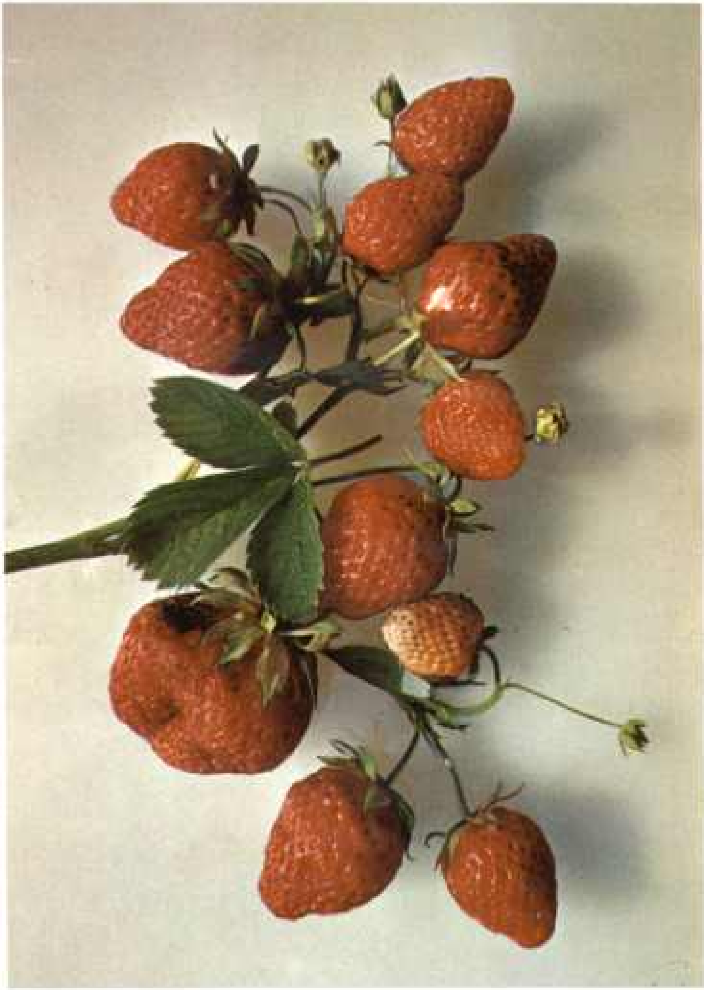
The Strawberry

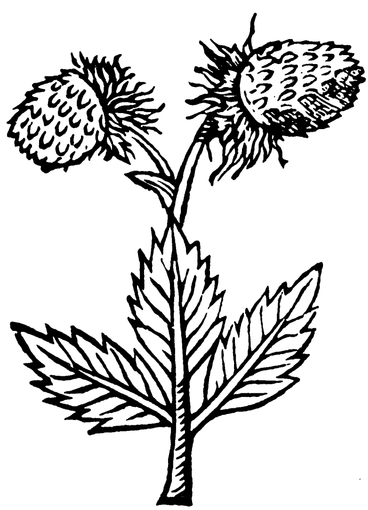


Howard 17 (Premier), the great strawberry of the first half of the 20th century. Though not so firm and not so tart or so well adapted to freezing and preserving, and not so widely grown, it was larger, more productive, better in fresh flavor, much more resistant to several diseases than most other varieties. Its germ plasm is in most American varieties now grown. Approximately half size. (Unless specified, strawberries in plates are full size.)

THE STRAWBERRY

History, Breeding and Physiology

BY GEORGE M. DARROW



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To the memory of
HENRY A. WALLACE
Who conceived this book
and nursed it to completion

A distinguished scientist,
farsighted statesman and
sincere humanitarian

Foreword

THIS BOOK is the result of collaboration between Dr. George M. Darrow, who is recognized as the foremost American authority on strawberries, and a group of other strawberry experts both here and abroad. It is published under the auspices of the New England Institute for Medical Research because of the Institute's interest in basic research in genetics which includes plants as well as animals. As a part of its program of interdisciplinary basic research, projects have been and are currently being pursued on the effects of radio frequency energy on germination of gladiolus bulblets, on genetic mechanisms in dividing cells of garlic root tips, and in germ cells of the fruit fly, Drosophila, in addition to cytogenetic studies of strawberry hybrids—the latter in conjunction with the Wallace Genetic Foundation.

It has been my privilege and great pleasure to serve as liaison agent between the various contributors, author, publisher, engravers, and sources of information and illustrations. Although it is impossible to recognize individually all those who have aided in one way or another, I am glad to give credit to those who have assumed major responsibility for various phases of the book.

First of all, Mr. Charles A. Madison, former Managing Editor of the College Department of Holt, Rinehart and Winston, Inc., has served as editor. His tireless efforts have been indispensable and invaluable. Mr. Hermann Kessler, Art Director of *Field & Stream,* has prepared and supervised the production of all color plates. His personal interest and devoted

efforts are greatly appreciated. Major credit is due Mr. Walter Von Egidy, President of Graphic Color Plate, Inc., whose craftsmen were responsible for engraving and printing the color plates; two other members of this firm must be thanked for their diligent and sympathetic assistance: Mr. O. C. Anderson, General Sales Manager, and Mr. Gerald K. Brown, Office Manager. The book has been designed by Mr. Ernst Reichl.

Among those especially helpful in research on historical features we must thank Dr. Alicia Lourbeig, Maitre des Recherches, Jardin des Plantes, Paris; Mrs. Elizabeth Hall, Associate Curator of Education, The New York Botanical Garden; Dr. William Stern, British Museum of Natural History; Mr. Charles Dyson, Scarsdale, New York; Mme. G. Duprat, Bibliothèque Centrale du Muséum National d'Histoire Naturelle, Paris; Mr. H. Jonkers, Horticultural Laboratory, Wageningen, Netherlands.

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DR. GEORGE M. DARROW is the former Chief Horticulturist in charge of breeding and cultural work with small fruits and deciduous fruits in the Crops Research Division, Agricultural Research Service, United States Department of Agriculture, Plant Industry Station, Beltsville, Maryland. Dr. Darrow is recognized as the foremost American authority on small fruits, particularly strawberries. During his forty-six years of service in the Department Dr. Darrow held many offices in scientific societies and was the recipient of numerous honors. He is past president of the American Society for Horticultural Science and of the Botanical Society of Washington. His society memberships also included the American Association for the Advancement of Science and a life-membership in the American Pomological Society. He served on the Editorial Board of the *Journal of Heredity and* was vice president of the American Genetic Association. In 1948 he received the Wilder Medal of the American Pomological Society for outstanding work on small fruits. In 1952 his services were requested by the Office of Foreign Agriculture to assist several Latin American countries in their work to improve native fruits. He was selected as an official U. S. delegate to attend the 13th International Horticultural Congress in London. In 1954 the U. S. Department of Agriculture awarded him its highest honor—the Distinguished Service Award. In 1963 the University of North Carolina conferred upon him the honorary degree of Doctor of Science. Since his retirement in 1957 he has continued to serve the Department of Agriculture as a collaborator and consultant. He lives on his farm in Glenn Dale, Maryland, where he not only continues to grow and evaluate new fruit varieties, but is interested in breeding ornamentals, especially day lilies and azaleas.

Dr. Darrow wrote all parts of the book not otherwise designated.

Miss D. Vivian Lee, Science Reporter for *Life* magazine, who received her Bachelor's degree from Stanford University and her Master's degree from Columbia, did extensive research in libraries and museums both in this country and in Europe in preparation for her chapters 3 through 6 on the historical background. She found the writings and drawings of Duchesne and recognized the great significance of his contribution to strawberry breeding and evolution.

The Honorable Henry A. Wallace, former United States Secretary of Agriculture in the cabinet of President F. D. Roosevelt, former Vice President of the United States, was a pioneer in the production of hybrid corn and hybrid chickens, who has long been interested in the breeding and genetics of many plants, particularly strawberries. He is now living at Farvue Farm, in South Salem, New York, and has contributed Chapter 1, as well as impetus and inspiration for the entire book.

Mrs. Mary Wallace Bruggmann, Chapponeyres, Vevey, Switzerland, wife of the former Swiss Minister to the United States and sister of Mr. Wallace, wrote Chapter 2, which describes the role of strawberries in religious paintings of the fifteenth century.

Dr. F. P. Cullinan, Associate Director, Crops Research Division, Agricultural Research Service, United States Department of Agriculture, Plant Industry Station, Beltsville, Maryland, wrote the biographical material on Dr. Darrow.

Dr. Clyde F. Reed, Botanist with the Crops Research Division, Agricultural Research Service, United States Department of Agriculture, Beltsville, Maryland, wrote the first part of Chapter 8, on strawberry species of the world.

Dr. G. Staudt, Institut für Vererbungs-und Züchtungsforschung der Technischen Universität, Berlin-Dahlem, Germany, contributed biographical material on Dr. Schiemann in Chapter 7. He also aided Miss Lee in preparation of her chapters 3 through 6.

Dr. Royce S. Bringhurst, Professor of Pomology, California Agricultural Experiment Station, Davis, California, wrote the portion of Chapter 15 dealing with California and collaborated with Dr. Darrow on strawberry breeding and industry in Mexico in Chapter 18.

Dr. Walter H. J. Hondelmann, Sengana GmbH, Züchtung und Züchtungsforschung, Hamburg-Volksdorf, Germany, contributed the part of Chapter 17 on strawberry breeding and industry in Germany.

Mr. John Meader helped Dr. Darrow to organize material for the book and to write Chapter 22 and also he prepared the index.

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Preface

The evolution of the strawberry from a wild to a cultivated plant can be illustrated in many ways, each contributing details toward the completion of the whole picture. Contrasts can be made between the size of fruit borne by wild and cultivated varieties, or the extent of the crop in 1850, 1900, and 1960. The breeding of better varieties can be traced back from present forms to their ancestors of much earlier times. What is known of character inheritance can be presented, along with the aims and methods of breeders who succeeded in obtaining better varieties. All these ways can help to explain how today's varieties originated, and each may suggest possible future improvements.

The objectives of this book can be understood best perhaps by the fact that it is designed to be what I would like to have available for my use, if I were starting a breeding program now; as such it is meant to serve others, just as Dr. S. W. Fletcher's book of nearly 50 years ago served me. By providing a helpful background, it is designed to follow the examples of Lambertye, Goeschke, and Millet, 75 to 100 years ago, and of Duchesne 200 years ago, all of whom offered the results of their study to aid the advance of others, and to add to the general body of knowledge. This book is designed to acquaint the reader with the strawberry, its origin and appearance, the structure of its fruit and plant, where and how it was developed and by whose hands, who is working with it now, and what can be expected of it. Will it continue as a major fruit? What are its weaknesses and its strong points? Is it worthwhile? How can we best take advantage of the present ease of interchange of ideas and germ plasm?

As answer to some of these questions, the book covers the early history of the strawberry in a review by Miss Vivian Lee, wherein we are made observers of the strawberry's slow evolution prior to the time when explorers of the New World searched for novel plants, and its dramatic progress, following the discovery of two new species, to the point where it became an important crop. In addition, the botany and early varieties of the strawberry are reviewed, in order that one may understand just how it progressed, in terms of intrinsic value, to its present status as a commercial crop, and may upon such understanding initiate a search for new qualities and, through them, further improvements. Serving a similar function are the chapters on morphology and physiology of the strawberry, its cytology, and the present sources of superior qualities. A considerable part of the book is assigned to present varieties, those who bred them, and the work being conducted at the experiment stations in the United States and other countries.

My association with various people in the preparation of this book has been pleasurable and of great help; with Miss Lee, who searched out the strawberry's early history; with Dr. Reed, an enthusiastic botanist of cultivated plants; with Dr. Bringhurst, who has led the research in California, where strawberry production competes for labor in a highly industrialized region; and with Dr. Hondelmann, who has written of the work of the Sengana Institute in Hamburg, Germany, where he is actively engaged in breeding, and from which successful varieties already have been introduced. And, of course, with those scores of breeders who are presently active who have been most generous in describing their work and in furnishing data and illustrations. I hope that I have presented their viewpoints correctly.

Thanks are due especially to Mrs. Neumann, my secretary for many years in the U.S.D.A., for her diligent typing of the manuscript; to Mr. William Reiss for his patience in obtaining many of the photographs; and to my associates in the berry breeding work of the U.S.D.A., who have discussed many of the problems of breeding with me. Also I must thank Mr. John Meader, who helped to organize the manuscript. I wish to thank my wife, Grace, especially for permitting the use of the dining room table for many months as an extension of my desk. Finally, I am deeply grateful to Mr. Henry Wallace for his penetrating questions and stimulating suggestions.

October, 1965 GEORGE M. DARROW

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The Strawberry

I

Introduction

by Henry A. Wallace

I AM DELIGHTED to write, by way of introduction, the first chapter of this book about strawberries because I have been curious about and have loved the strawberry plant ever since I ordered my first plants as a high school boy more than sixty years ago. Moreover, it has been a rare privilege to know intimately for many years one of the great strawberry experts of the world, Dr. George M. Darrow.

The problem of tracing the history and ancestry of strawberries is very difficult because there are so many kinds which are so similar in appearance and so distant in ancestry. Evolution from the ancestor of the wild strawberry of Europe to the wild strawberry of Eastern America, probably required hundreds of thousands of years; derivation of the wild strawberry of Chile may have required even longer.

The ordinary wild wood strawberry of Europe, the *fraise des bois* or *vesca,* is rarely tasted today except by epicures. And yet in the 1400's, as Mary Wallace Bruggmann briefly elaborates, this wild European wood strawberry was highly esteemed in religious art. The first person really to understand the relationship of this wild European strawberry to the wild American strawberries was Antoine Duchesne, a young French boy of the Court of Louis XV. His observations are fully described for the first time in English in a fascinating way by Vivian Lee in this book. He had a ringside seat when the modern large-fruited strawberry, based solely or almost solely on blood from North and South America, was brought together for the first time in Europe in the mid-1700's. Without this European work, which combined North and South American strawberries, our modern strawberry would not exist.

The mild maritime climate of Chile produced a non-hardy type of plant and the severer North American climate resulted in a plant more adapted to heat, drought, and cold. The possible permutations and combinations in the third, fourth, fifth, and sixth generations from the cross were infinite. For nearly a century this hit-and-miss work was done in Europe, and the first large-fruited, good tasting, but not very hardy, strawberries were grown chiefly in Northwest France, Holland and England. Although there is no historic record of the event, ship captains undoubtedly brought this new, large-fruited strawberry, which was commonly called pine or Ananas, to the American colonies in the 1760's or 1770's. There other doses of the wild North American strawberry were put in to make the North American large-fruited variety somewhat more hardy and more acid than the European large-fruited strawberry.

During the past 130 years many Americans have tried by repeated crossings to get more productive, more disease-resistant, better-tasting and larger-fruited strawberries. Doctor Darrow knows more about these men than anyone else, having studied their efforts for more than fifty years. He himself has produced many new varieties. He has observed year after year that no other plant is more sensitive to minute changes of environment, especially day length and temperature.

He has been deeply impressed with the fact that the mild, cool, coastal climate of California, benefiting from irrigation, produces nearly half the strawberries of America from April to December. The original breeding in California was done by Harold Thomas and Earl Goldsmith beginning in 1929. They wanted a large, firm berry which could be picked one-fourth green and which could stand shipping to the east coast. To do the job, they relied on the recombinations resulting from crossing two Massachusetts sorts, Howard 17 and Marshall, one Ohio variety known as Nich Ohmer, and a British kind known as Royal Sovereign. George Darrow had furnished several fundamental sorts based on Howard 17 and Royal Sovereign. Various other varieties were included also but these four varieties have been the backbone of California strawberry breeding. Many thousands of seedlings have been produced and careful selections of the best have been made. The result has been an unusual commercial triumph in the big city markets of the United States. The size is big and the flavor is moderately good, although not the best. If supremacy in the market is the criterion, Harold Thomas and Earl Goldsmith and their successor, Royce Bringhurst, must be given first prize.

From late December until March, nearly all the strawberries coming on the American big city markets are Florida 90, originated in 1948 by Dr. A. N. Brooks at Plant City, Florida. Florida 90 is one-half Missionary, which was a chance seedling picked up near Norfolk, Virginia, about 1900 by Mr. Gohn. While Missionary is better adapted to the Tropics than any other large-fruited strawberry, it has never done well in California. Missionary gave Florida 90 its tropic adaptation, but Florida 90 is larger and has a better flavor. While the male parent is not known, Florida 90 behaves as if the father might have been Klonmore. Florida 90 in the northeastern city market usually is better flavored than either the California berries or Missionary.

Outside of California and Florida, large-fruited strawberry breeding in the temperate areas of the world has been based on different varieties and theories. The one variety used more than any other in the United States has been Howard 17, originated by A. B. Howard, who died in Belchertown in western Massachusetts in 1907. More than a hundred years ago Howard learned to love strawberries from some of the Perfectionists who remained at Putney, Vermont, while he was still a high school boy. To Howard belongs the credit for recognizing the sturdy vigor of a variety called Crescent. Howard used Crescent again and again because it had no pollen and therefore was easy to cross. I remember growing Crescent as a boy and discarding it for lack of flavor. Howard kept it because of its great vigor and hardiness and ease of crossing. Crescent was the backbone of the success of A. B. Howard as a strawberry breeder.

Crescent was a combination of the first American bred variety called Hovey with one of the forms of the wild strawberry of eastern United States. Parmalee, the man who found the Crescent near his home in 1873, lived near New Haven, Connecticut. Hovey was originated in 1834 by C. M. Hovey, who lived near Boston, Massachusetts. Hovey was produced by crossing the most popular British variety of the early 1800's, Keens Seedling, probably with Methven Scarlet which was rich in the wild North American blood. Hovey was a man of learning associated with intellectuals of Boston; Howard was a dirt farmer, but he nevertheless associated with idealists, writers and college professors of western Massachusetts.

Dr. George Darrow and Mr. George Slate at the New York Agricultural Experiment Station recognized the importance of Howard 17 for breeding purposes. In nearly all strawberries north of Florida, Howard 17 is found to the extent of at least one-fourth. More than any one man, George Darrow recognized the high importance of the combination of Howard 17 with Missionary.

Dr. Darrow writes about many strawberry breeders in this book but not about himself. Therefore I asked Dr. F. P. Cullinan, one of the top men in the scientific work of the U.S.D.A., who has known Dr. Darrow in a close personal way for many years, to give me facts I did not know. Dr. Darrow is a genuine Yankee from southern Vermont, raised on a dairy farm not far from where A. B. Howard of Howard 17 fame lived all his life. His Horatio Alger boyhood will not be recounted here. Suffice it to say that he graduated in 1910 from Middlebury, Vermont, specializing in Botany. Then after getting a Master's degree in 1911 from Cornell, he went to the U.S.D.A. where he worked for 46 years. In 1926 he had the good fortune to be associated with some of the very first strawberry chromosome counting work as conducted by Longley. Darrow's work on physiology of the strawberry earned him a doctorate at Johns Hopkins in 1927. For more than 45 years Dr. Darrow has lived at Glenn Dale, Maryland, almost midway between Washington and Baltimore. There today he not only works with his son in producing commercial "pick your own" strawberries but he also hybridizes day lilies and azaleas. He associates joyously with his plants—he is that rare individual, a genuine *plantsman.* This title in my opinion is far beyond that of any Ph.D.

As a writer about strawberries, Dr. Darrow stands out as one of the leading contributors to scientific strawberry literature for 45 years. No one has written more abundantly and precisely. No one has had a wider acquaintance among the American strawberry breeders, north, south, east and west.

Dr. Darrow was in the forefront of the fight to help strawberry nurserymen bring out virus-free plants. He cooperated with experiment stations in the United States and Scotland to bring out varieties which would withstand the disease known as red stele. He cooperated with George Slate of the New York Experiment Station at Geneva on the problem of getting better flavor by crossing the virus susceptible Suwannee with Midland both of which were noted for their flavor and both were one-half Howard 17, a variety of great vigor but rather moderate flavor. Unfortunately no one has yet found a high-yielding, firm-fleshed, large-fruited, disease-resistant sort which has the very fine aroma of Suwannee. George Slate is still working on the problem and I have been in the field with him and Dr. Darrow to see the many thousands of seedlings.

During the past thirty years, strawberry growing in the United States has more and more drifted to areas where labor costs are low, where the soil is sandy, and where irrigation is readily available. More and more, strawberries have tended to disappear as a commercial crop in the midwestern states except on a "pick your own" basis (an exception is Michigan where acreage has been maintained) . The modern American back does not seem to adapt itself to strawberry picking.

For 160 years European strawberry breeding followed a different course from that in the United States. In both North America and Europe, the large-fruited strawberry was based on the same two American species combined by Europeans beginning about 1750. But from then on, the Americans have put in larger doses of the wild North American strawberry, whereas the Europeans held to a higher percentage of Chilean. The reason for this was because the European climate was milder. Again and again the best European crosses were brought to the United States only to succumb to the climate. The most notable exception was the highly flavored Royal Sovereign originated by Laxton of England in 1891, and it survived only in crosses. Even as a parent, Royal Sovereign has not survived except in California and North Carolina, and was not of any importance in eastern, southern, or central United States. Nevertheless, as an ancestor, it is found to some extent in every California variety. Keens Seedling, brought to the United States about 1826, was not adapted to our climate, but as a parent of Hovey it is to be found in nearly every American variety. Black Prince, another early English variety, a seedling of Keens Imperial, originated by John Wilmot of England, is also to be found in most American sorts.

Up until 1850 the European combinations of the North American wild with the large-fruited Chilean had been more or less a failure on the big city markets of the United States because they were not hardy enough to take our climate except under high, garden culture close to the coast. Before 1858 nearly all strawberries on the American market were large-fruited (by present standards very small) selections made in Europe from the North American wild strawberry.

James Wilson, a Scottish gardener and nurseryman who lived in what is now Albany, laid the foundation for a complete change in American commercial strawberry growing when he saved seed from a patch where two pistillate and one male or bisexual sort were growing. Each of the three was one-half either Keens Imperial or Keens Seedling, the British sorts which had done so well in England and had spread over the continent. The American effort had been to cross these tender British sorts with the better North American wild. But nobody had been commercially successful until James Wilson planted open pollinated seed from his 3-variety patch so rich in Keens blood. By great good luck he found a large-fruited, hardy, good-looking sort which won favor very rapidly on the city markets, although its flavor was mediocre. For more than 40 years the Wilson dominated the strawberry markets of the United States. It was the first real break-through on the road to a variety which would stand our climate and yet give large, good-looking fruit in abundance. Of course about 1880 or 1885 Crescent, which was also a grandchild of the British Keens Seedling with a wild North American sire, in part replaced Wilson and had the honor or furnishing $\frac{5}{8}$ of the blood of Howard 17. Genetically speaking Hovey and Crescent are all-important, far more important than Wilson. Commercially Wilson led the way. All honor to James Wilson, the Scottish gardener who knew a good thing when he saw it.

We may say therefore that importations of the British Pine or Ananas derived from the White Chilean laid the foundation for the large-fruited strawberry in the United States. To a degree this is also true of Europe. French sorts have rarely been imported into the United States, and not a single one has ever done well here. French breeders look with disdain on American strawberry varieties even though a few of them have been used with great success in crossing in England, Holland, and Germany.

The British have recognized the need of greater hardiness in their strawberries and have used American varieties, especially recently, in their breeding work. The most widely grown sort of French origin today, Madame Moutot, which is half Royal Sovereign, was introduced in the early 1900's. It has been very popular in the river valleys of Italy and Switzerland. It is a very large-fruited kind, but in spite of being half Royal Sovereign, has a rather poor flavor. It has never done well in the United States and none of its crosses has done well. A hundred years ago Jucunda, another British type, was widely grown in the United States in regions where the soil was rich. The European sort best adapted to American conditions in recent years has been Senga Sengana, brought out in the late 1950's by Professor von Sengbusch, the distinguished geneticist of the Max Planck Institute of Hamburg, Germany. Perhaps Senga Sengana's adaptability is due to the fact that it is one-half American by ancestry, and therefore has more hardiness. American varieties in Europe seem to lack flavor. Howard 17 has never been a success in Europe, either as a variety or as an ancestor. The climate of eastern United States is more different from that of Europe than most people realize.

The large-fruited strawberry has displaced the small-fruited, wild strawberries of eastern United States and the totally different wild strawberry of Europe. The flavor of the American wild strawberry is found represented to some extent in a few of the large-fruited varieties. Strawberry connoisseurs tell me that the unique flavor of the wild strawberry of Europe, the *fraise des bois* or *vesca,* is never found in our domestic large-fruited strawberry. It is challenging but probably not profitable to breed a large-fruited strawberry with a *fraise des bois* flavor.

An even greater challenge is to breed a large-fruited strawberry with the Muscat flavor. This is a second, but rarely found, wild strawberry in Europe which has a flavor quite different from the *fraise des bois.* The musky flavor is peculiarly appealing to a few people. It is never found on the market in the United States and rarely on the market in Europe. Scientifically, the musky strawberry was recognized as *moschata* by Duchesne 200 years ago. It has a rough leaf and carries its blossoms very high. Usually the blossoms of a plant are either all male or all female. The male plants have no fruit. The fruits are rather soft and do not attain their altogether unique flavor until quite ripe. The task of making a large-fruited, firm-fruited *moschata* is a very great challenge.

The French, because of their highly developed sense of the unique, have spent more time than anyone else on producing ever-bearing varieties of *fraise des bois*. Furthermore, they have worked harder than anyone else trying to introduce the *moschata* flavor into the large-fruited strawberry. An everbearing, non-running form of *fraise des bois* was first found in the wild about 300 years ago just east of Grenoble in the low Alps near the Swiss and Italian borders. These mostly have elongated, pointed fruits, and are the type grown by a limited number of epicures along the coast in northeastern United States today. They breed true from seed and are propagated by seed. But this pointed, alpine *fraise des bois* is not the kind usually seen in the paintings of the 1400's. Apparently the running, round-fruited type was more common in the 1400's.

It has only been since 1926 that scientists have had the techniques to know that the *fraise des bois* or vesca had only 14 chromosomes, whereas the Chilean, the wild North American, and the commercial large-fruited strawberry all have 56 chromosomes. Only since 1926 have we known why it was so hard to make the *fraise des bois* cross with the large-fruited strawberry. The *moschata* or musky strawberry, which has 42 chromosomes, will cross occasionally on the 56 chromosome berry, but the resulting plants are not productive. Charles Simmen of Montmorency, France, has had modest success along this line, but his varieties containing *moschata* blood usually have not survived very long.

Doctor Darrow is probably right in concluding that it is more practical to breed more flavor by selection into the ordinary 56-chromosome commercial strawberry than to try to introduce flavors from either of the two exotic wild European sorts with their 14 and 42 chromosomes respectively.

For myself I have long held the romantic idea that it would be good to go back to the source, to the original wild European 14-chromosome berry. How to do that and yet maintain size and firmness is the problem.

To me personally, the *moschata* has had an interest for thirty years because President F. D. Roosevelt first called my attention to it. He was one of the few people fascinated by the musky flavor, when he was a small boy traveling with his tutor in Germany. Following up on Roosevelt's suggestion with Doctor Darrow, I found that there was this other wild European strawberry, less well known than the famous *fraise des bois.*

I am sure that the very practical and very successful strawberry growers of California will never fool with either of the two wild European strawberries. Nor will the very successful strawberry growers of Oregon, Washington, Michigan, Florida, North Carolina, Louisiana, or Arkansas. They will follow the doctrine of "First things first." One look at these wild strawberries from Europe will convince them that there is nothing there for them. These small-fruited European sorts are hundreds of thousands of years removed from their large-fruited kinds so carefully evolved from the North and South American species and varieties by so many devoted breeders since 1750.

Nevertheless, a few men will try to go back to the early beginnings on the assumption that not everything good in the strawberry world originated in Chile and North America. Europe may have something to contribute. The religious artists of the 1400's loved the wild European strawberry. Perhaps it will yet contribute something more tangible than religious art.

The immediate future in the United States undoubtedly belongs to the strawberries originated by Doctor Darrow and his close friends and many associates in many states. On the continent of Europe, the future seems to belong increasingly to the varieties originated by Professor von Sengbusch in Germany. In the British Isles, varieties originated by the Cambridge Experiment Station, and in Scotland varieties originated by Robert Reid of Auchincruise, seem to dominate the picture.

Probably no domestic plant is more complex biologically, more sensitive in its adaptability than the strawberry. This means that a really good and comprehensive book is almost impossible. Fortunately, the history of the domestic berry begins only in 1760, and therefore we know more about this plant's history than we do about most other organisms. Doctor Darrow is deserving of great credit for getting the cooperation of so many strawberry experts in helping him write a story which is both scientific and romantic. In my opinion, the history of the strawberry has just begun. However, I doubt that the strawberry of the future will ever attain the size of the berries seen by Hieronymous Bosch's tortured imagination in the early 1500's.

2 The Strawberry in Religious Paintings of the 1400's

BEGINNING IN the earliest years of the 1400's the monks of Western Europe were using the round-fruited, wild strawberry in their "illuminated" manuscripts. Long before the large-fruited strawberry was brought from Chile to Europe, long before the scientists looked upon the *fraise des bois* or wood strawberry with a taxonomic eye, the monastic painters had gazed upon it and found it lovely, and worthy to share in their offerings to the Virgin Mary.

Toward the end of the 1300's a new spirit was spreading throughout Europe which was reflected in a freer and more natural artistic style. Emile Mâle, in his great work on Gothic art, calls it the awakening of human tenderness and suggests that it sprang from St. Francis of Assisi who loved all Creation, and who aroused in his brother monks the love of nature and the need to express it. The monks were the artists of the time and they were occupied with the brightening, or "illumination" of prayer books, and the paintings of tiny illustrations—"miniatures"—for the religious texts which they copied by hand. In their newly stirred feelings they began to look at the world around them, to see the details of nature and of everyday life, and they painted what appealed to them and what they thought beautiful.

Simultaneously with the flowering of human tenderness which began with St. Francis, we find the desire of the mystics to come nearer to the Virgin and to glorify her. They spent hours in contemplation of her and

This chapter was written by Mary Wallace Bruggmann.

the Infant Jesus. They wrote poems to her, giving her all the virtues and calling her by the names of all the flowers. They lost themselves in veneration of her, and when they made pictures of her, they adorned them with all that was precious and rare.

In a French miniature of about 1400 we see the strawberry, in the hand of Joseph who is holding it out toward the little Child Jesus, coaxing Him to take His first step.[1] In another, Mary, against a background of flowers, has her Child on her knee and angels are gathering strawberries, presumably for the Infant.

It may be that the monks first began drawing the strawberry plant because of its graceful form and pure colors, or it may be that the fruit was just becoming widely known. The French King, Charles V, was a patron of the miniaturists, and by 1386 he had 12,000 strawberry plants set out in his Royal Gardens.[2]

There was much traveling from monastery to monastery, from Italy to southern France, up toward Paris and Burgundy, to Germany and Flemish provinces and over to England. The influence of the miniaturists spread northward to the Rhineland, and it was there that the theme of the Mother and Child received its most charming portrayal.

So we come to these touching paintings of the School of Cologne: "The Madonna of the Roses," "The Garden of Paradise," and the "Madonna among the Strawberries." The Madonna is always a young girl seated in a closed garden (to indicate her virginity), holding the blessed Child in quiet but radiant joy. The artists, Lochner, Schongauer, and unknown masters, have surrounded her with a brilliant galaxy of flowers and plants among which is the strawberry. The Virgin's flower, the rose, is in predominance, but the thistle, carnation, lily of the valley, iris, primrose, and entire plants of the *fraise des bois* with its red fruit and white blossoms also are present. The plants may form the entire decoration as in our frontispiece, or a single plant may be placed in an important spot, at the feet of the Madonna or in the Child's hand. They are botanically exact, perfect likenesses of the original, round-fruited, wild, European *vesca,* which still fascinates the gardener of today. (See Plate 2–1.)

In her stimulating book on the symbolism in the pictures of the Middle Ages (*Symbol-Fibel*). Klementine Lippfert guides us into the meaning which flowers and plants as well as animals, colors and objects had for the people of that time. Elizabeth Haight, in her book, *Symbolism of the Great Masters* (1913), writes "the strawberry stands apart from all other symbolical fruits. It is found in Italian, Flemish and German art and also

1 Mâle, Vol. III, p. 153.
2 Hyams, p. 17.

in English miniatures. As a symbol it is not only widespread but of comparatively early origin . . . . It is the symbol of perfect righteousness." There is ample evidence that medieval art is permeated with symbolism and that every object had its own particular significance. Certain symbols, the Cross, the fish, the thorn, originated in the Scriptures and were carried on through Christian tradition. Others developed gradually in an atmosphere of intense religious feeling. The rose represented virginity and purity; the carnation, because of the shape of its calyx, suggested the nails of the Crucifixion; and herbs of medicinal virtue suggested the healing powers of Christ. The whole of the strawberry plant was used (the dried roots, the leaves and fruit). The *Symbol-Fibel* tells us that it was a cure for depressive illnesses, and its presence can be considered a reference to eternal salvation. "It stood for noble thought and modesty, for although it is conspicuous by its color and fragrance, it nevertheless bows humbly to the earth."[3] In a further quotation we read, "Künzle (the herbalist) writes that the people of the middle ages saw in the three partitioned leaf a reminder of the Holy Trinity; the fruits, pointed downward, were the drops of blood of the Christ; and the five petals of the flower, His five wounds."[4] (See Plates 2–2 and 2–3.)

With so many qualities attributed to it, it need not surprise us that we repeatedly encounter the strawberry, as entire plants in the foreground of a picture, or as individual berries and blossoms or garlands forming the border of a miniature. As far as we have seen, they occur most frequently in the presentations of the Madonna and of the Christ. They usually are the round *vesca,* but we have also detected the more elongated Alpine *vesca* which, quite properly, is in a Swiss tapestry of about 1490. It is apparently the same plant which grows on the hills around Lake Geneva today. The subject of the tapestry is the Resurrection. Around the tomb from which the Christ is rising, the strawberry and a variety of other plants are growing, the symbol of continuous life.

When we speak of medieval art we mean religious art, but we have one notable exception in the "Garden of Delights," or "Strawberry Tree" as it was first called, by the Dutch painter Hieronymous Bosch (1455–1516). It is an allegorical, complicated triptych with hundreds of details and with curious unclothed people. We mention it only because of the scenes which call such marked attention to the fragrance of the "fragaria." A naked group of three is kneeling beside a berry half as large as themselves, smelling it as though to take nourishment from it. Another group has formed a circle, and is balancing and playing with a gigantic, out-sized berry as

[3] Lippfert, p. 17
[4] Ibid., p. 57.

though it were a balloon. The accepted interpreter of Bosch, Wilhelm Fränger, thinks that the painter was using it, along with the grape, cherry and apple, as a sign of voluptuousness. (See Plate 2–4.)

Toward the early 1500's there was another evolution in man and in art. The Renaissance was developing a more worldly style which replaced the manner of the mystics. On the threshold between the Middle Ages and the Renaissance, A. Dürer (German School, 1471–1528) made a drawing of "Mary and the Many Animals." It is one of the last of the symbolical pictures in which we have seen the strawberry. It shows a more sophisticated Madonna sitting in her garden with animals all about her, and the little Christ-Child is reaching out from His Mother's knee to grasp the tri-parted leaf from a growing strawberry plant.[5]

[5] It was my brother Henry W. Wallace's interest in strawberries which first led me to see the plants in the Gothic paintings, and it was his delight when I would discover one depicting strawberries which induced me to write down, without any pretensions, these few observations. That—and a persistent affection for the flavor and fragrance of the *fraise des bois.*

3

Early History of the Strawberry

THE HISTORY of the strawberry goes back as far as the Romans and perhaps even the Greeks, but because the fruit has never been a staple of agriculture it is difficult to find ancient references to it. Theophrastus, Hippocrates, Dioscorides and Galen did not even mention it; nor did Cato, Varro, Columella or Palladius, the four Latin writers on agriculture. Apulius cited the strawberry only for its medicinal value. Although Virgil and Ovid did name the strawberry in their verses, they did so only casually in poems of country life where they associated it with other wild fruits. Virgil, for example, included the strawberry among the beauties of the field in his *Third Ecologue* where the shepherd, Damoetas, is warned:

> Ye boys that gather flowers and strawberries
> Lo, hid within the grass an adder lies.

Ovid mentioned it twice, once in his description of the Golden Age from Book One of the *Metamorphoses* as "Arbuteas foetus, monatanaque fraga legebant," (They gathered Arbutus berries and mountain strawberries). Later, in the thirteenth book of the same work, Polyphemus, Galatea's rebuked lover, sings to her of the settlement he wants to make with her:

> With thine own hands thou shalt thyself gather the soft strawberries growing beneath the woodland shade.

Pliny (23–79 A.D.) was the last known writer for many centuries to mention the strawberry. In the twenty-first book of his *Natural History,* he listed "Fraga," the fruit of the strawberry, as one of the natural products of Italy.

In a later section, Pliny confused the strawberry with the Arbutus or tree strawberry, "terrestribus fragis." Some natural historians believe that the strawberry was cultivated in Greek and Latin gardens and that it was served at banquets, but there are so few references to it that it is doubtful if much was made of it. The next surviving reference to the strawberry does not appear again until the thirteenth century in the writings of a Greek doctor, Nicholas Myrepsus. The literature of botany was often the literature of medicine, where plants were described for their use in treating ailments.

By the 1300's, the strawberry was in cultivation in Europe, for the French then began transplanting the wood strawberry, *Fragaria vesca,* from the wilderness to the garden. The plant was considered more ornamental for its flowers than useful for its fruit, although it was grown to some extent for eating. The financial accounts of a hospital or poorhouse in northern France in 1324 list an item "Pour Fraisiers à planter en la montaigne acatés à Pierot Paillet et Aelés Paiele XII d," which might have been planted for their fruit. In 1368 King Charles V had his gardener, Jean Dudoy, plant no less than 1,200 strawberries in the royal gardens of the Louvre in Paris. In 1375 the Chateau de Couvres, near Dijon, property of the Dukes of Burgundy, had four blocks of the garden assigned to the cultivation of strawberries. They received particular care and good fertilization and the runners were transplanted to vacant soil to perpetuate the plants. "Doubtless its cultivation was crude, but still, it existed. The strawberry was so appreciated by the Duchess of Burgundy that it was sent to her when she visited in Flanders," wrote Bruyerin-Champier (*De re Cibaria,* 1562).

England, too, was an early admirer of the strawberry. The Reverend John Earle compiled a list of early plant names from old lists appearing in documents and vocabularies between the tenth and the end of the fifteenth centuries. The successive modifications of the name from "Streowberige, Strea Berige, Streowberge, Streaw Berian Wisan, Streberi Lef," to "Strebere-Wyse" and "Strawberry" show a long familiarity with it there. The last name came from "A Pictorial Vocabulary of the Latter Part of the Fifteenth Century." The Anglo-Saxon word *streow* meant hay. According to one theory, the Anglo-Saxons in A.D. 900 called the strawberry the "hayberry" because it ripened at the time the hay was mown. Another guess is that the name derived from the way children strung the berries on straws of grass or hay to sell, a custom still practiced in parts of Ireland today. A more likely explanation is that the Anglo-Saxons used the name "strawberry" to describe the way the runners *strew* or stray away from the mother plant to find space in which to grow.

Londoners were buying the fruit from street vendors by 1430 when John Lidgate wrote the song of the "London Lickpenny." One verse quotes the cry of "strabery rype:"

There are fifty-two color plates in the book. Each plate is numbered by chapter and by priority within the chapter, corresponding to the numbering in the text. It should be mentioned that where possible the strawberries are reproduced lifesize. Great care was also taken to obtain exact shades of color throughout, although a number of them were taken by photographers at various times and places and had to be color-corrected specifically and with great care at the direction of the author.

Madonna among the strawberries. Painting at the Museum of Solothurn, Switzerland.

PLATE 2-1

Cursus de Eterna Sapientia, "Christ with Book and Orb," from *Liber Devotionis,* showing individual berries or garlands forming the border.

PLATE 2-2

Cursus de Passione Christi, "The Betrayal of Christ," from *Liber Devotionis,* showing individual berries or garlands forming the border.

PLATE 2-3

Then unto London I dyde me hye
Of all the land it bearyeth the pryse;
"Gode pescode," one began to cry,
"Strabery rype, and cherrys in the ryse."[1]

English royalty, like French royalty, had developed a taste for the fruit.

"When I was last in Holborn,
I saw good strawberries in your garden there:
I do beseech you send for some of them . . ."

the Duke of Gloucester asks the Bishop of Ely in Act III, Scene iv, of Shakespeare's tragedy *Richard III* of 1597, and the strawberries were sent for on June 13, 1483, according to Shakespeare authorities. The reference at least indicates that in the 1400's the Bishop of Ely grew strawberries with such success in his garden at Holborn that the fact drew the attention of writers, whatever the symbolic overtones of the passage. One of the first known botanical illustrations of the strawberry appeared in the *Mainz Herbarius* of 1485 (*Plate 3–1*).

By the 1500's references to the cultivation of the strawberry were more frequent; physicians and apothecaries discovered its supposed medical uses, and botanists began to name the different species. *The Grete Herball* appeared in London in 1526 as an English translation from the French work on the medicinal uses of herbs and was printed by Peter Treveris. Here is the description of "The Fragaria. Strawberyes"

> Fragaria is an herbe called strabery. It groweth in woodes and grenes, and shadowy places. It is pryncypally good agaynst all evylles of the mylt. The uice therof drunken with hony profyteth mervaylously.
>
> For the brethe
>
> For them that take brethe with payne as it were syghynge. The uice therof take in drinke white peper heleth it. Strawberyes eate helpeth coleryke persones, comforteth the stomake, and quencheth thyrst.

Perhaps King Henry VIII believed that royal pleasure led to royal health for in 1530, four years after the publication of *The Grete Herball,* he paid ten shillings for a "pottle of strawberries" according to the *Privy Purse Expenses of Henry VIII.* A pottle was a small basket, shaped like an inverted cone, and often held less than one-half a pint. This measure indicates that the fruits of the time were small, and must have been wood strawberries.

Ruellius, a botanist of the period, also referred to the cultivation of strawberries in his *De Natura Stirpium Libri* (1536). Describing them as "growing wild in shady places," he also notes that "gardens furnish a larger

[1] *Sturtevant's Notes on Edible Plants,* ed. by U. P. Hedrick. Albany, New York, 1919, p. 192.

fruit." By the mid-1500's in England, demand for the fruit had stimulated regular strawberry farming. In his "Five Hundred Points of Good Husbandry" (1557), Tusser recommended strawberry cultivation as an appropriate part of the "employment of women." Under "September's Husbandry" Tusser wrote:

> Wife, into the garden and set me a plot
> With strawberry roots, the best to be got;
> Such growing abroad among thorns in the wood,
> Well chosen and picked, prove excellent good.

In France in 1562, Bruyerin-Champier, physician to Henry IV, included the strawberry among the plants which had recently entered French gardens. Sixteen years later, instructions for its cultivation appeared in *L'Agriculture et Maison Rustique,* in which Charles Estienne and Jean Liébault prescribed replanting the fields with strawberries every three years and annual hoeing and fertilizing. Gallo wrote from Italy in the same decade that "strawberries can be easily had in abundance in one's garden."[2] By the end of the century the strawberry's popularity was general. Hyll gave the final evaluation in the *Gardener's Labyrinth* (1593):

> They be much eaten at all men's tables in the sommer time with wine and sugar, and they will grow in gardens until the bigness of the mulberry. [The strawberry] requires small labour, but, by diligence of the gardener, becometh so great that the same yieldeth faire and big berries as the berries of the bramble in the hedge.

While the 1500's have horticultural significance for establishing the strawberry as a common garden plant, in double service as an ornament and as a table delicacy, this century was also important for the progress in botanical knowledge of the plant. By the end of the century all three European species of *Fragaria—F. vesca, F. moschata,* and *F. viridis*—had been cited. The common garden strawberry was *F. vesca,* which was transplanted from the woods and propagated by runners, the plots restocked by fresh transplantations (*Plate 3–2*). Two subspecies of *F. vesca* were identified. The white strawberry, or *F. sylvestris alba* (*Plate 3–3*), was noted frequently, dating from Jerome Bock's, or Targus's, description in 1532 of *Fraga alba seu candida.* Ruellius was one of the earliest writers to name different kinds of strawberries, and in 1536 he distinguished between the red and white *F. vesca.* Conrad Gesner, Dodoens and Camerarius were other classicists among botanists who cited white *F. vesca* during this century. Gesner remarked that it was especially common in the mountains around Baden, Switzerland. John Gerarde in *The Herball* (1597) also included *Fragaria alba* among his strawberries.

[2] Lcsourd, Felicien, *Le Fraisier,* Second Edition, ed. by Charles Simmen. Paris, 1943, p. 36.

The everbearing strawberry, *F. sylvestris semperflorens,* was a second subspecies of *F. vesca* brought to attention in the 1500's. It was described by Jerome Bock in 1532, and in 1553 by Conrad Gesner, as a strawberry which flowered and fruited in the Alps throughout the growing season. Although they thought this everbearing quality was common to all *F. vesca* they must have had the Alpine specimen in mind. Later botanists noted that it differed from *F. silvestris,* the wood strawberry, only in its greater vigor. It flowered three to four months after germination and continued flowering, even in winter, bearing fruits until the severe frosts of November and December. The young runner plants often flowered before they could take root. Although cited by Bock and Gesner, *F. silvestris semperflorens* was not cultivated until a rediscovery in 1764 by a Mr. Fougeroux of Bondaroi.

So inclusive were the botanists of this period in their descriptions and collections of plants that even freak varieties of the wood strawberry had a place in their herbals. One such curiosity was *F. vesca sive sterilis* or the "Barren Strawberrie" described by Gerarde. Later, in 1766, when it had totally disappeared, it was cited as the Plymouth Strawberry of England (*F. silvestris var. muricata* Duch). It was a sterile, freak variety with apetalous flowers which produced ill-formed and sharp midget fruits with completely aborted ovaries and it had little of the flavor of the strawberry. Tradescant had found a specimen around 1620 at Plymouth, England, and for sixty or eighty years it was cultivated in all the botanical gardens of Europe. In 1629 Parkinson called it the Prickly Strawberry.

The green strawberry, *F. viridis* or *collina* Ehrh., the second of the three native species, also was described. Jean Thale in 1588 wrote of a strawberry he had seen in the Black Forest of Germany before 1530 which he named the *Knackelbeer Presling,* and in 1586 Joachim Camerarius spoke of *le fraisier tardif,* the late strawberry or "brossling." *Le Petit Fraisier* of Leonard Fuchs (1542) and *Le Fraisier à fruit doux* of Dodoens (1583) were other synonyms. So, too, was the "greenish strawberry," *F. subviridis* of John Gerarde in *The Herball* of 1597. He wrote, "there be divers sorts of strawberries, one red, another white, a third sorte greene and likewise a wilde strawberrie, which is altogether barren of fruite." Of the "greenish strawberry" alone he wrote: "There is another sort which bringeth forth leaves, flowers and strings like the other of his kind. The fruit is green when it is ripe, tending to redness upon that side that lieth to the sunne, cleaving faster to the stems, and is of a sweeter taste, which maketh the difference."

Caesalpinus, in his *De Plantis* (Florence, 1583), described a subspecies of *F. viridis* which he had found in the Bargemon Alps of France and which he called *Fragaria bifera* because it bore both spring and summer fruits. Years later, in the 1760's, the naturalist Duchesne had a correspondent collect specimens for him. Some were transplanted and cultivated in the gardens of Bargemon, a town at the foot of the Alps. There they "bear fruit in all seasons. Only the extremely rigorous winters present an obstacle to this continual fecundity," reported R. P. Antoine, the correspondent. Later botanists have noted that this twice-bearing quality is common to all specimens of *F. viridis.*

The musky-flavored strawberry, *F. moschata* Duch. or *F. elatior* Ehrh., was the third species noted in this century and is the third species indigenous to Europe. The only mention of it in the 1500's was by Matthias Lobelius in his *Observations sur les Plantes* (1570); that is, botanists believe that he referred to *F. moschata* when he designated a strawberry as *Fragaria E. Fraga majore alba.* Lobelius said that a common term for it was the "Gallobelgis des Chapirons," and Duchesne in 1766 noted that the flower merchants still called it the "Chaperon."[3] The musky strawberry was not cited again until 1613 in Besler's *Hortus Eystettensis,* which contained drawings of plants grown in the famous botanical garden of Aichstat in Francony. Besler had drawn a female specimen (the unisexual character of *F. moschata* was not recognized, however, until Duchesne's study of it in 1766). Besler called it the "Big-Fruited Strawberry" and referred to the very pleasant taste, odor and flavor of its fruits, which he said compared in size with certain plums. This description led Gaspar Bauhin in 1623 to call it the "strawberry with fruit as large as a small plum," and around 1640 Simon Paulli identified it by the same name. Paulli said he had seen it in Denmark where one year it gave fruits as large as peaches due to the excellent soil and the good weather that season.

The authors of the first *Catalogue du Jardin du Roi* called it simply "Fraisier étranger," or foreign strawberry. The wild habitat of *F. moschata* is still unknown. The Robins, who wrote the Catalogue in 1624, thought it came from Pannonie and gave their "foreign strawberry" the botanical name *Fragaria major pannonica.* Pannonie is a region of Europe between the Danube river to the north and the Illyria to the south. In 1629 Parkinson called it the "Bohemia Strawberry" or *Fragaria major sterilis seu bohemica* and he wrote:

> The Bohemia Strawberry hath beene with us but of late days, but it is the goodliest and the greatest, both for leafe next to the Virginian, [*F. virginiana,* a North American strawberry introduced in the 1600's to Europe] and for beauty farre surpassing all; for some of the berries have been measured to bee neere five inches about. Master Queester, the Postmaster, first brought them over into our country, as I understand, but I know of no man so industrious in the carefull planting and bringing them to perfection in that plentifull maner as Master Vincent Sion who dwelt on the Banck side, neer the old Paris garden staires, who from seven rootes, as hee affirmed to me, in one yeare and a halfe, planted halfe an

[3] Duchesne, Antoine Nicolas, *L'Histoire Naturelle des Fraisiers.* Paris, 1766, p. 52.

FIG. 3–1. LEFT TO RIGHT: *Fraga vulgaris,* common strawberries; *Fraga Bohemia maxima,* the great Bohemian strawberries; *Fraga acuseata,* the prickly strawberry.

> acre of ground with the increase from them, besides those he gave away to his friends, and with him I have seene such, and of that bignesse before mentioned. (*Paradisus in terrestris sole,* London, 1629)

F. moschata was always more popular in England where it was known as the "Hautbois" or "Hautboy" because of its long flower stems which rose high above the leaves. An illustration of its unpopularity in France is a passage from De la Quintinie, who wrote several works on gardening in the late 1600's and early 1700's: "I want even the Caprons (*F. moschata*) torn out or at least that no particular friendliness be held toward them. They are easy to know by their large, short and hairy runners, their very large flower, and their large, hairy, and almost prickly leaf."[4] "It has been known for a very long time in the gardens around Paris, but it is scorned there," wrote Duchesne in 1766. "The English cultivate it, on the contrary, to adorn their tables."[5] Its fruit was a deep, purplish red in color and had a pasty quality in the poorer varieties. Duchesne knew of specimens from England, Holland and Germany in the mid-1700's and Felicien Lesourd in 1943 said its distribution spread from England as far as Finland and that although it was then very

[4] De la Quintinie, *Instruction pour les Jardins Fruitier et Potagers,* Volume II. Paris, 1715.
[5] Duchesne, *op. cit.,* p. 164.

rare, it was still cultivated for its excellent, lightly musky aroma despite the infertility due to its unisexual character.[6] It has been reported as the main cultivated strawberry in the Vierlanden near Hamburg, Germany, until the late 19th century and it was frequently grown in Russia until the 1930's. In 1766 Duchesne knew of two or three perfect hermaphrodites, or bisexual ones, but he later noted they had become almost sterile.

At the end of the 1500's the two strawberries cultivated in gardens were the wood strawberry, *F. vesca,* and the musky strawberry, *F. moschata,* both characterized by small, distinctly flavored fruits. In all, the early botanists of that century had named three European species: *F. vesca* and its subspecies *F. vesca semperflorens; F. moschata,* just cited, and *F. viridis,* the green strawberry. The singular significance of the 1600's to strawberry history was the introduction to Europe of *F. virginiana* from eastern North America. for this berry was to sire today's modern, big-fruited strawberry.

Perhaps someone, someday, will discover the true story of the Virginia strawberry's journey to Europe. At present only a few works are known which suggest that it reached Europe in the early seventeenth century. The earliest of these is Gaspar Bauhin's *Pinax,* printed in Paris in 1623. There Bauhin designated the "Fraga acque magna ac in Anglia crescunt." Some botanists believe that Bauhin had in mind Besler's musky-flavored strawberry, *F. moschata,* from the *Hortus Eystettensis* (1613), and that Bauhin had not actually seen this strawberry as he did not include it in the enumeration of strawberry species. Yet his description shows that he had heard there were large strawberries in Virginia. No one even knows if the Virginian strawberry was introduced first into England or first to the European continent. Bauhin referred to England, and in 1656 John Tradescant noted a *Fragaria nova anglia nondum descripta* in the catalogue of his plant collection, *Musaeum Tradescantianum,* published in London. If this was *F. virginiana* then Tradescant would have been the first to refer to it. According to Pritzel, Tradescant died in 1638. Duchesne believed his catalogue was written about 1616, but not published until 1656 by his son. From the little that is known about Tradescant it seems likely that about this time he was making his famous collecting trips to the European continent. Thus he may have brought *F. virginiana* to England then.

An American strawberry, *Fragaria americana,* was cited in 1624 by Jean and Vespasien Robin, botanists to Louis XIII, in their *Manuel Abrégé des Plantes.* Five years later, John Parkinson in his *Paradisus in terrestris sole* designated "the Virginia Strawberry" in English and 1629 has been given traditionally for the introduction of *F. virginiana* to England. Parkinson wrote:

[6] Lesourd, *op. cit.,* p. 26.

> The Virginia Strawberry carryeth the greatest leafe of any other, except the Bohemian [*F. moschata*], but scarce can one Strawberry be seene ripe among a number of plants; I thinke the reason therof to be the want of skill or industry to order it aright. For the Bohemia and all other Strawberries will not beare kindly, if you suffer them to grow with many strings, and therefore they are still cut away.

The kind from Brussels, he went on to say, was brought by Tradescant. In seven years Parkinson had never known a berry to be fully ripened on all sides. One side was always rotten, although the plants flowered abundantly each year and the leaves were very large. Parkinson thus verified Tradescant's journeying to Europe and his importation of a strawberry from Brussels. Was this *F. virginiana*? Was more than one kind of *F. virginiana* then known? Or was this the first specimen of the Virginia Strawberry introduced by Tradescant? Parkinson did not say.

After Parkinson, references to *F. virginiana* followed thick and fast. Gui de la Brosse, head of the Jardin du Roi at Paris, in 1636 included a *Fragaria americana magno fructu rubro* in his *Catalogue of the Garden*. Ray gave a Latin translation of Parkinson, and Morison in his *History* called the plant the "Virginia Strawberry with Scarlet Fruit." Under this designation, Tournefort, Boerhaave and other botanists cited it in Latin in their catalogues. In 1738 Linnaeus identified it in the garden of George Clifford, a wealthy banker who had a large botanical collection in Amsterdam. Langley had a good engraving made of its flowers and fruits with an accompanying description in his *Pomone,* published in London in 1729.

The spread of the new species was very gradual and it remained little appreciated as late as the middle of the eighteenth century. Not until the end of that century would a rise in its popularity result in the introduction of new varieties, which increased from three to nearly thirty by 1820, for a time outnumbering other kinds.

The wood strawberry still predominated among strawberry growers in the late 1600's. The musky, the green and the Virginia strawberry were grown to a minor extent. No improvement of the fruit by raising new varieties from seed had been attempted seriously. Gardeners were satisfied to grow the wild species and the few varieties of them which had occurred naturally. The first half of the next century would bring the dramatic development of the commercial big-fruited strawberry. Meanwhile, the 17th century importation of *F. virginiana* had been the first step in bringing together the future parents of the modern strawberry. The Virginia strawberry was the sire of this modern cross. The journey of a French spy to Chile in 1712 resulted in the introduction of the female plant, the other American parent of *F. grandiflora* or *F. ananassa,* our present big-fruited strawberry.

4

The Strawberry from Chile

THE JOURNEY OF the Chilean strawberry, *Fragaria chiloensis,* from Chile to France in 1714 was the most important event in the history of the modern strawberry. The Chilean berry had one quality the European kinds lacked—size. The large berries attracted the notice of a French spy who had crossed the pirate-menaced seas to Chile in the early 1700's on a mission for King Louis XIV. Along with his observations on fortresses, armies, guns and supply routes, governors and Indians, he included a description and drawing of the Chilean strawberry. A collector as well as an observor, he spent six months caring for the specimens he took with him on the return voyage to France. Through the initiative of this young man, the New World strawberry, already cultivated for many years by the Chilean Indians, was brought as a bride to France where her marriage to North American *F. virginiana* took place.

In the early 1700's wild *F. chiloensis* grew over much the same area of Chile as it does today. The roots bind the sand along the coast of middle and southern Chile and then the plant advances inland, where it climbs as high as 5,100 feet in the Cordillera and wanders as far eastward as the Argentine provinces of Neuquen, Chubut and Rio Negro. At the time of the Spanish conquest of Chile in the mid-1500's, the only Indians who lived in the country of wild *F. chiloensis* were the Mapuche in the north and the Huilliche further south. These two tribes were very probably the first to cultivate *F. chiloensis,* since both distinguished in their languages between the wild-growing strawberry (*llahuen, lahuene,* or *lahueni*) and the cultivated one (*quellghen*), later called the *frutillar* by the Spaniards. At the time of the conquest another Indian group, the Araucanians, also grew strawberries along with maize, potatoes, pumpkins and beans, but they did not live in the area where *F. chiloensis* grew wild. For how many hundreds of years had the Mapuche and the Huilliche Indians cultivated *F. chiloensis*? Did this Indian culture of strawberries predate the European one, which seems to have commenced in the 1400's? No one knows, but when *F. chiloensis* was brought to France in 1714 it certainly had as long a history of cultivation as the European strawberry.

Until 1550–1551 the Mapuche and Huilliche Indians cultivated their strawberries undisturbed. Then the Spanish conquistador, Pizzaro, who had been attempting to conquer Chile for fifteen years, appointed Pedro de Valdivia supreme commander of the Spanish troops in Cuzco, Peru. Under Pizzaro they were able to penetrate the region between Rio Itata and Rio Tolten where the Mapuche put up a stiff fight. The Spaniards won, and as keen appraisers of South American culture, they counted the strawberry among the spoils of conquest. Soon after, the Chilean strawberry arrived in Cuzco, then the home of Garcilazo de la Vega, the son of an Inca princess and a Spanish conquistador. In his study of Inca culture, *Los Commentarios Reales de los Incas,* he described the fruits cultivated by the Incas of his day. Although de la Vega left Peru in 1559, he included in his descriptions a fruit called the *Chili,* which he thought probably had come to Cuzco in 1557, six years after Valdivia's conquest. According to him, this pleasant-tasting fruit bore small seeds on its surface like the fruits of the Arbutus. Both fruits were of the same size, but that of the Chili was rather long and heart-shaped instead of round, and the plant grew on low bushes which crept along the ground. Botanists are certain that de la Vega was describing the strawberry. As he was unable to give the fruit a Peruvian name, he called it instead the "Chili," thus supporting the evidence that the species was *F. chiloensis,* the strawberry of the Mapuche and Huilliche Indians.

In 1606 while in Spain, the sixty-eight-year-old de la Vega wrote his recollections of the Chilean strawberry as he first saw it in 1557 in Cuzco: "Another fruit which is called *chili* arrived at Cuzco in the year 1557. It is of excellent taste and very good to eat. It is borne on low plants, almost crawling on the ground; it has a berry like the arbutus, and is the same size but not round, longer, and shaped like a heart."[1]

1 "Otra fruta que llaman Chili llegó al Cuzco el año de 1557. Es de muy bien gusto y de mucho regalo. Nace en unas plantas bajas, casi tenidos por el suelo; tiene un granijado por cima como el madroño, y es del mismo tamaño, no redondo, sino algún tanto por longada en forma de corazon."

The "madrono" referred to by Garcilazo is the madrone or strawberry tree. *Arbutus unedo.* What Garcilazo called Chili was undoubtedly the Chilean strawberry. The original Spanish was obtained through the courtesy of Hector Lazo, a descendant of the father of Garcilazo, the Inca.

(Garcilazo de la Vega, "Los Comentarios Reales de los Incas." Chapter 11, Book 8, Part I, 1606.)

One of the first descriptions of the Chilean berries known to reach Europe was in the *Historia Relation del Reyno de Chile,* published in 1646 by the missionary Alonso de Ovalle, who wrote it during a trip to Rome. De Ovalle had lived in Chile until 1641. "Garden fruits are never, or only very rarely sold," he commented, "and anybody can go into a garden and eat as much as he likes without any restriction. Only strawberries, which are called *Frutilla,* are sold. Although I saw them growing wild for miles, they are very expensive when cultivated. Their taste and smell differ from those I saw in Rome. In size they are as large as pears and are mostly red, but in the territory of Concepción there are also white and yellow ones."

Another voyager, a Catholic priest named Louis Feuillée, provided a description of the Concepción strawberry. "Physical and Mathematical Observations with Several Remarks on Natural History Made at Concepción, January 1709," is the heading for Chapter 25 of his *Journal* in which the passage occurs. After noting the reversed order of the seasons south of the Equator, as compared with their sequence in the Northern Hemisphere, Père Feuillée continued: "Several fruits, like pears, apples, strawberries, etc. were ripe. For dessert we were served some strawberries of a marvellous taste, whose size equalled that of our largest nuts. Their color is a pale white. They are prepared in the same manner as we fix them in Europe, and, although they have neither the color nor the taste of ours, they do not lack excellence."[2] Feuillée had been sent out as King Louis XIV's official mathematician to explore and map the West Indies and South America. For two years he traveled the Chilean and Peruvian coasts, mapping cities, sketching panoramic views and collecting plants. But Père Feuillée failed to include the "excellent" strawberry of Chile in the collection he brought back to Brest. Fortunately, the curiosity of Louis XIV about the New World and his concern over Spanish defenses on the Pacific coast of South America remained strong. Four months after Feuillée's return, the King dispatched another explorer on a remarkably similar mission, this time with orders to report on the Spanish fortifications. Unlike the priest who preceded him, who was a trained botanist, Amédée François Frézier was an engineer, but he had the botanist's impulse for collecting. He was the only explorer known to bring specimens of *F. chiloensis* back to Europe, giving the Old World the large-fruited strawberries of the New.

Lieutenant Colonel Frézier was a thirty-year-old member of the French Army Intelligence Corps when in 1711 he was commissioned to sail to the Spanish colonies of Chile and Peru on a reconnaissance mission. King Louis XIV of France had paid vast sums to maintain his grandson on the Spanish

[2] Feuillée, Louis, *Journal des Observations Physiques, Mathématiques et Botaniques,* Volume I. Paris, 1714, p. 314–315.

throne and was determined to get full information of even the least known parts of the Spanish West Indies before the French, as well as other nations, could be excluded from those seas by the Spaniards.[3]

> For this end, he pitched upon our Author, an experienced Engineer and Mathematician in his Service, whom he knew to be in every way qualified to make Hydrographical Observations for the Use of Mariners, and for the Correction of the Charts, and also to take exact Plans of the most considerable Ports and fortresses along the Coasts whither he was going; to direct to their best Anchorages, and to point out their respective Dangers; (Things which might hereafter be of great Use to the French, if a War should happen to break out again between the two Nations.) And this Gentleman he sent at his own Charge on board a Merchant-Ship, in the Year 1712, to pass as a Trader only, the better to insinuate himself with the *Spanish* Governors, and to have all opportunities of learning their Strength, and whatever else he went to be inform'd of.

Thus read the 1717 English introduction to the book which Frézier had published the year before, entitled *Relation of the Voyage to the South Sea, Along the Coast of Chile and Perou, Made During the Years 1712, 1713, and 1714*. Other sources describe his assignment as the study of the defenses in Chile and Peru alone. Whatever its scope, this was a delicate mission for the young but well-qualified engineer.

Frézier never referred to the fact in his writings, but his family name was an ancient one, which derived from the French word for the strawberry—*fraise*. Perhaps he did not know the story of his ancestor, Julius de Berry, a citizen of Auvers who was knighted by the Emperor and King of France, Charles Simplex, in 916 for a gift of ripe strawberries. As the story goes, the Emperor Charles was returning home from Lyons where he and Cardinal Clemens de Monte Alto, Italy, had gone to settle a local dispute. The Emperor stopped at Auvers to prepare a sumptuous feast for the Cardinal. At the end of the entertainment Julius de Berry presented the Emperor with dishes of ripe strawberries. The Cardinal was greatly impressed, and, after seeing and tasting the berries, he declared that such fruit would certainly be a rarity in

[3] Throughout the seventeenth century the Bourbon rulers of France had tried to break the powers of the Hapsburg Empire which surrounded them on all sides. Then in 1700 Charles II, king of Spain, died childless and left his regency to the grandson of Louis XIV of France. Louis XIV defended the rights of his grandson for eleven years against an alliance of Austria, England, Holland and Brandenburg, from the outbreak of the War of the Spanish Succession until its settlement in the Peace of Utrecht, 1713–1714. The condition of the peace was that France and Spain should remain forever disunited, although Louis XIV's grandson was permitted to retain the Spanish throne. The French king knew his influence would be limited to the lifetime of his grandson. Frézier's mission represented the French king's efforts to get the most out of a temporary advantage.

Italy. He marvelled that such berries could be ripe in the early part of May. The Emperor was so pleased with Julius's timely offering that he knighted him and changed his surname from Berry to Fraise, a name which later became Frazer. The Emperor also gave the family three fraises or stalked strawberries for their coat of arms (*Plate 4–1*).[4]

Several of the Frazers emigrated to Scotland in the mid-1000's as members of the company sent by King Henry I of France with his ambassador, Count Chatère, to honor the reign of King Malcolm III who had vanquished Macbeth. The Frazers fought well in King Malcolm's battle against the invading Danes and he honored them with grants of land. He gave the family a shield and coat of arms of azure with a triangular field topped by a crown. Within this triangle was their original crest of three fraises. Later, in the sixteenth century, one of the Frazers returned to France to escape political troubles in Scotland. He settled in the southeastern Savoy region, on the Swiss-Italian border and from this ancestor there descended Amédée François Frézier, who by name was certainly the appropriate man to introduce from Chile the mother of the modern strawberry, *F. chiloensis.*

The father of Amédée François was a distinguished attorney of law at Chambery and he had wanted his son to follow him in the law. The son, however, showed an insurmountable aversion to law. The boy's precocious intelligence, exceptional aptitude for the sciences and his facility for foreign languages persuaded his father to send him to Paris to study at the center of the French academic world. For three years Frézier studied science with a strong complementary dose of theology. Under two famous teachers he wrote his first essay on a subject in which he became expert as an explorer some years later. It was entitled: "Treatise on Navigation and the Elements of Astronomy." His scientific studies completed, Frézier set off on a trip to Italy where he developed a taste for art. He took special notice of architecture and what he learned he later applied in his engineering of fortresses and defense structures.

Around 1700 Frézier returned to France and accepted a lieutenantship in an infantry regiment. Meanwhile, he exploited the leisure of garrison life to publish a *Treatise on Fireworks* in 1706. Until then pyrotechnics had mainly military uses. Frézier was interested in the spectacular fireworks displays for ceremonies. In his book he provided a review of earlier studies and their instructions for the manufacture of decorative fireworks. The book became a text for fireworks makers. The attention it received won for Frézier a transfer to the military intelligence corps, as military engineer for Saint-Malo. At last he was able to work exclusively with science. Garangeau, Frézier's

[4] Most of this information on the early history of the Fréziers or Frazers came to the author via Charles Dyson of Scarsdale, New York, who is an expert on the clans of Scotland.

superior officer, praised his zeal and skill in several reports and it was on Garangeau's recommendation that Mr. Pelletier de Souzy, the minister of fortifications, suggested Frézier as the man to study the defense fortifications of Chile and Peru—the mission from which Frézier would return to France with the Chilean strawberry.

After several false starts and delays caused by storms, calms and the loss of an anchor, Frézier sailed on January 7, 1712, aboard the *St. Joseph,* an armed merchant ship. The company finally reached the open sea without the feared attacks from pirates. Pirating was a sport the French enjoyed themselves when conditions were favorable, for Frézier recorded: "During that time, we discovered a small ship, which we judged to be Portuguese from the island of Madera, but the sea ran too high and we had too much business of our own to go about taking prizes."[5] After a long 160-day voyage round Cape Horn, Frézier arrived in Concepción, Chile, on June 16, 1712.

This was his base for more than a year and a half. He posed as a merchant captain so that he could visit the fortifications as a tourist. All the while he was studying them for Louis XIV, sketching maps which showed the best approaches for attack, where ammunition was stored and the routes of escape. He made friends with the Spanish officials who, had they known the true nature of his assignment, would have had his head. In his report Frézier was able to estimate the strength of the Spanish administration in each area he visited and he reviewed the organization of the government, its power over the Indians, and the unity and support that could be expected among the colonial governors. He noted that the Spaniards were just beginning to develop their gold and silver mines and he predicted these would become a source of great wealth to them. This part of his report was to be of such interest to the other European nations, that Frézier's book was translated immediately after its appearance in French, and within three years was available in English and other major European languages. In his excursions to the ports and capitals of Chile and Peru, the traveler also reported on the operations of the Church, the social organization and customs of the Indians, the physical geography of the area and its agricultural products. He remarked upon everything from earthquakes to the diversity of the seasons in the plains and in the Cordillera to the zoology of Peru. His book also contained several descriptions of new plants he had noticed. Among these was an exceptionally large-fruited strawberry plant which he found at Concepción.

The Indians called the site *Penco,* "pen" signifying "to find," and "co" meaning "water." Pedro de Valdivia, conqueror of Chile, changed the name to Concepción after he had subdued the neighboring Indians and founded a city there. Concepción is on the coast where a road by the same name leads

[5] *A Voyage to the South-Sea.* London, 1717, p. 6.

FIG. 4–1. Frézier's map of Concepción, Chile, where he found the *F. Chiloensis.* Note the valley to the left where the plants were discovered.

to the beach. The strawberries of which Frézier wrote were cultivated in the rich soil around Concepción (*Fig. 4–1*), soil which the officer described as "extraordinarily fertile, and so easy to till that they [the inhabitants] only scratch it with a plow."[6] The Spaniards called the strawberry plant the "Frutillar" and its berries the "Frutilla," meaning "little fruit."

> There they plant whole Fields, with a Sort of Strawberry Rushes, differing from ours, in that the Leaves are rounder, thicker and more

[6] *Ibid.*, p. 75.

downy. The fruit is generally as big as a Walnut, and sometimes as a Hen's Egg, of a whitish Red, and somewhat less delicious of taste than our Wood Strawberries. I have given some Plants of them to Monsieur de Jussieu, for the King's Garden, where Care will be taken to bring them to bear. Besides these, there is plenty in the Woods of our European Kind. And in Short, all manner of Garden-Product among us, grow there plentifully, and almost without trouble.

It was this description, quoted here from the 1717 English translation of Frézier's book, which was to fascinate European botanists and gardeners. Any

FIG. 4–2. Frézier's somewhat stylized but life-size drawing of the Chilean strawberry as he saw it growing near Concepción.

plant that could produce strawberries as big as a walnut had great value and so, as samples of *F. chiloensis* passed back and forth, each recipient would take care to note his experience with the plant.

Frézier accompanied his description with a somewhat stylized drawing (*Fig. 4–2*) of the "Fraise du Chile dessinée au grandeur naturelle," the Chilean strawberry drawn in its natural size, showing fruits, but no flowers, and which he described in Latin as *"Fragaria Chiliensis,* fructu maximo, foliis carnosis hirsutis, vulgo frutilla," Chile strawberry with big fruit and leathery hirsute leaves commonly known as Frutilla. Fifty years later Frézier discussed the cultivation of *F. chiloensis* at Concepción in a letter he sent on November 18, 1765, to Antoine N. Duchesne who was writing a book on strawberries:[7]

> They are found in the little valley plains where one can conduct a small stream to water them, as is done for the fields in several places in France, because it only rains in Chile during two months of the year, during three at most, in the wintertime, which corresponds to our summer, due to the situation of the southern temporal zone. . . . The berries are brought back in such abundance to the city of Concepción and the vicinity that people sell them at the market like other fruits. For half a real, which is the lowest money, one gets one or two dozens, wrapped in a cabbage leaf.

Frézier left Concepción on February 19, 1714, and after stopping off at Brazil and the Azores he reached Marseilles on the 17th of August. With him he carried several of the strawberry plants to which he played nurse throughout the voyage. He described the return trip in the same letter to Duchesne:[8]

> I returned in a merchant vessel from Marseilles, owned by the Bruny brothers, whereon they had placed as Supercargo, that is to say, entrusted with commerce, their nephew, M. Roux of Valbonne, who, after the captain, had the sole right to regulate the consumption of fresh water, which is very precious in a voyage of six months sailing . . . . through the torrid zone; so that if he had not taken it to heart to water these plants encased in a pot of soil, it would have been impossible for me to preserve them until our arrival at Marseilles, where there were five living ones, of which I had three and he two. I gave one of them on my arrival in Paris to my friend, M. Antoine Jussieu, to cultivate in the King's Garden, and one to M. Peletier of Souzy, our minister of fortifications, and kept the third for myself.

On his return, Frézier was honored by a presentation to Louis XIV, who had him explain the maps he had drawn. The king then marked his satisfaction with the mission by awarding Frézier 1,000 écus from the royal treasury.

[7] Duchesne, Antoine Nicolas, *L'Histoire Naturelle des Fraisiers*. Paris, 1766, p. 186.
[8] Duchesne, *op. cit.*, p. 182.

Louis XIV died before Frézier's observations could be published so in 1716 the book was dedicated instead to the Duke of Orleans, the regent for young Louis XV. Frézier's *Voyage to the South Sea* was praised by such scientists and geographers as Halley, Reămur, and Robertson and in such publications as Scevari's *Dictionary of Commerce,* the *Journal of Arevoux* (the Jesuit critical literary publication) and in the *Historical Atlas of Holland.* Perhaps the greatest tribute was its translation into German, Dutch and English within three years after the original French edition.

Meanwhile, Garangeau, Frézier's superior at Saint-Malo, again requested his services for defense construction. In 1719 Frézier was sent as Engineer-in-Chief to Santo Domingo on a two-year assignment to fortify the island. There malaria nearly killed him but he was too useful to his superiors to permit his return until nine years later when he was sent first to Philipsbourg and then to Landau, Germany, where he built twenty-six defense structures. This last assignment was the basis for a characteristically scholarly and precise work applying theories of architecture to practical engineering. Frézier married, was commissioned a captain, and in 1739 was named Director of Fortifications for the whole of Brittany. He finally retired from his sixty-four years of service at the age of eighty-two. At eighty-seven he was still writing on such diverse subjects as navigation and landing methods for the Lucayes Islands, the aesthetics of architecture, and on the purification of unhealthy water which could make even sea water drinkable. Even when his sight weakened, five years before his death in 1773, he made himself read at least six hours a day, especially books on travel and history.

Activity had always characterized Frézier's life and even in his last years he lived at a pace one would associate with a far younger man. An example is his correspondence which was extensive and which included literary men as well as scientists. They consulted him with confidence and found him pleased to share his insights. Always one to insist upon precision, he scorned presumptuous ignorance. He disdained envy as well, calling it a great and humiliating weakness. His associates said he was as delighted with a discovery as the inventor himself. One biographer described him as the representative of the universal character of the enlightened eighteenth-century man.[9] The Secretary of the Royal French Marine Academy, writing of Frézier in the flowery phrases of the era, said: "Amédée François Frézier has rendered his name dear to Letters, to Art and to Science, which he cultivated with success, to the Corps du Genie (Intelligence Corps), from which he acquired his fame, to the Marine Academy, of which he was the ornament for a long time, and to the Society of which he was the delight."[10] This was the remarkable man who

[9] *Nécrologe des Hommes Célèbres de France.* Paris, 1766.

[10] M. de Marguery, *Eloge Historique de M. Frézier,* p. 159.

had the curiosity and initiative to transplant the first Frutillar from Chile to France.

What did the plant from Chile look like? What characteristics would it communicate to its offspring, *F. ananassa*? Comparing it to the familiar European wood strawberry, botanists noticed that its brownish green leaves, though the same size as *F. vesca,* were much stouter, thicker and more stiff and leathery, with big teeth and with prominent veins on the very pale underside. The runners were also much bigger and at least triple the length of those of the wood strawberry. "It is not rare to see the nodes of these runners borne at 15 or 18 inches from the old plant," Duchesne wrote of the plant in 1766. The hardy pedicels were almost ligneous. Another obvious difference was the heavy pubescence of the *Frutillar,* which was covered with long, appressed, whitish hairs on the underside of the leaves and especially on the stems and sepals. These sepals were numerous and remained spread out flat on unfertilized flowers but closed again on fertilized ones once the petals fell.

And then there were the few, but enormous, flowers: "One often sees that an écu of six francs cannot cover it," said Duchesne, describing the diameter as more than one and three-fifths inches.[11] There were many petals, a single one equal in area to the entire flower of *F. vesca.* In cool sunny weather they gave off a strong perfume, which Dillenius also had noted in his *Hortus Elthamensis:* "Flores teneum Oxyacantha ordorem spirant." In the female flowers forty or fifty short stamens, instead of the usual twenty, pressed together in three or four mixed rows, and pointed in all directions around the young receptacle, itself the size of a small *F. vesca* fruit.

The fruits were proportionate to the flower in size, although Frézier found them to be smaller in Europe than those he had seen in Chile. The ovaries, though quite a distance from each other, formed only shallow pits in the solid flesh of the berry; each ovary was three to four times bigger than those of *F. vesca,* and a deep, dull red in color. In ripening, the berry was red above but yellowish-white below, with a most pleasant odor. The berries were commonly elongated and angular, some rounded and a bit pointed.

Another characteristic feature, and a remarkable one, was the strength of the pedicel. At the moment of ripeness, instead of hanging down with the weight of the fruit as in other strawberries, it bent upward so that the point of the berry faced toward the sun. The *Frutillar* began to flower in France at the time *F. vesca* bore its first ripe fruits and the berries were not mature until the end of June, a month later.

What happened to Frézier's *F. chiloensis* plants upon his return to Mar-

[11] Duchesne, *op. cit.,* pp. 170–176.

seilles in August 1714? As he wrote Duchesne in 1765, he gave two of the five plants to Mr. Roux de Valbonne, the officer in charge of the water supply, who had kept the plants alive by watering them during the long sailing. Another specimen went to the head of the King's Garden at Paris, M. Antoine de Jussieu. Frézier kept one plant for himself, and the remaining one was given to his superior, M. Pelletier de Souzy, the minister of fortifications at Brest. Between 1714 and the publication of Duchesne's monograph on the strawberry in 1766, a large prosperous strawberry industry developed at Brest, supplied by fruits from *F. chiloensis* pollinated by other species. Perhaps the plant sent to M. Pelletier de Souzy in Brest started this culture. Or perhaps Frézier's own plant was the mother of that industry. After publication of his book in 1716, Frézier returned to Saint-Malo in Brittany, in command of the construction of fortifications upon the request of M. Garangeau, his former patron. Was it then that he delivered runners from his Frutillar to the local gardeners of Brest, exciting them with his claims of the marvelous properties of his new strawberry? Or did he survey the Brittany coast until he decided that the port of Brest would best simulate the coastal climate of Concepción? He left for Santo Domingo in 1719, returned to France in 1726, and two years later he left for Germany where he remained until 1739, after which he returned to Brittany. Perhaps during one of these interludes the Chilean berry was introduced. In 1765, Frézier wrote Duchesne from Brest that "this city and its vicinity are so well provided with strawberries that one finds them for sale at the market."[12] According to Duchesne, Frézier had himself cultivated the Frutillar after his return to France.

The imported Chilean strawberries had a difficult time in Europe at first. They grew vigorously, but even at Brest produced none of the fruit "as large as a hen's egg" which had recommended it to Frézier. Indeed at first the plants produced no fruits at all. Unwittingly Frézier had selected female plants in Chile; at least the five which reached France were female. The botanists of the King's Garden at Paris, always eager to receive and exchange new plants, preserved several specimens of *F. chiloensis* in their herbaria and, according to Duchesne, these were all female. Antoine de Jussieu, head of the King's Garden, and true to the international spirit of eighteenth-century science, wasted no time in sending propagations of his plants abroad. In 1720, just six years after Frézier's return, the great Dutch botanist Boerhaave, published a description of *F. chiloensis* grown from runners sent to Leyden, Holland, from the King's Garden in Paris. He designated it as "Fragaria crassis rugosis soliis flore semine carens" and called it the "Chili strawberry without blooms or fruits."[13]

[12] *Ibid.*, p. 187.

[13] Boerhaave, Hermanno, *Index Alter Plantarum Quae in Horto Academica*. Lugduno-Batavo Aluntur, 1720, p. 165.

From Holland, Philip Miller introduced the plant to England. "I brought some of the plants from Holland, Anno 1727, which thrive and increase exceedingly, but as yet I have obtained no Fruit; the last Season, Anno 1729, they produced great Numbers of Flowers, which were larger than the Hautboy Strawberry, in proportion to the Bulk of its Fruit; but I am in Hopes next Season to obtain some Fruit in Perfection: I observe they thrive best when they have only the Morning Sun, and do require frequent Waterings in dry Weather," wrote Miller in the 1731 edition of his *Gardener's Dictionary*. In the 1752 edition Miller was more exact about his source and explained that "in 1727 I brought a parcel of the plants to England, which were communicated to me by Mr. George Clifford of Amsterdam, who had large beds of this Sort growing in his curious gardens at Hartecamp." Miller had given a specimen to Dillenius, assistant to James Sherard who owned one of most richly stocked gardens in the world at Eltham. Although the plant flowered in 1730, it was a female similar to Boerhaave's and bore no fruits. Thus Dillenius engraved a flowering specimen without fruits in the *Hortus Elthamensis* (1732), a descriptive catalogue of the plants in Sherard's garden (*Plate 4–2*).

All the botanical gardens were having the same difficulties: Frézier's female plants seldom produced fruits. Duchesne, in 1766, was to explain the trouble. Female plants had to be fertilized with the pollen of other strawberries and not all strawberries could pollinate *F. chiloensis*. Only strawberries with large fruits like *F. moschata, F. virginiana* and later, *F. ananassa* were successful. Meanwhile, no European before Duchesne seemed aware of the separation of sexes in strawberries. Philip Miller had cautioned in 1759 that if the gardener was careless and selected strawberry plants at random, the majority of the plants would become barren. "These are generally called blind, which is when there are plenty of smaller flowers but no fruit produced," he wrote, and described such flowers as well-supplied with stamens but lacking female parts with few if any styles and producing deformed fruit at best.

It was Duchesne who taught that the male flowers Miller described were valuable as pollinators. Probably Frézier, anxious to select superior specimens to introduce to France, had collected those plants which bore the largest fruits among the cultivated Frutillars of Concepción. These must have been females since males would produce no fruit.

Eventually some *F. chiloensis* plants in Europe did bear. Although disappointed in his barren plants in London, Miller wrote in the same 1731 edition of the *Dictionary* that the plant "has produced Fruit several Years in the Royal Garden at Paris, where Monsieur Jussieu assured me, it was commonly as large as a small Apple." Two years later in his 1733 edition Miller could add: "and this season there has been Fruit in several Gardens near London," but for many years the English lacked the success and consequent appreciation for the Frutillar which the French showed. Successive editions of Miller's *The Gardener's Dictionary* are like the readings of a barometer measuring the rise and fall of England's affection for the Chile strawberry. The comments on *F. chiloensis* from the third edition of 1737 are an example:

> I brought some of the Plants from Holland Anno 1727, which thrive and increase exceedingly; but these bear very indifferently and the Fruit being less delicate than the Hautboys (*F. moschata*), few Persons care to propogate this Sort in England. These plants have been placed in the Sun, and cultivated with Care, but have never succeeded where they have been thus treated. I have observed that they succeeded best where they have been grown under the Shade of trees, in a loamy Soil, and little more Care taken of them than to keep them clear from Weeds.

Three years later, in 1740, Miller observed that the Chile strawberry "is now but little esteemed in England, the Fruit being ill-tasted. This Kind has produced Fruit of Late Years in many Gardens; but in general the Fruit is not so large as those of the Globe-Hautboy Strawberry, and is of a very irregular Form."

In 1737 the Chile strawberry appeared in a descriptive catalogue of Clifford's garden at Hartecamp in Holland. The author of the *Hortus Cliffortianus* was none other than Linnaeus, the famed naturalist of Sweden. Linnaeus had recently received his medical degree in Holland and had then been hired by the wealthy Amsterdam banker, George Clifford, as his physician and botanist. Linnaeus cited first Frézier and then Dillenius and Boerhaave in describing the Chile strawberry but he called it *Fragaria chiloensis* instead of *Fragaria chiliensis* as named by Frézier. Perhaps Linnaeus thought the plant came from the island of Chiloe off the coast of Concepción, while Frézier had been careful to use *chiliensis* to designate the country itself.

In 1736 Linnaeus was sent to England to meet Philip Miller to whom Clifford had sent *F. chiloensis* and to whom he was later to send an early specimen of the modern strawberry, *F. ananassa*. Miller had been brought to London by Sir Hans Sloane to head the new London Apothecaries' Garden at Chelsea. The garden gained a leading position among the great botanical collections under Miller's supervision. Miller's *Dictionary* was for a long time the standard dictionary of English gardening, and its fame soon went beyond England. After the first awkward meeting with Miller, a great cooperation developed between Linnaeus and Miller, and the latter finally championed the Linnaean system of classification. Miller gave Linnaeus numerous specimens of plants for Clifford's garden as well as dried specimens for the herbarium. The close contact among the botanists of this period and their eagerness to exchange specimens from their collections were responsible for the rapid dissemination of the Chilean strawberry in Europe. Linnaeus enters the story again later. (See *Plate 4–3.*)

The French had much better luck than the English with *F. chiloensis.* The sharp-eyed gardeners of the Plougastel region of Brittany around Brest had observed that the Chile strawberry bore abundant fruit when *F. moschata* and *F. virginiana* were planted in between the rows of *F. chiloensis.* In a similar climate nearby at Cherbourg, M. des Nouettes-Grou wrote that he had been cultivating the Chile "with success by means of pollens from native berries which succeeded very well for me . . . in 1758 and 1759." Two of his berries were 7½ inches in circumference.[14] The botanist Du Hamel observed in 1764 that "in the better tended plantings, half the strawberries were of an entirely different sort, which are called regionally "Barbary strawberries." These proved to be *F. virginiana* and *F. moschata* plants.

The French found that *F. chiloensis* had a very determined preference for a marine climate and its cultivation remained confined to Plougastel. Attempts to cultivate it in Anjou, Touraine, and the lower-Loire areas failed. For more than a century, until about 1875, the Plougastel's harvest supplied the cities of Brittany and the English markets as well. After 1875 the popularity of *F. chiloensis* began to diminish as new, large-fruited varieties, of which it was the mother, replaced it. In 1887, Mme. Elisa Vilmorin[15] recorded that the strawberry fields planted to *F. chiloensis* still covered one hundred and eighty acres, while by 1900, of the three hundred acres devoted to strawberries in Plougastel, only fifty acres were planted to the Chilean strawberry.

By the mid-1700's the strawberry from Chile was no longer simply a curiosity in the botanical collections of the wealthy and of the universities. It was beginning to be grown commercially around Brest, the only place in Europe where it succeeded. Its hybrids, which were accidental results of using *F. virginiana* as the pollinator for *F. chiloensis* (there is little evidence that the cross of *F. chiloensis* x *F. moschata* ever produced fertile plants), were more adaptable, and gardeners in England, Holland and France made careful selections for large-fruited varieties of *F. ananassa,* as the hybrid was called. This led to the gradual abandonment of its parent, *F. chiloensis,* except around Brest.

As Captain Frézier was central to the story of the introduction of *F. chiloensis,* so Antoine Nicolas Duchesne is central to the story of its hybridization which followed, for Duchesne was both an active experimenter and a

[14] *Ibid.,* p. 187.
[15] Decaisne, Joseph, *Le Jardin Fruitier du Muséum,* Volume 9. Paris, 1862–1875.

chronicler of this period. Yet without European curiosity in New World botany, Frézier's five plants of *F. chiloensis* would not have been propagated and distributed so early to so many growers. For several centuries, large-fruited strawberries might have remained exclusive to the western coasts of the Americas.

5

Duchesne and His Work

ON JULY 6, 1764, Antoine Nicolas Duchesne (*Fig. 5–1*) personally presented King Louis XV with a pot of strawberries. The fruits were specimens of the Chilean berry (*Fragaria chiloensis*) and had extraordinary size and beauty. Fruiting *F. chiloensis* was a rare sight since the plants were female, but the seventeen-year-old boy had used pollen of the musky strawberry (*F. moschata*) with spectacular results. On the advice of his head botanist, Bernard de Jussieu, the king honored Duchesne by ordering Mademoiselle Basseporte, the famous botanical artist, to paint the berries for the collection in the Royal Botanic Library. In addition, he authorized Duchesne to raise more *F. chiloensis* in the royal kitchen garden at Versailles and to collect all varieties of strawberries known in Europe for the Trianon garden.

Two years later, research and experiments produced the most scholarly, complete treatise ever written on the natural history of the strawberry. For a nineteen-year-old boy it was a remarkable achievement, but it was more remarkable still as an illustration of the cooperation and enthusiastic involvement of eighteenth-century scientists, farmers, and home-gardeners in attempts to exploit the variation of nature. Duchesne wrote to all of them for his collection. He wanted their plants and their descriptions of the behavior of wild and cultivated strawberries in their regions. He pressed them to speculate with him about the directions nature had taken in the past and why. They did their best to answer him, from their chairs in the great universities, from the rounds of a village priest, from gardens in the countryside of England, France, Switzerland, Germany, and Sweden, and from the Office of Naval Defense in Brittany. Their lives and attitudes were not comparable in many

FIG. 5–1. Portrait of Duchesne, who at the age of nineteen wrote a study of the genus *Fragaria* which has become a classic in natural history.

respects, and when Duchesne asked them to consider the strawberry he found the same diversity in their experiences with it. Yet their replies to his questions were the materials for his balanced and reasoned discussion of strawberry evolution. The conclusions he derived generally remain valid today.

The discovery that strawberry plants could be unisexual as well as bisexual set Duchesne off on his study of natural history. He first found unisexual plants in the musky-flavored strawberry, *F. moschata* (*Fig. 5–2*), and then noticed the same condition in the foreign strawberry from Chile, *F. chiloensis.* There were no male Chilean strawberries in Europe, but with male *F. moschata* (*Fig. 5–3*) planted nearby, female *F. chiloensis* would produce the enormous fruit for which it was famous.

Fragaria chiloensis had not flowered in Duchesne's garden in the spring of 1764 so he and his father had asked M. Richard, the king's botanist-gardener at the Trianon, the Royal garden at Versailles, to send them some *F. chiloensis* to study. On the 29th of May Richard sent a single potted plant with one stem and two branches, which were divided into eight pedicels. In all there were eight buds, two of which were long past blooming and one which already had withered. No berries had formed. Duchesne recognized at once that the flowers were female and despaired of obtaining any fruit as he knew of no male *F. chiloensis.* The plant did resemble *F. moschata* and so he placed it in his collection of strawberries, next to male *F. moschata.* Hardly had the petals of one flower fallen when on June 6th he saw its receptacle beginning to enlarge, the first stage in the formation of a berry. A little later he was certain that the fruit had set. "I did not doubt for an instant that the

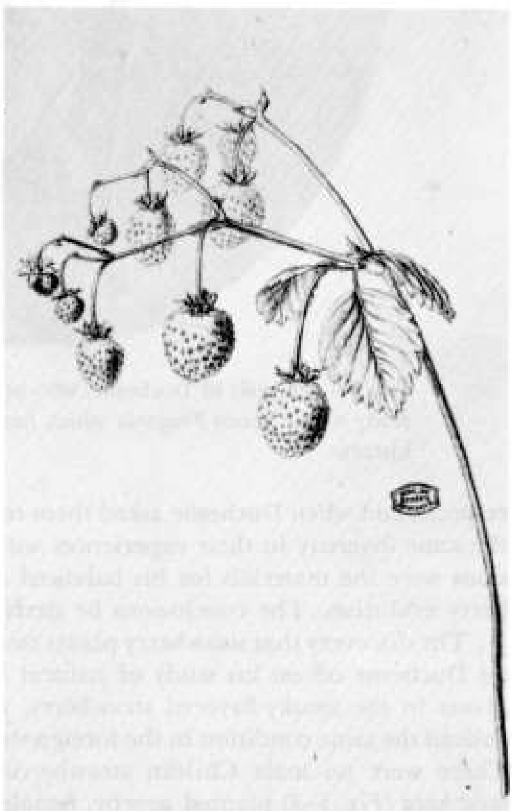


FIG. 5–2. A stem of female *Fragaria moschata.* Duchesne's discovery of unisexuality in this species helped him recognize the same characteristic in *Fragaria chiloensis.* (by Duchesne)

neighboring *F. moschata* had fertilized it," wrote Duchesne (*Fig. 5–4*).[1] The next three fruits also set. Duchesne removed the last two flowers so the plant could concentrate its strength and develop bigger berries from the flowers already fertilized. The first of the berries, which was very large, ripened during the first days of July and the others soon followed.

How did such experiments in natural history come to capture the Duchesne boy's attention in the first place? He was born October 7, 1747, at Versailles, where his father, an architect and painter, had inherited the post of superintendent of the king's buildings, an office created for his father by Louis XIV. Left motherless at birth, the boy received the devoted attention of his scholarly father, a man learned in Greek, Latin, and several modern languages, a lover of the fine arts and the natural sciences. All his knowledge was concentrated on his son's education. As a four-year-old the child could

[1] Duchesne, Antoine Nicolas, *L'Histoire Naturelle des Fraisiers*. Paris, 1766.

FIG. 5–3. A male *Fragaria moschata* plant. Gardeners in the early 1700's tore this plant from their strawberry beds because it did not fruit and so was said to be sterile. Duchesne found its pollen was necessary to fertilize the female plant and he used the pollen on female *Fragaria chiloensis* and made this "stubborn" strawberry produce fruit. (by Duchesne)

FIG. 5–4. Duchesne's drawing of the Chilian strawberry whose flowers he fertilized in 1764 with the pollen of a male *F. moschata*. This was a handmade pollination between the two species and Duchesne presented the fruiting *F. chiloensis* to King Louis XV, so remarkable were the large berries which resulted.

read, knew four hundred Latin words, and could recite numerous historical anecdotes which his father had taught him in discussions or in the instructive games he invented. His father kept him occupied constantly, varying his studies to maintain interest. As soon as the boy was old enough the two began a series of walking tours which took them around Versailles and Paris to public and industrial establishments; later they walked to Fontainbleau, Campiègne, Le Hâvre, and Reims, where the boy watched the coronation of Louis XV. M. Duchesne insisted that his son miss nothing, and urged him to puzzle over all he saw. He made a small notebook for him in which to describe their observations of each excursion. Soon the boy was recording his own observations from these walks (his father insisted they travel everywhere on foot). Meanwhile, lessons progressed in Greek, Latin, English, and Italian, and in history, geography, mathematics, drawing, and music. The zealous teacher made every childhood amusement and game a physical or moral means of instruction.

Natural history was the boy's favorite subject. In his free moments he would visit the Trianon Garden, which his father supervised as superintendent of the king's buildings. The collection of the botanic garden fascinated him. But more engaging than the garden itself was the kindly royal botanist, Bernard de Jussieu, who allowed the boy to follow him about the countryside in his gardening work. The shy, solitary scientist began to instruct his small companion in the botanical characteristics and methods of classification of the plants they handled. He taught him how to make plants reproduce and what to do with the seeds, bulbs, and runners. He pointed out strange features, like the separation of sexes on some plants, and insisted on precise notation of the particular seasons for transplanting, fertilizing, pruning, and the effects of temperature changes.

Good fortune had brought Antoine Nicolas Duchesne the finest teacher of natural history in all of Europe. Bernard was second in the five-member de Jussieu dynasty of botanists who occupied for nearly a century and a half a pre-eminent place in botanical science. Bernard's older brother, Antoine, to whom Frézier had sent an *F. chiloensis* plant, was "Professor and Demonstrator of the Interior and Exterior of Plants" at the King's Garden (a post formerly held by Tournefort). He was also a prosperous doctor with a large clientelle. In 1714 he brought his fifteen-year-old brother Bernard to Paris where he became "Assistant Demonstrator of the Exterior of Plants at the King's Garden." Bernard's job entailed the organization and inspection of all open-air and hot-house cultivation, the instruction of the gardeners in his charge, and the leading of botanical excursions into the countryside around Paris. Bernard also prepared all the courses taught by his older brother, the busy doctor. Bernard kept house, receiving their few but select friends: famous botanists like Le Monnier, Duhamel du Monceau, Malesherbes, and Poivre—along with foreign visitors passing through Paris. Their house became known as a salon dedicated to scientific discussion. Among the visitors from abroad was young Carl Linnaeus, who stayed with the de Jussieu brothers for a month following his departure in 1738 from Hartecamp where he had served as George Clifford's gardener and doctor. . . . A strong admiration and warm friendship united the two greatest botanists of the age and for thirty years Bernard and Linnaeus exchanged letters, living and dried plants, and seeds. Their correspondence included criticism of recent publications, comments on the activities of the French Royal Academy of Sciences (both were members), and discussions of scientific expeditions, particularly those of friends and students. Anything new in the world of science interested them—zoology, biology, and medicine, as well as botany.

Through interest in Linnaeus' sexual system of classification and his method of binomial nomenclature, Bernard de Jussieu had developed ideas of his own on a natural method of plant classification. The earlier botanists like Ray, Morison, Magnol, Vaillant, and finally Linnaeus himself, had foreseen such a relationship but had formulated no rules or descriptions. Bernard's interest had centered on this by 1759, when King Louis XV, an enthusiast for all the sciences but especially botany, requested him to collect all the plants cultivated in France in the Trianon Garden and to establish a school of botany there. For several years the king personally followed its development and encouraged de Jussieu with kindness and friendship.

Modest and hesitant, Bernard wrote only three small essays on botany in his whole life. He published nothing on his natural method of classification and left behind no record of the directing principles behind his research. He used his system in only one work, the catalogue of the plants in the Trianon collection, but this remained in manuscript form as a list of names which he revised continually right up to the last hour before his death. Bernard had refused the vacant professorship left by his brother, who died in 1758, and so he remained an under-demonstrator, passing most of the day in armchair meditation across the room from his studious young nephew. The two men broke their rigorously imposed silence only in the evening when Antoine Laurent de Jussieu read to his uncle, awaiting his comments and ideas.

By the time the seventeen-year-old Duchesne began his study of strawberries he already had published *Le Manuel de Botanique*. This manual described the characters and properties of plants cultivated around Paris and their nutritional, medical, artistic, and ornamental uses. With Bernard's approval, Duchesne had given common names to all these plants, carefully substituting new names for inaccurate or confusing older ones. The praise scientists gave the book encouraged him to continue his observations. With Louis XV's authorization to extend the collection of strawberries in the Trianon Gardens—the reward Duchesne received for his unusual strawberries and his eagerness to learn more about them—Duchesne wrote to botanists and gardeners all over Europe. Frézier, then in Brest, was asked for a detailed account of his collections of the Frutillar, fifty-one years earlier in Chile. The village curate from the Montreuil area was pressed into service. Could he discover the origin of the common market-garden variety of *F. vesca,* a large-fruited wood strawberry called the Montreuil strawberry? Von Haller in Switzerland was asked to send native species. A bishop from Bargemon, a town in the Alps du Var, searched the countryside at Duchesne's request to test the ancient report of a twice-bearing strawberry which grew in the neighboring mountains.

In his enthusiasm, Duchesne did not hesitate to approach the great Linnaeus himself, the old friend of his tutor, Bernard de Jussieu. The distinguished botanist proved most approachable and for ten years he corresponded with Duchesne, exchanging several species of plants and tolerating (though not accepting) the audacious youth's criticism of Linnaeus' own classification of strawberries. Linnaeus fully approved Duchesne's initiation of a depth study in botany, a most unusual attempt in an age devoted to classification and systemization. "When you have completed the history of the wild strawberries, you will have accomplished something which I long have hoped that some botanists would do; namely, that they would each choose their plant family and examine it most thoroughly; in this manner would soon be attained the ultimate knowledge of plants which now floods botanists with its abundance," he wrote Duchesne from Hammarby on September 24, 1765.[2]

Duchesne did study his plant family, the *Fragaria,* thoroughly. His book, which details this study under the title of *L'Histoire Naturelle des Fraisiers,* begins with a description of the genus as a whole, and then follows with an examination of each of the ten species and eight varieties with which Duchesne was acquainted. He intended to accompany each with a drawing of the plant as he had seen it growing at Versailles, but he lacked the money to do so. Several of these drawings, so realistic that botanists have since said they could survive microscopic inspection, were discovered by this author in the Paris Muséum de l'Histoire Naturelle and are published here for the first time. Yet Duchesne's botanical descriptions could not have been more exacting and precise. For each strawberry he tried to trace the history of its European introduction, cultivation, and distribution from the earliest botanical references in medical books and garden catalogues on up to the year that his book was published. He included notations of flowering and fruiting seasons and weather effects for each species. In a truly unusual attempt for his century, he pointed out what he thought to be the oldest and the newest species and then offered his reasons which were based on the differences among the species and their distribution. He went on to suggest which kinds might have descended from which. The order in which he discussed each species followed this system and the author summed up his ideas in the drawing of a genealogical tree.

He devoted the second part of his book to strawberry culture. Here he evaluated the different methods of fertilization, propagation, and the forcing and retarding of the fruiting time of different kinds. The final section of the book, entitled *Remarques Particulières,* he divided into four detailed little essays on puzzling aspects of the natural history of plants which his study of *Fragaria* had suggested.

The ten species (or "races" as Duchesne called them) in the order in which he described them were:

I. The Alpine or *Fraisier des Mois* (*F. vesca semperflorens*)

II. The wood strawberry or *Fraisier de Bois* (*F. vesca silvestris*) and its six "varieties"

a) the variegated (*F. vesca variegata*)

[2] Hylander, Nils, *Linné, Duchesne och Smultronen.* Svenska Linne-Sallskapets Arsskrift 28, 1945.

b) the white (*F. vesca alba*)
c) the double (*F. silvestris multiplex*)
d) the clustered (*F. silvestris botryformis*)
e) the Plymouth (*F. silvestris muricata*)
f) the *coucou* (*F. silvestris abortiva*)

III. The Fressant or Montreuil strawberry (*F. hortensis*), a cultivated garden variety of the wood strawberry with fruits which Duchesne said were fifteen to twenty times larger than the common Paris market variety of his day.
a) *le blanc fraisier de fressant,* a white variety of the above

IV. The runnerless wood strawberry (*F. efflagelis*).

V. The Versailles strawberry (*F. monophylla*), a wood strawberry with simple leaves.

VI. The green strawberry (*F. viridis*)

VII. The musky or Hautboy or Capiton strawberry (*F. moschata*)

VIII. The Chilean or Frutillar (*F. chiloensis*)

IX. The pineapple or ananas strawberry (*F. ananassa*)
a) The "fraisier pannaché," a striped-leaved *ananassa*

X. The scarlet or Virginian (*F. virginiana*)

Several discoveries important to the new science of plant breeding emerged from Duchesne's study, and he showed their practicality by applying them to the cultivation of strawberries. He was the first to recognize the separation of sexes in strawberries. Though rarely cultivated today, *F. moschata,* the musky-flavored strawberry, was common in eighteenth century gardens, as its fruits were considerably larger than those of the wood strawberry. It was a difficult berry to raise, however, since after a few years in a garden half of the *F. moschata* plants would be found sterile and had to be pulled out. Soon the remaining plants would bear less and less and the gardener would have to search again for new vigorous plants. By studying *F. moschata,* Duchesne discovered that the sexes were separated in this particular species. Unless some of the "sterile" plants were allowed to grow near the "fertile" fruit-bearing females, not a single berry could be expected in the whole bed of musky strawberries. Duchesne's teacher, Bernard de Jussieu, had pointed out cases of separate sexes in other plants, among them a peach tree which bore only male flowers and thus no fruit. Linnaeus had described the Latoch raspberry from Lapland in 1753 which had unisexual plants, the female flowers bearing only rudimentary stamens. The gardener of a friend of the Duchesnes, to whom they had given an *F. moschata* plant in 1760, had tried tearing out all *F. moschata* from the garden except one fertile plant. He propagated this plant from runners until he had filled a bed twelve to fifteen feet long with its offspring. The following year he could not find a single edible berry. "Then regretting the sterile plants which he had so carefully destroyed, he told me that doubtless they were necessary to fertilize the others," said Duchesne.[3] The gardener recalled that the stamens on sterile *F. moschata* were very hardy, but he had not suspected that the fertile individuals were absolutely barren of pollen.

To the young gardener's observation, Duchesne owed his first suspicion of the unisexual character of the female musky strawberry, *F. moschata.*

Duchesne began experimenting on *F. moschata* in the summer of 1765. He took a female, or fertile, plant from a garden where it was growing among males and set it in a pot. Eight of the flowers were in the process of developing into fruits, five or six were withered, and about twenty were still buds. Duchesne cut off those flowers which might have been already fertilized and five of the developing fruits. He marked the three remaining infant fruits with thread and placed the pot in isolation on the windowsill of his room. All the later flowers which opened there withered, but the three infant fruits that he had marked developed into mature fruit. This experiment convinced him that a fertile female plant, already bearing young berries, would form no additional berries when isolated from male plants of its species.

Duchesne next asked himself if *F. moschata* could be fertilized by pollen from other kinds of strawberries. He placed another pot containing a female plant on his windowsill and surrounded it with four *F. vesca* plants and a *F. virginiana.* No fruits formed despite the presence of the other species. About that time, while walking around Montlhéry, he saw some strawberries in the garden of the Lord of Villebousin and observed that there were two female *F. moschata* growing in a bed of Fressant (*F. vesca*) strawberries. As he suspected, they were unfertile through the lack of male *F. moschata* plants. "These last two observations," wrote Duchesne, "while confirming that the female Capitons (*F. moschata*) cannot fertilize themselves, seem to indicate in addition that common strawberries (*F. vesca*) are incapable of fertilizing them."[4] Independent of these experiments, close examination of the female flowers themselves showed Duchesne that they needed males as pollinators since the undeveloped stamens were totally lacking in pollen. He also noted a secondary sex characteristic—male *F. moschata* flowers were larger than those of the females.

In great excitement Duchesne wrote to Linnaeus describing his discovery. He received a stern injunction to examine his *F. moschata* "males" more closely. Linnaeus suspected them to be frost-bitten hermaphrodites (bisexual plants) which he said were easily mistaken for males. "While you are talking

[3] Duchesne, *op. cit.,* Part II, p. 28.
[4] *Ibid.,* p. 29.

about sex, I ask that you take care lest you are considering flowers consumed by a spring frost as masculine, which happens frequently in our country. I have never seen or observed masculine flowers in any strawberry," concluded Linnaeus in a letter of September 24, 1765.[5]

"No one, I believe, suspected before me the separation of the sexes in the Capiton," Duchesne stated in his book.[6]

Neither was Linnaeus of much help in answering Duchesne's other question about *F. moschata*. "Did it grow wild in Sweden?" Duchesne had asked, trying to trace the original source of the plant. Linnaeus, however, had confused *F. viridis* with *F. moschata* and thus could not give Duchesne a convincing answer. Linnaeus reported that the green strawberry "is very common here and completely spontaneous; it grows on all slopes but especially by roadsides and on the sides of larger ditches, while *vulgaris* (that is, the wood strawberry) occurs in open woods, clearings, and burnt woodlands, where

[5] Hylander, *op. cit.*
[6] Duchesne, *op. cit.* During this period the *F. moschata* had some popularity in English gardens. Either the English had solved the problem of dioecism unconsciously, by allowing male plants to remain in their gardens, or by calling another strawberry by the name *F. moschata.*

FIG. 5–5. A green strawberry of Sweden (*Fragaria viridis*). Linnaeus confused this species with the Swedish garden strawberry, *Fragaria moschata,* and thus led Duchesne to believe that *F. moschata* was native to Sweden and that in its wild state it was bisexual. (by Duchesne)

the green strawberry is never seen. I cannot distinguish the green strawberry from the usual wood strawberry through the plant itself, but only by the fruit, so similar are the two."[7]

In identifying the green strawberry, Linnaeus had cited Bauhin's *Fragaria fructu parvi pruni magnitudine,* the strawberry with fruit as large as a small plum, as his source. Duchesne believed this was *F. moschata,* the musky-flavored strawberry, and not the green strawberry as Linnaeus claimed. The origin of *F. moschata* was unknown. Rumors had described it as American or oriental. It was cultivated in France, England, Sweden and Germany, but certainly it was not native to France. Yet Linnaeus described it as "completely spontaneous" in Sweden.

In a discussion of the cultivated Swedish garden strawberry, which he called *F. hortensis,* Linnaeus said that this strawberry was grown both in French and Swedish kitchen gardens and that it differed from the wood strawberry and the green strawberry of Sweden only by the size of its fruits, since the fruits of the wood and green berries were the same size. He then said he thought the cultivated garden strawberry (which was really *F. moschata*) must be the green strawberry and he planned to plant a green strawberry from the wilds in his garden the next year to see if it would grow berries as large as the garden strawberry.

How could one of the greatest botanists of the day confuse two so different species as *F. moschata* (his garden strawberry) and *F. viridis* (his green strawberry)? As Linnaeus himself said, "the green strawberry is bleak in color compared to the wood strawberry, less perfumed, and comes off the plant with the calyx attached." The only obvious explanation for his confusion is the use of the common name "strawberries" in Sweden for both *F. moschata* and *F. viridis,* the green or wild hill strawberry of Sweden. Duchesne could never be sure that the green strawberry was the true wild *F. moschata* (*Fig. 5–5*).

The discovery of separation of sexes in the musky strawberry alerted Duchesne to the same possibility in other species and he easily recognized that the Chilean, too, was dioecious—at least only females had ever been seen in Europe. Other botanists before Duchesne had attributed the Chilean's sterility to its impotent stamens which lacked pollen. Duchesne was the first to discover a successful pollinating agent for it, thus remedying its sterile condition. Other botanists had tried to pollinate it with *F. vesca* pollen but had failed. Noting its resemblance to *F. moschata,* Duchesne used the musky strawberry as a pollinator for the Chilean and produced the famous berries which he presented to Louis XV in 1764. Noting also that *F. vesca* pollen

[7] Hylander, *op. cit.*

had failed to pollinate female *F. moschata,* Duchesne suggested that this mutual disinclination might differentiate them as species. With characteristic caution, he wrote: "Before concluding anything from these observations, it is doubtless necessary to repeat them (attempts to pollinate *F. moschata* with *F. vesca*), and it would be very useful if several persons should do so. But if the experiment confirmed this, it seems to me that one could hardly avoid regarding the common strawberry (*F. vesca*) and *F. moschata* as two species, despite their very intimate resemblance, just as one generally recognizes the dog, fox, and wolf as different species because they refuse to mate together."[8]

The Chilean strawberry had been grown successfully as a market variety in the Brest area of France for some years. What were the berries used as pollinators? Duchesne wondered. M. Duhamel, a famous botanist of this period, attested that in the better-tended plantings of *F. chiloensis* "half of the strawberries were of an entirely different sort, which has the regional name of Barbary strawberry."[9] He sent some of these to Duchesne who found them to be an assortment of *F. virginiana* and *F. moschata.* None was *F. vesca.* The dioecism present in *F. moschata* and *F. chiloensis* and their ability to cross suggested a genealogical relationship between the two species to Duchesne.

He wondered if *F. moschata* was dioecious in its wild state. Taking Linnaeus' word that the green strawberry of Sweden (*F. viridis,* also called the meadow or wild hill strawberry) differed from the cultivated garden strawberry there (*F. moschata*) only in the size of its fruits, Duchesne surmised that the green strawberry must be *F. moschata* in its wild state. According to Linnaeus, this was a perfect hermaphrodite and so Duchesne described it as *F. moschata* before its degeneration into the unisexual condition always found in cultivated *F. moschata.* "The solidity of the fruit, the large stamens and the hairiness of the plant leads me to believe that *F. moschata* owes its origin to the green strawberry rather than to any other," he wrote.[10] There was no wild *F. moschata* in France. Perhaps then, he reasoned, the adaptation to the climate change between France and Sweden was responsible for *F. moschata's* degeneration. Perhaps *F. chiloensis* cultivated in Chile was likewise bisexual and "perhaps the change in climate has caused the defect observed in ours (*F. cholensis* in France)," he said.[11]

In the Trianon Garden Duchesne had discovered a partially bisexual flower on one of the Chileans which had come from Cherbourg in 1764. In

[8] Duchesne, *op. cit.,* p. 40.
[9] Duchesne, *op. cit.,* Part I, p. 187.
[10] *Ibid.,* p. 157.
[11] *Ibid.,* p. 179.

1765 this particular plant had one flower that produced mature seeds while all the other flowers dried up and died. This one flower produced an imperfect fruit bearing fourteen ovaries or seeds, and consequently looked rather like a raspberry. Duchesne planted a few of its seeds which germinated successfully, proving to him that some of the stamens on the Cherbourg *F. chiloensis* must have been fertile. Thus he wrote: "Here is an example of an almost perfect hermaphrodite (bisexual plant) which supports the possibility of the preexistence of bisexual individuals which would have produced other unisexual or hermaphrodite-unisexual ones."[12] Duchesne kept this individual along with two runner plants. He also kept the young Chileans derived from its seeds to compare with seedlings produced by the fertilization of Chilean flowers with the musky strawberry's pollen.

"To settle this question" of whether a change in climate made Chilean plants unisexual in France, he was careful to add that "it would be important to import fresh seeds of the *Frutillar* (Chilean) from Chile, or better yet, living plants. . . . While supposing, as seems reasonable to me, that the separation of the sexes or at least of their potency, is natural to this species (*F. chiloensis*) and to the Capiton (*F. moschata*) it is very probable that the first has originated from the second." And he added, tongue-in-cheek, "One cannot object that if there were males and females (of *F. chiloensis*) in Chile, people surely would have perceived them in cultivating them, since people in Europe are still unaware that the Capitons are not hermaphrodites."[13] The hole in his genealogical theory, Duchesne admitted, was the lack of an explanation of the way *F. moschata* could have traveled to Chile to become *F. chiloensis*. Still, it is impossible to ignore Duchesne's observation in 1766 that *F. moschata* resembled *F. chiloensis* more closely than any other European strawberry. Genetics has since revealed that the somatic chromosome number of *F. moschata* is 42 while that of *F. vesca* is only 14.

Many questions arose in Duchesne's mind about cross-fertilization among strawberry species and the characters of the hybrids derived from them. He was certain that there were consistent laws permitting hybridization between certain kinds and preventing it between others. He wondered if the capacity for plants in a genus to hybridize with each other could be the guiding principle for distinguishing among species. Future observations, he believed, would answer four important questions: (1) Whether male Chileans existed and whether they could fertilize female *F. moschata;* (2) whether perfect flowers occur on female *F. chiloensis* plants, making them capable of self-fertilization. If so, this would suggest that there have been hermaphrodite *F. chiloensis* plants at other times, and that they might have descended from

[12] *Ibid.,* Part II, p. 42.
[13] *Ibid.,* Part I, pp. 179–180.

the hermaphrodite *F. vesca*. (3) Whether *F. vesca* is really incapable of fertilizing *F. moschata* and *F. chiloensis*. If *F. vesca* could not fertilize them it would invalidate the preceding theory, and consequently would prove *F. vesca* a distinct species. (4) Finally, "by examination of the Frutillar (Chilean) derived from seed fertilized by the Capiton (male musky) which I have sown, as have M. de Jussieu and M. Richard, and of which several have germinated already, one will see what changes foreign pollinations effect, and how the resemblance of children to their mothers and to their fathers is regulated in plants." Duchesne hoped that such observations truly would produce new insight on "that very agitated question: whether the crosses and hybrids in plants follow the same rules as in animals."[14]

The young author was able to observe several of the crosses between the Chilean and other species. As he had speculated, several of the progeny proved to be perfect hermaphrodites. These were *F. ananassa,* which through future breeding would give our modern, big-fruited strawberry, producing crops without dependence upon interplanting with other kinds for fertilization. Duchesne was the first man to identify the parentage of the new strawberry: "I suspect it to be a cross of the Scarlet strawberry (*F. virginiana*) and the Frutillar (Chilean)," he wrote in 1766.[15] It was the resemblance of the new "pineapple" strawberry, or *F. ananassa,* to both *F. virginiana* and *F. chiloensis* which persuaded Duchesne that it must be an intermediate between them and he so placed it on his genealogical tree of *Fragaria*. Duchesne described its resemblance to *F. chiloensis* as that of a son to a mother, fertilized by a foreign father which he believed could only be *F. virginiana* (*Fig. 5–6*).

Duchesne's botanical description of *F. ananassa,* the hybrid, follows: The flower stems, branches, and pedicels of *F. ananassa* resemble those of *F. virginiana* though due to their vigor they are larger than those of *F. virginiana* by half (*Fig. 5–7*). The flowers almost equal *F. chiloensis* in size, but are more regular, with six petals and a similarly reflexed calyx. The fruit has no resemblance to *F. virginiana* but has a pale red color with a brown and yellowish cast, with very watery but solid flesh, like that of the musky strawberry and the Chilean. In its center is a rather large cavity within which is a large, long central core which adheres to the calyx when the fruit is picked. The ovaries are almost as large as those of the Chilean and are spread quite wide apart over the surface. The flesh swells very little in their interspaces, however, and thus is compact. The perfume of the fruit is closely similar to that of the pineapple. Pyramidal in shape, the berries are only a little smaller than the Chilean in size. The leaves are larger than those of the Virginian with petioles nearly twice the length so that each

[14] *Ibid.,* Part II, p. 43.
[15] *Ibid.,* Part I, pp. 196–197.

FIG. 5–6. The Scarlet strawberry (*Fragaria virginiana*). Duchesne was the first to recognize this species from eastern North America as the father of the modern strawberry. *F. virginiana* pollen on *F. chiloensis* females from the coast of Chile produced the fertile hybrid *F. ananassa* or *grandiflora*. (by Duchesne)

FIG. 5–7. *Fragaria ananassa,* the large-fruited hybrid which Duchesne identified by its characteristics as a cross of *Fragaria chiloensis* x *Fragaria virginiana*. He said the fruit was shaped like a flattened oval, the first fruits "monstrous" in size, and the color a dull red and very pale on the underside. (by Duchesne)

leaflet goes in a different direction, although on a horizontal plane. The leaflets are more vigorous and thicker than the Virginian's, so that they have a rough leathery texture like the Chilean's. They lack the dense pubescence of the Chilean, having very little hair. The plants resemble the Chilean in its vigor and its runners are about as big and as long. In color the leaves are like those of the Virginian.

F. ananassa (the resemblance of the new strawberry to the pineapple in odor, taste, and berry shape gave it this name) had been introduced only a few years before Duchesne wrote *L'Histoire Naturelle des Fraisiers.* Philip Miller first cited it in the 1759 edition of the *Gardener's Dictionary* and included an engraving of it in his book of illustrations of the plants described in his *Dictionaries* (*Plate 5–1*).

Although Miller had heard that it had originated in Louisiana or maybe Virginia, he finally decided it had come from Surinam, for so he was told by George Clifford, the Amsterdam banker-gardener who had sent Miller a specimen of *F. ananassa* (*Plate 5–2*) just as he had given him *F. chiloensis* thirty years before. Because of its resemblance to two or three other species of strawberry, Miller refused to take the responsibility for naming it as a distinct species or a new variety from seed. In the 1759 *Gardener's Dictionary* he identified it with *F. virginiana* as a single species and in the 1760 edition of engravings he labelled it the "Surinam Strawberry."

Duchesne saw his first *F. ananassa* in 1765. M. Richard, the botanist-gardener of the Trianon, had some *F. ananassa* plants which he had brought from England for the king, but which Duchesne thought looked different from the one in Miller's drawing. In an article published some years later in Lamarck's *Encyclopédique Méthodique Botanique,* Duchesne discussed the wide variation common to hybrids of *F. virginiana* x *F. chiloensis,* some resembling one parent considerably more than they did the other.

When in 1764 *F. ananassa* was brought to Paris by two or three interested people, Duchesne was informed by M. Le Monnier, professor of the king's garden, that it came from the gardens in and around Aix-la-Chapelle (Aachen), Germany, near Rheims, where it had been cultivated for several years. Even before 1764, Daubenton had cultivated *F. ananassa* at Montbar in Burgundy. In the spring of 1762 Daubenton received three unlabeled plants from Baron de Worb, M. de Graffenried, of Switzerland, in a shipment of packaged trees. Baron de Worb grew several foreign strawberries in his garden, some from Canada and some from Virginia. Did the Baron receive this *F. ananassa* from another country or was it produced by an accidental cross of the Virginian and the Chilean in his own garden in Switzerland? When Sir Jansin saw a specimen of Daubenton's strawberry in the king's garden he recognized it as one the English had pointed out to him as the

Double Scarlet, as if to connect it with the Scarlet strawberry (*F. virginiana*) and to note that it was double in size. Other Englishmen identified it for him as the Bath Strawberry, associating it with the name of the city where it was first cultivated in England.

In 1766, Duchesne also knew of a strawberry from Holland which the Dutch merchants advertised in their catalogues as the Strawberry from Chile with fruit in the shape of a pineapple, "but it is known how little one ought to agree with their nomenclature," cautioned Duchesne.[16] He noted how much this Dutch berry resembled *F. ananassa* in the Trianon garden and suspected that the Dutch fruits would resemble the drawing of Miller's plant, since Miller had received it from Amsterdam. Duchesne knew also of a variety with leaves striped with irregular bands of whitish yellow which he called *F. ananassa variegata.* This had been brought to the Trianon Garden from Holland along with regular *F. ananassa.*

By 1771, when he published a supplement to his *L'Histoire Naturelle des Fraisiers* in Lamarck's encyclopedia, Duchesne knew several varieties of *F. ananassa.* These he now called *Quoimios,* a name he borrowed from the English Quoimio or Coamiau and which he applied to all the big-fruited New World strawberries and their crosses.

First he cited the Quoimios (pineapple strawberry) of Haarlem, Holland, from a cross whose fruit was the first to be called *Fragaria ananassa* in botanical literature. It resembled the Chilean in color and somewhat in the shape of its fruits, in its flesh, and in its very similar, though fainter, perfume, so fleeting that people ate the fruit while it was still green or downy. This variety was a perfect hermaphrodite and produced fruits when planted by itself. However, the topmost flowers of a cluster rarely developed fruits, and as this strawberry was late in flowering it was particularly suitable for pollinating the very late female Chilean. For this reason Duchesne thought these two ought to be planted in alternate rows. He believed that this Quoimio probably originated at Haarlem, Holland, and around 1762 spread to Germany, to Switzerland, and then to England.

A second *F. ananassa* variety he called the Quoimio de Bath (*F. calyculata*) (*Fig. 5–8*), a variety whose berries were often smaller than those of the Chilean, but whose plants surpassed all others in vigor and size. Its branches and runners, equal in size to those of the Chilean, were much less hairy and much more numerous. The leaves were much larger and the six-petaled flowers had remarkably large calyxes with sepals clothed on the underside with white hairs. In shape the fruit was round and a little conical and sometimes flat and palmate rather than angular. The flesh was very white and light, swelling a good deal between the ovaries (seeds). In color the berries were dull white

[16] *Ibid.,* p. 203.

Fig. 5–8. The delicately perfumed Bath strawberry was an early variety of *F. ananassa* thought to have originated in Bath, England. In the shade the berry remained a dull white but under the sun became a soft, even flesh color and in substance was very white and light. Duchesne said the plant surpassed all other varieties in vigor and size. (by Duchesne)

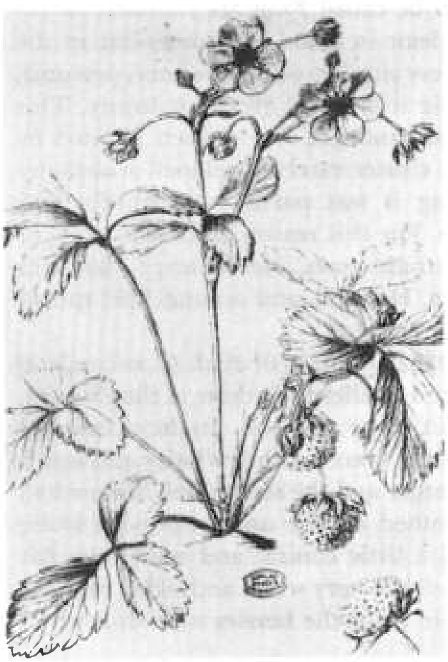


Fig. 5–9. The Carolina strawberry was an early variety of *F. ananassa*. Its berries were round and cherry-red in color with a flesh like the wood strawberry in substance and with a peculiar perfume. The compact flesh kept well after picking. Unfortunately, the plant was often sterile. (by Duchesne)

if kept in the shade, but under the sun became a soft, even, flesh color. They had a delicate perfume. The Bath strawberry was a prolific producer and formed crowns which lasted two to three years. It required sandy soil. The English had also recently cited a strawberry very similar to the Bath but with larger fruits which they called the Devonshire strawberry.

The Carolina strawberry, a third *F. ananassa* variety (*Fig. 5–9*), resembled both *F. virginiana* and *F. chiloensis* and had the regular, five-petaled flowers of *F. vesca,* although much larger. Its fruit was invariably round in shape with a light flesh almost like that of the wood strawberry in substance. It was less juicy than other berries and had a peculiar perfume. Since it did not swell much between the seeds, and thus, Duchesne noted, retained more color, its appearance was almost a cherry red. This compactness permitted the berry, if not bruised, to keep its quality two or three days after picking. Its small leaves, like the stem, resembled those of *F. vesca.* Unfortunately, the Carolina was often sterile. Since this occurred only in old plantings, Duchesne thought it might be remedied by planting the seeds in nurseries with sandy soil. He gave nothing about its origin.

A fourth variety of *F. ananassa* was the Quoimio de Cantorbéri (*Fragaria tincta* or *F. Quoimio*). This was the variety first called Quoimio or Coamiau in England. Duchesne knew nothing of its source. Very like the Carolina strawberry, its fruits were a little smaller and less regular, and they were not pointed at all. The fruit had a deeper color which penetrated well into the flesh so that the juice was red almost like that of the mulberry. The berries had a high, somewhat strong and wild perfume. All these characteristics made Duchesne suspect the Quoimio de Cantorbéri to be a pure species from some area in North America, or at least a naturally occurring variety.

A fifth *F. ananassa,* the Clagny Quoimio (*F. hybrida,* le Fraisier de Murmarais) Duchesne thought a hybrid variety probably derived from the backcross *F. virginiana* x the Quoimio de Haarlem (*F. ananassa*). It resembled the Virginian in the arrangement of its flowers, the substance of its fruits, and in its scarlet color. Although it bloomed the earliest of all strawberries, it gave a small yield. Duchesne first saw its fruits produced in 1770 near Versailles, in a garden called Murmarais, across from Clagny.

Why Holland is given exclusive credit for the introduction of *F. ananassa* (the Quoimio de Haarlem) is an unanswered question, especially since it would seem that the Brest *F. chiloensis,* fertilized by *F. moschata* and *F. virginiana,* must have produced some *F. ananassa* seedlings almost at once, which then most likely spread to other areas of France. Duchesne had been told that *F. ananassa* brought to Paris in 1764 came from Aix-la-Chapelle. Perhaps Holland is credited because Philip Miller received his first *F. ananassa* from George Clifford of Amsterdam, or because some of the early

FIG. 5–10. The single-leaved wood strawberry, or *Fragaria monophylla,* produced one leaf instead of the characteristic three leaflets. Duchesne named it the Versailles strawberry as he and his father discovered this sport growing among the wood strawberries in their garden at Versailles. His curiosity concerning the variation nature could produce started Duchesne on his study of strawberries. (by Duchesne)

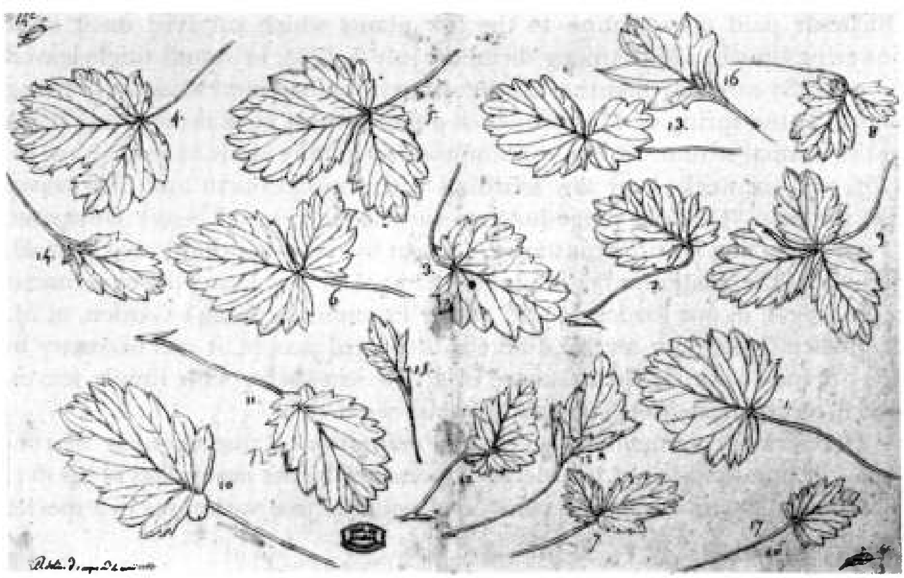
F. ananassa in the French botanical collection at the Trianon Garden and in the king's garden at Paris had been brought from Holland.

The Dutch might have made the acquaintance of *F. ananassa* in two ways. First, the plant might have been sent from Brest, as the Dutch seed merchants presumably imported new plants as well as exported them. If these merchants had requested *seed* from Brest, they would have received seed from either *F. chiloensis* x *F. moschata* or *F. chiloensis* x *F. virginiana* and Duchesne describes Dutch *F. ananassa* as intermediate between the latter two.

A second possibility is the cross of *F. virginiana* x *F. chiloensis* within Holland itself. Six years after Frézier's return from Chile, *F. chiloensis* from the Leyden botanical garden in Holland was noted in Boerhaave's botanical work of 1720. Antoine de Jussieu had sent to Leyden a runner plant of the female Chilean given him by Frézier. Assuming that the Dutch were then cultivating *F. virginiana,* as there is every reason to believe those marvelous gardeners did, circumstances favored natural hybridization of the two species. That this hybridization occurred accidentally seems most likely, since the Dutch merchants first called *F. ananassa, F. chiloensis ananaeformis* (*F. chiloensis* with the shape of a pineapple) in their catalogues.

Perhaps the most exciting ideas in Duchesne's depth study of *Fragaria* come from questions raised in his mind about the natural history of plants, for his acumen was such that he constantly sought relationships between strawberry varieties, and patterns of change and development in living things. Duchesne's first letter to Linnaeus, dated Versailles, December 10, 1764, concerned his discovery of monophyllous *F. vesca:*

FIG. 5–11. After careful observation of the single-leafed strawberry over the years Duchesne noted that sometimes the leaves became palmate, beginning to resemble the typical tri-foliate strawberry leaf. He sketched these exceptions as evidence of the continuing variation in plants. (by Duchesne)



"In the garden of my most adored father, there has originated an offspring from seeds of *Fragaria vesca,* which alone does not have ternate leaves but instead simple leaves. It has grown here for three years and exhibits, as it creeps with its innumerable runners, a descendant which does not differ from the mother plant. In the past months of May and June it has given flowers and ripe berries with a most delicious taste and a shiny, scarlet red color, and rich with fertile seeds. I congratulate myself most highly to be able to place before your eyes and subject to your sagacious judgment, this, if I may say so, new marvel of nature, this hitherto unknown mutation of *Fragaria vesca.* I send you some nodes of this Fragaria, collected by me, and a living root and at the same time a newly published little work of mine in botany (*Manuel de Botanique*), all this on the advice of our experienced botanist, B. de Jussieu."

And Linnaeus replied, "Your *Fragaria* pleased me immensely. I cannot sufficiently marvel as to how it has arisen from *Fragaria vesca.*"[17]

The discovery of the monophyllous Versailles strawberry, *F. vesca* (*Figs. 5–10, 11*), growing among a collection of wood strawberries in his father's experimental garden at Versailles first started Duchesne on his *Fragaria* research. In 1761 Duchesne and his father had planted some seeds of the wood strawberry, which had been in the garden for several years, to see if white *F. vesca* berries were produced frequently from plants with red *F. vesca* berries. Since the Duchesnes had replanted them too soon and had taken poor care of them, the seedlings almost all died. The experiment having failed, Duchesne paid no attention to the few plants which survived until their flowering time in 1763. Among them, on July 7, 1763, he found single-leaved *F. vesca.* By carefully planting all the runners, he had more than sixty living plants by the spring of 1764, of which about a third gave flowers and fruits in the normal season. Father and son planted mature seeds of it on June 15, 1764, and six weeks later saw seedlings with simple fourth and fifth leaves like the first. "One can judge how my surprise increased," wrote Duchesne. "I was expecting no such constancy. I began by doubting that it was general, because of the small number of plants I had raised, but seeing the experiment repeat itself, in our garden as well at the Trianon, the King's Garden, at M. de Jussieu's, and with several different interested people, it was necessary to give in and recognize the existence of a new strawberry with simple leaves, which reproduced itself constantly by its seeds."[18]

Here was experimentally supported refutation of the doctrine of constancy or immutability of the species as preached by the naturalists of his day. The Versailles strawberry was conclusive evidence that variations in a species

[17] Hylander, *op. cit.,* p. 19.
[18] Duchesne, *op. cit.,* Part II, pp. 12–13.

could come from seed and that these variations were preserved in successive generations. How should one classify the new strawberry? The question led Duchesne into a dissertation on the meaning of variety, species and genus, in which he pled for unilateral agreement of definition.

By means of hybrid sterility, so the naturalists believed, nature prevented the formation of new species. Not only did animals of different species ordinarily refuse to mate with each other, but when they did mate, their hybrid progeny resembled both father and mother but could not reproduce themselves. In regard to plants, Duchesne said, the doctrine of the fecundity of hybrids had replaced the law of constancy for the past twenty years, but he objected that the proofs of hybrid fecundity in plants were unreliable. Now he could offer the fertilization of *F. chiloensis* by *F. moschata* as experimentally supported and respectable evidence. He only was waiting to see if the seeds of this cross would be fertile like the parents. He believed that the cross of *F. chiloensis* x *F. virginiana* would be a second example. Linnaeus himself was put under fire in the book when Duchesne criticized the great naturalist for arbitrarily naming new species and identifying the parents of the hybrids by using subjective judgments based only on the appearance of the plant and not upon experimentally supported evidence.

Duchesne's *Fragaria* study had convinced him that "species appear fixed and immutable, but that accidents which make certain individuals vary, procure in others rather considerable changes which are perpetuated in their posterity, which thus form a new species." In agreement with Buffon, a famous French botanist, Duchesne said that "the crosses (*métis*) derived from the mating of two individuals of different species, but of the same genus, truly become the parents of new species, but the hybrids (*hybrides*) produced by individuals of different genera are deprived of the faculty of self-reproduction." From this conclusion Duchesne went on to recommend a method of distinguishing genera from species (or varieties) based on experiments in plant breeding. "The best without doubt for plants as well as for animals would be to make the experiment of mating," he said. "Those which together produce fertile crosses (métis) would be pronounced of the same genus and those which refused to do so would be regarded as different genera. It is to be hoped that experiments of this nature will increase. Botany could only gain a great deal from them."[19]

As such experiments were difficult, time-consuming and almost impossible for many plants, botany had taken recourse in examining those parts of a plant which distinguished it from other kinds. But Duchesne even proposed modifying the usual method of distinguishing among genera by the number, shape, proportions and locations of their various parts. Instead, he recom-

[19] *Ibid.*, pp. 21–22.

mended that the classifiers look first at the positions of plant parts and at their interior structure, since these characters should be as constant in plants as in animals, for which comparative anatomy served to distinguish among genera very well. Linnaeus had approached this suggestion in his statement that the inflorescence, or the arrangement of the flowers, revealed the most real differences. Why, then, asked Duchesne, were there so few differences so established in his works? Probably because he created too many genera and took for generic characteristics those differences caused by the influence of climate and cultivation, as these traits were perpetuated in the posterity of these plants. Such groups of plants, according to an axiom of Ray, another naturalist of the period, were qualified by the name "genus" since they could not be treated as varieties or as constant species. In the mid-1700's the botanist was really a classifier who derived his conclusions from the observation of the world as he saw it. Duchesne was ahead of his time, a scientist of the age of experimentation, when naturalists would ask how nature became as it is and would try to duplicate the process in their laboratories.

Although Linnaeus did not change his earlier statements, he did continue to correspond with Duchesne, tolerating the youth's brash challenges. Linnaeus planted Duchesne's gift of the single-leaved Versailles strawberry in a bed in front of the main building at Hammarby where the famous Peloria had been planted, a specimen which also confronted the doctrine of constancy of the species, although Duchesne called it unsatisfactory evidence as its progeny were not fully or consistently fertile.[20]

One of Duchesne's questions about the lines of plant development was whether a profound change in climate or soil could so alter a group of plants, isolated from the environment of its parents over a long period of time, that an entirely new species would result. He suggested that the effect of soil and climate in America had altered European *F. vesca* into *F. virginiana* and that European *F. moschata* had there become *F. chiloensis.* He hoped that future experiments in cross-fertilization would clarify the question. Erroneous as his theories on the origin of *F. chiloensis* and *F. moschata* may be, Duchesne had recognized the effect which isolation of a species, under altered environmental conditions, can have in preserving adaptive changes in plants, a principle appreciated by geneticists today.

Duchesne also showed foresight in his conviction that a fixed temperature could be determined to tell when strawberries would germinate, release their pollen, flower, etc. Michel Adanson, the great French naturalist and contemporary of Duchesne, had done this for certain other plants. In 1766, Duchesne wrote that he himself had not yet been able to discover these temperatures for strawberries. He tried to explain the everbearing quality

[20] Hylander, *op. cit.*

A painting by Hieronymus Bosch showing strawberries of fantastic size. Painting at the Prado Museum in Madrid.

PLATE 2-4

Frage ertberen Cap·clx·

Frage latine· Die wirdigen meister sprechen das ertberen syne kalt vnd feucht an dem dritten grade· vnd die natur an der frucht die fyndet man auch an dem krude· Diß krut hait subtyel stengel vnd kortz vnd glichet der odermynge alleyn ertberen krut grösser vnd breyter bletter hait· Diß krut weret eyn gantz iare vnd nit darvber· Plinius spricht das ertberen krut gar gut sy da mit zu baden fur den steyn Auch ist das wasser do von distilliert gut gedruncken fur den steyn vnd machet wol harmen· Der groß

Mainz Herbarius, "Gart der Gesundheit," printed by Gutenberg's employee, Peter Schoeffer, in 1485.

PLATE 3-1

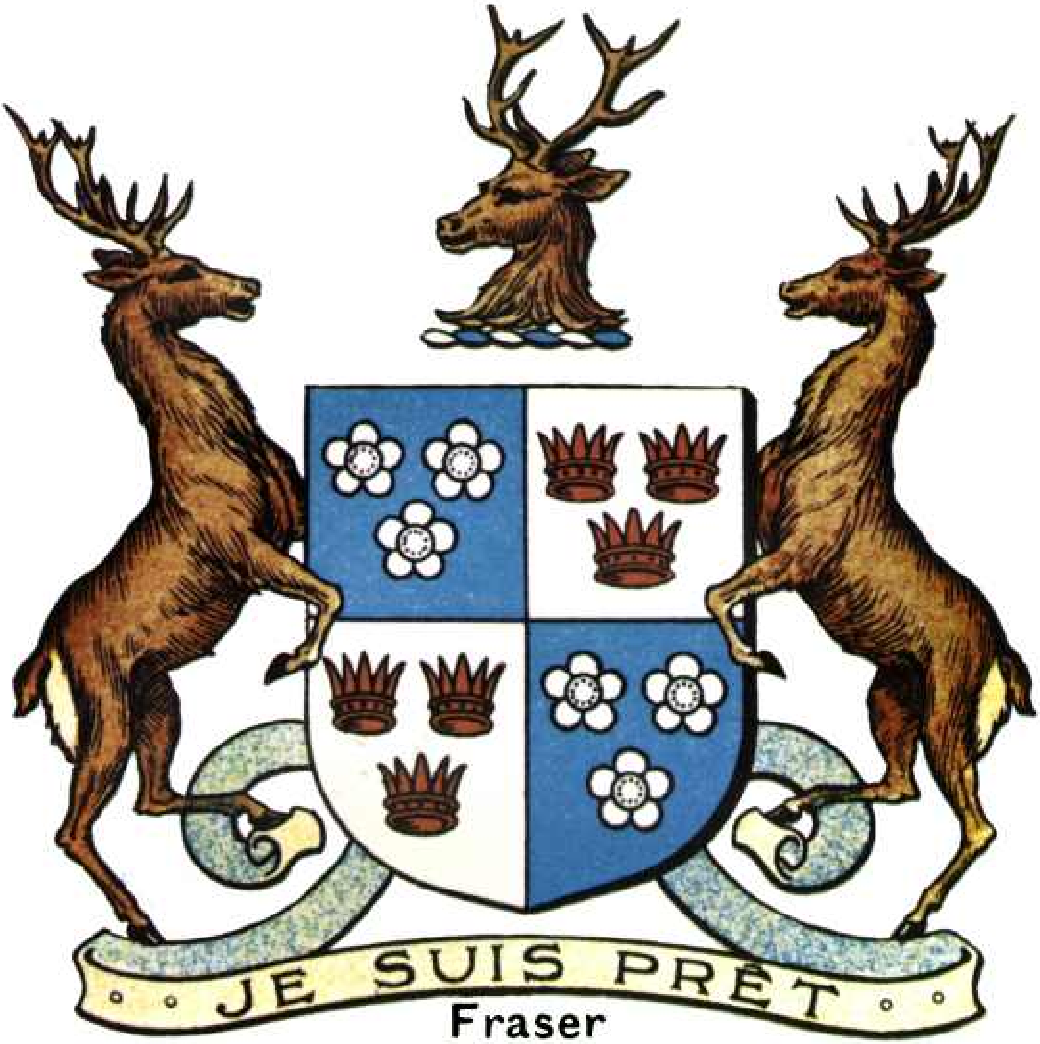
Fuchs's "New Kreuterbuch," first edition, 1543. *Fragaria vesca.*

PLATE 3-2

This white *vesca* (ABOVE) was photographed in Guatemala at 6000 feet above sea level.

PLATE 3-3

This white *vesca* was given to Walter Von Egidy by Henry A. Wallace and now grows in his garden in Connecticut, approximately 1000 feet above sea level. (photo by H. Kessler)



The Frézier coat of arms shows strawberry blossoms in an azure field and was awarded by King Charles V of France for a gift of ripe strawberries in 916. The motto reads "I am ready," as was the alert French navigator, Amedée Francois Frézier, who brought back the first *F. chiloensis* to Europe from Chile. (From the *Tartans of Clans and Septs of Scotland,* by W. and A. K. Johnston, Ltd., Edinburgh, 1906)

PLATE 4-1

Dillenius painted a specimen of the new strawberry from Chile in the *Hortus Elthamensis* in 1732, but was unable to show any fruits as English and European botanists were ignorant of the separation of sexes in strawberries and so did not pollinate female *F. chiloensis* with pollen from other berries. Instead they complained of the barrenness of the Chilean strawberry and let it go at that.

PLATE 4-2

From the British Museum (Natural History), London. Courtesy of Mr. R. E. Carr. *Color transparency* from Johann Simon Kerner's "Abbildung aller Oekonamischen Pflanzen," Stuttgart, 1788. Plate 171, *Fragaria chiloensis.*

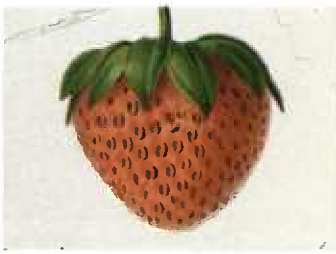
PLATE 4-3

Philip Miller included this painting of *F. x ananassa* in the 1760 publication of engravings of plants described in his *The Gardener's Dictionary*. He received the plant from Amsterdam, where he was told it came from Surinam, although he had heard that it was native to Louisiana or Virginia. Because of its resemblance to two or three species, Miller declined to name it as a distinct species or as a variety from seed.

PLATE 5-1

F. x ananassa as painted by Mme. Vilmorin in *Le Jardin Fruitier du Muséum,* vol. 9, 1862-1875.

Photo of the Ambato variety of *F. chiloensis* grown for centuries near Ambato, Ecuador.



Fraisier du Bath, also painted by Mme. Vilmorin; probably the same as *x ananassa.*

PLATE 5-2

The Downton strawberry was the first of Thomas Andrew Knight's selections to draw attention to the merits of experimental crossing. One of 400 seedlings Knight raised from crosses in 1817, the Downton had large, oblong fruits and resembled the Chilean strawberry in many ways. Uncertainty about the Downton's parentage discouraged Knight from calling it a definite example of *F. virginiana x F. chiloensis*. (From *Transactions of the Royal Horticultural Society,* vol. 3, London, 1820)

PLATE 6-1

The Elton strawberry, second of Knight's famous varieties, came to rival the Downton in 1828. Had it not been spotted in the Royal Horticultural Society's garden for its health, hardiness, bloom, and beautiful fruit, it might have passed unnoticed, for Knight had overlooked the berry growing in his own garden. (From *Pomological Magazine,* vol. 3, 1830)

PLATE 6-2

Keens Imperial, raised by Michael Keens, a market gardener of Isleworth in 1906, ranked as the first large-fruited market strawberry of any real quality. Keens grew it from seed of the Large White Chili. Although it lacked high flavor, it boasted a deep crimson fruit and symmetrical shape. Best of all, its projecting seeds made it a hardy traveler, armored against bruises. In 1819 seed from it produced Keens Seedling. (From *Transactions of the Royal Horticultural Society*, vol. 2, London, 1818)

PLATE 6-3

Keens Seedling won Michael Keens a silver cup from the Royal Horticultural Society when he introduced it in 1821. Almost a century later in the early 1900's it had yet to be replaced as a near-perfect berry. The sensation it created sparked other growers to attempt their own hybridizations. Keens Seedling blood is to be found in almost every outstanding variety of strawberries cultivated in the northeastern United States.

PLATE 6-4

Keens Seedling, the first modern strawberry started in England and introduced in 1821.

The Chilean, *F. chiloensis,* imported from Chile in 1714.

Viscomtesse Hericart de Thury, started in France and introduced in 1850.

F. vesca, the native wood strawberry and the first cultivated variety of wild strawberries.

The musky strawberry, *F. moschata,* of Europe.

PLATE 7-1

The musky strawberry, *F. moschata,* in full fruit, June 22, Geneva, N. Y.

A row of the wood strawberry, *F. vesca,* in full fruit at the Geneva, New York Station.

F. chiloensis plant with fruit, selected at Long Beach, British Columbia.

PLATE 7-2

TO RIGHT, fruits of *moschata;* TO LEFT, fruits of *vesca x moschata* with chromosome numbers doubled to give an octoploid. (Photo by Ellis)

Berries of a selected decaploid hybrid (10X) resulting from crossing a tetraploid (4X) *vesca* with the cultivated strawberry and crossing the resulting 6X back to the cultivated.

PLATE 7-3

of the strawberries of the Bargemon Alps by this reasoning. Since the temperature necessary for the flowering and fruiting of strawberries remained the same there from spring until winter, instead of becoming increasingly warmer accompanied by a sharp change with the approach of autumn as in the rest of the temperate zone, the plants continually flowered and fruited in these mountains until fall. To test this theory, he sent specimens of the strawberries in his collection to a correspondent in Bargemon to learn if the climate would produce an everbearing quality in them as well.

First-hand observation of the development of a new variety of strawberry from seed—the Versailles strawberry (*F. monophylla*)—led Duchesne to construct a theoretical genealogical tree (*Fig. 5–12*) which explained how all the different sorts of strawberries he knew were derived from a single kind—*F. vesca semperflorens* (the everbearing wood strawberry).

> For each of the races of strawberries I have been careful to indicate what seemed actually true on the subject, but I do not dare flatter myself with having always been accurate. To do this well, it would be necessary to have certain and precise knowledge of the native country of each strawberry, or at least from the time it has been raised from seed, and to know from which other strawberry this seed has resulted. I have demonstrated how much insight is still lacking about all this . . . One must first recall that I consider the alpine, Fraisier des mois I (*F. vesca semperflorens*) as the father of all the others. It is also at the head of the tree. The common wood strawberry, Fraisier de bois II (*F. vesca sylvestris*) which differs almost solely in its slower rate of growth [and in not flowering throughout the season he might have added], is immediately below, as if produced by it.

Duchesne considered the variegated and the white to be varieties of *F. vesca*. The double, the cluster, the Plymouth, and the "coucou" or abortive all seemed to him to be variants of *F. vesca,* the common wood strawberry. The Fressant, runnerless, and Versailles he considered to be simply varieties of *F. vesca*. But all these varieties, having several common characteristics, can thus be easily reduced to one common root. These are several branches of a single house. The ordinary Fraisier de bois (*F. vesca sylvestris*) is the only one of the eleven which grows naturally in wild places like the Fraisier des mois (*F. vesca semperflorens*).

> The green strawberry VI ought to form a separate line. I have said that it seems to hold particularly to the Fraisier des mois, as its vegetation is a bit more vigorous than that of the Fraisier de bois. . . . Other particular characters whose causes can hardly be determined, throw still more inde-

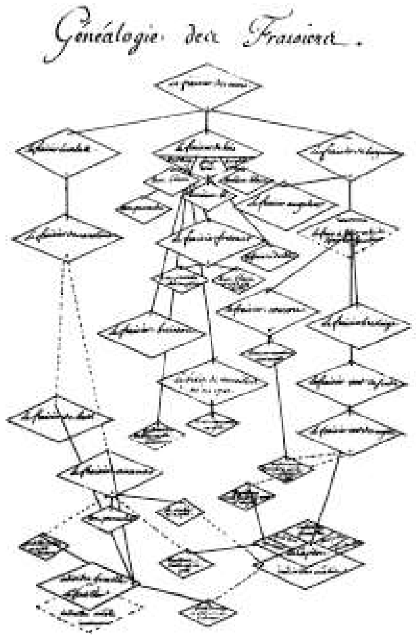


Fig. 5–12. Duchesne constructed the genealogical tree of strawberries to illustrate his theory that all the larger-fruited species had evolved from a single ancestor, the wood strawberry, *Fragaria vesca silvestris,* or its variant, the everbearing strawberry, *Fragaria semperflorens.* Geneticists agree that on the whole he was correct. (by Duchesne)

Fig. 5–13. The Maujaufe de Champagne belonged to a group which Duchesne described as intermediate between the wood strawberry and the green strawberry. The watery flesh of the berries and their long sepals which clung to the fruit reminded him of the green strawberry, while the bright red color and small size of the juicy fruits resembled the wood strawberry. This hybrid is X *Hagenbackiana* frequently found in central Europe. (by Duchesne)

cision on the origin of this strawberry. Here [in the chart] I suppose it to descend immediately from the Fraisier des mois.

If the musky strawberry (Capiton VII) is not a plant originally distinct in origin from the (common *F. vesca)* strawberry, we must believe that it is derived from the green strawberry (*F. viridis*) rather than any other, as one sees it in the genealogical tree. . . .

The Fraisier ecarlate X (*F. virginiana*), which is the common strawberry of Canada, and Virginia, differs, as I have shown, from the Fraisier de bois by a great number of minor characteristics. However, it can hardly have originated from any but this race, and so I mark it in the genealogical tree. The influence of climate seems to have produced the principal changes in it, since [such changes] are equally apparent in the two other American races.

. . . The Chilean (*F. chiloensis*) (VIII) originates from the Capiton (*F. moschata*) as does the Scarlet (*F. virginiana*) from the wood (*F. vesca sylvestris*). Indeed, it seems to have been subject to the same changes by the influence of the same climate, and the separation of the sexes on the Chilean males and females indicates this affinity.

The pineapple (*F. ananassa*) IX presents an affinity of a different nature [in the genealogical tree], because I suspect it to be a cross (métis) of the Scarlet (*Virginiana*) and the Chilean. I have stated the reasons for this: It resembles the former by its leaves, its stems, its flowers, and their sexes; it approaches the latter by its vigor and by all the qualities of its fruits—size, color, substance, and perfume.[21]

Duchesne's arrangement of *Fragaria* with diploid *F. vesca* kinds followed by hexaploid *F. moschata* and finally by octoploid American sorts—*F. virginiana* and *F. chiloensis*—is supported today by genetical studies.

Duchesne's *L'Histoire Naturelle des Fraisiers* of 1766 lists ten species of strawberries and nine varieties. In an article in the *Encyclopédie Méthodique Botanique* of Lamarck, which appeared only five years later, he lists twenty-five kinds of strawberries. Duchesne rearranged his classification system in this later and much more widely known article, based on his continued research in *Fragaria.* He divided *Fragaria* into two main groups: (1) Les Fraises—the pure wild strawberries with small and numerous ovaries and short stamens, and (2) Les Caperons—strawberries with large but few ovaries and with long stamens. The first group was composed of eight sorts. The second group was divided into four subgroups—the Maujaufes (*F. vesca* x *F. viridis*), *the* Breslinges (*F. viridis*), the Caperonniers (*F. moschata*), and the Quoimios, the American species and hybrids, in that order.

(1) The Maujaufes were the link between the Fraises (the first group, *F.*

[21] Duchesne, *op. cit.*, Part I, pp. 220–227.

vesca) and the Breslinges (*F. viridis*), and resembled the latter especially in their tendency to sterility, in their variability when raised from seed, and in their long, slender branches which bent with the weight of the fruit. They also resembled *F. viridis* in the large number and the arrangement of runners, in the long sepals which clasped and adhered to the fruit and in their watery flesh. In their small size, juicy tender flesh, bright red fruit color, and leaf color, they resembled *F. vesca*. The Maujaufe de Provence (*F. bifera*) and de Champagne (*F. dubia, Fig. 5–13*) were the two varieties Duchesne placed in this group.

(2) The Breslinges or green strawberry (*F. viridis*) had greenish fruit which turned red only when exposed to direct sunlight. The berries had extremely large ovaries, scattered fairly sparsely over their surface, and a very juicy, very firm flesh. The long calyx was so tightly clasped about the berry that it could be detached only with difficulty. The leaves were drier and firmer than those of *F. vesca* and the Maujaufes, with a duller, browner color, and they were covered with longer hairs. One portion of the berry frequently aborted and in general the green strawberry proved extremely variable when reproduced from seeds, although sometimes it reproduced exactly. The first of the Breslinges—coucou (*F. abortiva*)—was an intermediary berry between the Maujaufes (*F. viridis* x *F. vesca*) and the Breslinges (*F. viridis*). Then followed the Breslinge d'Allemagne (*F. nigra* of Germany), de Bourgogne (*F. pendula*), de Long-Champ (*F. hispida*), d'Angleterre (*F. viridis* from England), and de Suède (*F. pratensis* Linn.).

(3) Duchesne listed two Caperonnier (*F. moschata*) varieties: First came the Caperonnier Royal, a twice-bearing one from Brussels and the only hermaphrodite *F. moschata* he knew; secondly, the unisexual Caperonnier (*F. moschata dioica*).

(4) Then came the Quoimios, the strawberries of the New World, and their varieties from crosses, "of which none is constant, but which among them form a very recognizable race, intermediate between those of the Chilean and the Quoimios of Virginia," said Duchesne. "These two can be regarded as extremes, the first with very large fruits and very hairy foliage, the other with much smaller fruits and very smooth foliage . . . the Quoimios are all rather subject to sterility, especially those raised from seed. As for the rest, one can hardly cite a common characteristic among them."[22] The six Quoimios were comprised of the Frutiller, or Chilean (*F. chiloensis*), the Quoimio de Haarlem (*F. ananassa, F. chiloensis annaeformis*), de Bath (*F. calyculata*), de Carolina (*F. Carolinensis*), de Virginie or Virginian (*F. virginiana*), and lastly, the Quoimio de Clagny (*F. hybrida*).

[22] Duchesne, Antoine Nicolas, "L'Essai sur L'Histoire Naturelle des Fraisiers," *Encyclopédie Méthodique Botanique* of Lamarck. Jean Baptiste, Paris, 1783–1817, p. 534.

The publication of *L'Histoire Naturelle des Fraisiers* did not exhaust Duchesne's interest in strawberries. He continued to collect new specimens at the Trianon, the king's garden in Paris, to experiment with cross-fertilization, and to correspond with Linnaeus, whom he continually asked for new strawberries, especially those foreign to Sweden. Linnaeus' letters express his continual eagerness to obtain rare plant specimens from the Trianon collection and describe his pleasure when the plants arrived and grew successfully. Linnaeus' friend Bjornstahl visited the Duchesnes in the summer of 1769. Linnaeus wrote to Bjornstahl: "Give my regards to dear Duchesne, the amiable boy, who procured me the Calceolaria (from Chile), and which now stands in bloom and cries each hour, 'Duchesne.' Never has any plant pleased me more, never have I more carefully tended a plant in my window."[23] Duchesne in turn had requested that Linnaeus send specimens of the common wood and the green strawberry.

In the autumn of 1765 Linnaeus did send some *F. pratensis* (the green strawberry) plants, which arrived in wilted condition and soon died. Apparently such a fate was common in the long uncertain shipments with their poor connections, for the letters frequently discuss the problem. Duchesne made repeated requests to Linnaeus for new material, including suggestions and directions for packaging methods which would insure freshness and specific instructions for addressing the plants for the fastest possible delivery to Versailles. "He even called upon the postal minister in order to achieve faster postal service, a subject which interested the French sovereign as much as strawberries."[24]

Eventually on April 13, 1767, Duchesne could write that he had just visited the Trianon and seen three plants of the green strawberry from Linnaeus which M. Richard had saved. Their buds were ready to flower and Duchesne said he "devoured them with his eyes." In October he wrote that they had flowered once and now were flowering again, having produced a total of three berries. Their runners had "multiplied infinitely." This *Fragaria* differed from all other specimens in his collection. Finally, Linnaeus sent him the common wood strawberry and Duchesne's thank-you note, the last of his extant letters to Linnaeus, dated July 24, 1772, tells of his delight in the new strawberry plants which embellished his garden.[24] Duchesne received these two specimens after publication of his *L'Histoire Naturelle*. He described them in the "Essai sur L'Histoire Naturelle des Fraisiers" included in Lamarck's *Encyclopédie Méthodique Botanique.*

The senior Duchesne considered his son's varied studies as the necessary elements of a good liberal education. Now he wanted him to prepare for a

[23] Hylander, *op. cit.*
[24] *Ibid.*

worthy career and insisted that he study law. So when Linnaeus' friend, Bjornstahl, visited the Duchesnes in 1769, he found Antoine Nicolas a law student who "is already Baccalaureas and will be Licentiat within a month, after which his law studies will be finished, for botany is his avocation, while law is only for future advantage, since anyone who wishes to receive an important occupation has to have studied the laws."[25] Like the young Frézier, the navigator and engineer who brought back the first *F. chiloensis,* Duchesne too had parental pressure towards law. Like Frézier he resisted, and after graduation turned back with relief to natural history.

His interests spread beyond strawberries to research in the cultivation of other plants. For years he had been adding to a calendar in which he recorded the seasons of growth and the appropriate time of cultivation for each plant. Requests from gardeners for copies of it persuaded him to publish in 1770 *Le Jardinier prévoyant* (*The Foresighted Gardener*). It sold for six sous and was a widely used almanac in the eleven successive years of its publication. Intensive research on gourds and experiments in their cross-fertilization followed, then a catalogue called *Etrennes botaniques* (*Botanical Handbook*), giving the common names, descriptions, and uses of four thousand plants which had been grown at the Trianon, arranged according to Bernard de Jussieu's natural method of classification. In 1771 came a list of seeds sold by M. Andrieux-Vilmorin, founder of the great Parisian seed house of today. Years later, Eliza de Vilmorin would write extensive descriptions of strawberry varieties of the mid-1800's for an illustrated article in Decaisne's *Le Jardin Fruitier du Museum.*

A wonderful opportunity came to Duchesne in 1776—he was invited to visit the famous botanic gardens of England with Abbé Nollin. The voyage produced the essay "Sur la formation des jardins," the source of Delille's verses on gardening.

Duchesne's father continued to direct his son's life and Antoine's choice of wife was made to comply with his father's wishes. As the father of five children he became interested in education. He could not forget the thorough tutoring his father had given him and he wanted the same experience for his own children. He and a friend wrote a *Portefeuille des Enfants* in 1784 made up of pictures, articles, stories, and instructive games intended to familiarize children with the arts and sciences.

Eventually Duchesne inherited the family post as superintendent of the king's buildings (*Fig. 5–14*). The French Revolution in 1789 put him out of work. Moreover, the list of suspects doomed for the guillotine included the name Antoine Nicolas Duchesne. At first he had sympathized with the aims of the revolutionaries. Then the anarchy of June 20, 1792, made him conscious

[25] *Ibid.*

of the horror and fanaticism which led to the beheading of the king the following January. Duchesne realized that he had been supporting the forces which killed the man whom he and his father had walked to Reims to see crowned king years before. Although a devout Catholic, Duchesne refused to support the clergy who swore allegiance to the Civil Constitution. Only the reputation of his scientific achievements saved him from beheading.

When quieter days arrived, Duchesne became a teacher. Soon after the revolution the Écoles Normales were founded with the most revered scholars in France appointed to the chairs of learning. Duchesne was admitted to the bench of specially selected teachers. Later he taught at the École Centrale at Versailles where he helped develop a "natural" method of teaching based on the study of the psychology of learning in children and, following methods used by Duchesne and his father on their children, it introduced a broad range of subjects to students at an early age. At Versailles and later at the Military Academy of Saint-Cyr he taught all branches of natural history—minerology, geology, zoology, comparative anatomy, botany, and plant physiology—and emphasized new findings on physical and chemical operations in organisms.

His writings ranged over studies of rural economy and agriculture and included descriptions of local geology, dissertations on the metric barometer with explanations of the new decimal calculus and measurement systems, a guidebook to Versailles, and an article on the cultivation and preparation of dry land rice.

The death of his wife and of his oldest and youngest daughters in rapid succession affected Duchesne's health severely. He retired from his position as Supervisor at the Lycée de Versailles and returned to Paris where he concentrated on the education of his remaining three children and on new research in natural history. At this time he was almost destitute. He had never been a good businessman, always too willing to sacrifice his own interests in transactions and to lend money and the results of his research to his friends for their work. His disinterest in money bordered on neglect. The Revolution had destroyed the inherited post of superintendent of the king's buildings. Forced to borrow money, he repaid his loans by selling his Versailles property at a loss.

His research was his life, and with increased frugality he continued to study. There were memoirs to submit on a European nomenclature for natural history with suitable names for economic plants. He wrote on the direction of plant growth, especially on the tendency of plants to turn toward light. He pursued his early studies on sterility in plants and their causes. He had organized his strawberry history around the characters which linked the different kinds. Now he expanded this to studies of all organic life. Meanwhile he continued to help with the work of the Society of Agriculture of Versailles, of which he had been secretary for many years. Before the Society he read his articles on the cultivation and use of different species and varieties of potatoes, on decay in grain, on the industry of man and the instinct of animals, and a plan for a farmer's calendar.

With old age came successive illnesses, making him an invalid. Unable to rest idle, Duchesne tried to spend his mornings editing his cartons of extensive notes and manuscripts, but weakness hampered him. A series of strokes paralyzed him and affected his memory and his speech. He died in February of 1827, almost eighty years old. In a biography Baron A. F. Silvestre, the secretary of the Royal Central Society of Agriculture, said of him: "In dying he could applaud himself for having spent well his long career, and for leaving behind him useful literary productions which will perpetuate for a long time yet the memory of the services he desired to render to the friends of the natural sciences and to his country."[26]

FIG. 5–14. Duchesne intended to use his father's official emblem together with his own drawings of strawberries in the 1766 publication of *L'Histoire Naturelle des Fraisiers,* but he lacked the money to print them. The inscription on the emblem read "from the Office of Antoine Duchesne Superintendent of the King's Buildings," a post Duchesne inherited but which the Revolution abolished.

[26] Silvestre, A. F., *Notice Biographique sur M. Ant. Nicolas Duchesne.* Paris, 1827, p. 26.

6

Early Breeding in Europe

PREVIOUS CHAPTERS have indicated that the modern strawberry's development first occurred in France. It was the French who introduced *F. chiloensis* to Europe and by pollinating it with *F. virginiana* produced the first varieties of *F. ananassa.* Antoine Nicolas Duchesne was one of the earliest and most noted authorities on strawberry classification and history, and he must be credited as the first to identify *F. chiloensis* x *F. virginiana* as the origin of the modern strawberry. It was the English, however, who first produced the magnificent varieties of *F. ananassa* which started strawberry breeding in Europe and America. This English breeding work, in itself, is behind hundreds of varieties we enjoy today. After the French had seen the success of the English breeders they too began to develop their own varieties, but for half a century the "Fraises anglaises" such as Keens Seedling, the Downton, and the Elton dominated the markets of Europe and also provided a foundation for a vigorous strawberry industry in England.

The Strawberry in England

In the late 1700's and early 1800's, varieties of *F. virginiana*—the Scarlet strawberry—were the popular English garden strawberries. Attempts by English gardeners to raise new varieties from seed increased the number of varieties of *F. virginiana* from three to nearly thirty. James Barnet, undergardener for the Royal Horticultural Society, knew twenty-six varieties of the Scarlet in 1824. In quality most were markedly superior to the general type of Scarlets —but none surpassed some of the wild *virginiana* in flavor. In size the berries showed but little improvement over the best wild ones. Growers who found that raising new plants from seed sometimes produced variations superior to the parent type, conducted experiments with seeds directly imported from Canada and North America, instead of working with American varieties imported earlier. As E. A. Bunyard observed, though slight differences resulted, the variation of *F. virginiana* was "not more than might have been in the wild state."[1]

What were these varieties? In 1766, Duchesne noted a kind of Scarlet from Strasbourg which had somewhat elongated berries; and sometime before 1826, Mr. Gibbs, a nurseryman of Old Brompton in England, raised a similar variety called the Oblong Scarlet. William Atkinson introduced the Grove End Scarlet, which he originated in 1820 at Grove End, Marylebone. Other well-known Scarlets were the Duke of Kent's Scarlet, Knight's Large Scarlet, Wilmot's Late Scarlet, Common Scarlet, and the Austrian Scarlet. The Scarlet was preferred in jam making because of its acid flavor, retention of shape, fine aroma, and bright red color. It was also the earliest strawberry to fruit naturally, without forcing.

A few varieties of pure *F. chiloensis* also existed in England at this time. In 1824 Barnet knew of two, possibly three, kinds, such as the Yellow Chile, which differed, mainly in the color of its fruit, from the original Chilean introduced a century earlier. *F. chiloensis* was unpopular in England because under most conditions it did not blossom and the fruit it did bear was poor-colored, and poor-textured, and often had a mawkish flavor. William Cobbett wrote of it: "As to the Chili it is very little superior in flavor to the potato."[2]

Furthermore, the Chilean was not at all hardy and was difficult to grow inland (the reason for its failure in France except at Brest on the seacoast). Philip Miller commented on its delicate constitution back in the 1750's, complaining that protection against winter frost was a precaution "absolutely necessary to the Chile strawberry, which is frequently killed in hard winters, where they are exposed without any covering." He recommended covering the beds with tanners bark, sawdust, sea coal ashes, decayed leaves, or evergreen boughs to preserve them.[3] This lack of hardiness, bred into cultivated varieties, has been a major failing throughout the history of the modern strawberry.

The success of English horticulturists in producing variations of *F. virginiana* encouraged them in their efforts in breeding. They discovered that outstanding progress could be made when the neglected *F. chiloensis* was used as one parent, for these new hybrids of *F. virginiana* x *F. chiloensis* inherited characters of hardiness, sharp flavor, and high color from the Scarlet and of large fruit size from the Chile.

Behind the early, famous English hybrids lies the work of two men. The value of their contribution is seldom fully recognized, yet it is of greatest importance, for in one case a variety was produced which enters into practically all those of today, and, in the other case, breeding techniques were developed which are basic to much of the progress we now accept so casually. The first of these two men was Thomas Andrew Knight (*Fig. 6–1*). Although

1 Bunyard, E. A., "The History and Development of the Strawberry," *Journal of the Royal Horticultural Society,* Vol. 39, 1914, p. 545.

2 Fletcher, S. W., *The Strawberry in North America.* New York, 1917, p. 116.

3 Miller, Philip, *The Gardener's Dictionary,* Sixth Edition. London, 1771, n.p.

FIG. 6–1. Thomas Andrew Knight, the first man to practice large-scale, systematic strawberry breeding, which produced two famous varieties: the Downton and the Elton. As a founder and long-time president of England's Royal Horticultural Society, he encouraged others to breed better varieties of fruits and vegetables.

he became renowned as president of the Royal Horticultural Society from 1811 to 1838, his notable contributions to strawberry breeding have been little appreciated. Knight has been described as "the foremost pioneer in this breeding work,"[4] and as "a practical breeder of new hybrids in all the important vegetables and fruits must have done more to raise the standards of excellence of these crops than any other contributor in this country before or since."[5]

Knight's father was a Herefordshire clergyman who died when his son was five years old. The boy's education was neglected, and until he was nine he remained almost illiterate. Since he was unable to read as a child, he con-

[4] Pearl, R. T., *The History of the Cultivated Strawberry*. Wye, England, 1928, p. 6.
[5] Bagenal, N. B., "Thomas Andrew Knight," *Journal of the Royal Horticultural Society*, Vol. LXIII. London, 1938, p. 324.

centrated his curiosity on the plant and animal life on the family estate. One day, says a story, he saw a gardener planting beans. The boy asked why the man was planting sticks of wood and was told they would grow up to be beans. The gardener's prediction came true. Knight immediately planted his pocket knife and waited in anticipation for the miraculous growth of new knives. When the experiment failed he sat down to consider the difference in the two cases. Already he was engrossed with the mysteries of the vital processes in plants, a preoccupation which would lead later to his reputation as a brilliant plant physiologist.

Eventually he did catch up with his education and with his phenomenal memory he was able to graduate from Baliol College, Oxford, with a minimum of application. He then withdrew to country life, to his little farm and greenhouse at Elton, where he would have remained a modest experimenter and breeder had not Sir Joseph Banks summoned him out of hiding. Knight first met Banks, who was then president of the Royal Society, in 1795. In April of that year Knight read his first paper before the Society on "The Grafting of Fruit Trees." Banks was interested in his ideas and began writing to him in July of 1796. Their correspondence lasted twenty years. Knight was painfully shy and reserved, but before the interest of such a great man he forgot himself and paid close attention to Banks's suggestions and advice. For some years Knight refused to read the papers of other scientists on vegetable physiology, afraid of becoming prejudiced by them in his search for truth. Consequently, he had little idea that any of his experiments and conclusions were unknown to other men. Banks finally persuaded him to read reports of other research and to publish his own ideas. He invited Knight to his house, and thus gave him the opportunity to compare his observations and theories with those of some of the world's famous naturalists. In these early years Knight was already a general farmer, stock breeder, and fruit and vegetable grower. Practicality, which was always the aim of his research, gave him an interest in improving plants by crossing them, a very new idea in 1798. From this interest came his calling as a practical agriculturist and he was included among the founders of the Royal Horticultural Society in 1804. When a committee asked him to help define the objects of the Society, he said the chief need was for "scientific inquiry into the breeding, cultivation, and forcing of fruit . . . in which the practice of the modern gardener is conceived to be most defective!"[6]

Along this line he made the first scientific attempt at strawberry breeding on a large scale. Observing that all available varieties and species of large-fruited strawberries (with the exception of the musky one, *F. moschata*) would breed together, he considered them all to be varieties of the same species.

[6] Simmonds, A., "The History of the Royal Horticultural Society, 1804–1954," *Journal of the Royal Horticultural Society,* Vol. 79, London, p. 463.

From experimental crosses he raised over four hundred seedlings in 1817 in an attempt to disprove the common opinion that all European gardens were indebted to America for "three distinct species of esculent strawberry: the Grandiflora or Pine; the Chiloensis or Chile; and the Virginiana or common Scarlet."[7] From the 400 seedlings he made a number of selections. He sent runners of the most promising kinds to the Royal Horticultural Society's garden in London. Each selection was numbered and had an accompanying description and account of its parentage. "I possess at present only a single bearing plant of each of the above mentioned varieties," he wrote, "but should the fruit of any be found valuable, I shall be prepared to send a very large number of plants of all . . . and such will be much in the service of every Member of the H. S., who may wish to obtain them."[8]

One outstanding seedling became the Downton strawberry (*Plate 6–1*), whose mother was raised from seed directly imported from America. Its geographical source in America was unknown, but it was classed as a Virginian. The father was the Old Black, a strawberry of unknown origin. This uncertainty about the source of the Downton's parents prevented Knight from claiming it to be a definite example of *F. virginiana* x *F. chiloensis*. The Downton itself had large oblong fruits with many resemblances to the Chilean.

The second of Knight's varieties to win attention was the Elton (*Plate 6–2*), which in 1828 became the Downton's rival. Knight had overlooked it in his plantings and it remained unnoticed until someone "discovered" it in the Royal Horticultural Society's garden where it was prominent for its late blooming, its beautiful fruit, its health and its hardiness. It established itself as a good late variety, but its actual parentage was unknown.

Knight's success in improving the quality of fruits and vegetables encouraged other gardeners to experiment on their own and they found Knight ready both to applaud their successes and to abet their attempts. At the end of each meeting of the Horticultural Society the members voted on the most deserving paper read at the session, which was then printed, to be preserved along with the record of the Society's transactions. By 1810, forty-one papers had been printed, fifteen of which belonged to the most prolific contributor—Thomas Andrew Knight. The first president of the Society died in 1810 and in 1811 Knight was elected to fill his place, a position to which he was annually re-elected until his death 27 years later.

In 1806 Knight's older brother left him Downton Castle, the 10,000-acre family estate in Herefordshire. Here Knight spent the remainder of his life, journeying to London every spring for the meetings of the Society, but devoting most of his time to running the estate and its orchards and giving many hours of thought to planning his experiments.

[7] Bagenal, *op. cit.*, p. 207.
[8] *Ibid.*, p. 210.

His contributions to practical agriculture show a wide range of interests and help to explain his influence in leading other gardeners and livestock breeders to imitate his efforts. Some of the observations he made are now a standard part of plant physiology, for he made studies on the ascent and descent of sap in plants, the nature of the cambium, geotropism of roots and stems, and phototropism in tendrils. In practical horticulture "the originality and range of his investigations are practically staggering."[9]

In recognition of Knight's reputation and his broad knowledge, Sir Humphrey Davy, when asked to deliver a course of lectures on "The Chemistry of Agriculture" before the English Board of Agriculture in 1803, he went first, on Sir Joseph Banks's recommendation, to consult Knight on some of the points in his presentation. In 1806 Knight won the Copley medal for his papers on vegetable physiology. A close friendship developed between Knight and Davy, and in writing to him about plant physiology in 1810, Davy said: "In considering the physiology of the subject, I shall have little to do but to record your labours, for you have *created* almost all the *science* we possess upon that interesting subject."[10]

In 1814, Knight was awarded a gold medal by the Royal Horticultural Society for his papers as well as his gifts of grafts and buds of valuable new fruits. In 1835 a Knightian medal was struck in gold and awarded him "for signal services he has rendered to horticulture by his physiological researches."[11] Knight accepted on condition he could give a sum equal to the cost of the medal to help liquidate the Society's debts.

As the years passed, Knight spent more of his time at Downton and shortened his visits to London. The death of his only son in a shooting accident in 1827 only made him work harder. He corresponded with horticultural societies and plant breeders all over Europe and America and received medals from many parts of the world. Despite his retirement to Downton, he never stopped contributing to the Society. He died in his coach on the way to the General Meeting of the Horticultural Society, May 11, 1838. As one historian said, "It would be difficult to find any other contemporary author, in this or other countries, who has made such important additions to the knowledge of horticulture and the economy of vegetation."[12]

Knight wanted the chief emphasis of the Royal Horticultural Society put on the breeding, cultivation and the forcing of fruits. He used his influence, first as a founding member, then as president of the Society, to insist on the

[9] *Ibid.*, p. 224.

[10] Knight, Thomas Andrew, *Selection from the Physiological and Horticultural Papers, Published in the Transactions of the Royal and Horticultural Societies by the Late Thomas Andrew Knight, Esq.* London, 1841, p. 22.

[11] *Ibid.*, p. 32.

[12] Simmonds, *op. cit.*, p. 464.

awarding of medals, one of the earliest means adopted by the Society to promote horticulture. Papers and pertinent correspondence were published along with paintings of exceptional new varieties of fruits and vegetables, and silver cups went to their breeders.

The stimulus of the Royal Horticultural Society had its effect on strawberries. Michael Keens, a market gardener of Isleworth near London, raised the first large-fruited market variety of strawberry in 1806, eleven years before Knight began his crossing work, and he found the Society both interested and appreciative of his efforts. Keens became second only to Knight in his importance to the English development of the strawberry.

> Having frequently, in the course of many years' practice, observed the deterioration of several kinds of fruit, when propagated in the usual ways of slips, buds, cuttings, scions, or division of the parent root, I have for a considerable time employed myself in raising new varieties from seed, which has been not only a source of great amusement to me, but also very profitable in my profession,

Keens wrote to the Society from Isleworth on January 10, 1814. He then described how he had sown the seed of the White Chili strawberry along with a great many others in 1806 and had discovered that one of the Chili seedlings was very different from, and far superior to, its companions. This was the Keens Imperial (*Plate 6–3*).

In his letter to the Society, Keens described his berry as a very fine deep crimson in color and round in shape. The seeds projected above the surface of the fruit thus protecting it from bruises and suiting it for transport to the markets. Its growth was free and vigorous and its stalk was exceptionally erect and strong, better able to support the fruit than any other strawberry, "which alone would give it a decided superiority over others in wet weather," Keens pointed out.[13] Although it lacked a high flavor, the great beauty of its fruit and its probable usefulness for the London market persuaded the Society to publish a drawing of it.

In 1821 the Society had its artist paint another Keens variety, the Keens Seedling (*Plate 6–4*), raised in 1819 from the seed of Keens Imperial. The Society awarded Keens a silver cup and published a description of the berry in "Notices of New or Remarkable Varieties of Fruits, ripened in the summer and autumn of the year 1821," a review of fruits which had been exhibited at recent meetings. Thus Knight's proposed honors went to the breeder of a strawberry which is an ancestor of most of today's leading varieties.

The berries of Keens Seedling were large for the 1820's—up to two inches in diameter, one and a half inches in length and somewhat coxcomb in shape. The fruit was a very deep rich red in color and white at the center, though the

[13] Keens, Michael, *Transactions of the Royal Horticultural Society*, Vol. II. London, p. 102.

red color stained deep into the flesh. The flesh was tender, compact and very juicy at the center with a flavor like that of the Pine strawberry. The seeds were small, yellow and deeply imbedded and the calyx was large and partially reflexed. The plants themselves were prolific and free growers and possessed "the desirable habit of bearing their fruit high from the ground," read the description in the *Transactions of the Royal Horticultural Society*.[14] E. A. Bunyard, a strawberry expert of the early twentieth century, said that "the large size and excellent flavor of this fruit created a sensation which probably no succeeding strawberry equalled." In 1914 he noted that while other varieties might have surpassed it in individual qualities, as a near-perfect berry it had yet to be replaced.[15] Keens had raised the first modern strawberry but the Keens Seedling was more of a happy chance than anything like the result of the systematic breeding program used by Knight. Other growers, spurred on by Keens' success, would use Knight's methods in their breeding.

Keens grew his strawberries in gardens extending over more than sixty acres at Worton Lane in Isleworth, the chief of the market garden towns in the region just north of the Thames, known as the "great fruit garden" of the London markets. Michael Keens and John Wilmot, originator of Wilmot's Superb Strawberry, were the chief two gardeners in early nineteenth century Isleworth. Their strawberry plantings made the township famous as a strawberry-growing center. Most of Keens' gardens were devoted to the Keens Seedling strawberry and the Keens gooseberry. Sir Joseph Banks, the friend of Thomas Andrew Knight, also lived in Isleworth at his estate "Spring Grove," named after an apple raised by Knight (Spring Grove Codlin) and which Banks cultivated extensively. Banks also grew many strawberries and reintroduced an old abandoned practice of spreading straw under the fruit to keep it clean and to diminish the amount of evaporation from the soil, thereby reducing the necessary amount of watering. Both Keens and Wilmot received the Banksian medal from the Horticultural Society for the excellence of their fruit. Keens himself owned most of his gardens "which very considerable property he attained chiefly by industry and a judicious marriage, frankly avowing that he began the world without a shilling of capital."[16] His son-in-law inherited the land when Keens died in 1835 at the age of seventy-three.

Later Varieties of the 1800's*

Many excellent varieties appeared after the success of Keens Seedling. John Williams was one of the first to succeed in breeding new varieties of

[14] "XXXI Notices of New or Remarkable Varieties of Fruits," *Transactions of the Royal Horticultural Society*, Vol. V. London, p. 261.
[15] Bunyard, *op. cit.*, p. 547.
[16] Bate, G. E., *A Middlesex Medley*. England.
* This section was prepared by George M. Darrow.

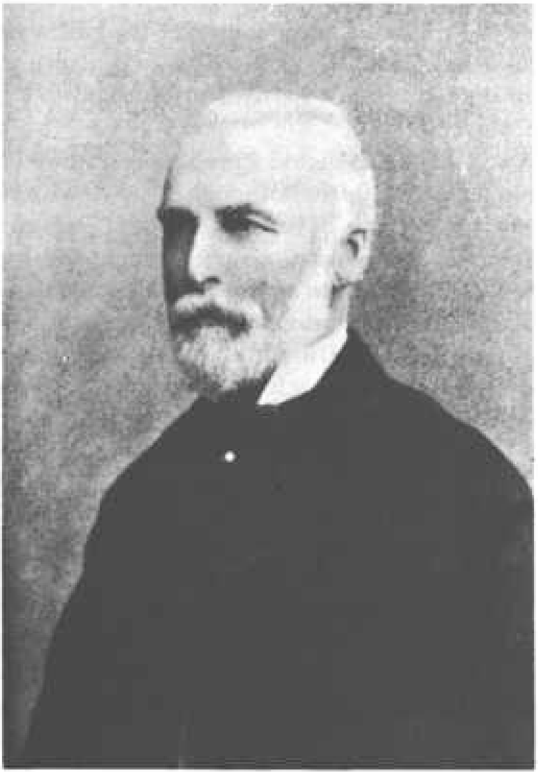


Fig. 6–2. Thomas Laxton began the most extensive and continuous strawberry breeding program ever attempted in the late nineteenth century in England and introduced such famous varieties as the Noble, King of the Earlies, and Royal Sovereign, ancestors of many modern English and European varieties. He used hardy American strawberries to strengthen European varieties. In the 1890's, when his sons took over his work, Laxton told of raising at least 10,000 seedlings in his thirty-two years of breeding work.

strawberries, which he named after his house, Pitmaston. His Pitmaston Black Scarlet was grown even as late as 1914.

In 1840, Myatt of Deptford introduced British Queen, his most famous strawberry, and one which Bunyard considered still among the best flavored in 1914. The Eleanor (1847), Admiral Dundas (1854) and Filbert Pine were other varieties raised by him. Admiral Dundas was an enormous pale orange-colored berry with pink flesh and good flavor. Eleanor was late blooming, bright red and acid and used for forcing for its very large fruits. Myatt's seedlings are supposed to have been raised from Knight's varieties. British

Queen dominated the whole strawberry market for half a century. Possibly if virus-free plants were available it would be widely grown yet for its unsurpassed flavor, even though it is not hardy. Introduced into France in 1848, it was widely grown there.

Between 1840 and 1850 the Bicton Pine was introduced by J. Barnes, a gardener at Bicton in Devonshire. Although its yellowish-white, soft fruit made it an amateur's variety, its flavor was excellent, suggestive of the Pine.

In 1854, Jucunda was introduced, a variety originated by John Salter of Hammersmith, England. It has been an important variety throughout Europe and the United States; its importance greater on the continent than in England. It was imported into the United States as early as 1858, and grown under high culture and protected with winter mulching. It was very productive and was raised there till the 1920's. It was light crimson with firm, red flesh of high flavor, late and capped the easiest of any variety, being picked without caps. It is still grown slightly for processing in Holland, but has been replaced largely by Senga Sengana. It has been crossed with others in Holland to get easy capping varieties.

In the 1860's two other famous English varieties were introduced: Sir Joseph Paxton (1862) and Dr. Hogg (1866), originated by Samuel Bradley, a gardener at Elton Manor near Nottingham. The first, Sir Joseph Paxton, was a midseason variety of brilliant glossy red and firm fruit, which made it a good market berry. It was a leading variety of England for seventy-five years, and in France was considered one of their best commercial varieties as late as 1944. Dr. Hogg was a long, somewhat flattened orange-red berry with pure white flesh, but although one of the largest of the late varieties, it was not as successful as the Paxton.

About this period, Thomas Laxton (*Fig. 6–2*) began the most extensive breeding of strawberries ever attempted in England. He began experiments in breeding in 1865 and conducted experiments for Charles Darwin, mainly with peas. He began introducing strawberry varieties from his work as early as 1872. His first great success and the only variety he introduced that was not a hand-made cross was the Noble (1884), a seedling of Excelsior that had been planted next to the American Sharpless. Until the last few years it was a major early variety of many countries. It was notable for its earliness, its resistance to cold and to disease. Even in 1960 many acres were grown in Italy and in Scandinavia. King of the Earlies (Vicomtesse Hericart de Thury x Black Prince) was introduced in 1888. In 1892, came Laxton's other great variety, Royal Sovereign, nearly equal to Keens Seedling in significance. It was a cross of Noble x King of the Earlies. It had an American variety, Sharpless, in its ancestry. The earliness, excellent flavor, beauty, productiveness, hardiness and relatively good handling quality made it of great importance in Great Britain and on the Continent. Its weaknesses are its great susceptibility to mildew and to virus diseases. After more than seventy years, it is still raised in many parts of Europe. Thomas Laxton originated seventeen varieties himself and after his sons took over the work in the 1890's, they and the grandsons introduced forty-seven more up to 1927. Scarlet Queen, Leader, Fillbasket, the Laxton, Latest, Latest of All, Bedford Champion and Duke, were some of the more notable of the other varieties. Better than other European breeders in the nineteenth century, Laxton understood the weakness of European varieties—they were not hardy enough and needed to be hybridized with the much hardier American varieties. In the 1890's, he told of raising at least 10,000 seedlings over the thirty-two years he had been breeding strawberries.

Breeding in France—1770 to 1900

Although the modern strawberry had its beginning in the great work of Duchesne in the 1760's and 1770's, research and breeding did not continue at the same high level in France. Except for the Chilean, grown quite extensively near Brest on the coast, the Pineapple (*ananassa*) was the chief variety and, for most of the time, almost the only variety grown in France from the time of Duchesne, about 1770, until after the introduction from England of Keens Seedling and other varieties in 1824 and the later introduction of the Elton. There was no Thomas Knight to stimulate hybridizing as in England, nor a Hovey as in America. Most of the breeding was just the raising of seedlings by amateurs and gardeners, with little of the systematic breeding of Thomas Laxton. We know now that most seedlings of perfect-flowered varieties are selfed seedlings and far less vigorous than the parents, so that just growing seedlings is discouraging work. Only accidental crossing by bees, or growing seedlings of pistillate varieties that had to be crossed to bear fruit, would give mostly vigorous strawberry plants. But even so, just by rais-

FIG. 6–3. Madame Elisa Vilmorin contributed descriptions of strawberries she had grown to Joseph Decaisne's magnificent work, *Les Jardins Fruitiers du Museum*. She also ran the famous Vilmorin-Andrieux seed firm of Paris single-handed after her husband's death and carried on Duchesne's work of testing new *F. ananassa* varieties.

ing seedlings, the French amateurs produced some superior varieties that were even grown in England.

In 1846, Gabriel Pelvilain, chief gardener of the royal palace at Meudon, raised the Comte de Paris and the Princesse Royale, with its hard core, both from seed of Keens Seedling and after their introduction the culture of the Pineapple strawberry soon ceased. In the same year, J. L. Jamin, raised the Vicomtesse Héricart de Thury, also from seed of the Keens Seedling, and it was introduced in 1849. This variety had excellent flavor, glossy red, firm berries, that made it the standard for flavor and preserving for one hundred years. It is still widely known under the name Ricart, from (He)ricart, and might still be a great variety if free from virus.

After 1849 the varieties grown were mostly of French origin until almost the end of the nineteenth century, for in the next twenty years many fine French varieties were introduced. F. Gloede introduced the Duc de Malakoff (Chilean x British Queen) in 1854, a variety of very large size. M. Lebreton selected Marguerite in 1859, from seedlings of Sir Harry x an unnamed seedling, because of its great size. It was said to average over ½ oz. (15 to 20 gms.) with exceptional berries of more than 1½ oz. (40 to 45 gms.). It had pink to white flesh and was quite acid. Dr. Nicaise of Chalons sur Marne, raised the Dr. Nicaise in 1863, another berry of largest size, up to 1½ to 2 oz. Berger obtained the Docteur Morère (Palmyre x Duc de Malakoff), in 1867 and it was introduced in 1871 as an early forcing variety of high flavor with dark raised seeds. Later it proved notable as one parent of Mme. Moutou.

Even though there was no systematic breeding in France in much of the nineteenth century, it was the French who produced during this period two great works on the strawberry. In 1864, Leonce de Lambertye, a man who used his retirement years for the intensive study Duchesne had conducted in his youth, published *Le Fraisier, sa Botanique, son Histoire, sa Culture.* The other work of importance was that of Decaisne, "Le Fraisier" in *Le Jardin Fruitier de Museum,* which included paintings of species and varieties with accompanying descriptions by Mme. Vilmorin (*Fig. 6–3, see* Chap. 5).

Three more varieties by three separate breeders complete the more notable ones up to 1900's. Joseph Riffaud obtained the General Chanzy (J. Riffaud x Madame Lebreton) in 1880. It was large, long ovoid, deep brilliant red, a good-flavored early sort used for forcing. Later it was the seed parent of Fukuba of Japan. Edouard Lefort originated the Edouard Lefort, a high flavored forcing variety, in 1889 and Louis Gauthier, of Caen, his Louis Gauthier, in 1889. The Louis Gauthier was a very productive, large white, very solid, rose-tinted variety, which capped with difficulty. It often produced a second crop in the fall, but on the runner plants.

At the end of the nineteenth century, Noble from England and Sharpless from America were introduced and these two and Marguerite were the main crop varieties. Docteur Morère, Marguerite and General Chanzy were the early and forcing sorts.

7

Genetic Research and Chromosome Number

THE EARLY HISTORY of the strawberry in Europe and the New World, including an account of its development in England and France up to 1900, appears in the preceding section, along with a review of the literature accompanying the strawberry's development. The early development of strawberry varieties in America and the men who bred them will be described in other chapters, as will later breeding work. First, however, it seems best to discuss *Fragaria* more fully, in order that breeding work of the past, present, and future can be properly appreciated, both for its accomplishments and the material limitations it must accept. To effect the basis for this appreciation it is necessary to describe strawberry species, both as they are distinguished by their genetic composition and by their gross morphological characteristics, for such description helps to clarify both the sources of characters and the possibilities displayed by the modern strawberry. Once this is done, the later discussion will rest on a broader base of information and will be more useful.

Genetic Research

For a clear understanding of the possibilities and limitations of strawberry breeding, the results of studies on strawberry genetics and cytology must be presented. The material which follows contains the findings of various investigators in this field; of Millardet, who obtained maternal and paternal inheritance in certain crosses, the descendant seedlings strongly resembling either the mother or father; of Solms-Laubach, who confirmed Millardet's findings; of Strasburger, who found normal union of egg and pollen in such crosses, but with dominance of paternal characters; of Richardson, who determined that the diploid *vesca* displays what we term simple Mendelian inheritance, while the octoploid garden strawberry displays a complicated inheritance; of Longley, who first obtained the chromosome numbers of several strawberry species. In such fashion, through the work of single investigators, basic information for breeders was gradually built up. Later investigations of the genetics and cytology of the strawberry were carried out on a considerably larger scale, especially by three centers of research: The Friedrich-Wilhelms University, beginning with Miss Elizabeth Schiemann around 1919 and continuing through her students, especially Dr. G. Staudt, until now; the Bussey Institute of Harvard University from 1921 to 1941, with Dr. East and his students, the Drs. Ichijima, Manglesdorf, and Yarnell; and the University of Manchester from 1950 to 1959, with Dr. Harland and his students, Margaret Smith and Drs. King, T. Smith, Ellis, Islam, and Jones. The studies at these research centers did much to establish the relationships among strawberry species. These studies also indicated the probable ancestors of the modern strawberry, and whether useful new types might be produced with different chromosome numbers, with different compositions of chromosomes from other species, or as hybrids with related plants such as *Potentilla*. Other genetic research is described under the country and institution where it was pursued, especially under North Carolina and the U. S. Department of Agriculture at Cheyenne, Wyoming, for methods of breeding; the U. S. Department of Agriculture, for production of productive *vesca*-flavored decaploids; and Russia, for cytogenetic studies.

A. Millardet, Professor of Botany at Bordeaux, France, was really the first modern strawberry geneticist. He began a study of hybrids of *Fragaria* in 1883 and continued this study eleven years. He published his paper *Notes on Hybrids Without Union or False Hybrids* in 1894. From the cross *vesca alba* x *chiloensis* he obtained one sterile plant similar to *vesca* and three plants like *chiloensis,* the pollen parent. In all, he obtained four cases of paternal plants where they resembled the *chiloensis* in all general characters.

In Germany, H. Solms-Laubach repeated Millardet's work and in 1907 reported that he also obtained only paternal plants from *virginiana* x *moschata,* all of which were sterile, as male plants of *moschata* characteristically are.

Strasburger (1909) sectioned flowers of the *virginiana* x *moschata* at

FIG. 7–1. Albert E. Longley, born in Paradise, Nova Scotia, Canada, March 12, 1883, graduated from Acadia in 1920, and received his Ph.D. from Harvard in 1923. He became a cytologist and botanist with the U.S. Department of Agriculture, at Washington, in 1923 and held that position until his retirement. He first worked on the cytology of strawberries and rubus and then became a specialist on the morphology of corn chromosomes and spent most of his years of service at the California Institute of Technology at Pasadena, Calif. Since his retirement he has lived at Columbia, Missouri.

twelve-hour intervals after pollination to determine if actual fertilization of the egg by the pollen took place. In the flowers he studied, he found union of egg and pollen typical of sexual reproduction, indicating that the so-called "paternals" were true hybrids, with the characters of the pollen parent remarkably dominant in the seedlings where *moschata* was a parent.

C. W. Richardson (1914, 1918, 1921, 1923) made a wise choice in the kind of strawberries he selected for his research. In studies of inheritance, he used the everbearing wood strawberry, *F. vesca semperflorens,* a diploid in which inheritance is clearest and simplest, involving runnered and runnerless, 3-leaflet and 1-leaflet, white and red-fruited forms. He found that the first gen-

Photo by André Snow

FIG. 7–2. E.M. East, born Duquorn, Illinois, October 4, 1879, graduated University of Illinois in 1900. He first became assistant chemist (1900–1903), then assistant plant breeder in the Illinois Experiment Station (1903–1905). He obtained his Ph.D. in 1907. He was agronomist at the Connecticut Station for four years (1905–1909), then in 1909 went to Harvard University as assistant professor of genetics and continued in this position until his death (November 9, 1938). Besides numerous articles, he wrote three books—the first, with D.F. Jones, *Inbreeding and Outbreeding* in 1919, was his most important to plant breeders. Dr. East's research was of great practical value, for his studies of inbreeding, hybrid vigor, selection, and self-sterility were basic. He was especially interested in proving that quantitative inheritance was also true Mendelian inheritance. He was known as "a careful worker, keen thinker, a scholarly writer and able lecturer," "a wise counselor and friend," and a great teacher.

eration of the cross "runnered x runnerless" plants always produced runnered plants, but when selfed these hybrid plants produced both runnered and runnerless seedlings in good Mendelian fashion. Likewise, 3-leaflet x 1-leaflet gave all normal 3-leaflet seedlings in the F_1, but 177 of 3-leaflet to 73 1-leaflet in the F_2; white-flowered x pink-flowered gave all pink-flowered in the F_1, but 77 pink to 10 white in the F_2; double-flowered x single-flowered gave 97 single to 37 double in the F_1; and white-fruited x red-fruited gave all red-fruited in the F_1 and 70 red to 20 white in the F_2. Thus, inheritance in the diploid strawberry was shown to be like that in other plants.

In contrast, when two large-fruited everbearers (octoploids) were selfed, more than a 3 to 1 ratio of everbearers (177 to 33) was obtained, while non-everbearing x everbearing gave 24 everbearing to 53 non-everbearing. All non-everbearing seedlings of this cross when selfed gave at least some everbearers. In crosses of female x perfect-flowered, Richardson obtained 183 female to 155 male, or perfect-flowered, about a 9 to 7 ratio. He obtained one cross with all large fruit, some reaching 32 cubic centimeters in volume. Royal Sovereign selfed gave 12 seedlings with flavor equal to their parent, three with somewhat better flavor, and 96 with no flavor or with a bad flavor. At the end of his research, he decided that it was not possible to judge the flavor of selfed seedlings because their fruit was too small.

When strawberry breeding began with the U. S. Department of Agriculture, at Glenn Dale, Md., the need for information about the chromosome numbers of the species and varieties was soon evident. In answer to this need, A. E. Longley (*Fig. 7–1*) began his studies about 1923. In *Chromosomes and Their Significance in Strawberry Classification* (1926) Longley first reported the chromosome number of *vesca, moschata, chiloensis, virginiana,* and of many varieties and hybrids. He considered *vesca* to represent the primitive form from which the others evolved, and held that dioeciousness (male and female flowers on separate plants) in the strawberry was associated with polyploidy. He also confirmed Millardet's results in obtaining maternal and paternal forms in crosses. *Fig. 7–3c,* left, shows the 28 chromosomes of pollen mother cells of the variety V. Hericart de Thury and the seven chromosomes of pollen mother cells on the right of two diploid seedling varieties of *vesca.*

Genetic Studies at the Bussey Institute, Harvard University

The report in 1894 by Millardet that some species-crosses of strawberries gave either maternal or paternal seedlings led E. M. East *(Fig. 7–2)* and his students at the Bussey Institute, Harvard University, to undertake a study of the genetics of *Fragaria.* Genetic investigations began in 1921 and con-

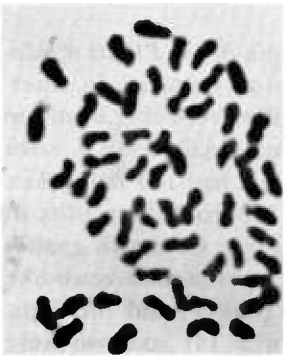


FIG. 7–3a. Photomicrograph of the chromosomes from a single cell from the root tip of a double hybrid strawberry cross which produced an octoploid plant with 56 chromosomes. Slide prepared by Mr. Henry Holden at the New England Institute for Medical Research.

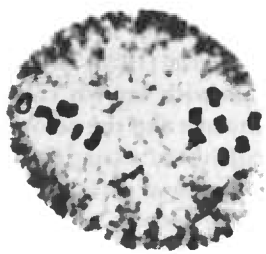


FIG. 7–3b. Photomicrograph of a pollen mother cell from *F. vesca,* a diploid plant with 14 chromosomes. This is a "squash" preparation of the second meiotic division metaphase (side view on left, polar view on right) showing the reduced number of chromosomes; *i.e.,* 7 in each group. Slide prepared by Mr. Henry Holden at the New England Institute for Medical Research.

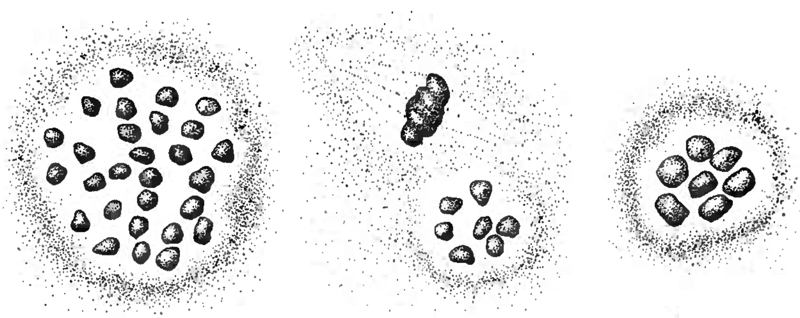


FIG. 7–3c. To left, the 28 chromosomes of the pollen of the variety V. Hericart de Thury; center and right, chromosomes of pollen of two varieties of the European *vesca.*

tinued through 1941. In 1930 East published *The Origin of the Plants of Maternal Type* which discussed maternal-type plants that occurred in interspecific hybridizations. East also described a diploid plant resulting from the cross *F. vesca* (2n = 14) x *F. virginiana* (2n = 56). The maternal parent *F. vesca* had white fruit, while the seedling resembled *vesca* but had red fruit. East then grew selfed seedlings of the red-fruited F_1 and reported the results in 1934 in the paper *A Novel Type of Hybridity in Fragaria.* Of the 18 greatly variable selfed seedlings raised, three did not flower, seven had *vesca*-like fruits, one of the seven having seeds in sets like *virginiana,* and the eight others were entirely sterile. Sixteen were diploid (2n = 14) and two were triploid (2n = 21). East concluded that one set of chromosomes of *F. virginiana* is so like those of *vesca* that pairing of chromosomes occurs and plant development follows.

In 1924 K. Ichijima began a study of the chromosome number of the species and hybrids then at Bussey. In *Cytological and Genetic Studies of Fragaria* (1926) he confirmed Longley's chromosome counts, and to the species with known chromosome constitution, he added the diploid *viridis* of Europe and the octoploid *ovalis* of the United States. He also examined eleven cultivated varieties; all were octoploid. In one cross of two diploid forms of *vesca* (*bracteata* x *rosea*) a tetraploid was obtained with larger, thicker, and more crenate leaves than the parents. It was vigorous and fertile. Doubling of chromosomes was noted in seven pollen grains.

In *Studies on the Genetics of Fragaria,* Ichijima (1930) reported that crosses of *nilgerrensis* with other diploid species were dwarfs except for three doubtful hybrids. Crosses of the musk strawberry, *moschata* (2n = 42) x diploids gave seedlings with the *moschata* chromosome number. One cross of a diploid x octoploid had the chromosome number of the pollen parent but was like the diploid in appearance. Three different forms, *vesca rosea, vesca alba,* and *nilgerrensis* had doubled chromosome number in pollen. *Moschata* had two kinds of chromosomes; two sets with dumbbell shape and one set with spherical shape. *Virginiana, glauca, chiloensis,* and Chesapeake also had genomes with the two shapes of chromosomes.

A.J. Mandelsdorf and E.M.East (*Studies on the Genetics of Fragaria,* 1927) made numerous crosses between diploids and concluded that they were entirely interfertile; however, the diploids under study were merely varieties of *vesca.* In crosses of pink-flowered x white-flowered, pink was dominant. In the F_2 they obtained 128 pink to 46 white, close to a 3 to 1 ratio. No crosses were obtained when *moschata* (2n = 42) was pollinated by a diploid species, but when the cross was a diploid x *moschata* seed was set. It gave poor germination (0.7 percent) and the few seedlings obtained died within two weeks. When octoploids were used as females, with diploids as males, none set, but the reciprocal was obtained without difficulty. Germination was poor; maternals were obtained; dwarfs did not flower; and all true hybrids were sterile. When the octoploid was crossed with the hexaploid *moschata,* a good set and a germination of 90 percent was obtained with vigorous, completely sterile plants and dominance of *moschata* characters. Maternal seedlings, both staminate and pistillate, were also obtained. Mangelsdorf and East, however, were not certain that pseudogamy was the cause.

In *Notes on the Somatic Chromosomes of the Seven-Chromosome Group of Fragaria* (1929), S.H. Yarnell found that the chromosomes he studied were all very similar in appearance. The only constant difference common to them was that of length; their lengths in microns averaging: 1.7, 1.5, 1.4, 1.3, 1.2, 1.0, and 0.9 for the seven. Usually it was impossible to distinguish differences except between the two shorter and the two longer ones.

Yarnell, in *Genetic and Cytological Studies on Fragaria* (1931), separated the diploids into four groups: (1) *vesca* and its varieties, *bracteata, californica, americana, rosea,* and *mexicana;* (2) *viridis* (= *collina*); (3) *nilgerrensis,* and (4) a *vesca* type from China. *Viridis* gave seedlings that were vigorous in crosses with the other diploids, but were only partially fertile. *Nilgerrensis* gave only dwarf hybrids in all crosses except those with *viridis,* and even these hybrids gave no flowers. No true hybrids were obtained in crosses of *moschata* with diploid species, but some maternals were obtained. The octoploids *virginiana* and *chiloensis* set no fruit when used as female parents with *vesca,* but, used as pollen parents on *vesca,* they gave both maternal and partially fertile plants. *Chiloensis* x *vesca* var. *bracteata* gave three sterile seedlings. *Virginiana* and *chiloensis* both gave vigorous sterile hybrids with *moschata* pollen, but no set was obtained when they were used as pollen parents. All types of crosses gave at least some completely fertile plants which were like the mother. Increased pairing of chromosomes occurred with increased temperature.

Yarnell (1930) also reported on studies of the tetraploid obtained from crossing two diploids, *bracteata* x *rosea.* The tetraploid was selfed and produced tetraploids. These were crossed with the diploids *vesca, viridis* (= *collina*), *bracteata,* and another diploid. All seedlings were triploids.

Genetic Studies at Friedrich-Wilhelm University*

In 1919 Prof. E. Bauer proposed that Dr. Elizabeth Schiemann (*Fig. 7–4*) ask for the strawberry collection of Prof. Solms-Laubach of Strasburg, Alsace,

* By Dr. G. Staudt.

FIG. 7–4. Elisabeth Schiemann was among the first girl-students officially admitted to study natural science at the Friedrich-Wilhelms-Universitat at Berlin during 1908–1912. During her studies she was greatly influenced by Erwin Bauer, one of the ablest of early geneticists in Germany, and through whom E. Schiemann became acquainted with the problems and great value of genetics for plant breeding. In 1912 she was graduated as a Ph.D. with the thesis *"Uber Mutationen bei Aspergillus niger."*

As an assistant of Prof. Bauer, E. Schiemann was in charge of the experimental work in barley. In 1925 she was granted the *"venia legendi"* with a paper entitled *"Zur Genetik des Sommer-Winter—Typus bei Gerste"*; in 1931 she became a full professor. In 1943 she was made head of the division for "development and history of cultivated plants" of the Kaiser Wilhelm-Institut für Kulturpflanzen-forschung, and after the war continued her studies of strawberries.

Besides her research work on strawberries, E. Schiemann added much to our knowledge of the genetics, history, and development of the cultivated plants. In 1932 her book, entitled *Entstehung der Kulturpflanzen,* was published. This book has been an approved standard work for research about the history and development of the cultivated plants; a supplement was published in 1943.

so that she could study further Millardet's "false hybrids." In 1930 and 1931 Dr. Schiemann demonstrated that Mangelsdorf and East's explanation for Millardet's patroclinous hybrids (by dominance of the higher polyploid parent) could not be generalized, because hybrids of *F. x ananassa* (8x) x *hagenbachiana* (2x) (the frequently found hybrid of *vesca* x *viridis*) gave some "diploid" types too, although all with 2n = 35 chromosomes. Another possible explanation for some of Millardet's "false hybrids" was given by Dr. Schiemann after she was able to show that the tetraploid hybrids of *moschata* (6x) x *viridis* (2x) could not be distinguished from *moschata*. These tetraploid hybrids gave fully fertile and more or less constant offspring.

From experiments published in 1931, Dr. Schiemann concluded that females and males (including hermaphrodites) were the two main groups of sex differentiation in *Fragaria* and, according to Kuhn (1930), suggested that the difference betwen maleness and hermaphroditism was organized by a different allel of the sex factor. Besides the sex factors, she proposed a number of factors for sterility concerning female and male organs as well. Sex changes in plants were often observed. Mutant changes in sex also were found by her. The development of sex organs of the strains used and the different progenies of Schiemann's experiments were investigated cytologically by Rudloff (1930).

From 1933 on Dr. Schiemann (1937) studied hybridization of both the diploid species *vesca* and *viridis,* x the hexaploid *moschata*. Similar to Lilienfeld's (1934, 1936) hybrid of *moschata* x *nipponica (elnipponica),* Dr. Schiemann succeeded in getting hybrids of *moschata* x *viridis*. These hybrids resembled in most characters *moschata* and in F_2 bred more or less true. The autohexaploidy of *moschata,* demonstrated by Lilienfeld, was confirmed by Schiemann's results, as was also homology between the genomes of *viridis* and *moschata*.

Homology of the genomes of *moschata* with those of *vesca* was concluded by Schiemann (1944) from a tetraploid hybrid (*vesca* x *moschata*) which produced normal pollen grains and had always fourteen bivalents in meiosis I. Thus, the homology of the three diploid species *vesca, viridis,* and *nipponica* could be established.

After 1945, Schiemann's associate, U. Nurnberg-Kruger, took over the hybrid material *vesca* x *nilgerrensis,* and G. Staudt started investigations on taxonomy and geographical distribution of the genus *Fragaria*. The need for an exact knowledge of taxonomy for the planned investigations on the phylogeny of the genus resulted in an extensive collection of strawberries from all over the world. Dr. Schiemann's experiments, in which *orientalis*-like plants originated in the F_2 of the pentaploid hybrid of *vesca* x *moschata,* initiated G. Staudt's investigations on the phylogenetic relationship and sex differentiation of the tetraploid *orientalis*.

Open questions in the genus Fragaria was published in 1951 in which Dr. Schiemann pointed out the main lines for further research: analysis of the diploid species in Europe, of the genome relationship between the European and Asiatic species, and analysis of the tetraploid *orientalis,* as the first steps in a study of the evolution of the polyploid species.

Schiemann's latest paper (1958) dealt with a subfertile hybrid which had originated in 1923 from *F. x ananassa* x *virginiana*. Besides having characteristic teratological malformation of the leaves, the plants, propagated vegetatively, came to flower for the first time after sixteen years. From that year on, the malformation of the inflorescences and flowers decreased.

G. Staudt, a student of Dr. Schiemann, in *Cytotaxonomy and Phylogenetic Relationships in the Genus Fragaria* (1959) concluded that American octoploids were not derived from American *vesca* types, but may have come from East Asia and may have been derived from East Asian *vesca* types. He suggests that the octoploids *virginiana* and *chiloensis* were derived from different ancestors. In a later paper, *The Origin and History of the Large-fruited Garden Strawberry in Germany,* Staudt traced the introduction of *virginiana* and *chiloensis* into Europe. He noted that the *chiloensis* plants "have no winter hardiness" and that in many places no flowers developed. The Mapuche or Huilliche Indians were the first to cultivate the strawberry in Chile. By 1759 *x ananassa,* the hybrid between *virginiana* and *chiloensis* was known. Staudt's *Taxonomic Studies in the Genus Fragaria* (1962) is a detailed study of *Fragaria* of America and Europe. Six species are recognized: *vesca* (with 4 subspecies), *viridis, moschata, virginiana* (4 subspecies), *chiloensis* (4 subspecies), and *x ananassa.* Included in *vesca* are subspecies *americana, bracteata* and *california.* Subspecies *glauca, platypetala,* and *grayana* are given for *virginiana* and subspecies *lucida, pacifica* and *sandwicensis* for *chiloensis.*[1]

Genetic Studies at the University of Manchester—1950-1958

Under the leadership of Dr. S.C. Harland (*Fig. 7–5*) and assisted by Miss Edna King, Miss M. Smith, Miss Thelma Smith and A.S. Islam, J.R. Ellis, and J.K. Jones a major genetical research project on the strawberry was undertaken along seven lines.

(1) Mildew resistance. Harland and Miss King (1957). Mildew susceptibility was found to be due to two dominant genes in the diploid *F. vesca.* Both genes must be absent to obtain a resistant plant. In the F_2 of resistant x susceptible a 15 to 1 ratio of susceptible to resistant was obtained. Cytoplasmic effects were noted: if the resistant plant was used as a female the F_1 was less susceptible than in the reciprocal. When accidentally a haploid with only seven chromosomes was obtained, it was immune to mildew, but when it was doubled to a diploid form again, it was partly susceptible. When redoubled

[1] Having grown hundreds of collections of *virginiana* and *chiloensis,* I prefer the botanical classification given on pp. 122–123, as being most realistic. No subspecies are kept, for the differences within the species are great in most areas. George M. Darrow.

FIG. 7–5. S.C. Harland.

to become a tetraploid, it was still more susceptible. The most resistant of all octoploids tested was a *chiloensis* from the Oregon coast.

(2) Studies in ploidy, J.R. Ellis, Thesis. (a) Commercial possibilities of decaploids. Decaploids had been produced by Darrow and by Scott, by obtaining 4x *vesca,* crossing it with cultivated octoploids to obtain hexaploids, then crossing the hexaploids with octoploids and selecting out the ten-ploids. Ten-ploids were then intercrossed and Scott raised several hundred seedlings from which commercial types could be selected. Other methods of obtaining decaploids were studied by Ellis, such as crossing 2x x 8x and doubling the resulting 5x to a 10x, or crossing the 4x *vesca* with 16x *virginiana* and with 16x cultivated varieties (obtained by doubling the chromosome number of *virginiana* and of varieties). The work had not progressed far enough to show the most promising method.

(b) Octoploids with some *vesca* chromosomes. Two methods were planned for obtaining octoploids from *vesca* and *moschata*—(1) doubling of chromosomes of *vesca* (2x) x *moschata* (6x) hybrids; (2) doubling of chromosomes of 4x *vesca* x *moschata* (6x) hybrids and then back-crossing to *moschata.* The first method was found to be difficult and only one hybrid was produced, a very vigorous octoploid. The second method was therefore followed. The cross 4x *vesca* and *moschata* (6x) gave only vigorous pentaploids, all fertile males. Ellis then theorized that *moschata* could have been derived from the allopolyploid of 4x *vesca* x *nubicola* (2x) as Staudt had suggested. *Moschata* would then contain 4 *vesca* genomes plus 2 others. The cross 4x (*vesca*) x 8x variety was also used to obtain 6x; these were crossed with *vesca* (2x), and then doubled to 8x. Two methods of obtaining octoploids from *vesca* and cultivated varieties were successful (see p. 109).

To obtain other kinds of octoploids, two methods were successful: decaploids were crossed with hybrid hexaploids, and hybrid tetraploids were doubled. The first kind of octoploid was highly sterile and the second octoploid types have not grown large enough to estimate their value. As Vilmorin (1898) and many others had suggested, Ellis concluded that it was unlikely that present octoploids had *vesca* in their immediate ancestry.

Ellis (1958) reported finding functional double unreduced gametes and suggests this as a possible way for *moschata* and *virginiana* and *chiloensis* to have originated, with no intermediate polyploid types, from diploids native to their habitat. *Moschata* would be derived from a double unreduced x, a single unreduced gamete, to give 4x x 2x = 6x and the octoploids from the union of two double unreduced gametes. He suggests the probable value of an octoploid with *vesca, moschata,* and *x ananassa* parentage.

(3) Intergeneric crossing. Ellis (1962) reviewed crosses between *F. vesca* and *Potentilla* made by others. Ellis obtained hybrids from the Sans Rivale strawberry x *Potentilla fruiticosa* and x *P. palustris.* Surviving seedlings were 5x and 6x. They were both female and male sterile. 4x *vesca* x *P. fruiticosa* seedlings were 3x. Octoploids x *P. palustris* (6x) were 7x with the most vigorous resembling *Fragaria.* Their rose-pink flowers were male sterile and slightly female fertile.

(4) Induction of haploids. No haploids have thus far been obtained. Islam (1961) studied the accidental haploid plant obtained from a *vesca* x *x ananassa* and compared it with the parent *vesca;* it was smaller in all its parts.

(5) Genetics of perpetual flowering on the octoploid level. Harland and Dr. Thelma Smith and Miss Margaret Smith, from a very limited crossing, obtained a possible 9 perpetual-flowering to 7 normal ratio with the perpetual being AB and the normal ab. Ellis then proposed that perpetuals x normal selfed would give 9 AB:3 Ab: 3 aB to 1 ab; the perpetual-flowering resulting from complementary genes AB.

(6) Propagation methods. Harland and Margaret Smith made a study of rapid propagation by using small one-inch long pieces of roots and small runner tips. The one-inch pieces of roots developed buds and made plants very slowly.

(7) Selfing. Through selfing some varieties lost little vigor, others had very weak progeny.

Effects of induced polyploidy: Islam, Jones, and Ellis found the constant characters associated with chromosome doubling in strawberry to be:

(1) Thicker leaves with larger serrations;
(2) Reduction in the length to breadth ratio of leaflets; that is, rounder leaflets;
(3) Increase in width of the basal angle of the terminal leaflet.

Islam in *Possible Role of Unreduced Gametes in the Origin of Polyploid Fragaria* (1960) reviewed the pertinent literature, and from this and his own studies concluded that "the frequent production of unreduced gametes may have been the principal method of origin of polyploids in *Fragaria.*" Their origin may be either the union of gametes with the full chromosome number of one parent and the reduced number of the other, or with the full number of both parents, called double non-reduction. As to the origin of tetraploids, Islam pointed out that Schiemann (1951) had noted 4x among the F_1 progeny of the cross 2x *viridis* (= *collina*) x 2x *vesca*. Accordingly, Islam suggested that the tetraploids *orientalis* and *moupinensis* may have originated through hybridization between the two diploids with overlapping habitats followed by chromosome doubling, or by the union of an unreduced with a double unreduced from two diploids. He suggests the latter method as the origin of hexaploids, for Lilienfeld (1933) obtained a hexaploid from the progeny of the 4x hybrids between the 6x *F. moschata* (*elatior*) and the 2x *vesca* (*nipponica*). Any of several diploid species may have been the progenitor of the hexaploid species. Octoploids could have resulted by non-reduction from undiscovered 4x or 6x (in crosses with diploids) American species, or by non-reduction from the Asiatic *orientalis* or *moupinensis* and subsequent migration of the 8x to America. The first seemed most plausible.

Among other articles concerned with cytogenetical research with strawberries is *A Contribution to the Question of Genome Relations in Some Species of Fragaria,* by N.A. Dogadkina, which reports that the cross *vesca* x *x ananassa* resulted in few seedlings, only four of which flowered. Chromosome behavior proved the homology of the genomes of *vesca* with one of those of *x ananassa*. The cross *orientalis* (2n = 28) x *elatior* (*moschata*) (2n = 42) was first made by Fedorova in 1932–33 in both directions. All the hybrids were pentaploid and twenty-seven plants were at least somewhat fertile. It was concluded that the two genomes of *orientalis* were homologous with two of *moschata* (*elatior*), that all three of *moschata* were homologous, that is from closely related species, but that *moschata* is not a true autohexaploid. Dogadkina points out that crosses made by Kihara (1930) and Fedorova (1934) indicate that three of the genomes of *x ananassa* are homologous with those of *moschata*. Fedorova obtained a tetraploid from *vesca* x *moschata* that indicated homology of the genomes of *vesca* with those of *moschata,* so that at least three of the *x ananassa* genomes seem closely related to that of *vesca*. Fedorova suggests that *orientalis* is a link betwen *vesca* and *moschata*.

Chromosome Number

Cultivated large-fruited strawberries and the species *Fragaria chiloensis, virginiana,* and *ovalis* from which they come, intercross freely and their hybrids, with certain exceptions, produce fertile seedlings. But the cultivated varieties and the octoploid species from which they come do not readily cross with diploid, tetraploid, and hexaploid species; seedlings of such crosses are nearly or entirely sterile. However, this does not mean that the latter species should be dismissed from consideration as breeding material. These other species need to be surveyed for qualities that might be useful in cultivated varieties. Then, methods of transferring desired qualities to cultivated varieties need to be found. Attempts were made as long ago as 1760 by Duchesne to make some of such crosses, but even today we do not know for certain of any successful attempts—success, that is, in terms of transferring desirable qualities from these other species to large-fruited commercial sorts. No progress was made along these lines until the hybrids were made by Dermen and Darrow in 1944, and later improved by Scott (Scott, 1951). More recently Lebedov in 1957 reported obtaining a hybrid of a cultivated variety x *moschata* variety that produced well and Katinskaja in 1963 reported obtaining useful sorts from cultivated varieties by *vesca,* by *viridis,* and by *moschata* (see under Russia).

The barrier to hybridization in large part has been differences in chromosome number. There are now four natural species groups known, and the phenotypic classifications of strawberry species by botanists constitute classes within these four groups. All such phenotypic classifications based on gross morphology are placed under the four chromosome number groups—2x, 4x, 6x, and 8x. There are in all about eleven strawberry species-classifications which seem to rest upon important enough differences to be valid, although more than 45 have been described. These eleven belong to the botanical and chromosome groups as follows:

Chromosome Groups	Species and Native Country		Geneticist Reporting
Diploid: (14)	1. *F. daltoniana*	—Asia	Darrow, 1937
"	2. *F. nilgerrensis*	—South Asia	Schiemann, 1951
"	3. *F. nubicola*	—" "	Staudt, 1959
"	4. *F. vesca*	—Circumpolar, north Africa, mountains of South America	Longley, 1926
"	5. *F. viridis* (= *collina*)	—Central Europe	Ichijima, 1926
Tetraploid: (28)	6. *F. moupinensis*	—East Central Asia	Staudt, 1951
"	7. *F. occidentalis*	—" " "	Petrov, 1934
Hexaploid (42)	8. *F. moschata* (=*elatior*)	—Central Europe	Longley, 1928
Octoploid (56)	9. *F. chiloensis*	—Coast Alaska to central California, south Chile, mountains of Hawaii	Longley, 1926
"	10. *F. ovalis* (=*cuneifolia, platypetala*)	—Western North America	Ichijima, 1926
"	11. *F. virginiana*	—Eastern " "	Longley, 1926

Some diploid species do intercross readily, but most hybrids have reduced fertility. The two tetraploids are said to be interfertile and their hybrids fully fertile. The three octoploids are entirely interfertile.

Diploids (2n = 14)

F. daltoniana is a little known, small, one-flowered species of South Asia. Its chromosome number is reported as diploid; botanically it belongs in the first group and its response as a parent places it there. The other four species in the diploid group (2n = 14) have in general small, usually thin-leaved plants which bear smaller berries than plants with higher chromosome numbers. *Nilgerrensis* is a many-seeded, tasteless, or ill-flavored species with white flattened berries on erect pedicels. Though *vesca* x *nilgerrensis* are usually dwarfs, Nurnberg-Kruger (1958) reported normal seedlings. *Nubicola* is similar in gross appearance to *vesca,* but hybrids with *vesca* are usually sterile. *Vesca* is of interest for its wide distribution, its aromatic, high-flavored berries, and its everbearing forms. *Viridis* has hard to cap, good-flavored, firm fruit. Though known for three hundred years, it has so far furnished no good garden varieties.

Triploids (2n = 21)

A single vigorous sterile triploid was found in eastern Oregon in 1949. It was collected by R.C. Rosenstiel and the chromosome count made by H. Dermen (unpublished). It resembled 4x *vesca* and probably resulted from the union of an unreduced with a reduced gamete of a diploid *vesca*. Triploids have been obtained by Dermen and Darrow from 2x x 4x crosses (Dermen and Darrow, 1938, *Fig. 7–6*).

Tetraploids (2n = 28)

Moupinensis and *orientalis* are hardy species of West and North China, Korea, Manchuria and Siberia. They undoubtedly have arisen from diploids, probably from crosses of two diploid species. Spontaneous tetraploids are known to arise from crosses of the diploids *viridis* x *vesca* and they resemble *orientalis*. Tetraploids have been produced from *vesca* (1) by using colchicine, (2) by crossing *vesca* (*bracteata*) x *vesca* (*rosea*) (Yarnell, 1929), (3) by crossing *vesca* x *moschata* (Mangelsdorf, 1927), (4) by crossing *moschata* x *vesca* (*nipponica*) (Lilienfeld, 1933, 1936), (Schiemann, 1951), and (5) by crossing *vesca* x *virginiana* (East, 1933, 1934).

Pentaploids (2n = 35)

Very vigorous sterile pentaploids (*chiloensis* x *vesca*) (Bringhurst, 1964) have been found in the wild on the coast of California. Pentaploids from

FIG. 7–6. A triploid *vesca* obtained by doubling the chromosome numbers of *vesca* and crossing back to the diploid *vesca*.

FIG. 7–7. A pentaploid obtained by crossing *vesca* 2x with Dorsett. Such hybrids usually are entirely sterile.

vesca x octoploids have been produced by Fedorova (1932), Dermen and Darrow (1938, *Fig. 7–7*), Scott (1951), Yarnell (1931a), Islam (1954), Ellis (1958), and by Mangelsdorf and East (1927). The latter also obtained pentaploids from *vesca* (both *americana alba* and *rosea*) x *ovalis* (*glauca*) and from *vesca* (*bracteata*) x *virginiana*. None that flowered was fertile. Usually the reciprocal cross of the octoploid x diploid fails entirely. However, in an attempt to produce apomictic seedlings of the Fairland and Temple varieties by pollinating with *vesca*, Darrow (unpublished) obtained a very large number of seedlings, all of which were vigorous true hybrids and set at least a few seeds. Only one had a fair development of fruit. Ellis obtained pentaploids from crosses of *vesca* x *moschata*, all very dwarf; from tetraploid *vesca* x *moschata*, all vigorous and all males; from *vesca* (2x) x *chiloensis, virginiana*, and *X ananassa* (Ellis, 1958).

Hexaploids (2n = 42)

F. moschata (*Plate 7–1*), the one hexaploid, is cultivated slightly in the gardens of Europe because of its vigorous plants and very vinous-flavored fruit. It may have originated by natural crosses of *vesca x viridis* or *vesca x nubicola* (Staudt, 1959), unreduced pollen or eggs of one parent furnishing the two extra sets of chromosomes, followed by doubling of the resulting triploids. Hexaploids have been produced by crossing cultivated varieties with 4x *vesca* (Scott, 1951) (34 seedlings) and by the reciprocal 4x *vesca* x octoploids *virginiana, chiloensis,* and cultivated varieties (Dermen, 1938–1939, unpublished) (*Figs. 7–8, 7–9*), (Ellis thesis, 1958), (Islam thesis, 1954), (Kluge, 1959).

Heptaploids, Seven-ploids (2n = 49)

These have been obtained by Scott and Darrow from (*F. x ananassa* x 4x *vesca*) x *x ananassa* and, although one was selected for its fertility, it was

FIG. 7–8. A sterile hexaploid (6x) obtained by crossing a tetraploid *vesca* with Dorsett. Rarely is it possible to obtain any seed from such a hybrid. *(See Fig. 5–9)*

finally discarded (unpublished). Ellis (1958) obtained seven-ploids from the 8x cultivated varieties x 7x hybrids and the reciprocal.

Octoploids (2n = 56)

Most cultivated varieties are octoploids and descendants of *chiloensis* and *virginiana*. A few varieties have *F. ovalis* in their ancestry also. The octoploids are native to the Americas and the Hawaiian Islands. Together they have the characters that by intercrossing have provided the basis for the present large strawberry industry. Dermen obtained an octoploid by doubling and redoubling an Alpine *vesca* by using colchicine *(Fig. 7–11)*.

To synthesize octoploids from lower chromosomal species, Ellis has suggested crossing hexaploids with pentaploids and looking for 8x seedlings from a union of hexaploid pollen, or egg, with unreduced pentaploid pollen, or egg. Other ways he suggests are:

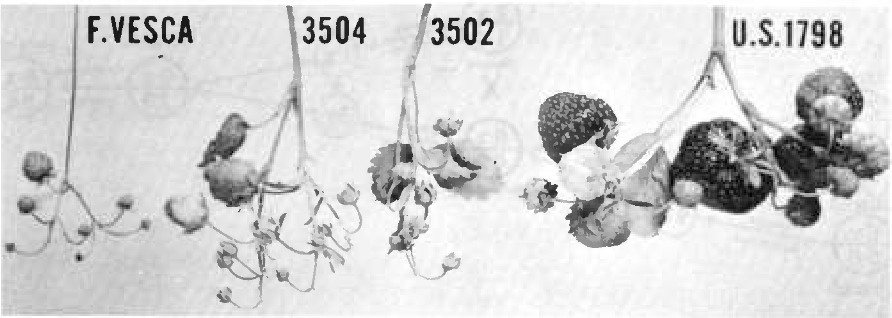
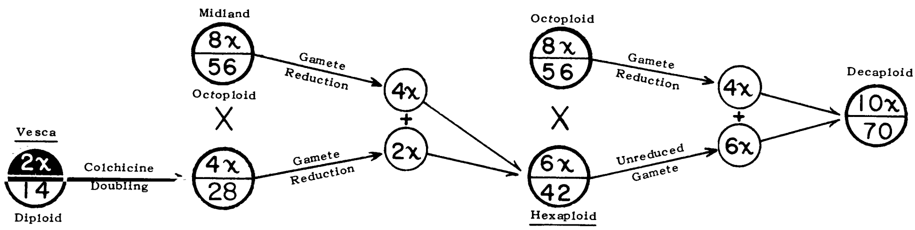
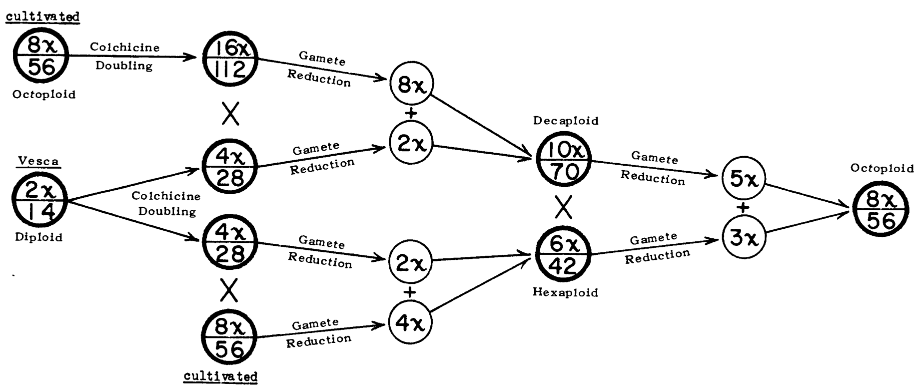


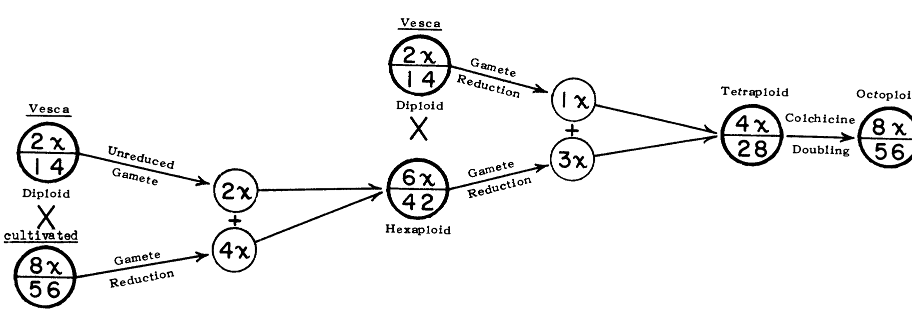
FIG. 7–9. Nos. 3504 and 3502 are selections from a cross of US-1798 (a pistillate selection of Ettersburg 904 x Howard 17 (Premier) with a tetraploid *Fragaria vesca*. They have 6 sets of chromosomes, 4 sets from US-1798 and 2 from a 4x *vesca*. When these were crossed with cultivated varieties, some seedlings were quite fertile and were found to have 10 sets of chromosomes, 2 from *vesca* and 8 from cultivated varieties. The 10x seedlings had the *vesca* fragrance. *(See Plate 7–2)*



A How to obtain A–Decaploids–2 parts *vesca* + 8 parts *cultivated*



B How to obtain Octoploids–3 parts *vesca* + 5 parts *cultivated*



C How to obtain Octoploids–4 parts *vesca* + 4 parts *cultivated*

FIG. 7–10. Three methods of obtaining decaploids and octoploids to combine the flavor and high aroma of the European wood strawberry with the size, flavor, and productiveness of the present cultivated varieties. Method A has been used by Darrow, Scott, and Dermen. Methods B and C have been tried by Ellis. *See Fig. 7–11* for another method used by Dermen.

2x x 6x, looking for non-reduction in both parents.

2x x 6x, looking for normal reduction division, but the 4x doubling in the embryo or by colchicine (*Plate 7–2b*).

2x x 6x, looking for normal reduction division to obtain a 4x, followed by unreduced egg and pollen uniting.

2x x 8x ⟶ 5x (unreduced) x 2x ⟶ 6x x 5x (unreduced) ⟶ 8x.

2x x 8x ⟶ 5x (unreduced) x 2x ⟶ 6x x 2x ⟶ 4x (unreduced) and doubled ⟶ 8x.

2x x 8x ⟶ 5x (unreduced and doubled) x 8x ⟶ 14x x 2x ⟶ 8x.

Ellis obtained octoploids from 6x (4x *vesca* x *F.* x *ananassa*) x 10x (4x *vesca* x 16x of cultivated). These octoploids were mostly vigorous and

FIG. 7–11. An octoploid obtained by doubling and redoubling the chromosome number of the everbearing Alpine *vesca.*

FIG. 7–12. An octoploid with 4 sets of chromosomes from *vesca* and 4 from the Dorsett variety obtained by H. Dermen. The plant was quite fertile.

FIG. 7–13. A decaploid produced by Dermen by doubling the chromosome number of a seedling of a 5-ploid *Fragaria vesca* (2x) x Dorsett (8x).

FIG. 7–14. A 12-ploid produced by Dermen by doubling the chromosome number of a seedling of 4x *vesca* x Dorsett by colchicine treatment.

highly sterile, completely female sterile, producing anthers with 3 per cent good pollen. Another octoploid was obtained from 2x *vesca* x hybrid hexaploid and the seed treated with colchicine to double the chromosome number. Fertility of the plant was not given. One octoploid was obtained from colchicine treatment of seed from *vesca* x *moschata* but this cross was not promising. Fedorova (1946) obtained octoploids, some of which were fully fertile, from selfing a partially fertile 7x seedling of *F. x ananassa* x *moschata.* Dermen (1938, unpublished) obtained a fertile octoploid by crossing Dorsett with an 8x *vesca* obtained by colchicine treatment of 4x *vesca* (*Fig. 7–12*).

9-Ploids (2n = 63)

No naturally occurring plants with chromosome numbers higher than fifty-six have been found. Scott obtained thirty-five plants all with sixty-three chromosomes (nine-ploid) from a ten-ploid x eight-ploid cross (1951). They were vigorous, but most were only slightly fertile. Another similar cross produced eighteen seedlings which were likewise only slightly fertile and he concluded that nine-ploid seedlings would be of little value. Fedorova (1946) and Ellis (1958) also obtained nine-ploids.

Decaploids (2n = 70)

Decaploids have been obtained by several methods:

4x *vesca* x 16x *virginiana*
4x *vesca* x 16x of cultivated varieties
6x (*vesca* 4x x cultivated varieties) x 8x varieties (see *Fig. 7–8* and *Plate 7–3b*).

Dermen (1938, unpublished) from the cross 2x *vesca* x 8x Dorsett variety obtained fully fertile 10x seedlings by colchicine treatment of seeds. He also obtained a decaploid by doubling the chromosome number of a seedling of a *vesca* x Dorsett (*Fig. 7–13*). Ellis (1958) reported obtaining five ten-ploid seedlings by treating with colchicine 2x *vesca* x *virginiana* and x *chiloensis,* and twelve twelve-ploid seedlings following treatment of 4x *vesca* crossed with the same species. The *vesca* x *virginiana* decaploids were highly fertile. In 1942 at Beltsville, Md., nearly sterile hexaploid seedlings (*Fig. 7–8*) (8x pistillate variety x 4x *vesca*) were crossed back to cultivated varieties (*Fig. 7–9*) and over seven hundred and fifty seedlings raised. About two hundred flowered in 1943. Seven of the more fertile were saved, of which Scott found one partially fertile with 2x = 49 (seven-ploid) and six fully fertile with 2n = 70 (decaploid) chromosomes. Most of the seedlings had spongy fruit like *vesca*, with large air spaces, and only six were selected for their large, firm fruit.

Scott (1951) repeated the cross octoploid variety (Midland) x 4x *vesca* and obtained eighteen probable hexaploids along with eight counted ones and eight octoploids; from a cross of an octoploid with two of these hexaploids he obtained thirty probable and twenty-three counted seven-ploids, eight octoploids, six decaploids, and one eleven-ploid; and from a decaploid x decaploid cross he obtained fifty-one probable and twenty counted decaploids. Decaploids x octoploids gave twenty-six probable and nine counted nine-ploids. Most of his hexaploids were very vigorous and failed to blossom or were sterile. He assumed that the ten-ploids originated as six unreduced gametes of the hexaploid uniting with the four reduced number of the octoploid (28) to make ten-ploid. Though he assumed that the fully fertile octoploid seedlings of his crosses resulted from self contamination, they may have resulted by apomixsis due to failure of the first reduction division of the egg-mother-cell.

Most interestingly, Scott, out of fifty-two fully fertile decaploid seedlings, obtained twenty-nine seedlings with a high per cent of good pollen. The plants were indistinguishable in foliage and growth habit from cultivated varieties. Although the fruit of most decaploid plants was spongy, all final selections had firm fruit with the high aroma of *vesca*; the fruit was not as large as that of the newer cultivated varieties. These decaploids had fourteen chromosomes from *vesca* and fifty-six from the cultivated octoploid. Fedorova (1946) also reported fertile decaploids.

It seems obvious, therefore, that it is entirely possible to breed decaploid strawberries with the high aroma of *vesca*. Breeding can be continued on the decaploid level by the continued combining of 2 genomes of *vesca* with 8 of the cultivated, while using different octoploid ancestors to increase the array of decaploids (*Plate 7–3a*).

16-ploids

Seedlings of cultivated octoploid varieties and of *virginiana* and *chiloensis* have had their chromosomes doubled to sixteen-ploids (Dermen and Darrow, 1938, Ellis, 1958). The 16-ploids of Ellis were hybridized with 4x *vesca* to obtain decaploids (see above). From colchicine treatment of seedlings of varieties crossed with *chiloensis,* Hull (1960) reported obtaining eighteen chimeral sixteen-ploid seedlings whose second apical cell layer was affected in sectors and nine seedlings where the second layer was affected in the entire crown. In a comparison of plants having sixteen-ploid at least in the second apical layer, with plants of the same seedlings having eight-ploid in the second layer, the sixteen-ploid had larger fruit, indicating a possible advantage of breeding at the sixteen-ploid level. Ellis (1958) obtained four sixteen-ploid selfed seedlings of *chiloensis,* five of *virginiana,* and three of cultivated varieties. The sixteen-ploid selfed *chiloensis* seedlings were very vigorous while those of selfed *virginiana* and of octoploid varieties were slower in growth. Seedlings of sixteen-ploid Huxley seedlings were, however, comparable in vigor to the normal Ettersburg 80 (Huxley). Dermen's (1938 unpublished) sixteen-ploid was from treating Dorsett seedlings with colchicine *(Fig. 7–15).*

Other chromosome numbers

Scott obtained one seedling with seventy-seven (11 genomes) chromosomes—an unreduced octoploid uniting with three sets from a reduced hexaploid. The seedling was only partially fertile and was less vigorous than the decaploids. Fedorova (1934) reported 7-, 8-, 9-, 11-, 12- and 14-ploids from *F. x ananassa* x *moschata* and 13x from the 7x crossed back to *moschata.* Ellis obtained three 11-ploid from a 6x hybrid x a 10x hybrid (*vesca* x *F. x ananassa*). Scott failed to find any aneuploids, but Ellis obtained odd chromosome numbered seedlings from the cross 4x *vesca* x 16x *virginiana,* most of which were stunted. He obtained 15-ploids from 5x x 10x (*vesca* x *F. x ananassa*), 18-ploids from 5x (unreduced) x 16x x *F. x ananassa.* Islam (1954) reported 12x, 13x, and 14x seedlings from open-pollinated F_1 of *vesca* x Bradley Cross (8x). Fedorova (1946) reported obtaining 12-ploid and 14-ploid from the selfed seedlings of *F. x ananassa* x *moschata.* Dermen (1939, unpublished) obtained a sterile 12-ploid (4x *vesca* x Dorsett) *(Fig. 7–14),* a fertile 32-ploid (of a 16-ploid Dorsett seedling) by colchicine treatment *(Fig. 7–16).*

Chromosome doubling

Chromosome doubling of germinating seedlings, especially of diploids, has been quite successful. Dermen and Darrow (1938) obtained tetraploid *vesca* by treating germinating seedlings with 0.2 per cent colchicine solution for twenty-four hours. A sixteen-ploid seedling of Dorsett was obtained by treating seedlings for five and six hours. Hull's sixteen-ploids resulting from colchicine treatment of seeds were chimeral. Ellis reported (1958) that 78 per cent of the surviving treated seedlings of *vesca* were tetraploid. He used 1 percent colchicine for twenty-four hours.

Octoploids or Decaploids

Ellis (1958) concluded that hybridization between the induced polyploid

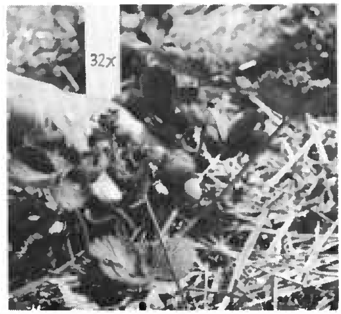


FIG. 7–15. A 16-ploid strawberry resulting from doubling the chromosome number of a seedling of Dorsett.

FIG. 7–16. 32-ploid resulting from the doubling of the chromosome number of a seedling of the 16-ploid Dorsett seedling with doubled chromosome number.

forms of *vesca* and cultivated varieties was a very favorable method for producing ten-ploids. Though Ellis pointed out that the ten-ploids of both Scott and himself produced smaller fruit than that of the present octoploids, this does not seem to warrant any conclusion as to the possible size of fruit borne by decaploids. The size of present cultivated varieties is the result of selection of the larger-fruited sorts from millions of seedlings and, given as long and as extensive a program, just as large-fruited decaploids with *vesca* aroma might be obtained as easily.

It would also seem entirely possible to obtain octoploids with the strong aroma of *vesca,* or of *moschata,* so that, by their use as intermediaries, stronger aroma could be transferred to cultivated varieties. This would seem more logical than the origination of separate groups of decaploid and octoploid varieties indistinguishable in appearance. Results so far indicate that decaploid x octoploid crosses would be sterile or nearly sterile, so that breeding would have to be continued within the separate groups. Far less confusion would result if all varieties were decaploid or octoploid.

8

The Strawberry Species

IN THE PRECEDING CHAPTER, results of genetical research with the strawberry are given; the four chromosome groups of species are described; and hybrids derived in various ways but having other chromosome numbers also are discussed. The subject of the two parts of this chapter is one of a narrowing scope of concern: the eleven species, placed in the four chromosome groups, are described in terms of gross morphology, then attention is focused on the three species out of the eleven, which compose the genetic source of the modern strawberry. Much of the material in this discussion of necessity must be of a technical nature. The modern strawberry is chiefly the result of crosses between two octoploids, with slight infusion of some characters of a third. These octoploids presumably came from ancient diploids, whether by doubling with unreduced gametes to tetraploid, and then doubling again to octoploid, or by some other process. Certainly the strawberry was not always the highly heterozygous plant that it now is. A trend to greater complexity and adaptability associated with higher polyploidy is evident. Out of the array of technical detail, patterns can be drawn; the causes of present weaknesses and reasons for the modern strawberry's strength can be traced to earlier sources.

Wild Strawberry Species of the World*

The genus *Fragaria* Linn. belongs to the Rose Family (*Rosaceae,* subfam. Rosoideae, tribe Potentilleae) along with its closest allies, *Duchesnea* Smith and *Potentilla* L. The wild species of strawberries fall into four groups, cor-

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related with their chromosome numbers, these being five diploids, two tetraploids, one hexaploid and three octoploids. Until recently (Ellis, 1961, Nature 190: 968) when sterile plants resulted from crosses with species of *Potentilla*, no certain hybrids with other plants had been obtained (though Burbank reported crosses with raspberries, *Rubus*).

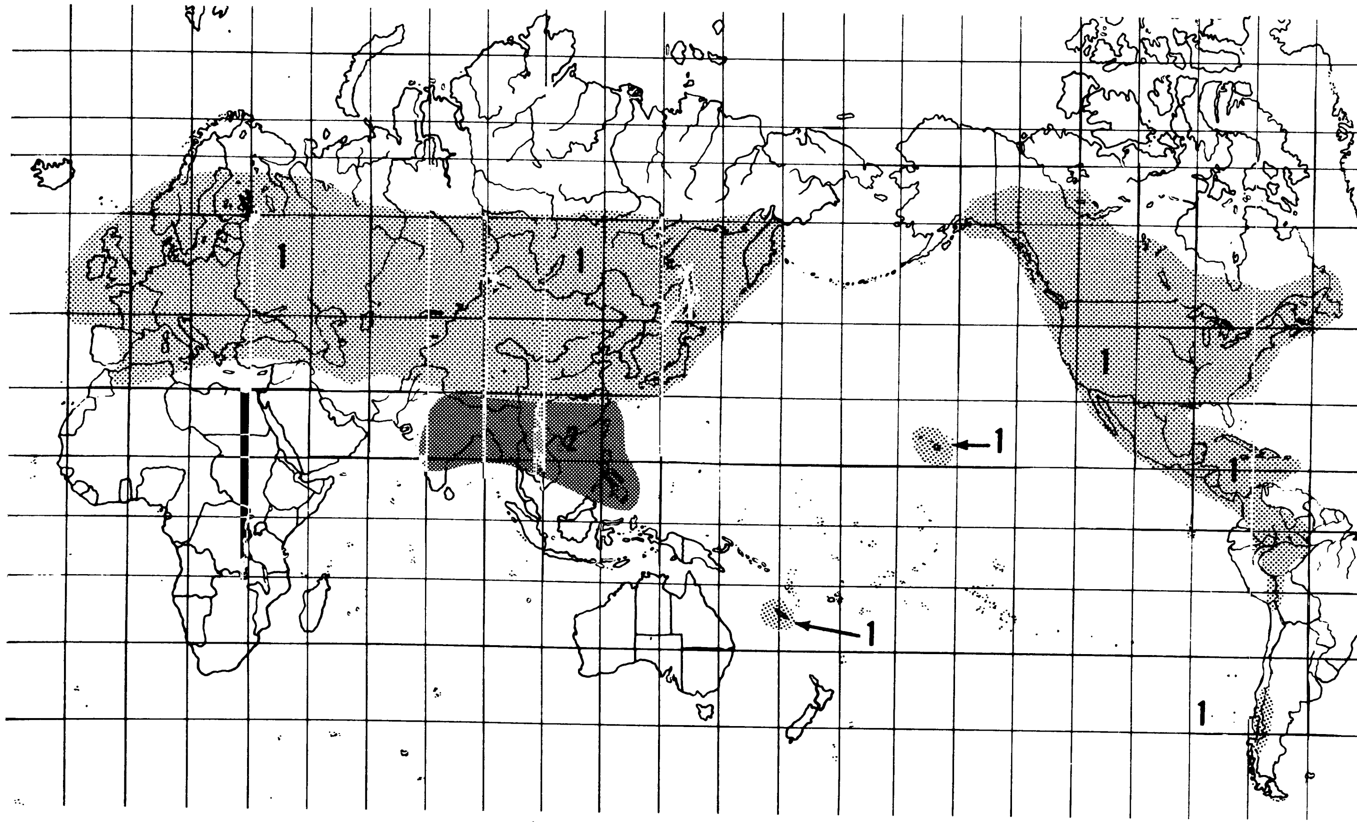
The cultivated varieties of commercial strawberries are almost all octoploids and are derived chiefly from the octoploids *F. chiloensis* and *F. virginiana,* usually recognized as *F. x ananassa.* A few have octoploid *F. ovalis* in their ancestry. A few "musk" varieties from the hexaploid *F. moschata* are grown very slightly, chiefly in Europe. A few of the very small-fruited, highly aromatic diploid varieties, derived from the European *F. vesca* and its everbearing form *F. semperflorens,* also are grown slightly. No cultivated varieties have come from the two tetraploid species, *F. orientalis* and *F. moupinensis* of Asia; none from the diploid species *F. daltoniana, F. nubicola* and *F. nilgerrensis* of India and Southeast Asia; none from the diploid *F. viridis* of Europe. The diploid species are the least variable and the octoploid, the most variable.

Many other strawberries have been described as new species, but most of them fall within the ranges of variability for the eleven species described below. The genetics and hybridity is unknown for most of these "species" at the present time and the exact placing of these species must await more extensive study and breeding.

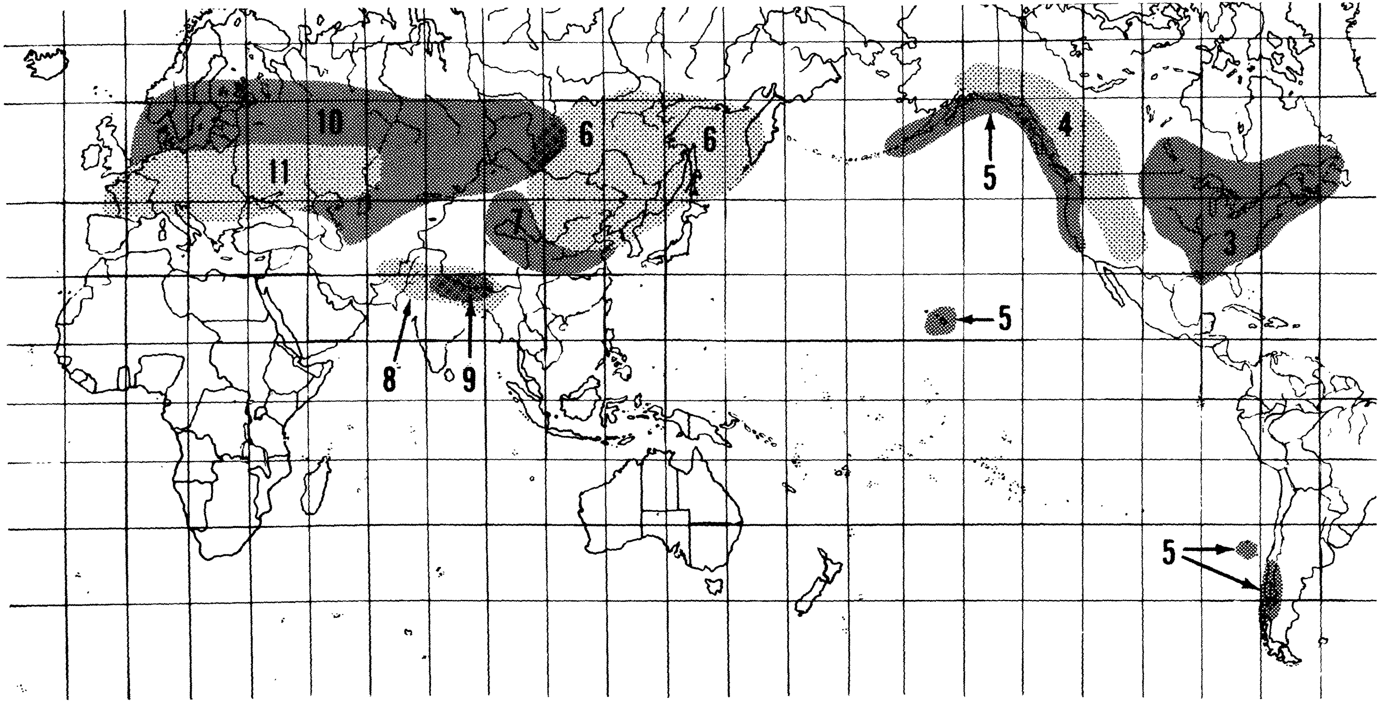
Diploids — 2n = 14 chromosomes

1. *F. vesca* L., 1753. (Sp. Pl., 494, *Fig. 8–1*). Wood Strawberry, *Frais. des bois.* This is the common wild woodland strawberry of Europe and Asia. It is the most widely distributed species of the genus, being circumpolar, appearing throughout Europe, northern Asia, North America and northern Africa. At present at least it is found southward in its botanical varieties at the higher elevations in the mountains of the West Indies, Mexico and South America. *Map 8:1.*

Plants are erect, 15–30 centimeters high, with runners; leaves are thin and light green with slender petioles, glabrous or becoming so above, lighter colored and lightly silky-hairy beneath, at least on the veins; leaflets are nearly sessile, rather small, relatively narrow, cuneate-ovate to rhombic-ovate with large sharp serrations; petioles and peduncles have few but generally spreading soft hairs; inflorescence is small, on usually tall inflorescences, equaling or exceeding the leaves, forking; flowers are about 1.3 centimeters in diameter, bisexual; fruit is hemispherical (in the type and seedling raised) flesh extremely soft, pulpy, generally aromatic to highly aromatic; seeds are small, raised, very prominent; calyx is reflexed, widely spreading.



Map 8–1.
1. *Fragaria vesca*
2. *Fragaria nilgerrensis*



MAP 8–2.

3. *Fragaria virginiana*
4. *Fragaria ovalis*
5. *Fragaria chiloensis*
6. *Fragaria orientalis*
7. *Fragaria moupinensis*
8. *Fragaria nubicola*
9. *Fragaria daltoniana*
10. *Fragaria viridis*
11. *Fragaria moschata*

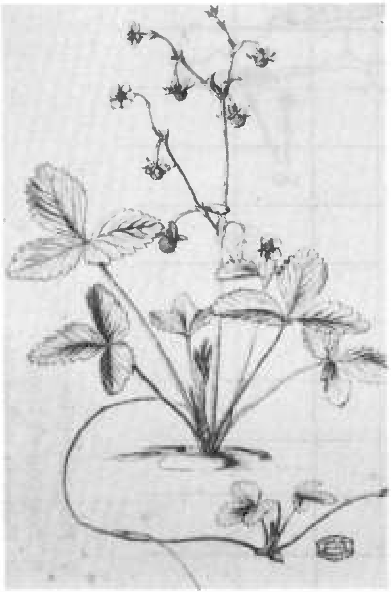


FIG. 8–1. *F. vesca.* (by Duchesne)

FIG. 8–2. *F. vesca semperflorens.*

Many allied species or varieties have been proposed, but they vary from the type only slightly: var. *californica* (Cham. & Schlecht., 1827) Staudt, 1962, with leaves silky below; *F. mexicana* Schlecht., 1839, with cuneate or oblong-obovate leaflets; ssp. *bracteata* (Heller, 1898) Staudt, 1962, and *F. insularis* Rydb., 1908, with the calyx spreading; ssp. *americana* (Porter) Staudt, 1962, with ovoid or subconic fruit red, occasionally white, with sub-appressed hairs on the peduncles and pedicels; var. *eflagellis* (Duch.) Ser., in DC., 1825, runnerless; *F. semperflorens* (Duch.) Ser. in DC., 1825, both runnered and runnerless (Alpine), flowering all summer; var. *monophylla* (Duch.) Ser. in DC., 1825, with a single leaflet; var. *muricata* (Duch.) Ser. in DC., 1825, with petals, stamens and pistils leafy (may be due to Aster yellows virus); var. *multiplex* (Duch.) Ser. in DC., 1825, with petaloid stamens.

Some forms, as *semperflorens, helleri* (Holz in Coult., 1896, *Fig. 8–2*) and *monophylla,* are known to differ by single genes from the typical *vesca.* Though not greatly variable genetically, *Fragaria vesca* is very adaptable and is the most widely native and naturalized of all the species of strawberries. The three most notable qualities for this strawberry are its adaptable plant, its highly aromatic fruit and its everbearing character. Its most undesirable characteristic is its extremely soft fruit, with large intercellular air-spaces throughout the berry. *Map 8:1–1.*

2. *F. viridis* Duch., 1766. (*Hist. Nat. Frais.*, 135). (Syn.: *F. collina* Ehrh., 1792, *F. bifera* Duch., 1790, *Fig. 5–5*). Capitan, Breslinge, Green strawberry. This species is native to most of Europe and to eastern (Caucasus) and central (Siberia) Asia; Canary Island, in open grassland hills, steppes, small forest areas and in brush. *Map 8:2–10.*

Plants are slender, with no or very few, short runners without nodes; leaves are deep green, silky beneath, thin, ovate to elliptic with curved and smaller teeth than *vesca*; inflorescence is erect, small; flowers are perfect, much larger than those of *vesca*, the petals are overlapping, usually somewhat yellowish-greenish when opening; stamens are longer and the anthers are larger than in *vesca*; fruit is green, greenish-white to red (in the sun) when ripe, small, the flesh firm, aromatic; achenes are set in pits; calyx is relatively large, long, hard to separate and clasping as in *chiloensis*, epicalyx spreading.

This species is native to grassy meadows and steppes and forest edges. Plants resemble *F. vesca* in general appearance. It commonly reflowers in fall. Though slightly variable, it seems rather distinctive and has no apparent characters that would improve present cultivated sorts, unless it may have a different everbearing or photoperiod response. Its firmness should be surveyed for new genes for that character. It is said to thrive on calcareous soils better than most species. *Map 8:2–10.*

3. *F. nilgerrensis* Schlecht., 1857. (ex J. Gay, *Ann. Sci. Nat.* IV, 8:206, *Fig. 8–3*). This vigorous species is native to southeast Asia from the mountains of the Philippines and central southern China (Yunnan, Hupeh, Szechman, Mingtsze) across to India, especially the hill region of southern India. *Map 8:1–2.*

Plants are often very robust; runners, petioles and peduncles are covered with long stout spreading hairs; leaflets are petiolulate, thick and rugose, round to obovate, small to medium, small serrations, very pubescent on leaves

FIG. 8–3. *F. nilgerrensis,* a 7-chromosome species of southern Asia. It is white-fruited, many-seeded, rather tasteless, and nearly sterile in crosses even with other 7-chromosome species.

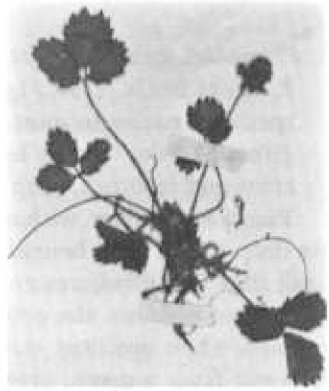


FIG. 8–4. *F. Daltoniana* from the Sikkim Himalaya area.

and petioles, dull green; inflorescence is small, three to four large flowers, white with a pink blush; stamens are short, pistils are very numerous; receptacle is large, flat; fruit is subglobose or depressed, white with a pale pink tint, tasteless to unpleasant, small, borne on erect pedicels; seed is small, numerous, set close together and in pits; calyx-lobes are large, often clasping, entire, spreading or suberect in fruit; forms with scarlet instead of white flowers and large instead of small fruits are known.

Little is known of the physiological characters of this species, such as its photoperiod and temperature responses. Its native distribution suggests it as one possible parent of *Duchesnea indica,* the false strawberry. Its large number of small seeds per fruit also suggests its value in breeding for large fruit, using as the other parent a variety with large fruit to furnish the most hormone per seed for swelling. Attempts to cross this have usually resulted in failure or in dwarf plants that do not fruit. However, in 1941 Nuremberg (1959) crossed *vesca* and *nilgerrensis* and obtained eleven normal and seven dwarf plants. Backcrossed to *nilgerrensis* he obtained seventeen hermaphrodites, four pistillate and seven male or sterile plants.

This diploid seems to have a tetraploid counterpart in most of its morphological characteristics in *F. moupinensis* from farther north and eastward (in China mainly). Some specimens from China (W. Hupeh) are huge (up to one foot tall with larger leaves and runners two feet long) and may prove to be octoploids of *F. nilgerrensis.*

4. *F. daltoniana* J. Gay, 1857. (*Ann. Sci. Nat.* IV, 8:204, *Fig. 8–4*). This species is native of Sikkim Himalayas at 10,000 to 15,000 feet. *Map 8:2–9.*

Plants have filiform runners, slender, hairy to nearly glabrous; leaflets are petiolulate, with few teeth; flowers are solitary; calyx lobes are toothed and bracteoles toothed, spreading in fruit; fruit is elongate-ovoid, or fusiform, often nearly 2.5 centimeters by 1.3 centimeters broad, bright scarlet, but with little flavor. *Map 8:2–9.*

This species seems to have only its relatively large fruit size and possible hardiness to recommend it to breeders.

5. *F. nubicola* Lindl., ex Lacaita, 1916. (*Jour. Linn. Soc. Bot.* 43:467). This species is native of the temperate Himalayas, 5,000-13,000 feet elevation. *Map 8:2–8.*

This species is described as being nearest *F. viridis*, although the specimens seen resemble *F. vesca*. Hooker (1879, Fl. Brit. India, 2:344) considered this species as a variety of *F. vesca*. Staudt (1959) by experimentation showed that *nubicola* was incompatible with *vesca*, and considered it a separate species.

Plants are slender, silvery, nearly glabrous, runners filiform, hairs on the petioles and the few-flowered peduncles densely silky appressed; calyx-lobes are narrow, spreading in the fruit.

No desirable characteristics for breeders have been noted.

Tetraploids — 2n = 28

6. *F. moupinensis* (Franch.) Card., 1916. (*Bull. Mus. Nat. Hist.* Paris, 22:397–398). Based on *Potentilla moupinensis* Franch., 1885 (1886). This is a species of eastern Tibet (Moupine), Yunnan and western China. *Map 8:2–7.*

The range of this species lies between that of *F. orientalis* to the north, of *F. nilgerrensis* to the south and of *F. nubicola* and *F. viridis* (*F. collina*) to the west. In leaf characteristics it is very similar to *F. nilgerrensis* and may represent a tetraploid form of that diploid species. Franchet had suggested that it resembled *F. collina* (*F. viridis,* a diploid), in which case it may be a tetraploid of that species. In this case the distribution of *F. viridis* would be extended eastward from central Siberia into western China.

Plants are slender; rhizome is short, stoloniferous; radical leaves are trifoliate, sometimes pinnately quinquefoliolate, with smaller leaflets on the petiole below, sericeous beneath, glabrous above; floriferous stem is more or less longer than the leaves, hirtellous, often two-flowered, sometimes as many as four-flowered, the peduncles are often with a smaller simple leaf or subtended by a bract, appressed sericeous; calyx is laciniate, the lobes are lanceolate-linear; petals white, subrotund, about twice as large as the calyx.

Although we know this species to be a tetraploid, its culture and cultivation in China is not too well known. More study and breeding of this species is needed before it can be properly evaluated.

7. *F. orientalis* Losinsk., 1926. (*Bull. Jard. Bot. Princ.* U.R.S.S., 25:70–72, *Fig. 8–5a, 8–5b*). This species lives in the forests and open mountain slopes, frequently in stony soil, of western Siberia, Mongolia, Manchuria and Korea. *Map 8:2–6.*

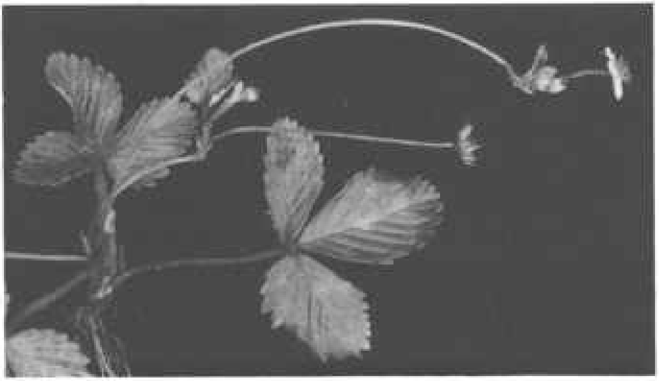


Fig. 8–5a. Plant of *F. orientalis* (from Manchuria) (2n = 28), with inflorescences which apparently started as runners, the tips of which were transformed into flower buds. Photo September 15, 1927.

Plants (in type) are only 3.8 centimeters high, the runners, long and slender; leaflets are ovate, rhomboid-shaped, with silky hairs below, almost sessile, with six to nine large, deep teeth on each side; inflorescence is few-flowered, bract at base of two to three leaflets; flowers are large, 2.5 to 3 centimeters, usually perfect, pedicel thick with thick spreading hairs; petals are up to 1 centimeter long, rounded, overlapping; sepals are tightly haired, lanceolate,

Fig. 8–5b. Berries of *orientalis* picked in the mountain near Hingan, Manchuria.

outer sepals linear-lanceolate, shorter than the petals, clasping; fruit is conical or round, red; seeds are sunken.

Its distribution in the cold dry areas of Asia suggest its hardiness and drought resistance. It is sometimes fall-fruiting in Maryland. Petrov, who found this species to be a tetraploid, later obtained an octoploid by colchicine treatment. This strawberry is used fresh in the Far East, but its culture is unknown.

Hexaploid — $2n = 42$

8. *F. moschata* Duch., 1766. (*Hist. Nat. Frais.,* 145, *Fig. 8–6*). (Syn.: *F. elatior* Ehrh., 1792). Musk, Capron, Capiton, Hautbois Strawberry. This species of strawberry grows in forests, under shrubs, in shaded places, in tall grass. It is found from Scandinavia and Atlantic Europe, eastward through central and eastern Europe (Volga, Dnieper, Don regions), and into Russia, Siberia (Region of Amur). *Map 8:2–11.*

Plants are vigorous, 10 to 40 centimeters tall, runners none or very few, even more vigorous than many *virginiana* and *chiloensis* clones; plants are dioecious but cultivated varieties usually perfect-flowered; leaves are broad, rhombic, strongly veined, rugose and very hairy; inflorescence is tall, umbel-like usually above the foliage; flowers are large, 20 to 25 millimeters in diameter; fruit is larger than in *vesca,* light red to dark dull brownish or purplish red, even greenish-red, irregular-globose (to ovoid), aromatic, strongly vinous or musky; achenes are raised; calyx is strongly reflexed.

Schiemann (1937) reported that hybrids of *moschata* and *viridis* are tetraploid and fully fertile and can hardly be distinguished from *moschata.* Most hybrids with the octoploid *virginiana* are completely sterile, but a small percentage of the seedlings produces fruit and a few seed, and such seedlings look like *moschata.* This species is very hairy, has great plant vigor, very large flowers and the most aromatic fruit of all. It has been cultivated to some extent since about A.D. 1600 for its vinous flavored fruit, liked by some, disliked by many. It is like the muscat grapes, which, with a slight muskiness, are considered by many the most delicious of grapes, but seedlings of which may have such a strong flavor as to be inedible. Notably most of the berries ripen together in *F. moschata.*

Octoploid — $2n = 56$

9. *F. virginiana* Duch., 1766. (*Hist. Nat. Frais.,* 204, *Fig. 5–6*). Scarlet or Virginian strawberry. This is the meadow strawberry of eastern North America from Louisiana and Georgia to Hudson Bay and the Dakotas. It is an octoploid with fifty-six chromosomes while the only other species of

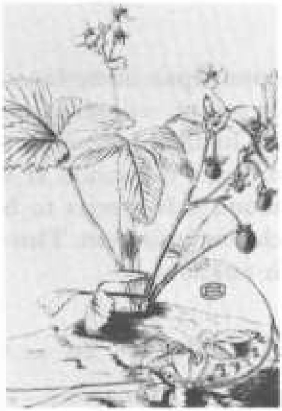


FIG. 8–6. *F. moschata.* (by Duchesne)

eastern North America is the diploid, *F. vesca* ssp. *americana* (Porter) Staudt, 1962 (*Canad. Jour. Bot.* 40:872) found in woodland and shady places from Newfoundland and Manitoba south to Virginia, a much more slender plant. *Map 8:2–3.*

Plant is from a subsimple caudex at end of a simple rhizome, making runners early; leaves are relatively thick, medium to dark green, usually petiolate, coarsely toothed, obovate to oblong; petioles are with spreading hairs; terminal leaflet is 1.5 to 10 centimeters long, with four to eight pairs of teeth; inflorescence is variable, basal to high branching, hairy; flowers are large, dioecious, occasionally polygamous, the strictly pistillate flowers much smaller than the staminate, 0.6 to 2.5 centimeters broad; borne below, with or above the foliage; calyx-lobes are 4 to 11 millimeters long; fruits are 0.5 to 2 centimeters in diameter, about twice the size of *vesca,* subglobose to ovoid, light to deep red, mostly scarlet, flesh usually white, pulpy, acid, aromatic, sometimes astringent; achenes are 1.3 to 1.6 millimeters long, sunk in deep pits below the surface.

The Virginian strawberry is quite a variable species and several botanical varieties have been described: var. *australis* Rydb., 1898, with nearly sessile leaflets; var. *illinoensis* (Prince) Gray, 1867, (var. *grayana* (Vilm.) Rydb., 1898), very vigorous, with spreading hairs on pedicels, terminal leaflets 5 to 10 centimeters with eight to fifteen pairs of teeth; var. *canadensis* (Michx.) Farw. with oblong-conic fruits; *F. multicipita* Fern., 1908 (many crowned), may be virus-affected plants (Gaspé); var. *terrae-novae* (Rydb., 1898), Fern. & Wieg., leaflets with short petiolules, scapes and petioles appressed to strigose-pubescent to glabrous; var. *glauca* S. Wats., 1871, with sparse pubescence.

Many notable characteristics appear in the various regional wild clones: from northern North America comes extreme resistance to low temperatures as well as to high temperatures; from southern United States comes the adaptation to short photoperiods; from the northern Great Plains comes drought resistance. Furthermore, the flowers range from susceptible to very resistant to frost. It has generally aromatic, rather acid, soft fruits, but firm selections can be obtained. Many selections cap very easily; many ripen all their berries nearly at the same time.

10. *F. x ananassa* Duch., 1766 (*Hist. Nat. Frais.,* 190, *Fig. 8–7*). (Hybrid between *F. chiloensis* and *F. virginiana; F. x ananassa* nm. *cuneifolia* (Mitt. ex Howell) Staudt, 1962, is a nothomorph). (Syn.: *F. chiloensis* var. *ananassa* (Duch.) L.H. Bailey, 1925; *F. grandiflora* Ehrh., 1792).

Most of our common cultivated strawberries with large fruits belong here. Duchesne (1766) had suggested *ananassa* as a hybrid between *F. virginiana* and *F. chiloensis. F. x ananassa* strongly resembles *F. virginiana* var. *illinoensis* but has heavier and slightly rugose foliage, coarser and blunter teeth, and more superficial pits of the larger fruit. It is often found escaped from cultivation along woodsides and railroads. Specimens have been seen from Europe, North America, Russia, Hawaii, Japan and China.

11. *F. chiloensis* (L.) Duch., 1766. (*Hist. Nat. Frais.,* 165, *Fig. 8–7*). This species is based on cultivated plants taken from Concepción, Chile, to France in 1714. This very variable species is abundant along the beaches of the Coast of Chile (but often somewhat inland) and in the Andes Mountains from the latitude of Concepción south 700 miles to below Coyhaique, even on the eastern slope in Argentina; in North America it is confined to the beaches from near Santa Barbara, California, north 3,000 miles to the Aleutian Peninsula of Alaska, but never inland off the beaches, as in Chile; in Hawaii it is on the mountain tops at 5,000 feet elevation up. Though cultivated in Peru and Ecuador and formerly in Mexico, the cultivated varieties of *F. chiloensis* were all from Chile and differ from most of the species in being more hairy, in having dull leaves that are glossy only at times, and in often having perfect flowers and large fruits. All these characters can be found in wild plants both in Chile and occasionally in California. *Map 8:2–5.*

FIG. 8–7. *F. ananassa.* (by Duchesne)

Plants are low, stocky, usually entirely silky, runners stout, short to long often perennial, mostly forming after fruiting; petioles are stout, 2 to 20 centimeters long; leaves are very thick and leathery, usually glossy, dark green, tending to be evergreen, large to small; leaflets are broadly obovate and the margin crenate with short rounded teeth above the middle, pale and silky beneath, petiolulate to nearly sessile; inflorescence is extremely variable, mostly silky haired, basal to high branching, few to many flowered, dioecious with occasional hermaphrodites, especially in Chile; flowers are mostly very large, 20 to 35 millimeters broad, borne below, with and above the foliage; petals are broadly obovate; calyx is clasping after petal-fall, quite silky; fruit is dull brownish red (especially on the sunny side) to pale translucent pink, flesh white, firm, mild, usually lacking in flavor, hemispherical to oblate, 15 to 20 millimeters in diameter, separating from the calyx very easily in most, usually larger than in other species; achenes are mostly raised above the surface, but may be in shallow pits, dark.

Many variants can be found along the coast and in the mountains of Chile, along the Pacific coast of North America and in the mountains (above 5,000 feet) of Hawaii: ssp. *chiloensis* f. *chiloensis* Staudt, 1962, cultivated in South America, especially in Chile; ssp. *chiloensis* f. *patagonica* Staudt, 1962, in Chile and Argentina; ssp. *lucida* (E. Vilm.) Staudt, 1962, Washington to California; ssp. *pacifica* Staudt, 1962, California to Aleutian Islands; ssp. *sandwicensis* (Decaisne) Staudt, 1962, Sandwich Isl., Hawaii. (This name cannot stand because of *F. chiloensis* var. *sandwicensis* Deg. & Deg., Fl. Hawaii, 1961).

This species is notable for its drought tolerance; adaptability to low temperatures (although some plants are not); adaptability both to long and to short photoperiods; resistance to cold when in flower and fruit in the Andes Mountains of Chile. Also notable, the inflorescences are often very large in Hawaii, the fruits usually cap easily, and are often quite firm. The limiting characters are susceptibility to leaf-scorch, plants usually tender to very tender to both cold and heat; berries dull red to white, with white flesh, dark seeds and very little flavor. Some clones found in California are reported as being highly flavored.

Fig. 8–8. *F. ovalis* in a hillside pasture near Corvallis, Oregon. This clone is chiefly male but some primary flowers are set.

12. *F. ovalis* (Lehm.) Rydb., 1906. (*Bull. Torr. Bot. Club,* 33:143, *Fig. 8–8*). Based on *Potentilla ovalis* Lehm., 1849. This species includes all the pasture and meadow strawberries from northern New Mexico in the mountains to Montana west to the beaches of California, and north to Alaska. It is fully fertile with *F. virginiana* to the East and with *F. chiloensis* of the beaches to the West and merges with those species on both boundaries. *Map 8:2–4.*

Plants are more or less glaucous; leaves are usually thicker than in *virginiana,* but much thinner than in *chiloensis,* usually with a bluish sheen, silky beneath; leaflets are subsessile, or short-petiolulate, oblong or cuneate, 2 to 3 centimeters long coarsely toothed above the middle; inflorescence is rather short, not over 5 centimeters high, usually below the leaves, flowers 1 to 1.5 centimeters in diameter, petals obovate, exceeding the sepals by a half; fruit is pale red, usually soft to extremely soft, subglobose, about 1 centimeter in diameter.

This species is as variable as *chiloensis* and *virginiana* are. Introgression of characters of *chiloensis* such as thicker leaves, firm, dark-seeded, dull fruit and clasping calyx can be found in *ovalis* as much as 100 miles from the beaches inland in Oregon, and of the characters of *virginiana* such as the thin leaves with toothing below the middle, with bright scarlet berries with reflexed calyx in Colorado and Wyoming, west of the range of *virginiana.* Hybrids between *chiloensis* and *ovalis* and backcrosses and segregates are abundant where *ovalis* meets *chiloensis* at the beaches. *F. ovalis* is notable for its drought tolerance, its resistance to low winter temperatures, its reflowering and everbearing character in very many clones, its early ripening, its flower-resistance to frost and its earliness, and can contribute these qualities to future strawberries.

Characters of *Fragaria virginiana, ovalis* and *chiloensis* in Strawberry Varieties

By 1920 strawberry breeders in the United States were interested generally in the systematic crossing of varieties and the use of qualities of the native species in breeding. In his breeding, A.F. Etter in northern California was using *F. chiloensis* (Clausen, 1915) which he had collected along the California coast (Etter's catalogue 1920), as well as a South American *chiloensis;* in 1900, Hansen and Haralson had begun their crossing of cultivated varieties with selected wild Virginians from Manitoba and North and South Dakota; Fletcher had recently published his book, *The Strawberry in North America* (1917) and also his monograph "North American Varieties of the Strawberry" (*Va. Tech. Bul.* 11, 1916); at the old U.S. Department of Agriculture Research Farm across the Potomac River in Virginia, W.F. Wight, during the years just before 1920, had established for study a planting of *Fragaria* species from various botanic gardens and other places of the world; D.N. Shoemaker, about 1916, selected superior wild plants of *virginiana* in the mountains of western North Carolina, and others made selections in Michigan, Minnesota, and elsewhere for Wight's collection; Georgeson, beginning in 1905, was using selected *chiloensis* and *ovalis* in his Alaskan breeding work; in 1920–1921 Popenoe surveyed the Chilean strawberries of Ecuador and Chile (*Jour. Her.* 1921) and sent plants to the United States; and Hedrick and associates were working on the monograph *The Small Fruits of New York* (1925).

By this time it seemed quite clear from Fletcher's book that *F. chiloensis* and *F. virginiana* were the two chief, if not the only, parent species of the cultivated strawberry. Then came the questions. Had the strawberry during the hundred years of breeding and selection in North America evolved toward *chiloensis* or toward *virginiana,* and had we lost valuable qualities in the process? Were there other qualities in the wild parent species which might be of value in cultivated varieties; qualities such as resistance to "black root" and leaf spots, to the humid semi-tropics, and to drought, resistance of flowers to frost, and of berries to rot? Could wild species furnish such qualities as hardier crowns to make mulching unnecessary, or flowers with more pollen and less sterility, to reduce nubbins and produce larger berries? Later, questions arose as to possible sources of resistance to red stele, Verticillium wilt, and viruses both in wild species and in cultivated varieties.

For the breeding work of the U.S. Department of Agriculture begun in 1920 at Glenn Dale, Md., the selections of *virginiana* made by Shoemaker proved especially interesting, for there were very productive pistillate and perfect-flowered selections among them. Crosses of these selections with cultivated varieties yielded seedlings which fruited as early as 1922 with some as large as the cultivated parent. Fifty or more of his varieties and hybrids, derived in part from *chiloensis* selections, were obtained from Etter and grown at Glenn Dale. A considerable population of crosses of many of these with eastern varieties was fruited at Glenn Dale, also as early as 1922. In 1923 as many as 1,268 seedlings with one parent *chiloensis* were set in the field. In addition many varieties were imported from Europe and used in breeding beginning in 1923. Some of these varieties, such as Louis Gauthier, White Pineapple, and La Constante quite evidently were derived in large part from *chiloensis.* During the years 1927 and 1928 through the courtesy of the Forest Service, forest rangers collected and sent about seventy-five lots of selected plants of *F. ovalis* from many parts of Western United States. Some of these were used in breeding. Before 1930, Prof. Schuster, at the Corvallis Station in Oregon, made many crosses of *F. chiloensis* and *F. ovalis* with cultivated varieties. From July 1930 to June 1932, further collections by Darrow were made of *chiloensis* along the coast of California, Oregon, and Washington, and of *ovalis* from the inland areas, to be grown at the Oregon State Station. Later, selections of *ovalis* were obtained and used from the extensive collections at the federal station at Cheyenne, Wyoming (*Plate 8–1*). G.F. Waldo (of the U.S.D.A.), who has been stationed at Corvallis since 1932, has made many additional collections of *chiloensis* and has used them in his breeding ever since. Of 765 selections made by him in his breeding between 1941 and 1956, 443 (about 60 per cent) were only two or three generations removed from the wild. A collection of *virginiana* selections from the wild in different areas of North Dakota was furnished by A.F. Yeager, and has been used in breeding both for frost-resistant flowers and basal flower-cluster branching habit. In 1957 over one hundred collections of selected clones and many seed collections were made by Darrow in Chile and some of these were used (*Plate 8–1b*). Many state and provincial stations have made selections of these species, especially, California, Washington, Alaska, British Columbia, Alberta, North Dakota, South Dakota, Iowa, Minnesota, New Hampshire, Louisiana, and Missouri.

Three Octoploid Species

The commonly accepted classification of the wild octoploid strawberries is that of three species—*F. virginiana,* the meadow strawberry of eastern North America, from the Atlantic seaboard west to about the western boundary of the Dakotas; *F. ovalis* (includes also most of *glauca, cuneifolia* and *platypetala*) from Montana, Wyoming, Colorado, and northern New Mexico west to the beaches of the Pacific and to Alaska; and *F. chiloensis* along the Pacific beaches, rarely half a mile inland, from Alaska to south central California, along the beaches of south central Chile, and eastward into the Andes Mountains, extending to include their Argentine side; and on the volcanoes of the Hawaiian Islands.[1] *F. ovalis* is completely interfertile with both *chiloensis* and *virginiana* and there has been an introgression of characters of *virginiana* into *ovalis* in its eastern range and of *chiloensis* into *ovalis* from the Pacific coast inland. Where the latter two species meet along the beaches of the Pacific coast the characters of *chiloensis* are most in evidence, while inland those of *ovalis* predominate. It would seem that some characters of *ovalis* prevented it from becoming dominant on the beaches, and some characters

[1] Staudt (1962) does not give *ovalis* specific rank but keeps only two octoploid species. On Hawaiian Mts. a form *sandwicencis* may be a hybrid or a separate species; a visit to Hawaii (Dec. 1965) suggests this to be derived from *chiloensis* x *ovalis* and carried by birds from Alaska. It has sharply toothed leaves and often at least very large inflorescences with relatively large berries.

of *chiloensis* prevented it from becoming dominant inland. All three octoploid species in the wild are almost entirely dioecious, but as early as 1624 perfect-flowered *virginiana* were selected and taken to Europe. The Indians of Chile also had selected perfect-flowered plants of *chiloensis* which they were growing when the Spanish came to the Concepción area of Chile in 1557. In Chile, besides the many "staminate" or male *chiloensis* that set from one to several berries to the inflorescence, a wild variant has been found at various places, in form much like the cultivated Red and White Chilean, which are grown in Chile today, but with duller, very hairy, thinner leaves and often perfect flowers. This variant also has been found in the south-central coastal area of California.

In the last sixty years, *F. ovalis* has entered into cultivated strawberries through the work of Georgeson in Alaska, Etter in California, Powers in Wyoming, and the federal-state work in Oregon. The Washington variety (one parent of Robinson) is considered to have *ovalis* as one parent. The Molalla of Waldo in Oregon and the Ogallala of Powers in Wyoming also have *ovalis* in their parentage.

Differences between *chiloensis* and *virginiana*

The plants of *F. chiloensis* and of *F. virginiana* are very different in appearance, chiefly due to the glossy, dark green, thick, leathery leaves of the former (*Fig. 8–9*) and the non-glossy, light green, hairy, thin, coarsely toothed leaves of the latter (*Fig. 8–10*). The leaves of *chiloensis* are relatively evergreen; its crowns, petioles, peduncles, and runners are usually relatively stout, while those of *virginiana* more slender. *Chiloensis* has silky fine hairs, while *virginiana* has coarse hairs. *Chiloensis* usually blossoms much later

FIG. 8–9. *F. chiloensis* (male) growing in sandy loam, Newport, Oregon.

FIG. 8–10. A pistillate clone of the wild strawberry of eastern North America, *F. virginiana*. (Photo by Crandall)

FIG. 8–11. *F. chiloensis* thrives and produces long runners on the sand dunes of the Pacific Coast.

(twenty to forty days); its flowers are usually larger; its stamens are larger with more pollen; the ripe berries (*Plate 8–1b*) have a clasping calyx, are larger, with dull purplish-red skin, white flesh and dark seeds that are raised, or at most slightly imbedded; the berries have only slight flavor and aroma. Fruit of *virginiana* has a recurved calyx, is aromatic, scarlet to crimson in color, often red-fleshed with seeds sunken in pits (*Plate 8–1c*). *Virginiana* is quite tolerant to both cold and the humid heat of the Eastern United States, while *chiloensis* usually cannot survive this heat and cold. In general, most *chiloensis* seem much more susceptible to cold, even though the species is very abundant in the fields about Cohaique, Chile, and other places in the Andes Mountains, as well as along the coast of Alaska, where very low temperatures in winter are the rule. On the other hand, *chiloensis* seems to endure drought far better than most *virginiana* varieties and survives the dry spells in dunes and sandy beaches of the Pacific Coast (*Fig. 8–11*). *Chiloensis* leaves seem adapted to drought conditions, for the thickness of their upper surface cuticle and epidermal cell wall runs about 6.9μ (*Fig. 8–12*), while that of the *virginiana* is 4.3μ. The thickness of the cell wall or the lower epidermal surface is 3.9μ for *chiloensis* and 1.6μ for *virginiana*. In *chiloensis* the entire wall of the upper epidermis is thickened.

F. ovalis vs. *chiloensis* and *virginiana*

Fragaria ovalis characters are in general so intermediate between *chiloensis* and *virginiana* that comparisons of contrasting characters are not so easily listed. Its characteristic bluish green foliage is rarely seen in *virginiana* and either is masked by the deep green or is not present in *chiloensis*. Its leaflets are much more wedge-shaped than is usual of those of the other two species. Two notable characteristics are the especially everbearing character of many of the *ovalis* at lower elevations and the drought resistance and hardiness of its plants.

The characters of the three species may be contrasted as follows:

	chiloensis	ovalis	virginiana
Leaves	—thick, leathery	thick to thin	thin
	thick cuticle and epidermal cell-wall		thin cuticle and epidermal cell-wall
	deep-set stomata		shallow-set stomata
	strongly netted		not strongly netted
	glossy	dull	not glossy
	dark green	bluish green	light green
	evergreen	dying with cold	dying with col
	silky	silky to hairy	hairy
	short teeth	coarse teeth	coarse teeth
Petioles	—thick	slender	slender
	not channeled		broadly channeled
Crown	—thick	less thick	less thick
Flowers	—large	medium	medium to small
	large stamens		medium stamens
Fruit	—dull red	medium red	scarlet to crimson
	seeds slightly sunken	sunken in pits	sunken in pits
	calyx clasping when ripe	clasping to reflexed	reflexed
	slight flavor	mostly strong flavored	strongly flavored and fragrant
Plant	—drought resistant	drought resistant	less resistant to drought
	heat susceptible	heat resistant	heat resistant
	low temperature susceptible (except in Andes)	low temp. resistant	low temperature resistant
	non-everbearing	often everbearing	rarely everbearing

Handmade F_1 hybrids between the *chiloensis* and *virginiana* species show hybrid vigor, the plants being far larger than those of either species. The fruit of hybrids, though far larger than that of the typical wild species, is not so much larger than that of the White Chilean grown in Chile, nor that of the Ambato, the Red Chilean as grown in Ecuador. However, the hybrids of cultivated varieties with *chiloensis* show still greater hybrid vigor than the species-hybrids themselves. The hybrids of cultivated varieties with *virginiana,* on the other hand, show less hybrid vigor than the crosses of cultivated forms with *chiloensis*. Even so they still show more vigor than most of the species-hybrids (*Plate 8–2*).

It would seem that during the past hundred years the wild strawberry of much of eastern North America has become extensively hybridized with the cultivated. Birds have carried seed of cultivated varieties to the wild, where the best adapted of the seedlings survive. Bees have carried pollen from cultivated to wild strawberries. Hybrids growing from such seed often have larger leaves and fruit than the pure wild *virginiana*. Some characters of cultivated sorts can be found in wild strawberries quite widely. Relatively, large-fruited and thick-leaved clones are common among wild strawberries of Eastern North America; many of these have been transplanted to gardens; and many varieties have been named from wild plants. Even a recent "Register of Fruit Varieties" (Brooks & Olmo, 1960) lists eight varieties as chance seedlings and five others as of unknown parentage. All of these thirteen would certainly have more characters of *virginiana* than of *chiloensis* in their ancestry, but to have large enough and firm enough berries for naming none could be entirely *virginiana*. Even in Western Oregon and Washington some natural hybrids between cultivated varieties and *ovalis* are being found (*Fig. 8–13*).

When large numbers of seedlings are grown at one place as in Maryland, those selected to be tested as varieties will naturally be the ones best adapted to that environment. Most strawberry breeding has been done in eastern North America where *virginiana* is native or, if in Western States, it has been done inland from the beaches and not where *chiloensis* is native. Hence it is to be expected that selections for naming contain more *virginiana* than *chiloensis*. Few American varieties resemble *chiloensis* closely; many are close to *virginiana;* all seem intermediate in some respects.

Characters of *chiloensis* and *virginiana* in cultivated varieties

A chart estimating the characters of these two species as they appear in a number of cultivated varieties will illustrate the differences in their genetic makeup in respect to the two species. F_1 seedlings, if grown both in Maryland and along the beaches of the Pacific Coast, would probably show this contrast

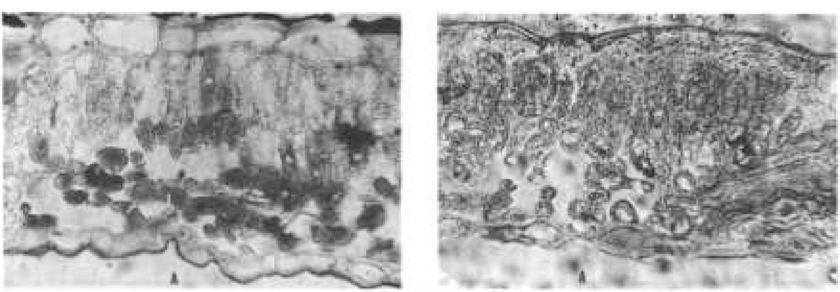
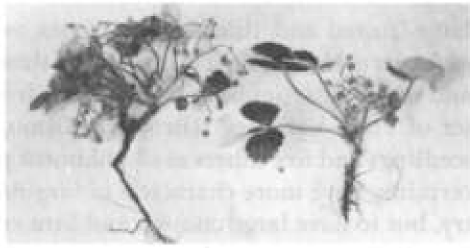


FIG. 8–12. (*left*) Cross-section of leaf of *F. chiloensis*. Note the relatively thick cuticle and cell walls of upper epidermal layer and the deeply placed stomata of the lower surface, both characteristics valuable for drought resistance. (*right*) Cross-section of leaf of *F. virginiana*. Note thinner cuticle of epidermal layer and less deeply placed stomata.

FIG. 8–13. Large-clustered *F. chiloensis* from the coast of Oregon; (*right*) 14 flowers, leaves above flowers; (*left*) 3 clusters with 23, 22, and 24 flowers—one berry developing. More than 40 flowers to the cluster have been counted.



of some characters, as well as the masking of others and the intermediateness of still others. The best test to show the true characters of varieties in relation to the species would be to compare plants grown on the Pacific beaches with the same kinds grown inland. Judging the characters as they appear in our plots is the best we can do now. The following table gives ratings of five varieties for several characters of *chiloensis.*

Rating of 5 varieties for characters of *chiloensis.* 100 = full *chiloensis* character. 0 = none of *chiloensis,* all characters from *virginiana.*

Characters	Fairfax	Earlidawn	Blakemore	Howard 17	Missionary
Leaf thickness	80	40	50	60	30
" glossiness	70	40	60	60	20
" toothing	30	20	20	20	10
" evergreenness	80	30	40	40	30
" hairiness	20	40	20	20	20
Flower size	80	30	30	30	30
Stamen size	80	20	20	20	30
Fruit color exterior	70	20	20	20	30
" " interior	0	0	0	20	20
" firmness	100	80	100	60	70
" flavor	40	30	30	30	30
" late-ripening	50	0	0	0	0
Seed color	30	10	0	0	20
" position	100	60	80	60	80
Calyx clasping	90	0	0	0	0
Plant draught resistance	50	50	80	50	50
Plant heat susceptibility	30	20	0	50	0
Plant cold susceptibility	20	10	10	10	20

According to this rating Fairfax expresses 57 percent of the characters of *chiloensis;* Earlidawn, 28 percent; Blakemore, 31 percent; Howard, 17, 31 percent; and Missionary, only 27 percent. This would seem to confirm the idea that, due to selection in an environment best suited to *virginiana,* North

American varieties have more characters of *virginiana* in them than of *chiloensis*. Yet Fairfax, which seems to have the most *chiloensis* in its characteristics of eastern varieties succeeds well in a rather wide area and it has been successfully used as a parent in North America, Japan, and Europe. Greater use of *chiloensis* in breeding for superior varieties seems indicated.

9

Early Varieties of the Americas, 1800–1900[1]

AS THE PRECEDING CHAPTER INDICATED, modern strawberry varieties have descended from the crossing of *F. virginiana* with *F. chiloensis*. The transition from these native species to the modern varieties now available is a long process, involving the hybridization of the two species, then hybridization of their descendants, and finally some back-crossing to the original parents and reselection. There has been almost no ingression of *F. ovalis* characters and that quite recently. Robinson in the United States is the outstanding example, being ¼ *ovalis*. This chapter describes the important early varieties of the Americas, some of which were closely related to the native species, from which all of them descend. These varieties composed the foundation of commercial strawberry production in the Americas in the nineteenth century, and many also appear in the ancestry of the strawberry varieties of today.

In the United States commercial strawberry production began about 1800. Its beginnings were small and its progress slow. Only selections of the native *F. virginiana* were raised commercially; most fruit came from plants growing wild in meadows and pastures. This continued to be the case until 1840, and then the change was only minor. Hovey was grown along with the native selections, its acreage equalling perhaps one tenth of that set to the native sorts. In 1858, however, came a real change and a great advance. In that year, the native Virginian varieties began to disappear, and their place was taken by Wilson, a fully hardy, large-fruited strawberry, precursor of the modern ones. This innovation expanded the industry from 1,400 acres to more than

1 See Appendix II, for Chronology of Strawberry varieties in the United States.

100,000, grown not just near the large northern cities, but as far away as Oregon, Louisiana, and Florida. Since then the history of strawberry varieties is comprised of an endless series of substitutions of new and better varieties for old ones, which then disappear, or survive only as the parents of more sophisticated plants which take their place. The major varieties that supplanted the Wilson were Crescent, Sharpless, Aroma, Dunlap, Marshall, Klondike, and Missionary, and these in turn have been supplanted largely by Blakemore, Tennessee Beauty, Klonmore, Headliner, Albritton, and Florida Ninety in the South; Howard 17 (Premier) Catskill, Sparkle, Robinson, Pocahontas, Jerseybelle, Dixieland, Earlidawn, Midland, and Armore in the North; and Northwest, Shasta, and Lassen on the Pacific Coast. Hundreds of other varieties have been grown.

A list of early varieties of the Americas properly includes (1) the Chilean, the original variety of *chiloensis,* which was being cultivated in Chile in 1714 when Frasier took plants of it to France; (2) Ambato which has been raised near Ambato, Ecuador, probably for about 400 years; (3) Methven Scarlet, one parent of the Hovey; (4) Hovey, notable both as the first American strawberry resulting from planned crossing, and as an ancestor of nearly all of our present varieties; (5) Ross Phoenix, the male parent of the Wilson; (6) Wilson, which was the first modern strawberry and which alone changed the strawberry from a minor to a major crop; (7) Large Early Scarlet, or New Jersey Scarlet, two early-ripening named varieties of the native Virginian strawberry; (8) Neunan, a probable seedling of Wilson adapted to southern states; (9) Crescent, a seedling probably of Hovey crossed with New Jersey Scarlet, through which most American varieties trace their ancestry back to Hovey and to the Virginian; (10) Charles Downing, from Kentucky and (11) Sharpless grown with Crescent to pollinate it and important in Europe (Poland) even today.

The earlier varieties, such as Hovey and Wilson, which at first were grown along with the native Virginian sorts and later replaced them, have a peculiar and interesting derivation. Although the strawberry is a gift of the Americas, most of its early development, as Miss Lee describes, took place in Europe. The ultimate sources, the Chilean and Virginian, were native to the Americas, yet the parents of the first important American varieties were originated in Europe. So it is that all early varieties in America have European varieties in their parentage. Carrying it one step further back, these European varieties derive from varieties imported from the Americas. Thus, the white Chilean and the Scarlet, popular in England in the late 1700's and early 1800's, were only slightly removed from *F. chiloensis* and *F. virginiana.* These two varieties fostered Keens Imperial, the parent of the notable Keens Seedling. Keens Seedling, in turn, was the progenitor of Hovey and Ross Phoenix, two important early varieties of America, which in their turn are presumed to be the parents of Wilson, the first modern strawberry of America. The sources of many early varieties in America are similar to those in this example, involving English varieties either indirectly or directly, and often native varieties of the Virginian, the English varieties descending from earlier ones from the Americas. The process is one of mixing characters and of enlarging gene pools, which so often leads to an increase in vigor and intrinsic worth.

The early history of the Chilean strawberry has been described in Chapter 4. The Chilean was probably not greatly different from the Ambato, still raised extensively in Ecuador, and the Red Chilean, still raised in the region of Santiago, Chile, today. Both these varieties are perfect-flowered, however, while the original Chilean as taken to France in 1714 was pistillate. The original Chilean, it must be remembered, was extremely susceptible to winter cold and to summer heat, and so unproductive in climates like that of the United States that it probably would not have produced a quart of berries per acre in most parts of the country. These non-hardy genes, which were introduced by the Chilean into most descendant varieties still trouble us and are still in the process of being bred out.

Ambato (*Fig. 9–1*) was probably brought to Ecuador soon after 1557, when it was carried from Chile to Peru. Like the original Chilean, it is extremely tender to winter cold and unproductive in the United States. Popenoe (1921) examined the several hundred acres of Ambato in 1920 and sent plants to the United States, where it was used to some extent in breeding and probably entered into the ancestry of Siletz. It may have entered also into the

Fig. 9–1. Fruit and flower of the Ambato strawberry in Guachi, Ecuador (*right*). Note the long conic shape of the fruit in contrast to its globose to globose-conic shape in Maryland (*below*). Note also the clasping calyx characteristic of *F. chiloensis*. This variety has probably been grown in Ecuador for nearly four hundred years, having been taken to Peru in 1557 by the Spanish from Chile as seeds or plants the year after the Spanish reached Chile in 1556. (After Popenoe)

parentage of Etter's varieties. Ambato is notable for several things: The amount of pollen in its flowers, the uniformity of its fruit, the firmness of its berries, and its adaptation to the very short photoperiods and to the constant low growing temperatures of the highlands of Ecuador. *Fig. 9–1* shows clearly the uniform shape of Ambato, which is due to thorough pollination of all the pistils made possible by the enormous amount of pollen in its anthers. The fruits usually are not as bright as those shown, and are rarely colored over the whole surface. As an indication of their firmness, the berries, with little or no injury, are often carried in boxes on mule back to the city of Ambato, for which the variety is named, and thence by truck to Quito and other cities. The plants grow not far from the Equator on mountain tops in volcanic soil and form flower buds after months at temperatures of 35° to 60° F., and photoperiods of about twelve and one-half hours. Normally they do not form flower buds in the latitude of Washington, D. C.

Methven Scarlet is probably the seed parent of Hovey. It was a seedling of the Hudson Bay, a pistillate, raised by Thomas Bishop at Perthshire, England, in 1815, so it had to be a hybrid. It was soon introduced into America where it was widely cultivated between 1820 and 1835. It was described by Fletcher as "large, round conic to coxcombed, dull scarlet; flesh light red, soft, poor; runners numerous . . . rather insipid, but large and showy" (1916). This description does not fit a pure Virginian, but rather some hybrid from the cross of Hudson Bay with some "pine," not so hardy as most Virginians, that Bishop happened to be growing at that time. A hardy pure Virginian in breeding should have produced a hardier variety than Hovey, especially since Hudson Bay itself was very hardy. Next to Large Early Scarlet, Methven Scarlet was the most widely cultivated of early grown sorts in North America and it did not pass out of cultivation until about 1870.

Hovey, originated in 1834 by C.M. Hovey (see Chapter 12), was probably a cross of Methven Scarlet x Keens Seedling. Though much hardier and more productive than Ambato or the Chilean, from which it was three or four generations removed, it was still not generally hardy. Hovey, however, was better adapted to the conditions around Boston than any European large-fruited variety. It was the first American large-fruited variety to be grown commercially, as well as the first variety of any fruit to be originated in America as the result of planned crossing. Hovey was notable for (1) its large size, (2) relative hardiness as compared with European varieties of that period, (3) productiveness under high culture, and (4) its fine flavor.

Ross Phoenix, perfect-flowered, was originated in 1837 by Alexander Ross, Hudson, New York, and is probably the male parent of the Wilson. It is reported to be a seedling of Keens Seedling, probably with a cultivated or a wild Virginian as its pollen parent. Being selected at Hudson, N. Y., it was probably one of the hardier seedlings of such a cross. Fletcher (1916) described it as "medium" (in size), "round-conic to coxcombed, very dark crimson, firm, very good." Ross Phoenix was "cultivated considerably 1845–55" and was grown by James Wilson near Albany. Much of its importance derives from its parentage of the Wilson.

Wilson, a perfect-flowered variety, was undoubtedly the first modern American strawberry and does not differ materially from those we now grow. The Wilson was originated in 1851 when James Wilson (see Chap. 11) sowed seed of Hovey, Black Prince, and Ross Phoenix and selected it from the resulting seedlings. As both Hovey and Black Prince were pistillate and Ross Phoenix was perfect-flowered, the latter had to be the pollen parent, unless other perfect-flowered varieties were in Wilson's garden. Both Hovey and Black Prince were dark red, and the flesh of Black Prince was very dark, so either variety could have been the mother parent of Wilson. Wilson was more acid than any of the three possible parents grown by James Wilson.

Wilson had many notable qualities: (1) it was extremely productive, far beyond other varieties of the day; the berries were (2) large and (3) much firmer than those of other kinds; (4) their color was an attractive deep red; (5) it was excellent as a preserving and canning variety; (6) its plant was hardier than that of any other large-fruited variety, so that it was dependably productive and growers could afford to raise it; (7) it was widely adapted and could be grown successfully farther south than other kinds; and (8) it could be grown on nearly any soil. As it was perfect-flowered, it could be grown by itself. Wilson changed the strawberry into a major crop grown from Florida and Louisiana to New York and Wisconsin, and on the Pacific Coast. Its one limiting character was the acidity of its fruit, which decreased as the berries matured (*Plate 9–1a* and *b*).

New Jersey Scarlet and Large Early Scarlet. The variety grown by Wm. Parmalee in Connecticut when he found Crescent was New Jersey Scarlet, originated by E.W. Durand (see Chapter 12) at Irvington, New Jersey, and introduced in 1868. Fletcher (1916) considered it practically the same as Old Scarlet, which about 1624, over 200 years earlier, was introduced into Europe where it was assumed to be the same as Little Scarlet, a variety still grown slightly in Europe for preserves. New Jersey Scarlet was described by Fletcher as having medium-sized, conic, necked, light scarlet berries with whitish medium-firm flesh with a good mild sub-acid flavor and it was early in season. Little Scarlet, like Old Scarlet, has similar but roundish berries (*Fig. 9–2*). Large Early Scarlet was also similar, but had earlier and larger fruit. It also was highly prized for preserves and its plants were notably hardy.

New Jersey Scarlet and some other Scarlet varieties may have been pure Virginian in ancestry, or may have been first or second generation backcrosses

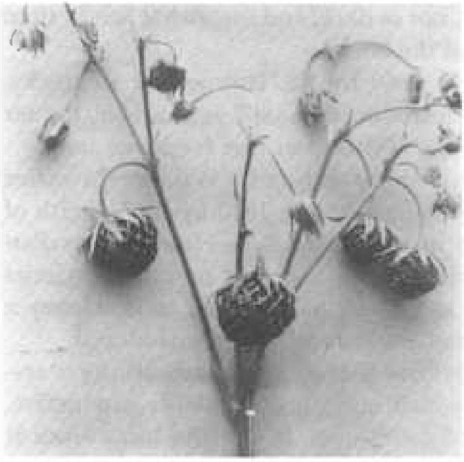


FIG. 9–2. A fruit cluster of Little Scarlet, a variety long grown in Europe and which may have been the original form of *F. virginiana* from which, crossed with the Chilean, our modern strawberry largely descended. Only five flowers of 19 in this cluster set fruit. On heavy soils at Geneva, New York, a much larger percentage sets fruit. (Photo taken June 12, 1924, at Glenn Dale, Maryland.)

to the Virginian. Knight showed that this could be so when he described similar Scarlet seedlings from crosses that he made in 1918 (see p. 76). In the development of the modern strawberry to what it is now, a substantial infusion of hardiness was necessary; and it was this that the Scarlet varieties provided, for these Virginian varieties were adapted to a rigorous climate.

Neunan, introduced about 1868 by a Mr. Neunan of Charleston, South Carolina, was probably a seedling of Wilson. It became the standard sort in much of the Southeast from Virginia south to Florida and along the Gulf

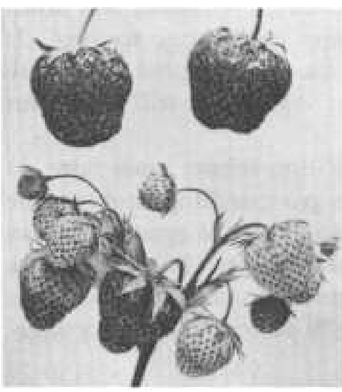


FIG. 9–3. The Crescent strawberry, one of the finest of the earlier varieties, which is in the ancestry of most American varieties.

Coast. Neunan was just enough better, not so dark, and somewhat firmer than Wilson to be grown by many instead of the latter.

Charles Downing was originated in 1860 by J.S. Downer, of Kentucky, from seed of Downer's Prolific. It was introduced in 1867 as a milder, lighter red, midseason variety, not so firm as the Wilson but fine for home use.

Crescent (*Fig. 9–3*) was found as a chance seedling by William Parmalee of New Haven, Conn., in 1873 and was introduced in 1876 by H.H. Smith of West Haven, Conn. Mr. Smith wrote in a letter to A.B. Howard that Parmalee grew only Hovey and New Jersey Scarlet and that no other varieties were raised near the Parmalee place, so that its parents had to be Hovey x New Jersey Scarlet, a Virginian that had just recently been introduced.

The Crescent had many of the qualities that made Wilson so popular—its high productiveness, its hardiness which made it dependably productive, and its adaptability to a wide range of conditions. It also was acid. Since it was pistillate, another variety had to be grown with it for pollination. Its fruits were scarlet, rather than the deep red of Wilson; they were not quite so large and they were softer. The plant was subject to leaf spot; however, it was earlier and made runner plants more freely than Wilson, and it was even more productive. As a pistillate, all its seedlings had to be hybrids; its vigor of growth, its hardiness and productivity, and probably its scarlet color, led to its use as a parent in breeding. These characters are now generally present in today's varieties.

Sharpless was raised in 1872 by J.K.S. Sharpless of Catawissa, Pennsylvania, from mixed seed of Jucunda, Charles Downing, Wilson, and Col. Cheney, and was introduced in 1877. It was thought to have Charles Downing as one parent. Its other parent could have been either the Col. Cheney or Jucunda, but not the much more acid and darker Wilson. The berry was relatively large, often hollow, irregular in shape, often with green tips, and bright scarlet in color. Its seeds were somewhat raised. It was mild and good in flavor, and late midseason in ripening. It was a good pollen producer and was grown extensively as a pollinator for Crescent. Crescent was much more productive, but Sharpless was much larger and better flavored. It required fertile soils and failed on poor ones. It was well adapted to hill culture, and was widely grown in Europe until after 1900 and is still important in Poland.

The success of C.M. Hovey, and of James Wilson twenty years later, in obtaining far better varieties, stimulated many to grow seedlings and in some cases to make crosses. By 1880 many new varieties began to appear. Wilson continued to dominate the market and was planted on about half the acreage almost up to 1900. Crescent and Sharpless were grown on about 30 percent of the acreage and other varieties on the remaining 20 percent. The other varieties were numerous. In southern states Hoffman, a seedling probably of Neunan, found by Mr. Hoffman of Charleston, South Carolina, was introduced in 1887. It was earlier, firm and acid, and better colored than Neunan, and replaced it in the South. Michel, Excelsior, Cloud, and Lady Thompson were other varieties better adapted to the South, with its shorter daily light periods, for they had less chilling requirement than northern sorts. In the North, besides Crescent, Warfield (introduced 1885), Bubach (introduced 1886), and Haverland (introduced 1887) were three other widely grown pistillate varieties and were pollinated with Wilson, Sharpless, Gandy (introduced 1888), Aroma (introduced 1892) and others.

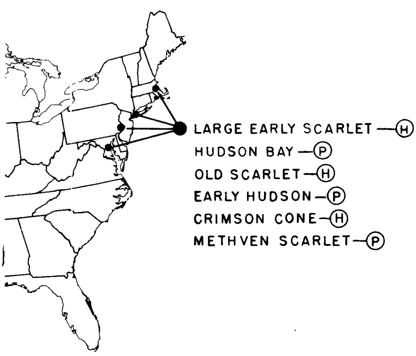


FIG. 9–4. Where strawberry varieties were grown to 1840. P = pistillate. H = hermaphrodite.

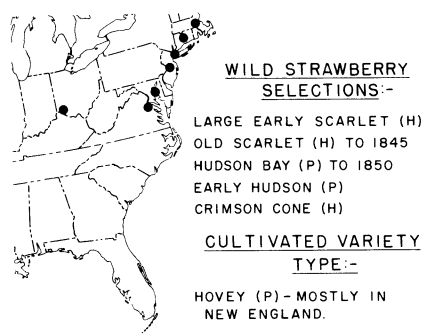


FIG. 9–5. Where strawberries were grown and varieties between 1840 and 1858. P = pistillate. H = hermaphrodite.

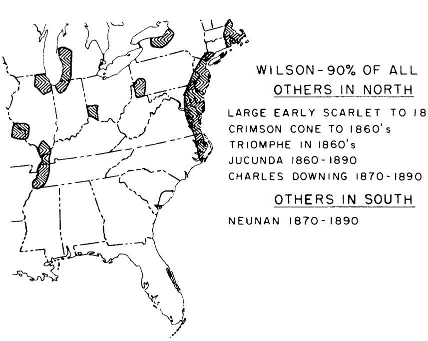


FIG. 9–6. Where strawberries were grown and varieties between 1858 and 1880.

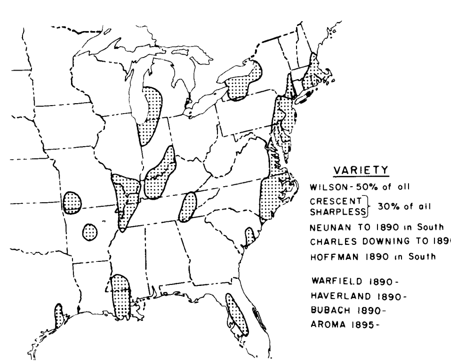


FIG. 9–7. Where strawberry varieties were grown, 1880 to 1900.

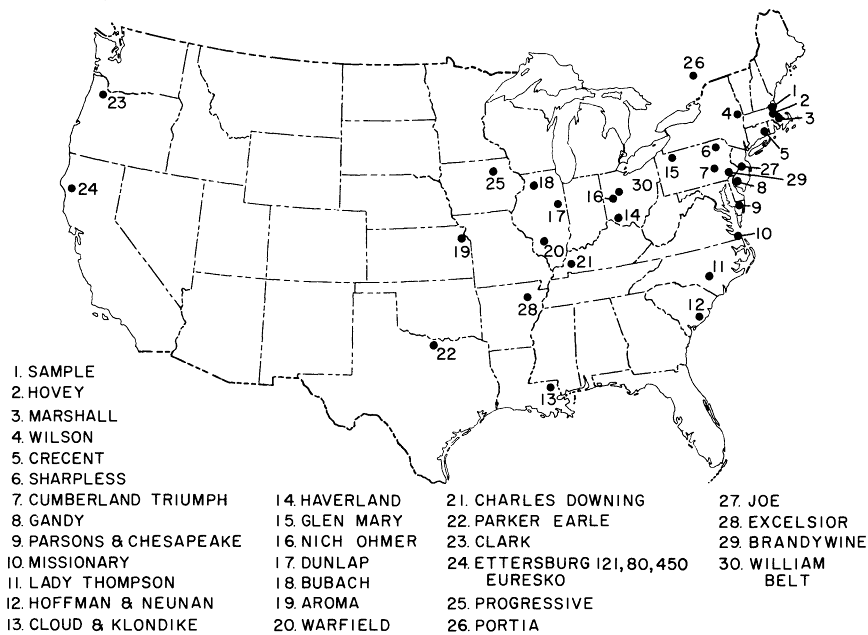


FIG. 9–8. Where older strawberry varieties originated.

Thus, in 1800 there were only a few garden plantings containing the Chilean, the tiny European wood strawberry, *vesca,* and selections of Virginian, either American or European, and these were in the gardens near the cities along the Atlantic seaboard. Most strawberries were gathered from the wild meadow and pasture areas. By 1820 there were very few commercial plantings of selections of the wild Virginian (*Fig. 9–4*). Though Hovey was bred and introduced in the 1830's it caused no real increase in the acreage except perhaps around Boston. Even when Wilson was introduced in 1854, the total acreage of the United States was estimated by Fletcher (1917) at only about 1,400 and the major sources of supply were the native wild ones. Owing to the superior hardiness, shipping quality and productiveness of Wilson, the acreage in the United States expanded quickly so that there may have been 10,000 acres in 1860, 50,000 by 1870, and 100,000 acres by 1880 (*Fig. 9–6*). Other berries were raised on a small percent of the total acreage, but on the whole Wilson dominated the markets until 1900 (*Fig. 9–7*). Figure 9–8 shows where the older varieties originated.

10

Later Strawberry Varieties, 1900-1965

THE NINETEENTH CENTURY in America witnessed the establishment of commercial strawberry production: from 1800 to 1858, the native Virginian varieties were mostly grown; then, with the advent of hardy, large-fruited varieties, came the great expansion from 1858 to 1880, when acreage increased 50-fold and growing areas extended to the farthest boundaries of the country; and lastly, toward the end of this period, the introduction of hundreds of varieties whose screening was necessary in order to determine their adaptability to certain areas. After 1900, and extending to the present, began the later period which involved on the part of breeders and breeding work the increasingly considered selection of varieties for their ability to replace older varieties in particular regions. This process still continues (*see Figs. 10–1 to 10–8*). For the whole country, acreage is not expanding, but areas of production shift, owing to advantages of labor, industrialization, and changing varieties whose adaptation to certain areas makes them especially valuable. Production per acre is increasing, owing mainly to better varieties and the development of agricultural techniques for intensive cultivation.

Varieties of North America, 1900–1950

Nine especially notable strawberry varieties were grown in the first half of the present century: Marshall, Klondike, Missionary, Dunlap, Howard 17

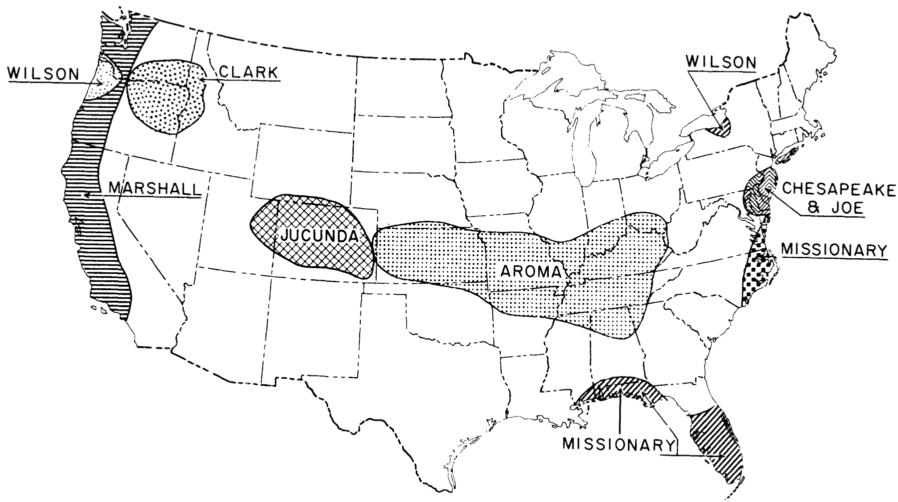


FIG. 10–1. Where strawberry varieties were grown, 1900 to 1920, part A.

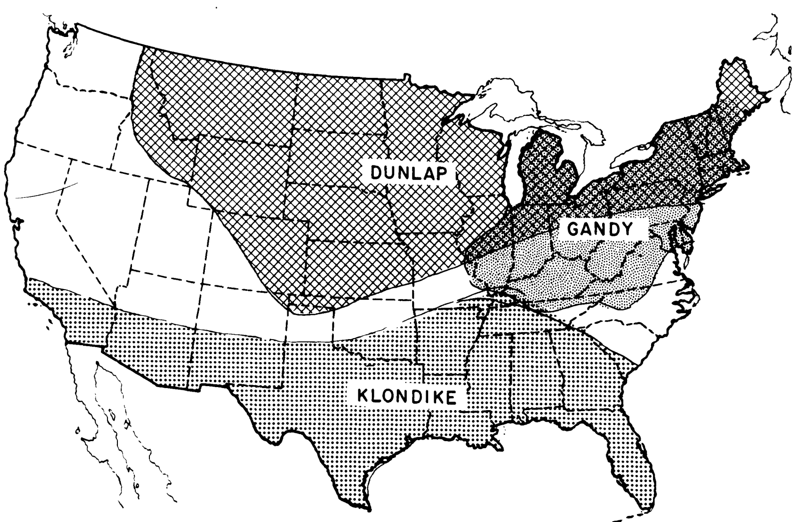


FIG. 10–2. Where strawberry varieties were grown, 1900 to 1920, part B.

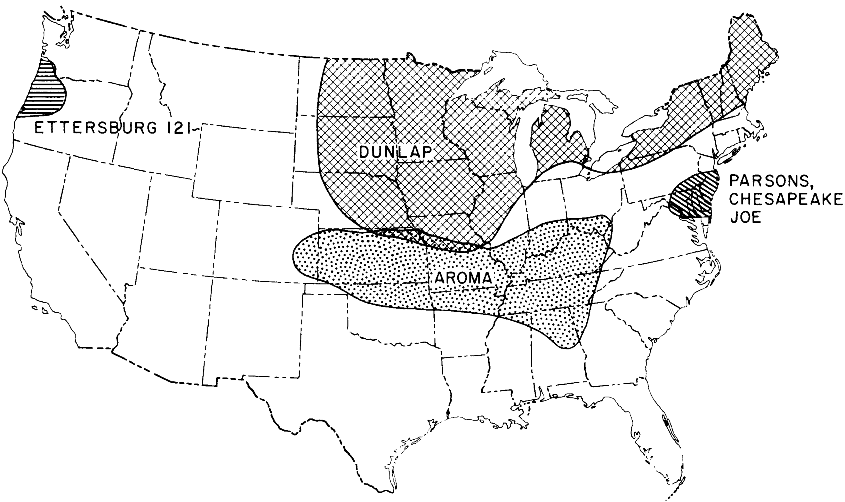


FIG. 10–3. Where strawberry varieties were grown, 1920 to 1940, part A.

(Premier), Aberdeen, Blakemore, Fairfax, and Aroma. All of these varieties are still known today; but the Blakemore alone of the nine is still important in acreage, having been replaced only in part. Although Dunlap has been most notable for its hardiness, and for its extension of strawberry growing farther north, it is also notable as a parent of hardy everbearing varieties. One other variety was outstanding as an ancestor. Nich Ohmer, introduced in 1898, was never widely grown but is found to the extent of 25 to 30 per cent in every California variety.

(1) *Marshall* (*Plate 10–1,* a chance seedling), was found in 1890 by Marshall F. Ewell of Marshfield Hills, which is just south of Boston, Mass., and was introduced in 1893. Though less hardy than many varieties, it was hardy enough to be widely, but not heavily, grown in northern states from about 1900 to 1910. Then it was found to be adapted to the milder climate of western Washington, Oregon, and California, where it became the dominant variety; from about 1905 to 1945 in California, and from 1905 to about 1958 in Oregon and Washington. In the 1940's, it was replaced in California by the larger, more productive and less virus-susceptible variety Shasta, and in Oregon and Washington in the 1950's by the hardier, more virus-tolerant, and more productive variety Northwest. At present it may still compose as much as 4 percent of the total acreage set to strawberries, but is being replaced rapidly by Northwest.

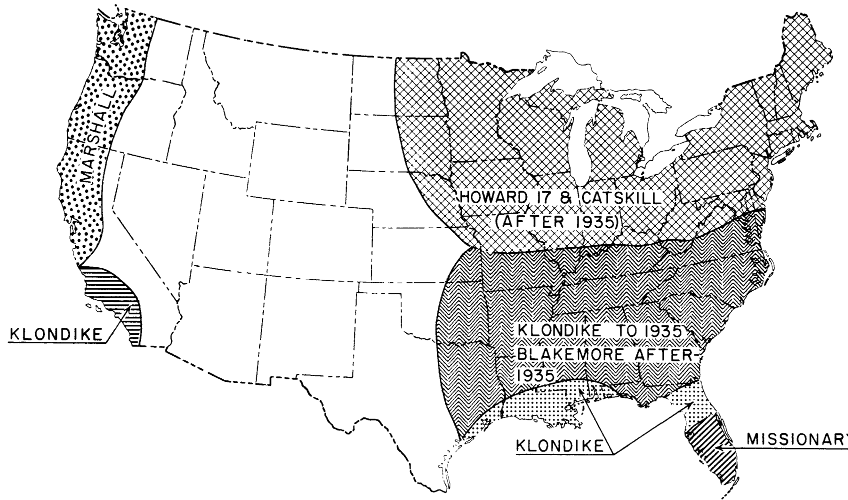


FIG. 10–4. Where strawberry varieties were grown, 1920 to 1940, part B.

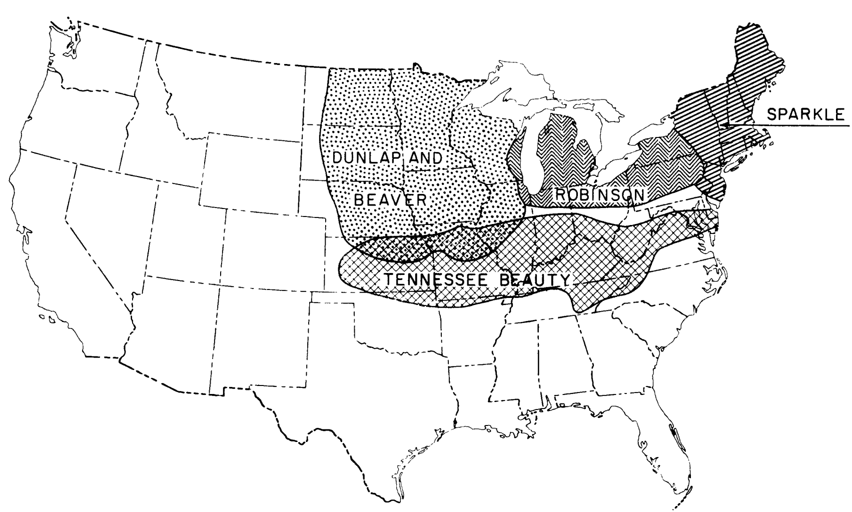


FIG. 10–5. Where strawberry varieties were grown, 1940 to 1960, part A.

As the Marshall is large leafed, relatively large-fruited, deep red, and of high flavor, its parents would have been varieties with these characteristics, and Marshall could hardly have been a cross with the wild Virginian. The varieties grown in the late nineteenth century which might have been parents of Marshall are now lost. Undoubtedly they were rich in Hovey blood. Among the likely larger-fruited, although lighter-colored varieties which could have been parents of Marshall would be President Wilder and Bubach, but other combinations of varieties of the 1880's may have been the source. Bubach, itself of unknown parentage, was like Marshall in being soft, irregular in shape, large and of high flavor, but its color was light red. President Wilder (Hovey x La Constante) was large but round-conic to obtuse, light scarlet with light flesh, sweet, and of high flavor also.

Marshall remained important for so long because of its high flavor and its suitability for freezing and preserving. The berries became mushy after freezing, but held their flavor and their deep red color. While it was important in the development of the great freezing industry of Oregon and Washington, its limitations were its soft flesh, average productiveness, and non-hardy, virus-susceptible plants. Marshall has entered into the ancestry of several leading varieties of today: Northwest, Robinson, Catskill and all the varieties grown in California, such as Shasta, Lassen, Siletz, Goldsmith, Solana, Tioga, Fresno and Torrey.

(2) *Klondike.* This variety, introduced in 1901, was originated by R.L. Cloud, a railroad shipping agent of Independence, Louisiana, who knew that a better shipping variety was needed and bred one. Its parentage was given by Mr. Cloud as Pickerproof x Hoffman. Very soon it became the standard variety of the entire southern United States, excepting the central and southern Florida areas; and for over 30 years, until after the introduction of the Blakemore, it was the leading variety in the United States. Probably over a million acres of it have been grown. The Blakemore, a still firmer variety, replaced it in most of the South in the 1930's, while Klonmore replaced it in Louisiana. It is now grown only in the plateau region near Irapuato, Mexico, for freezing.

Klondike possessed many of the characteristics of the Wilson—it was acid, deep red, of medium size, produced runners freely, and withstood neglect. It also was moderately productive and withstood the heat of southern summers. It was liked for freezing, because of its rich red color and its acidity. Its chief limitations were its susceptibility to leaf scorch and leaf spot, its medium size, and lack of firmness. Blakemore replaced it because of its firmer, brighter fruits and Klonmore because of its resistance to leaf spot.

Klondike is in the parentage of Klonmore, Headliner, and Dabreak—varieties that replaced it in the Louisiana region.

(3) *Missionary (Plate 10–1).* Missionary was found about 1900 as a chance seedling by Nathaniel Gohn, Deep Creek, near Norfolk, Virginia, and was introduced in 1906. At that time Hoffman was the standard southern variety and may well have been one of Missionary's parents. The other parent may have been some other southern variety, such as Lady Thompson or Michel, or it may even have been a native Virginian. Many varieties with Missionary in their ancestry have a flavor of berry not found in other breeding lines, and one which is distasteful to some people. Missionary quickly became the leading variety in eastern Virginia, eastern North Carolina, and in southern Florida. It was found to require less chilling; and it grew and fruited better than other varieties in the semitropics of central and southern Florida and central America with their shorter photoperiods. When ripe, it was acid, deep red, and pointed with a distinct shoulder. It was a fairly good shipping variety, especially as grown in Florida. Its limitations were that it became soft in warm weather and that it was only moderately productive in Florida. Along the Atlantic Coast, it was replaced by Blakemore and recently in Florida by Florida Ninety.

Missionary has been notable as a parent and has entered into the ancestry of many major varieties: Northwest, Blakemore, Headliner, Tennessee Beauty, Dixieland, Florida Ninety, Lassen, Pocahontas, Albritton, Earlidawn, Surecrop, Armore, Dabreak, and Klonmore. It is represented in the ancestry of present-day varieties more than any other variety except Howard 17 (Premier). California breeders do not think much of Missionary.

(4) *Dunlap (Plate 10–1).* Though originated in 1890, Dunlap was not introduced until 1900. It resulted from one of the crosses by Rev. J.R. Reasoner of Illinois; according to him, probably Crescent x Cumberland Triumph. Extremely hardy, widely adapted, highly flavored, irregular-shaped, rich red, and attractive, it made an ideal garden variety. For fifty years it has been an important variety in northern states and Canada. It is still grown to a slight extent in north-central states where hardiness is a major factor. Farther south, in Maryland, it is too soft, too subject to leaf spot, and does not have the high flavor it has in northern regions. Its softness is its most serious limitation; its susceptibilty to leaf spot is also serious. Howard 17 (Premier) proved more productive, and therefore it together with Catskill, and Sparkle gradually replaced Dunlap wherever they were hardy enough.

Dunlap has been most important as one parent of everbearing varieties, contributing hardiness, vigor, and high flavor. It was the pollen parent of Progressive and through Progressive has entered into the parentage of other everbearers: Rockhill, Gem, Red Rich, Twentieth Century, Ozark Beauty, Ogallala, and others. Its pedigree indicates that Dunlap has a rather low percentage of Virginiana blood, but its appearance and performance belie this.

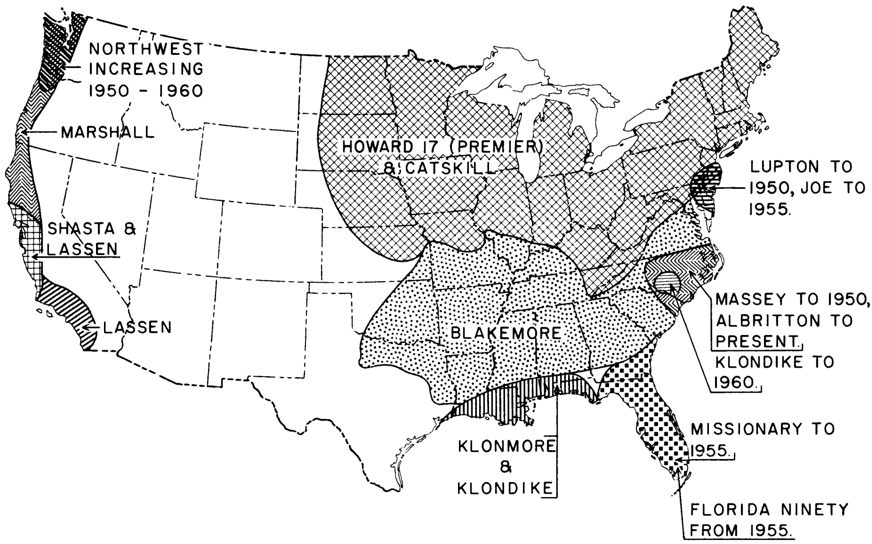


FIG. 10–6. Where strawberry varieties were grown, 1940 to 1960, part B.

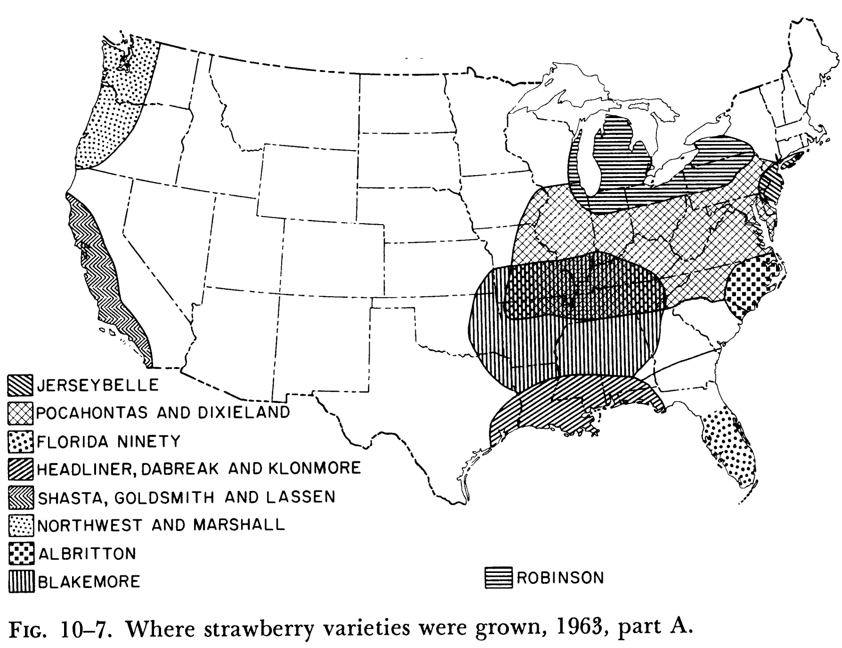


FIG. 10–7. Where strawberry varieties were grown, 1963, part A.

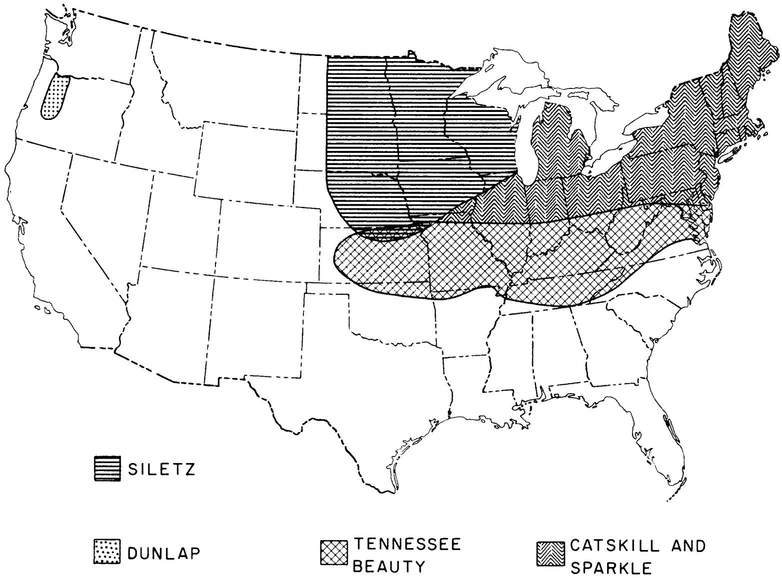


FIG. 10–8. Where strawberry varieties were grown, 1963, part B.

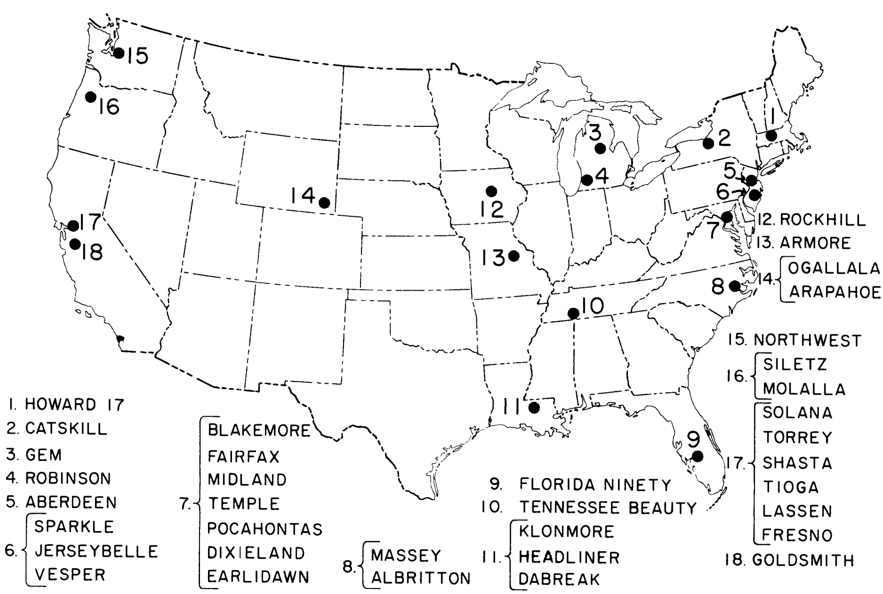


FIG. 10–9. Where today's varieties originated.

FIG. 10–10. The Klondike.

(5) The *Howard 17* (Premier) variety (*Plate 10–1*), originated by A.B. Howard and tested and introduced by his son (E.C. Howard) of Belchertown, Massachusetts, is and has been for forty years one of the important strawberries, both because of its wide commercial use and its value in breeding. It was a cross of Crescent x Howard 1 (see p. 181). Fletcher (1916) dates its introduction about 1909 when it and many other seedlings were given limited distribution by E.C. Howard. Among those obtaining plants was E.H. Riehl of Illinois. A little over two years later, in the summer of 1911, Mr. Riehl supplied the Kellogg Company of Michigan with fifty plants of "a seedling found in his vineyard . . . probably a seedling of the Howard 17 (Premier)." The Howard 17 (Premier) would have fruited first at Riehl's place in 1910. It is impossible that seed from the Howard 17 (Premier) could have produced a seedling clone that fruited first in 1911, that it could have been tested and then furnished Riehl fifty plants to send to the Kellogg Company the same summer that it was first selected. Premier was introduced in 1915. As Howard 17 it was introduced widely by C.E. Chapman of North Stonington, Connecticut, in the spring of 1918. A discussion as to the identity of the two varieties began in 1920; and most observers considered the foliage identical but the fruit different.

However, in general, through thirty years from about 1920 to about 1950 most people considered the two identical. Then, after virus-free plants of what was called Howard 17 were obtained and none was obtained of Premier, the two were compared and a discussion concerning them arose similar to that of thirty years earlier. The majority of careful observers now consider the foliage of the two to be indistinguishable, while what is called Premier does not usually make so many runner plants as the virus-free Howard 17: Some Premier stocks in fact made far too few. The majority of observers also consider the fruit of virus-free Howard 17 to be somewhat lighter red and softer, and, where stands of Premier can be obtained, they think it should be preferred.

If Premier and Howard 17 are identical, virus may have made the fruit of what is now called Premier somewhat darker. If plants of Premier could be freed of virus, comparable plants of the two might be tested. Again, possibly the virus in Premier might be transferred to clean Howard 17 by grafting and the resultant stocks then compared. As a third test, resistance to some disease, such as Verticillium, may be found in Premier but not in Howard 17, which would indicate a genetic difference.

However, the Howard 17 (Premier) is gradually becoming of less importance as promising new varieties with Howard 17 in their ancestry are being widely tested. Premier was widely tested from 1915 to 1919 and was mentioned as a new variety in the 1919 edition of *Farmers' Bulletin 1043* (written in 1917); in the 1926 revision (written in 1925) Howard 17 (Premier) was estimated to be grown on 16 percent of the total strawberry acreage of the country and as the second in importance in the United States. The estimate today is that it consists of not over 2 percent of the total acreage, and it is being steadily replaced by Earlidawn, Sparkle, Midway, Pocahontas, and Midland—all with Howard 17 in their ancestry.

Table 1 gives twenty-five principal varieties (based on acreage) in the United States in 1964—with the per cent of the total acreage composed by each variety. It also gives the parentage, if the variety had Howard 17 in its ancestry. This table indicates that varieties derived in part from Howard 17, and including Howard 17, make up at least 92 percent of the total acreage.

Two other tables pertinent to Howard 17 may be found in the appendix. Table 2 gives the names of thirty-nine varieties having Howard 17 as one parent, some of which have been introduced too recently to have been fully evaluated by growers and some of which have already been dropped. Table 3 lists eighty-two other varieties having Howard 17 in their parentage. Some varieties, as for example Fairfax, whose parentage is uncertain, or which trace back to Fairfax (as does Sparkle), probably have Howard 17 in their parentage. Florida Ninety is an open-pollinated seedling of Missionary and is perhaps a cross of Missionary x Klonmore. Of the important varieties of the United States not derived from Howard 17, Marshall, Klondike, and Dunlap are varieties older than Howard 17, and Aberdeen is of unknown parentage and may have Howard 17 in its ancestry.

The qualities for which Howard 17 so rapidly became a major variety in northern United States were: (1) high resistance to leaf spot and leaf scorch diseases; (2) relatively high tolerance to virus diseases; (3) early cessation of runner initiation with formation of many crowns, and early flower bud initiation (late August and early September) (see p. 332); (4) frost-hardy flowers; (5) relatively large, bright red, good flavored berries; (6) high productivity. New varieties (except for Earlidawn and Midland) replacing Howard 17

Table 1. Principal varieties of strawberries in the United States in 1964—parentage indicated where derived in part from Howard 17

VARIETY	PARENTAGE	PERCENT OF ACREAGE Non-Howard parentage	Howard 17 or varieties from it
Northwest	(Howard 17 in ancestry)		18
Blakemore	Missionary x Howard 17		14
Shasta	(Howard 17 in ancestry)		6
Headliner	L7-27 (Suwannee x Klonmore) x L7-42 (Suwannee x Konvoy)		5
Tennessee Beaut	Missionary x Howard 17		5
Dixieland	Tennessee Shipper x Midland		4
Marshall	Unknown	4	
Sparkle	(Howard 17 in ancestry)		4
Robinson	Howard 17 x Washington		4
Midway	Dixieland x Temple		4
Catskill	Marshall x Howard 17		3
Florida Ninety	Seedling of Missionary	3*	
Lassen	(Howard 17 in ancestry)		3
Pocahontas	Tennessee Shipper x Midland		3
Albritton	(Howard 17 in ancestry)		2
Earlidawn	(Howard 17 in ancestry)		2
Howard 17 (*Premier*)			2
Jerseybelle	(Howard 17 in ancestry)		2
Siletz	(Howard 17 in ancestry)		2
Surecrop	(Howard 17 in ancestry)		2
Armore	Blakemore x Aroma		1
Dabreak	(Howard 17 in ancestry)		1
Dunlap	Crescent x Cumberland Triumph	1	
Klonmore	(Howard 17 in ancestry)		1
Goldsmith	(Howard 17 in ancestry)		1
Others	(Nearly all have Howard 17 in ancestry)		3
		8	92

* Possibly Howard 17 in ancestry, see text

(Premier) are mostly later ripening. Howard 17 (Premier) is being replaced for the following reasons: Earlidawn and Midland are slightly earlier, firmer, and much better for freezing, and Midland, though not frost resistant, is much higher in flavor and far better for freezing. Like Howard 17 (Premier), both cease to initiate runners and start branch crowns and fruit buds in late summer. Catskill and Pocahontas are early midseason varieties of larger size, higher flavor, and better qualities for freezing. Pocahontas is also firmer than

Howard 17 (Premier). Sparkle, a late midseason variety, liked for freezing, has higher flavor, greater beauty, and is resistant to the presently common race of the red stele root disease. Thus, by 1965 standards Howard 17 (Premier) lacks size, flavor, firmness, freezing qualities, and beauty. It is still one of the most productive varieties, one of the most resistant to leaf diseases and to frost, one of the most tolerant to virus diseases, and it has the desirable habit of producing many crowns.

Howard 17 (Premier) has been affected by genetic variegation, which in the late 1920's and early 1930's was serious in this variety. In recent years no reports of variegation have been made and propagation from variegation-free stocks seems to have eliminated the trouble. Although the gene or genes for variegation have been passed on to many of its descendants, such a gene may, of course, have come from the other parent as well. Among its descendants variegation has been noted in Blakemore, Dixieland, Klonmore, Tennessee Beauty, Bellmar, Fairmore, and Wisconsin 537. It is possible that crosses using the present non-variegating strains of a variety may have less tendency to variegate than did the older stocks.

Howard 17 (Premier) is said to have been one of about 25,000 seedlings raised by the Howards and certainly it is one of the most important varieties in the history of the strawberry. George Slate in 1931 reported that Howard 17 (Premier) was an outstanding parent in his breeding work (Slate, 1931). Twelve years later he again emphasized the value of Howard 17 as a parent in breeding (Slate, 1943). The writer also noted that Howard 17 (Premier) was a fine parent and that about 40 percent of his selections being grown in 1933 had Howard 17 (Premier) as one parent (Darrow, 1934).

(6) *Aberdeen* (*Plate 10–1*). This variety was originated by J.E. Kuhns, a strawberry grower of Cliffwood, New Jersey, which is situated not far from the New Jersey Agricultural Experiment Station at New Brunswick, New Jersey. Mr. Kuhns was growing Glen Mary, Chesapeake, and Late Stevens about the time he obtained the Aberdeen and decided to introduce it. He was in the habit of testing many new varieties, of making crosses, and growing seedlings of those that interested him without keeping a record of their ancestry. He regularly had a field of several hundred seedlings under test. As early as 1910 he had promising varieties, some of which he introduced. A letter from his son, W.W. Kuhns, in 1963 states that the elder Mr. Kuhns had said that a cross with the vigor of Late Stevens and quality of Chesapeake would be a great berry. The son also said that if a seedling was from these two it had the vigor of Late Stevens but not much of the qualities of Chesapeake, though he grew it for twenty-five years as his most profitable variety. Seed must have been sown as early as 1910, for by 1917 Mr. Kuhns had tested the selections and had a row of Aberdeen about 300 feet long. Aberdeen was first reported as promising by J.H. Clarke, of the New Jersey Agricultural Experiment Sta-

tion, in 1924. In 1927 he reported that it had fruited for four years and was promising each year (Clarke, 1927). Its most serious weakness was that it was too soft to ship, even though it outyielded Howard 17 (Premier). Occasionally having high flavor, it is a free plant maker, producing large, medium red, soft, and mildly subacid fruit. In the 1930's it was grown in New Jersey quite widely on heavier soils and in other northeastern states. In 1935, Anderson of Illinois reported that Aberdeen was red stele-resistant, thus becoming of great importance. In that year, A.S. Colby, of the Illinois Agricultural Experiment Station, made the cross Mastodon x Aberdeen. A high percentage (63.5 percent) of the resulting seedlings showed resistance to the disease. Clarke, in New Jersey, was already using Aberdeen as a parent and had made selections that were introduced as Pathfinder and Sparkle, both of which showed resistance. The U.S. Department of Agriculture made the cross Aberdeen x Fairfax to produce Temple which was selected in 1939 and introduced in 1943. Temple, Fairland, and Sparkle replaced Aberdeen as desirable red stele resistant varieties.

(7) *Blakemore* (*Plate 10–2*). This variety was originated by G.M. Darrow, of the U.S. Department of Agriculture as a cross of Missionary x Howard 17, made in 1923 and selected in 1925. It was sent out for trial in the spring of 1927 and later that year tests by Lathrop of the National Preservers Association indicated that it was superior for preserving. In 1928, in tests by Dearing at the North Carolina Department of Agriculture Station at Willard, N.C., it was considered to be outstanding as a shipping variety for the South and it was introduced through that Station and cooperating nurseries in 1929. Its resistance to leaf spot and leaf scorch, its tolerance to virus diseases, its attractive scarlet fruit, its firmness for shipping, its superiority for preserving, and its greater productiveness as compared with Klondike, led to a quick replacement of Klondike by Blakemore except in southern Louisiana and in Florida. It replaced Missionary in Virginia and North Carolina. Blakemore was grown as far north as southern New Jersey, but has since been replaced there by newer varieties, first by Sparkle and then Jerseybelle, and in Maryland and Virginia by Pocahontas, Dixieland, Earlidawn, and red stele-resistant varieties.

When Blakemore was selected only 64 seedlings of the cross were grown. One other selection of the same progeny was named the Bellmar. It was larger, less acid, less firm, slightly deeper red, and several days later than Blakemore. It did not succeed, partly because it was not as firm and partly because virus diseases made it less productive under many conditions. Later large numbers of seedlings of the same cross were grown and the Suwannee was named for its very high dessert quality, which is perhaps the best in the United States. It is less tolerant of virus, however, and has nearly disappeared. A stock free of virus has been obtained by Dr. John McGrew.

Table 2. Varieties (27 in all) resulting from crosses with Aberdeen or descending from Aberdeen are:

Year introduced	Variety	Cross	Source
1938	Pathfinder	Howard 17 x Aberdeen	N.J. Agric. Expt. Station
1943	Sparkle	Fairfax x Aberdeen	N.J. Agric. Expt. Station
1943	Temple	Fairfax x Aberdeen	U.S.D.A. & Md. Agric. Expt. Sta.
1947	Auchincruive Climax	TD-8 x Aberdeen	Scottish Hort. Station
1947	Fairland	Aberdeen x Fairfax	U.S.D.A.
1949	Redcrop	Aberdeen x Fairfax	N.J. Agric. Expt. Station
1950	Vermilion	Redstar x Pathfinder	Ill. Agric. Expt. Station
1952	Maine 55	Howard 17 x Aberdeen	Me. Agric. Expt. Station
1952	Monmouth	Aberdeen x Howard 17	Me. Agric. Expt. Station
1952	Orland	Aberdeen x Howard 17	Me. Agric. Expt. Station
1953	Plentiful	Redstar x Pathfinder	Ill. Agric. Expt. Station
1954	Stelemaster	Fairland x Md-683	U.S.D.A.
1955	Jerseybelle	((Lupton x Aberdeen) x Fairfax x (Pathfinder x Fairfax)	N.J. Agric. Expt. Station
1955	Talisman	NJ-1051 x Auchincruive Climax	Scottish Hort. Station
1956	Puget Beauty	US-Oreg. 1765 x Sparkle	Wash. Agric. Expt. Station
1956	Redglow	Fairland x Tennessee Shipper	U.S.D.A.
1956	Surecrop	Fairland x Md-US-1972	U.S.D.A. & Md. Agric. Expt. Sta.
1957	Agassiz	Pathfinder x British Sovereign	British Columbia Expt. Farm
1957	Cavalier	Valentine x Sparkle	Can. Central Expt. Farm
1957	Guardsman	Claribel x Sparkle	Can. Central Expt. Farm
1957	Redcoat	Sparkle x Valentine	Can. Central Expt. Farm
1957	Juspa	Jucunda x Sparkle	Holland Inst. for Hort. Breeding
1957	Redgauntlet	NJ-1051 x Auchincruive Climax	Scottish Hort. Station
1959	Fulton	Starbright x Pathfinder	N.Y. Agric. Expt. Station
1960	Midway	Dixieland x Temple	U.S.D.A. & Md. Agric. Expt. Sta.
1960	Gorella	Juspa x US-3763	Holland Inst. for Horticultural Breeding
1960	Revada	Ada Herzberg x Auchincruive Climax	

The limiting characters of Blakemore are its relatively small size and its sporting to yellow plants, "June yellows" or "variegation," which was first noted in 1933 and rapidly increased in all sections of the United States. At first it seemed that the variety might be lost, but non-yellowing stocks were selected in several places and some of these proved relatively stable. Though the condition is inherited, research in North Carolina indicates that it is possible to use Blakemore in breeding non-yellowing varieties.

Blakemore has been used extensively in breeding and is in the ancestry of Northwest, Headliner, Dixieland, Pocahontas, Albritton, Massey, Earlidawn, Surecrop, Armore, Dabreak, Siletz, Goldsmith, Klonmore, and others.

(8) *Fairfax* (*Plate 10–2*), originated by G.M. Darrow, of the U.S. Depart-

ment of Agriculture, from a cross made in 1923, was selected in 1925 and introduced in 1933. Its parentage is probably Etters 450 x Howard 17 (Premier) or Howard Supreme x Etters 450 (Darrow, 1962). It is notable as one of the finest flavored of all strawberries. It does not keep its flavor so well as Suwannee in cool, cloudy, or in hot, windy weather. Fairfax is resistant to leaf diseases but susceptible to red stele root disease and to virus diseases and to fasciation in southern states. Fairfax is a good but not excessive plant maker, its flowers produce the most pollen of any; the berries are good sized, deep red in color, firm fleshed, and the least acid of common varieties. Since virus-free stocks of Fairfax have become available, it is being grown widely.

Fairfax has proved to be a good parent and Grenadier (of Canada), Redstar, Sparkle and possibly Kogyoku of Japan (24 in all) have Fairfax as one parent while Cavalier, Guardsman, and Redcoat of Canada, Redgauntlet and Talisman of Great Britain, and Arapahoe, Ogallala, Red Rich, Ozark Beauty of the everbearers, and Jerseybelle, Vesper, Midway, and Surecrop are among 38 others having Fairfax in their ancestry (Darrow, 1962). Fairfax transmits excellent dessert quality and freedom from leaf spot. Its limitations are that the berries turn purplish when over-ripe, it is not acid enough for a good freezing variety, and its excellent flavor does not develop under some weather conditions. Its descendants are being used more as parent varieties.

(9) *Nich Ohmer* was originated by J.F. Beaver of Dayton, Ohio, as a seedling of Middlefield and was introduced in 1898. It did not succeed in eastern United States because (1) the fruit was only of fair flavor, (2) its size was small after the first pickings, (3) it was subject to leaf spot, and (4) it needed high culture. It was much grown in the 1920's and 1930's in the coastal area of California near Watsonville, where its flavor was high, the berries large, firm, attractively glossy crimson, and where it produced well throughout the summer in the cool coastal climate. After the larger and more productive Shasta and Lassen were introduced, Nich Ohmer was no longer grown. It has entered into the ancestry of Shasta (25 percent of its parentage), into Lassen (25 percent), into Goldsmith (Z5A) (25 percent), into Solana (25 percent), and into Fresno, Tioga, and Torrey (31 percent each).

(10) *Aroma (Plate 10–3)* started in 1889 by E.W. Cruse, Leavenworth, Kansas, as a seedling of Cumberland x Triumph, was introduced in 1891. It became the leading variety in the southern Midwest and held that position for about fifty years. It was second in importance in the United States in 1919, and fourth in 1939, with 12 and 10 percent of the total acreage of the United States, respectively. Its foliage was resistant to leaf spot and leaf scorch; the plants were productive and the fruit firm, uniformly large, very attractive, and of good dessert quality. It succeeded especially well on silt and clay soils, but has been finally replaced by three varieties: in part by Blakemore, which is earlier,

somewhat more productive, and an even better shipper; in part by Tennessee Beauty, which is about the same in season, much more productive, good as a processing berry, and about as good a shipper; and in part by Armore, also of the same season but larger, not so smooth, much more productive, higher in flavor, but softer, more susceptible to leaf spot and much more subject to mildew. Neither Aroma nor Armore is suitable for processing. Probably 500,000 acres of the Aroma variety have been grown. Its one notable seedling is Armore, a cross of Blakemore x Aroma. Mr. Cruse also originated the Cyclone (1894).

Present varieties of North America—1965

Only four of the ten notable varieties listed and discussed in the first section appear in the list (see Table 1) of present important varieties of the United States. The others, except Catskill, are varieties introduced since 1940. The new varieties of today are being tested quickly for their adaptation and for grower acceptance. In part this is due to better understanding of local adaptation of varieties in terms of photoperiod and temperature, and in part to the control of virus diseases, which so often in the past destroyed all usefulness of a variety even before it was well introduced. Examples of this latter case are the Northstar, a superior freezing sort, and Starbright, a high flavored dessert berry introduced about twenty-five years ago, both of which were entirely infected by virus and which quickly became unproductive. Now, with modern techniques of producing virus-free stocks, the potential value of new varieties is more readily apparent when they are introduced.

Table 1 lists the chief varieties now grown in the United States. Besides these there are small acreages of Empire, Fairfax, Midland, Midway, Redstar, Solana, Vermilion, and Vesper and smaller acreages of Burgundy, Columbia, Erie, Fletcher, Fortune, Fulton, Frontenac, Fresno, Mollala, Puget Beauty, Ranger, Redglow, Stelemaster, Tennessee Shipper; and of everbearers, Arapahoe, Gem, Geneva, Ogallala, Ozark Beauty, Red Rich, Rockhill, and Twentieth Century. Figure 10–10 shows where many of these varieties originated.

Strawberries of the United States[1]

Northwest (*Plate 10–3*) was bred by C. Schwartze of Western Washington Experiment Station, introduced 1949. Since 1962 this is the most planted variety in the United States, but all in Oregon and Washington. It is highly productive of late-ripening berries very good for freezing. Plants are tolerant to virus diseases. It is very good but not best for freezing, and it needs larger

[1] For parentage see Appendix, Section IV.

size. Limitations: it is not red stele-resistant, and is susceptible to leaf spots and mildew.

Blakemore (see pp. 151, 407) was bred by George M. Darrow of the U.S. Department of Agriculture, introduced in 1929. From about 1937 to 1961 this was the most planted variety in the United States because of its early ripening, very firm, bright red, good shipping berries, good for freezing and preserving, high in pectin. Plants are virus-tolerant, resistant to leaf spot, leaf scorch, and Verticillium wilt. Limitations: its berries are too small, too acid for best dessert flavor, and the plants sport to variegation.

Shasta (*Plate 10–3*) was bred by H. Thomas and E. Goldsmith of the University of California at Davis, introduced in 1945. This is the third most grown variety in the United States because of its large, firm, attractive berries and plants which are somewhat tolerant to virus diseases. Shasta fruits all summer on the California Coast. Limitations: it is not high-flavored, and is only fair for freezing. Perhaps as many tons of this are produced as of any variety in the world.

Headliner was bred by P.L. Hawthorne and J.C. Miller of the Louisiana State University, and was introduced in 1957. It quickly replaced the Klonmore because of its early ripening, larger berries and more productive, leaf-spot-resistant plants. Limitations: it is subject to leaf variegation and is being replaced, in part, by Dabreak with its still larger, fine-flavored berries. It is not adapted north of Louisiana.

Tennessee Beauty (*Plate 10–4*) was bred by E.M. Henry of the University of Tennessee, introduced in 1943. This is fifth in acreage because its plants are extremely productive, tolerant to virus diseases; its berry is medium late, firm, glossy red, good in flavor, easily capped, and very good for freezing. Limitations: it is drought-susceptible and it runs down in size.

Dixieland (*Plate 10–4*) was bred by D.H. Scott and George M. Darrow of the U.S. Department of Agriculture, introduced in 1953. Now sixth in acreage, this variety was introduced because of its very productive plants and its early, firm, attractive berries; it is very good for freezing and much larger than Blakemore. Limitations: its leaf variegation is serious, and it is subject to leaf scorch and to red stele; its flavor is good but not high.

Marshall (*Plate 10–1*) (see pp. 141, 143) was found as a seedling just a short distance south of Boston, Mass., and introduced in 1893. Midseason. For over fifty years Marshall was the standard of flavor in the Pacific Northwest and even in 1962 it was the seventh most grown, but only in the Northwest. Its excellent flavor, large size, freezing quality, and its drought resistance made it important. Limitations: it is not firm, and is being replaced because of its susceptibilty to virus diseases and to leaf spot and its only moderate yields.

Sparkle (*Plate 10–4*) was bred by J.H. Clarke, of Rutgers University in New Jersey, introduced in 1942. Medium late. Its extremely high yields, attractive appearance, good freezing quality, high flavor, and resistance to one strain of red stele root disease have made it a leading variety in the Northeast. Limitations: it is too soft and often small in size south of New England.

Robinson (*Plate 10–5*) was bred by J.C. Haley of Michigan, introduced in 1948. Because of its medium late season, large size, productivity, beautiful light red color of fruit, and tolerance to virus diseases, it was the third most planted variety of the United States up to 1963. It is notable as the only well known variety with part *ovalis* ancestry. Limitations: it is too soft, not highly flavored, not good for freezing, not red stele-resistant. It is rapidly being replaced by the red stele-resistant Midway of much better flavor.

Midway (*Plate 10–5*), bred by D.H. Scott of the U.S. Department of Agriculture, was introduced in 1960 for its resistance to the common strain of red stele and for its productiveness, its early midseason, medium-large, deep red, medium-firm berries of good flavor, which are very good for freezing. Limitations: it is somewhat subject to leaf spots, leaf scorch, Verticillium wilt, and drought damage, and it is sometimes too bland as far south as Maryland. It is rapidly replacing Robinson, especially in Michigan.

Catskill (*Plate 10–6*) was bred by George L. Slate of the N.Y. State Agricultural Experiment Station, and introduced in 1933. Midseason. It is liked for its large size, good flavor and great productivity. Limitations: its softness and susceptibility to leaf spot and virus diseases.

Florida Ninety (*Plate 10–6*) was raised by A.N. Brooks of the Florida Agricultural Experiment Station from seed of Missionary. Its probable pollen parent is Klonmore. It was introduced in 1952 for its very long, large, early berries; under many conditions it has high flavor even after reaching northern markets. The plants are productive. It is the chief variety of Florida. Limitations: it is subject to leaf spot and Verticillium wilt; it is not firm enough in warm weather.

Lassen (*Plate 10–6*) was bred by H. Thomas and E. Goldsmith of the University of California at Davis, and was introduced in 1945. Because of its short rest period requirement and its high production of large berries along the coast of southern California, it has been grown extensively. Limitations: it is too soft, it is not adapted to freezing and it has only fair flavor; it is being replaced by Torrey, Fresno, and Tioga.

Pocahontas (*Plate 10–7, a* and *b*) was bred by D.H. Scott and George M. Darrow of the U.S. Department of Agriculture. Early midseason, it was introduced in 1953 because of its large, attractive, firm berries, which are very good for freezing, good in flavor when fresh, and because of its very productive plants. Limitations: it is not red stele-resistant; it has good but not best flavor.

Albritton (*Plate 10–7*) was bred by E.B. Morrow of the North Carolina Agricultural Experiment Station in a cooperative program with the U.S. Department of Agriculture, and was introduced in 1951 for its late, large, uniform, attractive, firm berries of excellent flavor, which are very good for freezing. It is one of the best adapted varieties. Limitations: it is not hardy northward, and it should be more productive and larger.

Earlidawn (*Plate 10–8*) was bred by D.H. Scott and George M. Darrow of the U.S. Department of Agriculture, and was introduced in 1956. It is the earliest large, attractive, very productive variety, which is good in dessert quality and very good for freezing. Limitations: it makes few runners, and it is susceptible to Verticillium wilt and red stele.

Jerseybelle (*Plate 10–8*) was bred by F.A. Gilbert at the New Jersey Agricultural Experiment Station (Rutgers University). It was selected in 1948 and was introduced in 1955 because of its large average size, great beauty, good yields, and lateness in New Jersey. Limitations: it is tender skinned, is not adapted to freezing, is very susceptible to leaf spot, leaf scorch, and Verticillium wilt, and it is susceptible to red stele.

Siletz (*Plate 10–8*) was bred by George F. Waldo of the U.S. Department of Agriculture at the Oregon State College, and was introduced in 1955 for its late ripening, deep-red berries of high flavor, which are adapted to freezing. Its plants are resistant to red stele root disease, and are adapted to the Pacific Northwest. Limitations: its berries are too soft and not very large.

Surecrop (*Plate 10–8*) was bred by D.H. Scott of the U.S. Department of Agriculture, cooperating with the University of Maryland, and was introduced in 1956. Of all American varieties it is the most resistant to diseases—to several strains of red stele root rot, leaf spots, leaf scorch, and Verticillium wilt—and is drought resistant. It is very vigorous. Midseason. Its berries are firm, glossy light red, have good dessert and freezing quality, and they are tart. It is productive. Limitations: its tartness, and it should be larger, firmer, and more productive.

Armore (*Plate 10–8*) was bred by H.G. Swartwout of the University of Missouri, and introduced in 1950. Midseason late. Its berries average large, and are irregular, medium firm, light red, mildly subacid, and highly flavored. It is very productive. Limitations: it is not firm enough, is not adapted to freezing, and is very subject to mildew and leaf spots.

Dabreak (*Plate 10–9*) was bred by P.L. Hawthorne and J.C. Miller of the Louisiana State University, introduced in 1961. Early season. It has quickly replaced a part of the Headliner acreage in Louisiana because of its greater production and its still larger, very attractive, good shipping berries which are sweeter and higher in flavor. It is quite resistant to leaf spot and good for freezing. Limitations: it is too new to judge.

Klonmore, bred by P.L. Hawthorne and J.C. Miller of the Louisiana State University, was introduced in 1940. Early. It is highly resistant to leaf spots, and its berries are medium firm, attractive bright red. Limitations: its small size and susceptibility to leaf scorch. It has been mostly replaced by the larger and more productive Headliner and Dabreak.

Goldsmith was bred by H. Thomas and E. Goldsmith of the California Strawberry Institute and is privately grown by members of that Institute. It was introduced as Z5A in 1958. It is grown because of its productiveness, especially in the summer and early fall along the California Coast, and its good shipping quality; it has large, firm, glossy, attractive berries of fair quality. Limitations: it has fair flavor only, and is only fair for freezing.

Midland (*Plate 10–9*), bred by George F. Waldo and George M. Darrow of the U.S. Department of Agriculture, was introduced in 1944 for its very early, high-flavored, large, deep red berries that are among the best for freezing. It is adapted to southern New England south to Virginia and west to Kansas. It is usually resistant to leaf spot and leaf scorch. Limitations: it is not fully hardy, not very firm, its color dulls after picking, and it is susceptible to virus diseases.

Empire, bred by George Slate of the New York Agricultural Experiment Station, Geneva, New York, was introduced in 1951 for its attractive, light red berries of good flavor, and its very productive plants. Midseason. Limitations: it is not firm enough south of New York and New England, and it is susceptible to leaf spots.

Redstar (*Plate 10–9*) was bred by George M. Darrow of the U.S. Department of Agriculture, and introduced in 1940 for its lateness, its attractive berries of medium firmness, which are rather tart but good to very good in flavor. It is resistant to leaf spots and scorch, and is tolerant to virus. It is adapted to northeastern United States west to Missouri. Limitations: it is not productive enough, and is not resistant to red stele disease.

Vesper (*Plate 10–10*) was bred by J.N. Moore while at the New Jersey Agricultural Experiment Station (Rutgers University), and was introduced in 1962 because of its very large size, very attractive appearance, its very high yield, and its very late season in the Northeast. Limitations: it is very susceptible to leaf diseases and to Verticillium wilt. It is not of high flavor, and is too soft south of New Jersey.

Donner, a variety bred by H.E. Thomas and E.V. Goldsmith of the University of California, was introduced in 1945 for its high flavor. It is not grown in California now, but it is the second most grown variety of Japan. Limitations: it is not so productive in California as Shasta.

Tennessee Shipper (*Plate 10–10*) was bred by E.M. Henry of the Tennessee Agricultural Experiment Station. It was introduced in 1942 for its early, very firm fruit, which is well adapted to freezing. It resulted from a backcross of Blakemore to Missionary and it is a notable parent for firmness. Limitations: it is too small and too tart for dessert.

Fresno (*Plate 10–10*), bred by R.S. Bringhurst and V. Voth of the California Agricultural Experiment Station, was introduced in 1961. It is a sister of Torrey and Tioga. It possesses low chilling requirement. It is more attractive, larger, firmer, caps easier than Lassen which it is replacing in southern California. Limitations: it is too new to judge.

Torrey (*Plate 10–10*) was bred by R.S. Bringhurst and V. Voth of the California Agricultural Experiment Station, and introduced in 1961. Like Fresno, it is more attractive, larger, firmer, and caps easier than Lassen. It has the lowest chilling requirement of California varieties. Limitations: it is too new to judge.

Tioga was bred by R.S. Bringhurst and V. Voth of the California Agricultural Experiment Station. It was selected in 1955 from about 900 seedlings of the same cross as Fresno and Torrey (Lassen x Cal. 42.8—16) and released in 1964. It is about 10 percent larger than Lassen and larger than Fresno, Shasta, and Torrey. Like Fresno, it is more attractive, much firmer, and caps easier than Lassen. It is more productive than Lassen and wider adapted in coastal California. Limitations: it is too new to judge but considered very promising.

Solana was bred by R.S. Bringhurst and V. Voth of the California Agricultural Experiment Station. It was introduced in 1957 for its high flavor, short rest period requirement, and tolerance to salinity and virus diseases. It is the chief variety in Oxnard and Fresno areas of California. Limitations: it is not a good freezing berry.

Suwannee (*Plate 10–10*), originated from the cross Missionary x Howard 17 (Premier) made by George F. Waldo in 1931, was selected in 1933 by G.M. Darrow and J. R. Magness and introduced in 1945 jointly by the Mississippi Agricultural Experiment Station and the U.S. Department of Agriculture. This sister of Blakemore was introduced for its high flavor, even under adverse conditions. It is similar to Blakemore in runner production, resistance to leaf diseases, and berry size, but it is more glossy and softer. It ripens about four days after Blakemore. It has been entirely free from the Blakemore yellow variegation. It is sensitive to virus diseases and all stocks were infected. Recently (1964) plants were freed of virus by heat and runner tip propagation. It is still the highest flavored of American varieties, though equalled at times by Fairfax, Midland, Rockhill, and Fletcher when at their best.

Strawberries of Canada

Until very recently, the varieties grown in Canada have been mostly the same as those grown in northern United States. In the 1920's Marshall, Magoon, Dunlap, and Paxton (Sir Joseph Paxton?) were leading varieties in British Columbia. The notable exception has been British Sovereign, a high-flavored, productive kind found in 1920 in a Magoon strawberry field in British Columbia. By about 1928 it had become an important variety there; and is even now (after Northwest) still their second most important sort, though subject to red stele and mildew and not adapted to freezing.

Agassiz (Pathfinder x British Sovereign) was introduced in 1957 by the Dominion Station at Agassiz, British Columbia, for its superior freezing quality, large size, and hardiness but it is susceptible to red stele and mildew. It is grown to a limited extent in British Columbia only.

Dunlap and Howard 17 (Premier) have long been the major varieties of eastern Canada but are rapidly being replaced by Redcoat, which was introduced in 1957, and which is a very productive, very attractive variety from the Ottawa Central Farms Station. Cavalier, Guardsman, and Grenadier from the same station, also introduced in 1957, are of some importance in eastern Canada. It seems probable that, just as in the United States, many well-adapted varieties have been originated only to be lost after being infected by virus diseases. Valentine [Howard 17 (Premier)] x Vanguard (Pocomoke X Early Ozark), introduced in 1941 by the Vineland, Ontario, Station for its earliness and large size, is one of these. It has proved to be a valuable parent both in Canada and in Scandinavia.

In the Prairie Provinces, though the acreage is not large, notably hardy varieties are being bred, up to now in large part by private breeders, among whom are W. Oakes, who introduced Glenheart (everbearing), Glenmore, and many others, and A.J. Porter who bred Sparta, Jubilee, and Parkland (all everbearers), and others.

Redcoat (Sparkle x Valentine, *Plate 10–11*) was introduced in 1957 for its extremely high yield, very good appearance, firmness in Canada and its earliness (of Dunlap season) and very good shipping qualities. It is rapidly replacing Dunlap, Howard 17 (Premier), and others over a wide area of eastern Canada as the major variety. It is resistant to mildew and is quite hardy. Limitations: it is too soft in United States, thus is not suited to processing. It is susceptible to Verticillium wilt and leaf spot.

British Sovereign (*Plate 10–11*) was found in a planting of Magoon in British Columbia, and introduced in 1923. It is one of the two main varieties in British Columbia (Northwest is the other) because of its large, attractive, high-flavored, firm fruit, and is about 40 percent of the total. Limitations: it is not well adapted to freezing and is susceptible to red stele and mildew. It is said to resemble the Sir Joseph Paxton.

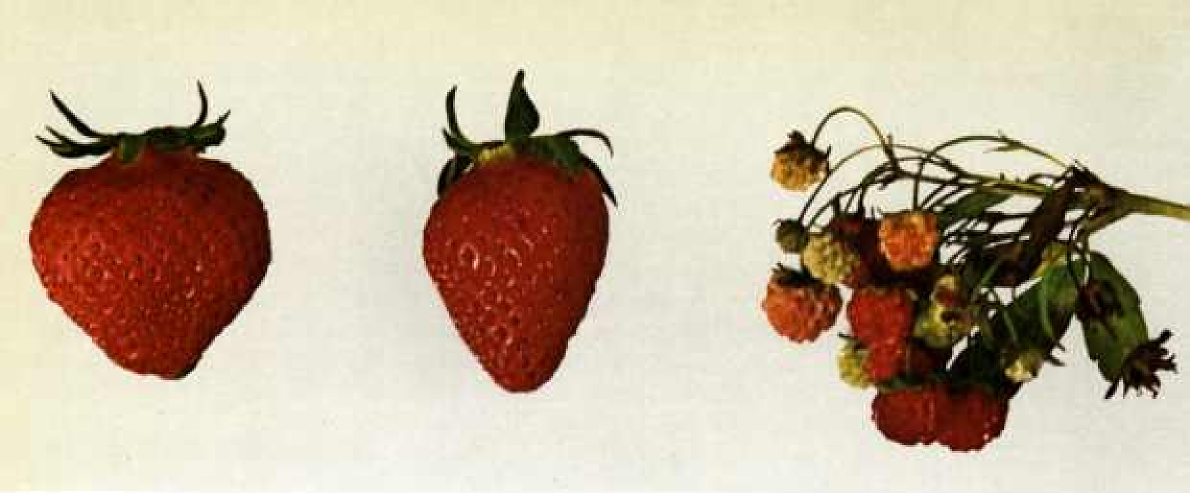
Cavalier (Valentine x Sparkle, *Plate 10–11*) was introduced in 1957. Its season is very early, about with Midland. It is firmer than Catskill in Canada, has good flavor and is good for processing. It is resistant to Verticillium wilt, but is susceptible to mildew, scorch, and leaf spots.

Des Alpes

Green Strawberry

American Scarlet

PLATE 7-4



ABOVE. It is possible to obtain selected seedlings from a cross of a variety with a selected wild plant as large as the variety parent. 3318 Blakemore x *Ovalis*. U.S.D.A. photo.

RIGHT. Selection from cross of Earlidawn x *chiloensis* (seedling of Red Chilean). U.S.D.A. photo. (See also Plate 14-2 and Plate 14-4.)

BELOW. A productive large-fruited pistillate Virginian #27, selected near Highlands, N. C. Note deep-set seeds in pits. (See also Plate 14-4.)

PLATE 8-1

(ABOVE LEFT) A fruit cluster of *virginiana* — (ABOVE RIGHT) "Sheldon" x Midland showing its great productiveness and low-branching fruit clusters (BELOW).

PLATE 8-2

A clone of the beach strawberry growing on the sand dunes of the California coast. This clone has held the sand for many years.

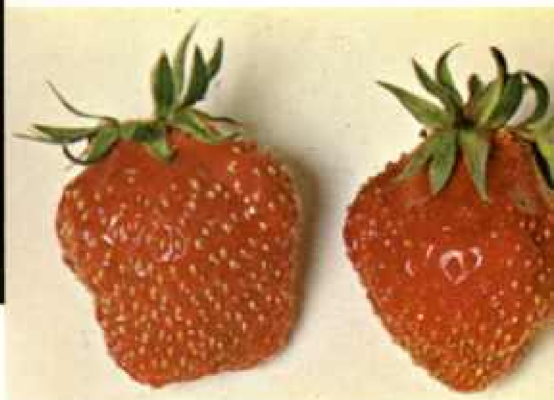
PLATE 9-1

A pistillate of beach strawberry on the California coast.

Marshall

Missionary

Aberdeen



Dunlap

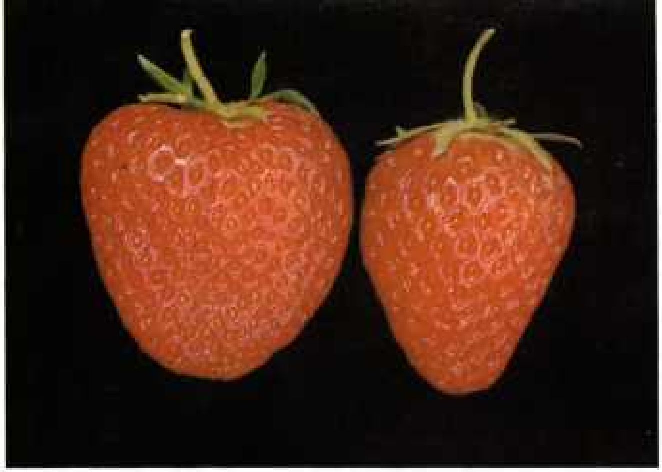
Howard 17

PLATE 10-1

Fairfax

PLATE 10-2

Blakemore



Northwest

Aroma (1/4 lifesize)

Shasta

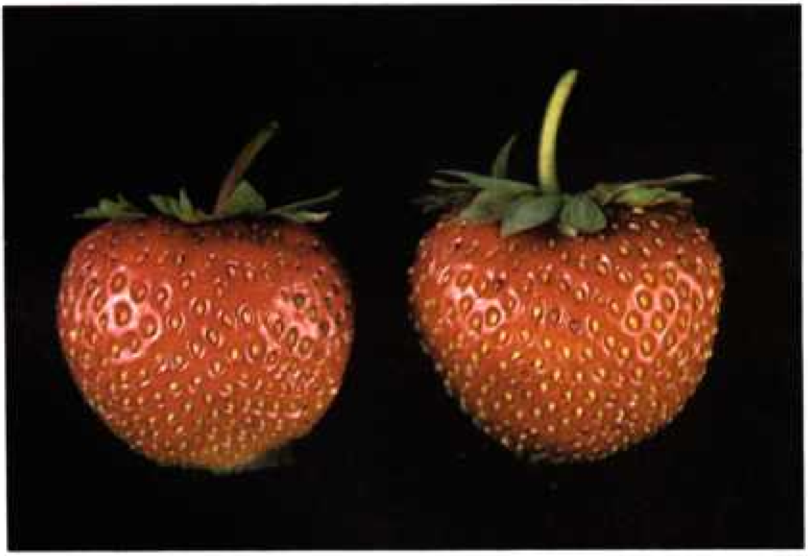
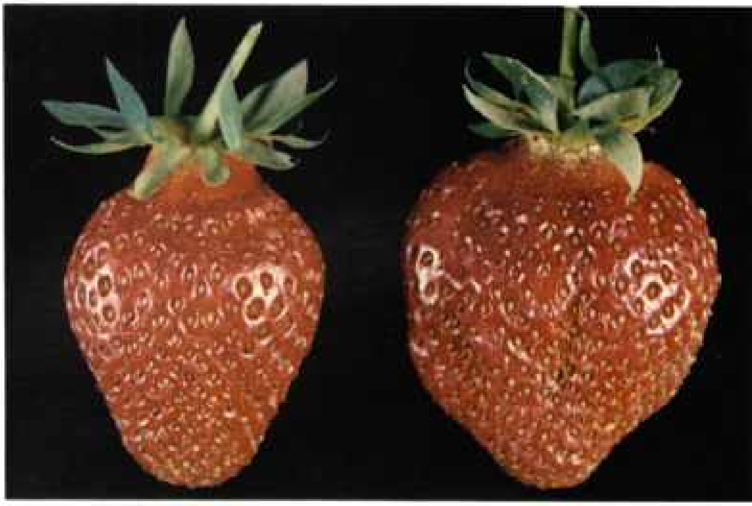


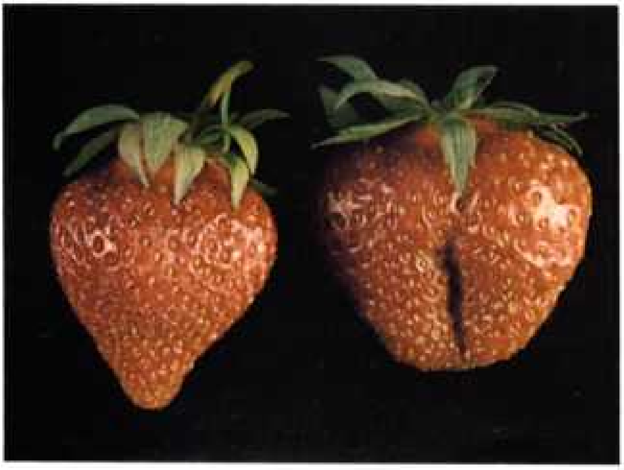
PLATE 10-3

Sparkle



Dixieland

PLATE 10-4

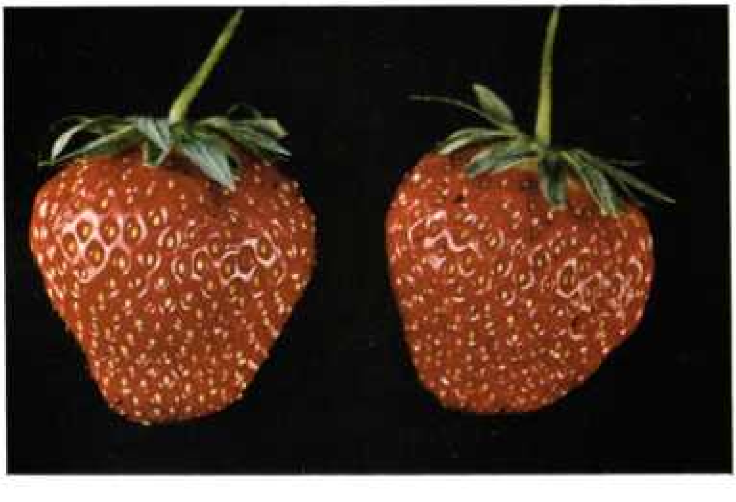


Tennessee Beauty

Robinson

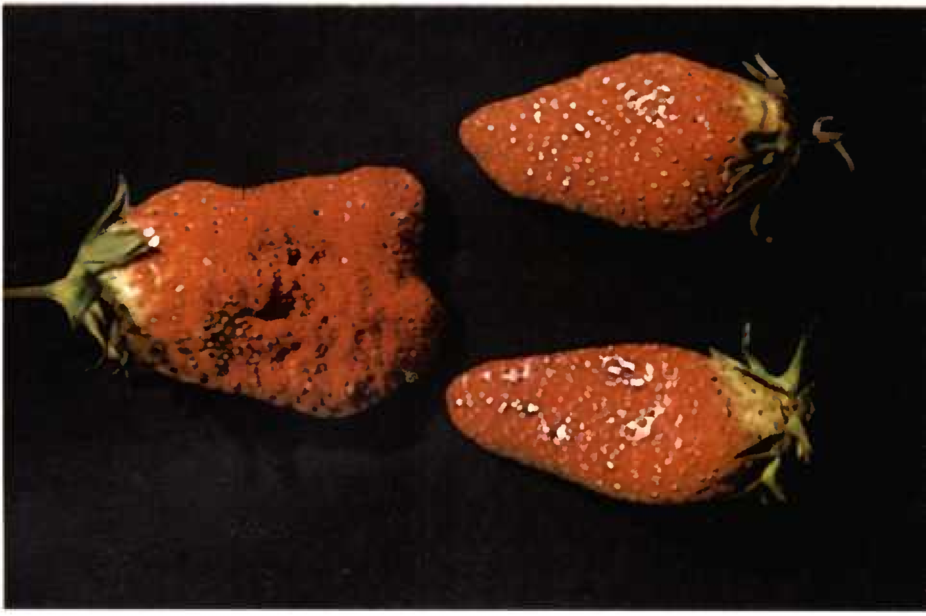
PLATE 10-5

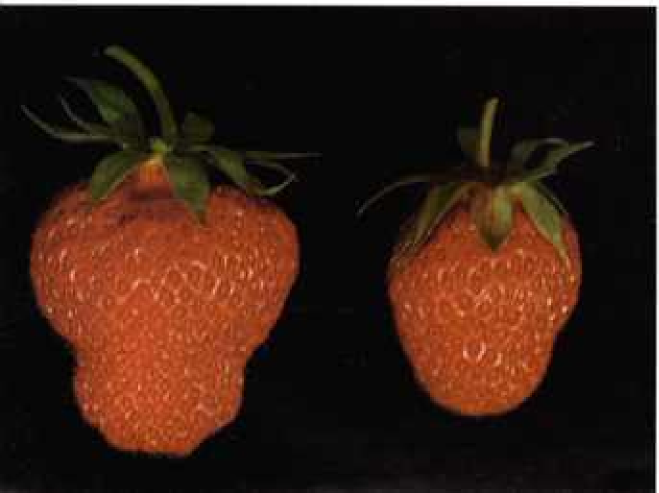
Midway



Catskill

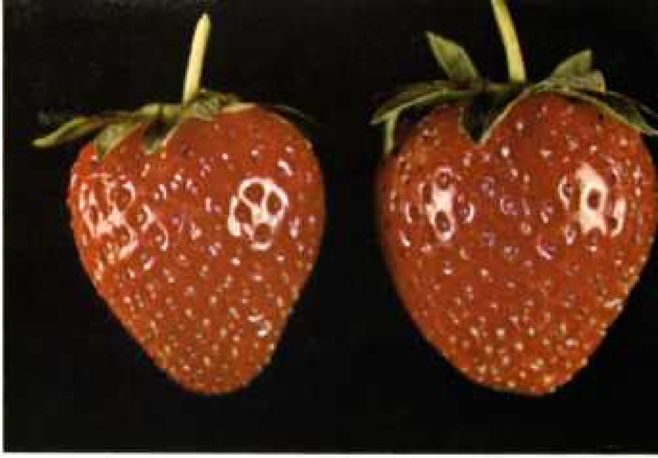
Florida Ninety





Lassen

PLATE 10-6

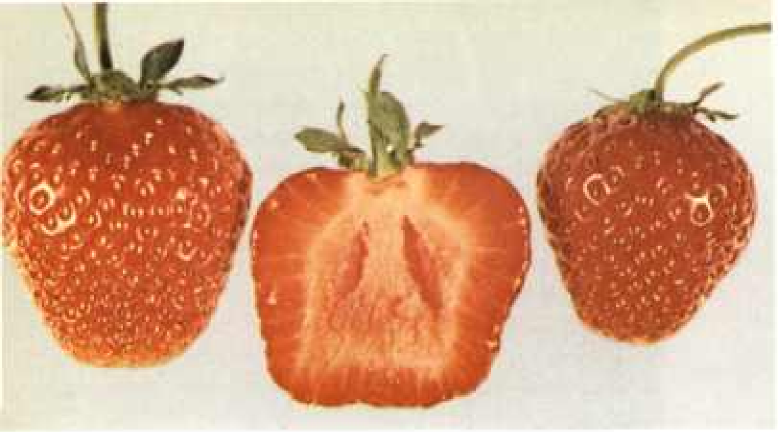


Albritton

PLATE 10-7

Pocahontas

Pocahontas in Basket



Earlidawn

Surecrop

PLATE 10-8

Jerseybelle

Siletz

Armore

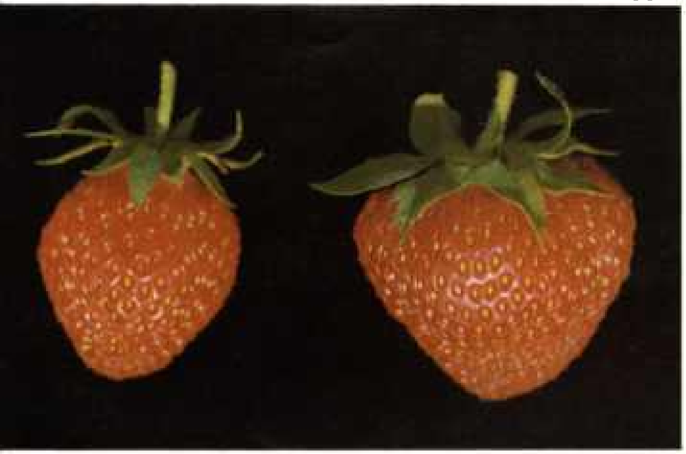
Redstar

Dabreak (½ lifesize)

PLATE 10-9

Midland

Tennessee Shipper



Vesper

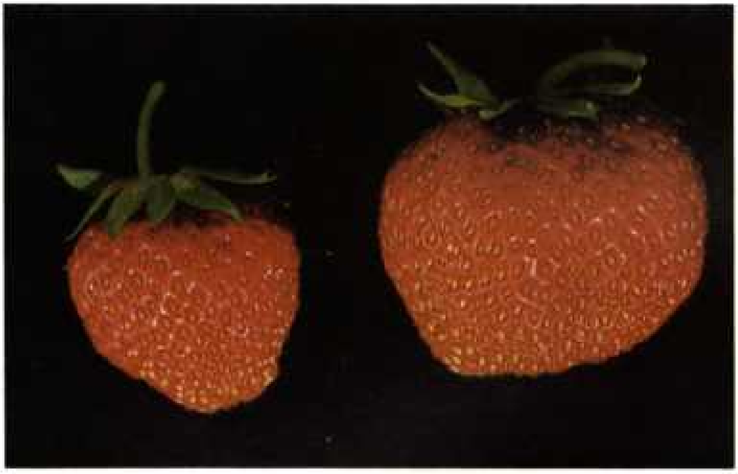
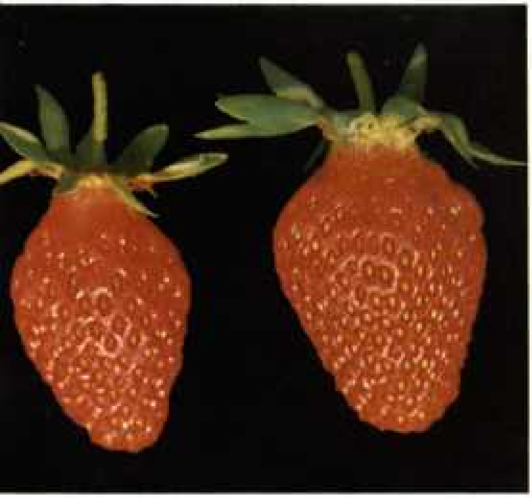


PLATE 10-10

Torrey

Suwannee



Fresno

British Sovereign

Cavalier

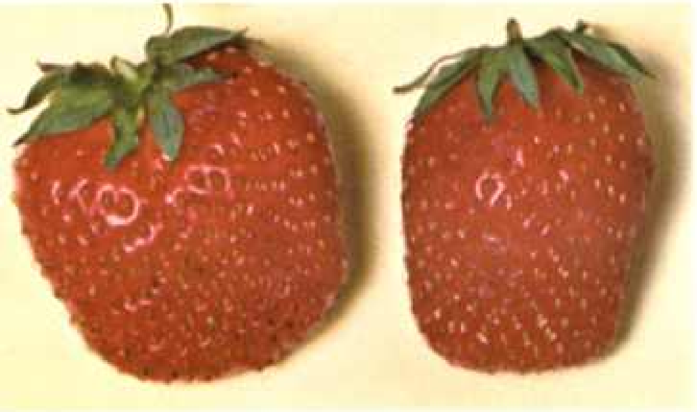


PLATE 10-11

Redcoat

Redcoat in Basket


Gem

Climax

PLATE 11-1

Guardsman (Claribel x Sparkle, *Plate 10–8*) was introduced in 1957 for its very late season, excellent flavor and very high yields. It is resistant to red stele and mildew, but is susceptible to Verticillium wilt and it runs down in size too quickly.

Grenadier (Valentine x Fairfax) was introduced in 1957 for its dark red, firm, good flavored berries. It is good for processing but is susceptible to mildew, and it drops in size quickly.

Mexico

Up to the very recent postwar (World War II) period, a small acreage of probably pure *chiloensis* varieties called "Negrita" and "Poderosa" or "Criollo" had been grown near Irapuato, a mile-high plateau region about two hundred miles northwest of Mexico City (Darrow, 1953). Since the war period, Klondike, Klonmore and Blakemore have been grown and now Klondike, Florida Ninety, and some Solana are the varieties grown. Klondike is liked by buyers because of its excellent freezing quality and most of the berries are frozen for shipment to the United States and Canada. But yields of Klondike are low. Florida Ninety has replaced it and others in large part, for it is good for freezing, though not equal to Klondike, is much more productive and ripens in November and December, so that large quantities are shipped fresh to the United States from November until berries from Texas, California, and Louisiana ripen.

Varieties for processing

The chief uses of processed strawberries are freezing for later preserving and packaging for dessert use. About half of the total crop of the United States is so processed and the other half sold in fresh fruit markets. Some berries are used in ice cream and for ice cream topping. At one time the very small berries of the Clark, grown near Hood River, Oregon, were separated out at harvest and sold for candy centers; the syrup drained from cans of frozen berries is used as a flavoring for soft drinks and candy; and, in Chile, one factory has canned the White Chilean for use as a berry in a glass of wine, but these are minor outlets.

Varieties for preserving should be medium to light red to the center. They should be firm, subacid to acid, and aromatic. Blakemore, Earlidawn, Dixieland, and Pocahontas are among the best in the United States. Some of the varieties used include: in the West, Northwest (too dark for best), Marshall (too soft but high flavor), Shasta (lacks acid and flavor); in the South, Florida Ninety (too soft in warm weather), Blakemore; in the Central and Northern

States, Tennessee Beauty, Pocahontas, Dixieland, Earlidawn, and Sparkle (too soft and dark). Senga Sengana is considered excellent in northern Europe.

Varieties processed by freezing for dessert and for ice cream topping should be somewhat deeper red and more red to the center (as Northwest) than those for preserving, but also should be firm. They should also be subacid to acid and aromatic. Actually, for the most part, the same varieties are used as for preserving.

Caldwell and Culpepper (1935) studied many varieties and suggested that medium-sugar, high-acid, and medium-astringency most nearly describes a variety desirable for preserving. They listed Klondike, Dunlap, and Missionary as meeting these specifications. Klondike was average in sugar content, but its high acid-astringency and acid-solids ratios made it the most acid of the group.

New Varieties in North America

New varieties just introduced include *Earlibelle* (U.S.D.A. and North Carolina, Albritton x Md.-U.S.–2101), an early high-flavored, attractive, firm shipping variety for eastern North Carolina; *Sunrise* (U.S.D.A. and Maryland, U.S.–4152 x Stelemaster), an early red stele-resistant dessert variety for the New Jersey to Missouri areas; *Tioga* (California, Lassen x Cal. 42.8–16), a general purpose variety for California of the same cross as Fresno and Torrey but larger. It is reported to be much firmer than Fresno and even more productive than Lassen.

Acadia (Nova Scotia) is the first variety introduced by Craig and Aalders of the Kentville Research Station—a Redcrop x Sparkle cross selected in 1959 and released in 1965. Compared to Sparkle it is two to three days earlier, as high in flavor, slightly larger, as productive but somewhat more susceptible to leaf spot and leaf blotch. *Citation* (Kentucky, Fairland x Tennessee Shipper) was selected in 1953 and introduced in 1964 as a very productive, firm, deep red, midseason variety with high processing quality and is suggested for the area where Pocahontas succeeds. It is not red stele resistant and is quite susceptible to mildew.

Strawberry Varieties of the World

The world acreage of strawberries is probably between 300,000 and 400,000 acres, of which about 130,000 are in North America, 20,000 in Japan, and the rest mostly in Europe. About 27 varieties each of which comprise 1 percent or more of the acreage are as follows:

Variety	Estimated acreage	Where chiefly grown
Madame Moutot	40,000	Europe
Northwest	20,000	Oregon, Washington, British Columbia
Senga Sengana	20,000	Europe
Blakemore	14,000	Southern United States
Purpuratka	10,000	Poland
Cambridge Favourite	10,000	England and Europe
Klondike	9,000	Mexico
Florida Ninety	9,000	Mexico and Florida
Kogyoku	8,000	Japan
Shasta	6,000	California
Donner	6,000	Japan
Sparkle	6,000	Northeast United States and Canada
Tennessee Beauty	5,000	Central United States
Headliner	5,000	Louisiana
S. de Chas. Machiroux	5,000	Italy
Jucunda	5,000	Yugoslavia. Holland
Surprise des Halles	5,000	France
Redcoat	4,000	Eastern Canada
Robinson*	4,000	Michigan
Midway	4,000	Michigan
Marshall	4,000	Oregon and Washington
Dixieland	4,000	Eastern United States
Regina	4,000	Europe
Cambridge Vigour	3,000	England
Catskill	3,000	Northeastern United States
Pocahontas	3,000	Eastern United States
Others	90,000 or more	

*Rapidly being replaced by Midway

These 27 varieties probably comprise about two-thirds of the world acreage, and in 1965 are the most important varieties. Why are they so widely grown? We do not know all the factors, but these 26 probably contain in varying degrees most of the important characters of ideal strawberries. Some of these varieties have certain qualities that helped make them important: M. Moutot, Shasta, S. de C. Machiroux have large size; Northwest, Senga Sengana, Blakemore, Purpuratka, and Klondike have fine freezing quality; Jucunda has fine capping quality; Blakemore and Dixieland have fine shipping quality; Florida Ninety has fine quality from December to March on the northern United States market; Donner, Sparkle, and Marshall have fine local market flavor; Redcoat and Senga Sengana have hardiness; Blakemore, Klondike, Florida Ninety, Headliner, and Surprise des Halles have low chilling requirements. But each must have many other qualities too. Of these 27, Mme. Moutot, Blakemore, Robinson, Marshall, Jucunda, and Klondike are being replaced by varieties of greater market value; the last three rather rapidly because they are less productive than newer varieties and Robinson because of its softness and low flavor. Cambridge Favourite, Senga Sengana, Midway, and Redcoat are increasing in acreage because they include in their makeup more of the desirable qualities that are needed to keep the strawberry an important world crop and food plant. As such, the strawberry is raised under intensive culture with a high return per acre, often on high-priced land near large centers of population, as well as in areas remote from the ultimate market where transportation costs are higher as a result.

For the strawberry to continue as a major crop with a high per acre return, some basic requirements are: still higher yields, moderate production costs, and more appealing berries for consumer demand. Much higher yields have been demonstrated as possible through improved cultural methods and breeding for higher yielding varieties. Much larger berries for cheaper picking costs; firmer berries for less rot in the field, in markets, and with the consumer; varieties of higher flavor for freezing and fresh use; berries holding high flavor for several days in shipment; and varieties resistant to the many diseases—these are some of the problems faced by breeders, whose solutions are being sought at research stations in widely different areas. And some answers already have been found in such varieties as Redcoat for Eastern Canada, Northwest for the North Pacific States, Catskill, Armore, Earlidawn, Sparkle, Midway and Pocahontas for the Northeast, Florida Ninety for Florida, Dabreak for Louisiana, Tioga and Goldsmith for California, Talisman and Redgauntlet for Scotland, Cambridge Favourite for England, and Senga Sengana for North Europe. These varieties give hope that still better answers will be found, such as a Northwest with lighter color for preserving, a firmer Catskill not so sensitive to viruses, a firmer Armore resistant to mildew, and an Earlidawn that produces more runners, etc. Ideal varieties would have the size of Senga Gigana in Germany, the length and size of Florida Ninety and Fukuba where they are adapted, the firmness of Dixieland, the market flavor of Florida Ninety in winter, the beauty of Jerseybelle and Albritton, the yield of Tioga, Armore, Earlidawn, and Catskill, and the red stele root rot and leaf diseases resistance of Surecrop.

We now know that there cannot be just one variety grown universally. Day-length and low-chilling requirements are such that there must be some varieties for the far south and others for different climatic complexes.

11

Everbearing Strawberries

FOR HUNDREDS OF YEARS varieties of everbearing strawberries have grown wild and under cultivation in Europe. Everbearing strawberries, however, are comparatively new to North America. The reason is: the wild everbearing form, *F. vesca semperflorens,* is native to Europe; in North America, however, no such character is fully inherent to native species. It wasn't until around 1900 that North America had a tenable commercial everbearing variety. This variety and the ones coming after it, however, were essentially different from the early European everbearers, for they were octoploids, whereas *F. vesca semperflorens* was a diploid. This small-fruited diploid has now been supplanted largely in Europe by octoploid everbearers, so everbearers in the United States and Europe since 1900 bear a "family" resemblance hitherto nonexistent. The material which follows describes everbearers, both those of the past, especially in Europe, and those which are grown today in North America as well as in Europe.

The Diploid "Everbearers": Alpine-Runnered and Runnerless

The mid-1700's in Europe and England saw the introduction of the Alpine, Quatre Saisons, or perpetual, autumn or everbearing strawberry, *F. vesca semperflorens.* These Alpines, which were among the first strawberries grown in Europe, found at several places in the Alps, are mutants of the European wood strawberry, *vesca.* They form flower buds and produce fruit from early summer to late fall. They are of two types; those that produce runners and fruit all summer, and those that produce no runners and are propagated by seed, or by dividing an old plant into its many crowns. This

FIG. 11–1. *F. vesca semperflorens.* The fruit clusters shown are of Erige du Poitou, a runnerless variety of the everbearing, or Alpine form of *F. vesca.* It is still quite widely grown in France because of its delightful vinous aroma. This is a 14-chromosome species which crosses with difficulty with 56-chromosome garden strawberries. Seedlings from such a cross bear imperfect fruit.

second type produces many secondary stems or branch crowns, unlike the type which produces runners.

Although mentioned as early as 1553, the runnered-type of everbearer was not well known until about 1765, when plants were obtained for the Royal Garden of France from Bargemon in Provence where it grew abundantly in the wild. Seed was also brought from Mt. Cenis in Italy in 1764. The original runnerless type called Bush Alpine or Gaillon strawberry was obtained at Gaillon in 1811 by Labaute. Possible mention of it dates back to 1652. The runnerless type forms large plants which bear berries of larger size than the runnered type. The berries of both types are borne on tall fruit stems well above the leaves (*Fig. 11–1*). The berries of the runnerless may be quite large for the wood strawberry and vary from blunt-conic to very long conic and may be even more than 1 inch long. Berries of both types are light and spongy, with air spaces throughout the flesh. The berries have little flavor until they are ripe, when the perfume, which differs from that of large-fruited varieties, becomes strong. For full flavor, Hyams (1962) suggests slightly crushing the berries, sprinkling them with sugar, then covering and leaving them for several hours.

Only slight differences exist between early varieties of diploid everbearers and those grown now. A well-known variety selected in Germany is Baron Solemacher and seed of it and others is available in the United States and England. A white variety of it is also known. In France Reine des Vallies and the red Gaillon are two well-known runnerless kinds, and Brilliant and Belle de Meaux are good runnered Alpines. Monstrueuse Caennaise with larger fruit is classed as a runnerless Alpine.

There may not be over fifty acres of the wood strawberry under cultivation in all the world and those fifty acres are mostly in France, northern Italy, and in Austria. One of the largest areas is near Tortoma in northwest Italy where selections of plants from the surrounding hills are grown for the highly flavored fruit for the Milan market (see p. 293). Besides the cultivated areas some fruit is still picked from native wild plants.

The Octoploid Everbearers in America

In the shortening days and lowering temperatures of late summer and early fall, strawberry plants normally respond by developing flower buds in their crowns. But the ordinary garden strawberry, being an exceedingly variable plant, has, in its development of flower buds, a great range of response to temperature and day length; a range which can be observed in all octoploid species in the wild, quite frequently in *F. virginiana* in the North, very commonly in *F. ovalis,* and at least to some extent in *F. chiloensis.* As a result, examinations during the summer and fall show many wild plants growing in various areas of North America to be in flower, some at one time, some at another. A large percentage of plants of *F. ovalis,* collected in many parts of the western United States, blossomed throughout the summer and fall when grown in Maryland; some also respond this way at Cheyenne, Wyoming. If the days are artificially shortened to eight hours, varieties like the Missionary initiate some flower buds in quite hot weather in midsummer in eastern United States, while other varieties do not form flower buds with eight hours of light unless the temperatures are much cooler; the Klondike will not form flower buds until October under normal conditions. The so-called everbearing strawberry varieties do not differ in kind from this general sort of response, but only in degree; they normally form flower buds even when days are sixteen or more hours long. The present everbearers grow very little in the short days of winter (*Fig. 11–2,* Chouard, 1943). In the breeding of everbearers, man has emphasized the character of summer and fall flowering. This character is actually just a specialized sort of response to the effects of temperature and day length, for all varieties can be made to be everbearing under short days and low temperatures; each variety having a certain day

FIG. 11–2. Growth of an everbearing (*left*) and a southern (*right*) variety during midwinter in the greenhouse, Washington, D.C. Most everbearers have been bred in the North, require a low-temperature rest period, and do not grow in the short days of midwinter.

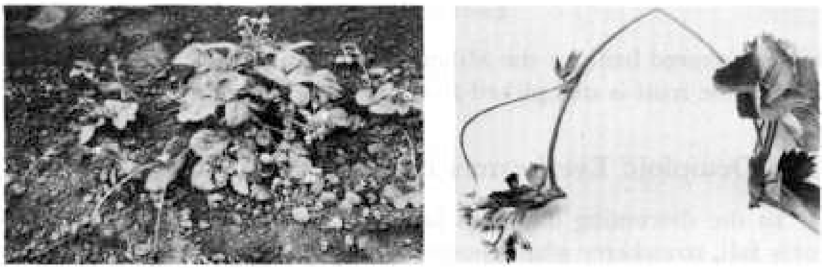


FIG. 11–3. (*left*) An everbearing strawberry plant set in the spring, showing runner plants blossoming soon after forming, even before rooting. Photographed July 16. (*right*) A runner plant of the Progressive variety at the left which has formed a flower bud. Everbearing varieties vary from those which produce throughout the summer on the mother plant only, to those which produce on all runner plants as soon as they are formed. Photographed in June.

length-temperature complex, whether very specific, or relatively broad, at which it succeeds best. Some varieties bred with emphasis on summer and fall blooming give the highest production in the world, under the cool temperatures along the California coast, but in the eastern states they produce only in the usual short season of June. In Europe some everbearing varieties produce all summer, but others are called "two-crop" varieties, for they seem to make no flower buds until after the longest days are past. In Holland growers take advantage of this response of some varieties by artificially shortening the days during the last of May to start new flower bud initiation for a fall crop.

Because so many genes are involved, the pattern of flower and fruit production is extremely variable. The everbearing varieties selected out and named are those that have the best production habit in the mind of the person selecting that variety for his latitude. Among the recent everbearing varieties in the United States, Ozark Beauty was selected in Arkansas for its adaptation to that climate. Although mother plants of this variety produce both runners and fruit freely, the runner plants do not usually produce any fruit the first year, as do those of most other kinds (*Fig. 11–3*). Other everbearing varieties produce fruit so continuously that few, or no, runners are formed, and the variety is difficult to propagate (*Fig. 11–4*). The most desirable varieties, besides producing a good crop, have enough vigor to produce a sufficient number of runners and flower buds for that variety's propagation. Runnerless varieties may be raised from seed or by crown division.

A valuable character of the everbearers of the United States and Canada is that they usually are quite hardy. If at any time it happens that their flowers are killed by frost, most varieties recommence flower and fruit production immediately. The American wild everbearing forms have yet to be utilized in the production of cultivated everbearing sorts, so their value is not yet known.

The history of everbearing varieties in the United States is given in the U.S. Department of Agriculture's *Farmers' Bulletin 901,* first issued in 1917, and as such, the history does not date very far back. Cultivated large-fruited everbearing strawberries have been known for only 75 years and have been important for fifty to sixty years. No European everbearers have become of commercial importance in the United States.

Although the Oregon Everbearing (a supposed seedling of Triomphe originated in 1882 in Oregon) was introduced in 1890, it was not generally successful. Pan American was the first important everbearing variety in the United States. It was selected by Samuel Cooper (*Fig. 11–5*) of Delevan, New York, from a patch of Bismarck where its unusual characteristics drew his attention to it. Its runners were flowering and fruiting on September 28, 1898. When he planted these apart they continued to flower and fruit throughout the growing season and he introduced the variety as Pan American in 1902. Both he and others who compared plants considered the Pan American to be a mutant of the Bismarck (reported to be Bubach x Van Deman). Van Deman was Crescent x Captain Jack (a supposed seedling of Wilson). Pan American was important especially as a parent. Mr. Cooper later introduced 9 other varieties, all descended from the Pan American, of which the (Superb autumn x *Cooper*) x *Sherman* (all *Pan American seedling*) succeeded best.

Another contributor to the development of everbearing strawberries was Harlow Rockhill (*Fig. 11–6*), who obtained the Pan American from Cooper in 1904, and in 1908 crossed it with Dunlap to obtain the Progressive, the leading everbearer for many years. Progressive, like Superb, was exceptionally resistant to leaf-spot disease and very hardy, obtaining hardiness from both parents. Later Rockhill introduced the Rockhill (*Wazata, Bonanza, Big Sweet, Fig. 11–7*) from the cross Early Jersey Giant x Progressive.

Many other fine everbearers have been introduced. Mastodon (Kellogg's

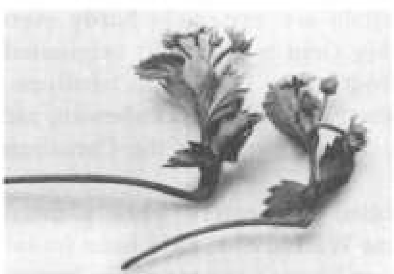


Fig. 11–4. Everbearers may fruit on runner plants. At the right, terminal bud of a runner plant which developed into a flower bud as soon as the first leaf had been differentiated. The runner plant at the left developed a second leaf before the terminal became a flower bud. June 21.

FIG. 11–5. Samuel Cooper of Delavan, New York, in a field of Superb, his most successful variety. Cooper started everbearing varieties in the United States when he found on September 28, 1898, a plant and its runners fruiting in his field of Bismarck and named the new variety Pan-American.

FIG. 11–6. The Progressive strawberry on the place of its originator, H. Rockhill, who is shown in the field, Conrad, Iowa, September 22, 1916.

Prize x Superb) was from a cross made by G. Voer of Indiana, selected in 1917, and introduced in 1921. Although the least flavorful of well-known everbearers, it was widely grown until recently, because of its disease resistance, large fruit, and free runner production. Twentieth Century, selected in 1926, was from a cross made by T. Kasuga. Gem was introduced in 1933 by Keplinger and reintroduced by him as Superfection (1946) and Brilliant (1951). It has been the leading everbearing variety since about 1945. Streamliner of unknown parentage, found in 1938 by Edgmond in Oregon and introduced in 1944, has high flavor. Red Rich, bred by M. Hagerstrom and introduced in 1949, has many characteristics of the Rockhill, but seems even more restricted to northern areas. Most of its fruits are tiny at Beltsville, Maryland. Geneva, bred by G. Slate and introduced in 1961 at the New York Agricultural Experiment Station, has high flavor, is large but soft.

Recently Ozark Beauty (1955), Arapahoe (1954), Ogallala (1956), and other new everbearers have been grown considerably. Arapahoe, Radiance, and Ogallala resulted from the breeding work at the Cheyenne, Wyo., Horticultural Station. Both Arapaho and Ogallala are extremely hardy even northward into Canada. Glenheart (probably Gem x Rockhill) originated with William Oakes, Manitoba, and was introduced in 1941 for its hardiness. Sparta, Parkland, and Jubilee from A.J. Porter, Parkside, Saskatchewan, are other very hardy varieties, of unknown parentage, grown in the Canadian prairie provinces.

In recent years, several privately controlled everbearers, when planted in December in coastal central California near Watsonville, have been found to produce heavy crops the first year, and have become commercially important there.

The shallow root system of the strawberry makes the everbearing sorts, which ripen in mid- and late summer when the transpiration rate is high, especially subject to drought injury. Often before the plants recover from one hot drought period another occurs to check growth and fruit production. The production of fruit over a long period also requires a fertile soil high in nitrogen. Because the flower clusters develop from buds in leaf axils in place of runners, everbearing sorts are shy runner producers. For these reasons everbearers are successful only where the rainfall is ample and the soil is fertile in northern United States and Canada and at high elevations in the Appalachians of North Carolina.

Present Everbearing Varieties of the United States

Gem (*Plate 11–1a*) reported as a bud sport of Champion by F.J. Keplinger of Michigan, introduced in 1933 and re-introduced as Superfection and Brilliant by him. In eastern states soft, rather small, irregular, acid but good flavored; in Great Plains and westward larger fruited. Plant very hardy. A leading everbearer since about 1940.

Rockhill (*Wazata*), bred by Harlow Rockhill of Iowa, was introduced in 1923, Early Jersey Giant x Progressive. It has excellent flavor, is attractive, plant is very hardy, resistant to leaf spot, makes few runners.

Red Rich (Rockhill x Fairfax), bred by M. Hagerstrom of Minnesota, introduced 1949. Hardy, excellent flavor, attractive, heavy crops of large to very small berries, resistant to leaf spots and leaf scorch, makes few plants.

Ozark Beauty (Red Rich x Twentieth Century), originated with J.B. Winn of Arkansas. Introduced 1955 for its runner-plant production, attractive, sweet good-flavored berries. Mother plant very productive, runner plants usually produce no berries.

Arapahoe (Cheyenne 1 x Selection 430–2) x (Rockhill x Cheyenne 3) (Selection 430–2 is (*F. ovalis* x Fairfax) x Fairfax), bred by L. Powers, E.D. Krouch and D.H. Scott, U.S. Department of Agriculture, Cheyenne, Wyoming. Introduced in 1954 for its extreme hardiness and drought tolerance. Berries

FIG. 11–7. To left, the Rockhill everbearing strawberry; to the right the Pres. Meuren, a variety of the Alpine everbearing strain of *F. vesca,* the wood strawberry of Europe.

medium size, firm to soft, glossy red, very good flavor. Usually produces many runners.

Ogallala, bred by L. Powers, U.S. Department of Agriculture, Cheyenne, Wyoming, selected by G. Viehmeyer of North Platte, Nebraska, and introduced in 1958; high flavored, medium to large, very hardy, resistant to leaf spots.

Geneva (NY-316 (Streamliner x Fairfax) x Red Rich), bred by George Slate of the New York Agricultural Experiment Station and introduced in 1961. Fruit large, high flavored, deep red, soft.

Twentieth Century (Berri Supreme x Rockhill), bred by T. Kasuga, Utah, introduced 1932, high flavored.

European octoploid everbearers ("Remontant" or "Perpetual")

France. According to Richardson (1914), the first perpetual strawberry, widely known in France was "Gloede's Seedling" (Ananas Perpetual), was introduced in 1866 by F. Gloede. It made an enormous amount of runners, but saw little success. Following this came Mabille (Limoges) and l'Inépuisable (1871), both of which also were not particularly successful. The Abbé Thivolet, a parish priest of Chenoves Seine-et-Loire, was the first to appreciate the possibilities of an everbearing strawberry. First, he raised the Roi Henri, then the Robert Lefort, and Leone III. Finally, in 1893 Abbé Tivolet obtained the St. Joseph, the first true large-fruited everbearer, also known under the names of Constante Feconde, Leone XIII, and Rubicunda. Although it was a true everbearer, as we know them today, and of high flavor, it was small-fruited and not productive by present standards. The Abbé himself was not fully satisfied and later introduced the St. Antoine de Padoue, which was still not productive by present standards. But these varieties did stir the imagination of others and many improved varieties soon followed.

In 1889, Louis Gauthier introduced his white-fruited Louis Gauthier, which might be called a two-crop variety, because it cropped in the fall on its runner plants. He crossed the St. Antoine de Padoue x Louis Gauthier to obtain the Merveille de France, introduced in 1904.

Roland Chapron of Caen obtained the Madame Poincaré (St. Joseph x Lucie Boisselet) in 1930, the very vigorous large-fruited Sans Rivale (General de Castelman x Madame Poincaré) in 1937, in 1938 the Triomphe (St. Fiacre x Madame Poincaré) and in 1950 the Inépuisable with still larger berries of good quality and of great vigor of plant.

Charles Simmen of Montmorency, a breeder of everbearing and non-everbearing strawberries, introduced about 1925 the Geant Simmen (Charles Simmen); in 1931 the Recorde (a non-everbearer x La France Pacifique), a very vigorous variety with high-flavored, dark-red berries, some of largest size; in

1945 the Saint Jean, said to be a cross of the musky *moschata* with an unknown variety; and recently the Bijou. Chouard (1943) states that the everbearers like Recorde initiate flower buds in shorter time than non-everbearers and require less illumination to start growth.

Other everbearers of some note were St. Claude, by Rivoire, a good flavored variety with berries hidden by its foliage, and the Profusion obtained by Ribichon and introduced in 1946. At present, Sans Rivale of Chapron is generally considered the best everbearer for all France and even for England. It begins fruiting about the same time as Madame Moutot and bears well through the summer and fall. Its berries are large, good flavored, aromatic and a glossy bright vermillion red when ripe. It sets so heavily that its fruit may be small.

The registration system for both everbearing (remontants) and non-everbearing for all France indicates the value of the different everbearing varieties there at the present time. There were thirty-nine everbearing varieties listed in the register in 1963. Only Sans Rivale is in Class 1, those recommended for all France. Class 2, which includes those with special characteristics, or which are of more local interest, has eight everbearing varieties:

Appelever	Recorde
Geant Franboisé	Saint Claude
Liberation d'Orleans	Sanvoir
Profusion	Truffant Prodice

Class 3, which includes varieties for special study has nineteen varieties and class 4, of varieties whose sale is to cease January 22, 1970, has eleven varieties.

Holland. In Holland, everbearing (remontantes) strawberries are grown only by amateur home gardeners. Three varieties, Repita and Revada introduced in 1960 and Elista in 1964, have been bred by Miss Kronenberg of the Horticultural Research Institute at Wageningen. They are productive enough to indicate the possibility of commercial production. The preferred varieties at present are Revada and Macherauchs Dauerernte and are considered better than Sans Rivale.

Germany. The everbearing varieties grown at present in Germany are Macherauchs Dauerernte, Hummi Trisca, Herzbergs Triumph, Ada Herzberg, St. Jean, and the Alpine Riigen, which is more grown than Baron Solemacher. Macherauchs Dauerernte was introduced in 1956 by O. Macherauch, a nurseryman.

Two-crop varieties of Europe

In France, varieties have long been known which produce some fruit in the fall on plants that bore in the spring. As far back as 1768, Duchesne recognized a botanical form, *bifera* (= twice bearing), which was probably the species *F. viridis,* the green-fruited strawberry. With two-crop varieties, flower buds are initiated in the relatively long and cool days of midsummer in northern Europe, and they continue to develop so that flowers and fruit are produced from late August on to frost. With protection provided by cloches or cold frames, a considerable fall crop can be obtained. The finest of these two-crop varieties in recent years was Auchincruive Climax, which gave a heavy crop in late summer and fall (*Plate 11–b*). In the 1950's, however, this variety was completely lost because of spring variegation. The new Talisman, of good flavor, and Redgauntlet, of fair flavor, bred by Reid of Scotland, are also fall-fruiting. The Early Cambridge originated by Sir Rowland Biffin of England and of French origin, the Abundance of Louis Gauthier, Victorie of Maillochon and Liberation d'Orleans of M. Joly, all have good quality and the fall-fruiting characteristics. Abundance (Constante Fecunde, apparently the St. Joseph x Louis Gauthier) is an early-ripening sort originated by Louis Gauthier in 1905. It or a variety under that name is notable for its great hardiness in Scandinavia. Fruit rot under the cool temperatures of fall is one of the more serious troubles of fall-fruiting production.

12

Notable Early Strawberry Breeders of America

IMPORTANT STRAWBERRY VARIETIES are numerous today, displaying many characters and adaptations; but this, of course, has not always been so. While most of the varieties presently grown were introduced by agricultural experiment stations, earlier varieties, both in the United States and abroad, were originated by private breeders. Some of these privately originated varieties are especially important for their service as parents; those who bred them are notable for their perceptiveness and foresight. It is these private breeders who did much to set in motion the strawberry breeding work which continues today in experiment stations in many parts of the world. The following chapters first chronicle the work of early breeders and those of today, then they proceed to describe the breeding work of North American agricultural experiment stations, as well as of those abroad. Lastly, in this section, some of the knowledge gained from this experimental work is described, along with the uses to which this knowledge has been and can be directed.

Six great breeders of strawberries belong to the pre-experiment station period of the nineteenth century. The first American fruit breeder was Hovey, who made six controlled crosses of strawberry in 1834 when he was twenty-two years old and obtained the Hovey. The second breeder, Wilder, made crosses over a period of at least thirty years and originated the President Wilder strawberry in 1861. The other four who were active somewhat later (partly in the nineteenth and partly in the twentieth century), made crosses for many years before obtaining their most notable varieties—Cloud, introduced the

FIG. 12–1. C.M. Hovey, America's first breeder, nurseryman, editor of a great horticultural magazine, and originator of the Hovey strawberry.

Cloud in 1889 and the Klondike in 1901; Reasoner introduced his Dunlap in 1900; Howard first fruited the Howard 17 (Premier) in 1906; and Etter introduced his Ettersburg 121 in 1907 and Ettersburg 80 in 1912. These six men were true strawberry breeders whose work met with notable success, although in the case of Wilder the President Wilder did not become a dominant variety. Other breeders may have done as much work, or even more than some of these, but they were not so successful in obtaining notable varieties, either because of the parental material available to them, or because of their environment, or because of their way of making and selecting crosses. Their contributions while not notable, nevertheless helped to make the modern American strawberry.

What different kinds of men these six were! Two were Bostonians, Hovey, a nurseryman and publisher of a fine early horticultural magazine; Wilder, a successful wholesale drygoods merchant, by avocation an enthusiastic amateur horticulturist; the third, Cloud, a railroad station agent of Louisiana; the fourth, Reasoner, of Illinois, an itinerant preacher who was also a scholar, an architect, and a builder of churches; Howard, a small fruit farmer and seedsman of western Massachusetts; and Etter, a mountaineer homesteader of northwestern California. All entertained the vision of finer strawberries and they, with the help of others, changed the strawberry from a wild fruit into the fine, modern, cultivated crop we have today. Of the many others who obtained fine strawberry varieties, Wilson, of the middle nineteenth century, was a small nurseryman of Albany, New York; Durand, somewhat later, was an artist; and Rockhill, at the beginning of the twentieth century, a grain farmer of central Iowa. These three are important, one for the notable Wilson variety, the second for the New Jersey Scarlet, the Virginian parent of Crescent, and the third, Rockhill, for advancing a special group of berries—the everbearers.

Charles Mason Hovey (*Fig. 12–1*), the first notable North American strawberry breeder, was born October 26, 1810, in Cambridge, Massachusetts.

At the age of twenty-two, he and his brother started a seed store at Cambridge and a one-acre nursery, which was greatly enlarged eight years later. Hovey envisioned a magazine that would develop an intelligent class of gardeners in America just as the *Gardeners Chronicle* was started about the same time in England. When he was twenty-four, he founded *American Gardeners' Magazine,* which later became *Magazine of Horticulture,* a great periodical by the best standards of today. He was its editor for thirty-four years, for as long as it existed. More or less concurrent with this, he began the publication of *Fruits of America,* which contained more than 100 color plates and was published in parts appearing from 1847 to 1856, two volumes were completed and a third begun. On his place in 1845 he is said to have had 1,000 pear and 400 apple varieties, as well as those of many other fruits. He grew 200 varieties of camellias, many of them his own originations, from which some were selected for exhibition in London. Many varieties of trees and shrubs had their origin with him. Throughout life he was an active member and supporter of the Massachusetts Horticulture Society and was its president for four years. He was an honorary member of the Royal Societies of London and of Edinburgh.

In 1832 Hovey had 12, and two years later, more than 50 varieties of strawberries in his tests. Another account states that he had three varieties when he was only twenty years old. He found that neither Keens Seedling, introduced in England in 1820, nor any other large-fruited strawberry was fully hardy. In 1833, he made the crosses that resulted in Hovey's Seedling and Boston Pine. He fruited his seedlings in 1836 and by 1838 he was convinced that one seedling was superior to all others and he introduced it as Hovey. So far as we know, he did no further strawberry breeding. The Hovey was a failure as a commercial variety, except in New England where it was the chief, or one of the chief varieties until about 1890. However, compared with other large-fruited kinds of 1840, the Hovey was hardier and larger, and its flavor was as high or higher. Under high culture it was productive. Compared with the native *F. virginiana* varieties, though, it was not hardy and it produced few runner plants. Moreover, although called perfect-flowered when introduced, it was pistillate under most conditions and needed another kind as a pollinator.

When Hovey made the six crosses which resulted in the Hovey, he somehow lost his labels for the seedlings. At first he felt certain that the Hovey came from the cross Melon x Keens Seedling, but later he stated that he supposed it came from the cross Methven Scarlet x Keens Seedling. Methven Scarlet originated in England and was probably a hybrid of Hudson Bay, a *F. virginiana* variety with some "pine." Hovey considered Methven Scarlet rather insipid but it was hardy, large, and showy. The Hovey was described as pistillate, very large, round or ovate, slightly conical, never coxcomb, a deep shining red, but paler when grown in shade, seeds inserted in a slight cavity, flesh scarlet, firm, agreeably acid, high flavored, not surpassed by others, leaves large, rather light green, plants very vigorous—more so than those of any other variety, perfectly hardy, ripening midseason two weeks after Early Virginia (Old Scarlet) and a week after Keens Seedling and Methven Scarlet.

In 1854 Hovey wrote that since 1834 immense numbers of seedling strawberries had been raised in the United States and at least 200 varieties introduced, but not a dozen were worth growing; that it was not easy to raise new kinds superior to old or even equal to them; and that nearly the maximum of excellence had been obtained. He looked to some improvement, but only with the most careful hybridizing and then only so slight as to be unobserved by many. He also noted that in England only Keens Seedling (1818) and British Queen (1834) were important at that time (see Chapter 6).

A major contribution of Hovey was his article "Some Remarks upon the Production of new varieties of Strawberries from Seeds," published July 1837 in his *Magazine of Horticulture.* He gave careful directions for making crosses and discussed the need for choosing the parents, suggesting Methven Scarlet for one parent because of its hardiness even though he noted that it did not have flavor. This and later articles by him undoubtedly stimulated others to start breeding.

Marshall P. Wilder (*Fig. 12–2*) was born in Ringe, New Hampshire, September 22, 1798, the eldest of nine children, and died December 16, 1886. He began school at four years of age. At sixteen he chose farm work instead of a college course. Soon he began work as a clerk in a store and by the time he was twenty-one, he became a partner. At twenty-six he moved to Boston, where

FIG. 12–2. Marshall Pinckney Wilder, a President of the American Pomological Society, a breeder of strawberries for over thirty years, and originator of fine varieties, especially the President Wilder.

he was a successful wholesale drygoods merchant, and in 1831 he moved to the Dorchester suburb where he lived till his death. He was, like his friend Hovey, greatly interested in pears. In his orchard he tested 1,200 kinds of pears and, at one time he had 2,500 trees, representing 800 kinds. He did far more crossing and originating of new varieties than did Hovey. He was one of the founders of the American Pomological Society and was its president, except for one term, from its organization in 1850 until his death. He was a founder of the Massachusetts Agriculture College (now the University of Massachusetts) and was a trustee of the Massachusetts Institute of Technology. He is said to have continuously bred strawberries for over thirty years, and to have raised thousands of seedlings. His notable variety, President Wilder, was raised in 1861 and was a cross of Hovey x La Constante. It was perfect-flowered, large, light scarlet, high flavored, and was grown many years for its large, attractive berries of high dessert quality. Like the Hovey, it had to be grown in very fertile soils to obtain good crops and was probably not fully hardy. Like the Hovey also, it was grown chiefly by amateurs and by some for the Boston market.

Robert L. Cloud. Up to the time of the Civil War, only a few strawberries were grown in Louisiana and these were the very aromatic Old Scarlet (Early Scarlet, a selection of the wild Virginian). As early as 1868, the Wilson had been introduced and small lots of strawberries were shipped to Chicago, but carloads were not shipped until the 1880's. Robert L. Cloud was born December 6, 1854, in New Orleans. In 1866 he moved with his parents to Tickfaw, where he helped his father grow strawberries for the Louisiana market. About 1886, when he was the railroad shipping agent at Independence, Louisiana, he superintended the loading of the first iced refrigerator car of strawberries ever sent to the northern markets. By this time he had already started growing and testing seedlings, and about 1885 had introduced Big Bob, a cross of Cumberland Triumph x Neunan. He made no hand crosses, but instead depended on bees to pollinate pistillate varieties, and grew seedlings from them and from other seed. His Cloud, thought by him to be Crescent x Wilson, was introduced in 1889 and was widely grown in the South until about 1900. Except as parents, Lulu, introduced in 1895, and Pickerproof, introduced about 1898, never became important. In 1901 he introduced Klondike which quickly became the major berry in all the South and was the most grown variety in the United States from about 1905 until about 1935, when it was replaced by Blakemore and, to a slight extent, by Missionary. In Louisiana, however, Cloud's varieties were the leading ones, from the time of the introduction of Cloud until Klonmore was introduced in 1940. The Klondike was also a leading variety in southern California, southern Illinois, Maryland and

Delaware. It is still raised extensively in Mexico. Cloud's later varieties, Payday and Perfect, which he was testing in 1915, never became important.

Cloud's great variety, Klondike *(Fig. 10–10)*, was said by him to be a cross of Pickerproof x Hoffman, both Southern varieties. He gave its ancestry as follows:

```
                                              Hovey
                                    Crescent    x
                         Lulu ....       x    New Jersey Scarlet
          Pickerproof            x    Neunan (probable seedling of Wilson)
Klondike       x         Hoffman
          Hoffman (probable seedling of Neunan)
```

To have grown and fruited seedlings, made and propagated selections, and to have enough plants to introduce his first variety by 1885, Mr. Cloud must have started raising and testing seedlings as early as 1880. He continued raising seedlings at least until 1915. He succeeded admirably in his main objective of obtaining a much better shipping variety that would grow vigorously after a relatively short rest period and under the relatively short photoperiods in southern States.

Rev. John Rogers Reasoner (*Fig. 12–3*) was born on a farm at West Union, Ohio, March 2, 1835, and died January 12, 1925, at Urbana, Illinois, when he was almost ninety years old. His early days were spent on a farm but he was also a plasterer by trade. When he was twenty, he settled along the southern border of Kentucky. During the Civil War, he joined a Kentucky regiment, of which he was chaplain for a while. He was also in the Sanitary Commission, the forerunner of our Red Cross. He joined the Methodist Conference and was first a pastor at Maysville, Kentucky, and then at two other places in Kentucky. Next, for two years, Reasoner was a builder and an architect. Then he returned to the ministry, holding pastorates in Ohio and Illinois and often serving as supervisor and laborer in the building of churches. Rev. Reasoner acquired a wide knowledge of history, sciences, and Greek and Hebrew literature, and had a splendid library. He gave talks on plant breeding and genetics and tried to instill a love of horticulture in his parishioners.

In 1901 Reasoner retired from the Ministry at Urbana and the last twenty-four years of his life were spent in following his special interests, especially plant breeding. He had always been interested in the strawberry. When he was six, his mother made him supervisor of strawberries in the home garden, but they did not bear a single berry, being probably all males. He began serious breeding about 1886, using Cumberland Triumph, Crescent, Capt. Jack, Sucker State, Warfield, Glendale, Sharpless, Windsor, and others. He had to

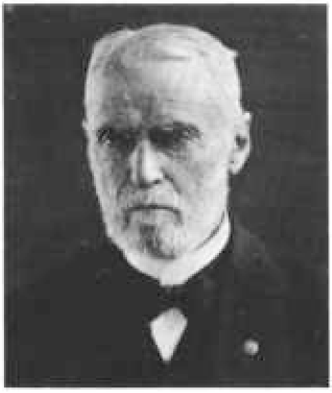


FIG. 12–3. Rev. John Rogers Reasoner, farmer, plasterer, pastor, architect, builder, classical scholar, lecturer on genetics and horticulture, practical breeder, originator of the Dunlap strawberry.

work on parsonage lots, doing what he could in the time and space allotted. In 1890 he originated Dunlap, which he thought to be a cross of Crescent x Cumberland Triumph, and he introduced it in 1900. The Burrill, a cross of Crescent x Dunlap, made in 1909, was introduced in 1916. It was very similar to Dunlap and the nursery trade soon used the names interchangeably, but Dunlap, probably rightly, was the only name to persist. Rev. Reasoner was for a time Director of the Illinois State Horticultural Society Central District Experiment Stations. Dunlap is still grown somewhat, for it proved to be the hardiest of all standard varieties and of high quality.[1]

Arthur B. Howard (*Fig. 12–4*), the originator of the Howard 17 strawberry, was one of the very few Americans who started systematic berry breeding work before 1900. He had in mind an ideal strawberry, and he pyramided the good qualities of the varieties he knew and propagated until he fruited his selection number 17 in 1906. He is said to have thought it the ideal strawberry. And it was the "ideal" strawberry for his location and time, more disease- and frost-resistant, more handsome, larger, and more productive than most other varieties of that day, and of good flavor. The Howard 17 was all this, and more, for it became the great parent of American strawberry varieties.

Arthur B. Howard was born of idealistic parents June 1, 1836, on a farm in Belchertown, Massachusetts, about nine miles from Amherst. At the age of fifteen, he went to live for a little over a year in the Putney, Vermont community of the Perfectionists (about twenty-six persons at this time), which was composed of people with strong religious belief, including the union of its members into one large family who held all things in common. At least during the winter, he attended the community school, whose library had the best available books and agricultural papers on gardening and fruit culture, Hovey's *Magazine of Horticulture* presumably among them. The community

[1] From *Illinois Horticultural Society* 59:279–328. 1925.

FIG. 12–4. A.B. Howard, Belchertown, Massachusetts, 1837–1907, foremost strawberry breeder in America of his time whose variety Howard 17 is in the ancestry of most American strawberries and was the most important variety in the Northeast for a generation.

raised large gardens, and the head gardener of the community gave Howard the benefit of his long experience in gardening. What interested young Howard most was the raising of strawberries, for, in addition to the value of what the community consumed, $150.00 worth was sold from the community patch in one year. Plants also were sold. When he returned to the home farm, his father allowed him to use a third of an acre on which he set five varieties of strawberries—Early Virginia (Old Scarlet), Burrs New Pine, Hovey, Chester, and a few Wilson. The next spring he planted another third of an acre, which he set all to Wilson. From 1,600 to 1,800 quarts were harvested for the first crop from the first field, and the following year from the combined fields over 3,200 quarts were picked, for which he received over $500.00. His interest in the strawberry thus proved well-founded and lasted the rest of his life.

Through the years, Howard's thirty-five-acre farm became a fruit farm. Because he was interested in the best varieties of each fruit he grew large collections of apples, pears, peaches, cherries, plums, grapes, and berries, adding new ones as they came to his attention. He wrote many articles on fruit growing and on general subjects for the *New England Homestead,* the leading agricultural paper of that day. A friend of its editor, he represented the paper as subscription agent and was even offered the position of co-publisher. He became a close friend of S.T. Maynard, the first professor of horticulture of Massachusetts, and of J.G. Holland, editor of the *Springfield Republican* and one of the founders of *Scribner's Monthly*. Maynard took his classes to Howard's farm, and among the students was S.W. Fletcher, who was in charge of the variety tests at the college where Howard's selections were being tested.

Howard began his strawberry breeding, at least in the 1880's, and later he was joined by his son Everett as a partner in his fruit and farm work—breeding and growing fruit, flowers, and vegetables, and producing and selling flower and vegetable seed. He was an extensive exhibitor at fruit fairs and received more than 2,000 premiums for his exhibits.

In his strawberry breeding Howard used the best varieties and the best of his own seedlings. He is said to have raised and tested over 25,000 seedlings. He even sent seedlings to others to fruit. His crossings were carefully recorded hand pollinations made in a greenhouse. Selections were sent out to be tried by strawberry specialists and experiment stations, and were reported on by the Ontario Station as early as 1894. Two varieties only were named, the Dighton (soon dropped) and the Howard 17. They were selected in 1906 from about 800 seedlings of a cross made in 1904 and were not named and introduced until after Howard died, June 11, 1907. It is said that he had about 1,000 plants of the No. 17 by the spring of 1907. He also named and introduced the Howard apple, Howard Star petunia, Royal Splendor verbena, Lilliput zinnia, and the Bay State tomato. Everett Howard carried on his father's work, sending out the Howard 17 for trial in 1909 and making additional crosses. In 1907, the cross Howard 103 x Howard 17 was made by Everett and about 1,000 seedlings were grown, from which the Howard Supreme was selected and introduced in 1931. It was a large, attractive, high-flavored, very productive variety but was not so popular as it would have been twenty-five years earlier, for it was a pistillate and in 1931 perfect-flowered varieties were preferred. In 1929, the American Pomological Society gave the Marshall Wilder Medal for notable fruit varieties

to A. B. Howard and Son
Premier or Howard 17
Most widely grown of
All strawberries 1908

Albert F. Etter (*Fig. 12–5*) was born on November 27, 1872, at Shingle Springs, Eldorado County, California, of a family of eleven boys and one girl. In 1876 the family moved to Coffee Creek and later to Salt River, south of

Fig. 12–5. Albert F. Etter, mountaineer and homesteader of northern California, originator of the Ettersburg 121, Ettersburg 80 (Huxley), and other strawberries.

Eureka in Eel River Valley. In 1894 he filed a homestead claim to five hundred acres at Ettersburg and was joined there by his brother, August. In 1924 he married Katharine A. McCormack of New Jersey. He died on November 13, 1950.[2]

He lived forty miles west of the railroad and six miles inland from the ocean, just back of the Coast Range in the dry hill country of northern California, at an elevation of about 1,000 feet. He had made Ettersburg his home in 1894, and it was here that he established the fruit breeding farm and nursery which subsequently supplied new genetic material to breeders and growers in this and foreign countries. One of his varieties is now grown in Europe and Australia, and others are in the ancestry of many of America's widely grown varieties.

At thirteen he was interested in breeding dahlias, red currants, and gooseberries. He left school two years later and worked at the home place in Ferndale for the next seven years. At fifteen (1887) he grew his first seedling strawberries, from a cross of Sharpless x Parry. He early obtained and used in his breeding what he called the Peruvian Beach strawberry, said to have been brought to Eureka, California, from Callao, Peru, by a Captain Cousins. As the Peruvian beaches are desert and have no strawberries, this variety probably came from cultivated fields in the interior of Peru or possibly an irrigated field near Lima. Etter (1908) described this as a white, solid-fleshed, fragrant variety with a peculiar pineapple flavor, less drought- and cold-resistant, not fruitful, and less vigorous than the local beach strawberries. Using this form of *chiloensis* pollinated with third generation seedlings from Sharpless x Parry, he fruited his first variety, Rose Ettersburg, in 1895, and introduced it in 1903. Later he used in his crosses selections of *chiloensis* from various spots (Pigeon Point, Point Arena, Cape Mendocino) along the coast of California.

Etter also used one other species in his breeding: *F. ovalis,* the native octoploid of western United States, which he called by the names *cuneifolia* and *platypetala,* and possibly also at times *californica,* a name properly applied to a woodland diploid *vesca* type. He had also the true *californica* as well as the *F. vesca semperflorens* of Europe. Both of the latter two were said to have been used in his crosses, but there is no evidence that either was successfully crossed. He also told of using *F. chiloensis,* or *F. duchesne* in crosses, but what he actually had was *F. nilgerrensis,* a diploid. It does not seem to have entered into his varieties. At one time he gave the parentage of Red Cross as Etters 80 x *F. duchesne,* at another time as Etters 216 x Trebla. The latter seems most likely.

[2] Adapted from an article in *Fruit Varieties and Horticultural Digest* 17:69–72. 1963.

Varieties which Etter reported as entering into his varieties include Sharpless, Crescent, Northfield Junior, Dorman, Bederwood, "Michel's Early" (not true, as he records it as pistillate), Fendall, Parry, Wm. Belt, Dunlap, and Chesapeake. He discontinued his strawberry breeding about 1926, but continued his strawberry nursery, his apple and pear breeding, and at least his testing of seedlings for some years. During the early 1920's, many of his varieties and selections were tested at the U.S. Horticultural Station at Glenn Dale, Maryland, and more of them later. Dr. R.E. Clausen described Etter's work for the July, 1915, *Journal of Heredity*. Etter, himself, issued a few catalogues and wrote several articles in which he expressed some of his ideas.

Anyone who has seen hybrids of cultivated varieties with the cultivated forms of *F. chiloensis* from Ecuador, Peru, or Chile, will understand the excitement of a boy of 15 and the concentration of his interest upon strawberry breeding. Crosses of selections of *F. chiloensis* from the Pacific Coast beaches may give seedling plants of enormous vigor, with the pistillate ones extremely productive of medium-sized, pale, mostly soft berries, but crosses of the South American varieties of *F. chiloensis* with cultivated varieties give seedlings not only with enormous vigor of plant, but with fruit of large size and a great range of firmness and flavors, some of which are even vile. For the most part, Etter grew seedlings of pistillate-flowered sorts. In crossing, he placed a flower of the male parent on one of the mother parent and kept them in place with cloth tied over both. It is probable that the recorded ancestry of many of his varieties is incorrect. We are quite certain of this in some cases: Ettersburg 121 is reported as Alpine *vesca* x Cape Mendocino *chiloensis,* and Trebla is reported as having both the Alpine *vesca* and the native *californica* form of *vesca* in its parentage. Both parentages seem wrong.

We do not know why Etter discontinued his breeding about 1926. We suppose that when he brought in plants from various sources he brought along with them virus and fungus diseases, and insects, such as aphids, which spread virus diseases. Virus diseases were noted at his place in 1932; also what was thought then to be rhizoctonic root disease, but which could well have been red stele root rot, in part at least. Diseases such as these probably puzzled him as they did everyone else, but he was isolated and may have lost some of his enthusiasm because of such troubles.

The Etter variety still grown today is supposed to be Ettersburg 80, called Huxley in Great Britain and on the continent and called E–89 or Ettersburg in Australia. It is much like the original *F.* x *ananassa* or Pine varieties—a large, rather ovate-shaped variety with a bright-red glossy-surface color and a white, smooth-textured, firm flesh. The plant is very vigorous and its leaves large, deep green, and glossy. It is quite tolerant of virus. It is the mother parent of Southland, which was introduced in 1931 by the U.S. Department of

Agriculture, but which proved frost-susceptible. Though reported by Etter as [(Rose Ettersburg x *californica*) x (Rose Ettersburg x Cape Mendocino beach, a *F. chiloensis* selection)], it probably was not such a cross, although it was apparently derived in part from Rose Ettersburg.

Fairfax is also indirectly derived from Etter's work, for it probably resulted from a cross of Ettersburg 450 (E-450) x Howard 17 or Howard Supreme x E-450. E-450 and E-904 were sweet, high-flavored, rich red, very firm, rather small-fruited varieties (as grown in Maryland) but neither was very vigorous. They were much like Red Chilean in plant and fruit except that the berries were far higher flavored and were rich red to the center.

During the 1920's and early 1930's, the Ettersburg 121 was extensively grown for canning, chiefly in western Oregon. It was a firm-fleshed berry with high flavor and a color that held well in canning. Its cap came off easily, leaving little scar, and was usually left on the plant in picking. It was best adapted to the heavy, well-drained soils in the Willamette Valley. Trebla and Ettersburg 80 were also grown in Oregon and Washington. Etter's varieties were too subject to leaf spot to be of direct value in eastern states. E-445 and E-450 were the most resistant to leaf spot in Maryland.

In the 1937 *Yearbook* of the U.S. Department of Agriculture (pp. 491–492) the 52 varieties and selections known to have been sent out by Etter by 1937 are listed, along with their parentage and a few of their characteristics. Other of his selections under number are known to have been sent out by him.

The value of Etter's work (aside from E-80 and E-121, grown as varieties, and these and other selections which have entered into the parentage of varieties of other breeders) is in the attention it drew to the hybrid vigor and new characters obtainable in crosses of cultivated sorts with *F. chiloensis.* Georgeson, in Alaska, had obtained some of the same results but his selections, made under the long photoperiods of Alaska, were less usable than those of Etter.

In his writings, Etter emphasized the exquisite flavor of E-450, E-904, Bederarena, Bederarena Junior, and Kalicene; the excellent canning quality in E-121 and said to be in Trebla, Redfour, E-450, Red Sugar, and Kalicene; the solid flesh with tough skin of E-450, E-904, and Lnge; the lasting color of flesh of E-121, said to be in Trebla and Lnge also; the ease of capping of E-121, Lnge, Alcatraz, and Trebla; the blossom frost-resistance said to be in Trebla and E-59; alkali resistance said to be in Rose Ettersburg and E-80; the mildew resistance of Fendalcino; and the drought resistance said to be in Red Cross, E-84, and E-500. Etter called attention to the deep root systems which he thought derived from *F. chiloensis,* and to runners of some *F. chiloensis* and its hybrids, that lived to the second year.

While ill during 1938, he lost most of his strawberry material and only a

Strawberry varieties originated by Albert Etter, and those having Etter varieties in their parentage

Etter's Varieties	Varieties derived in part from each
Bederarena	Nectarena
Delecto	Simcoe, King, Great Bay, Blaze, Strafford
E-80	Albritton, Louise, Southland, Jubilee
E-121	Corvallis, Claribel, Northwest, Guardsman, Sharon, Wisc.-214, Wisc.-251
E-214	Elgin, Tupper, Phelps, Merrimack
E-450	Probably Fairfax and its descendants
E-512	Wright
Euresko	Redheart, Cal. Institute-Z4
Fendalcino	Cupertino, Lassen, Cal. Institute-X2, Z4 and Goldsmith
Golden Gate	Black Lee, Canal
Norg	Borden
Red Sugar	Simcoe, Howe

few of his varieties and selections are known to still exist. His genetic material now exists in E-80 and E-121 and in varieties of other breeders derived in part from some of his varieties.

Some of the germplasm from Etter's varieties is in varieties introduced by D. Boyes of England (see ASHS register #15). The more important crosses of the writer and associates, Carl Schuster and George Waldo, with Etter's varieties were with Bederarena, Cream, Delecto, E-80, E-121, E-450, E-904, Euresko, Kalicene, Lgne, and Trebla (see *Jour. Her.,* Nov. 1934).

Etter also did some apple and plum breeding and, at least, grew cherry and pear seedlings, and perhaps did some breeding with them. During his later years he gave most of his time to these fruits.

James Wilson, about the middle of the nineteenth century, was a Scottish gardener and nurseryman in Albany, New York. He sowed seed of Hovey, Black Prince, and Ross Phoenix and from the resulting seedlings two years later selected the variety that bears his name, which alone changed the strawberry from a fruit grown for the few by few, into a fruit grown by hundreds of thousands from Florida to Maine and west to California and Washington.

Little is known of James Wilson except that he exhibited his seedling June 22, 1953, at a meeting of the Albany and Rensselaer Horticultural Society where it did not attract much attention. He showed potted plants of it in full fruit the following year. It was then considered outstanding and named Wilson's Albany, later shortened to Wilson. He divided his stock with neighbors in 1854. In 1856, when the demand for plants was great, his nursery had fewer plants than some of the neighbors, he having died in 1855 and left the nursery to his son, John Wilson, who continued to propagate the Wilson for several years. As in the case of Hovey, who made one series of crosses in one year, Wilson grew only one set of seedlings in 1851 and from it obtained his great variety. (See Chapter 9)

Elias W. Durand of Irvington, New Jersey, a suburb of Newark, was an artist who for reasons of health had to seek an out-of-door life. Beginning about 1857 through his friendship with Seth Boyden, a strawberry grower and breeder, he also grew strawberries and made many hand-made crosses to originate varieties that were introduced between 1865 and 1880. His most important variety was New Jersey Scarlet, introduced in 1868, which was the pollen parent of Crescent, and which with Hovey and Howard 17 are the three great ancestors of modern strawberries. So far as can be determined now, New Jersey Scarlet was very similar to Large Early Scarlet but was described by Fletcher as conic instead of roundish oval. It is supposed, but not known, to be a pure Virginian. (See Chapter 9)

Harlow Rockhill (*Fig. 12–6*), who was born August 28, 1866, in Marshall County, Iowa, and died there March 1, 1944, was chiefly a breeder of strawberries, bush cherries, plums, and peach-plum hybrids, though he worked also with gladiolas, peonies, raspberries, nuts, and pears. He had a broad view of horticulture in general, both of his grandfathers being small nurserymen. His father planted many windbreaks and his mother worked with flowers and plants in the garden. As a boy he cared for a herd of Angus cattle, kept their records, and raised strawberries and melons. He never married. In 1904 he obtained plants of the Pan American everbearer and began his important work with strawberries in 1908 when he crossed the Pan American x Dunlap and selected the Progressive (see Chapter 11). This was introduced in 1912 and was the leading everbearer in North America for a generation. On all counts but that of size, Rockhill considered the Progressive an ideal everbearer for his conditions. It was one of the hardiest of all strawberries; it made runner plants freely; its foliage was resistant to leaf diseases and its fruit was high in flavor. To improve on this, Rockhill started breeding for larger size, and crossed the Early Giant x Progressive in 1918. About 500 seedlings fruited in 1920, from which he selected the Rockhill, which was introduced in 1923. The Rockhill (= Wayzata, Bonanza, and Big Sweet) proved to be as hardy as the Progressive and much larger in size. It was one of the best flavored of all strawberries and attractive in appearance, but it did not make runners as freely as Progressive. It is still grown somewhat. Mr. Rockhill introduced four other everbearers—Americus (very fine flavor) and Francis, both Pan American x Louis Gauthier, but they were not hardy; and Iowa (Dunlap x Pan American) and Standpat (Pan American x Dunlap), both of which were

FIG. 12–6. Harlow Rockhill, originator of the first widely grown everbearing strawberry in the United States, the Progressive, and of the larger Rockhill variety.

hardy, but inferior to Progressive. Early Bird, a mixture in the Rockhill when it was introduced, and June Rockhill, a June-fruiting variety (selected in 1932, introduced in 1947) resembling Rockhill, were both Rockhill's varieties. The June Rockhill was considered by Mr. Rockhill to be a non-everbearing sport of the Rockhill (probably correctly), for its fruit was very high-flavored and similar to the everbearing, and the plant was also similar, except that it produced runners freely and did not build up large crowns as did the Rockhill. The Rockhill had another characteristic developed to the highest degree known: all of its flowers set fruits. Most wild octoploid strawberries have the male and female flower types on separate plants. All flowers of female plants usually set, but the male plants rarely develop fruit even on the primary flower. By crossing and selection of seedlings, productive varieties developing fruit from primary, secondary, and often tertiary flowers of staminate plants have been obtained, but sterility of the later flowers has

FIG. 12–7. S.W. Fletcher, teacher, researcher, author of *The Strawberry in America,* later director of Pennsylvania State University Experimental Station and Dean of Agriculture.

always persisted. Rockhill is the nearest that we know to the pistillate as regards its high degree of setting.

During his later years, Rockhill centered his interest more and more on stone fruits, crossing *Prunus tomentosa,* the Manchurian cherry, with the sand cherry, *P. besseyi*; inter-crossing apricots, peaches, plums, and prunes to obtain new types of plums. He named one red gladiolus the Cherry Red and left one late-flowering peony selection.

Others who obtained great varieties, whether by finding them in or around their fields, or by growing seedlings, were Downer, of Kentucky, who grew seedlings for several years and in 1860 obtained the Charles Downing as well as Downers Prolific, introduced in 1858, and the Kentucky, introduced in 1869; Neunan, of South Carolina, who raised seedlings about 1868 and introduced Neunan; Parmalee, of Connecticut, who found Crescent in 1870 (see Chapter 9); Sharpless, of Pennsylvania, who grew seedlings in 1872 and selected out Sharpless (see Chapter 9); Warfield, of Illinois, who found Warfield about 1882; Bubach, of Illinois, who grew seedlings in 1882 and obtained Bubach; Haverland, of Ohio, who grew seedlings in 1882 and introduced Haverland; Hoffman, of South Carolina, who found Hoffman in 1884; Gandy, of New Jersey, who grew seedlings in 1885 and obtained Gandy; Cruse, of Kansas, who grew seedlings in 1889 and obtained Aroma; Ewell, of Massachusetts, who found Marshall in 1890 (see Chapter 9); Thompson, of North Carolina, who found Lady Thompson in 1894; Black, of New Jersey, who originated Joe, introduced in 1889; and Gohn, of Virginia, who found Missionary and introduced it in 1906 (see Chapter 10).

After 1900 the notable breeders are, except Haley, of Michigan, entirely those who did systematic breeding over many years. Etter, Cloud, Howard, Reasoner, and Rockhill all continued their breeding work after 1900. Hansen, of South Dakota, and Georgeson, of Alaska, were the first notable breeders of the state and federal experiment stations, Hansen making his first crosses in 1900 and Georgeson his first in 1905 (see Chapter 15). S.W. Fletcher (*Fig. 12–7*), although not specializing in strawberry breeding, achieved a unique position as the historian of the strawberry in the United States (see Appendix 6).

13

Strawberry Breeders of Today

TAKEN AS A LOT, the strawberry breeders of today display as varied a background as did the breeders of the past. Although methods of breeding and testing advance, and the body of knowledge concerning the strawberry expands, the earliest causes of interest in strawberries and the background of these causes remain much the same from generation to generation. Many of today's breeders came from the farm; most of them have college training; many are from agricultural colleges, and most have trained beyond four years of college. The training itself is highly varied, ranging from straight agriculture to plant pathology, genetics to botany. Some breeders owe their special interest in strawberry breeding to work with strawberries at college, as a way to help meet expenses, or as a research project accompanying college courses. All in some way acquired the vision of production of better strawberries.

While breeders work with a highly heterozygous fruit and generally know in what species or varieties desirable germ plasm can be found, the breeders themselves, considered as an ideal type still in development, have a still more heterozygous makeup. Imbued with the vision of better berries, many a student has the germ plasm that could produce the excellent breeder of tomorrow. As the bulk of data grows from the increasingly sophisticated experiments, studies, and breeding programs, and as the difficulty of improving upon an already highly developed fruit increases, the breeder will have to advance by developing new techniques on the basis of wider training; this probably will have to include computer technology, biochemistry, and biophysics, as well as an intensive study in systematic botany, genetics, and strawberry varieties. Such demands will require a highly heterozygous quality of breeders, for in this quality lies the possibility for adaptation to particular needs.

The following biographic sketches, most of them accompanied by photographs, give a fair listing of today's breeders. Two of recent breeders whose photographs are shown, Morrow and Goldsmith, have passed on, but we are richer because of them.

Lewis E. Aalders, cytogeneticist, Small Fruit Section, Canada Department of Agriculture Research Station, Kentville, Nova Scotia, was born at Kentville on July 19, 1933. He obtained his B.Sc. and M.Sc. at Acadia University in 1952 and 1953, respectively, and his Ph.D. from Cornell University in 1957. He has been with the Kentville Research Station since 1953, conducting research related to the breeding of small fruit crops, including the strawberry. With the strawberry, the work has been focused on an inbreeding program and on a program of recurrent reciprocal selection jointly with Dr. Craig. The production of an F_1 hybrid variety that can be improved in a step-wise fashion by backcrossing has been the aim of this work. He and Dr. Craig introduced the variety "Acadia" in 1965.

Dr. Sadao Abe, originator of the Chiyoda and Yachido strawberries at the Horticultural Research Station, Kurume, Japan, is now chief in Floriculture at that station.

Prof. Enrico Baldini, director of the Department of Horticulture at the Agricultural University of Bologna and professor of Horticulture at the same university, was born in Florence, Italy, in 1925. He is a member of the Italian "National Agricultural Academy," of the "Georgofili's Academy"

Fig. 13–1. Aalders, L. E.

Fig. 13–2. Abe, Sadao

Fig. 13–3. Baldini, Enrico

FIG. 13–4.
Blake, Roland C.

FIG. 13–5.
Bringhurst, R. S.

and of the "Italian Horticultural Society." His main publication on strawberries is Baldini, B., and Branzanti, C.: *A monograph on the principal non-everbearing strawberry varieties.*

Roland C. Blake was born March 8, 1920, at Rowland, Maine; graduated in 1949, University of Maine; obtained his Ph.D. at the University of Minnesota, 1954. From November 1938 to October 1941, when Dr. LeRoy Powers was making his studies of strawberry genetics, he helped in berry research at the Cheyenne, Wyoming, Horticultural Field Station and became interested in berry breeding. His thesis at Minnesota was on the evaluation of strawberry varieties as parents. From 1954 to 1957 he was in charge of the berry research at the Northwestern Station at Mount Vernon, Washington; from 1952–1959 he was in charge of the federal pear breeding and research at the Southern Oregon Station at Medford, Oregon; and since 1959 has directed the federal berry and grape research at Carbondale, Illinois. In the spring of 1964, at Carbondale there were about 173 strawberry selections from 22,000 seedlings, with 8 of the selections to go into advanced tests. About 6,000 seedlings are fruited each year.

Royce S. Bringhurst, professor of pomology in charge of the strawberry research of the University of California, was born in Murray, Utah, December 27, 1918; he received his B.S. at Utah State University in 1947; his Ph.D. at the University of Wisconsin in 1950. Since 1953 he has been with the University of California in charge of small fruit research, most of which is concerned with the strawberry. Besides the introduction of the Solana (1958), Fresno (1960), Torrey (1960), Wiltguard (1960), and Tioga (1964), and breeding larger berries for California conditions, he has been interested in the native species, especially *chiloensis* and *ovalis*, and has found natural pentaploid *chiloensis* x *vesca* hybrids along the coast of California. He and his associate, Victor Voth, have been especially interested in the response of varieties to planting dates and temperature.

FIG. 13–6.
Brooks, Albert N.

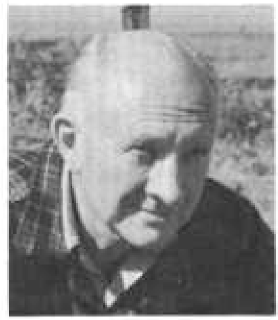


FIG. 13–7.
Clarke, J. Harold

Albert N. Brooks, originator of the Florida Ninety strawberry, was born October 16, 1897, College Hill, Ohio. He received his A.B. at University of Cincinnati, 1921, and was instructor in botany, plant pathology, and bacteriology there for two years. Then he went to the University of Wisconsin, obtaining his Ph.D. in 1926, majoring in plant pathology. For two years (1925–1927) he was with the Florida State Plant Board. In 1927 he went with the Florida Experiment Station where he has worked on all phases of strawberry research—diseases, insects, culture, varieties, and breeding—at a field laboratory at Plant City, the older strawberry growing section of Florida.

Though Dr. Brooks had done breeding work with strawberries in earlier years in Florida, his one great variety—the Florida Ninety—came in 1948 from seed of open-pollinated Missionary growing near Klonmore but in a field containing over 60 other varieties. In the winter of 1948–1949, 1,075 seedlings from this seed were tested and of these 120 were retested. No. 90 was finally selected for introduction in 1952.

J.H. Clarke was born June 12, 1899, at Lafayette, Indiana, and grew up on a general farm. Severe asthma brought on by contact with both cows and sheep caused him to choose horticulture as a major in college. After graduation in 1921, he was for two years assistant horticulturist at the University of Delaware and received an M.S. there in 1923. From 1923 to 1946 he was small fruit specialist at Rutgers University, becoming full time specialist in small fruits in 1928. He obtained his doctor's degree in 1942 at Columbia University. In 1946 he became general manager of the Cranguyma Farms, with about 100 acres of cranberries at Long Beach, Washington. In 1954 he started a rhododendron and azalea nursery which he still operates with his son, and they also have some twenty acres of cranberries. Dr. Clarke has written two books—*Small Fruits in the Home Garden* and *Getting Started with Rhododendrons and Azaleas*. While at Rutgers, he originated the Pathfinder in 1928, introduced in 1938; Sparkle, 1931, introduced 1942; and other varieties (Julymorn, Crimson Glow, Redwing, and Redcrop). Sparkle is still one of the important varieties of the United States.

Donald L. Craig, head of the small fruit section of the Canada Department of Agriculture Research Station, Kentville, Nova Scotia, was born in Kentville on December 18, 1923. Formal schooling included a B.Sc. (Agriculture) from McGill University and a M.Sc. and Ph.D. from the University of New Hampshire in 1955 and 1959. He has been at the Kentville Research Station since 1947 where his chief interest is in strawberry and raspberry breeding. Dr. Craig and Dr. Aalders introduced their first strawberry variety (Acadia) in 1965. Dr. Craig is interested in all aspects of horticultural research. He pioneered the first strawberry certification program in Canada.

George M. Darrow was born February 2, 1889, Springfield, Vermont; graduated in 1910, Middlebury College; obtained a Master's Degree at Cornell University in 1911 and his Ph.D. in plant physiology at Johns Hopkins in 1927. He started with fruit research of the U.S. Department of Agriculture July 1, 1911, and continued with this until retirement. For the summer of 1911 he assisted in sweet cherry, loganberry, and prune careful handling and storage investigations and later in storage and handling investigations with apples in Oregon. In the winter of 1911 he was assigned to careful handling with citrus in Florida and in 1912 began a four-year study of the physiographic regions of Tennessee, Kentucky, and West Virginia, mapping the fruit regions and describing the varieties in each state. Beginning in 1916 a study was begun of the cultural practices and varieties of berries in each producing region of the United States. After military service (1918–1919) these studies were resumed and the first strawberry breeding begun in the winter of 1919–1920. Strawberry and blueberry breeding and physiology were his chief interests. For the period 1946 to 1955 he was in charge of the research

FIG. 13–8.
Craig, D. L.

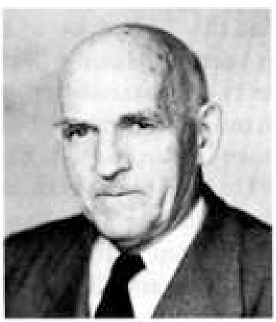


FIG. 13–9.
Darrow, G. M.

FIG. 13–10.
Daubney, Hugh A.

FIG. 13–11.
Galletta, G. J.

FIG. 13–12.
Gilbert, Frank

of all deciduous fruit production in the U.S. Department of Agriculture. In 1956–1957 he surveyed the native strawberries of Chile and retired March 31, 1957. Since that time he has been breeding hemerocallis and azaleas at his home in Glenn Dale, Md., and assisting his sons with a twenty-acre "pick-your-own" strawberry project.

Hugh A. Daubney was born on December 6, 1931, Nanaimo, British Columbia. He received his B.S.A. in 1953 from the University of British Columbia, his Ph.D. at Cornell in 1958. Since then he has been with the farm of the Canadian Department of Agriculture, Agassiz, breeding strawberries and raspberries. He has been especially interested in sources of resistance to mildew and red stele and in selecting superior clones of the native *chiloensis* along the beaches of the Pacific.

Gene J. Galletta was born on July 3, 1929, Philadelphia, Pennsylvania. He received his B.S. at the University of Maryland, 1951; his M.S. at Rutgers University, 1953. After service in the Army (1954–1956), he obtained his Ph.D. at the University of California, 1959. He worked in the Galletta Bros. Blueberry Farms 1942–1951; he was research assistant in pomology at Rutgers University, 1951–1953; and at the University of California, 1953–1954 and 1956–1959. Since 1959 he has been professor at North Carolina State College and in charge of the blueberry and strawberry breeding cooperating with D.H. Scott of the U.S. Department of Agriculture.

Frankin A. Gilbert was born in Burlington, New Jersey, June 8, 1919; he received his B.S. at Rutgers University in 1942, and his Ph.D. in 1952. He was a field agent in horticulture for the U.S. Department of Agriculture in 1942, in the U.S. Army Air Force from 1942 to 1944, extension specialist 1944 to 1946, instructor and research assistant 1946 to 1950 at Rutgers University, and since 1950 professor of horticulture at the University of Wisconsin in charge of the Branch Experiment Station at Sturgeon Bay, Wisconsin. In New

FIG. 13–13.
Goldsmith, E. B.

FIG. 13–14.
Hagerstrom, Marion

Jersey Dr. Gilbert made the cross and selected the seedling later named and introduced as Jerseybelle.

P.L. Hawthorne was born September 15, 1912, Provencal, Louisiana. He obtained his B.S. in 1938 and his M.S. in 1949 at Louisiana State University. From 1938–1940 he taught in Amite High School; from 1940–1946 he was assistant horticulturist at North Louisiana Experiment Station at Calhoun, Louisiana. From 1947–1948 he was assistant horticulturist, Western Tennessee Experiment Station, and from 1948 to present, professor of horticulture, Louisiana State University. In 1935, as a student, he was associated with the strawberry breeding work and has been working with strawberries ever since. He became project leader for strawberry breeding at Louisiana State University in 1948. Subsequently the Headliner and Dabreak were originated, each of which in 1965 constituted about half the acreage in Louisiana. Three new selections are being tested by growers at the present time.

Earl B. Goldsmith was born December 9, 1892, in Santa Cruz, California, and died on March 25, 1954. He went to grammar school but not to high school. When the experiment station at Santa Clara (a suburb of San Jose) was established about 1928, he was a ranch foreman for a prune grower at San Jose, and was hired by Dr. Thomas as foreman of the station for field trials. Darrow had sent many selections to Thomas for trial and on his own initiative Goldsmith began crossing and raising seedling strawberries. He made his first crosses in 1929 and the work was made official as a part of the research program in 1930. He continued to look after the breeding of strawberries under Dr. Thomas as research assistant at Santa Clara and later at Davis and Wheatland. In January 1944 he became an employee of E.F. Driscoll, a strawberry grower, and when Dr. Thomas became Director of the Strawberry Institute, Goldsmith became the strawberry breeder of the Institute under Dr. Thomas' direction. He was a rather small man, full of energy, a keen observer and an individualist. He was an idealist and devoted his entire energy to his strawberry work—to breeding ideal varieties. As each year's seedlings seemed better than those of the year before, he kept on—the level of accomplishment never quite reaching his ideal.

Marion Hagerstrom, Monticello, Minn., was born October 7, 1910, in Wisconsin. He is one of the few private strawberry hybridizers who still competes with some success with the state and federal breeders. While his Red Rich everbearer has not gained wide acceptance south of Minnesota, it has been used as a parent of the successful everbearers Ozark Beauty and Geneva. His crosses of Red Rich with Midland, while not yet named, have done better for H.A. Wallace in northern Westchester, N.Y., than most of the Geneva and New Jersey varieties. Hagerstrom has spent nearly all his life on the farm near Monticello, where his great interest is fruit breeding. His varieties have great hardiness.

D.D. Hemphill was born at Crane, Missouri, November 8, 1918. He received his B.S. from the University of Missouri in 1940 and his Ph.D. in 1948. He was assistant horticulturist at the University from 1940 to 1942, was in the army 1942 to 1946, and has been professor of horticulture since 1946 at the University of Missouri. He has been especially interested in plant hormones, growth regulators, herbicides, and small fruit research. Since 1953 he has been in charge of strawberry breeding.

S.C. Harland was born in Snainton, England, June 19, 1891. He received his B.S.C. in Geology in 1912 and his D.S.C. in applied botany in 1920 at the University of London. In 1913 he became Pomological Assistant in the St. Croix Experiment Station, Virgin Islands; in 1914 Assistant Soil Chemist, Department of Agriculture, Nova Scotia; in 1915 Assistant Superintendent of Agriculture, St. Vincent, West Indies; 1920 to 1923 Head of Department of Botany of the British Cotton Industry Research Association, Shirley Institute, Manchester, England; 1923 Professor of Botany and Genetics, Imperial Col-

FIG. 13–15.
Hawthorne, P. L.

FIG. 13–16.
Hemphill, D. D.

lege of Tropical Agriculture, Trinidad; 1926–1935 Head of Genetics, Empire Cotton Research Station, Trinidad; 1935–1939 Adviser on cotton to State of Sao Paulo, Brazil; 1939–1949 Director, Institute of Genetics of National Agricultural Society of Peru; 1950 to 1958 Professor of Botany, University of Manchester; retired 1958 as Emeritus Professor. His most important work was on cotton genetics and he published a book on Genetics of Cotton (1939), but also developed a school of research on the strawberry at the University of Manchester. His present address is Plant Breeding Station, Correo Nana, Kilometer 22, Carretera Central, Peru.

Edward M. Henry was born October 7, 1906, on a farm at New Market, Tenn. He obtained a B.S. degree from the University of Tennessee in Agriculture. He was with the Experiment Station at Knoxville from 1931 to 1934 as assistant horticulturist under Dr. Brooks Drain, with his chief responsibilty the project in strawberry breeding. The Blakemore was already the most popular variety in Tennessee and it was decided to try the same cross and to backcross Blakemore to each of its parents. He stayed with the breeding project long enough to make the selections later retested at Jackson and named the Tennessee Shipper and the Tennessee Beauty. Mr. Henry then worked for the Farm Security Administration for ten years and with the Agricultural Extension Service fourteen years. He is now agricultural county agent, living at Jonesboro in east Tennessee.

Walter H.J. Hondelmann was born in Hamburg, Germany, April 17, 1928. He studied horticulture and botany (1952–1956) in Cologne and Berlin, and received his doctoral degree (1958) at the Institut fur Vererbungs- und Zuchtungsforschung at Berlin-Dahlem. In 1959 he joined the Sengana GmbH. in Hamburg-Volksdorf, where he was junior breeder of strawberries and now is head of the breeding and research unit.

FIG. 13–17.
Henry, Edward M.

FIG. 13–18.
Hondelmann, Walter H. J.

FIG. 13–19.
Johnson, Harold A., Jr.

FIG. 13–20.
Kronenberg, Hester G.

FIG. 13–21.
Lalatta, F.

FIG. 13–22.
Meader, Elwyn M.

Harold A. Johnson, Jr., was born January 30, 1923, Riverside, California. He attended Santa Barbara State College and University of California and received his B.S. at Davis; he did graduate work at the University of California, and has worked in plant pathology to the present. He became interested in strawberries while manager of the McCrea Seed and Chemical Company at Santa Maria and helped the Sheehy Berry Farm, the largest berry farm at that time, with their insect and fertilizer problems. In June, 1955, he became strawberry breeder for the California Strawberry Institute.

Miss Hester G. Kronenberg was born in 1912 at Rotterdam, Netherlands, and studied horticulture at the Agricultural University in Wageningen, taking her degree in 1936. In 1938 she began a study of strawberry disease problems at Beverwijk in the old strawberry area of Kennemerland. Since 1943 she has been at the Institute of Horticultural Plant Breeding in charge of breeding and variety research in small fruits.

Prof. F. Lalatta, Director of the Institute for Fruit Culture at Rome, where strawberry breeding is carried on at Ciampino, about twenty kilometers from Rome.

Elwyn M. Meader was born March 31, 1910, Rochester, New Hampshire, adjoining the farm where he now lives. He received his B.S. in 1937 from the University of New Hampshire; his M.S. in 1941 from Rutgers University, where his thesis was "A Method for Determining the Relative Cold Hardiness of Dormant Peach Fruit Buds"; from 1938 to 1941 he did research on peaches for the U.S. Department of Agriculture at Rutgers, from 1941 to 1945 on berries at Beltsville, from 1945 to 1946 he was associate professor at the University of Vermont, from 1946 to 1948 he was horticulturist, U.S. Army in Seoul, Korea, from 1948 to the present he has been professor of horticulture at the University of New Hampshire. A native love of plants, a Yankee view of their good and bad points, and the desire to improve them, plus contact with A.F. Yeager, made him a plant breeder. He was associated in the work of the U.S. Department of Agriculture when the Midland and Temple varieties were introduced and when the major emphasis was put on breeding for red stele resistance and Fairland was selected. He has specialized in breeding everbearing strawberries without runners.

Julian C. Miller was born November 29, 1895, Lexington, South Carolina. He was in the Navy 1917–1919; at Clemson College he received his B.S. in 1921 and his Ph.D. at Cornell University in 1928. He was an instructor in horticulture, North Carolina State College 1921–1923; county agricultural agent, South Carolina 1923–1925; graduate assistant, Cornell University 1925–1928; professor of horticulture, University of Oklahoma, 1928–1929; professor of horticulture, Louisiana State University, 1929 to present. He was born on a farm six miles outside of Columbia, South Carolina, where strawberries were grown in the garden and in 1935 he initiated the strawberry breeding program that has resulted in the introduction of Klonmore, Konvoy, Marion Bell, Headliner, and Dabreak.

James N. Moore was born June 10, 1931, Vilonia, Arkansas. He received his B.S.A. in 1956, M.S. in 1957 at the University of Arkansas, and his Ph.D. from Rutgers University in 1961. Growing up on a farm, he became interested in strawberries when he was put in charge of the strawberry breeding project at Rutgers University and had as his research project the effect of gamma irradiation and photoinduction on auxin levels during the vegetative and reproductive growth of the strawberry. From September 1961 to January 1964 he was with the U.S. Small Fruits Research Unit at Beltsville and helped in the strawberry breeding. In January, 1964, he became associate professor of horticulture at the University of Arkansas in charge of small-fruit production work, including breeding.

Fig. 13–23.
Miller, Julian C.

Fig. 13–24.
Moore, James N.

Fig. 13–25.
Morrow, E. B.

Prof. Emmett B. Morrow, born in Rowan County, North Carolina, in 1898, passed away July 1956. He grew up on a cotton, grain, and dairy farm with four brothers and four sisters. Even as a boy he was interested in horticulture, helping in the garden, planting shrubs and fruit. He graduated from North Carolina State College in 1921 and obtained his M.S. at the University of California in 1924. He was for one and one-half years assistant in statistics in the Market Division of the North Carolina Department of Agriculture and then, until 1936, horticulturist in the Extension Service. In 1936, with the North Carolina Experiment Station, he began his research work on blueberries and strawberries, in full cooperation with the U.S. Department of Agriculture. New varieties resulting from this cooperative work were: Ivanhoe, Walcott, Murphy, Angola, and Croatan blueberries, now the chief varieties in the State; and the Fairmore, Daybreak, Eleanor Roosevelt, and the Massey and Albritton strawberres, of which the last two have been almost exclusively grown in eastern North Carolina since their introduction. His work on strawberries, beside the varieties introduced, has resulted in notable publications, including: (1) "Fruit-bud differentiation in deciduous fruits" (*Hilgardia,* 1925), (2) "Effect of age of plant on flower production and yield of strawberries in North Carolina" (*Proc. Amer. Soc. Hort. Sci.,* 1931), (3) "Relation of number of leaves in November to number of flowers the following spring in the Blakemore strawberry (*Proc. Amer. Soc. Hort. Sci.,* 1939), (4) "Inheritance of some characteristics in strawberry varieties" (*Proc. Amer. Soc. Hort. Sci.,* 1941), (5) "Effect of renovation of beds after harvest on yield and grade of strawberries" (*Proc. Amer. Soc. Hort. Sci.,* 1942), (6) "Rating system for the evaluation of horticultural material" (*Proc. Amer. Soc. Hort. Sci.,* 1949), (7) "Effect of limited inbreeding in strawberries" (*Proc. Amer. Soc. Hort. Sci.,* 1952), (8) "Genetic variances in strawberries" (*Proc. Amer. Soc. Hort. Sci.,* 1958), (9) "Genetic variation in an asexual species, the garden strawberry" (*Genetics,* 1958), and (10) "A quick method of cleaning berry seed for breeders" (*Proc. Amer. Soc. Hort. Sci.,* 1954).

Donald K. Ourecky was born in Sterling, Colorado, September 11, 1932. He grew up on a small fruit farm in Oregon and worked in the lily and iris fields of Jan De Graaff Bulb Farms. He obtained his B.Sc. from Oregon State University in 1954 and his Ph.D. from Washington State University in 1961. He was a junior horticulturist at the Coastal Experimental Station at Long Beach, Wash., 1954–1956; research assistant at Washington State University, 1956–61; and research geneticist with the U.S. Department of Agriculture at Tifton, Georgia, 1961–1962. Since then he has been at the New York Experimental Station at Geneva, working with George Slate and John Watson on berry breeding.

Robert D. Reid (center) was born February 14, 1902, at Carlisle in the

FIG. 13–26.
Ourecky, D. K.

FIG. 13–27.
Reid, R. D.

FIG. 13–28.
Scott, Donald A.

County of Lanark, Scotland. A berry grower who began studying diseases of strawberries at Auchincruive College in southwest Scotland in 1930, he noted the resistance of Frith to the red core (= red stele) root disease. In 1933 he began crossing and testing his seedlings for resistance. His numbered seedlings, which resulted from this work, were the basis of the Scottish Industry until after he introduced the Auchincruive Climax in 1947. His Redgauntlet and Talisman now are widely grown in Scotland and elsewhere, and the Templar was just introduced in 1964.

Donald H. Scott was born at Buxton, North Dakota, December 3, 1911. He received his B.S. from the University of North Dakota in 1936 and his Ph.D. from the University of Maryland in 1949. He was instructor in horticulture at the University of North Dakota from 1936 to 1937, and geneticist for the U.S. Department of Agriculture in peach breeding at the New Jersey Experiment Station, New Brunswick, 1937–1939, and at Beltsville, Maryland, 1940–1942. From 1943 to 1945 he was in charge of the U.S. Dry Land Horticulture Station at Cheyenne, Wyoming, working especially with tomato and strawberry breeding and shelter belts. Since 1946 he has been associated with the small-fruit research at Beltsville and in charge since the retirement of Darrow in March 1957. Even though allergic to strawberry pollen, he still makes the crosses.

Chester Druse Schwartze was born March 13, 1902, in the great tree-fruit region of Yakima, Washington, and was raised in his parents' fruit orchards near Yakima, as well as in his maternal grandfather's (D.L. Druse) pioneer orchard of many varieties. He obtained his B.S. in horticulture in 1924 at Washington State University, engaged in orcharding 1924–1930, and was fruit and vegetable inspector in 1930–31. In January 1932 he enrolled for graduate work, becoming a half-time research assistant at Washington State University in charge of strawberry and raspberry breeding. He obtained his doctor's degree in pomology in 1935, his thesis being "Rest period response and cold resistance in the red raspberry in relation to breeding of hardy varieties." He was appointed horticulturist at the Western Washington Experiment Station at Puyallup in charge of strawberry and raspberry breeding in 1935. Beginning in 1940, Arthur D. Myhre, B.S. in horticulture, assisted him and they jointly made crosses, raised and judged seedlings, made selections, and introduced varieties until 1957 when Myhre became head of the ornamental plant section there. Myhre's contribution was recognized in joint credit for the Puget Beauty strawberry and several raspberries and publications.

Having been brought up in a fruit environment, Dr. Schwartze's interest in fruit was crystallized by his reading, as a boy, about Luther Burbank's work, and later by courses in plant breeding, genetics, and cytology, and by his being in charge of strawberry and raspberry breeding while a graduate student.

Approximately 150,000 strawberry seedlings have been grown since he has been in charge and four varieties of especial promise have been named and released: Northwest (1949), which beginning in 1962 has had the largest acreage of any variety in the United States and is processed in larger quantity than any other sort; Puget Beauty (1956), Cascade and Columbia (1961). He has cooperated closely with other breeders in testing their selections, and varieties and selections of other breeders have entered into the parentage of his varieties. Dr. Schwartze is also well known for the raspberry varieties he has originated and for his blueberry work, for his willingness to test raspberry selections of other breeders for resistance to aphids that spread virus, and for his interest in the beauty of flowering crabapples at his home.

Reinhold von Sengbusch was born at Riga, Latvia, February 16, 1898, studied agriculture at University of Halle 1918–1919, where he graduated

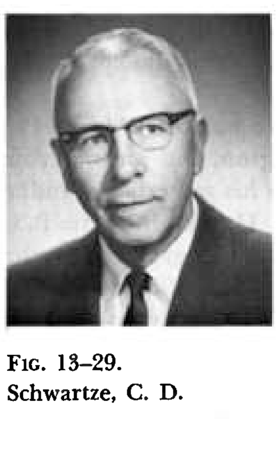


FIG. 13–29.
Schwartze, C. D.

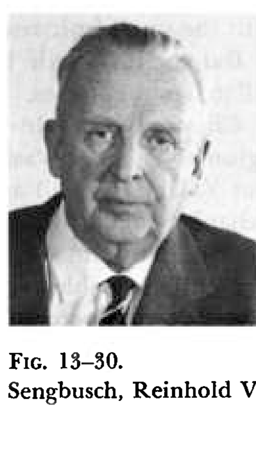


FIG. 13–30.
Sengbusch, Reinhold Von

FIG. 13–31.
Slate, George L.

FIG. 13–32.
Spangelo, L. P. S.

(Dr. rer. nat.) 1924, under Prof. Roemer. He was head of the department at Kaiser-Wilhelm-Institut fur Zuchtungsforschung at Muncheberg 1927–1937, where he originated the sweet lupin (alkaloid-free lupin). After that he was owner and head of a research station at Luckenwalde until 1945.

In 1942 he first started breeding work with strawberries. Other objectives of those years were polyploid rye, hemp (monoecious, fiber-rich types), spinach and asparagus. For the next three years he was head of State Experiment Station for breeding sweet lupines at Luckenwalde. He moved to Hamburg in 1948, where a research station of the Max-Planck-Gesellschaft (successor of Kaiser-Wilhelm- Gesellschaft) was founded, which was given the rank of Institute (Max-Planck-Institut fur Kulturpflanzenzuchtung) in 1959 under his directorship. In 1954 he also founded the private Sengana GmbH., where strawberry breeding work and propagation and distribution of new strawberry varieties are carried out. Under his auspices the strawberry work continued on a large scale. At the institute, research with cultivated mushrooms (physiology, breeding, cultivation methods) is a considerable part of his work.

George L. Slate was born at Barnardston, Massachusetts, June 27, 1899, grew up on a dairy farm where an assortment of fruit varieties for home use were grown. He came to Geneva, New York, from the Massachusetts Agricultural College in 1922 and assisted in the preparation of *The Small Fruits of New York*. This gave him a love for books on fruits, especially on the strawberry, of which he has one of the best collections. It also gave him an understanding of the evolution of the strawberry as a cultivated fruit and started him in breeding. He still continues to breed strawberries, fruiting about 11,000 seedlings and over 100 selections in 1962. Of these (many of selfed lines) over half were for better everbearing varieties. Present objectives especially emphasize firmness of berry, though high flavor and everbearing qualities were important too. In all he has introduced 16 varieties, of which his best known, Catskill, is the standard midseason variety of the eastern United States. His hobbies are gardening, breeding lilies, and writing for garden magazines. His assistants are J.P. Watson and D.K. Ourecky.

L.P.S. Spangelo was born at Morden, Manitoba, in 1919. His father was for a time an apple breeder at the Morden Farm. He obtained his B.S.A. and M.Sc. from the University of Manitoba and as an undergraduate worked during vacations at the Morden Farm for Mr. Kerr, the senior pomologist, in crossing fruit and taking records. He joined the federal staff at Ottawa in 1948.

H.G. Swartwout was born in Springdale, Arkansas, May 12, 1895. He received his B.S. and M.A. at the University of Missouri, and he has been plant pathologist at the University from 1918 to the present. He is the originator of Armore, which was introduced in 1930.

K. Tamari, originator, about 1938, of the Kogyoku, the leading strawberry of Japan, now retired.

Harold E. Thomas was born at Watsonville, California, March 25, 1900. He grew up on a small farm about six miles from the city. After high school he spent one year on the ranch and went to the University of California in 1920, obtaining his M.S. in 1924 and his Ph.D. in 1928 in plant pathology. He became a member of the plant pathology staff in 1927, working on strawberry diseases and continued in the work until he resigned to become director and pathologist of the non-profit Strawberry Institute of California, at Morgan Hill. The Institute, organized by E.F. Driscoll, a far-sighted strawberry grower who cooperated with the University beginning in 1930, was designed to conduct breeding and provide scientific assistance to the growers. In 1945 the University introduced 5 varieties of strawberries resulting from Thomas' and Goldsmith's work—the Shasta, Lassen, Tahoe, Donner, and Sierra. Of these,

Fig. 13–33.
Swartwout, N. G.

Fig. 13–34.
Tamari, K.

Fig. 13–35.
Thomas, Harold E.

FIG. 13–36. Voth, Victor

Shasta and Lassen became important in the United States. Some Donner and Tahoe were grown in the early 1950's and Donner has now become important in Japan. The Goldsmith (Z5A) was patented and introduced by the Strawberry Institute commercially in 1958 as Z5A and named in 1963. Solana, named in 1957 by the University of California, was selected in 1937 by Thomas and Goldsmith.

In 1934 there were between 3,000 and 4,000 acres of strawberries in California. Just before World War II the strawberry acreage in California was about 5,000, most of which was Marshall (Banner) in central California and Klondike in southern California. By the end of the war the acreage was down to 900 acres. The five new varieties, introduced in 1945 as a result of Thomas' and Goldsmith's work, were relatively virus-free and were far more vigorous and productive than Marshall. The acreage increased steadily until there were 22,500 acres in 1956, composing 55 percent of the national production, with Shasta and Lassen as the chief varieties. With the passing of years, Shasta and Lassen also became infected with virus and a virus-free nursery program was put into effect. The acreage has stabilized in recent years at about 10,000 acres.

A second organization, Strawberry Institute Nursery, has been set up in recent years for propagation of the highest grade plant stocks for growers. Dr. Thomas is director of this also. Patented varieties originated by the Institute are propagated for members of the Institute only. About twenty million plants are propagated annually.

Victor Voth, research specialist in pomology of the University of California, in charge of the research on strawberry in southern California, under Dr. Bringhurst, was born at Shafter, California, September 7, 1920. He obtained his B.S. from the University of California at Davis in 1942, and has been in strawberry work since 1946, first at Davis with Baker, next at Torrey Pines in 1952, and later, in 1956, with headquarters at the South Coast Field

FIG. 13–37.
Waldo, George F.

Station, Santa Ana, south of Los Angeles. Since January 1952 he has been in charge of the strawberry work in southern California, including Santa Barbara County. About half the seedlings raised each year are grown at either Torrey Pines or at the South Coast Field Station and the other half at Winters, near Davis. More than 10,000 seedlings are evaluated annually. His studies have shown Lassen to be the most salt-tolerant and have demonstrated this trait to be heritable. They have proved that the sprinkler system now used by 75 percent of the growers lessens the alkali problem.

George F. Waldo was born December 2, 1898, at Drayton, in the northeast corner of North Dakota. When he was fourteen, the family moved to a small-fruit farm at Dayton, in western Oregon; and a year later he planted the first strawberries, growing up to two and three acres at times. He graduated with the B.S. degree at Oregon State College in 1922, was assistant to the horticulturist at the Oregon State Hospital, Salem, Oregon, for one year, then began graduate work at Michigan State College in March 1924, obtaining his M.S. in 1926, at which time he entered the U.S. Department of Agriculture, working at the Glenn Dale, Maryland, Station, 1926–1932. He was in charge of the work there from 1930 to 1932, while George M. Darrow was in charge in Oregon. Since September 1932 he has been in charge of the cooperative breeding work of the U.S. Department of Agriculture and the Oregon Station for the Northwest at Corvallis, Oregon. His work on flower-bud formation in berries has been especially notable, as has been his breeding for better varieties for the Northwest. Although his raspberry and blackberry breeding has been his most successful work, his breeding with strawberries has been important in building up the desirable qualities of strawberries in selections used by himself and others. He has utilized selections of the native beach (*F. chiloensis*) and western field (*F. ovalis*) strawberries more than most breeders and has found selections of *F. chiloensis* that are more resistant to the red stele root disease than any others known for use in breeding.

FIG. 13–38.
Watson, John P.

FIG. 13–39.
Wallace, Henry A.

George Waldo's graduate work at Michigan State College on flower bud formation in everbearing strawberries was what was needed in the federal work at Glenn Dale, and after he became a member of the staff in 1926 he surveyed the initiation and development of flower buds in varieties and species. This made breeding more intelligible and led later to a better understanding of the effects of photoperiodism on the growth cycle and adaption of strawberry varieties. In this research he had a large part. He originated the idea of testing seedlings in greenhouse benches, to see whether they possessed resistance to the red stele root disease, a method that has greatly advanced the breeding for resistance to this trouble. Over the last twenty years, probably ten times more seedlings have been tested this way than could have been without this technique. Only the resistant seedlings are saved for field testing for other plant and fruit qualities.

Henry A. Wallace has been interested in growing strawberries since 1902 but began producing them from seed in 1935 when he went with Dr. Darrow to the U.S.D.A. experimental plots and was greatly impressed by a row of plants which was inbred out of Howard 17. He expanded his strawberry breeding when he moved to South Salem, New York, in 1946 using cross pollination in an attempt to produce virus-resistant strains. He felt that there was a chance of revolutionizing the strawberry industry by growing strawberries commercially from seed, an idea derived from his earlier success in producing hybrid corn.

To Wallace, his most intriguing project in recent years has been his effort to introduce *vesca* and *moschata* flavors into the domestic strawberry. Based on the work of Haig Dermen's application of colchicine to produce polyploids, that of Darrow in crossing tetraploid *vesca* with the domestic berry, and that of D.H. Scott in making a 10-ploid form which was ¾ American and ¼ wild European, Mr. Wallace converted the 10-ploid plants into 8-ploids in order to cross with other octoploids which he hoped could furnish size, firmness and color while retaining the taste of the wild European berry.

John P. Watson, who assists George Slate in the breeding work at the New York Experiment Station at Geneva, was born October 21, 1922, at Worcester, Massachusetts. He graduated at the Stockbridge School of Agriculture in 1942, was in the Air Force 1942–1945, obtained his B.S. at the University of Massachusetts in 1948 and his M.S. at Rutgers in 1950. His breeding work has included work with plums, peaches, grapes, and strawberries, as well as with other berries.

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U.S. Department of Agriculture Strawberry Breeding

PRIOR TO 1920 most breeding work with strawberries was conducted by private breeders. However, a comparison of the chapter on early breeders with that on breeders of today indicates that a change had taken place in the interim, for today's breeders are almost all employed at experiment stations where the work is supported by either the federal or the state governments. Tax-supported experimental work originated most of the varieties grown today; and the work continues, producing new varieties and adding to the knowledge about strawberries in general. Central to this work, is that conducted by the U.S. Department of Agriculture at Beltsville, Maryland, where extensive systematic breeding has been proceeding without interruption for forty-five years. Much of the work done there has affected, either directly or indirectly, the work at the state experiment stations, for the U.S. Department of Agriculture works cooperatively with many stations on the strawberry, and in the past has done much to disseminate breeding materials, ideas, and techniques to all those actively engaged in breeding. (See also under North Carolina and Wyoming.)

LOCATION AND PERSONNEL. A project for the improvement of the strawberry was undertken by the U.S. Department of Agriculture early in 1920, with George M. Darrow in charge, and the work located at Glenn Dale, Maryland, fifteen miles out of Washington, where Dr. Walter Van Fleet was breeding roses and chestnuts and had made some strawberry crosses. Before his federal

Fig. 14–1. An unheated sash greenhouse at Glenn Dale, Maryland, used for strawberry breeding, beginning in 1920. The house was later moved to Beltsville and was used for berry breeding until 1963. Left to right, George M. Darrow, George F. Waldo, Mr. Rifenbach (deceased), and C.E. Woods (resigned). April 22, 1930.

service, Dr. Van Fleet had bred strawberries in New Jersey, and had named the Early Jersey and Late Jersey varieties. After Dr. Van Fleet's death in January 1922, the strawberry work was greatly expanded. The first crosses were planted at the Glenn Dale Horticultural Field Station in 1921 and one-half acre fruited in 1922. For two years (1921 and 1922) crosses were made in the field, but the loss of crossed flowers by frosts was so great that the later crosses were made in an unheated sash glasshouse (*Fig. 14–1*). The seedlings also were raised in it. In 1922 four acres and the following year about eight acres of seedlings were grown. G.F. Waldo joined the team in 1926.

In 1928 strawberry breeding was initiated at Willard, North Carolina, in cooperation with Charles Dearing of the North Carolina Department of Agriculture, and later, in 1936, in cooperation with the North Carolina State Experiment Station, of which Prof. E.B. Morrow was in charge until 1956. In 1928 also breeding was begun at Corvallis, Oregon, in cooperation with the Oregon Experiment Station, with Prof. Carl Schuster in charge. In 1932 the central breeding work was moved from Glenn Dale to Beltsville, both in Maryland, where it has been continued ever since. From 1930 to 1932, George M. Darrow was in charge at Corvallis. Since then G.F. Waldo has been in charge there. From 1941 to 1945 E.M. Meader was associated in the work at Beltsville. From 1946 to 1957 D.H. Scott was associated with the work, and has been in charge from 1957 to the present. Dr. R.J. Knight, now at Chapman Field, Miami, Florida, assisted from 1957 to 1961, and Dr. J.N. Moore was associated in the work from 1961 to 1963. In 1939 cooperative breeding was begun with the University of Maryland, with the resulting seedlings being grown near Salisbury, Maryland. Since about 1946 most of the seedlings, first tested in the Beltsville greenhouse benches for red stele resistance, have been fruited at the University of Maryland Research Farm at Salisbury. In 1959 cooperative work was started at the University of Southern Illinois at Carbondale, with Dr. R.C. Blake in charge.

The staff at present is:

Beltsville, Maryland
- D.H. Scott, in charge
- E.D. Lusby, aide—field foreman (Fig. 14–3)
- D.P. Ink, aide—breeding (Fig. 14–2)
- R.O. Mullikin, aide—greenhouse
- R.H. Converse, pathologist—red stele disease
- J.R. McGrew, pathologist—virus diseases
- G.M. Darrow (retired), consultant

Corvallis, Oregon
- G.F. Waldo, in charge
- Francis J. Lawrence, associate

Willard, North Carolina
- G.J. Galletta, (of North Carolina Experiment Station, Raleigh) in charge

Salisbury, Maryland
- Directed from Beltsville and by Dr. I.C. Haut at College Park

Carbondale, Illinois
- R.C. Blake, in charge
- J.W. Hull, associate

Cheyenne, Wyoming
- G.S. Howard, in charge

OBJECTIVES. In the early years of the work the three specific objectives were origination of a commercial variety of superior dessert quality for eastern states, origination of improved canning varieties, and origination of superior freezing varieties. A survey of all the commercial strawberry areas of the United States in 1914 to 1917 showed Marshall as the standard dessert variety. Thus, on the Boston Market in 1916, ordinary market berries were selling for

FIG. 14–2. Ink, D.P.

FIG. 14–3. Lusby, Edward.

8c a quart and those of Marshall at 35c a quart. Marshall is not fully hardy and is very subject to leaf and virus diseases in eastern states. As a result of breeding for higher flavor, four dessert varieties—Dorsett, Fairfax, Narcissa and Southland—were introduced in 1932 and 1933. Southland proved frost-susceptible, all Dorsett plants lacked hardiness and were found to have virus, and both have been discarded. But clean stocks of Fairfax were found and propagated; and it continues to be grown as a standard dessert variety of northeastern United States. Narcissa was grown to a slight extent in Oregon, but was too soft. Redheart was introduced in 1932 as a very firm, high flavored, canning variety, but canning of strawberries has decreased substantially in the United States and with it the need for a canning variety. It is still grown in Italy. Furthermore Redheart is very subject to virus diseases. Blakemore was introduced as a shipping and freezing berry in 1930, and soon became the leading variety in the United States, a position which it held until 1962, when Northwest became the leading variety.

This first early work indicated that breeding for a specific objective was practicable and through the years varieties have been bred and introduced to fulfill specific objectives. In general, since 1940, the breeding work has had as one ultimate overall objective, the replacement of all varieties with new varieties resistant to the red stele root disease. Another objective for the South has been ideal shipping varieties—firm, large, high-flavored, attractive, and productive. Although the first ones, Daybreak, Eleanor Roosevelt, and Fairmore, failed due, at least in part, to infection with virus diseases, Massey and Albritton have succeeded in North Carolina. The objectives listed for the federal work in 1937 were: "(1) greater resistance to leaf, crown, and root diseases; to virus diseases, and possibly to nemas (eelworms); (2) greater resistance to high and low temperatures and to drought; (3) better adaption to long and short days; (4) better dessert quality under adverse weather conditions; (5) increased firmness and toughness of skin; and (6) better adaption to specific uses." (Darrow, 1937). Present objectives are similar: varieties resistant to red stele, firmer than Blakemore, larger than Pocahontas, more productive than Midway, as highly flavored as Suwannee, and as good for freezing as Midland. At Cheyenne, Wyo., (see also p. 253) beginning in 1932 the objective has been a home garden and local market variety that would stand –40° F. without mulch protection just as the wild ones do. Cheyenne 1, 2, and 3, Sioux, Arapahoe, Radiance and Ogallala were introduced and served the purpose. The latter three are still grown. Still larger, firmer, and more productive varieties are being bred.

METHODS OF BREEDING IN MARYLAND. As stated above, since field crossing was found in the early work to be hazardous, an unheated greenhouse (*Fig.*

14–1) was used. Vigorous plants were potted (usually in 5-inch pots) in late summer and fall and placed in the cold greenhouse. They received enough cold to break their rest period and crossing began in March, about a month earlier than was possible in the field. Low temperatures and low light intensity of midwinter caused the first flowers of many varieties to open without stamens, and emasculation of such flowers was unnecessary. By screening the ventilators insects were largely excluded; regular spraying for insect control was used; and the work of crossing was consequently made far easier, since protection of flowers against insect crossing was also rendered unnecessary. In the greenhouse, stamens rarely open before the petals unfold, and it is thus possible to emasculate and pollinate at the same time, just as the flowers first open. Most of the crossing and harvesting of seed is done before field work begins outside. Although the unheated greenhouse was moved from Glenn Dale to Beltsville, when the work was transferred there, and was used until 1963, heated greenhouses for crossing have been used at all stations for many years. The use of four to six hours of supplemental light, during the winter when light intensity is low, helps the flowers to develop more anthers and pollen, and is used particularly in Oregon.

Each year the crosses are planned, and a breeding chart is prepared which outlines these proposed crosses. As an example of breeding method and objectives, a part of the breeding chart used as a guide for 1945 at Beltsville, Maryland, is given below.

Strawberry breeding, 1945, Beltsville, Maryland

Mother parent*	Pollen parents	Purpose
1 Midland (62)	x Oreg. *1491, 1509,* 1765, *1775* (continued)	
	x Fairpeake & *F. virginiana* Sheldon, N.D.	Size
2 Md-3205 (52)	x Oreg. 1491, 1509, 1775, US-3366, & x self	Production
5 Aberdeen (35)	x " " " " & Fairpeake	Resistance
9 Massey (67)	x Eleanor Roosevelt, Midland	Size
14 US-2827 (66)	x Midland	Aroma
15 Suwannee (72)	x " (also x *2189*)	Flavor
20 *F. virg.*, Sheldon, N. Dak.	x Midland	Production

* Note: The number preceeding the mother parent variety indicates the group cross number; other crosses (Nos. 3, 4, 6, 7, 8, 10–13, 16–19, 21–28) omitted. The number following the mother plant variety and enclosed in parentheses indicates the Vitamin C content of the mother plant.

A total of 28 sets of mother parents were planned. Potted plants were brought into the greenhouse and the above plan followed as fully as possible.

When emasculating, the thumb nail is generally used to remove the stamens, corolla and calyx at one operation. If done with ordinary care no resulting injury to the pistils has been observed. When working with small flowers, such as those of *F. vesca,* sharp-pointed scalpels or tweezers sharpened to a cutting edge are used to remove the flower parts. Even though emasculation may not be necessary, the calyx and petals are always torn off when the flowers are pollinated in order to identify the crossed flowers (*see Fig. 14–4a and b*).

Especially when grown under glass, the first flowers to open on clusters of many varieties are pistillate (the stamens, if present, do not contain good pollen). For this reason it is often difficult to obtain pollen at the beginning of the season. The first flowers of Marshall and Fairfax contain abundant pollen, while the first flowers of such varieties as Howard 17, Missionary, Blakemore, Bellmar, and the everbearing varieties usually contain none. The primary and secondary flowers contain far more pistils than the later flowers on a cluster, and hence can set far more seed when pollinated. Many of the later flowers on a cluster do not set at all. Thus, every effort is made to pollinate the earliest flowers on each cluster, using the late flowers of the perfect-flowered varieties as source of pollen.

To obtain pollen, the practice has been to pick flowers having pollen-bearing stamens just as the petals are unfolding. The stems are left about a quarter-inch long and if the pollen is to be used within a few hours the flowers are allowed to wilt. As they wilt the anthers crack open and more pollen is available than if the anthers dehisce on the plants. If pollen is needed later, it can be held from one to four days by placing the flowers and large buds in shallow vessels of water and allowing them to open. When examination shows the anthers fully opened, the flowers are used directly on those to be crossed, being held so that the stamens touch the pistils. The flower is twirled by its stem in such a manner as to cover all the stigmas with pollen. A flower with abundant pollen may be used to pollinate four to six flowers or even more. Some breeders first collect pollen, then use camel's hair brushes to apply it (*Fig. 14–5*). When pollen is scarce, brushes may be used to advantage. There has seemed to be a greater chance for error, through accidental mixture of pollen, when using brushes, than when using the flowers themselves.

The comparative ease with which an abundance of pollen may be obtained, owing to the readiness with which blossoming may be advanced or retarded by placing the potted plants in warmer or cooler parts of the greenhouse, and by bringing in additional plants from the field, have made studies of pollen storage unnecessary. It has been observed, however, that pollen spoils soon under moist conditions, but when kept dry it apparently has

FIG. 14–4a. Emasculating.

FIG. 14–4b. Emasculation completed.

been fully effective even when held for several days. Crandall (1912) has reported slightly better results with pollen four days old than with fresh pollen.

At first seed was saved by mashing ripe berries on paper toweling, or newspapers, but since Morrow's use of an electric blender all seed is cleaned by putting berries in a blender from one half to two thirds full of water (*Plate 14–1*), turning on the blender for about twenty seconds, and saving only the seed that sinks. The seed is surface dried, then stored in vials, or small envelopes, and placed in a refrigerator until used. In one test by Meader the germination was 92 percent after ten years storage.

The seed is sown in sterilized soil or on pulverized sphagnum, about 1,000 seeds to a 12 x 18 inch flat. Since Piringer's tests at Beltsville showed the need of light on moist seed for their germination, care is taken that strawberry seed is sown on top of sphagnum or very shallowly, so that light can penetrate to the moist seed.

The speed of germination varies greatly, depending chiefly on the mother parent. Seed of *F. virginiana* germinates more rapidly than any other we

FIG. 14–5. Though direct use of pollen-shedding flowers on the flowers to be used to produce seed is common, camel's hair brushes are often used to advantage, especially when pollen are scarce.

FIG. 14–6. Giving seedlings a red stele test in the greenhouse bench to determine their resistance; to left, some resistance, to right, many seedlings with most of roots rotted and the leaves of some wilted. The affected seedlings will be discarded when the plants are dug.

have observed, seedlings sometimes appearing four days after sowing (Darrow, 1927). Seed of some garden varieties and of some strains of *F. chiloensis* may not germinate for two, or even four weeks.

When two or three leaves have grown, the seedlings are pricked into greenhouse benches, or into flats (*Plate 14–2a*).

Waldo devised a test for red stele resistance about 1940. In late fall seedlings are planted in greenhouse benches whose soil has mixed into it the roots of red stele affected plants, or is taken from a field in which the red stele disease had killed out plants, or whose soil is inoculated with cultures of specific strains of the fungus. After a growing period of two to three months the temperature is lowered to a range of 35 to 50 degrees for four to eight weeks and the soil kept wet. The roots of vigorous plants grown in such soil become affected, if susceptible, and only resistant seedlings are saved (*Fig. 14–6*) for a fruiting test. Because occasional seedlings escape infection, all selections are retested.

FIELD TESTS OF SEEDLINGS. Various methods of growing and fruiting seedlings have been used. The two most used in the U.S. Department of Agriculture are (1) growing single plants of each seedling and (2) growing and fruiting small blocks of runner plants of each. Both methods have advantages—the single plant approach because of the large numbers (about 8,000) which can be grown per acre at an 18-inch spacing between plants, as opposed to the small numbers grown at the 4- x 4-foot spacing for small blocks (about 2,750). Single-plant selections however, must be propagated; hence their second fruiting is delayed until the third year. At the 4- x 4-foot spacing, second-test rows of selected seedlings can be set at once and the second fruiting test made the very next year. Tests in North Carolina indicate that this method is quite efficient in selecting superior seedlings (*Plate 14–2b*).

In making first selections of seedlings, wooden stakes are usually placed beside each selected plant, to be left or removed at subsequent surveys of the seedlings (*Plate 14–4a*). Each field of seedlings is surveyed as often and as thoroughly as possible, with an ideal period of twice weekly. When a seedling is to be saved for further testing, it is given a serial number by which it is known thereafter. Notes are made of critical characters of each selection and usually of the cross as a whole, but not of each seedling. Often, detailed notes are made of each seedling, or of samples, of particular crosses that were made for special reasons (*Plates 14–3a and 14–3b*).

Second tests of selected seedlings are usually conducted in short rows, five plants set in a 10-foot row proving to be sufficient. Third and later tests are in replicated 10-foot rows set for comparison with other selections and varieties.

NUMBER OF SEEDLINGS. In the early days of breeding work small numbers of seedlings of many crosses were used. Later, larger numbers of fewer crosses have been grown. The original cross of Howard 17 x Missionary, from which Blakemore and Bellmar were selected, had a population of only 64 seedlings, while the cross of Tennessee Shipper x Midland, from which Pocahontas and Dixieland were selected, had about 3,000 seedlings and 107 selections were first made in 1948. But later, large numbers of seedlings of the Howard 17 x Missionary were raised from which the Suwannee was selected and named. Very much greater numbers of seedlings are now necessary, since the infected-soil bench test for red stele resistance has been adopted. Since the bench tests started, probably not over 10 percent of the seedlings have been set in the field for fruiting, with the remaining 90 percent discarded as too susceptible to red stele.

NUMBER OF SELECTIONS. Before 1933 for the six years (of twelve) when records were complete 37,084 seedlings were fruited and 1,013 selections made, of which 400 were still under test. A total of 1,126 selections were still being tested out of the 1,880 selections made up to 1933.

Consecutive numbers are usually given selections; thus selections in 1922 were numbered 1 to 100, of which No. 44 was later named Southland. Now selections at Beltsville are labeled as *U.S.* 25; those selected at Salisbury, Maryland, *Md.-U.S.* 25; at Corvallis, Oregon, *Oreg.-U.S.* 25; at Willard, North Carolina, *N.C.-U.S.* 25; etc.

Not all selections saved are chosen for possible naming and introduction as home garden or commercial varieties. Some are the best seedlings of the crosses that were planned in attempts to incorporate new qualities into the commercial strawberry, and are to be used in further crosses (*Plates 14–4a, 4b, and 4c and 14–5a, 5b, and 5c*). Up to 1934 as many as 20 selections of species were used in breeding to explore their possible value in a breeding program. Selections of these, and other species crosses made in later years, have been used for further breeding.

RESULTS. Up to 1965 about 1,500,000 seedlings have been grown from crossed seed, many thousands of selections made, and 40 varieties introduced. Since selections have accumulated more and more desirable genes over a period of forty-five years it is to be expected that many selections now being tested contain a great many of the desirable genes, and many varieties may be named from the selections now on hand. Of the 38 varieties already introduced, 23 are still in the trade and 15 have been dropped.

Two new varieties, Sunrise and Earlibelle, are just being named and released for propagation and introduction. Sunrise, for introduction in the fall of 1965, originated from a cross of US 4152 x Stelemaster made in 1952 and selected in 1954 at Salisbury, Maryland. It ripens early, about with Dixieland and Blakemore, is medium in size, light bright glossy red, firm, light pink flesh, but too pale for frozen pack, and is resistant to three races of red stele and to Verticillium wilt. It is susceptible to spot and is suggested for the area from Maryland west to Missouri. Earlibelle, for introduction in the spring of 1965, is from the cross Albritton x Md-US2101 and was selected in 1956. It is earlier and more productive than Albritton in eastern North Carolina. It is medium large, glossy bright red turning deep red, firm with bright red rather tart flesh, and adapted to frozen pack. It is resistant to leaf spot and leaf scorch and is suggested for the area from North Carolina southward.

About 100,000 seedlings a year are being grown, including those at all stations, but of course far fewer are fruited as a result of the red stele bench tests.

Some of the discarded varieties were dropped because of specific reasons. Narcissa, introduced for Oregon and Washington, although hardier than Marshall was not sufficiently superior to it in flavor and productivity; therefore Marshall continued to be the variety widely grown there. Redheart, Northstar, Daybreak, Maytime, and Starbright were all lost because they were not tolerant of virus diseases. Southland proved too frost-susceptible.

The reasons for the failure of Eleanor Roosevelt, Fairmore, and Brightmore are not so clear, though Fairmore may have been too susceptible to virus and Brightmore too small. Fairland and Temple are still grown but, as all stocks are infected with virus, they may be dropped soon in favor of Midway, Surecrop, and other new sorts resistant to red stele. The four varieties, Cheyenne 1, Cheyenne 2, Cheyenne 3 and Sioux, although small and soft-fruited, were hardy and high flavored. In their place Arapahoe, Radiance, and Ogallala are hardy, good flavored, larger, and everbearing and have much wider appeal. Massey has been replaced in North Carolina by the larger, firmer, still more handsome and more reliable Albritton. Bellmar, which is still raised a little, although large and less acid than Blakemore, is not so firm and not quite so early.

Beginning about 1946 at Beltsville, Salisbury and Willard and about 1950 at Corvallis, seedlings and selections have been kept relatively free of virus by isolating and spraying them to control insects.

Undoubtedly many selections of the past would have become important varieties if they had not become infected with virus which weakened them before they were introduced. In addition, much good genetic stock also was lost because of this. Now that techniques are used to keep the seedlings and selections free of virus, advances should be more rapid.

Keeping Seedlings and Selections Free of Disease. In the 1940's when techniques first made it possible to tell whether plants were approximately virus-free and when control measures were available, seedling and selection fields were isolated and regular spraying programs adopted. Later, when damage by the meadow non-gall-forming nematodes was found to be more serious than that of gall-forming ones, nematode control was added to the program. Plants of selections to be introduced are now indexed by grafting to indicator plants to make sure they are free of virus. Virus-free runner plants are rooted in sterilized soil, and propagating stocks for nurseries raised in screenhouses to ensure, as far as possible, clean stocks.

Nurseries introducing new varieties obtain plants from screenhouse stocks and propagate them in fields isolated from non-virus-free stocks. They observe a regular dusting, or spraying, schedule, to control vectors of virus diseases, and treat their fields for nematode control. Recent research has shown that a so-called "latent virus," which produces no distinctive symptoms, greatly reduces plant vigor and yield of some varieties and steps are being taken to eliminate this virus where it occurs. New varieties free of this virus are already being introduced. A chief problem at present is the attainment of complete freedom from the non-gall-forming nematodes in virus-free stocks sold by nurseries to growers.

INTRODUCTION OF NEW VARIETIES. In 1928 when it was proposed to introduce the Blakemore, a committee of the *American Nurserymens' Association,* instituted to cooperate with the U.S. Department of Agriculture, was asked to suggest three established nurseries of the eastern United States, where Blakemore seemed adapted, who were large propagators of strawberries and who might be willing to help introduce the variety. The Committee suggested three nurseries on the Delmarva Peninsula and all agreed to cooperate. Blakemore was introduced in 1930, using stocks propagated at the North Carolina Coastal Plain Station at Willard, North Carolina. The arrangement was satisfactory and was continued for other varieties with the approval of the nurserymen and the Committee of the Nurserymen's Association. These nurserymen have introduced many of the later varieties, always at a nominal price. Other nurseries have attempted to propagate virus-free stocks of the new varieties, but have found the necessary procedure too difficult for their conditions. However, some are doing this through cooperation with their states.

The U.S. Department of Agriculture has issued Circulars and Releasal Notices concerning each introduction giving the name and a brief description of the variety, the purpose for which it is adapted, the area where it has been tested, and often the varieties it should supersede. Methods of introduction have been worked out for varieties resulting from the work at Cheyenne, and those resulting from the cooperative work at Willard, North Carolina, and at Corvallis, Oregon.

SUMMARY. During forty-five years, continuous breeding has been carried on by the U.S. Department of Agriculture with specific objectives: (1) firmer, higher-flavored, commercial shipping varieties; (2) varieties for processing, both freezing and preserving; and later, (3) red stele resistant and hardier sorts. Since the first variety was introduced in 1929, from 25 percent to 40 percent of the United States strawberry acreage has been planted to varieties of U.S. Department of Agriculture origin. Much firmer, much better processing varieties and many good varieties resistant to some strains of red stele are available. Desirable genes have been concentrated in current varieties so that the level of available varieties is much higher. As an example, the firmer Blakemore replaced Missionary in eastern North Carolina, then the larger and higher-flavored Massey replaced Blakemore, and finally the still larger, more attractive and firmer Albritton has replaced Massey. Efforts are being made to breed hardier, still larger, and more productive varieties, which at the same time, still retain the high flavor, firm skin and flesh, and superb glossy color of the Albritton.

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Strawberry Breeding of North American Agricultural Experiment Stations

THE BREEDING WORK of the U.S. Department of Agriculture, with the varieties and techniques developed there, is of importance, but no account of strawberry breeding is adequate without a description of the work conducted for the past forty-five years by the research stations of the United States and Canada. What follows is such a description, including brief accounts of the experiment station work and some material about originators of important varieties. This account is not intended to be exhaustive by any means, but it should indicate where breeding work is, or was, conducted, how extensive the work is and toward what goals it is directed. For the breeder, knowledge of the work pursued by contemporaries, especially the material, objectives, and progress of their programs, can be very helpful, for it may serve to persuade him to initiate some projects and to put aside others, which evidence seems to indicate as holding little value.

United States

In the United States, research stations concerned with strawberry breeding are located in Alaska, California, Oregon, and Washington, in the far West; Wyoming, South Dakota, Minnesota, Iowa, Missouri, Texas, Louisiana, Mississippi, Tennessee, Kentucky, Wisconsin, Michigan, and Illinois in the mid-West; Florida, North Carolina, Maryland, New York, New Jersey, Vermont, New Hampshire, and Maine in the East. Important varieties have resulted from the work of:

Schwartze and Myhre, Washington	Northwest, Columbia
Darrow, Scott, Waldo, & Meader, U.S.D.A.	Blakemore, Fairfax, Midland, Dixieland, Earlidawn, Pocahontas, Surecrop, Midway
Waldo, Oregon & U.S.D.A.	Siletz, Mollala
Thomas & Goldsmith, California	Shasta, Lassen, Goldsmith
Bringhurst & Voth, California	Solana, Fresno, Torrey, Tioga
Hawthorne & Miller, Louisiana	Klonmore, Headliner, Dabreak
Henry, Tennessee	Tennessee Beauty
Slate & Watson, New York	Catskill, Erie, Empire
Brooks, Florida	Florida Ninety
Morrow & Darrow, North Carolina & U.S.D.A.	Massey, Albritton
Clarke, New Jersey	Sparkle
Gilbert, Moore, Hough, New Jersey	Jerseybelle, Vesper
Swarthout, Missouri	Armore

Of today's important varieties, only the Robinson, Marshall, and Howard 17 (Premier) have not come from experiment station work and all are rapidly becoming less important.

The first actual breeding work by an experiment station in the United States was that begun at the New York Station at Geneva in 1889. The early work in New York was intermittent, however, and although some 12 varieties were originated and named by 1917, none became important. Soon after 1900 however, Hansen (1907), of South Dakota, and Georgeson (1910), of Alaska, learned that hardy varieties could be originated through breeding, and by 1917 Anthony (1917), of the New York Station, saw that promising varieties could result from breeding. These findings were important.

Perhaps 1920 should be used to date the beginning of long-continued systematic breeding, for it was at this time that breeding was started in a greenhouse of the U.S. Department of Agriculture. Schuster, of the Oregon Station, began his work then also. Though not fully continuous in the 1920's, the work at Oregon has been nearly continuous since about 1929. Systematic New York Station work began in 1924 with Slate and has been continuous since.

At present it is generally recognized that continued strawberry breeding is a necessary part of experiment station work. It has been economically valuable both to the United States and to the states where important varieties have resulted. The federal work has resulted in important varieties that have advanced the industry, especially in such better shipping varieties as Blakemore, Dixeland, Massey, and Albritton, and in red stele root-rot resistant varieties such as Temple, Fairland, Siletz, Midway, Surecrop, and Mollala. The Northwest of the Washington Station has become the leading variety in Washington and Oregon; Shasta and Lassen and more recently Fresno, Torrey and Tioga of the California Station are the most important varieties in California; so, also, with the Florida Ninety in Florida, Headliner and Dabreak in Louisiana, Jerseybelle in New Jersey, Albritton in North Carolina; and the list could be extended greatly to include more varieties and states. Though the over-all qualities of the present varieties may be 100 percent better than the varieties they replaced, advances already in sight may again double and redouble the value of varieties of the immediate future. Advances are looked for along the lines of firmer berries, resistance to red stele root rot in most or all varieties, and higher dessert quality with a retention of high flavor under varied weather conditions, and ability to hold up after reaching the market. Other advances are possible in larger berries, frost-hardy flowers, cold-hardy plants, higher yields, and easier capping to eliminate some of the hazards of production and furnish the consumer a better berry. The only limits are those of breeders' imagination, industry, and support, and the germ plasm available in the varieties and species of the world.

Alaska

No commercial varieties from other States survive in Alaska where the minimum temperatures reported are −60° F. at Fairbanks and −42° F. at Palmer, with annual rainfalls of 12 and 15 inches, respectively. Differences in winter temperature averages are great: as high as +16° for January at Palmer and −12° at Fairbanks. During the winter, warm spells followed by low temperatures, or deep freezing with low rainfall, kill out ordinary varieties near the coast, while deep freezing with low temperatures, or just very low temperatures kill them in the interior. Experimental work was started in 1901 by C.C. Georgeson with a collection for testing at Sitka of 150 *F. chiloensis* plants on the Yakutat Beach. In good soil these native plants were extremely vigorous but produced few flowers and no fruit. When reset in a sterile volcanic soil, they bloomed and fruited, with the largest fruit being one inch in diameter. Plants of this species were hardy in the wet coastal climate where temperatures drop to −20° to −25° F. Plants of *F. ovalis,* from the interior of Alaska where the temperature goes to −65° F., thrived when planted in the interior near Fairbanks, being extremely vigorous but with few flowers or fruit; yet three years after some were planted in the wet, mild coastal climate of Sitka only three weak plants remained. *F. ovalis* is, in general, very susceptible to leaf spot and mildew.

Crossing was started by Georgeson in 1905, using a cultivated variety from the States called Hollis, of unknown origin. It was pollinated with the Yakutat *chiloensis*. In later years he used several other varieties with *chiloensis*. Seedlings produced no fruit until 1908 and but few until 1909. About 10 percent of this F_1 had large berries that were reported to be of delicious flavor. The hybrids had extraordinary vigor, growing even to 18 inches high. *F. chiloensis* gave the best results as a parent; and the hybrids were reported as perfectly hardy both on the coast and in the interior where the temperatures often went to −50° F. In 1910 hybrids of *F. ovalis* were made and showed improvement over the wild *ovalis*. One of the best selections was an F_1 of Magoon x *ovalis*, which produced large, deep red, firm berries of good flavor. Contrastingly, in a letter of September 3, 1923, Georgeson stated that hybrids with *chiloensis* were soft, very light colored, but unsurpassed in flavor. When the work ended in 1923, over 11,500 seedlings had been raised, and the best selections had been widely distributed under number to be grown commercially. Most of these have been lost but several are being grown commercially still. One called Sitka 275, which may be a seedling resulting from Magoon x *ovalis*, is still known. In general, near the coast these Sitka hybrids are hardy, vigorous, productive; the fruits are very small to large, very soft, mostly pale colored.

Recent breeding work has been carried on by C.H. Dearborn at Palmer, near the coast, and by A. Kallio at College, near Fairbanks in the interior. Many additional plants of both *ovalis* and *chiloensis* have been collected; and *ovalis* resistant to mildew along with perfect-flowered *ovalis* and *chiloensis* have been found.

At Palmer, tests of 74 varieties from other states indicated that none was hardy enough for Alaska, even when mulched. Sitka hybrids, from Georgeson's work, that had survived for thirty years, were collected and observed at Matanuska from 1950–1953. Crosses were first made in 1952 to obtain winter-hardy, red-fruited varieties. Several hundred selfed seedlings of these hybrids were tested; also, about 30,000 seedlings of crosses of Sitka D with varieties from other states, which included Midland, Jerseybelle, Sparkle, Gem, Radiance, and Marshall, were set in the field at Palmer. Fifty-two selections were made by 1955. Sitka D x Midland seedlings appeared to be among the most hardy at Palmer and best flavored. No plants of progenies of 23 crosses of commercial varieties survived when left unmulched. Crossing has been discontinued.

In 1950 Kallio also began collecting plants for the station at College near Fairbanks—Sitka hybrids resulting from Georgeson's work as well as native *ovalis* and *chiloensis*. Some *chiloensis* came through the winters at College and, although many do not flower and fruit, a few do. Hybridization work was started in 1953. Objectives are hardiness, drought, leaf-spot, and mildew resistance, and firm, good-flavored fruit. By starting seedlings in January in the greenhouse under lights, seedlings large enough for the field are obtained by June and early July, and the first selections can be made the next year. Of 13,088 seedlings set in 1962, 94 percent, or 12,316, survived the very cold winter of 1962–1963, and 769 were selected in 1963 for further study. The summer temperatures are low enough so that many are everbearing.

California*

Strawberry breeding in California presents an interesting case. Intensive breeding work, along with related investigations, is conducted at the California Experiment Stations; more breeding work proceeds at the private grower-supported Strawberry Institute of California and both are closely allied to the strawberry industry of California which in some places produces the heaviest yields per acre in the world. Much of the material about the Strawberry Institute and the strawberry industry of California is outside the avowed subject of this chapter, but because of the almost symbiotic relationship of industry to experimental work, descriptions of both, as well as descriptions of some of their techniques, are considered pertinent.

Strawberry breeding began at the Davis Station in 1925–1926 and has continued to the present. William T. Howes and A.G. Plakidas initiated the first work. Some selections were made of their crosses in 1927 and W.T. Horne made further crosses that year. He was succeeded by Dr. Harold E. Thomas and Earl V. Goldsmith, 1928–1945, Department of Plant Pathology, Berkeley. After they left the University to establish the Strawberry Institute of California in 1945, Dr. Richard E. Baker, Department of Pomology, Davis, was in charge and was assisted by Victor Voth. Baker resigned in 1953 and was replaced by Dr. Royce S. Bringhurst, who has continued the work in collaboration with Victor Voth from 1953 to the present. In 1952 a temporary branch strawberry research station was established at Torrey Pines, near San Diego in southern California with Victor Voth in charge. The southern California headquarters was moved to the South Coast Field Station of the University of California at Santa Ana in 1956, but work has continued on a reduced scale at Torrey Pines to the present.

* By R. S. Bringhurst.

The first Thomas-Goldsmith seedlings were fruited in 1930 at the San Jose Station near Santa Clara. The first crosses, made in 1929 by Goldsmith, were actually unauthorized, but were the result of his curiosity when he was foreman of the Deciduous Fruit Field Station of the University of California at San Jose. These were followed by systematically building up the desirable characters toward an ideal type which resulted in the release of the Shasta, Lassen, Sierra, Tahoe, and Donner in 1945. Of these, Lassen (originated in 1936) proved to be best in southern California because of its low chilling requirement, relatively high tolerance to salinity, wide adaptation under a variety of planting systems and high productive capacity. The fruit is mediocre to poor in quality, soft, ships poorly, tends to roughness and is unsatisfactory for freezing. Shasta, originated in 1935, proved to be best in coastal central California because of continuous production under the prevailing conditions, where fruit is harvested from the same plants from April through November. The fruit is good in quality, ships well, and is passable for freezing. Sierra, Tahoe, and Donner failed as varieties in California but Donner is a leading variety in Japan. From the Thomas-Goldsmith selections, Campbell and Cupertino were released by Baker in 1949 and both failed. Solana, which originated in 1935, was released by Bringhurst and Voth in 1958 because of its high dessert quality. Solana is established as the dominant variety in the Oxnard district of Ventura County and around Fresno, replacing Lassen in both areas, and is grown to a limited extent in other areas including the central coast near Watsonville. The fruit is not satisfactory for freezing.

Bringhurst and Voth continued the systematic building of ideal types to improve on the qualities of Shasta and Lassen, and to obtain varieties for special conditions. In addition to Solana, they introduced Fresno, Torrey, and Wiltguard (see p. 159) in 1961 and Tioga (see p. 159) in 1964. Fresno, Torrey, and Tioga were all selected in 1955 and all have the same parentage. Their plant habits and adaptation are similar to those for Lassen. Their fruit resembles that of Lassen in color and general shape, but they are larger, more attractive, firmer, better flavored, easier to harvest and all of them cap easier than Lassen. Torrey is darker than Fresno or Tioga. Wiltguard, selected in 1954, is resistant to Verticillium wilt and the fruit is particularly high flavored.

Fresno has rapidly become the dominant variety in southern California, replacing Lassen. Torrey has also become established, but to a more limited extent; since it has an even lower chilling requirement than Lassen it performs best at warm winter sites near the sea. Tioga has the greatest potential of the group because of wide general adaptation (including the Shasta area of the central coast), higher yielding ability, and exceptionally firm fruit. Wiltguard is not succeeding.

The success of the new "University" varieties is largely due to the development of planting systems which favor their best performance. Most noteworthy have been the summer planting of cold-stored plants and the use of clear polyethylene bed covers to raise the winter growing temperatures.

The present program conducted by Bringhurst and Voth involves research facilities in every important environment of the state. Detailed performance testing is carried out at the following locations: *Davis,* interior valley; *San Jose,* central coastal valley; *Salinas,* central semicoastal; *Watsonville,* central coastal; *Santa Ana,* south semicoastal; and *Torrey Pines,* south coastal. Most of the crossing is done in the greenhouse at Davis. From eight to fifteen thousand seedlings are fruited each year; about half are grown at Winters (near Davis) and half at Santa Ana or Torrey Pines. Foundation stocks are maintained at Davis, at Winters, and at the Antelope Valley Field Station of the University of California near Lancaster in Los Angeles County. Virus-free stocks are maintained at the latter site.

Computer technology can play an important role in large scale breeding work. This view is supported by various factors, some of which cannot yet be fully realized in terms of their potentialities. First, the computer can be programmed to reduce into a comprehensible form, at minimum cost, the large quantities of data which breeders amass each year. In the California program, field data are summarized, the standard deviations are calculated for the various fruit traits that are measured, and "performance," a value which is weighed heavily by yield but considers appearance, fruit size, and firmness as well, is calculated. Data can be recorded on cards in the field to reduce the cost of obtaining analyzable data. At the end of the harvest season (four to seven months), the values can be obtained for seasonal summarization by machine.

Meaningful genetical studies also are possible. Using the parent-offspring method, heritability values can be calculated for various traits, and correlations between pairs of traits can be determined. Many genetical problems can be subjected to analysis. As an example, in the California program there is interest in a possible negative relationship between Verticillium wilt resistance and desirable performance traits. It has been noted that, with intensive selection for desirable traits, most of the selected clones are susceptible, even though both parents may be resistant. Genes conditioning wilt resistance may be linked with genes that condition undesirable performance traits. Since the latter are quantitative in nature and the relation among them is probably complex, an appropriate computer program will aid in interpretation. Without the computer, a much less satisfactory evaluation would be possible economically.

It is conceivable, but not presently feasible, to program a computer to scan all possible combinations of heritable characters. However, by weighting some of the important characters according to their occurrence and distribution in the breeding population, effective predictions concerning the outcome of particular breeding programs can be made. This at least would introduce an element of control into breeding projects that has previously been impossible. And, beyond this, realistic estimates of potential progress can thus be made, providing guidelines for further experimentation, saving the waste of much needless investigation.

The Strawberry Institute, a non-profit institution located at Morgan Hill, was organized by E.F. Driscoll in 1944; at that time H.E. Thomas became its director and pathologist, and E.V. Goldsmith, its plant breeder. The Institute was organized to assist the growers belonging to it (Driscoll Strawberry Associates) in solving their disease, insect, variety, and other problems. The Institute has also furnished disease-free stock to their growers. Thomas and Goldsmith continued strawberry breeding along lines they started at the University, using the same breeding stock—growing seedlings (up to 45,000 in some years) and testing selections. At first the varieties grown by Institute members were Shasta, Lassen, and other standard varieties; now they are mostly varieties originated by the Institute—including Goldsmith (Z5A), a patented variety, and D4, and 5, true everbearers. In 1959 a profit corporation, "Strawberry Institute Nursery," also with H.E. Thomas in charge, was organized to separate the plant propagating work from the strictly service work. Plants are furnished to the Institute members at cost, but sold to non-members at the market price. In 1962 Institute members had about 1,600 acres in production. The Goldsmith variety occupies almost two-thirds of the acreage, and performs best in central coastal sites near the sea. It is unsatisfactory in southern California. Goldsmith is liked for its heavy mid-summer production (later than Shasta), large size, high gloss, and remarkable carrying quality. It is weak in spring production, unsatisfactory for freezing, and is subject to "transient yellows." D4 is important in the Oxnard area where it competes with Solana. The everbearers yield well, but do not hold large size as well; one has high flavor.

The development of the California strawberry industry began about 1910 after the Marshall, then called Banner, had been introduced into the Watsonville area near the coast south of San Francisco. Later it was grown in the Sacramento area as the Oregon Plum and in the Fresno area as Marshall. It was the leading variety for thirty years until after the introduction of the Shasta and Lassen in 1945. Nich Ohmer was also grown during the latter part of this period as a shipping variety. In 1918 the Central California Berry Growers' Association was organized and from 1920 to 1947 E.H. Haack was its manager. E.F. Driscoll and Ed Reiter were especially helpful in testing the early selections of the California Station.

In the 1940's before World War II, the California acreage was about 5,000. Marshall (Banner) and Nich Ohmer were the chief varieties in central and northern California and Klondike in southern California. With the removal of the Japanese from the Pacific Coast, during the World War II period, the strawberry industry dwindled to less than 1,000 acres. Yields were low in the prewar years because of the lack of suitable adapted varieties; most planting stock was infected with virus and the Marshall (Banner) variety was particularly sensitive to the prevalent viruses.

A sound basis for expanding commercial production in California was established in 1945 with the release of five varieties by the University of California for commercial use; these were soon reduced to Shasta and Lassen. The new varieties were tolerant of the prevailing viruses and relatively free of virus infection. Their pattern of production in the central coastal area was much more desirable than that of Marshall (Banner). About 40 percent of the fruit is produced in the July to November period on second-year production and no runners are produced by Shasta plants after the first year. The acreage expanded rapidly during the postwar years following the release of the "University" varieties and the return of the Japanese farmers. Improved culture and the expanding market also stimulated the increase in production. By 1956, twenty-two thousand acres were in production and yields of twenty to twenty-five tons per acre were obtained by the best growers, with returns of as much as $10,000 to $12,000 per acre. In 1956, California produced 55 percent of the nation's crop on about 12 percent of the acreage with a value of nearly $45,000,000; this from a total investment by the California Experiment Station of only $72,000 over a fifteen-year period for the five varieties introduced in 1945. Production in California now constitutes about 40 percent of the national total, produced on less than 10 percent of the acreage with a value up to $45,000,000 annually. Southern California produces the early crop and finishes about July 15, when harvest is stopped to prepare the soil for the new plantings. Central California starts in April and continues to November or December.

The greatest concentration of the industry is around Monterey Bay in central California, where about half the total crop is raised. This is due to the effect of the interaction among (1) the relatively low extent of winter chilling, (2) the cool summer growing conditions, and (3) the day length on flower bud formation of certain varieties. Strawberries have a response to chilling or lack of chilling similar to deciduous fruit trees. Under the cool coastal California growing conditions lack of sufficient winter chilling is expressed in the production of flower buds and fruit on many ordinary non-everbearing varieties throughout the longer days of summer. Although the Marshall (Banner) produced some fruit throughout the summer, the Nich Ohmer produced more consistently after July 1 and it is the Nich Ohmer type of response in Shasta, Lassen, and other varieties that has made them so valuable. These varieties have not proved so tolerant to virus as at first supposed, and planting of virus-free stocks has become important in recent years.

Nearly all fields are fumigated with mixtures of chloropicrin and methyl bromide under polyethylene film before planting, at a cost of up to $400.00 per acre. The fumigation essentially solves the replant problem since new plantings on properly fumigated soil respond about like plantings on good soil never planted to strawberries; the cost is more than offset by the increased yields. Good soils that would be unsatisfactory without fumigation because of previous crop history (tomatoes, etc.), or disease problems (Verticillium wilt, etc.), can be used. In nearly all cases, the plants grow better after fumigation.

In the Los Angeles-Orange Counties where Lassen has been the important variety, annual planting is universal, and fruit is harvested for only one year—rather for only three to four months out of that year. Plant density ranges from about 24,000 per acre on summer plantings to over 30,000 on some winter plantings. Clear polyethylene bed-covers, machine-laid, shortly after the plants are set, on all winter plantings and about January on summer plantings, are used on almost all plantings. For summer plantings, plants are cold-stored at 28° to 30° F. from the time they are dug in December and January until planted in August. Yields from summer plantings are extremely high, and the fruit quality is good. Winter plantings yield much less but the fruit quality is often better than from summer plantings. In southern California, where only high-valued land is available, growers plant strawberries every year on the same land, fumigating between the plantings. It is convenient to rotate winter plantings with summer plantings in this regard, since there is time to prepare the soil for a summer planting after harvest has been terminated on the previous year's winter planting, but not time to prepare the soil for summer planting after the harvest has been terminated on the previous year's summer planting. It is for this reason primarily that almost half the southern California acreage continues to be winter plantings despite the lower yields and income.

It has been said that the yields in California have declined since the peak year of 1953, and that much of the decline was due to increasing virus problems. Actually, record production of about a ten-ton per acre average for the state was realized in 1962, and that record was broken in 1963 with an average of over twelve tons per acre. Costs in California are $2,000 to $4,000 per acre but returns may be twice or three times that.

The so-called "virus reduction" of yields during the 1950's was at least in part due to a successive series of warm winters, which were particularly damaging to the Shasta variety. The record yields of 1962 and 1963 are due to a combination of cultural factors including: the use of clean planting stock, soil fumigation, control of the cyclamen mite, the use of polyethylene mulch in connection with annual planting in southern California, the adoption of the summer planting system of culture, the use of high elevation plants and the proper timing of winter plantings. In addition, the winters were relatively cold in the central coast area and plants of the Shasta variety received sufficient chilling to invigorate the older plantings.

Virus is a serious problem in the strawberries of California as was recognized nearly forty years ago. Practices to keep nursery stock clean have been used for over thirty years. Isolation of seedlings in breeding has long been used and most nursery stock is propagated in northern California, two hundred miles from the fruiting areas. An extensive indexing and control program is in effect by the State Nursery Service regulatory Department. Freedom from virus of planting stocks is considered the most important means of keeping high production.

Thomas feels that although varieties have been produced that are being used successfully, until perfection is reached, breeders will continue to improve California varieties, for the grower will not cease to want better varieties than he has.

Southern California needs an early high-producing variety with large showy berries that will start in late February or early March and continue to the end of June. At that time most plantings are plowed under, the soil fumigated, and the fields reset in August. The Fresno, Tioga, and Torrey varieties look very promising.

In central California a high-producing sort is needed that starts in mid-April, peaks in May, and continues through June. Then production ceases in the hot interior valley, but along the coast, with its cool climate, production can continue through the summer and fall. The fruit is used for both fresh market and processing, but the fresh market price averages much higher so the best fruit is shipped fresh. The Solana, Lassen, Fresno and Torrey varieties are grown in the hot interior valleys. The Shasta and the Goldsmith varieties are grown along the coast of central California and they produce heavily until late fall frosts and cool weather stop fruit ripening.

In the Central Coast, plantings have been harvested for three or even four years. The cost of harvest increases with the age of the planting, and in general the quality of the fruit decreases. Experimentation by growers following

University recommendations, has demonstrated that the profitable life of a planting often does not exceed two harvest years. Summer planting has increased greatly in popularity because of the high first-year production of quality fruit. As new varieties such as Tioga are used with this system, considerable change can be anticipated in the next decade.

The outstanding characteristics of the California varieties are their large average size and their periods of production—the Southern California fields producing the highest yields in the world and over a period of about four months, the Central California fields nearly as large yields but extended over a period of over six to seven months, with about 40 percent of the crop coming after July 1.

Florida

Breeding work with strawberries becomes difficult when attempted in the subtropical climate of Florida, which lies outside the range of native strawberries. It is very difficult to keep seedlings alive over the long, hot Florida summer with its flooding rains, and it is even more difficult to evaluate the seedlings. However, if it becomes possible to raise planting stock of Florida Ninety, or of seedlings of southern parentage, in Florida with or without cold storage, the improvement of varieties may be rapid, and in Louisiana and southern Japan as well.

Dr. A.N. Brooks, plant pathologist at Plant City, has been in charge since the breeding work started. Many selections and varieties of other breeders were tested in the early years, and seedlings were raised at times. All the earlier breeding work, however, was drowned out by floods in the 1930's. In 1948, one lot of 1,075 open-pollinated seedlings of Missionary was grown from which 120 were saved for further testing. From these, the Florida Ninety was finally selected and introduced in 1952. In 1954, Dr. Scott, of the U.S. Department of Agriculture at Beltsville, Md., made crosses of Missionary x Florida Ninety and x Albritton and of Albritton x Florida Ninety, and 1,937 of their seedlings, plus seedlings from open-pollinated Florida Ninety and Florida 45, were grown by Brooks at Plant City. In 1955, 1956, and 1957 additional seedlings were raised; these from over 35,000 seeds of crosses, with each other and with other varieties, of Missionary, Florida 45, and Florida Ninety. In 1964 a new strawberry and vegetable field laboratory was opened for research with about twenty acres of land and new laboratory buildings at Dover, just east of Tampa.

Florida Ninety originated from open-pollinated seed of Missionary from the Experiment Station planting containing over 60 other varieties in 1948. It is undoubtedly a cross of Missionary with some other variety (probably

Klonmore) because selfed Missionary seedlings are generally weak and their yield and fruit size far too small to be commercially useful.

According to Fletcher (p. 70), commercial strawberry production began in Florida about 1878 and the berries were shipped in open crates by rail, taking about three days to Philadelphia, New York, and Boston. The Wilson was firm enough to stand the trip. By 1888, 20,000 bushels were shipped and in 1889 the first refrigerator car of berries was sent north. Most of the berries were raised in the north-central area near Starke and Lawtey. After 1896 berries were raised near Plant City also, and, beginning about 1960, in southeastern Florida. In 1961, 62 percent of the acreage was in the southeastern area, 27 percent in west-central Florida, and 11 percent in Bradford County of North Florida. By 1933, at the greatest expansion of the industry in Florida, about 2,043 carloads were shipped from about eleven thousand acres. In recent years the shipments by months have been December 2 percent, January 13 percent, February 26 percent, March 43 percent, April 16 percent, May about ½ percent.

The recent expansion in strawberry production has been due to far higher yields from the Florida Ninety (selected in 1948 and by 1960 almost the only variety grown) when grown under black plastic mulch and in soil previously fumigated to kill nematodes. Two years after its release in 1952, it composed 65 percent of the acreage of the Plant City area and now is about 95 percent of the total Florida acreage. It is also grown extensively in Mexico.

Florida Ninety took over the acreage quickly because of its vigorous high-yielding plants, its very large fruit size (small size in Maryland), its bright scarlet color and its high flavor, at times with a delightful aroma even after shipment to northern markets. Its yields may be as much as three times those of the Missionary variety it replaced.

Yields per acre Pounds	Acreage Acres	Year
1,300	2,000	1957–1958
5,100	1,400	1959–1960
8,300	2,000	1963–1964

Plants are obtained from northern nurseries and are set during January or February in central Florida, or March or April in north Florida. Then runner plants from this planting are set in a new runner bed in May to June. Plants from this May-to-June plantings are used to set fruiting beds in September and October. To obtain freedom from nematodes, it is important to use only plants grown in fumigated soil, planting them in fumigated soil to keep them free. Black plastic is put on when plants are set; before planting if it is done by hand, or after setting if done by machine. If planting is done by machine, the plastic is slit and the tops pulled through at once to prevent sun burning of plants. Use of plastic ensures that beds aren't washed down with heavy rains, that there is less leaching of fertilizer, and more moisture is available. More vigorous growth with earlier ripening, higher yields, and cleaner fruit follows the use of plastic. About 10 percent of the crop has been shipped by air freight in recent years.

In 1962, J.W. Strobel, at the South Florida Homestead Station, began breeding especially for resistance to Verticillium wilt which had become a major problem in south Florida, especially when the susceptible Florida Ninety was grown as a winter crop on the fields formerly used for tomatoes.

Illinois

Beginning in 1935, notable work in breeding was done in Urbana by A.S. Colby, who proved that resistance to red stele root rot was inherited. His work culminated in the introduction of Vermilion in 1950. It was a Redstar x Pathfinder cross, late ripening, medium sized, soft, very good in flavor, vigorous, and productive. The plants, however, have become variegated and it is not widely grown. Plentiful, of the same parentage and also resistant to red stele disease, was introduced in 1953, but is little grown.

In 1958 Prof. Zych began strawberry breeding for varieties adapted to Illinois, but especially for high-flavored sorts. Crosses include high x low acid varieties and high x high soluble solids varieties. From 1,000 to 6,000 seedlings are raised each year.

U.S.D.A.-Illinois cooperative breeding work was begun in 1958 at the University of Southern Illinois with Roland Blake, of the U.S. Department of Agriculture, in charge and J.W. Hull assisting. The work at Carbondale is planned to complement that of the U.S. Department of Agriculture at its Beltsville, Maryland, Willard, North Carolina, Cheyenne, Wyoming, and Corvallis, Oregon stations as well as that of the Urbana Station. (See under U.S.D.A., pp. 214–215.)

Iowa

In 1894 Budd and Hansen crossed two wild strawberries from Manitoba, one perfect, the other pistillate, with five cultivated sorts and grew over 1,000 seedlings. They hoped to obtain the hardiness, remarkable fragrance, and high color of the wild. Three years later they reported that they obtained the hardiness but not the size needed in the F_1. Hansen continued this work in North Dakota. In 1903 Irvins reported using Buback, Bederwood, Haverland, and others in breeding. In 1937 T. J. Maney began breeding strawberries and had eight selections at the time of his death in 1945. Though all eight selections were used in crosses of E.L. Denisen, who began work in 1949, they had virus and were discarded. Two of Maney's selections, Iowa-1-3713 (Rockhill S_1) and Iowa-68-3702 (Beaver x Dorsett), were the parents of Cyclone, an easy capping home garden variety introduced by Denisen in 1959. Denisen's objectives at first were improved everbearing varieties, as well as runnerless varieties, to be grown from seed that could all be harvested at one time by machine and that would be easy capping. Limited inbreeding was begun later. Other later objectives include easy capping, freezing and dessert quality, market and shipping qualities, larger size, resistance to disease, and irradiation to obtain mutants. Up to 6,000 seedlings are raised annually. Some *ovalis*, *"glauca,"* and *chiloensis* selections are being used in crosses. A study of berry flesh and seed colors is under way by R.L. Macha. A study of inheritance of short nodes is also in progress.

Louisiana

In 1935 Dr. Miller and Mr. Hawthorne began strawberry breeding and their first selections were made in Baton Rouge in 1936. Their main objectives were varieties resistant to leaf spot and leaf scorch, with as good shipping qualities as Klondike and less acidity. Major varieties have been introduced as a result of this work—Klonmore in 1940, Headliner in 1957, and Dabreak in 1961. The Klonmore replaced most of Klondike acreage in Louisiana and in turn was quite rapidly replaced by Headliner, when it was introduced. By 1963, Dabreak constituted about half the acreage.

The objectives of the breeding work have been obtained quickly by raising large numbers of seedlings and repeatedly spraying the young seedlings with spore suspensions of leaf spot so that susceptible ones could be discarded and only resistant ones fruited. Spraying with spore suspensions of leaf scorch was added and recently angular-leaf-spot resistance was added to the program. The seedling numbers were further reduced by discarding all seedlings that did not produce a good stand of runner plants and at times not over 5 to 10 percent were saved for a fruiting test at Hammond. Thus, Klonmore was produced from the cross Blakemore x Klondike by first discarding seedlings in the seed bed that showed leaf spot susceptibilty, and by discarding those that produced few runners under their relatively short, hot summer days. Klonmore is highly resistant to leaf spot but susceptible to leaf scorch. It is less acid than Klondike and is more attractive.

Headliner replaced Klonmore and others because it was 30 to 50 percent larger than the older varieties and was superior to them for processing. In tests it averaged 91 percent greater yield than Klonmore over a four-year period. It is not so resistant to leaf spot as Klonmore, and many plants had variegated foliage. Headliner's ancestry is:

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                     Suwannee                    Blakemore
          L-7-27        x            Klonmore       x
                     L-6-30-45-7        x        Klondike
                                     Klondike
Headliner   x                       Missionary
                     Suwannee          x
          L-7-42        x           Howard 17 (Premier)        Blakemore
                                 Fairmore . . . . . . . .         x
                     Konvoy         x                          Fairfax
                                 Klondike
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Dabreak, introduced in 1961, has replaced Headliner in part, for it is still more productive (42 percent more over a four-year period in one test) in southern Louisiana; and the berry is more attractive and superior in shipping and preserving qualities. Its ancestry is:

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          Headliner
Dabreak      x         Klonmore                  Suwannee
          L-3-1169        x         L-7-42          x
                       L-0-242        x          Konvoy
                                    L-117-1-45-3 (Marion Bell selfed)
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Other varieties introduced by the Louisiana Experiment Station are Konvoy, which is soft but rich red, for processing, and Marion Bell (a one-generation inbred of Fairmore); seedlings of both lack vigor and fruit size. Size, flavor, and disease resistance in good shipping varieties continue to be objectives in the Louisiana work. Each year about 14,000 to 15,000 seedlings are raised, but relatively few are fruited. Some years 3,000 to 3,500 are placed in the nursery and 2,500 to 3,000 fruited.

Maine

A breeding project was started in Orono under Russell Bailey in 1936 with the objective of obtaining varieties resistant to red stele and better able to survive the winter. About 100 selections were carried through the winter in 1940 without mulch, using Howard 17 (Premier) as a check. Howard 17 (Premier) was badly injured and only 10 percent of its plants survived, while

22 selections showed good survival. Three varieties (Orland, Monmouth, and Maine 55), all resistant to red stele and higher yielding and hardier than Howard 17 (Premier), have been named and introduced. Later breeding was for firmer berries with a stronger fruit stem, but only one selection has been saved. When virus-free stocks of Howard 17 (Premier) and Sparkle became available, the survival and yields of these two varieties were better; cold storage of their plants resulted in better stands and the new varieties faced stronger competition from them. Maine-55 is superior in flavor and freezing quality but its berries are soft and lie on the ground, making them subject to rot. Sparkle is the chief variety, but the Maine varieties are grown locally.

Maryland

Presently I.C. Haut is leader and F. Lawrence* in direct charge of breeding work at College Park. Since 1938 cooperative breeding with the U.S. Department of Agriculture has been carried on; crosses are made by the U.S. Department of Agriculture at Beltsville, Maryland, and most seedlings grown in red stele-infested soil in greenhouse benches at Beltsville. Susceptible seedlings are discarded and the resistant ones grown to fruiting at the Maryland University Farm at Salisbury, Maryland. Usually 3,000 to 4,000 resistant seedlings are fruited annually and selections for further testing made at the first fruiting. At times seedlings have been grown, and tests for strains of the red stele organism made in the University of Maryland greenhouses.

The University of Maryland, beginning in 1952, has had a separate breeding program. At first the objectives were varieties adapted for high elevations in western Maryland and everbearing varieties. More recently the objective has been directed toward obtaining late-ripening varieties, 2,500 to 3,500 seedlings being raised annually. No varieties have been introduced. Some 30 to 40 selections are under test.

* Transferred to U.S.D.A. at Corvallis, Oregon, September, 1965.

Michigan

The breeding work, begun in 1950, is carried on jointly by J.E. Moulton at East Lansing and Stanley Johnston at South Haven. The crosses are made and the young seedlings grown in the greenhouse at East Lansing. The seedlings are now fruited at South Haven with both Moulton and Johnston evaluating the seedlings and selections. Objectives are varieties for early, mid-, and late season suitable for both freezing and fresh market, with large, glossy, bright red, firm, tough skinned, and red-to-the-center berries. No varieties have been introduced yet, though selections are under test by growers.

From 1950 to 1953, 132 crosses using 27 varieties and eight selections were made, 19,398 seedlings fruited, and 361 selections made. Howard 17 (Premier) was an outstanding parent in 20 combinations, and the seedlings were notable for resistance to mildew and leaf spot diseases. Fairland x Tennessee Shipper was notable for being productive and for giving firm, smooth, bright red, red-to-the-center fruit. Tennessee Shipper was an unusually good parent in eight of the nine crosses tested. Redcrop, Midland, Sparkle, and Marshall also gave high percentages of good seedlings (1955).

Some modifications of breeding technique were described by these workers (1955). The plants for crossing are dug just before severe weather (late October or early November), bundled and stored in sphagnum at 32° F. until early December. They are then potted and held at 54° F. for two weeks to establish roots, then the temperature is raised to 70° F. Supplementary light is used through February from four P.M. to midnight to give a sixteen-hour day to lengthen the peduncles and to develop more pollen. As pollen is not shed until after the flowers open, the flowers are emasculated and pollinated at the same time. Berries in the white stage have mature seed and are harvested. When sowed as soon as harvested, seedlings begin to appear in about two weeks. When large enough to handle, they are flatted, 80 to a flat, and in ten to fourteen days are ready for the field—late May to early June. Four to five runner plants per seedling are allowed to root and later ones removed.

Minnesota

Hybridization was begun at Excelsior in 1908 and has continued up to recently. Charles Haralson did the early breeding and was followed by A.N. Wilcox. W.D. Valleau, 1914–1925, also worked in the breeding program, particularly on the inheritance of sex types. In the early work, varieties were intercrossed to originate hardier varieties and 5,000 to 10,000 seedlings were raised between 1909 and 1924. This kind of breeding was continued on a limited scale still later. Selection within self-fertilized lines was begun in 1922 and continued until Wilcox's death in 1963. The principal varieties used in selfing were Belt, Chaska, Dunlap, Minnehaha, and Howard 17 (Premier); others used were Beaver, Campbell, Duluth, Early Bird, Mastodon, and Minnesota. Although there was reduction in vigor in the first generation, the later generations averaged more vigorous than the first selfed generation. The more vigorous S_1 were selected for further selfing. Inbreds were selected for firmness, productivity, winter survival, and resistance to disease. Besides research on inbreeding, a study of value of selections of the *F. virginiana* for breeding was one part of the program. In the early 1920's M.J. Dorsey was associated with the breeding work and helped in the selection of Duluth (everbearing) (Pan American x Dunlap), Minnesota (Dunlap x Pocomoke), Minnehaha, Chaska, Easypicker (Crescent x Dunlap), Nokomis, and Deephaven. At various times, W.H. Alderman, J.H. Beaumont, E. Angelo, W.G. Brierly, and F.E. Haralson assisted in the work. In the later work, though inbreeding was emphasized, Evermore (1945) (Duluth x Dunlap), Arrowhead (1946) (Duluth x Dunlap), and Burgundy (1944) (Easypicker x Dunlap), varieties from outcrossing, were introduced. Dunlap was notable in transmitting phenotypic characters, especially hardiness, vigor, and runner production. It seemed also to transmit more earliness to its seedlings than most parents. On the whole, Dunlap was less productive of good inbreds than several others.

Some research publications on the strawberry are discussed below.

"Sterility in the strawberry," by W.D. Valleau (1918), is an intensive study of the morphology of sex types of the strawberry. Valleau noted that the flower parts were in multiples of five except for the pistil; that the native parental species were dioecious; that staminate (male) plants have pistils that are only rarely functional; that pistillate plants have undeveloped stamens that rarely develop pollen; that there is a correlation between flower position and pistil fertility, fertility decreasing in the later flowers to open on an inflorescence; that sterility of the later flowers is more general in hermaphrodites than in pistillates, suggesting that hermaphrodites have been derived from staminates; that the percentage of aborted pollen is not constant in the anthers of a single flower, nor in the flowers of any variety; that there is no evidence of physiological self-sterility in the strawberry, and that nubbins are due to pistil sterility.

"How the strawberry sets its fruit," by Valleau (1918), shows the arrangement of the flowers and berries on a cluster. The first flower to open, the "primary," is the largest and develops into the largest and earliest berry to ripen. The second two, the "secondary," are next largest flowers and fruits and ripen next, the next four are the "tertiary" and have still smaller flowers and fruit.

"The inheritance of flower types and fertility in the strawberry," by Valleau (1923), indicated that hermaphrodites do not carry the factor for femaleness, but that pistillate do carry hermaphroditeness as a recessive, so that a one to one ratio results when pistillates are crossed with hermaphrodites.

In "Breeding behavior of the strawberry with respect to time of blooming, time of ripening, and rate of fruit development," by R.M. Peterson (1953), nine inbreds of varieties were selfed and intercrossed to determine whether studies of the progenies would furnish evidence of genetic differences. All three characters were quantitatively inherited with no heterosis. Between varieties there were significant differences in each character, the most important being in rate of development from time of pollination to ripe fruit. The difference here was as great as 8.8 days.

In "The breeding value of selected inbred clones of strawberries with respect to their vitamin C content," by T.H. Anstey and A.N. Wilcox (1950), selfed and crossed seedlings from five original varieties were tested: Marshall (inbred three generations), Dunlap (inbred three generations), Minnehaha (inbred two generations), Chaska (inbred one generation), and Howard 17 (Premier) (inbred one generation). High vitamin C was partially dominant to low vitamin C. Some selfed and some crossed seedlings had higher vitamin C content than the parents, indicating a recombination of favorable genes within a parent or from both parents, with vitamin C content as high as 165 milligrams per 100 grams in some seedlings of crosses involving each parent.

E. Angelo and associates, in "Studies on some factors relating to hardiness in the strawberry" (1939), tested varieties for hardiness to cold and Gibson was considered hardiest, hardier than Dunlap.

Mississippi

In 1948 Jean P. Overcash started a breeding program at State College to obtain varieties capable of withstanding the hot, dry summers. Some seedlings, 500 to 3,000, have been grown nearly every year since. About 30 selections are in replicated tests in one or more locations and about 60 more selections are in single-row plots.

Missouri

Early breeding at the Columbia station was begun by J.W. Clark in 1890 and reported by Charles A. Keffer in 1893. Open-pollinated seedlings of Gandy, Bubach, Crescent, Lady Rusk, and Warfield were fruited in 1892. Of 4,300 seedlings, 245 were saved for later testing. No varieties resulted from this early work but information on inheritance of sex did. Seedlings of four pistillate varieties gave 1,714 perfect (41 percent) and 2,420 pistillate (59 percent) seedlings, somewhat more pistillate seedlings than the one to one ratio usually obtained.

Later breeding was begun in 1934 by H.S. Swartwout. About 10,000 seedlings were fruited up to 1946, about 40 selections were made, and one variety —the Armore, large-fruited, very productive, high flavored but mildew susceptible—was introduced in 1950. Swartwout's objectives were (1) a variety with good yielding, dessert, and shipping qualities to replace Aroma in the Ozark region; (2) a local market variety to replace Dunlap and Howard 17 (Premier) in north Missouri; and (3) a superior processing variety. Parents used in his work were Howard 17 (Premier), Aroma, Blakemore, Progressive, Dunlap, and Klondike.

In 1953 D.D. Hemphill took over the breeding work. About 40,000 seedlings have been fruited, 262 selections made, of which 29 are being evaluated in replicated tests for comparison with standard varieties. No varieties yet have been named from this work. Hemphill's objectives have been (1) a good-flavored, home garden variety resistant to red stele and leaf diseases; (2) for south Missouri, a commercial variety to replace Blakemore, resistant to red stele and leaf diseases with good shipping and processing qualities; and (3) a local market variety for north Missouri resistant to red stele and leaf diseases with excellent flavor, size, and appearance.

New Hampshire

Strawberry breeding in Durham began about 1940. L.P. Latimer was in charge until 1949, when E.M. Meader took over the work. E.G. Corbett (1962) assisted from 1959 to 1962. The primary objective was late varieties. Merrimack, Blaze, Strafford, Jamboree, Phelps, and Great Bay were named. None is of more than local importance. Beginning in 1955 another objective has been to obtain runnerless, seed-propagated varieties, because loss due to virus might be avoided if all plants were grown from seed. All runnerless material to date has been everbearing. By the use of a 17-hour photoperiod most potential runner-making seedlings can be eliminated. In each generation of breeding with this objective there have been fewer runner-making plants. One combination of runnerless parents gave 95 percent runnerless seedlings; and one inbred progeny gave only 1 percent with runners. About 10,000 seedlings have been grown so far. A naturally occurring twelve-ploid seedling was obtained among the selfed seedlings of NH-2 [Lee Gem x Macedonian (seed from Greece)] x Sans Rivale, a line being bred for non-runnering. It was not fully fertile.

New Jersey

Since the initiation of breeding work, eight varieties have been introduced by the Experiment Station at New Brunswick: Pathfinder, Redwing, Julymorn, Crimson Glow, Sparkle, Redcrop, Jerseybelle, and Vesper. The first crosses were made in 1928 by J.H. Clarke, using as parents Howard 17 (Premier), Aberdeen, Lupton, Mastodon, Chesapeake, Gandy, Wyona, and Pearl, the last three for their lateness; and 1,800 seedlings were grown and tested. Additional crosses were made in the following years, using other varieties, as well as selections of the earlier seedlings, as parents. By 1937, over 22,000 seedlings had been set. In 1939, 138 were still being tested and 70 were discarded. Gandy, Chesapeake, and Lupton were disappointing as parents; and Howard 17 (Premier), Aberdeen, Pearl, and Fairfax were considered good parents. Lupton, used as a parent for its excellent shipping quality, transmitted its poor dessert quality but not its good shipping quality. Though five varieties were named by Clarke, only two became commercially important—Pathfinder (Howard 17 x Aberdeen), named in 1937, and Sparkle (Fairfax x Aberdeen), named in 1942. Sparkle is still an important variety in all northeastern United States. A sixth variety, Redcrop, was named and introduced in 1949 but did not succeed, probably being weakened by virus.

Following J.H. Clarke, F.A. Gilbert was in charge from 1946 to 1950. The cross made by him in 1946 (or 1947) from which Jerseybelle originated was NJ-953 [(Lupton x Aberdeen) x Fairfax] x NJ-925 (Pathfinder x Fairfax). It was selected in 1948 and introduced in 1955 because of its attractive color, high gloss, and large size. It quickly became the leading variety in New Jersey and in 1963 constituted 60 percent of the acreage there; Dixieland, Pocahontas, Surecrop, Earlidawn, and Sparkle comprising most of the rest. The importance of virus-free stock of Jerseybelle is illustrated by the contrast in yields of 5,130 quarts per acre in 1959 and 14,338 quarts per acre in 1961 after virus-free stocks were available for test plantings.

Since 1950, L.F. Hough has been in general charge but several, including J.N. Moore and H.H. Bowen, have been in direct charge, making the crosses and selections. Beginning in 1955, larger numbers of seedlings have been grown. In 1957 about 20,000 were fruited, from which Vesper was selected. Vesper (Utah Shipper x Jerseybelle, introduced in 1962) is still larger and later than Jerseybelle and also has great beauty. Though both Jerseybelle and Vesper have the deep color of Fairfax with a superior gloss, neither has its high flavor nor its resistance to leaf spot, leaf scorch, and Verticillium wilt, to which both are very susceptible. Jerseybelle is moderately productive, while Vesper is highly productive where leaf diseases are not too severe.

Two soil-borne fungus diseases, Verticillium wilt and red stele, are serious in New Jersey. Since 1958, E.H. Varney, plant pathologist, has cooperated in the breeding program for resistance to these diseases; and in this work there has been close cooperation with the staff of the strawberry breeding project of the U.S. Department of Agriculture, at Beltsville, Maryland. Catskill, Surecrop, and Vermilion were found resistant to Verticillium wilt and were used in crosses; the seedlings screened for resistance in a heavily infested field. Similar breeding and screening for resistance to red stele is being carried on.

At the present time the general objectives are (1) superior fresh market varieties, (2) processing varieties easily capped, (3) earlier and later varieties, (4) home garden everbearing varieties. Other objectives include frost hardiness of flowers, very large berries, true breeding lines for F_1 hybrid seed-propagated varieties, and runnerless seed-propagated varieties.

In 1963 there were about 600 selections (32 for advanced testing) and 25,000 seedlings in the field for fruiting in 1964, with H.H. Bowen in direct charge.

In "Inheritance of the so-called everbearing tendency in the strawberry," J.H. Clarke (1938) reported that in most crosses everbearing behaved as a dominant character. No homozygous everbearers were found. One produced no everbearing seedlings. In one, everbearing was recessive and in one the percentage of everbearers was lower than in most.

New York

Crosses were first made at Geneva in 1889, before any other experiment station in the United States. Other crosses were made in 1892, 1893, 1898, in 1906, 1907, 1910, 1911, 1913–1915, 1920, 1924, 1926, 1928, and nearly every year since. Up to 1917 R.D. Anthony reported that nearly 2,000 had been selected for a second test, but only 12 had been named. None became widely known. Slate began his extensive breeding in 1923. Since 1950 he has been assisted by J.P. Watson and since 1960 by D.K. Ourecky also.

The most widely known variety, Catskill [Marshall x Howard 17 (Premier)], introduced in 1933, has steadily gained in importance because of its large, attractive berries and great productiveness. It has been the standard mid-season variety from the Pennsylvania-Maryland line northward for over twenty-five years. Other varieties are Clermont, Empire, and Eden, grown to a slight extent; the new Fletcher (Midland x Suwannee), late mid-season, introduced in 1959 for its high flavor and good freezing quality; Frontenac [Erie x (Fairfax x Dresden)], late, introduced in 1959 for its large, firm, attractive berries that freeze well and for its productive plants; Fulton (Starbright x Pathfinder), mid-season, introduced in 1959 for its firm berries; Fortune [U.S.D.A.-2827 (Dorsett x US-367) selfed], early mid-season, named in 1961 for its attractive, high-flavored berries of only fair freezing quality; Geneva (N.Y.-316 (Streamliner x Fairfax) x Red Rich (Rockhill x Fairfax)), late mid-season and everbearing, introduced in 1961 for its excellent-flavored, large, attractive berries. This last variety makes runners freely at Geneva but few plants, except under high culture, farther south.

In "The best parents in strawberry breeding," Slate (1931) summarized his breeding work: the crossing of 28 varieties to produce over 13,000 seedlings from 1924–1931. He called attention to Howard 17 (Premier) as an outstanding parent, transmitting smooth regular-shaped berries to its seedlings.

In 1943 he reported on the years 1936–1942, in which he raised 11,761 seedlings and selected 292 for further testing. Again Howard 17 (Premier) was reported as an outstanding parent, but Fairfax and Sparkle were also considered notable.

In "Inheritance of Sex in Strawberries," R.D. Anthony (1917) reported on the inheritance of sex in strawberries. For 48 crosses of imperfect (pistillate) x perfect, 1,591 perfect to 1,621 imperfect were obtained, close to the 1 to 1 ratio, and from 23 crosses of perfect x perfect 2,190 perfect, 9 semiperfect (having some functional pollen), and 5 imperfect seedlings were obtained. But from 22 perfects selfed, there were 3,159 perfects, 685 semiperfects, and 474 imperfects.

North Carolina

Although W.F. Massey began testing seedlings as early as 1893, continuous strawberry breeding began at Willard (*Plate 15–1*) in 1928, when the U.S. Department of Agriculture in cooperation with the North Carolina Department of Agriculture, with Charles Dearing in charge for North Carolina, began planting seedlings which had been raised in Maryland. In 1936, the work was made cooperative with the North Carolina Experiment Station with E.B. Morrow in charge for North Carolina. Thereafter, seedlings were raised at both Raleigh, North Carolina, and Glenn Dale, Maryland. The Blakemore, sent to Willard in the spring of 1927 as a selection, was introduced from Willard in 1930. The Fairmore, Daybreak, and Eleanor Roosevelt were introduced in 1939, the Massey in 1940, and the Albritton in 1951. The Fairmore and Daybreak were soon discarded, having been weakened by virus diseases, while the Eleanor Roosevelt, although very large and firm and producing large berries only, was too dark and dull. The Blakemore, Massey, and Albritton succeeded, the Blakemore because of its superior shipping quality and bright color, and the Massey and Albritton because of their large size, high flavor, and good shipping quality. The Albritton is one of the most beautiful of berries with a high gloss over a scarlet surface. This variety, by Morrow and Darrow, is notable because it resulted from limited inbreeding, raising selfed progencies of Southland and Massey, crossing the best of these seedlings, No. 1065 x No. 1053, and selecting the best from the resulting population. After its introduction, Albritton quickly replaced Massey, since it had a tougher, glossier skin, equally high flavor and was more productive. Although the Albritton has succeeded remarkably in North Carolina, where it is an almost ideal variety, it is far less hardy than other varieties grown farther north.

The objectives of the work have been large, attractive, good shipping, disease resistant, high-flavored, productive varieties for the Southeast.

After Morrow's death in 1956, Schneider was in charge from 1956 to 1958, and was followed by Correll in 1959, and by G.J. Galletta from 1959 to the present.

Among the results of several notable breeding projects are these publications:

In 1941 Morrow and Darrow reported on "Inheritance of some characteristics in strawberry varieties" that seemed important in the breeding work in North Carolina. During mild periods in the winter in eastern North Carolina flower clusters of Blakemore and Missionary develop to the flowering stage and these flowers are killed by later freezes. As the early flowers develop into the largest berries, it seemed that studies might indicate a better genetic control of this character. Selfed seedlings of 7 varieties and various crosses of Blakemore, Daybreak, and Fairfax were observed. The complete flower history of any selfed line or cross showed that plants with the most flowers killed generally produced later the most flowers in both early and crown crop. Thus, conditions favorable for early flowering were favorable for further extensive flower bud formation and earliness of selfed seedlings gave a correct index of genetic earliness. Fruit characteristics of 100 seedlings (*Plates 13–3a* and *13–3b*), usually of 9 selfed and 11 crossed lines—shape, color, seed color, seed placement, firmness, separation of calyx, size of calyx, hollowness, flesh color, and size—were all studied and the best sources of the most desirable characters determined.

"Effects of limited inbreeding in strawberries" (1952), by E.B. Morrow and G.M. Darrow, indicated that selfed, backcrossed, and sib-crossed progenies resulting from inbreeding usually have greatly decreased vigor when compared with the parent varieties. However, seedlings with the highest rating for vigor could be selected in all progenies (*Plate 14–1*). It seemed possible to utilize the superior qualities of Howard 17 (Premier) and Blakemore, even though they and many of their seedlings mutate to variegated plants. None of eight inbred selections tested for yield approached the parents. The value of inbreeding seemed to be (1) the evaluation of a variety for its breeding value and (2) in concentrating desirable characters in the inbreds.

"Genetic variances in strawberries" (1958), by Morrow, Comstock, and Kelleher, indicated that the "seedling square" method of testing seedlings is an entirely adequate basis for first selection, that there is sufficient genetic variation to allow great improvement in yield, that measured yield was the most effective measure of improved yield, and that family selection is not likely to be more effective than selection among individual genotypes. A suggested plan of recurrent selection for fruit yield was given.

Another notable publication is: "Genetic variation in an asexual species, the garden strawberry," *Genetics* 43, 634–646, 1958. Comstock, R.E., et al.

Oregon

There are five agencies in the United States doing active breeding of strawberries on the Pacific Coast and all have long-continued programs. In Oregon and Washington the objectives are similar and the work closely coordinated. In general, the work of the California Strawberry Institute and of the California State Experiment Station is likewise coordinated and with similar objectives. In Alaska work is under way at the College Station near Fairbanks in the interior, and some testing of selections is being done at the Palmer Station, on the coast. A sixth agency, the Canadian Agricultural Experiment Station at Agassiz, British Columbia, also has strawberry breeding with objectives similar to those in Oregon and Washington, with emphasis on resistance to red stele and on hardiness (see Canada).

About 95 percent of the Oregon and Washington strawberry crop is produced for commercial processing, these two states producing the world's largest volume of frozen strawberries. The annual production is about 100,000,000 pounds from about 24,000 acres and the harvest season is June 5 to July 25. Fifty to 60 percent of the crop is frozen in 10 to 16 oz. dessert packages and the rest goes for preserving, ice cream, and institutional trade. From about 1905 to 1955, Marshall was raised on 90 percent of the acreage. Beginning in 1908, barrels of frozen berries were shipped to eastern preservers. Later, freezing in small containers developed. When prices dropped after World War II, higher yielding varieties were necessary and in 1950 the Northwest was introduced—a firmer berry with a much heavier yield and more tolerant of virus diseases. It composed 75 percent of the acreage in 1962 and was replacing Marshall rapidly. In 1962 Marshall made up 15 percent, Siletz 6 percent, Puget Beauty 3 percent, and others 1 percent of the acreage. Breeding programs in the two States have similar objectives—high yield, resistance to plant diseases, and high processing quality.

The work at the Oregon Station was begun in 1911 and continued to 1918 by V.R. Gardner, and again started by C.E. Schuster in 1920. It was made cooperative with the U.S. Department of Agriculture in 1928. When Schuster began nut research in 1930, the work was continued by George M. Darrow, 1930 to 1932, and then by George F. Waldo, 1932 to present. Gardner used the native *ovalis* and probably *F. chiloensis* in crosses with named varieties, with the objectives of superior shipping varieties. Schuster was breeding for a canning variety at the beginning, and obtained the Corvallis (Marshall x Ettersburg 121) from his first crosses in 1920. Later the work, in cooperaion with the U.S. Department of Agriculture, was expanded with the objectives of originating better freezing and preserving varieties as well as better shipping varieties. In all, Schuster grew about 50,000 seedlings. He used *F. ovalis* and *chiloensis* in his later crosses and their use was continued in later years, but not to obtain shipping varieties. Waldo has named the Brightmore (1942), Siletz (1953), and Mollala (1961) varieties for their freezing qualities. Since 1944, breeding for red stele root disease resistance has been a primary objective and from 1944 through 1963 a total of 240,948 seedlings were grown in infected soil and examined for red stele. Both Siletz and Mollala were selected from this work and are resistant to this disease. Siletz is the standard variety for soils where red stele may be serious in Oregon, Washington, and British Columbia. In some places after a few years in the same soil new races of the red stele organism appear that can infect even Siletz. Waldo has used selected *chiloensis* and *ovalis* more than most breeders in his crosses.

South Dakota

N.E. Hansen (1907) in 1895 collected wild strawberries (*virginiana*) near Brookings and later obtained plants from North Dakota near Manitoba. These were compared with a large number of varieties at Brookings in 1899 and 1900 and found much hardier. Hansen's first crosses were made in the winter of 1899–1900 and others the following and succeeding winters. Eight thousand seedlings were planted and about 225 selections made. All seedlings endured −40° F. with no snow cover. Two were sent out for trial beginning in 1905 as South Dakota #1 (Jessie x Manitoba wild) and #2 [Glen Mary x Cavalier (North Dakota) wild]. Though hardy at the station, they were injured at some other places. Many thousand seedlings, produced by backcrossing selections to their parents, were grown. They seemed less hardy than the F_1 but the non-hardy were weeded out by winter's cold. Dakota #1 became known as Dakota and was about one inch in diameter, too small to be grown except where the other varieties were not hardy. No breeding has been done by the South Dakota Station in recent years.

Tennessee

Strawberry breeding began in 1928 and has continued to the present. Its objectives have been to obtain attractive, firm, high-flavored varieties suitable for processing and shipping that are resistant to leaf and root troubles (Drain, 1934). Five varieties have been named: McClintock (1932) (Aroma selfed), Tennessee Supreme (1940) [Missionary x Howard 17 (Premier)], Tennessee Shipper (1941) (Missionary x Blakemore), Tennessee Beauty (1942) [Missionary x Howard 17 (Premier)], (*Fig. 15–1*), and Tennessean (1950) (Tenn.-230 x Tenn.-586). Of these, two are important, Tennessee Shipper (a

FIG. 15–1. Tennessee Beauty was selected in this field of seedlings of the cross at the University of Tennessee Agricultural Experiment Station in 1933. Note the growing of blocks of each seedling.

backcross of Blakemore to Missionary) and Tennessee Beauty [Missionary x Howard 17 (Premier)], the former as a parent for firmness, the latter for its productiveness and commercial use. Under the general direction of B.D. Drain, crosses were made at the main experiment station at Knoxville by E.M. Henry in 1933. The seedlings fruited and selections were made by him in 1935. About 12,000 seedlings had been fruited by 1935 when the work was moved to Jackson, Tennessee, where the selections were retested. L.A. Fister and Drain made the final selections and naming. Strawberry breeding has been continued at the Jackson branch; more recently by J.P. Overcash (1942–1945), E.H. Hanchey (1946), P.L. Hawthorne (1947), and W.E. Roever (1948 to present). Now the breeding work has been moved back to Knoxville with Roever in charge.

In "Some strawberry breeding progeny data," by B.D. Drain and L.A. Fister, data are given on characteristics of large selfed populations of Klondike and Aroma, small numbers of Blakemore selfed, and on intercrossing Aroma and Klondike, Blakemore and Aroma, and Dorsett and Aroma. Selfed Blakemore had 14.2 percent highly flavored seedlings, Klondike 8.0 percent, and Aroma 1.1 percent. Selfed Blakemore had 83.7 percent of seedlings free of leaf blight, while Missionary had 63.3, Klondike 67.4, and Aroma 66.3 percent free. Blakemore x Aroma had only 7.5 percent high-flavored, Dorsett x Aroma had 16.7 percent and Klondike x Aroma 12.7 percent. Selfed Klondike had 6.1 percent vigorous plants, Aroma selfed 4.4 percent, and Blakemore selfed 6.8 percent, while Klondike x Aroma had 54.3 percent and Blakemore x Aroma had 23.0 percent vigorous. Missionary x Howard 17 (Premier) had only 12.6 percent firm vs. Missionary x Fairfax 31.2 percent firm-fruited.

In "Strawberry breeding and the inheritance of certain characteristics" (1942), Overcash, Fister, and Drain reported on plant and fruit characteristics of crosses between Tennessee selections and between Tennessee selections and varieties. The cross of Tenn.-384 (Missionary selfed) x Tenn.-388 (Fairfax selfed) gave a vigorous progeny and many good-flavored seedlings. Eighteen percent of the progeny was saved for further testing.

Texas

In 1933 and 1934 crosses were made by Mortenson to obtain varieties that would produce sufficient runner plants able to survive under the high temperatures of south Texas. In 1938, eight selections were still being tested and three were named and introduced. Alamo (1937) was Blakemore x Ettersburg 80, Ranger (1937) was Texas x Missionary, and Riogrande (1937) was Blakemore x Ettersburg 80. Of these, Ranger is still being raised in south Texas.

Vermont

In Burlington, Dr. Charles Blasberg started strawberry breeding in 1945 and continued until his death in 1961. A main objective was late varieties for northern regions; later objectives were both early and late varieties. A number of selections of *F. virginiana* were used in breeding. A promising cross was U.S.-3366 x Temple. Selections from Blasberg's work are being tested currently under the direction of R.J. Hopp and B.R. Boyce.

In "Sterility of strawberries; Strawberry breeding" (1923), Cummings and Jenkins reported a study of the inheritance of sterility in strawberries. In crosses of the pistillate with perfect-flowered, 54.7 percent of the seedlings were perfect-flowered. Studies of inheritance of fruit characters were made with very small numbers, but large fruit size seemed to be clearly heritable.

Washington

The work at this station in Puyallup was begun by a graduate student, M.B. Hardy (1929–1931), and has been continued since 1932 by C.D. Schwartze, assisted 1940–1957 by Arthur S. Myhre. The objectives were firm, high yielding, red-fleshed, virus-tolerant, red stele-resistant varieties for freezing and preserving. The first variety, Northwest, was the result of a cross of 2 U.S.-Oregon selections: Brightmore x U.S.-Oreg.-456. Puget Beauty (1956) is a cross of Sparkle x U.S.-Oreg.-1765; Cascade (1961) is Shasta x Northwest; and Columbia (1961) is Wash.-157 x Wash.-175 (both selections resulting from crosses of U.S.-Oregon unnamed selections). The Northwest variety by 1962 constituted about 75 percent of the acreage in strawberries in Oregon and Washington, and it is also grown in British Columbia. It is much more productive than Marshall which it is replacing, and much more tolerant of virus. It is also firmer, has good processing qualities, and in 1962 was processed in larger quantity than any other variety in the world and constituted the largest acreage of any variety in the United States. It is not resistant to the red stele root disease, while Marshall is somewhat resistant. The new Columbia is similar to Northwest in processing qualities, but in addition is resistant to some races of red stele and to mildew and is highly tolerant of virus diseases. It ripens one week later than Northwest and is reported as somewhat resistant to the Botrytis fruit rot or gray mold. About 150,000 strawberry seedlings have been grown in the breeding program.

Up to 1962 it was estimated that 273,000 tons of the Northwest had been produced with a total farm value of $71,000,000. For 1962 the total was about 52,000 tons with a farm value of $13,500,000 and a processed value of $18,-720,000. From the beginning, in the 20 years before the Northwest was released, a total of $100,000 may have been spent on the strawberry breeding work by the Washington Station.

Wisconsin

Professor R.H. Roberts, now emeritus, has done limited strawberry breeding for many years at Madison and in 1950 he introduced two varieties, Wisc.-214 and Wisc.-537. Another, Wisconsin Queen, was introduced in 1959. These have been grown to a limited extent only. No virus-free stocks are known. Wisc.-214 was introduced for its large, attractive fruit which freezes well. Its parentage is Corvallis x Wisc.-7128 [Wisc.-78 (Beaver x Howard 17 (Premier) x Wisc.-134 (Vanguard x Howard 17 (Premier)]. Wisconsin Queen (Wisc.-214 x Wisc.-6-2) was introduced in 1959 for its attractive, good-flavored fruit, adapted to freezing.

Beginning in 1956, F.A. Gilbert, who in New Jersey made the cross and selected the Jerseybelle, has made crosses and fruited about 17,000 seedlings at the University Farm at Sturgeon Bay. Up to 1963, 205 selections in all have been made, 50 are under advanced tests, and three are being studied for possible introduction. The objectives are for large size, high yield, firm fruit, freezing quality, and high flavor.

Important varieties grown in the state are Robinson, Catskill, Howard 17 (Premier), and Sparkle. Wisc.-214 and Wisc.-537 are grown to a limited extent. The newer varieties Jerseybelle, Earlidawn, and Surecrop are being suggested for trial in some areas.

Wyoming

Collections of native strawberries (mosty *ovalis*) for possible hardiness in breeding was begun by A.C. Hildreth as early as 1932. Extensive systematic collections took place in 1936 after the severe winter of 1935–1936 had killed, or badly injured, all of the more than 150 commercial varieties, while the collected native plants remained uninjured. In all, about 42,000 plants from more than 1,100 localities in Wyoming, Colorado, Montana, New Mexico, and Utah were collected and planted in trial plots at Cheyenne, the U.S. Department of Agriculture Station. None was suitable for cultivation but they showed "extreme variations in horticultural characters, differing in size, shape, color, and flavor of fruit and in season of maturity, fruiting habit, prolificacy, tendency to produce runners, resistance to disease, and tolerance to soil alkalinity" (Hildreth and Powers, 1941). Some were everbearers, others June bearers. Most of the *ovalis* were pistillate or staminate, but a few were true perfect-flowered. Some showed considerable drought resistance and the majority proved hardy without protection.

Under Drs. Hildreth and Powers, during the winter of 1937–38, three varieties, Gem, Dorsett, and Fairfax, were crossed with three different collections of *F. ovalis* selected for winter hardiness, one of which had high flavor and a second larger than average size. The F_1 varied greatly. During the winters of 1938–1939 and 1939–1940 over 80 percent of the Dorsett and Fairfax and about 30 percent of the Gem plants were killed. In contrast, there was no appreciable killing of the F_1 nor of the native plants. In fruit size the F_1 were mostly intermediate, but ranged from as small as the smallest *ovalis* to nearly as large as the Fairfax, and some, with Fairfax and Dorsett as one parent, were superior in sweetness and flavor to either variety. Powers concluded that *ovalis* could be used to improve the cultivated strawberry in earliness, runner production, sweetness, flavor, and aroma. Different *ovalis* collections had different values as parents in crossing with cultivated varieties. The backcross method seemed to offer the greatest possibilities for the most rapid success of a breeding program. Double crosses were shown to offer far more promise than F_2 populations. On the average, 1 in 100 seedlings recombined six desirable characteristics: winter hardiness, large fruits, vigorous plants, high runner production, early maturity, and high flavor. Winter hardiness and production of many runners were almost completely dominant.

From this work, three varieties were released in 1944, one in 1948, two in 1954, and one in 1956, all for home garden use. The three varieties—Cheyenne 1 (Dorsett x *F. ovalis*), Cheyenne 2 (*F. ovalis* x Fairfax), and Cheyenne 3 [Fairfax x (Fairfax x *F. ovalis*)]—were introduced in 1944 as high-flavored varieties to cover a season of over a month, but were much smaller than the Fairfax. In 1948, the Sioux [(Fairfax x *F. ovalis*) x Fairfax] was introduced in cooperation with the North Platte Experiment Station of Nebraska. It was very hardy, soft, productive, high-flavored, but also smaller than commercial varieties. These are not now in the trade.

Three everbearers have since been introduced: Radiance [Montana x Cheyenne 1 (*F. ovalis* x Fairfax) x Fairfax] and Arapahoe [(Cheyenne 1 x ((*F. ovalis* x Fairfax) x Fairfax)) x (Rockhill x Cheyenne 3)] are very hardy everbearing varieties and were introduced in 1954. The berries of these are as large as commercial varieties. They are drought- and alkali-tolerant and the flowers are somewhat frost-hardy. Ogallala, introduced in 1956 (Rockhill x Cheyenne 3) x (Midland x Cheyenne 2), a third everbearer of high quality, was selected from 4,300 seedlings that were sent to North Platte, Nebr., Station where they were grown by Glen Viehmeyer. It is also hardy and is drought-tolerant, with berries the size of Fairfax. It and the other two everbearers seem adapted to eastern Colorado and to western Kansas north to Canada. More than most others, the work of Powers indicates the methods by which wild native selections can be utilized by breeders (Powers, 1944, 1945).

Dr. Powers was in other work from 1942 to 1946, during which time Dr. D.H. Scott was in charge of the strawberry breeding. Dr. Powers left finally in the fall of 1954; the work was continued by E.D. Krouch to January 1957, then by Brown to 1961, and since then by G.S. Howard. Since 1956 about 32,000 seedlings have been grown, 254 selections made, and a few are being more widely tested. The breeding work was still being continued in 1964.

Canada

In Canada the total acreage planted to strawberries in 1961 was given by the census as 13,051 acres, as 15,853 in 1951, and as 10,652 in 1941. Imports in 1961 were 25,140,820 pounds as contrasted with the 30,112,000 pounds produced in Canada. The acreage by provinces was:

Prince Edward Island	— 682	acres
Nova Scotia	— 703	"
New Brunswick	— 557	"
Quebec	—4,296	"
Ontario	—4,381	"
British Columbia	—2,253	"

Ripening begins about June 10 in Ontario and British Columbia, and in Nova Scotia and Prince Edward Island extends into August. The major production area of British Columbia is the Lower Fraser Valley with 1,600 acres in 1963.

Until about 1950, when some of the varieties bred at Ottawa and Vineland began to be grown in Eastern Canada, and British Sovereign became the dominant variety in British Columbia, the varieties grown in Canada were much the same as those grown in the northern part of the United States. In 1897 Haverland, Warfield, Crescent, and Wilson were considered the chief varieties, and Parker Earle, Gandy, and Williams the favorite late ones. In 1909 Bederwood, Splendid, Warfield, Williams, Greenville, Bisel, Sample, Buster, Pocomoke, and Parson were recommended. In 1919 the chief varieties grown were: *Maritime Provinces,* Dunlap, Splendid, Glen Mary, Sample, Warfield, Belt; *Quebec,* Dunlap, Parson, Splendid, Bederwood, Sample, Pocomoke, Warfield; *Ontario,* Parson, Glen Mary, Williams, Dunlap, Bederwood, Splendid, Howard 17 (Premier), Sample, Enhance; *Prairie Provinces,* Dunlap, Dakota, Bederwood, Haverland, Warfield, Tennessee Prolific; *British Columbia,* Magoon, Dunlap, Marshall, Paxton.

In 1950 varieties grown were:

Nova Scotia: Howard 17, Dunlap, Catskill, Jessie.
New Brunswick: Howard 17, Dunlap.
Prince Edward Island: Dunlap, Tupper, Louise, Elgin.
Quebec: Howard 17, Mackenzie, Dunlap, King, Louise, Elgin.
Ontario: Howard 17, Dorsett, Dunlap, Parson, Fairfax, Valentine.
Manitoba: Dunlap, Glenmore, Gem,* Sparta.*
Saskatchewan: Dunlap, Dakota, Gem,* Sparta.*
Alberta: British Sovereign, Dunlap, Howard 17, Gem,* Mastodon.*
British Columbia: British Sovereign, Marshall, Magoon, Dunlap, Gibson, Parson, Paxton.

In 1962 the varieties recommended were:

Newfoundland: Howard 17, Dunlap, Sparkle, Louise, Red Rich.*
Prince Edward Island: Cavalier, Dunlap, Redcoat, Catskill, Sparkle, Guardsman, Red Rich.*
Nova Scotia: Cavalier (14 percent), Catskill (25 percent), Redcoat (31 percent), Sparkle (29 percent), Surecrop (promising), Gem,* Red Rich.*
New Brunswick: Cavalier, Redcoat, Grenadier, Sparkle, Catskill, Guardsman, Red Rich,* Gem.*
British Columbia: Northwest, British Sovereign, Puget Beauty, Marshall, Agassiz; Northwest 60 percent and British Sovereign 40 percent of acreage.
Quebec: Cavalier, Redcoat, Sparkle, Guardsman.
Ontario: Redcoat (for main crop); Earlidawn, Erie, Catskill, Sparkle, Cavalier, Guardsman, Howard 17 (Premier).

* Everbearers.

Since 1960, Cavalier and Redcoat, both bred at Ottawa, have rapidly become the leading varieties of eastern Canada. In 1887 W.W. Hilborn reported having about 90 seedlings in the test planting at the Central Experimental Farm at Ottawa. As early as 1889, 650 seedlings were fruited there and 40 saved for further testing. John Craig was horticulturist in charge from 1890 to 1897, and in 1897 about 1,400 seedlings were raised. In 1898 W.T. Macoun became horticulturist and selections were made. M.B. Davis became his assistant about 1915 and took over the breeding work soon afterward. One-half acre was in breeding plots in 1917. Davis was made Dominion Horticulturist in 1933. Dr. A.W.S. Hunter took over the strawberry breeding in 1936 and L.P.S. Spangelo succeeded him, making his first crosses in 1949. Ray Watkins joined the breeding staff in November 1963.

The wild strawberry, *F. virginiana,* is native in Canada as far north as the 64th parallel, the latitude of Iceland, Stockholm, and Helsinki. Selections of native *virginiana* plants from Nova Scotia, New Brunswick, Ontario, Manitoba, and British Columbia have been used in crosses. The objectives in breeding were hardier varieties for northern latitudes, sweeter berries with higher aroma. Varieties were introduced as early as 1913. Presently, objectives include increased yield, firmer and more attractive berries, good dessert and processing quality, easy capping, and resistance to foliage diseases. Commercial varieties and Ottawa selections are used as parents. Promising crosses have been Sparkle x Valentine, Howard 17 (Premier) x Fairfax and x Valentine, Valentine x Fairfax, Claribel x Sparkle, Howard 17 (Premier) x Temple, Temple x Dresden. One variety, Louise, seems of some importance. The others failed, probably because of infection with virus diseases. Louise (1942) (Ettersburg 811 selfed) is a pistillate, late, attractive, medium to large berry of good dessert quality. It is very susceptible to leaf scorch and leaf spot, and virus-free stock is not available. It is grown to a very limited extent.

In 1957, four new varieties—Cavalier (Valentine x Sparkle), Grenadier (Valentine x Fairfax), Guardsman (Claribel x Sparkle), and Redcoat (Sparkle x Valentine)—were named and introduced. Guardsman, the latest and best in dessert quality, has been highest yielding, but Redcoat is a close second. Cavalier has been the best for early ripening, and Redcoat the most attractive and important commercially.

Cavalier is a very early, attractive variety whose fruit is much firmer than Catskill, Dunlap, or Howard 17 (Premier) (in Canada, but not in New York), and earlier than Howard 17 (Premier), good for dessert and processing. It is resistant to Verticillium, susceptible to mildew, scorch, and spot, and has dead caps in New York. It drops off in size too quickly.

Grenadier is a mid-season, dark red, very firm variety about the size of Howard 17, with good dessert and processing quality, but susceptible to mildew. The calyx is clasping like its Fairfax parent, but the berry is more tart and deeper red within. Like Cavalier it drops in size too quickly.

Guardsman is a very late, attractive and firm variety which is highly acid until ripe and then is high-flavored and good for processing. While resistant to some races of red stele and mildew, it is susceptible to Verticillium. It too drops in size quickly.

Redcoat is a mid-season, very attractive, glossy, light red variety with firm meaty flesh, good dessert quality. It is fair for processing, but susceptible to Verticillium and leaf spot. It is resistant to mildew. Because of its very productive plants, large average berry size, very attractive, glossy, bright red appearance, firm flesh and good shipping quality, equal to that of Sparkle, Howard 17 (Premier), and Dunlap, it is already the leading variety of eastern Canada.

Inbreeding has received considerable attention at this farm (Spangelo, 1958). As early as 1920 Parson, Bederwood and Valeria were being selfed and an F_2 generation fruited in 1924. Beginning in 1949, inbred lines of Howard 17, Sparkle, and Fairfax have been carried to the S_5 level. Valentine was crossed with seven Howard 17 (Premier) S_2 clones and three Sparkle S_2 clones, and in 10 of the 12 progenies the percent of selections was higher than in progenies obtained by crossing the originals. Phenotypes as a measure of genotypes of selfed lines is under study. For 1964 there were 17 S_5 progenies of Howard 17 (Premier) and two of Sparkle to be fruited.

For the University of Minnesota in 1963 Spangelo, in his Ph.D. thesis entitled "Combining ability in strawberries," reported on selfing and intercrossing five varieties, and on an S_2 of Early Bird (1963). Leaf scorch resistance and fruit quality did not show combining ability, but leaf spot resistance, number of runners, early ripening, fruit size, appearance, and firmness did. Accordingly, comparisons of self progenies can be used for selecting parents for any of these characters. The best cross indicated for several characters of the varieties tested seemed to be Howard 17 (Premier) x Fairfax followed by Fairfax x Dresden and Howard 17 (Premier) x Dresden.

In 1950 a study of the possibility of growing seed-propagated, instead of clonally propagated, varieties was begun. Seedlings of some crosses were quite uniform, and commercially acceptable, especially Sparkle X Valentine. At the same time isolation of variety testing, and control of vectors of virus was begun, since indexing for virus showed that most previous selections and varieties were completely or partially virus-infected.

Some publications are:

"Suggested infection scales for roguing strawberry seedlings susceptible to *M. fragaria* and *D. earliana*," *Phytopath:* 93:345–347. 1953, by L.P.S. Spangelo, and A.T. Bolton.

"Studies in strawberry bud differentiation," *Canada Department of Agriculture Bul.* 110, 1929, by H. Hill, and M.B. Davis, 1929.

The first sign of flower bud differentiation was noted September 19 in the Pocomoke variety. Runner plants rooted on September 19 showed initial flower bud stages in three weeks, and those rooted on October 10 showed initial stages October 24.

Nova Scotia

KENTVILLE, D.L. Craig has reported two phases of the breeding program here. (1) Inbreeding for seed-produced varieties of uniform type and (2) variety crossing for improved early and late maturing varieties. Inbreeding started in 1953 and 40,000 selfed seedlings had been evaluated by 1963. From 10 named varieties there were 30 S_3 lines, 184 S_2 lines, and 53 S_1 lines. Variety crossing started in 1951; 10,000 seedlings had been evaluated by 1963 and two appeared promising, one having a season like Sparkle and the other later.

D.L. Craig, E. Aalders, and C.J. Bishop (1963) have reported on their inbreeding up to 1963. They state their outlook as follows: "As the available varieties become more and more highly selected and further improvement becomes progressively more difficult, larger and larger populations are necessary. . . . One phase of the strawberry breeding program at Kentville is, therefore, presently aimed at surpassing this plateau of breeding advancement through development of a strawberry variety of desirable type which can be grown from seed." The project was begun in 1953. Five selections were made of each of two crosses, Valentine x Sparkle and Valentine x Fairfax, and then all selections of each cross were crossed with all others. The No. 3 selection of the first cross x No. 4 of the second was judged the best. Then 500 selfed seedlings of each of these (No. 3 and No. 4) were grown and six selections of each made. Each of these six selections of No. 3 selfed was crossed with each of the six selections of No. 4 selfed, then the two best of these selections, as judged by their seedlings, were crossed. Finally, 30 feet of matted row of each of four sets of seedlings was compared as follows:

		FRUIT RATING		PLANT RATINGS		
	Yield lb/plot	(1 to 5) Uniformity	Appearance	Stand percent	Health of foliage	Uniformity of foliage
Sparkle x Fairfax	26.5	2.55	3.31	78.8	88.6	76.6
F_1 of original selection	36.7	2.80	3.40	83.1	82.7	78.2
F_1 of sibs	38.5	2.89	3.72	88.2	90.2	84.2
F_1 of selfs	40.8	3.24	4.26	92.2	94.3	90.5

A consistent improvement in yield, fruit uniformity, and appearance, in plant stand, in health of foliage, and in uniformity of foliage was obtained. Aalders and Craig (1964) reported that in 1964 the inbreeding then involved 32 S_4 lines, 180 S_3 lines, 51 S_2 lines and 2000 S_1 seedlings. The recurrent reciprocal selection program was at the S_2 level of inbreeding and test-crosses to select S_2 parents with superior combining ability were being planted. Acadia (Sparkle x Redcrop) from the regular crossing program was named in 1964.

Strawberry breeding was carried on at the Saanichton Experiment Farm, 1935 to 1955, by E.R. Hall and 1955 to 1960 by J. Harris, when the work there was discontinued. No variety was named from this work.

AGASSIZ. At the Canadian Department of Agriculture Farm at Agassiz the work was started in 1946 by T. Anstey and continued by J.A. Freeman until 1959, and since then by H.A. Daubney. Present objectives are to originate varieties (1) of high yields and high quality, especially for the processing (freezing) trade which uses 90 percent of the crop, (2) with resistance to red stele races prevalent in British Columbia, (3) with resistance to mildew, along the lines of Puget Beauty and Siletz, (4) with sufficient winter-hardiness. Northwest is ideal for frozen pack, but is not fully hardy and is susceptible to red stele and mildew. British Sovereign, of high flavor, is not suitable to freezing and is susceptible to both red stele and mildew. Siletz is resistant to some races of red stele but lacks high flavor. Agassiz was released in 1956. It is superior for freezing, is winter hardy, but susceptible to red stele and mildew. It is grown to a limited extend in the Salmon Arm area because of its preserving quality. Puget Beauty is high flavored, winter hardy, resistant to mildew, but susceptible to red stele and not a reliable yielder. Since 1959 between 15,000 and 20,000 seedlings have been screened each year for red stele and mildew resistance (Daubney, 1961). About 3,000 screened seedlings were planted in the field in 1963. Fifty selections from the 1959 crosses and 80 from the 1960 crosses are being retested.

Tests of sources of red stele resistance and the use of these sources in breeding are considered of primary importance. Additional collections of *F. chiloensis* from the Pacific beaches are being made for study. The Yaquina clone of *F. chiloensis* for red stele resistance, Puget Beauty for mildew resistance, and Puget Beauty x Northwest for fruit, have been outstanding. Close coöperation with Schwartze, of Puyallup, Washington, and Waldo, of Corvallis, Oregon, is maintained.

Publications include:

"Resistance to Verticillium wilt in F_I generations of self-fertilized species of Fragaria," *Can. J. Bot.:* 36, 1958, by W. Newton and M. Adrichen.

Selfed seedlings of the species *vesca, vesca* var. *bracteata, virginiana, ori-*

entalis, ovalis including *yukonensis,* and *chiloensis* were tested for resistance to Verticillium wilt. No resistance was found in the seedlings of *vesca* or *virginiana*. Tolerant seedlings of *orientalis* were found and resistant seedlings, as well as tolerant seedlings in *ovalis, ovalis yukonensis,* and *chiloensis.*

"Effect of parentage in breeding for red stele resistance of strawberries in British Columbia," *A.S.H.S.,* 84, 1964, by H.A. Daubney.

Daubney evaluated 25 parents from the following four sources of resistance, Aberdeen, Frith, *F. chiloensis,* and *F. virginiana,* as well as Magoon, Perle de Prague, and Oberschlessein of unknown origin.

Ontario

Strawberry breeding at the Vineland Station began in 1913 and has been continued to the present, although no crosses were made in 1916 and 1921, or from 1931–1939. Five breeders have been successively involved in the work: F.S. Reeves, 1913–1922; W.J. Strong, 1921–1948; J.F. Brown, 1949–1956; E.A. Kerr, 1956–1958; and C.L. Ricketson, 1958 to present. The early objectives were large size, better flavor, greater yield, firmer, and more attractive berries. Early Ozark was the outstanding parent. Four varieties were introduced: Vanguard (Pocomoke x Early Ozark) in 1924, Vandyke [seedling 1467 (Dunlap seedling) x open] in 1928, Vanrouge (seedling 180,115 x Bliss) in 1938, and Valentine [Howard 17 (Premier) x Vanguard] in 1941. Seedling 180,115 was Admiral x 1563 (Dunlap x Early Ozark). Crosses for the first two varieties were made by Reeves and the next two by Strong. Only Valentine was important, because it was very early, large, soft but resistant to gray mold (Botrytis). Valentine is no longer grown commercially in Ontario, but it is one parent of Cavalier, Grenadier, and Redcoat, of the Ottawa Station, and is an important parent in other countries. All selections previous to 1958 have been discarded because of virus infection. Up to 1944, 37,555 seedlings had been fruited. The objectives in 1944 were better early varieties, higher flavor through use of English varieties, easy hulling, better preserving qualities, resistance to root rot and suitability to quick freezing. Present objectives of Ricketson are high yields and higher flavor, especially for preserving. Since 1958 some 3,790 seedlings have been fruited and 85 selections are still under test. About 10,000 seedlings were to be set in the field in 1964.

Manitoba

As in other Prairie regions with extremes of drought and temperatures, hardiness is all-important. Although only about one hundred and twenty acres of strawberries are grown in Manitoba, they are an important fruit for the home garden and small market gardener. Throughout more than forty years varieties from other areas have been tested for hardiness at the Dominion Research Farm at Morden. Dunlap, tested as early as 1920, proved a reliable variety and Howard 17 (Premier) has also been widely grown.

Up to 1950 Dunlap, Gem, Howard 17 (Premier), Sparta, Glenheart, Arrowhead, Burgundy, Evermore, and Valentine were used extensively in breeding. Rockhill was used for its high flavor and everbearing habit, and Cheyenne 1 and Cheyenne 2 for their hardiness. Most selections were lost due to virus infection and no superior selections were found. A *diallelcross* system using Valentine, Glenheart, Sitka Hybrid, Robinson and Morden selections 65–54 is being tried. Progenies with the greatest mean hardiness had Glenheart as one parent.

W.R. Leslie was the breeder from 1926, when breeding started, to 1943, then C.R. Ure from 1943 to 1962; D.D.F. Williams under Dr. Ure from 1950 to 1956. H. Quamme is now in charge and is mainly testing varieties and selections from other areas.

Two private breeders have been active in obtaining new varieties for prairie areas. William Oakes, of Miami, Manitoba, now in his eighties, introduced 17 varieties from 1940 to 1950, of which two, Glenheart and Glenmore, are still of some importance because of their hardiness. Glenheart, everbearing of unknown parentage, introduced in 1946, is widely grown in Manitoba. Glenmore, a June bearer also of unknown parentage, is recommended still for both Alberta and Saskatchewan. A.J. Porter, Parkside, Saskatchewan, is still an active plant breeder. He introduced 6 varieties of unknown parentage between 1940 and 1960. His Sparta, an everbearer introduced in 1940, is still extensively grown as a commercial variety. Parkland, introduced in 1954, is recommended as a hardy everbearer for Saskatchewan, and Jubilee as a hardy everbearer for Alberta and Manitoba.

Alberta

R.E. Harris is in charge of strawberry breeding at Beaverlodge. Prior to 1954 some open-pollinated seedlings had been grown. In 1954 a study was begun of the combining ability of cultivated varieties and of wild x standard varieties. Two promising selections have been made. Mildew-resistant *virginiana* was crossed with standard varieties in 1959 to improve hardiness. Selfing, followed by intercrossing, was started in 1961.

Premier, Glenheart, and Sitka hybrids proved best for transmitting vigor, and Northerner for yield. Fairfax and Red Rich transmitted the largest number of desirable fruit characters. Glenheart x Cheynne 2 was the most promising cross for considerations of hardiness, vigor and large fruit.

Although so far north (55° 13″), with an annual rainfall of 17.5 inches, of which 5 inches runs off with the spring thaw, with temperatures from 98° to −53° F., and soil temperatures as low as 15° at 4-inch depth, *F. Virginiana* is native and abundant. Many collections of *virginiana* have been made. Even *vesca* is native, but it is not as abundant as *virginiana*. Critical temperatures for killing well-hardened plants in October ranged from −15° to 5° F. Crown hardiness is considered to be most important.

16

Strawberry Breeding and Industry in Great Britain

England

THE NINETEENTH CENTURY in England saw the origination of varieties which were quite extensively grown in the twentieth century as well (see Chapter 4). The appearance of Keens Seedling in 1821 dates the time when both England and Europe had their first fine strawberry variety. Most other varieties of lasting use, however, were originated somewhat later: Myatt's British Queen (1840); Bradley's Sir Joseph Paxton (1862), Jucunda introduced by John Salter (1864, *Fig. 16–1, 16–2*) and Doctor Hogg (1866); and the varieties Noble (1864) and Royal Sovereign (1892) originated by Laxton, whose work and that of his sons bridges the two centuries. Such varieties as these, including the older ones such as Keens Seedling and Black Prince, plus numerous others were grown in England up until virus diseases and red stele root rot became very destructive in the 1920's and 1930's. Then, plant losses and low yields eliminated most varieties from commercial plantings as well as from home gardens. Research work indicated the major sources of trouble. As a partial solution, Royal Sovereign stocks that were relatively free of virus were found and propagated. The red stele-resistant Auchincruive Climax, bred by Reid of Scotland and introduced in 1947, proved to be adapted to England, and it was so superior in flavor, size, beauty, and production that it replaced

Fig. 16–1. Jucunda, the oldest commercially grown strawberry in the Northern Hemisphere, originated in the 1850's, seeds slightly raised, rather glossy, the easiest of all to cap.

most other varieties very quickly. Auchincruive Climax for general market and Royal Sovereign for early fruiting and highest flavor became standard.

A little breeding work was being done inside England at this time, at first simply in an effort to originate better varieties; an effort which later became directed to the production of varieties that were resistant to red stele and tolerant to virus diseases. Sir Rowland H. Biffin, Professor of Agricultural Botany at the School of Agriculture, University of Cambridge, crossed Ekey (of the United States) x Royal Sovereign and in 1937 released the Early Cambridge, which was notable for its vigor and resistance to the red stele root rot. Though still grown, it is no longer an important variety, except as a parent. D. Boyes, who succeeded Sir Rowland Biffin, was Director of the Cambridge Research Station from 1930 to his retirement in 1951, bred many successful vegetable varieties, especially of Brussels Sprouts. He started breeding strawberries about 1930 and was the originator of numerous varieties, including the Cambridge Favourite, Cambridge Vigour, Cambridge Prize-

Fig. 16–2. Jucunda, a very old, very easily capped variety, used in freezing for preserves and ice cream topping, though far from ideal for such use.

winner, Cambridge Rival, and others, which together made up 80 percent of the commercial crop of England in 1962. By 1953, of the 42 selections of Boyes' that were tested by the trade, 20 were named; No. 42 being named Cambridge Favourite. Boyes, as did Laxton and Reid, notably appreciated the need for hardiness. Consequently, he used many American varieties in his breeding, especially those of A. F. Etter and of the U.S. Department of Agriculture.

About 1950, Auchincruive Climax plants began to turn yellow with "June yellows" or "variegation." An attempt to obtain non- or slow-sporting stocks was made, but none proved available and the variety was lost. Reid then named Talisman (introduced 1955) and Redgauntlet (introduced 1956–1957), both of which are resistant to red stele, with Talisman the more resistant. Tests by this time were showing which of the Cambridge varieties were best and virus-free stocks were soon obtained and propagated. At present about 80 percent of the acreage consists of the Cambridge varieties, 15 percent of the Reid varieties, and 5 percent of others, chiefly of Huxley (Ettersburg 80) near Wisbech only, and a little of Royal Sovereign. The acreage planted to Merton Princess, released in 1956–1957, and bred by Hedley Williams, is said to be increasing somewhat. For freezing, Talisman, Cambridge Vigour, and Cambridge Prizewinner are satisfactory. For jam, Talisman, Redgauntlet, and Early Cambridge seem preferable.

The Cambridge Varieties

Cambridge Favourite (34–4–5) [(Etter seedling x Avant Tout) x Blakemore]. (*Plate 16–1b*) The plant is vigorous, very resistant to mildew, subject to "green petal" virus; streaky-yellows have been seen in it. The berry is large, maintains its size well, and is of medium red, firm flesh, and good flavor. It caps fairly easily, travels well, and is productive. It produced about 70 percent of crop of England in 1962.

Cambridge Vigour [US–3378 (Aberdeen x Fairfax) x Early Cambridge] (*Plate 16–2c*), is large, most resistant to red stele of all, very subject to Verticillium wilt, sensitive to drought, and has some variegation. The berries are large, run down in size, are very attractive light red, of firm flesh and good flavor; it caps fairly easily, early to midseason, and is fairly productive. The crops are early and heavy on maiden plants, so it is preferred in cloche culture. It produced 20 percent of the crop of England in 1962, and less now.

Cambridge Prizewinner [Early Cambridge x Howard 17 (Premier)]. The plant is vigorous and productive; the berry is of medium size, bright light red, runs down in size, is soft, of fairly good flavor, caps easily, and is early. It produced less than 5 percent of crop of England in 1962.

Cambridge Rival (Dorsett x Early Cambridge). The plant is tall, susceptible to Verticillium wilt, and productive. The berry is large, glossy bright crimson, fairly firm, sweet and rich, caps fairly easily, and is early to second-early. It produced less than 5 percent of crop of England in 1962.

Some other varieties and their parentage:

Cambridge Aristocrat (Fairmore x Early Cambridge)
Cambridge Early Pine (34–4–5 x Blakemore)
Cambridge Epicure [Early Cambridge x (Euresko x Ettersburg 121)]
Cambridge Forerunner (Early Cambridge x Bellmar)
Cambridge Late Pine (34–4–5 x Fairfax)
Cambridge Premier (Royal Sovereign x Blakemore) x Euresko x B–15 (a U.S. variety x Royal Sovereign)
Cambridge Rearguard (34–4–5 x Northstar)
Cambridge Regent (Fairmore x Royal Sovereign)
Cambridge Sentry (Dorsett x Early Cambridge)

Hedley Williams, who was an assistant to Boyes, was transferred to John Innes Institute where he has continued to breed strawberries. In 1956–1957 he released Merton Princess, a seedling of Royal Sovereign (*Plate 16–1a*), which is very large, light red, rather soft, and is a home garden variety of fair flavor. Williams is also seeking general red stele resistance, is breeding everbearing varieties, is testing sib-crossing and other limited inbreeding, and is working with *Potentilla*-strawberry hybrids.

Scotland

The strawberry industry in Lanarkshire began about 1870 and by 1880 developed into a boom that lasted until about 1910. In 1908 there were 1,439 acres (the peak) and in 1927 there were 1,193 acres in Lanark and 300 in Perth, with 2,670 acres in all of Scotland. Popular varieties before 1920 included Overton (Dunbarton Castle), Scarlet, Queen, Bedford Champion, Leader, Laxton, Paxton, President, Lexington, and others. There was a constant succession of introductions and many, if not most, growers had several varieties. The variety most widely grown during the 1920's was the John Ruskin, introduced about 1900, a very early, firm, dark, small, fair-flavored variety liked for jam. Then the red core (red stele) disease became all important, making necessary the breeding of resistant varieties. From about 1938 to 1950, several Auchincruive selections were grown; from 1950 to 1956 Auchincruive Climax was almost exclusively grown, and since 1956 the Redgauntlet and Talisman have been the chief varieties. In 1962 the crop in all of Scotland was 1,671 acres, with the greater part in the counties of Angus (446 acres), Perth (340 acres), Lanark (272 acres), and East Lothian (259 acres).

Although a few crosses were made in 1928–1929 and a few hundred seedlings grown, practically all of the strawberry breeding in Scotland is the work of one man, Robert D. Reid. In 1930 at the West of Scotland Agricultural College at Auchincruive, Reid began his work on the diseases of strawberries. This work was made a part of the Scottish Horticultural Research Institute in 1951. When Reid began his work, a root trouble, which had been first recorded in the Clyde Valley in 1921, was becoming widespread and it was identified as the fungus disease, red core, caused by *Phytophthora fragariae*. In a test of varieties, one was found to be resistant to the disease. This little-known variety named Frith had been found in 1918 as a strawberry seedling at Cudham, in Kent, near a Royal Sovereign field and where Givon's Prolific was said to have been grown. In 1933 Reid began systematic crossing with it as one parent to obtain more desirable resistant varieties. His selections—Auchincruive 1, 2, 4, 5, and 6—were planted in infected soil in 1934 and remained free of the disease until 1939 when slight infection was found. In 1938 A.M. Sutherland joined Reid and has assisted him since. In 1941 there was a collapse of selected resistant plants in two fields. In later years similar breakdowns of resistance occurred in other kinds, following their selection for resistance, indicating the appearance of new races of the fungus to which the selections were not resistant. Up to 1948, the numbered Auchincruive selections were the mainstay of the Scottish industry.

In 1938 the Aberdeen was imported from America and in 1939 a cross of TD-8 [CC-6 O.P. (Frith O.P.)] x Aberdeen was made and seedlings grown, from which the Auchincruive Climax was selected. It was introduced in 1947 for its resistance to red stele and its other good qualities. Reid found the qualities of the Aberdeen to complement those of Frith. Auchincruive Climax was a remarkable variety, large in size, attractive, high-flavored, productive, late, tolerant of virus diseases, and producing a large second crop in late summer and fall in northern Europe. It quickly became the principal variety of Great Britain and was extensively raised in northern Europe, also in New Zealand, Tasmania, and Australia. In Scotland it stayed relatively free of red core, but in its first test in the United States it was completely susceptible, not being resistant to American strains of the red stele fungus. Unfortunately, it showed some June yellows in 1950 and by 1954 nearly every plant in all fields showed this variegation. With Auchincruive Climax, crop yields reduced rapidly and non-yellowing stocks were not found as they had been with Howard 17 (Premier) and Blakemore in America, and Madame Moutot in Holland.

As Auchincruive Climax began to fail, Reid was already testing selections from his later breeding. Talisman, raised in 1946, was named in 1955 and Redgauntlet in 1956–1957, both from the same cross. Both are resistant to some strains of red core, but Talisman to more strains than Redgauntlet;

both are mid-season to late, firm-fleshed, and very productive. In 1964 another resistant variety, the Templar, was introduced.

Scottish Varieties

Talisman. (*Plate 16–2a*) It is of medium size, has high flavor, is difficult to cap, susceptible to Botrytis, resistant to Verticillium wilt, and mildew. Runners come freely. It is liked in Holland, France, New Zealand, Tasmania, and Australia.

Redgauntlet. (*Plate 16–2b*). It is large, handsome, and ships well; it is only fair in flavor, picks easily, and is least subject to Botrytis. It is liked for the fresh fruit market, being considered too large for best processing. It is grown in Belgium, Holland, France, and New Zealand.

Templar. It is a cross of Auchincruive 11 x Cambridge Vigour, made in 1957, and introduced in 1964. It has a globose to short conic, a large to very large berry, becoming dark red when fully ripe; it is firm, rich, and of slightly acid flavor; produces a late main crop; is resistant to several strains of red core root disease.

- **Redgauntlet and Talisman**
  - **Auchincruive Climax**
    - **TD-8 (CC-6 O.P.) Frith O.P.)**
    - **x**
    - **Aberdeen**
  - **x**
  - **New Jersey 1051**
    - **NJ-674**
      - **NJ-370**
        - **Aberdeen**
        - **x**
        - **Fairfax**
      - **x**
      - **NJ-147**
        - **Pearl**
        - **x**
        - **Howard 17 (Premier)**
    - **x**
    - **NJ-314**
      - **Pearl**
      - **x**
      - **Fairfax**

Parentage of Redgauntlet and Talisman, by percentages:

Aberdeen	31¼%	Howard 17 (Premier)	6¼%
Fairfax	18¾%	Frith, Open Pollinated to	
Pearl	18¾%	F_2—25%	

In 1954 Reid reported having tested 30,111 seedlings from 1943 to 1954 with 7,609 seedlings still under test; 538 selections were still free of red core. From 1954 to 1962 over 102,000 more were tested. Three methods of testing for resistance to red core are used by Reid: (1) Roots of young seedlings are immersed for forty-eight hours in a solution with a suspension of zoospores of the fungus and then planted in vermiculite. After 14 days they are examined for infection. (2) Seedlings are planted in the greenhouse in concrete benches containing naturally infected soils and after 6 to 8 weeks with temperatures below 50° F., the plants were examined and those susceptible discarded. (3) Seedlings are planted in a field which has been infected for over twenty-five years. In field retests of plants from test groups (1) and (2), seedlings are set 3 x 3 feet, allowed to make a group of runners, and kept until fruiting. From crosses made in 1954, 8,314 seedlings were raised and these reduced to 2,755 before field testing. Over a period of several years, the percentage discarded for red core ranged in bench tests from 16 to 54 percent, followed by a further 12 to 44 percent discarded from field tests of those whose susceptibility was not indicated in the earlier test. *F. virginiana* seedlings gave the greatest number of resistant seedlings. Dr. I.G. Montgomerie has been associated in the testing of seedlings for resistance to red core, which has resulted in nine strains or races of red core fungus being isolated. Other sources of resistance to red core were found by Reid. In early tests Oberschlesien and Pillnitz were found the most resistant, and Perle de Prague resistant in a later test. Two plants of *virginiana* and one of *ovalis* have been found immune to the most pathogenic race, and a *vesca* from Jugoslavia has been immune to all so far. By selfing F_1 seedlings from *virginiana* and Auchincruive No. 11, 12 percent and 58 percent of seedlings have been obtained which are immune to some race of red core.

The acreage of certified plants grown for sale indicates the demand for the different varieties. For 1963 this was:

	England and Wales Acres	Scotland Acres
Cambridge Favourite	98	45
Cambridge Vigour	29	8
Redgauntlet	20	15
Huxley (Ettersburg 80)	18	1
Royal Sovereign	12	2
Talisman	8	18
Cambridge Prizewinner	5	0
Merton Princess	4	0
Cambridge Rival	3	0

A.B. Wills, of the Horticultural Research Institute at Mylnefield, has attempted strawberry-*Potentilla* crosses, using four diploid, four tetraploid, and three hexaploid *Potentilla* species with four cultivated varieties, *virginiana, chiloensis,* and *vesca*. He reported in 1963 that Auchincruive Climax x *P. fruiticosa* gave 19 seedlings, two of which were vigorous.

17

Strawberry Breeding and Industry on the European Continent

WHILE BOTH BREEDING WORK and commercial cultivation of the strawberry continued without interruption for a considerable period in England, much of the breeding work on the European Continent is rather recent, some beginning after early work by amateurs and private firms had largely ceased, as in the case of France, and some coming as a first attempt toward the origination of varieties adapted to a particular location, as in Italy. In Germany, continuous breeding dates back a hundred years. Of course, in the past France, Germany, and in fact all Europe, maintained an exchange of advances with England; each benefitting from the other's work, and each helping to stimulate it, but the European industry was to a large degree founded upon varieties imported from England. Now, the Continental industry and much of the breeding work, with only a few exceptions, is based upon varieties originated on the Continent. Introductions from England and the United States have proved of great value as parents, but not many are in commercial use. Royal Sovereign, for instance, is now grown slightly in England and in France, but its present importance on the Continent comes from serving as a parent with Docteur Morère, of Madame Moutot. Redgauntlet, Talisman, Jucunda, Cambridge Favourite, and Cambridge Vigour have been imported from England and are grown in Holland, while Pocahontas, from the United States, and Regina, from Germany, are of some importance in Italy. Regina is also cultivated to a minor degree in France and Holland. Some of the more recent German work has utilized American varieties, namely Sharpless and Sparkle, but Siletz, Sharpless, Pocahontas and to a slight extent Redheart are the only American varieties which have proved at all useful on terms other than those of breeding material. Many of the German introductions are commercially important throughout Europe.

In his article published in 1960, entitled *Basic Principles for Crossing for Long-continued Research,* Dr. Friedrick Gruber called attention to the importance for European breeders of the crossing of European and American varieties and listed some varieties resulting from such crosses:

(1) GREAT BRITAIN: Royal Sovereign, Climax, Talisman, Redgauntlet;
(2) NETHERLANDS: Oranda, Glasa, Juspa;
(3) GERMANY: Oberschlesien, Sieger, Regina, Macherauchs Frühernte, Senga-Sorten, Senga Sengana;
(4) DENMARK: Ydun;
(5) SWEDEN: Indra, Julia;

Others that could be listed are Cambridge Favourite and the other Cambridge varieties of England.

France

Breeders and Varieties, 1900–1965

After 1900 the succession of varieties in France was still largely the result of work by amateur growers of seedlings, rather than that of systematic breeding. Three breeders, however, produced continuous work over a considerable length of time: Louis Gauthier, R. Chapron, and Charles Simmen. Louis Gauthier pursued his work well into the 1900's. He raised the Ville de Caen (Empereur de Maroc x Madame Moutot) in 1922. This variety was firm-fleshed, large, aromatic, and late, but it was subject to mildew and often fasciated. It now has been replaced. Noble from England, Sharpless from America, and Marguerite for main varieties of the early 1900's were soon largely replaced by new French varieties: Sharpless by Madame Moutot, soon after Madam Moutot's introduction about 1910, and Noble in part by various earlies and by Surprise des Halles, introduced in 1929.

Madame Moutot (also called Tomate, La France, Madame Kooi, etc., *Plate 17–1a*), was originated by Charles Moutot, gardener to M. Vanderbilt of Poissy. It came from the cross Docteur Morère x Royal Sovereign in 1906. Although it has great varieties in its ancestry, some like British Queen and Royal Sovereign of the highest flavor, it is of ordinary flavor in most of the areas where it is grown. Madame Moutot is still the most grown variety in France (60 percent) and in several other countries of Europe because of its size and productiveness, but it is being replaced widely by Senga Sengana, especially in the north, and to some extent by Cambridge Favourite and Talisman.

A really fine advance came when Guyot of Dijon raised Surprise des Halles (*Plate 17–2b*) about 1925 and introduced it in 1929. Surprise des Halles is the most cultivated early variety of France today (18 percent of total acreage) because of its earliness (twelve days before Madame Moutot), its rather large, fairly firm fruit, and its very productive plants. The plants, however, are subject to leaf spot. It is reported to be replacing Ladette in southeast France.

The work of R. Chapron of Caen resulted in a number of varieties, among them in 1930 the variety Fertilité, a cross of Empereur Nicolas x Leader. It is grown locally in the Paris area in Brittany, but is decreasing in importance. Chapron's Ville de Paris, originated in 1929, is not now productive and is passing out of cultivation. His Sans Rivale (1937, General de Castelman x Madame Raymond Poincaré) is now the leading everbearer of France. It is vigorous, very everbearing, large and of good quality. Madame Poincaré, one of the parents of Sans Rivale was St. Joseph x Lucie Boiselet, obtained in 1930. It is subject to leaf diseases. Chapron's Reine des Précoce (Madame Moutot x Noble, 1937) was a very early forcing variety.

In the Brest region, J. Le Gall originated the Général de Gaulle, a cross of Reine de Précoce x Fertilité, made about 1940 and introduced about 1947, that is a locally adapted, early variety, sensitive to virus and having only average flavor.

Charles Simmen of Montmorency, France, has been primarily interested in breeding everbearers. His Record, originated in 1931 (a non-everbearer x La France Pacifique) is an everbearer with exceptional vigor and very large fruit. He has introduced several varieties with musky flavor: Muscade (Tardive de Leopold x Madame Moutot), originated about 1940 but not very productive, and Hercule (Record x Muscade) about 1946. Hercule is very resistant to leaf spot, has large fruit of excellent flavor, but it not very productive. It bears a small second crop. Saint-Jean, which was introduced in 1945, was a rather unproductive everbearer said to be a cross of the musky *moschata* with an unknown variety. Regal is an early, aromatic productive sort obtained in 1936, but not attractive. Précose Musquée, a descendant of Muscade, was originated about 1950. It is very subject to mildew, but has a very musky flavor and fragrance. It is a home garden variety.

The Strawberry Industry

In recent years the strawberry crop of France has averaged about 22,240 acres (9000 ha) with an annual production of about 43,000 tons. The chief production areas of France are:

Moselle (East)	25%	Massif (Central)	8.0%
Vaucluse (Southeast)	16%	Loire Valley	4.0%
South West	15%	Paris area	3.5%
Rhone Valley	12%	Other areas	5.5%
Finistere (Brittany)	11%		

Before the last world war production was below 20,000 tons. Along with the increase in production there has been a decrease in export (22 percent in 1949 to 3 percent in 1960) and an increase in import.

Present varieties and the percentage each composed of the total acreage grown in 1963 were:

Madame Moutot	60.0%	Général de Gaulle	4.0%
Surprise des Halles and Ladette	18.0%	Fertilité	1.0%
Royal Sovereign and Gauthier	9.0%	Reine de Tardive	0.5%
Saunier (St. Geniez)	7.0%	Sieger	0.5%

Others grown slightly are Souvenir de Charles Machiroux, Talisman, Tardive de Leopold, and Vicomtesse Héricart de Thury; of the everbearing, Sans Rivale, Saint-Claude, Record, and Profusion; and of the *vesca,* La Brillante and Reine de Vallées (Alpine).

The official catalogue of strawberries for France recommends only four varieties: Cambridge Favourite (English), Madame Moutot, Surprise des Halles, and Talisman (Scottish), for main crops, and Sans Rivale for everbearing. Eighteen other non-everbearing and eight everbearing are in Class 2 (those of local or of special interest) and include for the non-everbearing:

Fertilité (Empereur Nicolas x Leader), grown near Paris
Général de Gaulle, grown near Brest
Hercule (Record x Muscade), for gardeners
Huxley (= Nouveau Morére) (= American Ettersburg 80)
Ladette, early, being replaced by Surprise des Halles
Louis Gauthier, white, for amateurs only
Major
Pocahontas (a recent American), general culture
Reine de Carpentras
Saunier (Vicomtesse de Saint-Geniez), local in Lot Valley
Souvenir de Charles Machiroux (Belgian) (Tardive de Leopold x Ville de Paris), very large, general market
Supermonstrueuse Hative, an early
Surprise Vaucluse, early local at Vaucluse
Tardive de Leopold (German), female, very glossy, decreasing
Triomphe de Tihange
Vicomtesse Héricart de Thury, too small, not productive now
Ydun (Danish) (Tardive de Leopold x Deutsch Evern), productive, large, not high flavored

Madame Moutot is still the most widely grown variety in France because of its productiveness, large size, and its good growth, but it is often misshapen, poorly colored, not of high flavor, and not suited for freezing and jam, although so used. Its plants are subject to variegation. Surprise des Halles is grown because it is early and produces best of early varieties, but its flavor is inferior to that of the early Glasa and Senga Précosa and its size in the later pickings is small. Cambridge Favourite, a relatively new variety but the chief one of England, ripens with Madame Moutot. It is large, orange-red, caps easily, is fairly firm, a good shipper, and good in flavor. Talisman, a new variety of Scotland, is large, bright red, a fairly good shipper, hard to cap but a good processor, and late. Resistant to red stele, Senga Gigana (the very large new German) was the most productive and most promising in southern France trials.

Present Breeding Work

Official breeding work at present is carried on only at the Vaucluse Station at Montfavet by Miss Georgette Risser. It is directed toward obtaining an early variety adapted to the Montfavet region with its mild winters. A study of factors for earliness includes attention to the time of initiation of flower buds in autumn, the effect of winter cold on the development of inflorescences, their development in the spring, and the period from flowering to ripe fruit. Other work includes studies on methods of selecting varieties for intensive culture. Seed is sown in the greenhouse in March after treatment with sulfuric acid, and the seedlings are set in June so that they can each make at least six runner plants, considered a minimum for study of the fruit characters and of their susceptibility to mildew, leaf spot and botrytis. The next year the seedlings finally selected are planted in three plots of nine plants each, on three separate planting dates. Yields are obtained and the selections are compared in these plots. The first stage of selection is the most difficult because of the number of seedlings to be judged and the many characters to be observed. Successive elimination after noting each character is practiced. From 15,000 intervarietal hybrids since the start of the breeding work, 22 were tested for yield and one early and one late were considered worth further tests. Inbreeding decreased seedling vigor in the I_1 and further inbreeding depressed vigor still more, so that fruit qualities could not be evaluated. Crossing I_2 and I_3 showed seedlings much more uniform than those of crosses between two varieties, making possible a study of inheritance of earliness and production.

In a study of factors that might affect the yield of selections in tests, virus-free plants for the first two crops yielded 126 percent more than virus-infested ones; plants set August 22 yielded 140 percent more than those set September 29; and a stand of 47,750 plants per acre yielded 77 percent more than a stand of 19,300 plants per acre.

A comparison of six early varieties set October 4 in cold frame culture showed Surprise des Halles as 70 percent more productive than the next, Deutsch Evern, but less attractive and less highly flavored than Glasa and Senga Précosa (G. Risser, 1963).

Non-everbearing varieties of strawberries registered in the catalogue of species and varieties, their identification and their description, Ann. Amelior, Pl. 1962, 142 pp., Brossier, J.O. This notable study, begun in 1953 at Versailles and continued at Montfavet in 1959, reports on observations for seven years on 53 varieties and includes keys for identifying varieties. It has been followed by a supplement by G. Risser (1963) with a description of 16 other varieties.

Germany*

It is said that George II, King of Hanover, introduced the first large-fruited strawberries to Germany in 1751. Before that time no *ananassa*-forms were known; instead other species, mainly *Fragaria moschata* were cultivated. Some varieties of these species were grown even until the end of the 1930's in old growing areas, for instance "Vierlander Strawberries," but all varieties grown in Germany before 1870 originated in France and England.

The first German-bred varieties were introduced by Gottlieb Goeschke (*Fig. 17–1*), Köthen (Saxony-Anhalt), about 1870. Of the more than 20 varieties which he bred in the following years, the Hohenzollern and König Albert von Sachsen were known until the early 1950's. Beginning in 1902 Franz Goeschke (*Fig. 17–2*), son of Gottlieb Goeschke, continued the work until 1912 and produced about 30 varieties, of which Königin Luise (1905), Roter Elefant, Panther, Zarathustra (1926), Osterfee (1917), and Amazone were cultivated until the end of the 1950's.

These two, father and son, were comparable to Laxton and the Laxton Brothers of England. The father, Gottlieb, was the owner of a nursery in Köthen and did his breeding there. His more notable varieties were mostly those for amateurs. The son, Franz, was director of horticulture and lecturer at the horticultural school at Proskau. Königin Luise and Osterfee were widely grown commercially.

The introductions of Johannes Böttner *(Fig. 17–3)*, a well-known nurseryman at Frankfort, Oder, were also important. The author of *Gardening for Beginners,* from 1866 on he was editor of the magazine *Practical Advisor for*

* By W. H. J. Hondelmann.

Fig. 17–1. Gottlieb Goeschke (1818–1898), horticulturist at Köthen, the first strawberry breeder of Germany.

Fig. 17–2. Franz Goeschke (1844–1912), Royal Horticultural Director at Proskau.

Fruit Growing and Horticulture. His strawberry introductions began about 1897; his two most famous varieties being Sieger (1897) and Deutsch Evern (1902). The latter became the most important early variety of Germany and adjacent countries for the next five decades. Some other varieties originated by Böttner were: Aprikose (1897), Rotkäppchen (1910), Sauerling (1913), Flandern (1916), and Masuren.

Beginning in 1919 varieties originated by Prof. O. Schindler *(Fig. 17–4)* at Pillniz (Saxony) became very important. Until the end of the last war his Oberschlesien (1919) was a most notable variety for its high yield and its wide

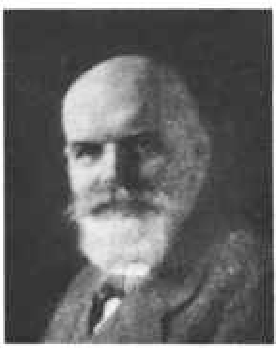


Fig. 17–3. Johannes Boettner (1861–1919), horticulturist and Horticultural Editor at Frankfurt/Oder.

Fig. 17–4. Prof. Dr. Otto Schindler (1876–1936), Director of Horticultural Experiment Station at Pillnitz.

adaptability. Frau Mieze Schindler (1933) was very popular in home gardens because of its excellent flavor and good fruit quality. Schindler's varieties Johannes Müller, Herbstfreude, and Mathilde should also be mentioned.

Besides these varieties, French varieties played a significant part. The most important has been Madame Moutot, which for several decades was widely grown in the Rhineland and Southern Germany, and, in some old growing areas, even until the present, along with Madame Lefebre. Some varieties of other German breeders also came on the market, for instance (1904) Späte von Leopoldshall by E. Lierke, which was a notable variety with its late ripening season, and (1905) Hansa, originated by Buhk (Vierlanden near Hamburg). In the 1930's varieties produced by the nurseryman O. Macherauch and by P. Krechen deserve mention; Eva Macherauch was produced by the former in 1931 at Legefeld, near Weimar, while Prinz Julius Ernst was originated by Krechen in 1935 at Oberkrassel. During the second part of the 1930s at the Kaiser-Wilhelm-Institut fur Züchtungsforschung in Müncheberg (now Max-Planck-Institut fur Züchtungsforschung, Köln-Vogelsang) crossings were made, with the aim of producing new varieties for the early ripening season. Two early varieties resulted: Regina, which was introduced by the Fey nursery at Meckenheim near Bonn in 1951, and Macherauchs Frühernte, which was introduced by O. Macherauch also in 1951. Since 1948 at the Institute an objective has been the production of decaploids (Bauer), of which various types are existing. Macherauch later introduced the varieties Macherauchs Dauerernte, an everbearer (1956), Macherauchs Späternte, an extremely late ripening variety (1957), and Macherauchs Marieva (1962) a midseason one. In 1942 the variety Georg Soltwedel was introduced by the breeder, a nurseryman of same name, at Deutsch Evern near Lüneburg.

A development, comparable to the breeding at U.S. experimental stations, arose in Germany in 1942, when Prof. von Sengbusch began to breed varieties, to meet the specific demands of the industry for freezing, which had developed at that time. The first results of breeding were introduced in 1951 as Senga-numbered-varieties, e.g., Senga 29, Senga 54, Senga 188, etc. All these varieties were replaced by the all-round variety Senga Sengana in 1954. From that year the strawberry work of von Sengbusch was continued at the Sengana GmbH., and the lines of breeding have been enlarged. In 1960, Senga Precosa was introduced as a very early ripening variety and in 1963 Senga Gigana, as a very large-fruited variety.

Some varieties of other breeders in recent years should be mentioned—the Direktor Paul Wallbaum (by K.P. Thiele, Hanover) (1953), and Lihama (1960), Asieta (1960), and Vigerla (1963) (by M. Etscheidt), which were introduced by various nurseries.

From the beginning the everbearers were of importance for home gardens. The more important everbearers of recent years are, Ada Herzberg (1942), Heinemanns Unerschöpfliche (1943/44), and Herzbergs Triumph (1942), by G. Herzberg at Wefensleben, and Hummi Trisca (1961) by R. Hummel in Stuttgart.

Since the early 1950's the variety picture in Germany has been changed in character. Patented (copyrighted) varieties, "Hochzuchten", are becoming more important. For the encouragement of breeding new valuable varieties of crop plants, protection of variety is granted under certain conditions. In this way the breeder's title to his variety is protected and his private initiative is promoted. On the other hand the customers for seed and clone material, farmers and horticulturists, are protected from poor quality and untrue seed or clonal material. In 1953 a seed law was enacted for this purpose. Strawberries were not included. As similar regulations were needed for the private strawberry breeders and as biological protection was impossible because of its vegetative propagation, a system of propagation and distribution according to civil law was established, mainly at the initiative of Dr. R. von Sengbusch. It has been in operation successfully for about 10 years. Several legal steps are taken to guard the title of a variety; these involve a standard agreement for propagation and distribution and the obtaining of a licensed title, by which the costs of breeding are paid. Specifically, the following is done:

(1) Protection of Variety. Patents can be given for strawberry varieties. The variety name can be protected by trademark, and the design of package (in the case of commercial marketing) can be secured by legal protection. The law against unfair competition is used in general jurisdiction. Finally, the breeder is protected by Art. 14 of the constitution, which safeguards property, in this case intellectual property.

(2) System of Propagation. The breeder enters into agreements concerning propagation with nurseries, farmers and so on, and only such firms are allowed to propagate the variety. Propagators are subject to fixed conditions, to keep the quality of plant material on a high level in accordance with the seed law. The breeder maintains the original stock. From this stock "Elite-plants" are sold to propagating firms, who propagate the "Elite" material once only to "Hochzucht," (highly selected) which is sold to customers. At all levels of propagation, that of the breeder as well as that of the propagating nurseries, the plants are tested by the agricultural department. All certified plant material is labelled.

(3) System of Distribution. The breeder makes license agreements with distribution firms, chosen by him and only these are allowed to offer and sell plant material. The licensed firm is obligated to sell only certified plant material. In most cases rights for propagation and rights for distribution are

given to the same nurseries. Breeders have in nearly all cases made a price maintenance agreement with reference to anti-trust law. All licensed nurseries therefore sell at the same price. They settle accounts for license with the breeder twice a year.

In other European countries somewhat similar systems are exercised so that by international trade marks and agreements with a general representative of other countries, the distribution of a variety is under control. Before a new copyright variety is released, it is tested by the Federal State Variety Office to ascertain whether it actually is a new variety.

Copyrighted varieties are: Asieta, Direktor Paul Wallbaum, Georg Soltwedel, Hummi Trisca, Lihama, Macherauchs Dauerernte, Macherauchs Früherernte, Macherauchs Marieva, Macherauchs Späternte, Regina, Senga Gigana, Senga Précosa, Senga Sengana, Vigerla.

The principal strawberry varieties of the Federal Republic of Germany based on percentages of the commercial acreage in 1963 are:

	Variety	percent
1	Senga Sengana	56
2	Senga Precosa	10
3	Oberschlesien	8
4	Regina	6
5	Madame Moutot	6
6	Macherauchs Frühernte	3
7	George Soltwedel	2
8	Direktor Paul Wallbaum	1
9	others[1]	8
	total	100

1 These include: Macherauchs Dauerernte, Macherauchs Späternte, Macherauchs Marieva, Lihama, Hummi Trisca, Asieta, Gartenbaudirektor Meymund, Ada Herzberg, Herzbergs Triumph, Sieger, Hansa, Deutsch Evern, Frau Mieze Schindler, Madame Lefèbre, Ydun, Talisman, Redgauntlet, Gorella, Siletz.

Foreign varieties have been tried on countless occasions and a few have been grown for some years, but none of the newer introductions reached an importance comparable with the old Madame Moutot, though all were *unpatented varieties.*

Among such should be mentioned are: Auchincruive Climax, Talisman and Redgauntlet (all from Scotland), Cambridge Favourite, Cambridge Late Pine (both from England), Ydun and Xenion (both from Denmark), Siletz (from Oregon, U.S.A., the only U.S. variety with satisfying yield in Germany), Gorella (from the Netherlands).

The heaviest-producing areas are indicated on the map of Germany (*Fig. 17–5*).

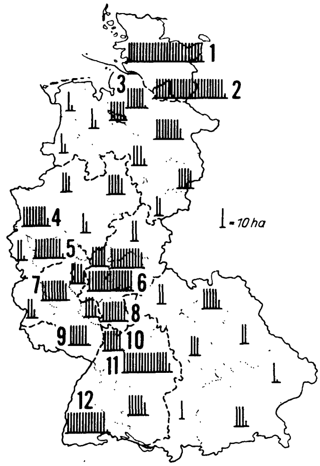


FIG. 17–5. Strawberry growing area in western Germany in 1964.

Description of German Strawberry Varieties*

IMPORTANT VARIETIES

Senga Sengana (1954, *Plate 17–2c*). This early mid-season variety has good flavor, a hardy plant, and great adaptability. It is grown commercially for fresh market and especially for processing (deep freezing, canning, jam etc.), as well as for home gardens. It is grown not only in Germany, but in all north-central and north-western Europe, and to some extent further south. Though Madame Moutot is still most grown, Senga Sengana is rapidly becoming the most important European variety.

Fruits are large to medium, blunt conic to heart-shaped, dark red, firm flesh; medium acid, good capping quality, has averaged about 30 percent greater yield than the next German variety over three-year periods, and over 100 percent greater than the old variety Oberschlesien, in ten field trials (1952–1956). It is resistant to mildew, verticillium and insect infections, but susceptible to botrytis (Copyrighted).

Senga Precosa (1960, *Plate 17–2a*). This variety is very early ripening, three to four days earlier than Regina and Macherauchs Frühernte and mainly grown for the early season in south and south-western Germany. Its berries are light to medium red, blunt conic, medium firm, and sweet; it is not so susceptible to mildew as other early varieties; its capping quality very good, and its yield medium (Copyrighted).

Regina (syn.: Brandenburg, 1951). Macherauchs Frühernte and Regina replaced Deutsch Evern as the standard early varieties until the introduction of Senga Precosa. Regina ripens about two days before Deutsch Evern; it is medium in size, light to medium red, and medium firm; its flavor is good,

* Parentage of German varieties appears in the appendix, Section V.

sweet to subacid; it is productive for an early variety, but is susceptible to mildew, and the very early blossoms and even the flower buds are endangered by late frost (Copyrighted).

Macherauchs Frühernte (syn.: Müncheberge Frühe, 1951). This variety has the same parentage as Regina and has about the same qualities: medium large, soon becoming smaller, glossy, medium red, and blunt conic; its flowers are not so susceptible to frost as Regina's, but infection with mildew is much more severe than with Regina (Copyrighted).

Georg Soltwedel (1942, *Plate 17–1b*). This midseason variety had wide distribution in the late 1940's and was preferred for fresh market; it has good flavor, glossy, bright red, large, wedged or blunt conic fruit; its first fruits are very large and irregular in shape; it is susceptible to red spider, and is high in ascorbic acid (Copyrighted).

Direktor Paul Wallbaum (1953, Pistillate). This is a late ripening berry of Mieze Schindler type and grown for its lateness and its good quality; it is medium red, large, rather uniform conic to round; its flowers are susceptible to frost, but the plants are hardy. This variety gives a medium yield (Copyrighted).

Oberschlesien (1919). This variety is medium late, and was the highest yielding variety for commercial growing until the early 1950's. Due to its good adaptability it was widely grown; its flavor is just passable; its berries are large to very large, medium red, uniform blunt conic shape, the first fruits being broad and wedged. For several decades previous to 1950, it was widely used for processing purposes and is still an important variety.

Other Varieties

Frau Mieze Schindler (1919, Pistillate). This is a notable older, late ripening variety; it is grown because of its good flavor; its fruits are medium size, round to kidney shape, deep red, firm; it is hardy but not productive; it is susceptible to *Mycosphaerella*.

Sieger (1898). This is an early variety, three to four days later than Deutsch Evern. Because of its sweet aromatic flavor it was popular for commercial and amateur growing, mainly in early growing areas; it shows higher yields than Deutsch Evern; its berries are light red, medium to large, round, and very soft. Its yield is only medium.

Deutsch Evern (1902). Until the introduction of Regina and Macherauchs Frühernte, this variety was the standard early variety of northern Europe; and still is a major variety for forcing under glass (*Plate 17–1d*); its berries are long conic, light red, medium to small; its early blossoms are sometimes endangered by frost; it is susceptible to mildew.

Hansa (syn.: Schwarze Ananas, 1905). This is a mid-season variety, which before introduction of Senga varieties, was the best variety for preserving; its fruits are medium sized, round to broad round, dark brownish red, and rather firm, mildly subacid.

Asieta (1960). This is a medium late type, whose fruits are large, blunt conic to broadly round and wedged, deep dark red, very firm, and acid; it is susceptible to *Diplocarpon* (Copyrighted).

Macherauchs Marieva (1962). A medium early variety, this possesses fruits which are blunt conic, red, medium large, medium firm, and aromatic; it is susceptible to red spider and less susceptible to mildew, mites, and nematodes (Copyrighted).

Lihama (1960). This early variety has berries which are dark red, medium size, blunt conic, acid to subacid; it produces a good yield; it is susceptible to *Mycosphaerella* (Copyrighted).

Macherauchs Dauerernte (1956). An everbearing type that resembles "Heinemanns Unerschöpfliche" in many ways; this variety is blunt conic, medium to dark red, subacid, and aromatic; it is susceptible to *Diplocarpon* and red spider and nematodes (Copyrighted).

Ada Herzberg (1942). This is an everbearing sort, similar to Mieze Schindler; its fruit is subacid; its yields are good for an everbearer, but about 30 percent lower than Junebearers; it is susceptible to *Mycosphaerella, Diplocarpon,* and red spider.

Hummi Trisca (1961). This is an important everbearer because of its large fruits, which are blunt conic, wedged, medium red, rather firm, and subacid; it is best adapted to southern Germany; it is susceptible to nematodes (Copyrighted).

Macherauchs Späternte (1957, Pistillate). A late ripening type, this form has berries medium red to red, often *cat-faced* because of non-pollination of its female flowers; it is susceptible to mildew (Copyrighted).

NEW INTRODUCTIONS OF 1963

Senga Gigana (*Plate 17–3b*). This is an early midseason type whose berries are extra large (average weight 30 grams, first fruits up to 55 grams), which is grown for fresh market and home gardens; its fruits are highly glossy, medium red, long conic, very attractive, medium firm, mildly subacid; it has a high yield, exceeding Senga Sengana in the first cropping year; it is susceptible to Botrytis but is resistant to other diseases; it prefers the drier soils (Copyrighted).

Vigerla. This is a medium early ripening variety with fruits, long conic, primaries wedged, bright medium red, medium sized, firm flesh, and subacid; it has high yield, and good capping quality but is susceptible to mildew (Copyrighted).

The Sengana Story*

In 1942 Dr. R. v. Sengbusch contacted the newly developed deep-freezing industry, which was looking for vegetable as well as strawberry varieties suited to its purposes. None of the varieties grown at that time, so it seemed, met freezing requirements. With the financial support of Messrs. Andersen & Co., a sub-company of Ph. F. Reemtsma, strawberry breeding was started at Luckenwalde near Berlin. First v. Sengbusch tested the varieties used in the canning industry. One of these, named Markee (after the German village where it was grown) had an extremely firm flesh and kept its shape very well after thawing, but it was unsatisfactory in flavor and yield. This variety was crossed, therefore, with some well-flavored European varieties.

In 1944 an F_1 generation of about 40,000 seedlings was planted to be used for selection. All plants weak or poor in yield were discarded. Then the berries of the about 10,000 remaining single plants were tested for deep freezing at −20°C. About 1500 were found to be good and were propagated in clones. In 1945 the first clones were tested. In order to extend the basis of selection, the selection work was done at three different localities:

1. At the project center at Luckenwalde, in a 3 ha. (ha. = 2.47 acres) breeding field.
2. At Glienicke with about 1.5 ha. on a very light sandy soil.
3. At Barby (Elbe) with 1 ha. on heavy loamy soil.

Testing was very difficult because of the war. Luckenwalde itself was occupied by the Russian army in April, 1945, and the first testing of the clones was done under the Soviet-Russian soldiers' eyes. Even so, v. Sengbusch was able to select the numbered varieties 29, 54, 145, 188, and 242 from among the clones grown that summer. Since it was, of course, impossible to keep exact records of yields, simply the number of pickings was marked on labels, to obtain some records. By this method the high cropping of Senga 54 was noted in the first test year.

In 1948 transfer of the breeding material to Hamburg was started. Andersen & Co. arranged an experimental field at Wulfsdorf, just behind the Hamburg State border, to test the clones for freezing. In these tests Senga 29 and Senga 146 proved to be the most suitable. In the meantime the freezing industry was stopped as a consequence of the end of war and breeding work had to be directed to new objectives.

From 1950 on the emphasis was upon selection of types which had high market value. The aims were: high yield, good disease resistance, sufficient

* By W. H. J. Hondelmann.

quality of berries, and above all, plants suitable for general cultivation. In 1949 there was a very heavy infection by mites (*Tarsonemus pallidus*). Since successful control of mites was not yet possible, all but three clones became stunted. These three were from the cross Markee x Sieger. In the second cropping year these three averaged over 5,000 kg. per one-fourth hectare. The heaviest bearer of these was propagated and half a hectare was planted in 1953. One year later it was introduced under the trade mark Senga Sengana.

In the same year, 1954, v. Sengbusch founded the Sengana GmbH. This company, of which v. Sengbusch became president, took over the strawberry work, especially the distribution of newly bred varieties. In 1955 Gerhard Mellenthin joined the company, and later he became head of the propagation and distribution section; in 1959 Walter H.J. Hondelmann joined and is now head of the breeding and research section. Greenhouses are available for crossing (*Plate 17–3a*). The breeding fields of Sengana GmbH now occupy seven hectares, the plantations for propagation sixty hectares; the first year of propagation is for runner production, the second and third for berry production.

It soon became obvious that breeding strawberries with no support by industry or state was only possible by procuring a license and even this could only be profitable with a high price for plants. Since the commercial grower, after having bought a new variety, will at once propagate more plants for himself (at least in virus-free locations, such as northwestern Germany)—and this is not liable to license— new breeding objectives were given first consideration. These entailed breeding varieties for the home gardener, who prefers a change of plants and varieties more frequently than do commercial growers. The area set to strawberries in home and other private gardens in Germany is estimated to be twice as great as the commercial area, and is therefore of importance. The commercial area has been 3,000 hectares in the last few years and rather constant, so that the total growing area in the Federal Republic of Germany is about 10,000 hectares (24,700 acres, *Fig. 17–5*).

First results of the expanded work were Senga Precosa (1960), a very early ripening variety, and Senga Gigana (1963, *Plate 17–3*), an extremely large-fruited variety. At present, in the company three breeding lines are being carried on:

1. Varieties for home gardening (private growing)
2. Varieties for fresh market (horticultural commercial growing)
3. Varieties for processing (agricultural commercial growing).

Within these three lines characters needed for growers and consumers may be seen in the following table:

Breeding lines and characteristics

HOME GARDEN (PRIVATE GROWING)		FRESH MARKET (HORTICULTURAL COMMERCIAL GROWING)		PROCESSING (AGRICULTURAL COMMERCIAL GROWING)	
grower	**consumer**	**grower**	**consumer**	**grower**	**consumer**
Different ripening seasons. Large Fruits. Everbearer. Resistance.	Flavor. Consistency of shape and color.	High yield. Different ripening seasons. Suitability for agric. growing. Shipping quality. Resistance. Self fertility.	Shape. Color. Flavor.	High yield. Capping quality. Suitability for agric. growing. Shipping quality. Resistance. Fruit size. Self fertility.	Consistency of shape and color. Uniformity of fruits. Juice keeping quality. Cooking quality. Flavor.

Tests at all levels of selection are continued for two years, since the performance of clones in the first cropping year is not correlated strongly enough with the second year, and the second year is the main cropping year. A sample of one year's work is about as follows:

Fruiting year—20,000 seedlings selected for earliness, yield, everbearing, disease resistance.
Second test —3000 to 4000 selections (in 5-plant clones), selected for yield, size, disease resistance.
Third test —300 selections in 20-plant clones, selected as above, for flavor, self-fertility.
Fourth test —20 selections in 100-plant clones, selected as above, in a triple lattice, in a first propagation.

Since their introduction, the Senga varieties have been maintained true to name. In 1962 the Federal Chambers of Agriculture decided that each new strawberry variety must be maintained on a four-year cycle. It starts with Maintenance A, next Maintenance B, then Super-elite and Elite to "Hochzucht." In each of the levels propagation is made in the ratio 1:10. Three years of running Super-elite is followed by a new Maintenance A in the fourth year. No clone has yet been discarded. The virus test is conducted by grafting on *vesca* indicator plants.

Hitherto no virus has been detected on the propagation fields of Sengana GmbH. This is due to the position of the fields in northern Germany (north and east of Hamburg), where the aphid vector (*Pentatrichopus fragaefolii* Cock.) cannot survive the winters and has not yet been found. This facilitates the breeding work considerably.

Besides the pure breeding, such problems of breeding research are studied as heritability, estimation of important economic traits, correlation between these and estimation of the relation of environmental variance to total genetic variance.

Hondelmann, W. "Investigations on breeding for yield in the strawberry *Fragaria x ananassa* Duch." Zeit. Pflanzenzüchtung 84, 1965. Investigations were carried out on F_1-clones in connection with breeding for yield in the strawberry on the genetic potential, the variety-environment interaction and the inter-relationship between five characteristics which are important for yield.

The genetic potential (as expressed by the genetic variance, the coefficient of variation, heritability in the broad sense and the selection gain (S), is large for yield of fruit as well as for factors of yield: number of crowns, number of inflorescences on a crown, number of individual flowers on an inflorescence and size of fruit.

In the interaction of variety and environment (year and location), the relation of variety to year is the most important.

The relationship between the yield of fruit and the four other corresponding yield factors is analysed by means of the path coefficient method. From this it appears that the number of individual flowers is the most important factor, followed by the size of fruit.

The conclusions for practical strawberry breeding are briefly discussed.

Netherlands

The Strawberry Industry

Since the west European sea climate of Holland has cool summers and mostly mild winters, very hardy strawberry varieties are not considered to be of foremost importance. Frosts occur in early May, so that frost injury to flowers may occur, but the hazard is a minor one. Strawberries are raised chiefly in the southern provinces, one center of production being in western Brabut, south of Breda. The production in 1964 was about 33,000 tons from field culture and about 1700 tons from glass houses. About 50 percent is consumed fresh and 50 percent processed, mainly for jam.

The steady growth of the industry in Holland is seen by the increase in acreage through the past fifty years.

1912— 3000 acres (50 acres under glass)
1927— 5840 acres (55 acres under glass) = 2336 ha.

1938— 6083 acres
1955— 9400 acres (200 acres under glass) = 4088 ha. (93 ha. under glass)
1964—11,525 acres (370 acres under glass) = 4516 ha. (74 ha. in glass houses, 76 ha. frames)

The production in 1964 was about 3.5 tons per acre for fields in bearing.

Irrigation, control of pests and of weeds, and the use of clean plants (virus, nematode, and cyclamen mite-free) have in recent years improved the industry. Most strawberry fields are cultivated under the hill system, and fruit from about June 1 to July 15, while in glass houses and frames ripening starts about April 1 and continues to about June 1 (*Plates 17–5a to e*). Strawberries are grown in both heated and unheated greenhouses and in unheated glass frames (the so-called "Dutch lites"). Cloches (*Plate 17–5b*) are used in home gardens in all of northern Europe.

About 1948 the varieties grown were:

Deutsch Evern, Madame Lefèbre (cold frames and early)
Madame Moutot (late, main crop, tart, not good flavor)
Oberschlesien (midseason, main crop, tart)
Jucunda (late, main crop, preserving, not for freezing)

About 1955 there were four important varieties: Deutsch Evern, Auchincruive Climax, Oberschlesien, and Jucunda. Auchincruive Climax quickly disappeared after variegation appeared. Jucunda was grown for pulping and jam chiefly because it capped well, but its fruit is white inside and its flavor only fair. It is not suitable for freezing or canning.

Present varieties (1964, with an asterisk indicating the five most important) are:

Field culture
  Early—Regina
    Macherauchs Frühernte (decreasing)
  Medium early—Gorella* (for field culture)
  Midseason—Senga Sengana* (for field culture)
    Redgauntlet* (for field culture)
  Late—Talisman
    Jucunda (decreasing)
Under glass—Glasa*
    Cambridge Vigour*
    Deutsch Evern (lessening rapidly)
Best Everbearing—Revada and Macherauchs Dauerernte

Senga Sengana has become the dominant variety for field culture; it produces well, regularly, and has intense red color. Its limitations are that it has an unusual flavor, it is only fairly easily capped, and it is susceptible to Botrytis fruit-rot. It is eaten fresh and is processed. Large quantities are exported to Germany. Processed berries are capped in the field.

Strawberry Breeding

WAGENINGEN. The work at the Institute of Horticultural Plant Breeding was begun in 1946 by Miss Hester G. Kronenberg, assisted by L.M. Wassenaar, with the objectives of obtaining (1) easily capped, good colored preserving varieties; (2) varieties for the fresh market; and (3) everbearing varieties.

For the years 1960 to 1963 about 4,100 seedlings were raised annually and in 1964 about 24,000. Six varieties have been introduced:

Juspa (Jucunda x Sparkle), 1957
Oranda, 1957 (Deutsch Evern x Temple), (little grown)
Gorella (Juspa x US-3763), 1960 (early)
Repita (Ada Herzberg x Auchincruive Climax), 1960 (everbearer)
Revada (Auchincruive Climax x Ada Herzberg), 1960 (everbearer)
Elista ((Jucunda x self) x US-3763), 1964 (everbearer)

The notable characters of the five varieties now grown are:

Gorella (1960) (Juspa x US-3763)—healthy foliage, very large, compares with Madame Moutot, fairly good capping, medium early; susceptible to Verticillium

Juspa (1957) (Jucunda x Sparkle)—good capping, only fair quality, very productive

Repita (1960) (Ada Herzberg x Auchincruive Climax)—fair grower, second crop earlier than Revada. Fruits of fairly good size, bright red, good flavor. Susceptible to *Diplocarpon*

Revada (1960) (Auchincruive Climax x Ada Herzberg)—vigorous grower; fruits light red, brisk subacid, healthy foliage

Elista (1964) (Jucunda x self)—open plant, fairly late. Productive, flesh red, brisk in flavor. Fresh market, capping difficult until fully ripe

In 1952 Miss Kronenberg reported that selfed seedlings of Blakemore, Brightmore, and Temple did not show loss in vigor, but that seedlings of some others did. June yellows showed in Blakemore, Howard 17 (Premier), and Madame Moutot selfed seedlings (Kronenberg, 1952).

In 1955, crosses giving good results, except for flavor, were given as follows:

PLATE 14-1

Electric blender used to clean strawberry seed. The blender is filled about half full of water, the berries are poured in, the current is turned on for 20 seconds, and then the pulp is poured off. The good seed which sinks to the bottom is taken, its surface is dried, and the seed is then stored in a refrigerator until used.

Seedlings of the cross Temple x Midland germinated on sphagnum moss, the largest with two leaves about ready to transplant into flats or greenhouse benches.

Seedlings of Albritton x Ambato planted at a 4′ x 4′ spacing and each is allowed to make a small mat of plants.

PLATE 14-2

100 berries of the backcross of Blakemore x Missionary, each berry from a different seedling, to get the surface color. (1/3 lifesize)

100 berries of the cross Blakemore x Fairfax, each berry from a different seedling and cut to get the color of the flesh. (1/4 lifesize)

PLATE 14-3

Selected seedling of Albritton x Ambato to be used for later breeding.

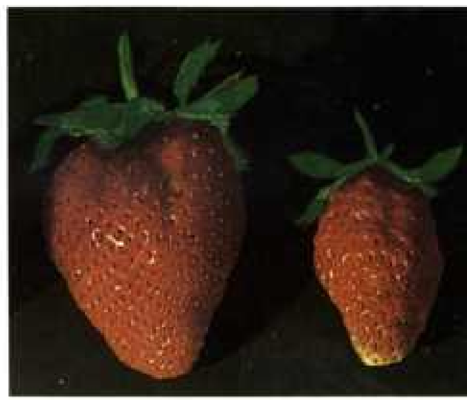
Backcross of U.S. #3563 to Midland. Berry size may often be regained in a single backcross to the variety parent. (See also Plate 8-2.)

F. virginiana #27. A productive pistillate selection of the Virginian from western North Carolina.

PLATE 14-4

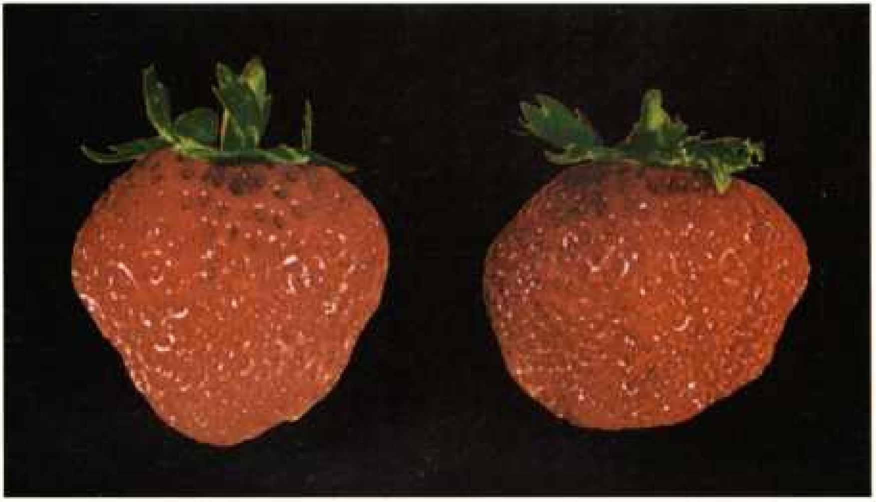
U.S. selection #3563, a first-generation cross of a frost-hardy *virginiana* x Midland. This selection was very vigorous and very productive but small. (See Plate 14-4, center photo, and Plate 8-2.)

Crosses of large with large give large-fruited seedlings. Here Massey (LEFT) x Eleanor Roosevelt (RIGHT) gave this very large U.S.-N.C. #1158 selection.



Selfed seedlings of Eleanor Roosevelt showing the enormous difference in vigor; few were as vigorous as that to the left and very few survived that were as weak as the one to the right.

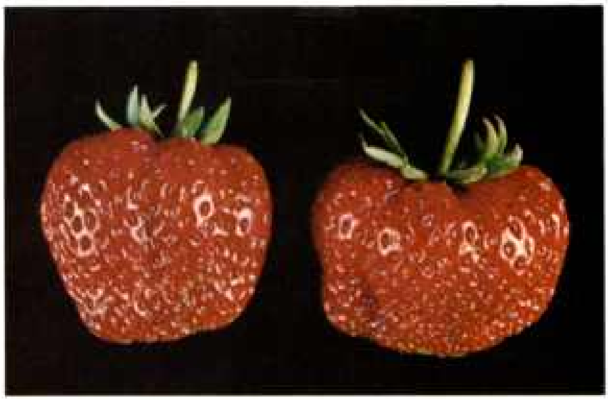
PLATE 14-5



Merton Princess

PLATE 16-1

Cambridge Favourite



Redgauntlet

Talisman

Cambridge Vigour

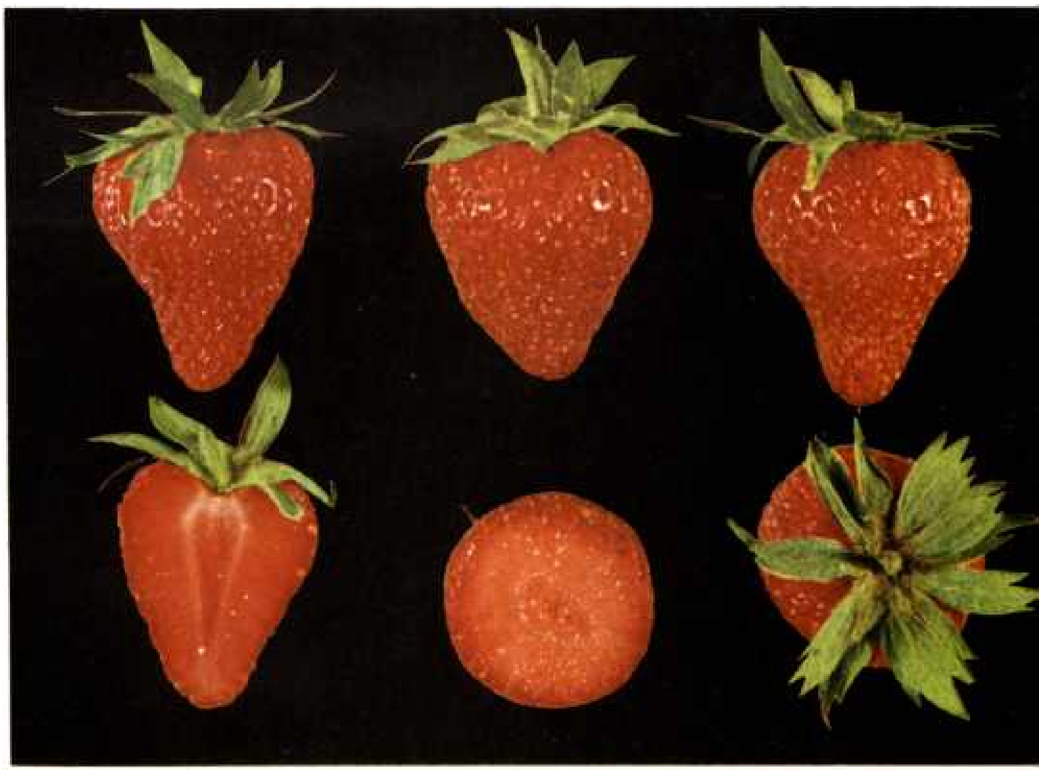


PLATE 16-2

Madam Moutot, a French variety, the most grown variety of Europe because of its productiveness. It is very large and of wide adaptation, but is gradually being replaced in part by the Senga Sengana, the Cambridge Favourite, the Talisman, and the Souvenir de Charles Machiroux.

PLATE 17-1

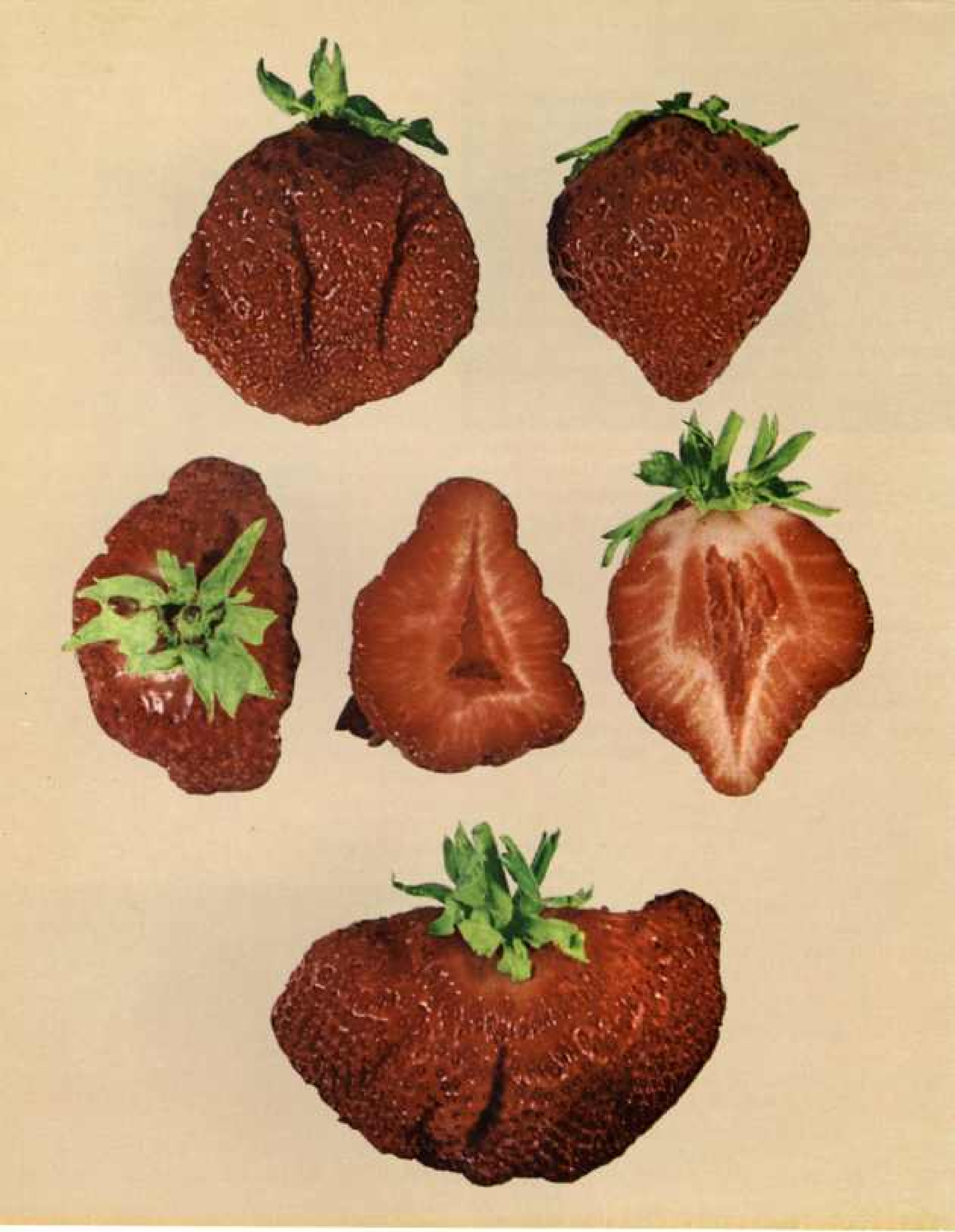
Georg Soltwedel, a good-flavored midseason, large berry high in ascorbic acid and well adapted for the fresh fruit market. Copyrighted.

Senga Sengana, a late midseason ripening just after Madam Moutot. It is deep red, highly productive, hardy, well adapted to freezing, resistant to mildew and Verticillium wilt. It is rapidly becoming the standard of Continental Europe.

Surprise de Halles, the chief early variety cultivated in France.

Senga Precosa, a very early, light-red variety. Copyrighted.

PLATE 17-2



Souvenir de Charles Machiroux, a Belgian variety, widely grown in northern Italy because of its very large size and its extreme lateness in ripening and good production. This variety is gradually replacing part of the Madam Moutot acreage.

PLATE 17-3

Crossing parents in the greenhouse at Sengana GmbH.

Senga Gigana, an early midseason variety introduced for its extremely large size and attractive berries. Copyrighted.

PLATE 17-4

Plants of Dutch Evern set about August 1, 12" x 12" for Dutch lites, produce about five pounds per Dutch lite. Subirrigated. Photo Sept. 17. (Stock #19)

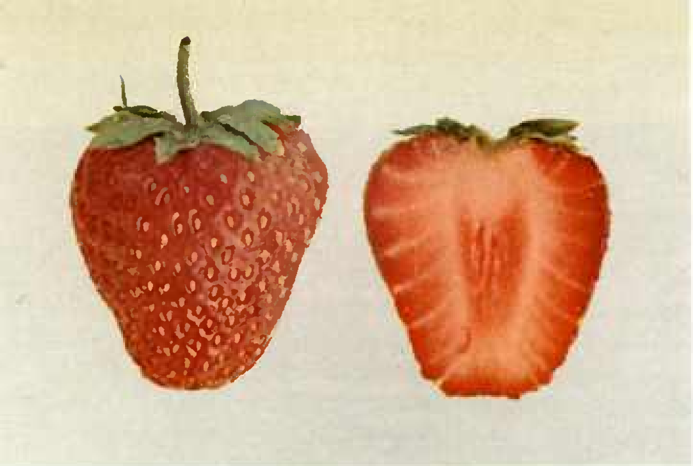
Cloche culture by gardeners of northern Europe for a fall crop of two-crop varieties when as much as half the spring crop may be harvested. Photo taken September 13, in vicinity of Chertney, England, of Auchincruive Climax.

Strawberries grown in 12" x 24" flats to be moved into the greenhouse in January for ripe berries April 10 to May 10, produce about one pound to the flat.

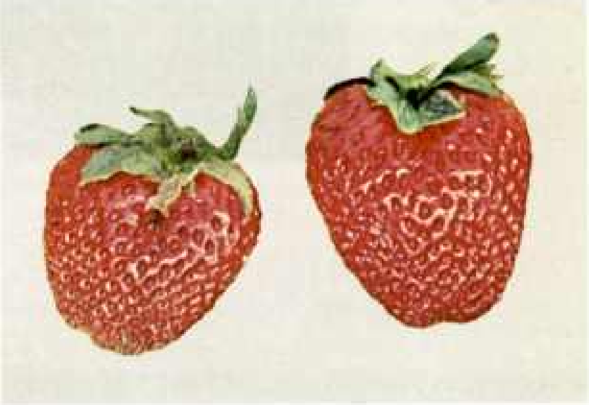
Strawberries set in beds to be covered by Dutch lites over cold frames. In some fields days are shortened to 12 hours by covering the beds from about June 1 to July 1 for a second crop in the autumn.

Forcing the Dutch Evern variety for the early market in the Netherlands.

PLATE 17-5



Donner, the second most grown variety of Japan, was originated by Dr. Thomas of California and is liked for its high flavor and productiveness.



Kogyku, the most grown variety of Japan because of its large early ripening berries, which are of only fair flavor.

Fukuba, for 40 years the leading variety for cement block hillside culture in Japan. It may reach 3 inches in length.

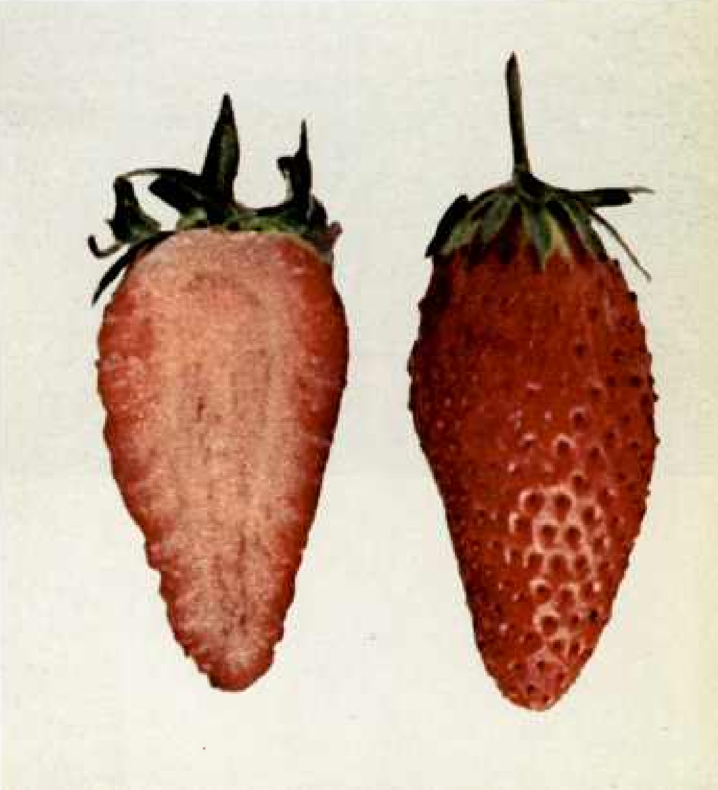


PLATE 18-1

Florida Ninety, grown under black plastic near Bradenton, Florida, to encourage extensive root development.

PLATE 19-1

Perfect flower cut lengthwise to show the green stem end which later develops into the strawberry.

A close look at the ripening berry surface showing fully grown seed at right of photo and non-pollinated seed at left.

Fully developed stamens containing pollen.

PLATE 19-2

Hermaphrodite flower containing very few good stamens.

A perfect or hermaphrodite flower with anthers shedding pollen.

Pistillate strawberry flower showing a poorly developed stamens.

Petals have shed and pistil ends are drying up.

Berry starting to grow.

Flower stems above foliage. Flowers are exposed to frost, but berries are less likely to rot.

Pineapples and Missionary strawberries growing together in Costa Rica.

PLATE 20-1

Cambridge Premier x Deutsch Evern
Elsa Schneider x Deutsch Evern
Cambridge Premier x Elsa Schneider
Silva x Elsa Schneider

Jucunda is being used in breeding to combine its good capping qualities with other desirable ones.

ZALTBOMMEL. The work at the Experiment Station started in 1939, is under the close supervision of J.D. Gerritsen and is carried out by J. Blommers. The objectives are for fresh market varieties for field culture and under glass. The introductions are:

Bowa (1952) (unknown parentage)
Glasa (1957) (Howard 17 x Deutsch Evern)—very early, for forcing
Vola (1961) (Bowa x Empire)—midseason, good flavor, fresh market

The number of seedlings grown was about 2,300 each year, 1960 to 1963, 5,200 for 1964, and 7,000 for 1965.

MIDDELRODE, BERLICUM, AND NORTH BRABANT. The work at the Experiment Station here is done by G. Th. Op't Hoog under the supervision of H.J.A. Slits, with the objective of obtaining preserving varieties easily capped with good color. Six to eight thousand seedlings are grown annually. Several varieties were introduced but none is succeeding.

ALLIED RESEARCH. Extensive research was published in 1942 by E.W.B. van den Muyzenberg, Agricultural University, Wageningen, on the effect of external growing conditions on the periodic development of the Deutsch Evern variety. On the basis of the results of this research, he evolved growing methods making possible the production of ripe strawberries throughout the year.

L. Smeets, at Wageningen, is studying the day-length-temperature effects on varieties from different regions.

Belgium

According to Habran (1912), there were 6,175 acres (2,500 ha.) of strawberries grown in Belgium with several major centers of production, especially the Valley of the Meuse, the region of Tournai, in Brobaut, in Limbourg, and the region of Gent. In the north of Campine, about 2,000 acres (about

800 ha.) are grown for processing. Production under glass is decreasing. The varieties grown are:

Early
1. Surprise des Halles
2. Mme. Lefèbre
3. Regina

Midseason
4. Senga Sengana
5. Triomphe de Tihange
6. Ville de Paris
7. Cambridge Favourite
8. Redgauntlet

Late
9. Souvenir de Charles Machiroux
10. Talisman

Souvenir de Charles Machiroux (*Plate 17–4*), a late Belgium variety of very large size, is the leading variety grown.

Breeding objectives given in the 1961 report of the Ministry of Agriculture have been to obtain varieties for the fresh fruit market and for processing—large in size, productive, easily harvested, early where needed, tolerant to viruses.

Sources of Desirable Qualities

Resistant to virus—Siletz (seems immune), *F. chiloensis,* Huxley.

Highly productive—M. Moutot, Triomphe de Tihange, Record, Souvenir de Charles Machiroux, Oberschlesien.

Early—Deutsch Evern, Madame Lefèbre, Early Cambridge, Regina, Surprise des Halles, B-26/6.

Good shipping—Ville de Paris, Souvenir de Charles Machiroux.

Resistant to root disease—Talisman and Auchincruive Climax.

Good processing—Ville de Paris, Senga 188, 54, and 29.

Breeding began in 1952 and has continued since. As many as 5,493 seedlings had been raised in a year and 309 selections were under observation in 1960.

Lemaitra and Sirouval (1955) showed that by regulating the amount of supplemental light, berries could be matured by Christmas of Triomphe de Tihange, Deutsch Evern, and Surprise des Halles.

Switzerland

The principal variety of Switzerland is Madame Moutot. Other varieties grown are Wadenswil 6 (large, soft, high flavor, introduced about 1960) and Wadenswil 7, bred by the federal station at Wadenswil, and Senga Sengana, Senga Precosa, Senga Gigana, Macherauchs Frühernte, Macherauchs Marieva, and Surprise des Halles. Nurseries are propagating virus-free plants for growers. Dr. F. Kobel bred the series of Wadenswil varieties but the breeding work is not being continued at present.

Wadenswil 1 was reported as Deutsch Evern x Ostersee, Waldenswil 2 as Wadenswil 1 x Hansen, and Wadenswil 3 as Tardive de Leopold x Wadenswil 1. Wadenswil 4 (released 1948) was introduced for its resistance to leaf spot and to drought and for its productiveness.

Senga Sengana is gradually replacing Madame Moutot in Switzerland.

Denmark

The strawberry acreage in Denmark is about 3,700 acres (1,500 ha.). About half the crop is processed. The main crop varieties are Senga Sengana for late midseason and Dybdahl for early midseason. Early forcing varieties are Xenion, Senga Precosa, and Regina.

Dybdahl was bred by H.H. Larsen, Rislund, Aarhus, and introduced about 1909. It is large, bright red, mild, excellent in flavor, early midseason, average in yield, susceptible to mildew and gray mold.

Breeding at the State Experiment Station "Spangsberg" near Esberg began in 1919 with Edv. Christiansen and Akeel Henriksen. Four varieties, Spangsberg 5, Freja, Rubin, and Ydun, were introduced in 1948 from their breeding work, the last three resulting from the cross (Spate von Leopolshall x Deutsch Evern) x Culver. Ydun was the most productive and was grown extensively. It is bright deep-red, conical, tart, soft, large, and late. Freja is earlier and Rubin later than Ydun. Ydun has been largely replaced by Senga Sengana. Beginning in 1949, A. Thusen has had the breeding work and is assisted, since 1959, by Miss Madsen.

In 1960 Xenion (Deutsch Evern x Valentine) and in 1965 Zefyr (Valentine x Dybdahl), were introduced, being earlier than Deutsch Evern, good flavored and good for processing. At present, breeding work is directed toward easy capping varieties for processing, making diallel crosses of about 30 varieties.

Italy

Commercial production as known in the United States is new in Italy. In 1920 there was almost no commercial production except for local markets, but the acreage of strawberry plantings has increased rapidly in recent years. By 1940, about 1,500 acres were grown. After the war the acreage began to expand, especially for exports to West Germany and to Switzerland; in 1959 there were 13,813 acres, in 1960 16,158 acres, in 1961 17,848 acres, in 1962

19,815 acres, and in 1963 there were 21,102 acres. About 40 percent of the berries are exported, mostly to Germany (66 percent of exports) and Switzerland (29 percent of exports), where they arrive about a month before the varieties of those countries have ripened. The production in 1962 was about 56,500 tons, or about three tons per acre.

The largest areas are in the Northeast; 60 percent of the total acreage is in the Province of Emilia-Romagna and Veneto near Bologna, Ferrara, Forli, Ravenna, Modena and Verona; 18 percent in the Province of Lazio near Rome; 13 percent in Piemonte in the Northwest; and 9 percent in the other Provinces. Recently plantings have been made in the far south, in the Provinces of Puglia and Lucania. A non-everbearing variety of *F. vesca* and another of the musky *moschata* are grown in Tortona, Italy—Magiostrina de Milano and Profumata di Tortona—and each makes up about 10 percent of the production of that area. Magiostrina de Milano is quite large for a pure wood *vesca* and Profumata di Tortona is of good size, larger than the *vesca.*

In 1962 over half, or about 12,500 acres, were of the Madame Moutot variety. About 2,000 acres of Regina de Verona, an early variety (in part a German variety American Seedling II x Deutsch Evern), were grown, chiefly around Verona; about 2,000 acres of Souvenir de Charles Machiroux (very late, of large size), of Belgian origin, mostly in Emilia; and about 2,000 acres of Senga Sengana (midseason), of German origin, were also grown, along with a smaller acreage of Nobile (of England) and other varieties. In trials, Pocahontas from the United States is reported as productive and as good for shipping as Madame Moutot, and it is four days earlier, much more attractive, much better flavored and well adapted to processing.

Chief varieties

From the report of Branzanti in *L'Italia Agricola,* the importance of the varieties in Italy changed from 1960 to 1964 as follows:

	1960 percent	1964 percent
Madame Moutot	61	42
Souvenir de Charles Machiroux	14	23
Regina (Tredesca)	9	15
Nobile	6	1
Perla	3	—
Senga Sengana	—	4
Others	7	15

Madame Moutot (of French origin). Though most grown (42 percent in 1963–1964) of all strawberry varieties in Italy, it is less important relatively than in 1960. It is grown because it is very productive and the berries are very large though rough. It is widely adapted. However, it is quite susceptible to virus. It is not very firm and must be picked when unripe to ship well. It is not very attractive, nor high in taste and aroma.

Souvenir de Charles Machiroux (of Belgian origin). Its production is increasing rapidly and it forms over 20 percent of the total production, mostly near Emilia. It is liked because of its productiveness (not equal to that of Madame Moutot in the first year), its good color, very large size, and good flavor. It is irregular in shape. It ripens about 4 days later than Madame Moutot.

Regina. There are two kinds grown, one originating in Germany, the other of unknown origin, but which is liked better. Both are early, seven days before Madame Moutot, and together are about 15 percent of the Italian production. The fruit is uniform in size and shape and its flavor is high, described as a mixed sweet-sour taste. It is susceptible to mildew and late frosts.

Senga Sengana (of German origin). This variety has been increasing, especially because of its processing quality and is about 4 percent of the total production. It begins to ripen about four days after Madame Moutot, is smoother, richer colored, with good red flesh and good flavor.

Near Tortona in northwest Italy, about 10 percent of the production is a variety of *vesca,* called Magiostrina di Milano. It is supposed to come from the wild plants of the surrounding hills and is important in the Milan market. It is grown in matted rows. The plant is said to be resistant to drought and to disease. The fruit begins to ripen 3 to 4 days after Madame Moutot. It is small, scarlet, sweet, and aromatic.

A variety of *moschata,* the musky strawberry, called Profumata di Tortona is also grown around Tortona and occupies about 10 percent of the acreage. It has been cultivated a long time there. It is resistant to drought and to disease. It is a pistillate variety and has large flowers and large flower clusters. The fruit is small but about twice the size of the *vesca,* mostly spherical, reddish violet, very aromatic. It also begins to ripen just after Madame Moutot. It is quite productive and is used largely for ice cream flavoring.

Extensive research on all phases of strawberry culture is carried on at Bologna, Verona, Rome, Torina, Bari, and other research stations, and breeding for improved varieties adapted to the climate of Italy has recently been started at Bologna and at Rome. Virus-free stocks of 11 varieties are being increased at the Bologna and Verona centers.

The breeding work in Italy began about 1960; at Bologna it is under the Direction of Dr. Enrico Baldini, professor of horticulture at the University of Bologna, and that at Rome is under the direction of Dr. F. Lalatta, of the

Institute for Fruit Culture. At the University of Bologna the varieties Director P. Walbaum, Machiroux Spaternte, Nobile, Prof. Dott Settgast, and Freja have been crossed with Cambridge Favourite, Madame Moutot, Redheart, Blakemore, and Pocahontas. At the Pomological Institute at Rome, beginning in 1960, Cambridge Favourite, Huxley (Ettersburg 80) and Climax have been intercrossed by Mrs. Maria de Ranieri and Mrs. Elisa Venezian to obtain new varieties—firm, productive, and of good quality. About 110 selections were still under test in 1964. Six hundred inbreds have been raised. Three groups of runner plants have been exposed to 10,000 and 20,000 r of Cobalt 60 for twenty days in the period preceeding flowering to obtain somatic mutations. The 700 seedlings raised in 1961 from this work were reduced by selection to 60 in 1964.

Notable recent publications are: (1) Report of the Second National Congress on the strawberry, June 1962, published by the Chamber of Commerce of Bologna. (2) A report of 150 pages on many phases of the strawberry industry in *L'Italia Agricola* 101:633–782, July 1964. Especially noteworthy are the two articles by Branzanti describing and illustrating in color the cultivated non-everbearing and the everbearing varieties of Italy and promising new sorts. (3) A monograph containing excellent colored illustrations and descriptions of the varieties tested and grown in Italy, by E. Baldini and E.C. Branzanti, and entitled *Monografia Delle Principali Cultivar de Fragola Non Rifiorenti,* Institute for Tree Culture, University Bologna 1964, p. 237. In this are shown some of the characters considered most useful in describing and identifying varieties.

Sweden

The acreage of strawberries in Sweden for 1964 is estimated to be 8,645 acres, of which about 3,700 acres are commercial. Senga Sengana is the chief variety comprising more than 50 percent of the total, while Abundance remains the leading variety of northern Sweden. Talisman is increasing in popularity. Early ripening varieties such as Senga Precosa, Lihama, Regina and Macherauche Frühernte have low yields and are grown but little.

Breeding work was started at Alnarp by Prof. C.G. Dahl and Dr. Emil Johansson early in the 1920's; the first variety to be named was Stella, raised in 1924 and followed by Silva in 1930, and Indra in 1936. Work at Alnarp was discontinued in 1962 when Dr. Johansson retired and since then all breeding work has been concentrated at Balsgard. E.J. Oldén began breeding at Balsgard in 1959 and Miss A.L. Koch took over the work in 1960. About 100,000 seedlings have been grown there in 10 years. The 2 major objectives are (1) high yielding varieties for each region of Sweden and (2) varieties resistant to gray mold (Botrytis) which destroys over 50 percent of the crop in some years.

In cooperation with Dr. Bauer, of Germany, during 3 seasons 9 varieties have been intensively studied at Cologne and at Balsgard for their response to the different environments. Valentine has been a good source of resistance to gray mold (Botrytis), and resistant selections of Senga Sengana x Valentine are being studied. A performance index "yield capacity" is being used to evaluate varieties, seedlings, and selections. This is based on branch crowns per plant x number of flower clusters x number of fruits per cluster. This index was 63 for Sparkle, 164 for Abundance, and 264 for Senga Sengana. Punch cards are being used for the various characters. Valentine has proved to be an outstanding parent (Koch, 1963) for earliness and for resistance to Botrytis and mildew.

F_1 and F_2 clones are being used for selfing, backcrossing and sibling crosses in detailed programs, using mainly Senga Sengana, Valentine, Sparkle and Fairfax. Interspecific crosses using 4x *F. vesca* with cultivated varieties are being made in an attempt to transmit the *vesca* flavor into decaploids.

Poland

As in Italy, there has been a great expansion of strawberry production in Poland. The yield in 1964 is given as 60,000 tons as contrasted with 6,000 tons in 1954, and only 30,000 tons in 1961. Large exports go to West Germany, Sweden, England as well as to East Germany, Czechoslovakia and the U.S.S.R. The last report on acreage was about 31,000 acres for 1961. The varieties grown are:

In the Older Plantings	In the Newer Plantings
Madame Moutot	Madame Moutot
Purpuratka	Purpuratka
Sharpless	Regina
Deutsch Evern	Macherauchs Frühernte
	Georg Soltwedel
	Talisman
	Ydun
	Cambridge Favourite

Purpuratka, an old variety of unknown origin, is said to produce a superior frozen product because of its dark red flesh and because all berries are firm under their cool climate. The aphid that spreads most virus diseases is said not to survive in Poland.

Strawberry breeding has recently started at the Research Institute of Pomology, Skierniewice, Poland under K. Smolarz.

Hungary

Inbreeding began in 1952. In 1963 Porpaczy and Szilagyi reported crossing inbred American and European varieties. The most productive hybrids (over two and one-half times Madame Moutot as standard) were from crosses between European I_1 (I=inbred) and I_3 but highly productive selections were obtained also from American varieties x European I_1 (over twice Madame Moutot as standard). In the final score the two top ranking selections were American varieties x European I_1 inbred for one generation.

Yields were obtained from "KN" (clone square) plot tests which consisted in transplanting three plants per replication and allowing each to make four runner plants. A weighted evaluation considering fruit size, firmness, color, smoothness, and taste was used in scoring.

Simon in 1963 reported on the variety Kátai (Brigaderos), a large-fruited everbearer of unknown origin which is highly variable in flower and fruit size and other characters. Its pollen mother cells had n = 7, 14, 21, and 28 chromosomes as well as aneuploids. Variable numbers were found at the two poles.

Russia*

According to T.P. Filosofova (1962, pp. 104–105) strawberry breeding began in 1924 at the Moscow Station with the objective of hardier varieties in the central belt of the country. The varieties originated are said to constitute about 90 percent of the area of all plantings in the central regions and are grown in other zones as well. The best known are the four: Komsomolka, Mysovka, Pozdnyaya Zagorya, and Krasavitsa Zagorya. Many experiment stations have been breeding strawberries for diverse climatic zones. The stations in the Chernozem belt and in the Volga area have bred drought-resistant varieties and stations near Leningrad have bred hardy varieties.

The main breeding method has been repeated crossing between local varieties and then crossing with varieties from other climatic zones of the U.S.S.R., or of other countries. Crossing with varieties from other areas is emphasized. The Moscow Station had about 500 selections under test. For

* From Reports of the 16th International Congress of Horticulture, Moscow 1962.

earliness, crossing the local early varieties Mysovka and Krasavitsa Zagorya with early varieties from the Ukraine had greatest promise; for lateness, the local Pozdnyaya Zagorya crossed with the German late ones, Georg Soltwedel and Frau Mieze Schindler, gave the most late selections. Large-fruited, high-yielding midseason selections came from Pozdnyaya Zagorya x Rozovaya.

Skvortzov (1929) described *orientalis* and illustrated its fruit.

Fedorova (1935) in 1930 obtained four hybrid seedlings from 5,430 seeds of the wood x musky (*vesca* 2x X *moschata* 6x) and in the second generation had seedlings 6x, 8x, 9x, 11x, 12x, and 14x, the 14x being the least vigorous and the 8x and 9x the most vigorous.

Petrov and Tukan (1937) noted that the diploids supposed to make up the tetraploid *orientalis* are perfect-flowered yet the *orientalis* has the sexes on separate plants; also, in the hexaploid *moschata* and in all octoploids the female is heterozygous for sex, yet in the tetraploid *orientalis* the male is heterozygous.

Dozadkina (1940) followed up the crosses of Fedorova of *vesca* (2x) x White Pineapple (8x), made in 1933. Four seedlings were obtained. All were pentaploid (5x) and some had 10 to 20 percent normal pollen. One set of *vesca* chromosomes paired with one set of the White Pineapple. Fedorova had crossed *orientalis* with *moschata* in 1932–33 both ways, and had suggested that *orientalis* was a link between diploid and hexaploid species. Dozadkina supported this from his studies and concludes that three sets of chromosomes of the cultivated strawberry are homologous and are closely related to those of *vesca*.

Sangin-Berezovsky (1963), among other species crosses, tried cultivated varieties x *orientalis* but obtained only one sterile hexaploid hybrid.

Philosophova (1941) suggested the use of *moschata* x *vesca* (*neglecta*) selections ($2n = 28$) to cross with the garden strawberry to get the desirable qualities of the musky and wood strawberry into the cultivated. *Orientalis* was crossed with F_1 of *moschata* x *vesca* (= *neglecta*) and good fertility of seedlings resulted.

Lichovitzer, V.G. (1934) reported on hybrids of cultivated x *moschata* that had 44 and 46 chromosomes.

Smolyaninova (1946) stated that Michurin first attempted to cross the garden and the musky *moschata* strawberry, and that in 1927 Petrov succeeded, but that the hybrids were mostly sterile. Smolyaninova continued this crossing, beginning in 1938. The hybrids ranged from entirely sterile to fertile, had intermediate vegetative characters but the berries were like the musky. In the exception, Bakhimutka (a Virginian type) x musky the seedlings were like the seed parent.

Lebedov (1957) reported obtaining the variety Podmostovnaja from the cross Komsomol x *moschata* and stated that it produced well, had good flavor, and the aroma of *moschata*.

Saks (1961) in a test of 12 species and varieties noted that three cultivated varieties were salt tolerant, Aborigen Attaja, Kolhoznaja, and Sinena, and that *orientalis* and *virginiana* were also. In a test of frost resistance, *orientalis, virginiana, vesca,* and cultivated varieties Sejanee Komsomolki, and Kieoskaja raunjaja, *moschata* Milanskajo were the hardiest.

Reports from several research stations of U.S.S.R. describe new varieties and the best varieties, old and new, of their region. Transmontane Beauty, Virginian, and Taskent were reported the most resistant to Botrytis (gray mold). Katinskaja (1956) reported the variety Leningradskaja Pozdnjaja (Victor x Saxon) as resistant to Botrytis. Useful varieties were reported by Katinskaja (1963) as obtained from cultivated varieties x *vesca,* also x *viridis* and x *moschata.* The high yielding Festival was reported as drought-resistant by Gorustovic (1963). The average ascorbic acid content for 27 varieties for three years was 67.4 ± 16.7 to 70.9 ± 16.3 with the highest being Purpuratka 113.4.

In an experiment beginning in 1934 no strain of six inbred varieties was better than the parents (Duka and Sokolovsky, 1938).

Sbitnev (1960) reported that Neiscerpaemaja was the highest yielding everbearer.

East Germany

Strawberry breeding in East Germany is carried on at present only at Muncheberg at the Institute for Field and Crop Breeding. A summary by Dr. Murawski in charge of work follows.

Summary (pp. 146–148)—53 combinations with 6207 seedlings were tested for their breeding values. The more important results were:

1. The combining ability of varieties differ. Some have specific characters for general combining ability; others have a special combining ability. From the present analyses Senga Sengana has the common or general combining ability for height of bloom and for fruit color; Sengana 29 for fruit color and number of fruits per plant. Most characters have a specific combination value. These include powdery mildew resistance, total fruit weight, fruit size, number of fruits per cluster, and fruit weight per cluster. Because the genetic value of a variety is judged by its most important characters, it is necessary to make continuous test crossing with the best combining partners.

Through analysis of selfed lines it may be possible to judge the genetic value of strawberry varieties and obtain at the same time more information on their combining value. More research on this is necessary.

2. Genetic analysis shows that the phenotypic characters are due to different genes. A few varieties possess a complex dominant gene for certain characters which reflects on the behavior of the selfed strawberries. General combining ability depends on favorable dominant genes, which show in crosses additive effects. It is possible that specific combining ability is determined by gene interaction and superdominence because the characters are distinguished in different crossings. Especially favorable further results in strawberry breeding are to be expected from the occurrence of transgressive segregation.

3. The results of regression analysis of tests showed that the total crop is determined mainly by the number of fruits. The exactness was B = 0.80–0.87. Also, the numbers of flower stems had great influence on the total yield; as measured it was B = 0.61–0.71. Individual fruit weight had a minor effect on total yield, B = 0.29. Research showed further that single fruit weight was not affected by number of flower stems nor was the number of fruits per plant affected by the number of fruits per flower stems. Repeated means of regression analysis likewise showed that the crop was determined mainly by the number of fruits per plant. Repeated regression coefficient determinations show little effect of single fruit weight on the total fruit weight per plant, on the number of flower stems, and on the number of fruits per flower stem. It is easier for the breeder to increase the crop per plant through increasing the fruit number than through individual fruit weight. Fruit size is inherited independently of fruit number. This makes it possible to select the best from a progeny having a high fruit number as well as acceptable fruit size. Thus, at present in strawberry breeding highest yields have not been reached.

4. The average rank of a few important characters was obtained for combinations that gave the best results. The value of new breeding was established for many characters. The appearance of seedlings with several good characters could be expected with high probability in combinations which show average performance in all important commercial characters. Combinations with very high rank may be lacking in value because of one inferior character. Of the 53 examined combinations, the following are of value for practical breeding:

Brandenburg x Georg Soltwedel
Georg Soltwedel x Senga Sengana
Klon 3587/74 x Senga Sengana

Senga 29 x Senga Sengana
Deutsch Evern x Senga 29
Sachsen x Senga Sengana

For a practical breeding program, it is necessary to use only such varieties for crossing that have more than average breeding value for single or combinnig characters. The genetic divergency of the varieties for crossing has an important role. Among such genotypes are to be expected specific advantageous gene changes. Varieties of American origin are valued breeding parents for European varieties.

18

Strawberry Breeding and Industry in Other Countries

BESIDES THE CONCENTRATED strawberry breeding work of some European countries and the extensive culture of strawberries in most of them, and besides the work in the United States and Canada, there is considerable culture of strawberries and some breeding work in other countries. All of these other countries have benefitted to some degree from varieties imported from the United States, England, or Europe, or from all of these; while in some of these countries no breeding work whatsoever has been done, and the country's industry was entirely founded upon varieties developed elsewhere. Japan, Mexico, South Africa, New Zealand, and Australia, the countries represented in this chapter, display various relationships of breeding and industry; from a country such as Mexico, whose industry is based upon varieties originated in the United States, to Japan, where government-supported breeding has proceeded for a considerable time in order to advance a highly developed industry based on American and European varieties. Where breeding work is conducted in these five countries, objectives are usually the same as elsewhere; the development of virus-tolerant plants adapted to the particular region. In the case of Mexico, an extensive strawberry industry exists because varieties have already been bred in the United State which can be grown there, even if they are not well suited to the industry's needs. There is little doubt but that much better adapted varieties could be bred for Mexico.

FIG. 18–1. *Dr. Hayato Fukuba,* was born December 16, 1856 in Tsumarro-Machi Shimane-ken, Japan, and was educated in Baitatsu Gijuku, 1872, Tokyo Gakunosha, in 1875; and in the Versailles (France) Horticultural School, 1887. He began work at the Mita Breeding Station in Tokyo in 1879, and the Banshu Grape Garden, Hyogo-ken, in 1882, where he became chief in 1886. In 1896 he went to the Shinjuku Gyoen (plant industry station). In 1904 he became a norin-gishi (agricultural engineer) at that station and chief in 1906. He retired in 1917 and died in 1921. Although Dr. Fukuba worked with other fruits and vegetables, his breeding work was confined to the strawberry.

Japan

It is said that strawberries were first cultivated in Japan about 1727 and that some more were grown in 1856. As a commercial crop on a large scale, however, strawberry growing is relatively new to Japan. The first varieties were introduced from the United States in 1872 and 1875, followed by the small-fruited *F. vesca* from France in 1884. Dr. Hayata Fukuba (*Plate 18–1c* and *Fig. 18–1*) of the Shinjuku Imperial Gardens imported four varieties into Japan in 1889; included among them were Docteur Morère and General Chanzy from France. Dr. Fukuba also introduced the Fukuba about 1899, growing it from seed of General Chanzy. Fukuba is high-flavored and of immense size as grown under cover and on the hillsides with cement-block culture. It is similar in shape, size, and appearance to the Florida Ninety, but it is not as early as the Florida Ninety is in Florida. It has been the most important forcing variety in Japan for over forty years. Later, Louis Vilmorin, Saint Joseph, Louis Gauthier, and Marguerite were introduced from France and Royal Sovereign, Sir Joseph Paxton, and Victoria were introduced from England. Royal Sovereign was grown until the 1930's. In recent times Donner, Fairfax, Marshall, Shasta, and Robinson from the United States have been grown.

In 1939 the acreage set to strawberries was given as 17,500. In 1963 the reported planting in strawberries was about 20,800 acres. The centers of the strawberry industry, the varieties grown in each, and the kind of culture given each is shown on the map (*Fig. 18–2*). It should be noted that strawberries are grown from Hokkaido, about the latitude of central Michigan, south to Kyushu, about the latitude of southern Georgia. The varieties now used are as follows (1 = most important for each culture; 2 is next; etc.):

Varieties for field culture

1. Kogyoku
2. Donner
3. "Marshall" (America)
4. Chiyoda
5. Yachiyo
6. Hokowase
7. Aga
8. Holei
9. Koro
10. Miyazaki
11. Robinson
12. Shasta
13. Takane
14. Fairfax

For matted row culture

1. Mimakigahara No. 1
2. Fujisaki
3. Shunko No. 1
4. Chikuma

For hillside cement-block cover culture

1. Fukuba
2. Benizuru
3. Hottawander
4. Shikinari (word means everbearing)

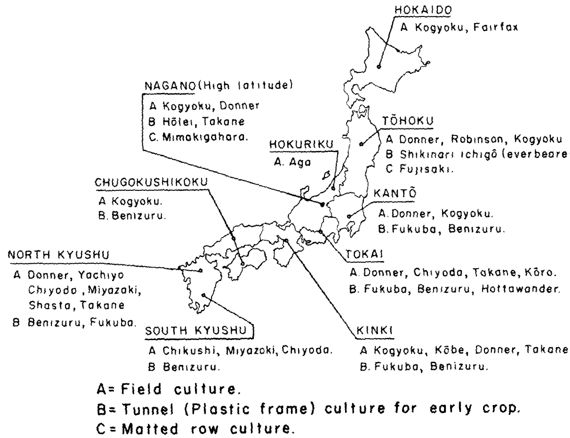
For tunnel culture

1. Kogyoku
2. Donner
3. Benizuru
4. Yachiyo
5. Hottawander
6. Shikinari

In percentage of total acreage Kogyoku composed about 40 percent, Donner about 30 percent, "Marshall" about 5 percent, Chiyoda about 5 percent, Yachiyo about 3 percent, Hokowase about 3 percent, and the others 14 percent.

Kogyoku (*Plate 18–1b*) was obtained in 1940 by Mr. K. Tamari (*Fig. 13–34*) and is of unknown parentage. One report is that Kogyoku was raised from seed of Fairfax. It is the most widely grown variety because of its very large, early-ripening berries. Although its fruits have only fair flavor, Kogyoku has a vigorous, widely adapted plant which is easy to raise. Donner (*Plate 18–1c,* see page 228) is a high-flavored variety originated by Thomas and Goldsmith in California. Recently Donner has been replacing Kogyoku in all parts of Japan because of its better flavor. "Marshall," also called America, is probably not the same as the Marshall variety of the United States. It was the most important variety about 1955.

In recent years breeding work has been carried on at four principal experiment stations in Japan, the first three national and the fourth a state one: Morioka, Iwate-ken; Okitsu Branch, Shimizu, Shizouka-ken; Kurume Branch, Fukuoka-ken, and the Kik Yogahara Branch, Nagano-ken. A little breeding work is carried on at some other state (ken) stations. The varieties resulting from this work are becoming important in commercial culture. The map (*Fig. 18–3*) shows the location of the principal experiment stations now breeding strawberries and some of the varieties originated at each station.



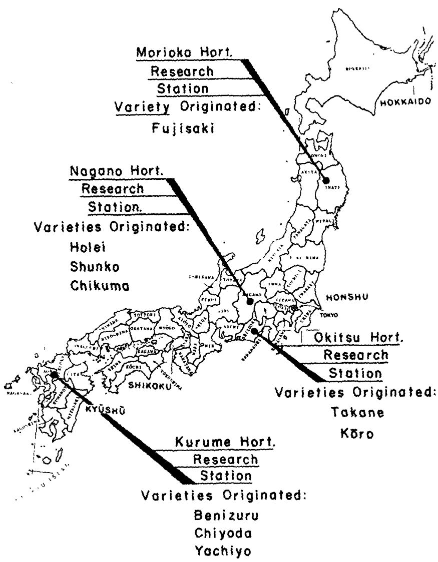


FIG. 18–2 (above). Map showing where the principal strawberry varieties are grown in Japan by H. Katsumata

FIG. 18–3 (left). Location of 4 experiment stations breeding strawberries and the varieties originated by each

Kurume Branch, Hort. Res. Sta. Strawberry breeding for warm climates began at the Kurume station in 1950 (*Fig. 18–4*) and the Howard 17 (Premier) was found to be a valuable parent there. By 1954, 24,000 seedlings had been grown and 14 clones released for trial as "Kurume 1 to 14" for dessert and preserving use. From this work, Chikushi (tested as Kurume 1) for dessert use, was named. Kurume 102 and Kurume 103 are grown to a slight extent. Chiyoda (*Plate 18–1e*), Benizuri, and Yachiyo were later introduced. The next crosses of this station were made in 1956 and a total of 49 selections for fresh market and for processing had been made from crosses up to the end of

Some varieties originated at the Japanese Experiment Stations with the date of their introduction

Variety	Year Introduced	Experiment Station	Variety	Year Introduced	Experiment Station
Aga	1960	Nigata	Holei	1961	Nagano
Benizuru	1960	Kurume	Hogyoku	1956	Tokushima
Chikushi	1951	Kurume	Koro	1953	Okitsu
Chiyoda	1958	Kurume	Shunko No. 1	1852	Nagano
Chikuma	1952	Nagano	Takane	1959	Okitsu
Fujisaki	1952	Morioka	Yachiyo	1961	Kurume
Fukuba	1899	Shinjuku Imperial Gardens, Tokyo			

1961. In addition, 140 selections for forcing had been made. In 1962, 3,269 seedlings were grown from crosses, a sample series being Chiyoda x #7–3–17, x Dixieland, x Donner, x Shelton, and x Sioux. Objectives of the breeding of this station are fresh market, preserving, and freezing varieties for warm climates, and forcing varieties.

Okitsu Branch, Hort. Res. Sta. Objectives of breeding at this middle latitude station have been processing and disease-resistant varieties. In much of the breeding, Temple, resistant to red stele root rot, has been used as one parent. In 1961, there were 37 selections made from 6,101 seedlings of Okitsu x Temple and 573 selections from 1,542 seedlings of other crosses. Two varieties from this station, Koro in 1953 and Takane in 1959, have been named and introduced.

Morioka Branch, Hort. Res. Sta. Work at this station (formerly at Fujisaki) began in 1938. Objectives of this station have been processing varieties for northern cooler Japan and an evaluation of inbreeding. To obtain processing varieties, 10 varieties were used as mother plants in 60 crosses, 8,330 seedlings raised, and 683 first selections made; Hanaoka Tamotsu is the strawberry breeder here. Fujisaki (Dorsett x Ettersburg) from this station has been quite successful as a processing berry in northern Japan and Hokkaido.

Kik Yogahara Branch, Nagano-ken Agr. Exp. Sta. Breeding for fresh market and for processing varieties of large size, high flavor, and color for northern latitudes have been primary objectives. Combining ability of varieties is being studied. Over 4,500 seedlings were planted in 1961. Two varieties, Holei (1961) and Shunko No. 1 (1962) have been named and introduced.

Varieties Introduced by Experiment Stations

The Benizuru originated at the Kurume Station as a cross of (Miyazaki x The Sun) x Fukuba and introduced in 1960, is a very early variety that by forcing under tunnels and with plastic on the ground is harvested from the end of November through the winter months. It is far more vigorous than the Fukuba now, and is earlier by two weeks; it is resistant to high temperatures and produces runners freely. It is equally good in flavor, has glossy crimson, long conic necked fruits somewhat like Fukuba but with red flesh. Its production in February under plastic is heavier than under "Ishigaki" (concrete block hillside) cultivation.

Yachiyo. This plant, also from the Kurume Station, was selected in 1957 from seedlings of the cross Lassen x "America" and was introduced in 1961. It is firm-fruited, blunt conic with a neck, attractive, deep glossy red, and preserves well. It is early and adapted to forcing for table use and preserves, but is grown in field culture also.

Chikushi, from the Kurume Station, is from a cross of Miyazaki x Fairfax. It is extremely large, irregular blunt conic, bright scarlet with a pale flesh, firm, good in flavor, and producing few runner plants.

Chiyoda. This plant was selected also by the Kurume Station from a cross of America x Midland. It is round, blunt conic, deep-red with red flesh, firm, a good shipper, high-flavored, and suitable for preserves and freezing. It is liked for its early crop in the paddy fields.

Others bred at experiment stations are:

Aga—Fukuba x Fairfax
Chikuma—Daikanko x Fairfax
Fujisoki—Dorsett x Ettersburg
Hogyoku—seedling of Fukuba (selected in 1956)
Holei
Kobe
Koro—"Morsholl" x Fairfax
Shunko No. 1—Mimokigahoro x Dorsett
Tokone—Haikara x Foirfox
Mimokigahoro

FIG. 18–4. Crossing inside a screened house at Kurume.

FIG. 18–5. Ordinary field culture in sandy soil in Hyogo. Berries mature four to five days earlier than in paddy fields of heavy soil.

THE INDUSTRY. In northern Japan and Hokkaido the main systems of culture, especially when fruit is raised for processing, are the matted row systems. Hill culture (*Fig. 18–5*) is also used in these locations, but chiefly for fresh market berries. In southern Japan the plants usually are raised in the nursery and transplanted into the paddy fields after rice has been harvested (*Fig. 18–6*). After berry harvest in early spring, the plants are pulled out and vegetables or rice are set to be grown in the summer. During the cold season, nearly a third of the field culture is covered with plastic stretched over split bamboo to hasten the ripening (*Figs. 18–7 to 18–9*). This is called "tunnel" culture. It has many variations, especially in the size of tunnels. Cement block culture or Ishigaki culture (Ishigaki = stonewall) is a type of forcing on steep hillsides (*Figs. 18–10 to 18–12*), originated soon after 1900 in the Kuno area in Shizuoka-ken, using stones to retain heat. After 1920 cement blocks took the place of stones.

A report on acreage for 1963 gave three classes of culture—cement-block culture or hillside culture, with 470 acres (yield 6,381 quarts per acre for 1961), tunnel culture with 6,200 acres, and field culture, with 14,100 acres (yield 4,940 quarts per acre for 1961). There were 109 acres of cement-block hillside culture in Shizuoka and 126 acres in Kanagawa. Field culture is widely distributed; Shizuoka had 2,020 acres and, in the north, Hokkaido had 2,045 acres.

FIG. 18–6. Winter strawberry growing in paddy fields in Hyogo. After berry harvest, young rice plants will again be set in late June.

Fig. 18–7. Wide plastic covers several rows in "tunnel" culture, a form of forcing.

Red stele root rot (negusare disease) has become serious in some fields in the southern part of Japan.

The chart that follows shows the varieties, the planting and harvesting seasons for each type of culture.

Chart of planting and harvesting dates for different systems of culture

Culture type	Planting dates	Harvesting dates	Varieties
Forcing by concrete blocks on hillsides	Sept. 10–30	Nov.–Dec.	Shikinari, Hottawander, (Fig. 18–7) Benizuru
	Sept. 20–Oct. 10	Dec.–March	Fukuba
Forcing in tunnels	Sept. 10–30	Dec.-March	Shikinari, Hottawander, Benizuru
	Oct. 1–Nov. 10	March 20–May 10	Kagyoku, Yachiyo
Forcing under mulch	Oct. 10–Nov. 10	April 10, May 10	Chiyoda
Field	Oct. 10–Nov. 30	May 1–June 10	Kogyaku, "Marshall," Chiyoda
Late	Oct. 1–20	May 20–June 20	Danner, Kagyoku
Cold storage; in tunnels	Sept. 1–20	Oct. 10–Nov. 20	Kogyoku, Chiyoda, Takane
	Sept. 20–30	Nov.–Dec.	
Matted row	—	June–July	Mimakigahara, Fujisaki, Shunko No. 1, Progressive, Chikuma

Fig. 18–8. Inside a wide plastic tunnel. The ground beds are also covered with plastic, with holes cut for the plants.

Fig. 18–9. A low plastic tunnel for forcing.

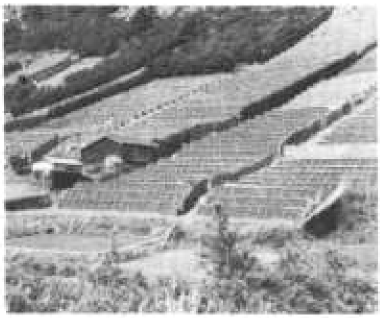


FIG. 18–10. Forcing culture by hillside cement blocks at Kuno-zan, Shiyuoka-ken.

Mr. K. Ninomiya, of the Shizuoken-ken Experiment Station, has published (1961) a book on the strawberry for growers in which he describes the 28 leading varieties and briefly discusses strawberry breeding.

Australia

The acreage in strawberries for 1962–1963 for all of Australia was reported as 1,041 acres of which 567 acres were in Victoria, 270 in Queensland, 100 in Tasmania, and lesser amounts in the other provinces. Breeding at present is carried on by I.A. Bonner at the Redland Horticultural Research Station, Ormistan, Queensland, and by J.E. Cox and V.C. Austen at the Horticultural Research Station, Narara, New South Wales. About 1,000 seedlings are raised each year at this latter station.

FIG. 18–11. Forcing by concrete-block culture. Blocks are 5 x 1.5 feet. Girl is thinning flowers and removing old leaves. Choice berries are protected in bags.

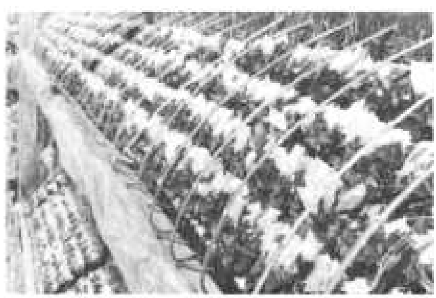


FIG. 18–12. Hillside cement-block culture, covering with plastic for further protection. Single berries are covered with bags for fancy fruit.

New South Wales

In 1962 Holbeche and Cox reported that the main varieties grown were the following:

Richmond Red, originated by N.S. Shirlow of the Hawkesbury Agricultural College, Richmond, N.S.W. (Fendalcino x British Sovereign, named about 1936), is medium-sized, blunt-conic, dark-red, fair-flavor, firm, and transports well, but is subject to leaf spot.

Ettersburg, one of the Etter varieties, is medium-sized, blunt-rounded, bright-red, and subject to leaf spot.

Auchincruive Climax, of Scotland, is medium in size, fair flavor, and subject to leaf spot.

Phenomenal, of Queensland, is of good flavor and bright red.

Majestic, of Queensland, is large, conic, and subject to mildew and leaf spot.

Bountiful (Fendalcino x Wamberal Beauty), was originated in New South Wales by J.E. Cox and V.C. Austen and introduced in 1958. It is good-sized, long-conic, fair-flavored, light-red, soft, and resistant to leaf spot.

Kendall, originated by the New South Wales Department of Agriculture and introduced in 1961, is an open-pollinated seedling of Richmond Red selected in 1958 and raised by J.E. Cox and V.C. Austen of the Narara Horticultural Research Station near Gosford. It matures from June to January with a flush of crop in October, and is recommended for the Coastal Districts. It is reported as highly resistant to leaf diseases but susceptible to gray mold. Holbeche (personal letter) stated that in 1965 Redgauntlet, Cambridge Vigour, Massey, Auchincruive Climax, and Midland were recommended for inland and Kendall for the coastal areas.

Queensland

The Phenomenal, a variety originated in Queensland, has been the widely grown variety. Majestic, introduced recently, has outyielded Phenomenal and is increasing in popularity. It led to breeding at the Redland Station where it has demonstrated its value as a parent.

New Zealand

The acreage for New Zealand is given as 421 in 1963–1964 and the average yield over four years as 4.7 tons. About half (48 percent) of the production is in North Auckland, much of it near Auckland and the rest scattered in Wellington, Auckland, Canterbury, and Hawke's Bay.

No strawberry breeding as carried on in England and Scotland is being done in New Zealand. Some breeding to obtain varieties tolerant to virus and resistant to red stele root rot was reported in 1958. Marguerite and Melba and then Capt. Cook were formerly the chief varieties; now the chief varieties are Redgauntlet, Cambridge Favourite, and Talisman, of Great Britain. Talisman does not yield well and is declining in importance. Bedford, Shasta, Chapman's Seedling, Solana, and Merton Princess are known.

South Africa

No figures of acreage set to strawberries in South Africa were found, but in the 1957–1958 season 445 tons were reported as used by the canning industry. From about 1944 to 1954 "Everbearing" was by far the leading variety grown. Having a light-red, soft, medium to large berry of poor flavor and a plant tolerant of virus, it was reported as composing 90 per cent of the total production in the early 1950's. Another variety, Koeal, was also grown to a limited extent.

Beginning in 1940, breeding for adapted varieties was started at Stellenbosch, Western Province Fruit Research Station, by P.A.L. Steyn and has continued there on a limited scale to the present. From the early crosses, three selections were released in 1954:

(1) Bien Donné No. 1. [(Tardive de Leopold seedling x German strawberry) x Everbearing] It is a very large, deep-red, good-flavored variety suitable for jam as well as fresh. It is virus tolerant.

(2) Bien Donné No. 2. (Same parentage as above) This is a pistillate plant with fruit medium to large, light red, and good flavor, which is suitable for jam. It is resistant to leaf spot.

(3) Bien Donné No. 3. (Corvallis x Everbearing) Its berries are medium to small, with very good flavor, and suitable for jam; it is productive, virus tolerant, and leaf-spot resistant.

These three replaced the "Everbearing" almost entirely by 1960. Two of the Bien Donné varieties (Nos. 1 and 2) were used in further breeding and in 1954, 1,747 seedlings were planted and by 1959 reduced to eight selections, four of Bien Donné No. 1 x Missionary and four of Bien Donné No. 1 x Massey.

Publication: "Strawberries in South Africa," *Bul.* 372; 26 pp., 1960, by P.A.L. Steyn.

Mexico*

For perhaps one hundred years, strawberries have been grown in the vicinity of Irapuato, Guanajuato, which is about two hundred miles northwest of Mexico City; the older varieties being selections of *F. chiloensis,* called Negrita and Poderosa, and grown to supply domestic markets. Commercial strawberry production in quantity began in 1948, with the opening of the first freezing plant in Irapuato which is located at about 5,700 feet on a plateau area irrigated from streams and deep wells.

Beginning about 1953, the industry expanded to the region about Zamora, east of Guadalajara, in the State of Michoacán, about two hundred miles from Irapuato, and, on a more limited basis, to Obrajuelos, in the State of Querétaro. The Zamora area is higher than that around Irapuato.

By 1954 there were about 2,400 acres planted to strawberries. Foreign Agriculture Circular of April 1964 gave the 1964 acreage as some 14,000 acres, about 9,000 of this is Guanajuato, and about 5,000 in Michoacán. The production per acre, though low, is increasing from 2.0 tons in 1960 to 2.6 tons in 1964. A high yield for the Klondike is 3.5 tons with 4.5 to 6 tons for the Florida Ninety.

Importation of frozen strawberries into the United States from Mexico increased from about 14,000,000 pounds in 1959 to over 45,000,000 pounds in 1964. Canadian imports from Mexico were over 4,000,000 pounds in 1963. In 1963 the total frozen pack was 44,000,000 pounds, of which about 5,300,000 pounds were used in Mexico. There were thirteen strawberry freezing plants in Mexico in 1964. Although the Klondike is preferred for freezing, most packers will accept Florida Ninety, with the same price being paid for all varieties. Florida Ninety and Solana may yield 50 percent more than the Klondike. Normally, most of the frozen berries are packed during March and April.

Shipments of fresh berries to United States markets have also increased in recent years. The Florida Ninety and, to a limited extent, Solana have been used for this purpose. In 1958, 13,000 pounds were exported and 2,449,000 pounds in 1963. In some years a few berries begin ripening by November; 41,000 pounds being exported in that month and 103,000 pounds in December of 1962; 576,000, 702,000, 318,000, 595,000, and 113,000 pounds were exported in the months January to May, 1963, respectively. The fresh packs shipped into the United States compare favorably with those of U.S. origin and compete primarily with fruit from Florida and other southern states. In contrast, the fruit marketed in domestic Mexican markets, usually in baskets

* By R. S. Bringhurst and George M. Darrow.

holding 12 to 14 pounds, is generally badly packed and poorly handled. Nevertheless, an increase in domestic sales from slightly over 2,000,000 pounds during the early 1950's to 12,600,000 pounds in 1962 was reported. One day's work by strawberry labor in Mexico currently (1963) costs about the same as one hour of similar work in California. Nearly all the cash cost of strawberry production is financed by companies which pack frozen berries or ship fresh ones.

Plants are usually set from May through August, but mostly in July and August, and picking begins in November. Most fields are kept for a single crop. Because of the short days and the cool climate due to the elevation, flower buds and fruit are produced the year through. Berries could be harvested the year through, but harvesting stops when the rainy season begins in late May or June. A common system of planting is in double rows with the plants 8 inches apart each way on raised beds which are spaced about 36 inches from the center of one to the center of the next. All runners are removed. The two principal hazards are frosts, which average seventeen per winter, and the rainy seasons. In 1964, about 90 percent of the plantings were grown as an annual crop; only the remaining 10 percent were bearing their second crop.

Although the soil is alkaline, summer rains are sufficient to leach out the salts. Salinity, Verticillium wilt, the absence of suitable planting stock, relatively poorly adapted varieties, and a need for the experimental evaluation of cultural practices constitute the greatest problems of this area. No breeding work with strawberries is conducted in Mexico; the industry being entirely founded on varieties originated in the United States, none of which is fully adapted to the region of their cultivation.

19

The Morphology and Physiology of the Strawberry

It is very difficult to assess the value to breeders of the particular knowledge which is available concerning the morphology and physiology of the strawberry. This knowledge ranges from facts about minute states and processes to general descriptions of the larger complexes in which these facts exist. The difficulty lies in making decisions as to which facts are germane, and which facts are not. It would seem that much of this problem persists because choices have to be made concerning for what sort of people the facts are intended and what uses this information could have for them.

The material in this chapter is supplied either to answer, or to point the way to answering questions that strawberry breeders or investigators might find important. This chapter describes the strawberry plant and its fruit, presenting in an orderly way much of the information which intensive studies have supplied. Such an ordering of information provides a general structure for those who pursue specialized investigations, while, at the same time, the data of special study is included for those who wish it.

The Plant

Figure 19–1 shows the plant of a strawberry, a bit of its root, its crown, leaves, and a fruit cluster with eight fruits, plus three flowers that did not set. There is a great deal more to a strawberry plant however than is revealed in this photograph. In all its parts it is one of the most changeable of all crop plants, and for this reason it is one of the most widely adapted and widely raised of all crops. The following pages contain a survey of some of our

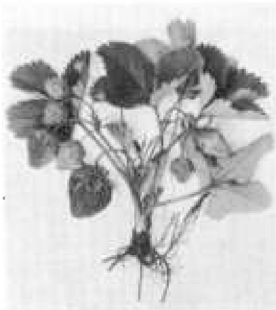


FIG. 19–1. Runner plant of Howard 17 strawberry rooted in September, which produced one cluster with 8 fruits and 3 flowers which did not set. Late-rooted plants average much fewer fruits than do early rooted plants.

knowledge of the strawberry's root, crown, leaves, flowers, and fruit as they affect our understanding of what to breed for in a variety.

The Root

Different species and varieties have very different-sized root systems, depending largely on whether they make runners freely and express their vigor in number of runner plants, or whether they make few runner plants and express their vigor in making large individual plants. Within limits, each form can be changed into the other—by restricting runners in the one case, and, in the other, by forcing more runners with nitrogen and by other means.

At the Iowa Experiment Station plants of different ages and with different root systems were compared. Succulent young plants with few lateral rootlets were not anchored as well as the older ones with a large root system, and were injured much more by heaving and by winter's cold. Figure 19–2 shows the two types of roots—the large primary ones which originate in the crown can be seen best in the youngest plant at the right, and, on the other plants, the small secondary lateral roots that make up the mass of the root system and which arise from the primary roots. There are usually 20 to 35, but there may be up to 100 or more primary roots and thousands of small rootlets in a

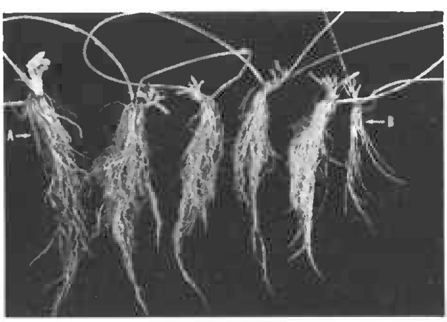


FIG. 19–2. Different root systems of a runner series in Dunlap. A) First runner plant to root; B) Last runner plant to root and the most liable to winter injury. A and all the older plants display secondary as well as primary roots, while B shows just primary roots.

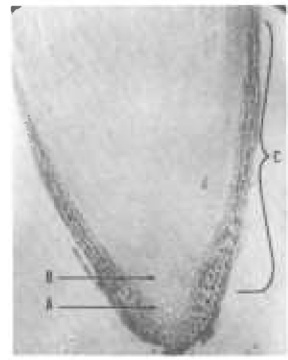


FIG. 19–3. Parts of a root. Longitudinal section showing parts of a strawberry root: A) root cap; B) growing point; C) active absorbing area.

good root system. Though the root is elastic, stretching and contracting as much as a centimeter (Kerner and Oliver, 1895), roots are often seriously broken when alternate freezing and thawing occurs. Mulching with pine needles, straw, or hay helps to prevent this sort of damage.

In general, root development is rapid in the fall and spring when there is not too great a demand for water by the leaves. Darrow (1929) found extensive root development as far north as North Carolina during December and January. Lineberry (1944) showed that ample available nitrogen greatly increased root growth during this period.

The primary roots push out rapidly from the crown and may become several inches in length before they branch. Van Tieghman and Douliot (1888) state that the primary roots arise only at the two sides of a median leaf trace, and White (1927) reports that they arise from the younger portion of the crown just outside the vascular cone. Proper depth of planting is the depth at which the plant formerly grew; if too deep, the crown may rot and the leaves fail to push through; if too shallow, the roots may dry out and be cold-injured in winter. After planting, both new primary and new secondary roots appear.

PARTS OF A ROOT. The wide adaptation of the strawberry is due partly to its variable root system, which is perennial, but perennial only in part.

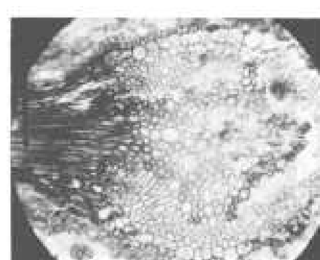
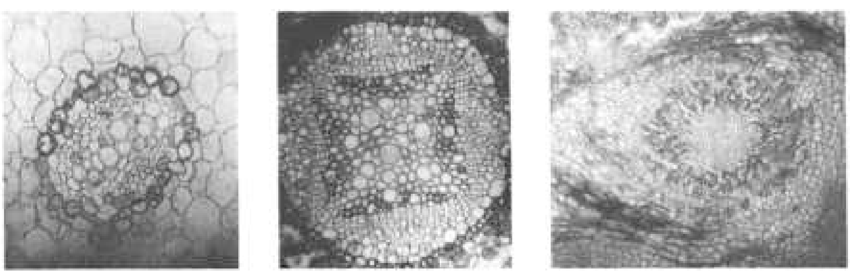


FIG. 19–4. Lateral root arising from tetrarch (having four main groups of vascular bundles) primary root. *Photo by White.*

Along the beaches of the Pacific Coast, *chiloensis* grows in sand dunes and sandy beaches, and roots of these plants may live for many years. In eastern states, *virginiana* has many primary roots, most of which live for but one or two years. The leaves of *virginiana* die with cold weather and in the spring new leaves appear from whose base new roots can grow. In general, cultivated varieties follow the pattern of *virginiana*. Nelson and Wilhelm (1957) describe the development of secondary tissues in the fall or early winter in California. First, vascular cambial strands are laid down, next a complete vascular ring develops, and finally a cork cambium. These outer cambium layers develop into a polyderm, the outer part of which is composed of a protective covering of dead cells, and the inner part of living storage tissue.

The macroscopic parts of a root are (1) the root tip, which is the region of very active growth (*Fig. 19–3*), (2) the white rootlets which take in most of the water and nutrients, often through root hairs, and (3) the corky-covered region which absorbs some water but is mostly a conducting part. Though Nelson and Wilhelm found starch in primary roots, none was found by White (1927) in Maryland, but only in the secondary roots which he considered to be the overwinter storage organ. A very short exposure—less than a minute in sunny, dry air—may kill all roots not partially corked over. A plant with only old roots absorbs water so slowly that if planted in dry, sunny weather most, or all, leaves must be removed. Figure 19–3 shows a root tip and Figs. 19–4 and 5 are of cross sections of young roots. Figure 19–4 shows a branch root arising opposite a vascular bundle in a tetrarch primary root. The vascular bundles become heavily lignified and fill the center of secondary roots. White

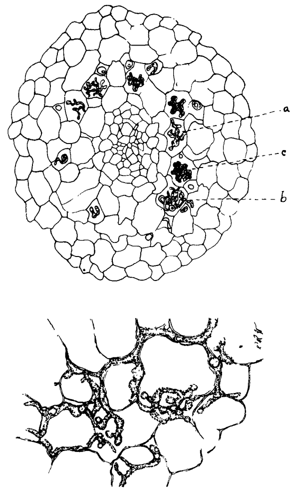
FIG. 19–5. (cont.) Cross-sections of young roots showing A) diarch, B) tetrarch steles of fibrous roots, C) polyarch stele of a primary root through which water and nutrients are transported. (After White)



A) Diarch stele of fibrous root.

B) Tetrarch stele of fibrous root considered to be usual.

C) Polyarch stele of large root.



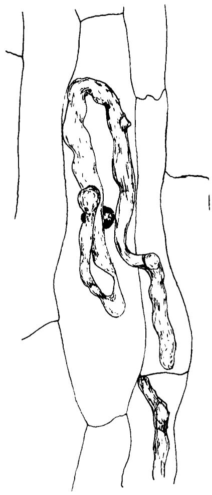


FIG. 19–6. (right) Mycorrhizal fungi in strawberry root. (After White)

FIG. 19–7. (far right) Mycorrhizal fungus within cells. (After White)

noted that the pericycle of primary roots is usually several layered and that of secondary roots few layered. The endodermis is usually distinguished only in very young roots. The root hairs mostly arise from fibrous rootlets, but some may arise from the primary roots.

SYMBIOTIC RELATIONS. Many investigators have found a certain type of fungus (Endogne sp.) in the roots of the strawberry and have suggested that it is mycorrhizal in nature (*Figs. 19–6* to *8*), that is, the fungus may furnish nutrients to the host plant. The mycorrhizal fungus is commonly called Rhizophagus or the Phycomycetous mycorrhizal fungus. White (1929) noted the restricted distribution of *chiloensis* and its association with mycorrhizal plants as an indication of a possible special need for the fungi. The possibility of the mycorrhizal fungi becoming parasitic under some conditions also was noted by him.

LIFE OF ROOT SYSTEM. In general strawberry roots grow one year and die the next, during the fruiting season. But when all flower clusters are

FIG. 19–8. Arbuscule showing apparent digestion by the host. (After White)

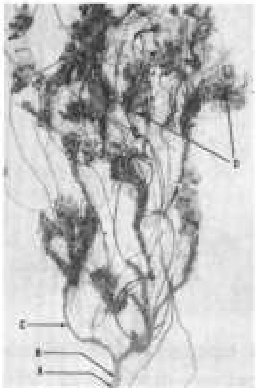


FIG. 19–9. A plant of *F. chiloensis* at least twenty years old with 33 living plants attached through living runners and roots. Main plant grew in the sand dunes of the Oregon coast. Much older plants than this one can be found.

removed from a mature plant, most of its root system does not die at fruiting time. Conditions are extremely variable and some roots may die when a few weeks old while some at least may become woody and live many years (*Fig. 19–9*). Plantations of the Ambato strawberry in Ecuador in a volcanic soil are very old and under such conditions the individual roots live for many years.

USE OF PLASTIC. Roots of the strawberry grow chiefly downward in well-drained sandy soils and a few roots may be found as deep as twenty-four inches. In clay soils they spread more horizontally. Ball and Mann (1927) found 90 percent of the roots in the top six inches of soil. In late fall, when the water table rises and the oxygen in the deeper layers becomes low, root growth is shallow. The oxygen content of the air in the soil where root growth is active is nearly that of the air above the soil, but where soil is water-logged, it may be as little as $\frac{1}{10,000}$ the normal. Black plastic in Florida and clear plastic in Japan and southern California are used to cover the soil over thousands of acres of strawberries. The sun warms the soil, and the heat does not radiate so rapidly off the soil under plastic, so that with several degrees warmer soil for several months, more extensive root and crown development occurs (*Plates 19–1a* and *b*). Root growth continues much later in the fall than does leaf growth. The plastic serves also to conserve soil moisture, and prevent soil washing and weed growth.

WHERE PRIMARY ROOTS ARISE. Under favorable conditions new primary roots grow from the crown at the base of each new leaf. About six such roots grow from each leaf base, three from each side. However, if the crown of the plant is above the ground, the new roots may not start, or may dry up before they reach the soil. If soil is drawn up around the crowns, new primary roots can grow to supplement or replace old roots. If a new runner plant (*Fig. 19–10*) lies on moist soil, roots quickly push out; if the soil dries out, the root

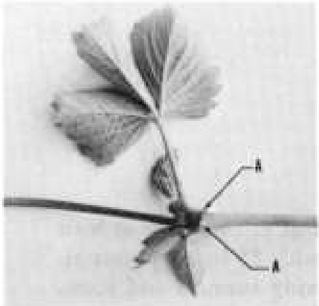


FIG. 19–10. A strawberry runner plant. Root tips pushing through at A.

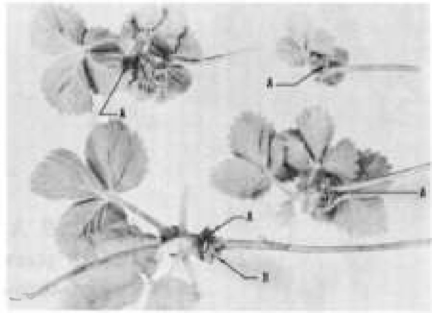


FIG. 19–11. Root tips of runner plants killed by dry weather—dead at A, still alive at B.

tips die (*Fig. 19–11*). Root distribution around the plant occurs in a characteristic fashion because the leaf arrangement is in a $\frac{2}{5}$ spiral and the roots come from the leaf bases (*Fig. 19–12*).

Top Growth of Plant

ANNUAL CYCLE OF GROWTH. In the North when a plant is set in the spring, new leaves appear with a bud in the axil of each leaf. During the summer some of the buds stay dormant, some develop into runners, and occasionally one develops into a branch crown. In the fall, depending on variety and conditions, the buds in leaf axils develop more often into branch crowns and into flower buds. In Howard 17, development of buds into runners ceases about the middle of August and bud growth from then until winter is by development of runners already initiated, by branch crowns, or by flower-bud initiation. Varieties like Howard 17 develop very large individual plants with many branch crowns that are especially productive, but make their runner plants relatively early in the season only. In northern states no additional flower-bud initiation takes place in the spring. In Maryland, a little spring flower-bud initiation occurs but it is of small value, if any. In eastern North Carolina and southward the days are short enough when spring comes, so that extensive initiation occurs and good fruit develops from winter- and spring-formed buds.

DEVELOPMENT OF PLANT AND RUNNERS. The development of a clone of the Howard 17 is shown in *Fig. 19–13*. The mother plant was set April 1, started its first runner May 27, had four runners on June 10, and by September 15 had a clone with 11 runners and 109 runner plants. The mother plant was not as large on September 15 as on June 10; its energy went to make

FIG. 19–12. Young runner plants of Klondike showing arrangement of leaves around the crown. The arrangement is a 2/5 spiral; every sixth leaf directly over the first, insuring maximum light use. Roots arise from the base of each leaf, which gives maximum root distribution. Runners from buds in leaf axil have a similar distribution.

new plants of the clone. A mother plant making as large a clone (*Fig. 19–13*) does not produce as much fruit as one which has had its runners kept off, or which does not normally produce many runners, such as plants of Midland or Earlidawn.

RUNNER PLANTS. The swollen end of a runner normally develops into a runner plant with roots from the under side and leaves and growing point at

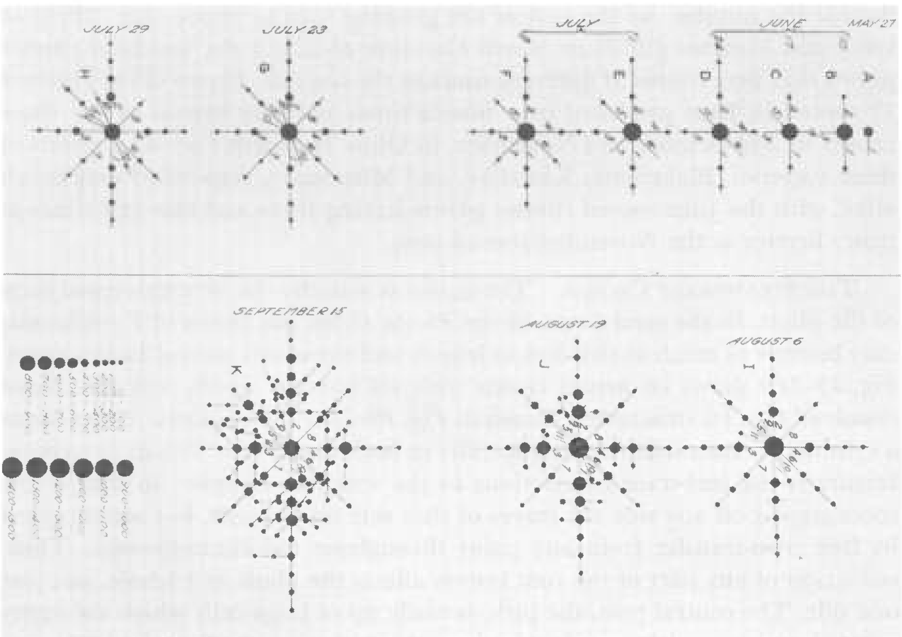
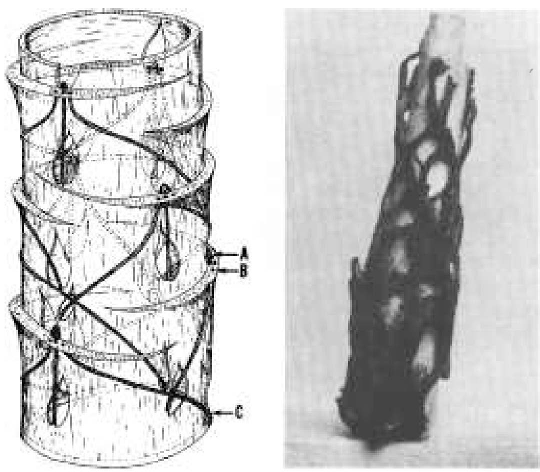


FIG. 19–13. The development of a strawberry plant and clone of Howard 17 set April 1, showing runners and runner plants from May 27 to September 25. Size of dots indicates the relative size of the plant through the season.

FIG. 19–14. A diagrammatic reconstruction of a strawberry crown showing the leaf-trace connection to the vascular cylinder of the plant. Each leaf draws its water from three distant parts of the crown, about 3/5 of the way around. With a 3–5 phyllotaxy the next leaf completes the encirclement of the crown with its vascular strands. In this diagram A is a bud, B the leaf base, and C the vascular strand. B is an actual crown with all but the xylem tissue dissolved out. (After White)



the tip. When plants are set in early spring in Maryland, runners begin to appear by the end of May and are produced throughout the summer and with most varieties until September and October. Plant propagators can often make counts of the number of runners about September 1 and expect to double the number by the end of the growing season. Shoemaker (1929) in Ohio and Morrow (1937) in North Carolina obtained the yields of runner plants that were rooted at different times in the summer. Plants of the Howard 17 rooted in June produced over fifteen times as many berries as did those rooted in late October and November, in Ohio. In North Carolina, plants of three varieties, Blakemore, Klondike, and Missionary, responded very much alike, with the June-rooted runner plants having three and one-half times as many berries as the November-rooted ones.

THE STRAWBERRY CROWN. The crown is actually the very shortened stem of the plant. In the sand dunes of the Pacific Coast the crown of *F. chiloensis* may become as much as two feet in length and the nodes several inches apart. *Fig. 19–14b* shows an actual crown with all but the woody vascular tissue dissolved out. Its structure is shown in *Fig. 19–14a.* This vascular tissue forms a cylinder with strands running spirally in both directions. The most striking feature is the leaf-trace connections to the vascular cylinder, so that if the roots are cut off any side the leaves of that side do not wilt, but are supplied by free cross-transfer from any point throughout the circumference. Thus, reduction of any part of the root system affects the plant as a whole, not just one side. The central part, the pith, is made up of large cells which are easily injured and turned brown by the formation of ice crystals in late fall and winter (*Figs. 19–15* and *19–16*). The narrow cambium layer outside the pith does not seem to be injured quite so readily by freezing as the pith, but if browned, the water and food conducting tissue of the plant is destroyed and

FIG. 19–15. Dorsett strawberry plants injured by low winter temperatures. All three plants shown were about the same size in November 1935, each having 10 leaves, but the one at the upper right was nearly killed by 0° F. temperature in December; the one at the lower right was very badly injured and bore only a few berries; while the one at the left was not injured seriously enough to damage its crop.

the plant may die. Freezing injury is easily seen by cutting the crowns lengthwise. Uninjured pith at the center is entirely white. With slight injury to the crown, but not measurable in its effect on the plant, browning of the lower part of the pith occurs; with more severe injury, deeper browning, and with real damage to the plant, browning and blackening of the outer cambium occurs. Enormous differences in hardiness of strawberries exist, from the Ambato and the Red Chilean that are extremely susceptible to freezing, to the Dunlap, Ogallala, and the native strawberries of the far North, where temperatures of below −40° are withstood, even without snow cover.

THE STRAWBERRY LEAF. As stated above, and shown in *Fig. 19–12,* the leaves are arranged in a ⅖ spiral, each 6th leaf being just above the first, for maximum light exposure. Leaves of *vesca* are thin, those of *chiloensis* thick, and of *virginiana* intermediate (*Figs. 19–17* and *19–18*). The thin leaves of *vesca* are characteristic of the humid woodland plant which *vesca* is, while those of *chiloensis,* with thick cuticles and deep-set stomata, are characteris-

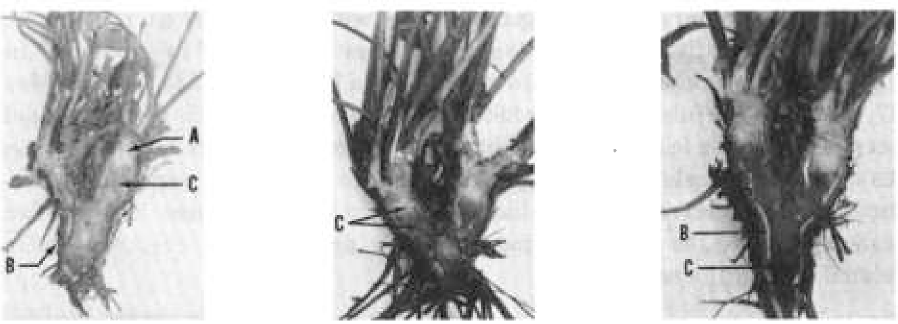
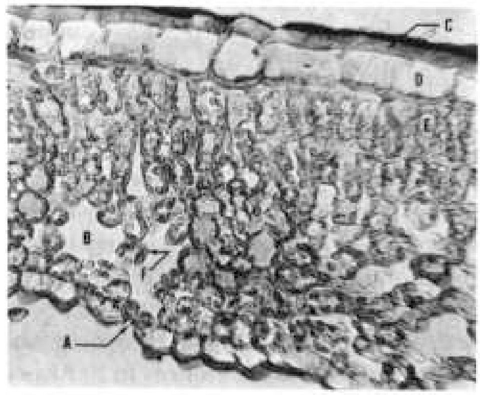


FIG. 19–16. Cold injury to strawberry crowns. Uninjured crowns would have white centers at A. 1. The most serious injury occurs when the cambium that carries sap and food is killed. Slight recovery is shown by new cambium in 1 and 3 at B. Plant 2 would not have recovered. The darkening of the centers of the crowns (C) is caused by the formation of frost crystals that break through the cell walls and oxidation follows, as in the browning of sliced apples.

Fig. 19–17. Section through a young leaf of *F. chiloensis.* A) stomata, B) air space, C) thick cuticle of upper leaf surface, D) upper epidermal cell, E) palisade cell, F) mesophyll cell. The interior cell surface exposed to air space is from 2.2 to 4.4 times greater than the exposed outer surface; in *F. chiloensis* it is about four times greater. Oxygen in the air enters through the stomata, comes in contact with the cell walls, and enters the cells. Carbon dioxide and water are given off and go out through the stomata.



tic of a dryland plant. Measurements of leaf thickness, at Corvallis, Oregon, were *F. chiloensis,* 220 μ; *F. virginiana,* 143 μ; *F. vesca,* 99 μ; Marshall, 163 μ; Blakemore, 192 μ, and *F. nilgerrensis,* 163 μ (unpublished).

The leaves of *F. chiloensis* are characteristically evergreen and live through relatively cold winters, those of *virginiana* die soon after severe frosts occur in the fall. Leaf characters of varieties and hybrids range from those like *chiloensis* to those like *virginiana.* Leaves of most varieties of the eastern United States are nearer those of *virginiana.* In the spring the embryonic leaves, enfolded by stipules, push out with warm weather, both by cell enlargement and to some extent by cell division, and in two to three weeks of warm weather reach full size. The individual leaves live for one to three months—those of Howard 17 in Maryland averaging 54 days with a range of 21 to 77 days. Though frequently killed by fungi, the leaves usually die in sequence. In *Fig. 19–13* the mother plant, Howard 17, had a leaf area of 530 sq. cms. May 27, 1311 sq. cms. July 8, but only 880 sq. cms. on September 15. If runners had been kept off, the leaf area would have been many times this. Overwintering leaves may be scarlet, purple, or green without a trace of purple, or intermediate. Most leaves are trifoliate, but some varieties have four or five leaflets; usually the latter are most recently derived from or most closely related to *F. chiloensis.*

Fig. 19–18. Stomata of strawberry leaf *(F. chiloensis),* 300 to 400 per square mm. on the lower surface, and none on the upper surface. When moisture loss through them is great enough to start incipient wilting, their openings close.

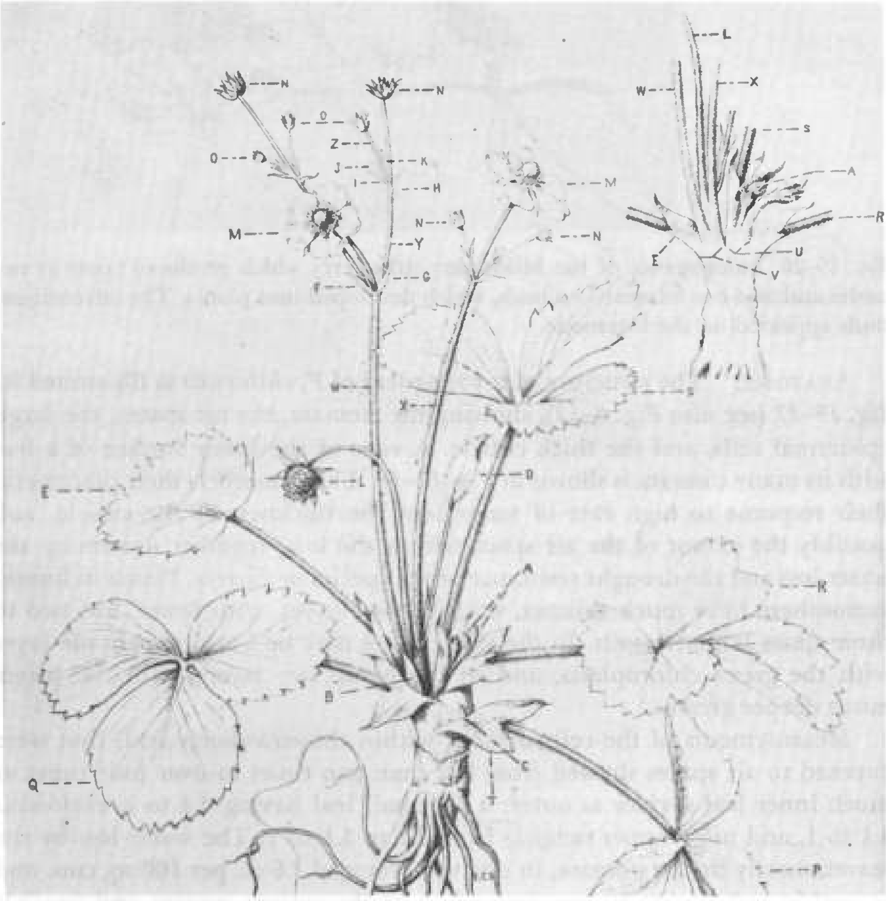


FIG. 19–19. Plant of Dunlap strawberry in flower, with a basal branching inflorescence. In the upper right-hand corner the longitudinal section of the same crown shows details of structure. April 28.

A) growing point in axil of leaf R.
B) growing point in axil of leaf Q.
C) growing point in axil of leaf P.
E) first bract of inflorescence
J and K) bracts at nodes on branch Z.
L) primary flower
MM) secondary flowers
NNNN) tertiary flowers
OOO) quarternary flowers in longitudinal section (*above right*)
P) oldest leaf of main crown
Q) next oldest leaf of main crown.
R) youngest leaf of main crown.
S) new leaf on new growing point A.
T) stipule of leaf P.
U) new crown in axil of leaf R from V to base of E = very short pedicel.
V) inflorescence terminating original crown
W) branch of inflorescence from axil of E.
X) branch of inflorescence from axil of bract D
Y) branch of branch W from axil of bract G.
Z) branch of branch Y from axil of bract I.

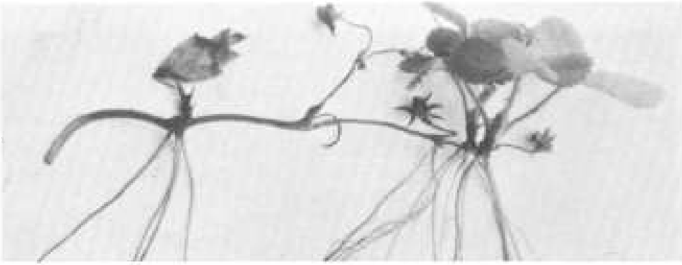


FIG. 19–20. Inflorescence of the Missionary strawberry which produced roots at two nodes and also two adventitious buds, which developed into plants. The adventitious buds appeared on the internode.

ANATOMY. The structure.of a young leaf of *F. chiloensis* is illustrated in *Fig. 19–17* (see also *Fig. 8–12*), showing the stomata, the air spaces, the large epidermal cells, and the thick cuticle. A view of the lower surface of a leaf with its many stomata is shown in *Fig. 19–18.* Their number, their placement, their response to high rate of water loss, the thickness of the cuticle, and possibly the extent of the air space within the leaf, together determine the water loss and the drought resistance of the species or variety. Plants in humid atmosphere have much thinner, much larger leaves, with fewer, but two to three times larger, vessels. In the shade there may be but one palisade layer with the green chloroplasts, and in the open, two layers, with the leaves much deeper green.

Measurements of the cell surfaces, within the strawberry leaf, that were exposed to air spaces showed from less than two times to over four times as much inner leaf surface as outer; a Marshall leaf having 4.4 to 1, *chiloensis* 4.1 to 1, and *nilgerrensis* ranging from 2.2 to 3.1 to 1. The water loss by the leaves, mostly by the stomata, in one test averaged 7.6 cc. per 100 sq. cms. and ranged from 5.3 cc. to 10.8 cc. depending on the variety, species, and weather conditions (Darrow & Sherwood 1931). The strawberry has more stomata per square millimeter than many plants, 300 to 400 versus 246 for the apple, by way of example.

The amount of water a plant uses in a day is dependent on its leaf area, the extent of its root system, the water supply, the temperature, the intensity and duration of light period, and the humidity. On sunny days in August, a plant with ten leaves may use a third of a pint of water, but on cloudy days not over half as much. With loss of water greater than the intake, the plants wilt, and if it continues for several days the older leaves may die. When wilting is this severe the smaller roots are in dry soil and die. Such a plant has a restricted root system for taking in water and nutrients, and a restricted top for manufacturing food. Many weeks may be required for such a plant to regain lost leaves or roots.

The chlorophyll of the leaf manufactures the food just as long as the sun furnishes energy and as long as water supplies the nutrients and carbon dioxide to the leaf and carries the food and waste away. When it is dark, the chlorophyll stops food manufacture. Also, if the supply of carbon dioxide from the air stops, as when the stomata close, food manufacture stops; so also when the nutrient or water supply ceases, or the sugar is not carried off, or the temperature is too high or low, or poisons injure the chlorophyll. Carbon dioxide in the air goes into the interior of the leaf, chiefly through the stomata. The extensive air spaces of the interior of each leaf make possible the circulation of the carbon dioxide, which forms about three parts per 10,000 of the air volume, to much of the plant. The carbon dioxide is dissolved in the water in the cell walls which makes it available for plant processes.

LEAF NUMBER AND YIELD. The number of leaves per plant in late fall is used as a measure of leaf area, which in itself is directly related to the number of fruits borne by the plant the next year. Many of the buds in leaf axils turn into flower buds, and usually, under average conditions within a variety, the more leaves, the more flower clusters. The older runner plants in general have the most leaves and greatest leaf area and produce the most fruit. A two-leaf plant in October may have one small fruit cluster of three to five berries, while a fifty-leaf plant may bear a quart of berries. Different varieties have different numbers of fruit clusters per crown and different types of flower clusters (see page 335).

In the spring the embryonic leaves within the bud of each crown develop as soon as growth commences. By the time the first willows and narcissus are

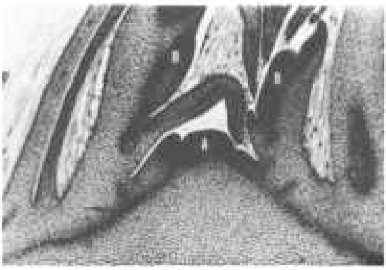


FIG. 19–21. Section through a crown of the Kalicene variety showing a flower bud just starting to develop on September 1 in Maryland. The broad point at A is the flower bud; B is an embryo leaf, magnified many times.

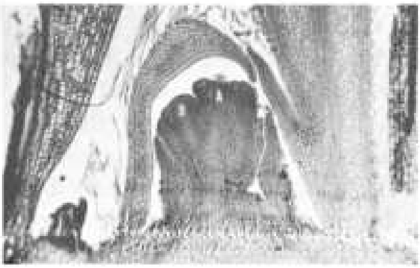


FIG. 19–22. Section through a strawberry crown after the flower cluster started to develop. This stage is usually reached seven to ten days after that in FIG. 19–21. A) primary flower bud, B) secondary flower bud. Highly magnified.

in bloom, one or more of the overwintering leaves have unfolded. Leaf growth and production of new leaves is rapid from then on.

Development of Growing Points. A drawing of a plant as it appears at the blossoming season is given in *Fig. 19–19.* This plant developed from a runner tip during the previous summer. In the fall the growing point at the end of its short stem was transformed into a flower bud which, in turn, in the spring developed into the flower cluster shown. Because its growing point became a flower bud, no further vegetative development of the plant could take place except as new growing points appeared, and, except through such new growing points, no leaves in addition to those already initiated could develop (see p. 327).

In the plant shown, the three leaves P, Q, and R had already been initiated in the fall before a flower bud formed. In the spring these quickly unfolded and reached full size at the time the drawing was made. The oldest leaf labeled P is the lower one, the next younger Q and the youngest R. It should be noted that the broad petiole bases of each of these three leaves encircle the entire stem or crown of the plant. Before unfolding, these petiole bases together with their stipules cover and protect the growing-point. In winter this protection is especially important.

The plant illustrated in this figure had sufficient vigor in the fall to start the bud in the axil of leaf R, which is just below the terminal. This developed to such an extent that a fourth leaf S has now expanded. The base of this leaf, however, encircles only the bud A. Growing-points B and C may be seen in the axils of leaves Q and R. If growing point A also turned into a flower bud then growing-point B would continue the growth of the plant. This has actually occurred, as can be seen in the longitudinal section of the crown in the upper right-hand corner of the drawing. Bud A is seen to consist of a rudimentary leaf and the small flower buds of a second inflorescence. Still other growing-points can be found under the old leaf bases shown circling the crown below the leaf P. If the plant should be given exceptionally good growing conditions, growing-points B and C might both develop into additional crowns. If growing points develop during the summer they are runner tips, but in the fall with shortening days and lower temperatures they become flower buds.

Guttridge (1959) exposed one plant each of pairs of runner plants joined by runners to long daily light periods. The effect of the long light period on one plant of each pair was to increase petiole lengths and leaf size and to delay flower initiation in the other plant of each pair exposed to a short day, and he concluded that there was good evidence for the existence of a growth-regulating substance(s) that promoted vegetative growth and inhibited flower initiation and that this substance controlled the vegetative-fruiting responses of the strawberry. By cutting the tops off in August soon after the previous harvest and so removing the flower inhibition produced by leaves, yields were increased from 10 percent to about 100 percent.

Runners. Runners are produced all summer from buds in the axils of new leaves, and in succession as the leaves develop. Guttridge suggests that the first axillary bud to differentiate in the spring becomes the first runner. These runners are two nodes and two internodes in length. The more rapidly the plant grows the more runners are produced. Their size and final length depend on growth conditions and varietal characteristics. Long runners may be advantageous in placing the runner plants that develop at their tips at a distance from the mother plant. Leading varieties have runners of medium length. The two internodes making up the runner are on the average about equal in length. The bud at the first node is usually dormant, but may develop into a runner; such branch runners are usually much smaller than the primary runner; if the runner tip is cut off, a plant may form instead of a branch runner. In the spring, plants with no flower buds start leaves and runners before those with flower buds, and those with few flower buds before those with many. Plants producing runners as early as the first fruit ripens, usually produce less than those starting runners after harvest. The *virginiana* normally starts runners much earlier than *chiloensis*; and the runners of *virginiana* are much more slender than those of *chiloensis*. The runners of both are variable in length; both have long or short runners, depending on conditions of growth. Most runners survive until winter, though in the southern United States many die earlier. Runners of *chiloensis* tend to survive winter's cold, and often do on the Pacific Coast. Its runners may even become part of the stem of an old clone and live for many years (*Fig. 19–9*). Also, in mild climates, by forcing them to grow erect, the runners of ordinary varieties may live for a full year. (The ridiculous "climbing" everbearing strawberry!)

Because flower buds, runner buds, and branch crowns all arise as buds from leaf axils, intermediate structures might be expected and are known (*Fig. 19–20*). Under moist conditions the inflorescence may root at one or more of its nodes and even produce plants. Etter reported a variety having inflorescences that produced runners. Roots are often produced by inflorescences when the first internode is short and the first node has contact with soil under the leaves. *F. orientalis* in Maryland often had long inflorescences that rooted.

Anatomy. The runner has a thick cortical layer surrounding a cylinder of very large vessels arranged in bundles separated by rays; the cylinder in turn surrounds a central pith of thin-walled cells. The whole structure is well adapted for carrying the large amounts of water and nutrients necessary to establish runner plants. Food and water may be carried freely in either direction, and the parent plant may support, or be supported by, a large clone of runner plants for months.

Gay (1857) first described the development of the runner series. At the runner tip a new plant is formed, the first leaf of which is a scale, or bract-like structure, but whose leaf traces arise in the crown of the new plant. The bud in the axil of the first leaf is well placed to receive water and nutrients, and is most likely to become a runner and to continue a runner series. It is, however, a new runner, not a continuation of the original runner. In everbearing varieties the bud in the first leaf axil may be a flower bud. Gay noted that in *F. viridis* of Europe the first runner may be two nodes long, but that the next runners are one node long.

FLOWER-BUD DEVELOPMENT. In Maryland, the first visible change of a strawberry plant's growing point into a flower bud is a broadening of the very tip as shown in *Fig. 19–21,* in this case occurring September 1. In seven to ten days this has developed as shown in *Fig. 19–22.* By October 1 the parts of flowers can be distinctly seen *(Fig. 19–23)* even with the unaided eye, and by November 20 most of the fall development has taken place (*Fig. 19–24*). Crowns of Howard 17 showing flower buds natural size are shown in *Fig. 19–25.* In the spring the parts of each flower in a cluster enlarge but most of the differentiation has already taken place the previous fall. In southern England (Robertson, 1954) early-rooted runners began to form flower primordia as follows: Auchincruive Climax in early August, Royal Sovereign early to mid-September, and Sir Jos. Paxton in late September.

Development of Inflorescence

In *Fig. 19–19,* a basal-branching flower cluster is shown, the details of the branching at the base being illustrated in the longitudinal section in the upper right-hand corner. The method of development of such a cluster may be understood best by comparing it with a flower bud as it develops in the fall in the crown of a plant. Such a flower bud is shown in *Fig. 19–22.* Here the primary flower has clearly developed from the terminal stem growing-point while the secondary flowers developed from lateral buds. As shown in *Fig. 19–22,* the pedicel of the primary flower L does not often elongate to equal those of the branches, especially when the branching is basal.

In the strawberry buds arise only from leaf axils and the branches of the inflorescence arise only from bract axils, the leaves being modified into bracts.

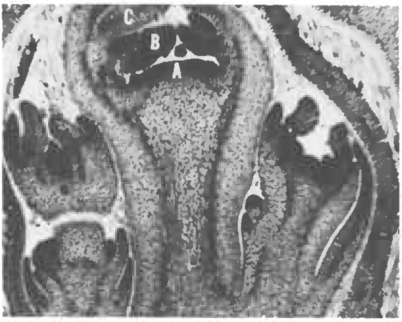


FIG. 19–23. (left) A still later stage showing the individual flowers on October 1. A) part that develops into the berry, B) stamens of the flower buds, C) petals. Highly magnified.

FIG. 19–25. (right) Crowns of Howard 17 with flower buds on November 15 in Maryland.

In *Fig. 19–19,* branch W arose from the axil of bract E and branch X from the axil of bract D. On branch W the flower M is terminal, but two branches had originated—the first in the axil of bract F and the second in the axil of bract G. Each of these branches has terminated in a flower N, but each has also branched.

In the inflorescence shown each branch has three internodes—a relatively long, a very short, and a second relatively long one. Thus branch W terminates with flower M. At W is a long internode, between the bases of F and G is a very short internode, and between flower M and bract G a second relatively long internode. Branch Y terminates in flower N. It has a relatively long internode at Y, a very short one between H and I, and another relatively long one between I and N. Though the inflorescence in the drawing has a

FIG. 19–24. Primary and secondary flower buds of the strawberry on November 20 in Maryland. A) basal-branching primary crown, B) secondary crowns, a) primary flower bud, b) secondary flower buds. Magnified several times.

very short peduncle (from V to the base of E in the longitudinal section) in most varieties of the strawberries a fairly long peduncle is usually produced. Typically, then, the primary axis and all of its branches have the long, short, and long internodes. Where the peduncle is very short, as in *Fig. 19–19,* the inflorescence is said to be basal-branching.

The inflorescences of many strawberry varieties, however, are quite irregular. Instead of two, several branches may start out at the base or at any point on the peduncle. The primary axis may then have one or two long internodes and several very short ones. Occasionally the primary axis may have several long internodes, but this is not common, at least in most varieties. (See p. 335 for further discussions of inflorescence types.)

Flower Buds, Light, and Temperature. With most varieties, when in late summer and fall the photoperiod shortens to eleven to thirteen hours, the bud in a leaf axil instead of becoming a branch crown or a runner becomes a flower bud. Van den Muyzenberg (1942) found that at least six days and up to 14 days of short photoperiods (six to twelve hours) were necessary for flower bud initiation, with six to eight weeks needed for the beginning of flowering in the Deutsch Evern variety. Commercial growers of Deutsch Evern shortened the days for four to five weeks from the last of May to about July 1 to start flower bud initiation and to initiate enough flower buds for a fall crop. Experimentally Moore and Hough (1962) were able to obtain flower bud initiation in the Sparkle variety by shortening the day from sixteen to eight hours at 70° F day and 65° night temperature, after twelve to fifteen daily cycles. They had previously obtained initiation within twenty-one days. If large plants are dug September 1 and placed in a warm greenhouse with supplementary electric light for four to five hours, the flower buds already initiated develop, but no new ones do. Studies by Waldo (1930) and others have shown that for the latitude of Maryland the first flower buds of Howard 17 are initiated in the latter part of August and additional ones are initiated later. All continue to develop until freezing weather. Actually, flower-bud initiation results when either the daily light periods are shortened, or the temperature is lowered. Along the coast of California with its cool climate, many varieties initiate flower buds all summer long. Such varieties are especially sensitive to temperature. However, up north, along the coast of Oregon and Washington where the temperatures are as cool, the light periods of midsummer are enough longer so that the same varieties do not produce as well. Likewise, southward at Irapuato, Mexico, the light periods are enough shorter in midsummer, and the elevation high enough for moderate temperatures, so that varieties like Florida Ninety, Klondike, Missionary, and others make flower buds and produce a crop the year through. From Mexico south to the equator and to about 15 to 20 degrees south of that at elevations

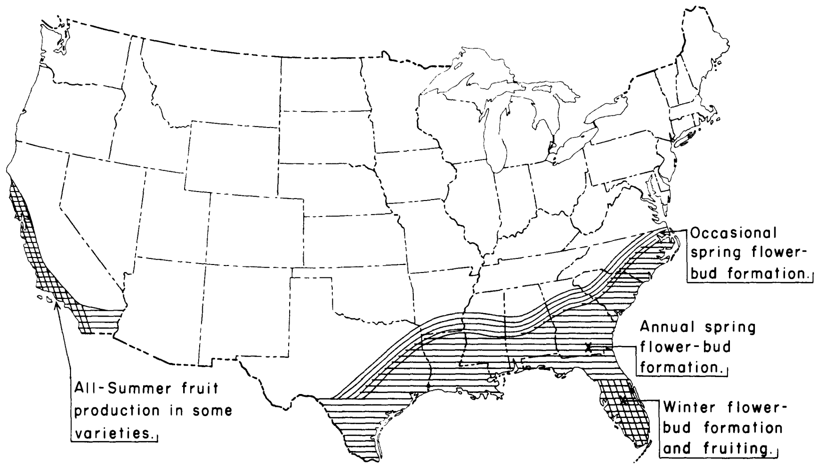


FIG. 19–26. Map showing regions of sufficient winter and spring flower bud formation for a commercial crop in southern states and in California. In the cross-lined area spring flower bud formation usually or always occurs with some varieties. The series of lines along the border of this area in the South represents areas where winter and spring fruit bud formation occurs in years of mild winters. In the cross-lined area of California, fruit bud formation continues throughout the summer in some varieties. Though occasionally flower buds form in early spring as far north as Washington, D.C., most flowers are sterile and no commercial crop occurs.

above 3500 ft., most strawberry varieties bear the year through. However, the elevation must be sufficient to make the temperature cool enough for the particular variety. Missionary grows and fruits probably best of any variety in the warmest temperatures under short days, Florida Ninety may do as well in some tropical areas.

Flower buds initiate in the short days of fall, winter, and early spring whenever the temperatures are high enough. The map (*Fig. 19–26*) shows where in southern states initiation continues all winter, or intermittently all winter. In Florida it continues all winter, in southern Louisiana nearly all winter, and in eastern North Carolina it occurs when warm periods occur. In Louisiana and North Carolina temperatures are high enough for plant growth to occur often in late February and through March, when days are short enough for flower-bud initiation. What is called a "crown crop" is harvested, usually, in May. To increase this crop growers use plastic covers to warm the soil and increase root and crown development. Further north in Maryland, flower bud initiation in March, and probably in cool Aprils, may occur, but never enough to be worth harvesting; flower clusters from such buds are mostly sterile and those that do set, produce small berries. Along the coast of California, with low temperatures that are still high enough for flower bud initiation, commercial crops are produced by many varieties all summer (see California industry, p. 231).

Darrow and Waldo (1929), after testing about 140 varieties, suggest that the response to daily light periods, to temperature, and to a rest period is so characteristic that the regional adaptation of new originations could be determined by growing them in the winter in the greenhouse. Later (1934) they state that "the Blakemore has not grown as well as Missionary in the short days of low light intensity of winter and this may be interpreted to indicate that it will not succeed as well in Florida as the Missionary. In actual tests (and by grower experience) in Florida this seems to be borne out." Northern varieties do not grow under the short days of winter even under a high temperature unless first given a rest period. Southern varieties may grow so vigorously so late in the season in the North that few flower buds are formed, and they are relatively unproductive.

Downs and Piringer (1955) reported on responses of everbearing and June-bearing strawberries to photoperiods in summer. When grown at photoperiods of eleven, thirteen, fifteen, and seventeen hours, all three everbearers produced flower clusters, but produced more under the longer light periods. Red Rich produced 5.0 clusters at thirteen hours and 23.2 at seventeen hours. They tended to produce the most runners at thirteen-hour photoperiods. Three June bearers produced their most runners at the fifteen-hour photoperiod. Climax produced a few flower clusters at the eleven- and thirteen-hour photoperiods, but none at fifteen- and seventeen-hour ones.

The response to daily light periods and to temperature is so characteristic that it has been suggested that by growing varieties in the winter in the greenhouse their regional adaptation would be indicated.

Rate of Flower Bud Development. Waldo (1930) found that in Maryland different varieties initiated flower buds at different times, but that in general the degree of development at the end of the growing season was correlated with the time of initiation. A physiological test of initiation (referred to above) consists of placing plants in a warm greenhouse at stated intervals, such as September 1 and 15, October 1 and 15, and lengthening the daily light period with artificial lights. Under these conditions only flower buds already initiated develop flowers. In Maryland, in one comparison, Missionary took 15 days to develop from initiation to a stage showing primary, secondary, and tertiary flower buds, and fifty-five days to fully developed buds, while for Dunlap the periods were six and thirty-five days. In Oregon the Marshall begins to initiate flower buds by September 1, but Ettersburg 121 not until about November 1. However, the latter was more evergreen and continued development at lower temperatures than Marshall (Waldo and Darrow, 1932).

FLOWER-BUD DEVELOPMENT AND SIZE OF PLANT. Davis (1922) first called attention to the relation of time of runner-plant formation to yield. Runner-plants formed in October produced less fruit than those produced in August. Morrow (1931) extended this study, and Sproat and others (1935) showed that the yield per plant was related to the number of leaves as a measure of leaf area; the older runner plants having the most leaves and the most fruit the following year. However, if the older plants are crowded, they may have few leaves and few fruits. Leaf number in the fall has been found a good measure of possible yield the following spring.

FLOWER BUD DEVELOPMENT AND MOTHER PLANTS. In both Florida and California plants are set and handled so that large individual plants having no runner plants are fruited. These produce maximum crops. In one study (Darrow, 1929) mother plants with runners kept off produced 132 fruits while mother plants with runners allowed to root to September 1, produced 43 fruits. This relation also holds true for northern regions, but so far it has been difficult in the Northeast to bring to fruiting a full stand of fully developed plants. Losses of plants from insects and diseases and weakening of plants from these and unknown causes have so far prevented this sytem from being generally adopted in northern states, even though ideal varieties for this system—Earlidawn and Midland—are available for some areas.

INFLORESCENCE TYPES. The number of crowns, inflorescences, and flowers per plant in matted rows produced by 48 varieties at Glenn Dale, Md., averaged 1.6 crowns, 2.4 inflorescences, and 23 flowers under one set of conditions (Darrow, 1929). The inflorescence is really a modified stem and at each node of the inflorescence a bract replaces the leaf, while the bud in the axil of the bract develops into a branch of the inflorescence. The bract at the first node is often as large as a leaflet of a true leaf. Sometimes it consists of three leaflets. Bracts at the second, third, and later nodes are progressively smaller. The branching of a typical inflorescence has one primary, two secondary, four tertiary, and eight quaternary flowers. However, different varieties have different types of inflorescences and even any one variety may have many types depending in part on where it is grown. Each branch has three internodes: a long, a very short, and a long one. The effect of the very short internode is to make it appear that there are opposite branches at the nodes; however, the lower branch has the larger bract and the flower and berry on

FIG. 19–27. Diagram of the strawberry flower, according to Schaffner. The pistil-bearing swollen axis, or stem end, is expanded to form the receptacle. The sepals, petals, stamens, and pistils are arranged on the 5-spiral plan just as the leaves of the plant are.

the lower branch are slightly larger and earlier. The first internode of many inflorescences and even of their first branches may be very short, and the inflorescence be basal branching. Darrow (1929) found 76 types in 323 inflorescences of Howard 17, of which 76 inflorescences were basal branching, and 124 types in 536 inflorescences of Dunlap, of which 88 were basal branching.

FLOWER STRUCTURE. The flower arrangement of the strawberry is typically five-parted as shown in *Figs. 19–27* and *28*. In vigorous plants extra flower parts are common both in wild and cultivated kinds (*Plates 19–2c to d*). Under unfavorable conditions, as in poor light and at low temperatures, flower parts are suppressed in a regular pattern, first the stamens, next petals, then sepals, and epicalyx, and finally the pistils. When growth is slow at flower-bud development, the calyx and epicalyx may become foliar. How wide petals, sepals, and epicalyx open is in part genetical, in part environmental.

FLOWER TYPES. Flower types have already been referred to as male or staminate, perfect-flowered or hermaphrodite, and female or pistillate; all the higher chromosome numbered (hexaploid and octoploid) species have

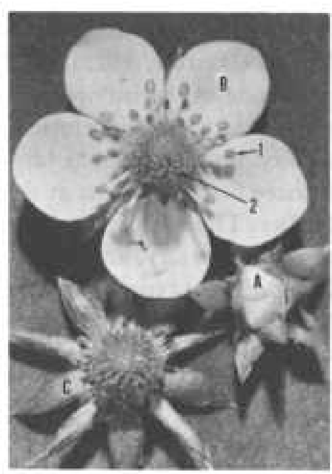


FIG. 19–28. A) a strawberry bud just opening, B) a fully opened flower, C) pistils pollinated, petals fallen off. The pollen which comes from the anthers at the ends of the stamens (1) is carried by bees to the stigmas at the ends of the pistils (2) to effect pollination. If all pistils are pollinated, a perfect-shaped berry may develop. If few are pollinated, an irregular-shaped berry develops.

these types in the wild. Pistillates tend to set all flowers. Males set none, but the fertility of flowers with stamens grades from pure males with no pistils through all degrees of pistil development and fertility to those setting practically all flowers as in Rockhill (*Fig. 11–7*). Longworth (1854) reported that on the average not one in 10 flowers of hermaphrodites set fruit. Today hermaphrodites develop far more of their flowers into fruit than that.

Several records for the average set of flowers of perfect and imperfect-flowered varieties have been made: in Minnesota, 67 percent vs. 72 percent; at Salisbury, Md., 66 percent vs. 88 percent; at College Park, Md., 64 percent vs. 82 percent; and at Glenn Dale, Md., 72 percent vs. 94 percent, 64 percent vs. 95 percent, and 61 percent vs. 90 percent in different years and conditions. At Glenn Dale, Md., one season, seven pistillate varieties averaged 31.7 fruits per plant and 1.7 flowers not set. Twenty-one perfect-flowered varieties averaged 10.2 fruits and 8.8 per plant did not set. If allowance is made for non-setting equal to that of the pistillate, then perfect-flowered varieties averaged about 70 percent fertile and 30 percent infertile.

Change of locale affects flower set also. At Glenn Dale, Maryland, the European variety La Constante set three fruits, and 39.8 flowers did not set; and the European White Pineapple set 1.2 fruits, while 18.4 flowers did not set. Also, Ettersburg 121, which succeeds in Oregon, set 0.2 flowers, while 17.2 did not set. The Howard 17, which replaced many varieties, set 16.4 and 2.7 did not set. It is not yet known why a variety like Ettersburg 121 that was so productive on clay soils in Oregon is so unproductive in Maryland and the same is so for the affected European varieties. Often the earlier formed flower buds on a plant develop flower clusters that set more fruit than do the later flower buds on the same plant.

Under some conditions varieties called pistillate develop a few stamens with pollen. Duchesne observed this (see p. 49). Meehan stated that in moist air and under favorable surroundings pistillate varieties often become hermaphrodite. Hovey and Crescent were apparently such varieties. Some-

FIG. 19–29. An intermediate, part pistillate, part hermaphrodite seedling. Two flowers to the left are pistillate, others have abortive stamens only and still others are good ones. (Portia x Kalicene)

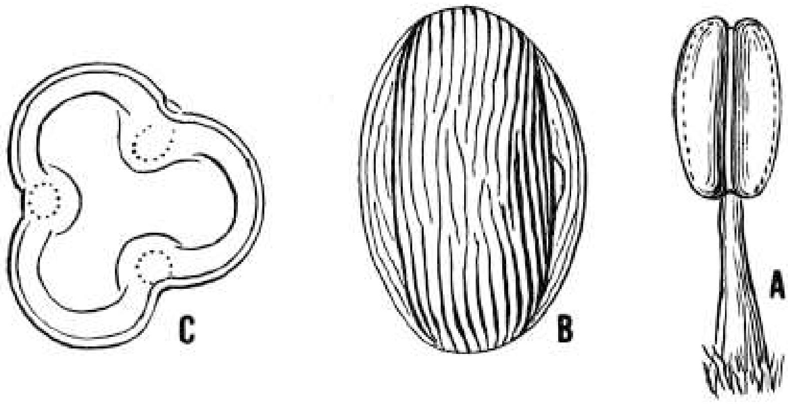


FIG. 19–30. A) Strawberry stamen-anther, opening by longitudinal slits along the sides. B) Pollen grain, general view, × 2250. C) Pollen grain, cross-section, × 2250. Drawn by A.R. Mann, who gives the size of a pollen grain as 16μ by 24.7μ.

times varieties like Glen Mary that seem to have good stamens under some conditions do not set well by themselves and set far better when cross-pollinated. Its flowers are functionally pistillate part of the time. By growing Dunlap in pure sand Gardner obtained 91 pistillate and only 2 hermaphrodite plants. *Fig. 19–29* shows two flower clusters from one plant with pistillate flowers on one and hermaphrodite flowers on the other.

STAMENS. The stamens in multiples of five, commonly 20 to 35, are usually arranged in three whorls (*Figs. 19–27* and *19–28*), although Shaffner shows but two (*Fig. 19–27*). They differ in size and length and are of a deep golden color when they contain good pollen (*Fig. 19–28* and *Plate 19–2a*). When pollen degenerates at a late stage the anthers are not full sized and are pale yellow (*Plate 19–2f*). Poorly developed stamens—"staminodia"—and stamens with good pollen may be found in the same flower (*Plate 19–2e*).

FIG. 19–31. Anthers cracking open with pollen coming out. In cracking, some pollen is thrown onto the pistil tips as shown here. Bees are essential for the best pollination in the field.

Pollen is mature before the flower or the anthers open, but usually the anthers do not crack until after the flower opens and the anthers dry a little. The anthers open at the sides (*Figs. 19–30* and *19–31*), sometimes under tension so that pollen is thrown onto pistils and petals; the pollen is at first heavy and sticky but later becomes dry and is carried by air currents. Pollen (*Plate 19–1*) remains viable for several days under ordinary conditions but if dry can be kept in a refrigerator for weeks. Valleau found abortive pollen in anthers of all 120 varieties he examined, the range being from less than 1 percent to 100 percent and the average being a little over one-third. No self-incompatability was found in cultivated varieties.

STERILITY AND PARTIAL POLLINATION. When the first flowers of perfect-flowered varieties open and set well, but the later flowers only partially set or do not set at all, natural sterility is the primary cause. But if the first flowers develop into nubbins, and yet the later flowers produce good berries, the poor development is probably due to partial pollination (*Fig. 19–32*). Petals and calyx may cover some of the pistils and prevent pollination. Frost and insect injury may also cause nubbins and both as well as fungi may kill the flowers. Sterile flowers are soon infected by fungi which makes diagnosis as to the cause of non-setting often difficult.

Pollen Production and Climate

Those who have worked with the strawberry have learned that plants of the same variety vary in their pollen production in any one area, as well as in different areas. The first flowers to open in the spring of many varieties may develop good anthers with abundant pollen in some seasons, but almost none in other years. Pistillate flowers that have abortive stamens may under other conditions have good stamens. Castle (1904) noted that Crescent and Stirling Castle were pistillate in the United States, but perfect-flowered in England. Hovey, Longworth, and others noted this response to conditions, in the early 1800's.

PISTILS. The pistils are arranged in a regular spiral on the stem end of the receptacle and the seeds also, as may be noted by examining well-shaped berries (*Fig. 19–34*). The general structure of a pistil is figured by Winston as shown in *Fig. 19–33*. The stigma is rough and sticky. Strasburger (1939) pollinated flowers of *F. virginiana* with pollen of *moschata* and found typical fertilization twenty-four to forty-eight hours later. The pistil base, the achene, commonly called the seed, contains one ovary. The ovary contains one ovule. The achenes are attached on the underside to the receptacle by fibro-vascular

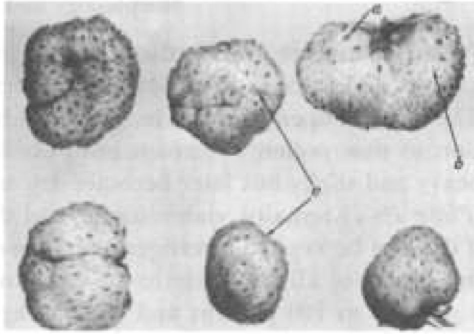
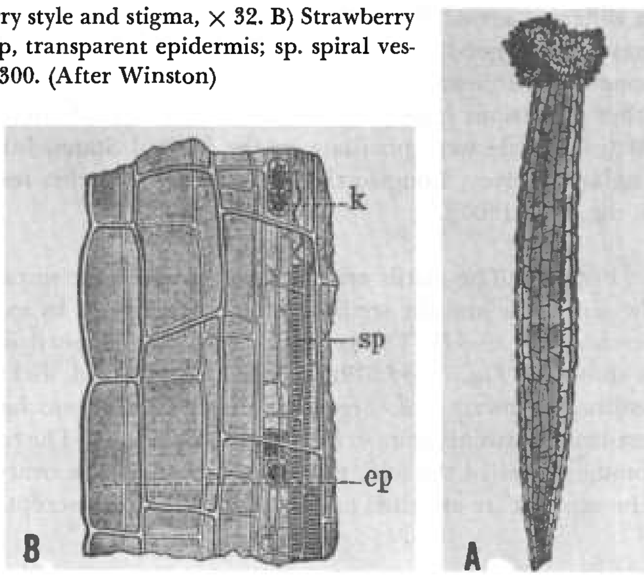


FIG. 19–32. Poor pollination causing nubbins. Relatively few pistils on these fruits were pollinated. Fully pollinated, the berries would have been 2 to 5 times as large. a) large seed, from pollinated pistil, b) small seed which did not develop because pistil was not pollinated, c) sunken areas where many pistils were not pollinated.

strands as well as by the epidermal layer. The style is also on the underside of the achene near its attachment to the receptacle. The style commonly persists until the berry is ripe. The achene is fully developed several days before the berry is mature. Each achene contains a single seed; as described by Winston (1902), there is a many-layered outer hard pericarp, next a soft thin testa, and then a single-layered endosperm enclosing the embryo. The food is stored almost entirely in the two cotyledons in the form of protein and fat with no starches.

No true after-ripening period at low temperatures is necessary for most of the seed and seed may be sown as soon as the berries are ripe, or held in the refrigerator dry for years. However, quicker and more uniform, but no greater, germination is obtained if the seed is stored moist for a month in an ordinary

FIG. 19–33. A) Strawberry style and stigma, × 32. B) Strawberry style in surface view. ep, transparent epidermis; sp. spiral vessels; k. crystal cells. × 300. (After Winston)



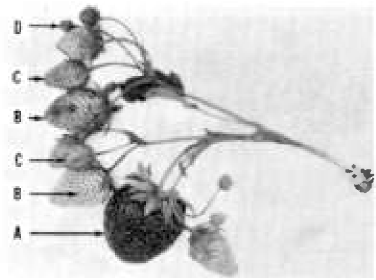


FIG. 19–34. Fruit development. A) Primary berry; it is the largest and ripens first. B) Secondary berries; these ripen next and are next largest. C) Tertiary berries; these ripen still later and are next smallest. D) Quarternary berries which ripen last and are smallest. *See also* FIG. 19–1.

refrigerator at 32° to 40° F. Seed of the different varieties and species vary greatly in speed of germination beginning in four days and continuing for three to four weeks. Henry (1934) reported that 25° C. (= 77° F.) gave the best germination; the amount of germination of hybrid seed ranging mostly from 58 to 94 percent, with one cross as low as 22 percent. Scott (1948) reported that treating with sulfuric acid for fifteen minutes hastened, but slightly lowered germination, and soaking in chlorine solution for eight hours also hastened germination (1955). Bringhurst and Voth (1957) in California obtained maximum germination after two to four months' storage moist at 32 to 34 degrees F.

THE BERRY, SIZE, POSITION, AND NUMBER OF SEED. After fertilization, the ovules develop rapidly. A hormone is produced quickly and the flesh around each fertile seed starts swelling (*Fig. 19–32*). Valleau (1918) and Gardner (1923) both pointed out that the primary berry of a cluster is the largest and that the secondary, tertiary, and quaternary are progressively smaller (*Figs. 19–1* and *19–34*), in their tests averaging 80 percent, 47 percent, and 32 percent of the primary. Darrow (1929) reported 48 percent and 33 percent as compared with the primary for the average of secondary and tertiary of one variety. However, Darrow (1929) also reported that for basal branching clusters secondary berries were 91 percent of the primary by weight. In general, the berries on basal branching clusters average far larger than on high branching ones (*Fig. 19–36*). No basal branching was observed in Klondike in Maryland, yet it regularly produces basal branching in the deep South. For some varieties high branching clusters indicate that they are being grown north of the area where they succeed best. Vigorous plants of varieties with many basal branching inflorescences bear more large fruit than similar plants of varieties with chiefly high branching clusters (*Figs. 19–35* and *19–36*).

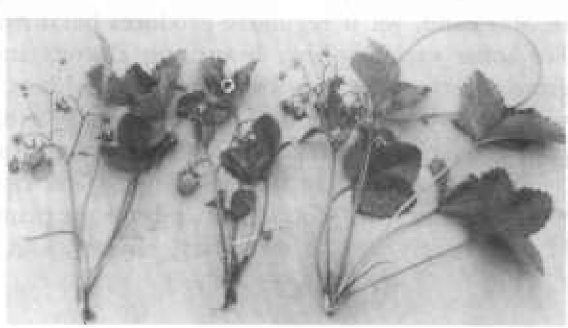
Primary berries are not only largest and ripen first, but have the most seeds. Valleau (1918) found 382 seeds for the primary berry, and 224, 151, and 92 successively for the secondary, tertiary, and quarternary berries of one

FIG. 19–35. Basal branching cluster of a plant of *F. virginiana* #13. Nineteen fruits set while six flowers did not. Nine of the secondary and tertiary fruits were as large or nearly as large as the primary fruit. Nearly life-size.

variety. Gardner (1923) reported an average for Gandy of 518 pistils for the primary, and 83 for the last flowers. Not only is it important for the breeder to cross the first flowers that open because they have far more seed than the last flowers, but also because the primary flowers are the most likely to set. As stated above, in nearly all varieties some of the later flowers and in some varieties most of the later flowers do not develop into berries. They are functionally males.

BERRY DEVELOPMENT. The primary flower, the first flower of those varieties that open in the spring, may have little pollen, less than later flowers of the same variety. However, the stamens are so placed that as they crack open they readily scatter pollen onto many of the pistils; and, as pistils remain receptive for several days, bees usually can get pollen from the later flowers to complete the fertilization of these primary ones. Pollination of all pistils of the flower are necessary for maximum berry size. Although blossoms may remain receptive for even ten days in cool weather if not pollinated, the reaction to fertilization is quite rapid, usually resulting in petal fall and the drying up of the pistils, sometimes within as short a time as twenty-four to forty-eight hours. However, flowers pollinated after the pistils have been receptive for one to several days develop into berries quicker than those pollinated as soon as the flowers open, and, as a result, they mature nearly at the same time as those pollinated when the pistils are first receptive.

FIG. 19–36. Three crowns from the same plant as in FIG. 19–35 of *F. virginiana* #13, with high branching clusters. The secondary and tertiary fruits of these clusters are far smaller than those in the cluster in FIG. 19–35.



GROWTH PERIOD—FLOWER TO RIPE FRUIT. At the beginning of the strawberry season in Maryland, the average period from flower opening to berry maturity is about 31 days, and at midseason, with longer days and higher temperatures, five to six days less. In Oregon for three years (1912, 1913, and 1914) the average periods for many varieties were twenty-nine, thirty-three, and thirty-five days. Everbearing varieties that mature their fruit in twenty to twenty-five days in the long days and high temperatures of mid-summer take 60 days in the autumn. Though Kerner and Oliver (1895) gave 2671

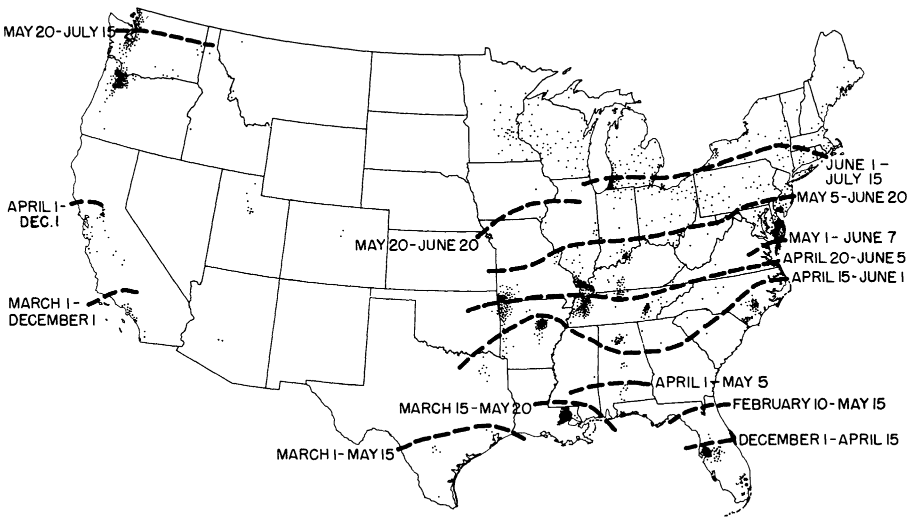
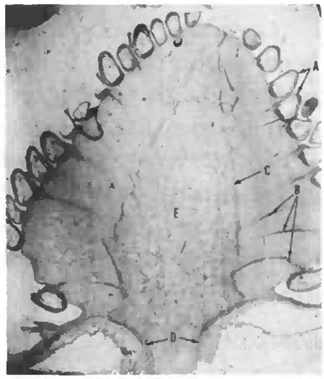


FIG. 19–37. Map showing the location of the principal strawberry-producing regions, the approximate ripening time in each region, and the northward progression of the strawberry season.

as the total daily hour-degrees after January 1 to ripe fruit of *F. vesca* in Germany, for a true index it would be necessary to establish the relative effect of different degrees of temperature on plant and fruit development and how much those effects are modified by other conditions. Records at College Park, Maryland, indicate the variation in seasons, the effect of environment and of varieties:

Year	First Blossom	First ripe berry	Days (number)
1910	Earliest variety—April 4	May 14	40
	Latest variety—April 25	May 27	32
1911	Earliest variety—May 3	May 23	20
	Latest variety—May 13	June 5	23

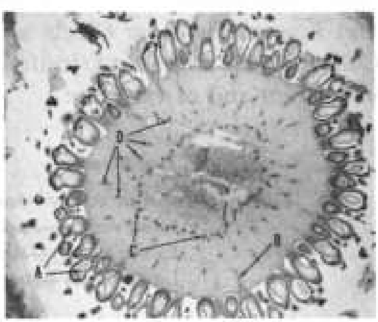
FIG. 19-38. Cross-section (enlarged about eight times) of a small green Marshall strawberry showing: A) seeds, B) fibro-vascular bundles to the seeds, C) central cylinder or ring of fibro-vascular bundles, and D) fibro-vascular bundles to seeds connecting with the central ring farther down. These vascular bundles, composed of longer, tougher cells than is the flesh, help to hold the berry together and make it firm. In breeding work, berries with very tough or very weak bundles are discarded. (Darrow)



The approximate ripening period in the United States is best shown by the map (*Fig. 19-37*) based on the time when shipments are made from each section. Along the Atlantic Coast for central and south Florida this period is four months, one and one-half months for eastern North Carolina, and 1 month for New Jersey. This difference in ripening period is based on the length of time of flower-bud formation in the different regions due to temperature and photoperiod differences and interaction.

BERRY GROWTH. Tschiercke (1886) has given the detailed structure and development of the berry (see *Figs. 19-38* and *19-39*). The flower base, which is the receptacle, develops into the edible part of the strawberry and consists of a fleshy pith at the center; next a ring of vascular bundles with branches leading to the achenes, the seeds; then a fleshy cortex outside the ring and an epidermis bearing a few hairs and connected to the superficial achenes. From the flower stage the pith cells increase in size, especially in length, and the narrow intercellular spaces already present increase in width, especially toward maturity. The cells of the cortical layer are similar to those of the pith, but are thinner walled and increase in size about twice as fast as the pith (Havis, 1943). The meristematic tissue, next to the epidermis, has no

FIG. 19-39. Lengthwise section (enlarged about eight times) of a small Marshall strawberry, showing: A) seeds, B) fibro-vascular bundles to the seeds, C) central cylinder or ring of fibro-vascular bundles, D) fibro-vascular connections to the stem, and E) pit or core of the berry with only tiny air spaces showing. The fibers conduct water and food from the stem through the central cylinder to the flesh and seeds. (Darrow)



intercellular spaces, but the cells continue dividing after those of the pith and cortex cease. The reason for differences in shape and size of different varieties depends not only on their early development when flower buds are forming, but on the duration of cell division in each layer and on how much the cells enlarge and how much they pull apart. In *F. vesca* cell division ceases when the receptacle is the size of a pea, while in the garden strawberry cell division continues slightly longer. The cells of the cortex become 4 or 5 times as wide in the garden strawberry as those in *vesca*. Havis (1943) found little cell division from just before fertilization until maturity and concluded that only 15 to 20 percent of the growth after fertilization was due to cell division, and was not significantly different in the four varieties studied. The size of air space affects berry size also. The air spaces in *vesca* are so large that the berry is extremely light weight compared to large-fruited varieties. Even large-fruited varieties vary greatly in density, and a few varieties like Fairfax have so little intercellular air space that some berries may sink in water. Redheart also has almost exactly the specific gravity of water. Berries selected for canning have less air space and less oxygen inside and keep their color and flavor better than most varieties.

The length and diameter of the developing fruit was measured at Willard, North Carolina, to establish a measure of the size at different stages, from the time of pollen shedding to the stage of full ripeness, as shown in the table below:

Size of the Strawberry Fruit at Different Stages in Its Growth
Willard, North Carolina (unpublished, Darrow)

Stage of Growth	Length Cms.	Diameter Cms.	LENGTH x DIAMETER Sq. cms.	% increase
Pollen shedding	.93	.72	.70	—
Calyx clasping	1.24	1.04	1.38	97
Berry swelling	1.73	1.43	2.62	90
Berry white	2.34	1.76	3.36	28
Berry reddening	2.68	2.15	5.90	76
Berry full red	2.90	2.37	7.15	21
Berry full ripe	3.27	2.50	8.16	14

FROST DAMAGE. Frosts may either kill the flowers outright or injure them so as to cause nubbins or misshapen berries. When a flower is injured by cold the pistils, which are the tenderest part, are killed first. If most pistils are killed, a nubbin with a wisp of dead pistils may result, or, if killed after fertilization, the embryos do not develop and a seedy spot on the berry results

FIG. 19–40. Cold injury to berries. A, frosted flower; B, C, D, three berries frozen while green which later partially developed; E, frost injury which prevented development of the berry near the tip, but which did not prevent enlargement of the seed coat. At center, F, frost injury as in E plus non-pollinated pistils and slight splitting as in G. G, frost injury which killed the pistils at the tip. Because the pistils did not develop, the berry finally split.

(*Figs. 19–40* and *19–41*). The achenes, however, are empty. Great differences in frost hardiness of flowers of wild strawberries of *F. virginiana* are known: flowers of Selection Sheldon from North Dakota being uninjured in Maryland at temperatures of 18° F. while flowers of ordinary varieties are killed at about 28° F.

AUXIN CONTROL OF GROWTH. Nitsch (1950) removed all achenes from fruits four days after pollination and growth stopped. Growth also stopped when the achenes were removed seven, twelve, nineteen, and twenty-one days after pollination. Although growth was stopped when removed at twenty-one days, the berries turned red at the usual time, twenty-six to thirty days after pollination. When one ovule was fertilized the flesh around it developed (*Fig. 19–42*); when three ovules were fertilized three areas developed; when only a ring of ovules was fertilized only the ring of flesh developed. When seeds were removed and an auxin like beta-naphthoxyacetic acid (100 p.p.m. in lanolin paste) was applied nine days after pollination, the berry grew to almost full size and ripened like normal berries. Nitsch (1949) found the greatest auxin activity and the greatest amount of auxin in the achenes twelve days after pollination and separated seven different growth substances

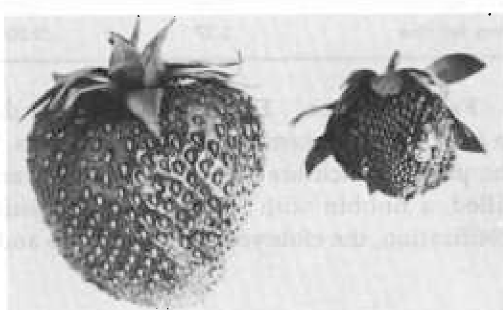


FIG. 19–41. Frost injury when the berry is very small may stop it from enlarging, as is shown here. The berry on the right should have been as large as that on the left. The seeds are empty.

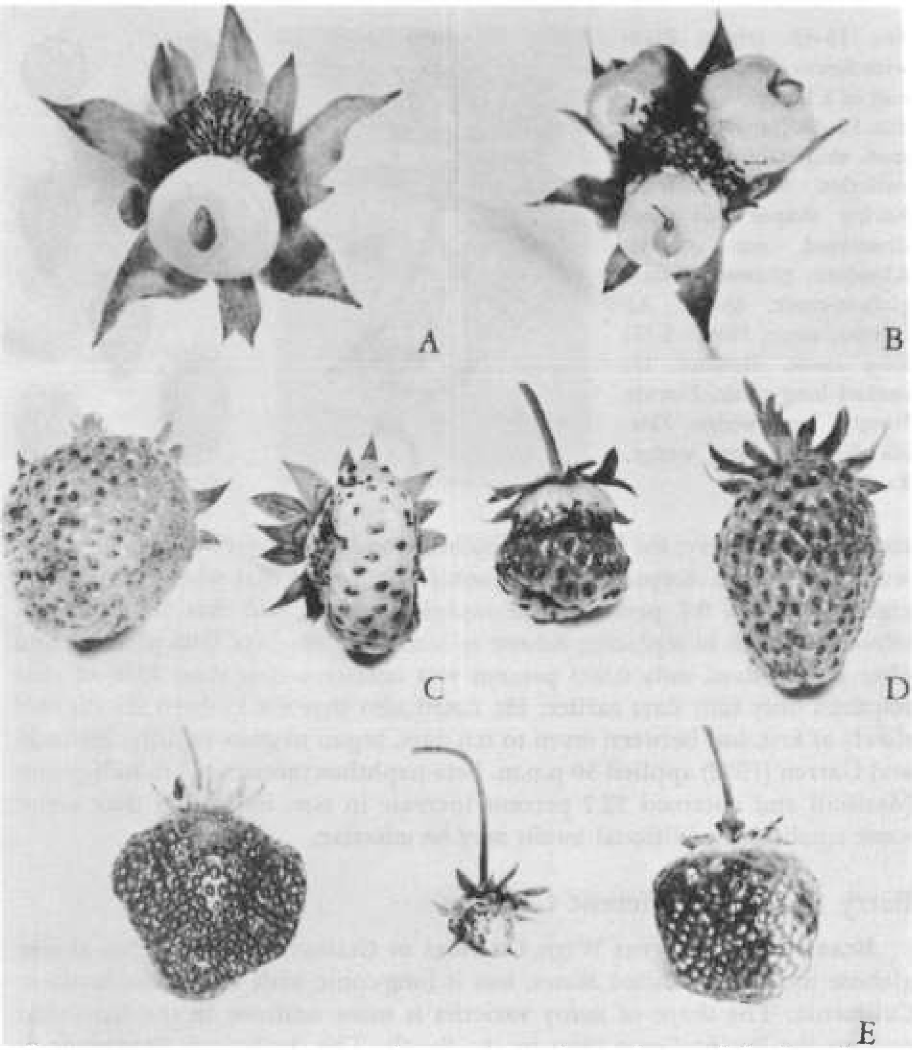
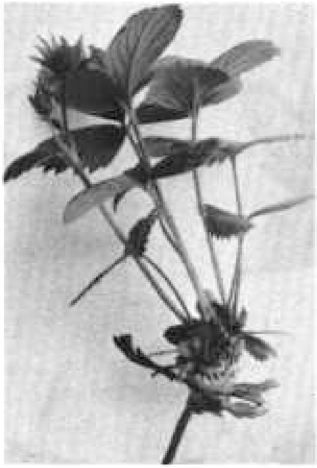


FIG. 19–42. A. Growth of the strawberry receptacle induced by one single fertilized achene. (Magnified three times.) B. Growth induced by three fertilized achenes. (Magnified three times.) Note the difference in size between the fertilized and the non-fertilized achenes. C. (Right), growth induced by three rows of achenes left in a vertical position, the others having been removed. (Left), control. D. (Left), strawberry having had all its achenes removed but two rows in a horizontal position. (Right), control. E. Strawberries of the sage age: (left), control (middle), strawberry which had all its achenes removed and replaced with lanolin alone, (right), strawberry which had all its achenes removed at the same time, but replaced by a lanolin paste containing 100 p.p.m. of beta-naphthoxyacetic acid. (After Nitsch)



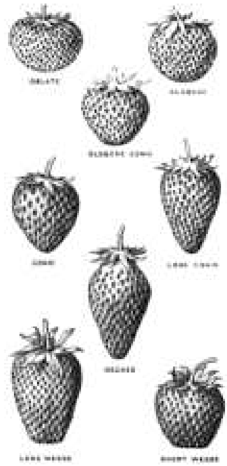


FIG. 19–43. (right) Plant with flower cluster from the end of a berry.
FIG. 19–44. (far right) Common shapes of strawberry varieties. Some varieties having shapes like those illustrated are: oblate, Klondike; globose, Shasta; globose-conic, Shasta, Albritton; conic, Howard 17; long conic, Howard 17; necked long conic, Florida Ninety; long wedge, Florida Ninety; short wedge, Earlidawn.

natural to the berry; the most prominent being indole-3-acetic acid. No auxin was found in the receptacle. Thompson (1963) found that when berries were eight days old, 0.1 percent of 2-naphthoxyacetic acid was necessary for effective growth in replacing achene effects; after ten days, 0.03 percent; and after twelve days, only 0.003 percent was necessary—less than 1/30 of that required only four days earlier. He noted also that the embryo sac divided slowly at first, but between seven to ten days, began to grow rapidly. Zielinski and Garren (1952) applied 50 p.p.m. beta-naphthoxyacetic acid to half-grown Marshall and obtained 32.7 percent increase in size, indicating that under some conditions additional auxin may be effective.

Berry Shape in Different Climates

BERRY SHAPE DIFFERS WITH CHANGES IN CLIMATE. Klondike is almost globose in eastern United States, but is long-conic with a neck in southern California. The shape of many varieties is more uniform in the Northeast and on the Pacific Coast than in the South. The Ambato is long-conic at Ambato, Ecuador, but short, globose-conic in Maryland (*Fig. 9–1*).

The tip of the berry may be meristematic under some conditions, especially when growth is checked in periods of cool weather. Leaves or even a plant may grow from its tip (*Fig. 19–43*). The development of bracts instead of seeds is usually due to the aster-yellows virus disease.

BERRY SHAPE. The common shapes of strawberry varieties are shown in *Fig. 19–44*. Most berries of Klondike are oblate, of Shasta globose conic, and of Florida Ninety long conic with a neck. The general shape of the berry is indicated to some extent by the shape of the receptacle in the small flower bud

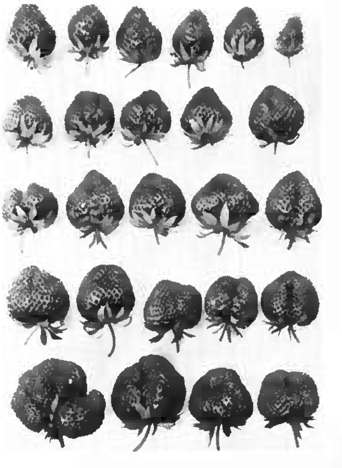


FIG. 19–45. Variations in shape of the Howard 17 (Premier) strawberry. The primary berries are shown toward the bottom and the later berries, one to a cluster, at the top; the primary berries, being more irregular, tend to have a broad wedge shape, and the later berries to conic or long conic forms.

the previous fall. The shape of the berries on the cluster depends on their position (*Figs. 19–45* and *19–34*), the primary berry tending to be irregular and broad wedge-shaped, and the later berries much more uniform. However, the shape may be affected by conditions in the fall and during the growth of the fruit in the spring. The multiple-tipped shapes of Marshall shown in *Fig. 19–46* were probably caused by cold, dry weather in the autumn affecting the flower buds. Irregular shapes of berries also result from conditions affecting the fall growth.

FASCIATION. Fasciation (*Fig. 19–47*) results from favorable growth conditions in late fall when days become too short for normal development of the particular variety and is most serious from Eastern Virginia southward. The flower bud broadens and in severe cases no fleshy fruit develops in the spring at all and the plants are barren. All gradations are found from a slightly flattened stem of the primary berry (*Fig. 19–47A*) to a coxcomb berry shape as in *Figure 19–47B* (see also *Fig. 21–15*). Fasciation is a varietal characteristic, some varieties, like Missionary and Blakemore, never fasciating. Many varie-

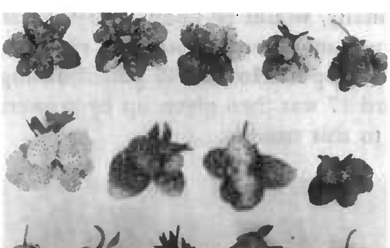


FIG. 19–46. Not genetic but abnormal berries due to injury to the developing flower buds by weather conditions in the previous fall. The entire crop in a field of Marshall was of this shape. The berries may be double or triple as in the lower row, quadruple or quintuple as in the center row, or there may be six, seven, or even more parts, as in the upper row. Note that in contrast to berries in FIG. 17–32, nearly all pistils have been pollinated.

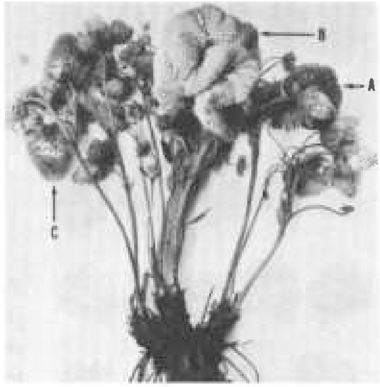
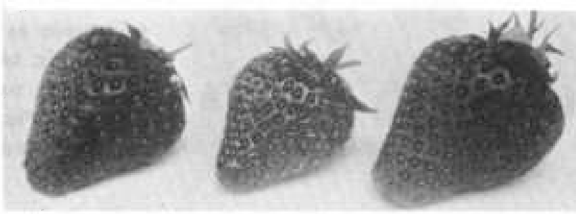


FIG. 19–47. A) Howard 17 strawberry plant with 2 crowns (*center* and *right*) fasciated. The wedge-shaped primary berry at A) is starting to fasciate, at B) is coxcomb in shape, and at C) is a normal one of conic shape. When a berry is as badly fasciated as at B, the other berries rarely develop.

ties succeeding in the North cannot be grown in the South because of this trouble and all Southern varieties must be quite resistant to fasciation. In the spring, insects, disease, lack of pollination, drouth, humidity, and frost all affect the shape of the berry.

IRRIGATION AND BERRY SIZE. Irrigated berries are not as firm as non-irrigated ones, though the difference is not usually great. The average water content of several strawberry varieties in Maryland ranged from 92.6 percent to 89.7 percent in 1929; 91.3 percent to 88.1 percent in 1930; and 92.5 percent to 91:8 percent in 1931. The primary berries normally had the highest water content and the later berries slightly lower water content. In 1929, for four successive pickings the average water content of all varieties was 92.6, 92.2, 90.9, and 89.7 percent (Darrow, 1936). In 1925, in Maryland, in a period of low humidity and very high temperature the ripening berries even dried on the plants to resemble raisins, a condition seldom observed. Because most of the root system is in the top six inches of soil, and because the leaves develop rapidly in the spring and transpire water freely, they pull water from

FIG. 19–48. Missionary strawberries. Center berry normal; outside, "puffed" berries with seeds far apart. Such puffed berries are much softer than the center berry, whose seeds are closer together, and, if developed normally, would be about half the size shown. "Puffing" occurs in ripe berries when warm humid weather occurs at ripening time. About 1933, on the Delaware peninsula, the crop of Howard 17 puffed during such a period and was almost a total loss. Howard 17 was then given up by growers in favor of Blakemore, which is more resistant to this trouble.



berries in very dry weather and cause smaller than maximum size. Irrigation to keep berries growing to maximum size may be needed as often as every three to seven days, if sufficient rain does not fall.

FIRMNESS OF BERRY. Though breeding has resulted in much firmer berries, little is known of the structure or chemistry of a firm berry. The cell walls of firm berries like those of Blakemore, Albritton, and Dixieland, do not pull apart as much when growing as do the cell walls of softer berries. As a consequence, such varieties do not become as hollow and thus have less air spaces inside. Their epidermis is tougher. Low water-soluble protein is usually associated with firm berries (Sistrunk, 1962). The larger berries of a variety are softer than the small ones, for they have a higher moisture content and probably have a different skin composition. High rates of application of nitrogen may produce larger berries. Temperature and humidity both affect firmness greatly. Sparkle is considered to be a firm berry in the northern United States, but it is too soft to be a market berry in the warmer climate of Maryland. In a very warm humid period berries of some varieties puff and are unmarketable (*Fig. 19–48*). Rains in cool weather, unless long continued, do not greatly soften berries, but in warm rainy weather berries may absorb water through the skin and become soft. Darrow (1932) reported on tests in North Carolina that where leaf growth is greatest the berries are softest, presumably because of the shading effect of the leaves. Berries soften as the

Contrast between temperatures of strawberries and of the air, Hammond, La., April 23

		BERRY TEMPERATURE	
Time	Air temperature	In shade	In sun
6:00	61	55	63
8:00	74	73	91
10:00	77	84	100–108
12:00	79	86	98
2:00	84	94	102–111
4:00	87	87	97–103
6:00	68	70	—

temperature rises. Thus, when the air temperature at 8 A.M. was 74°F., inside a shaded berry it was 73°F. and inside berries in the sun it was 91°F. At ten o'clock with an air temperature of 77°F. berries in the shade were 84°F. and from 100°F. to 108°F. in the sun. Pressure tests indicate that for each rise of the temperature by 21.7°F. the toughness of the skin is doubled. Not only is the skin more resistant to injury at lower temperatures, but the respiration rate is lower, fungi that cause rots grow more slowly, and the berries keep much longer. Popenoe (1921) has told of the remarkable firmness of the Ambato variety (*Fig. 9–1*) which grows slowly in the cold arid climate of highland Ecuador with a day length of just over twelve hours. The berries could be carried in large 26- to 33-pound boxes on mule back for many miles with no apparent injury. When grown in humid climates, the Ambato is no firmer than ordinary sorts. In Chile, with its cool, dry climate, the White Chilean is as firm as the Ambato. Various means have been devised to measure firmness but most breeders still judge firmness by feel—the friction of the thumb rubbing the surface of the berries in the field until the skin breaks, and by shipping tests. Firm-fruited wild plants have been found in both *ovalis* and *chiloensis* and relatively firm ones in *virginiana*. These have yet to be utilized by breeders. The Wilson of the United States and La Constante of Europe were relatively firm 19th-century varieties. Neunan, Hoffman, Missionary, and Klondike, of earlier varieties, were also relatively firm; Blakemore and Tennessee Shipper are much firmer and Massey, Albritton, and Dixieland are among the firmer large-fruited ones. Recently when grown under short days in the South, Klonmore, Headliner, Dabreak, and Florida Ninety have proved to be firm.

Dessert Quality. The dessert quality or flavor of strawberries is dependent both on inherited characteristics and on how they are affected by conditions. Caldwell and Culpepper (1935) concluded that best flavor was dependent on the sugar-acid-tannin ratio combined with volatile esters that make up aroma. As the berry matures, the acids decrease and sugars increase. When unripe berries lose chlorophyll and turn whitish, they have maximum water content. From the white stage on, sugars increase rapidly and continue until the berries are fully ripe. Acidity declines rapidly and astringency slowly.

The tests of Went (1957) on Marshall also serve as a guide to the development of aromas. Different varieties have been originated that are best in different regions; that is, that develop high flavor under the average weather conditions of those regions. Although the development of flavor of some varieties may follow that of Marshall, some may not. Suwannee has high flavor under a very wide range of conditions. Fairfax has very high flavor under a much narrower range of conditions and probably follows more closely the general development of flavor in Marshall, although the latter has high flavor under a wider range of conditions.

Dessert Quality of Ripening Berries. Smith and Heinze (1958) studied the development of berries from quarter-colored to fully colored. Berries of three kinds left to mature on the plants increased their size 23 percent to 57 percent, from quarter color to full color, depending on variety, and 12 percent to 23 percent from three-quarters color to full color. Quarter-colored berries of four varieties were harvested and stored until fully colored and rated 72 percent as good in flavor as those fully colored when picked. Also, the quarter-colored of two kinds stored until fully colored averaged 78 percent as much sugar and 33 percent more acid than the fully ripened ones.

Austin and others (1960) found that even greenish-white to 10 percent pink berries of the Sparkle developed full color at 85°F. in forty-eight hours, 90 percent of full color at 65°F. in ninety-six hours and did not develop good color at 55°F. The flavor was considered as good as of those ripened on the plant.

VARIETIES FOR PROCESSING. The chief uses for strawberries have been freezing for later preserving and for dessert use. Varieties for preserving should be medium to light red to the center, and for packaging for dessert, varieties somewhat deeper red should be used. Varieties with white soft flesh and low in acid are unsatisfactory for processing. They should be firm, sub-acid, and aromatic. The varieties used are listed under *Sources for Superior Quality.*

CAPPING. Berries of the wood strawberry, *vesca,* separate from the cap or hull when ripe and are always picked without the cap. Many of the wild Virginian cap easily, although most do not. The native commercial *chiloensis* of Chile mostly cap with ease, and in picking the caps are left on the plant. Yet the cultivated Chilean of South America usually cap with some difficulty. Jucunda, an old variety of England, and still grown in Europe, is regularly picked without caps. Miss Kronenberg has used it successfully in breeding to obtain Juspa and Gorella, but they do not pick without caps as easily as Jucunda. In drought periods berries are more easily picked without caps than in moist weather, and under irrigation in the Pacific Coast berries of Marshall, Northwest, and others are harvested without caps because of this response (*Fig. 19–49*). The varieties having the best capping qualities are listed on page 394.

Vitamin C. Varieties differ greatly in their vitamin C content and, in one study, ranged from 39 to 89 units (mg) per 100 grams (Ezell, 1947). The average for strawberries has been estimated at about 60 units with Catskill having a high content, Midland about average, Blakemore slightly low, and Aberdeen very low, about half that of Catskill. Breeding for much higher vitamin content was shown to be possible by Darrow and associates (Ezell, 1947). Berries on the plant ripening in the sun have higher vitamin C content than those ripening in the shade. After picking, berries injured by bruising

FIG. 19–49. A test of the capping qualities of strawberry varieties and crosses. In the lower row (*left to right*) are: 1) berry badly torn when capped, 2) berry with large core pulled out, 3) berry with smaller core pulled out, 4 and 5) berries capping very easily. All five berries came from different seedlings of one cross.

tend to lose vitamin C rapidly. Uninjured berries lose no vitamin C for at least three days when stored at 40° to 75°F. Uninjured half-red berries increase in vitamin C but not so much as if they were ripened on the plant. Capped berries at about 75°F. lost between 10 and 15 percent of vitamin C in twenty-four hours and between 85 and 90 percent in forty-eight hours.

FLAVORS. For the esters or volatile compounds, Winters (1964), states that about 35 odorous substances have been isolated so far, but that it still is impossible to reconstitute a really fresh flavor. Only the chief and most stable compounds have been isolated. When berries are crushed, the finest flavor is developed in one minute; in five minutes a noticeable change has occurred, and in ten minutes a marked change. By using low-temperature steam distillation a distillate (12 to 15 percent of fresh weight) is obtained which by dilution yields natural strawberry flavor.

Teranishi and associates (1963), of the U.S. Department of Agriculture at Albany, California, have recently reported on studies of volatile substances from strawberries. A direct chromatographic method of analysis of vapor from a single strawberry was developed to study the more stable components. The report lists 24 compounds of zone A of the chromatogram of strawberry oil which had over 150 components.

20

Climate and the Strawberry

Adaptability

AT AN ELEVATION OF 9500 feet to 10,500 feet in the volcanic soil of the mountain tops at Guachi, which is only a few miles south of the equator in Ecuador, the Indians have long raised one of the original strawberry varieties, the Ambato. The hundreds of acres planted to Ambato are on mountain tops in a very cold, dry climate, mostly above the areas where any other crops are grown, and even above where the Indians make their homes. Strawberries are grown also in many areas where semi-tropical crops are raised. They are raised extensively with citrus fruits and avocadoes in the arid areas of southern California, and they are raised in other humid semi-tropical areas, such as Japan, India, Colombia, Australia and Florida, where mangoes and pineapples (*Plate 20–1*), as well as oranges and avocadoes, are grown. For many years several hundred acres of strawberries have been grown under glass in the Netherlands, either in ground beds of strawberries covered by movable greenhouses from about January to June, or in beds which during the winter have cold frames and sash placed over them. On the coast of Japan, fancy strawberries are grown for the early market by terracing the very steep hillsides facing south and setting the plants between concrete blocks which cover the slopes. Instead of glass, mats protect the plants from winter cold and unseasonable frosts. In much of Japan, strawberries are a part-of-the-year-crop alternating with rice.

Because the cultivated strawberry is a hybrid of two highly variable octoploid species, it is possible to raise strawberries profitably under extremely

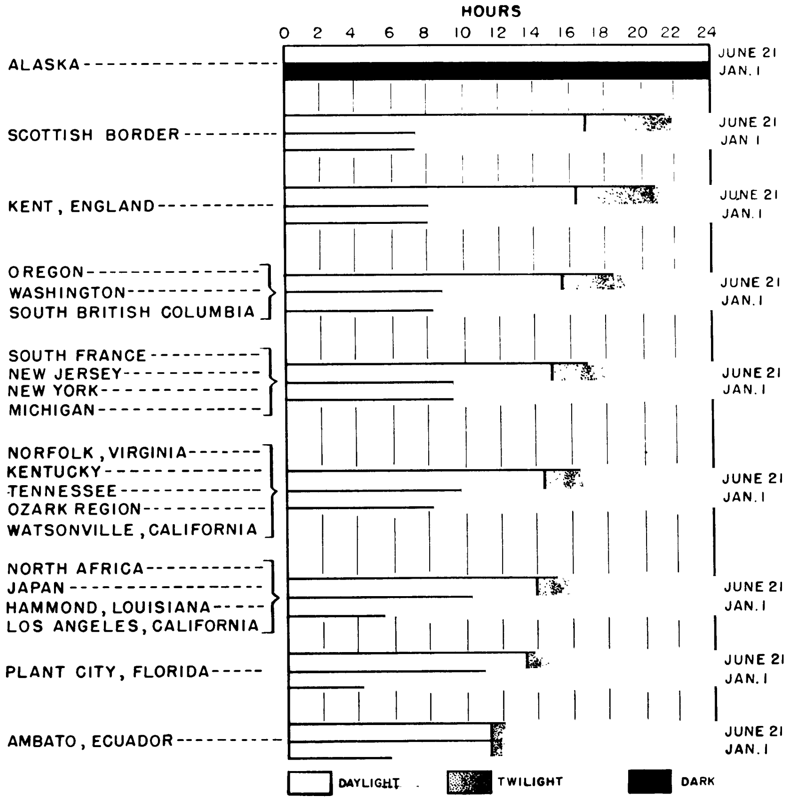


FIG. 20–1. Length of the light and dark periods (June 21 to January 1) in various areas where strawberries are grown.

different conditions: from irrigated desert to areas receiving 100 inches of rainfall; from sea level to elevations of 10,500 feet; from cold areas with −50°F. to the semi-tropics; under the continuous light of summer in the Arctic to the twelve-hour day under the Equator (*Fig. 20–1*); in glass houses and under glass or plastic covers, with concrete blocks, and with plastic ground covers as mulches; as a six-month crop, and as a crop occupying the same soil for hundreds of years. The same variety may be continuous-fruiting in one location and fruit for two or three weeks only in another. Other varieties may be everbearing under most conditions, so long as temperatures permit growth.

In part this remarkable range of adaptation is due to genetic variability, but it is also due to the high adaptability and plasticity of the strawberry plant itself. In the preceding chapter the structures of the strawberry plant have been described, thus providing a background for the subject-matter that follows: essentially, a description of the strawberry plant's relationship to its climatic environment. The most important and obvious climatic factors, as far as they affect the strawberry plant, are those of temperature and of daily light period, and it is these which are studied most extensively in this chapter. Other factors of varying importance are also treated. These are moisture (drought, heavy rainfall, high and low humidity) and the quality and intensity of light.

Temperature

Maps showing the areas of the world where the strawberry species are native indicate the geographically wide adaptation of the strawberry. *Fragaria vesca,* assumed to be the basic diploid species, or similar to the basic species from which the octoploid strawberries were derived, has the widest distribution (see *Map 8–1*), while the hexaploid *moschata* has one of the most limited distributions. The parents of the cultivated strawberry display an extremely wide adaptation. *F. virginiana* and *F. ovalis* are found from the tundras of Canada and Alaska south to the very mild climate of southern Louisiana and New Mexico. Low temperatures in central Alaska where the strawberry is native reach –60° F. in winter and high temperatures are up to 100° F. In south central Louisiana the range is from 0° F. to 110° F. For *F. chiloensis* temperatures range from –30° F. in winter to 90° F. in summer, along the coast of Alaska, and from about 23° F. to 115° F. in south central coastal California. In Chile, where the Chilean is native, temperatures range from the no-frost areas near Concepción to very low temperatures (–30° F. and lower) in the Andes Mountains. Cultivated strawberry varieties have not been developed for all these temperature extremes in which the wild kinds are found, but they are grown, even extensively, where the wild is not native—in southern California, in Florida, in parts of India, and in parts of Japan.

Low Temperature Effects

Effects of low temperatures on crowns are discussed on page 323 (*Figs. 19–15* and *19–16*). Relatively low temperatures may occur at any time from fall to spring. Angelo (1939) showed that the varieties tested completed their hardening at 32° F. within seven days, but that twelve hours at 68° F. (relatively warm temperature), then 12 hours at 32° F. produced greater hardiness than continuous exposure at 32° F. Gibson and Mastodon hardened the most and Aroma the least. Droughts seemed to lessen the rate of hardening. As protection from low temperatures, mulches could be applied after a week of severe frosts.

The ability of plants to harden is also important in winter and spring. In the North, the plants usually remain dormant all winter. They are still living, but at a very slow rate. If the temperature reaches 16° F. inside the plant of cultivated varieties, injury may occur, with the killing point about 10° F. Tests in Minnesota indicated that Burgundy was the hardiest; Beaver, Dunlap, and Howard 17 slightly less; and Gem and Catskill considerably less hardy to low temperatures. With a rise in temperatures above 32° F., plant functions increase rapidly, even though top growth may not be evident. However, after some growth has occurred in early spring, successive night frosts still can harden the plant. Severe frosts after such hardening do not injure the plants, but such frosts without previous hardening can cause serious injury, when the flower buds within the crowns may even be killed. Slight differences in the rate and extent of hardening of varieties in the fall, winter, or spring may be all important for a variety's success.

Winter-Hardiness

By using selections of the native western strawberry in crosses with cultivated varieties, the Cheyenne, Wyoming, Station has originated varieties that withstand temperatures of –40° F. without snow cover or mulch. Several varieties have been introduced for Manitoba, Alberta, and Saskatchewan that withstand the low temperatures of these areas, but with covering of mulch or snow. Likewise, similar crosses have resulted in varieties for central Alaska, which survive six weeks of continuous light in summer and winter temperatures to –50° F. Flowers of selections of the native strawberry of North Dakota have been found to withstand temperatures of 18° F. without injury, while flowers of ordinary varieties are killed at 28° F. (Darrow and Scott, 1947). Flowers and berries of the wild *chiloensis* of the Andes Mountains of Chile are uninjured by freezing temperatures in midsummer, and the berries can be harvested the day following such temperatures. As has been discussed elsewhere (pp. 177, 157), older cultivated varieties such as Keens Seedling and Hovey and even the Albritton of today have the non-hardy Chilean in their ancestry. It is probable that, with two highly heterozygous octoploid parental species, hardiness will be an important factor to be considered in strawberry breeding for a long time to come.

Photoperiod

Relatively little is known of the photoperiods for different species of strawberries. Different clones of all species may be expected to react differently (*Figs. 20–2* and *20–3*). At least some clones of the diploid *F. vesca* grow

FIG. 20–2. Effect of photoperiod. The contrast between the rest period and photoperiod requirements of Howard 17 (left) and of Missionary (right) is shown by these plants brought into the greenhouse November 7 and held until March 10 during the short days of winter. Howard 17 does well in the North after a long winter cold rest period and thirteen- to fourteen-hour daylight periods at the time growth starts, while Missionary succeeds in Florida where there is a very short rest period and the daylight periods are about 10 hours when they blossom and fruit.

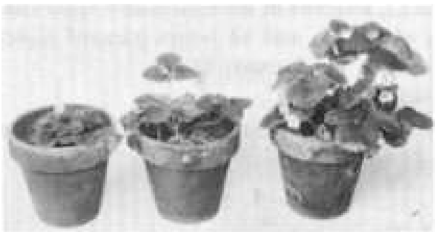


FIG. 20–3. *(left)* Effect of a rest period on the Fairfax strawberry in the winter in the greenhouse; *(left)* no rest period with normal daylight; *(center)* no rest period but a long day of light; and *(right)* a rest period and then normal daylight.

at all day lengths. In a greenhouse in Washington, D.C., they made greater growth under the longer daily light periods, but made a fairly vigorous growth under the shortest days of midwinter (Darrow and Waldo, 1934). *F. moschata* showed more response to long light periods than *vesca,* but less than cultivated varieties. The clones of *F. virginiana* (*Fig. 20–4*), which were studied, showed greater response to longer periods in winter than did *moschata* and *vesca,* while those of *chiloensis* showed the greatest differences, some growing well under the short days of winter and others showing response to longer light periods. Undoubtedly a greater range of selection of *virginiana* clones, as from Louisiana, Maryland, and northern Canada, would have shown equal increase in range of response.

Light Intensity

Though the length of the daily photoperiod in general has the greatest effect on the growth and annual cycle of plant development, light intensity seems of special importance to the everbearing varieties, which grow less vigorously than ordinary June-bearing varieties after being given a low-temperature rest period and extended light periods with artificial light. Everbearing varieties have been bred mostly in northern areas with longer days and relatively intense light. They grow poorly in winter (*Fig. 20–5*).

Fig. 20–4. Effect of photoperiod. *F. virginiana* 27, selected in western North Carolina, under normal day (*at left*) and normal day plus 4, 7, and 14 hours (*toward right*) and 24 hours artificial light (*at right*). November 11 to January 31.

The cultivated strawberry is so variable that even everbearers should show great variation in response to intensity.

Response of Varieties to Light and Temperature

The result of hybridizing two species with highly variable responses to temperature and photoperiods is the modern strawberry whose immense reservoir of genes makes possible the selection of varieties extraordinarily adaptable to local conditions. Consequently, the variety best adapted to a region is usually one selected in that region, with its particular complex of day length and temperature. Everbearing varieties are "long-day" plants forming flower buds under the long days of summer in northern states, more flower buds at seventeen-hour-days than at fifteen hours (Downs and Piringer, 1955) and relatively few at eleven and thirteen hours. Ordinary varieties are "short-day" plants forming flower buds when the days become short and the temperatures are low, in late summer and fall.

Fig. 20–5. The Progressive everbearing strawberry under normal winter days in the greenhouse, showing six flowers with undeveloped stamens and petals on February 25. Even the pistils on most flowers are not developed enough to set.

FIG. 20–6. Note the "ground fruit" and "crown bloom." In North Carolina the flower bud, which develops into the "ground cluster," is formed in the fall, and an additional flower bud, which develops into the high-branching cluster, as shown in this plant, is laid down in late winter or early spring.

Runners are initiated only when the day length is twelve hours or longer and when temperatures are above 50° F. Downs and Piringer (1955) found runner production to increase with increasing day length, up to 15 hours. A temperature of at least 73° F. and a fifteen-hour day is effective for rapid runner production. Branch crowns in ordinary varieties tend to form most freely when the days are too short for runners and yet too long for flower buds. If plants are brought into the greenhouse as early as September 1 in Maryland and given artificial light to lengthen the daily light period, normal summer growth is induced and no flower clusters are produced, in most varieties at least. If plants are brought into the greenhouse after January 1 and exposure to cold weather, normal summer growth is induced, even without additional light (*Fig. 20–3*).

Varieties have characteristic temperature-day length responses which determine their regional adaptation. Southern varieties grow under short days at relatively low growing temperatures and need little or no rest period. Northern varieties grow very little under short days and, if first exposed to short daily light periods, require a low-temperature dormant period to break their rest period. The rest period is caused by one or more plant hormones produced by a short-day low-temperature complex and is broken either by long photoperiods at growing temperatures, or by temperatures near the freezing point, either in light or darkness. Plants of over 80 varieties and species when not given a full rest period in Maryland continued to flower and fruit until July and some until August, but plants of the same varieties given a low temperature rest period formed no more fruit buds at normal temperatures.

Response of varieties to light conditions during October and November in the field is considered somewhat indicative of their regional adaptation. During this period varieties adapted to southern states produce relatively large leaves with long petioles while northern varieties grow little or not at all. In southern states fruit clusters are large and branch basally when developed from buds formed under short daily light periods of fall and early winter, but late-winter and spring-formed flower buds usually develop into high-branching clusters (*Fig. 20–6*). Late falls with long periods of sunny days and cool nights are considered favorable to extensive fruit-bud development and to large crops in the following spring, but it also induces fasciation in varieties subject to this trouble.

At various latitudes with their differences in photoperiod, light intensity, and temperature, the plant responses are different also. At Ambato, Ecuador (see *Fig. 9–1*), almost directly under the Equator with days of just over twelve hours of light and where temperatures are below 60° F. much of the time, flower buds and fruit are produced by the Ambato variety the entire twelve months of the year. In Maryland it is barely possible to obtain a single flower on this variety. The Missionary is everbearing in Colombia at 4° north latitude and in Guatemala at 14° north latitude. In Mexico at 20° latitude at 4000 feet elevation the strawberry is still everbearing, with a day length of about eleven hours in December and thirteen and one-half hours in June. Fruit production there begins in January and continues to June, when it is stopped, in part by the rainy season. In Florida, at 26° to 28° latitude, near sea level fruit production is heaviest from January through March, but continues to some extent to April and May, when it ceases with high temperatures. In California, from 34° to 37° latitude, along the coast with its cool climate, some varieties have a fruiting season of about two months but others initiate flower buds and produce fruit all summer and fall, for six to eight months, until stopped by low temperatures. In northern states from 40° to 45° and northward, where no flower buds are normally produced in the spring, the fruit production period is about three weeks.

Because the daily light period and the amount and quality of light received varies so widely for early, mid, and late winter, and because varieties respond so characteristically to additional light, the regional adaptation of varieties may be determined by their response to additional light and temperature in the greenhouse in Maryland (Darrow, 1929). New selections and varieties may be taken into the greenhouse September 1 and be given artificial light to make a fourteen-hour day; their growth can then be compared with that of standard varieties of each area. For still more specific tests for local adaptation, the light periods may be varied from thirteen to sixteen hours and the average temperatures from 55° to 65° F. at night and 70° F. during the day.

Studying the field growth of nine varieties—two southern (Missionary and Klondike), two middle latitude (Aroma and Gandy), and five northern ones (Howard 17, Dunlap, New York, Parsons, and Sample)—during the summer, Darrow (1930) concluded that daylight temperatures of about 73° F. were optimum and that high growth rates were made from about 68° to 79° F., while at daylight temperatures above or below this range, growth rates were generally much lower. Went (1957) obtained the best leaf development of the Marshall at 57° to 63° F. He found that Marshall flowered and fruited throughout the year at 42° to 50° F. with continuous light, but with temperatures of 57° F. at a sixteen-hour day no flowers were initiated. Flowers were initiated at all temperatures tried with an eight-hour day.

Experimentally lowering the temperature to a constant 60° F. under fifteen-hour days induces flower-bud initiation in June-bearing varieties. Likewise, shortening the daylight period to ten hours with a constant 70° F. temperature induced flower-bud initiation in all the varieties tested except Fairfax. Tests of many species and varieties indicate that both photoperiods and low temperatures are all-important in inducing flower-bud initiation in June varieties. Short days in the fall cause the strawberry to become dormant. In a test of 51 varieties none became dormant when placed in the greenhouse September 1 and exposed to electric lights, in addition to day light, until 10 P.M.

Fruit Development Period (see also pp. 343–345)

The period from first blossoms to first ripe berries varies greatly with temperature, so that in areas of very low temperature, 60° F. or below, berries may take weeks longer to mature than in areas where much of the daylight-temperatures is above 60° F. For most of the United States and Canada, the period from first blossom to first ripe berry is approximately one month and lessens as the season advances and the weather becomes warmer. Clarke (1931) in New Jersey found the five-year average for Howard 17 to be 31.2 days from first bloom to first picking. The period varied from twenty-nine to thirty-five days for different years, and for 20 varieties for three years the range for all varieties for all years was twenty-five to thirty-eight days, with an average of 32.1 days. Though the two varieties with the shortest periods were late kinds, late varieties in general were among those with the longest periods.

Wilson and Giamaloa (1954) in Louisiana tagged flowers as they opened and obtained the days to ripe fruit. Their total range for four varieties for three years was eighteen to forty-one days with most of the berries ripening in twenty-three to twenty-eight days. Temperatures were not given.

Though the fruit development period of different varieties seems to vary slightly, in most strawberry-growing regions the difference is probably not often important and certainly far less important than the time of first and full bloom in determining the season of ripening of varieties. In areas where temperatures after flowering are low, the period of fruit development would be exaggerated and might be important.

Vitamin C Content

The vitamin C content of strawberries is relatively high and varies with temperature, light, and variety. In general, conditions that favor the production of a large crop of large and high-flavored berries also favor a high vitamin C content. Highest flavor is obtained with sunny days and cool nights. Production of vitamin C on sunny days in general parallels the production of high sugar content; and vitamin C (as in the case of sugar) is retained when the nights are cool and respiration is low. Long days of sunlight increase the vitamin C content. In general, therefore, vitamin C may be somewhat increased in the longer days toward the end of the strawberry season, but it may actually be higher at the beginning of a season with cool nights and sunny days than at the end of a season with cloudy weather and warm nights.

Flavor

The rate at which sugar accumulates in berries depends on the rate of transport of sugar from the leaves (governed by temperature and sunlight) and on the rate of loss of sugar by respiration (governed largely by temperature). Flavor is affected very little by soil type and that little only because soil type affects moisture supply, temperature, and plant growth. Flavor is also affected relatively little by fertilizers. However, in one test on sandy coastal plain soils in North Carolina, berries from plots receiving muriate and sulfate of potash, or potash plus nitrogen, seemed sour and lacking in flavor, while those from superphosphate plots were sweeter and better in flavor. The berries from the superphosphate + nitrogen fertilized plots seemed much the sweetest and finest flavored. Preserves made from the berries from phosphorus + nitrogen plots scored higher in flavor than those from control plots and still higher than those from the potash plots.

Went (1957) studied flavor of the Marshall at three different daylight temperatures, 62.6°, 73.4°, and 86° F., at three different night temperatures, 50°, 57.2°, and 68° F., and at three different light intensities of supplemental light added to eight hours of daylight. He concluded that sugar content was entirely a function of light intensity during the day and was independent of the day or night temperature, or photoperiod; and that acidity was a function of ripeness, the riper the berry, the less its acidity. At eight hours of daylight high aroma was produced, but the light intensity had to be fairly high—above 600 foot-candles. Most important, the eight hours of daylight had to be at a temperature of less than 59° F. for good aroma; even 50° F. for the eight hours was sufficient. The rest of the light period could be at a higher temperature. Finally, in a further test, two hours of 1500 foot-candles of light at 50° F., or eight hours at 700 foot-candles was sufficient for high flavor.

Just as wine vintages of some years, due to favorable light and temperature, are much superior to those of other years, the flavor and character of strawberries of some years are much superior to those of others. The frozen and preserved berries reflect these differences. Because of the effect of climate in rating varieties for flavor, it is important to indicate the region where they were grown. Thus, Darrow (1947) rated Marshall 9 in flavor (10 = highest, 1 = lowest) in Oregon but only 3–5 in flavor in Maryland, while Howard 17 was rated eight in Massachusetts, but only six in Maryland.

21

Breeding for Resistance to Strawberry Pests

STRAWBERRIES ARE ATTACKED by many pests, both insect and disease, which vary widely in their destructiveness and their distribution. Many of these pests are world-wide, while some are more serious in particular locations. The examination which follows reviews those pests known to the United States. Characters, such as resistance which are shown by certain varieties and noted by associates, are also included.

Very little is known of resistance to insects. Consequently resistance to specific insects is not discussed. Varieties that have thick leathery leaves seem to be more resistant to leaf mites. No real resistance to aphids is known, although they seem to multiply less freely on some varieties than on others. The bud weevil, which feeds on pollen, does not affect pistillate varieties, but all perfect-flowered varieties seem to be affected.

Knowledge of diseases which affect strawberries is somewhat more comprehensive. The lists on pages 390, 391 indicate what varieties are known to be resistant to various diseases. This information is important, for many diseases are being and others can be controlled by raising resistant or tolerant varieties. Systematic breeding is under way in many places to obtain more varieties resistant to various troubles. In the case of some diseases the need is urgent and breeding for resistance is more extensive than with other diseases. The demands to be met vary. For instance, all varieties introduced on the Pacific Coast, because of the difficulty of controlling aphids there, must be relatively tolerant to virus diseases, that is, slow to lose vigor when infected.

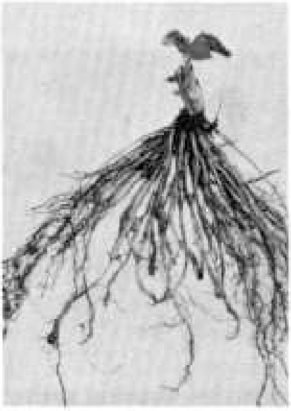


Fig. 21–1. Root-knot disease is caused by the root nematode, which lives in the tissues and destroys much of the root system. Note the absence of root-growth beyond many of the swellings. The root-knot nematode causes far less serious injury than the meadow nematode which causes brown areas rather than knots. In Florida the sting nematode, which shortens the roots to about 2 inches, is so serious that fields are treated before planting.

In the U.S. Department of Agriculture program at Beltsville, Maryland, since 1940 all breeding work has been directed toward varieties resistant to the red stele root-rot; and this is now a part of the program at Corvallis, Oregon, and other places. Once the knowledge of diseases, especially viruses, is more complete, the present means of dealing with them may seem clumsy stop-gap attempts, but these means are what seem presently most appropriate in respect to the amount and kinds of information now available.

Nematodes

Nematodes are threadlike worms too small to be seen easily by the unaided eye. Many species live in the soil and several attack the roots of the strawberry; many others live on the above-ground parts of plants, and several cause serious damage to the buds and leaves of the strawberry. Sanitary measures are the usual method of control.

Root Nematodes. The northern root-knot nematode (*Fig. 21–1*) and the meadow or root-lesion nematode enter strawberry roots to feed. They stay alive when plants are dug and shipped, and consequently are readily spread in nursery stocks. Other nematodes, like the sting and dagger nematodes, feed on the surface of roots and are usually dislodged when the plants are dug. Most root nematodes are more destructive in sandy than in clay soils. Soil fumigation to kill the sting nematode has been found necessary to raise good crops in Florida. Black root in many soils is due to meadow nematode, since the black-root fungi enter roots injured by this nematode (Chen and Rich, 1962). Fumigation of the soil is generally practiced in California to control the complex of soil troubles, including black root, and is beginning to be a standard practice in the eastern United States also. Little is yet known of resistant varieties. Fresno, Torrey, Siletz, and *F. ovalis* (Canada 5157 selection) may have some resistance.

FIG. 21–2. To the left a healthy plant, to the right a plant affected with southern bud nematode. Both the southern and northern bud nematodes cause similar injury by feeding on the very small leaves before they emerge from the buds.

BUD, LEAF, AND STEM NEMATODES. The bud nematodes, causing spring and summer dwarf, live in the most succulent tissues of tiny buds and very small leaves. The flower buds are often killed by the feeding of the "spring dwarf" species, resulting in flowerless plants. Buds and small leaves are killed or dwarfed by the "summer dwarf" (*Fig. 21–2*). Both diseases are commonly spread by infected stocks. The bulb and stem nematode is chiefly a pest in the Pacific Northwest. No resistance to these nematodes is known in varieties. Leaf nematodes are important in parts of Europe, but not in the United States, so far as is known.

Red Stele (Brown Core) Root-Rot Resistance

This disease of the root system was first noted in Lanarkshire, Scotland, about 1920, in Illinois in 1930, and in California and Maryland at about the same time. Its country of origin is still unknown. It is serious as far south as eastern North Carolina and Arkansas.

In moist, cool weather of late winter and early spring, this fungus disease grows rapidly up the center part of the roots, the stele, which turns reddish while the cortex of the root appears normal (*Figs. 21–3* and *21–4*). If the season is dry, infected plants may die before blossoming; if the season is wet they may blossom, but die before the fruit ripens. Affected plants at first show the dull, bluish-green color of wilting plants and may die in a few days. The fungus spreads through soil by swimming spores so that wet or low spots in a field are usually first affected. The disease is spread by drainage water, by soil on machinery and shoes, and by infected plants. In well-drained sandy soil it is rarely serious; yet, when the soil freezes deeply and then the top soil is thawed but wet, it may be severe. In the summer the disease is inactive except in areas with very cool summer temperatures. Summer spores of the fungus may live in the soil for many years.

The fungus has from several to many races which differ in their ability to infect different varieties; all named varieties are susceptible to some race.

Because of Reid's (1933) and Colby's (1935) and Darrow's (1937) success in early tests of breeding resistant varieties, extensive breeding work was promptly started. Hundreds of thousands of seedlings have been grown, and most desirable characters of strawberries are now in resistant varieties. Progeny of a cross of two resistant parents gave twice as many resistant seedlings as a cross with but one resistant parent.

When it was realized that this fungus produced races that differed in their infectivity, resistance tests of many species, of hundreds of varieties, and of hundreds of thousands of seedlings were made. Resistance to some strains was found in both *chiloensis* and *virginiana* and in a few varieties, chiefly Frith, a little-known variety of Scotland, and in Aberdeen of unknown parentage of New Jersey. Marshall, Oberschlesien and Perle de Prague show resistance to some strains. Highest resistance in species has been found in the Yaquina *chiloensis* selected by Waldo on the coast of Oregon. So far this selection has been resistant to all strains in the West but not to all in the East. Its seedlings in crosses with varieties have shown the highest percentage of resistance yet found. Resistant varieties grown on the Pacific coast have obtained their resistance largely from selections of *chiloensis,* those of eastern states from Aberdeen, and those of Europe from both Frith and Aberdeen. On page 390 are listed varieties known to be resistant to some strains. General resistance, that is, resistance to red stele disease and not just to certain races of the fungus, may occur.

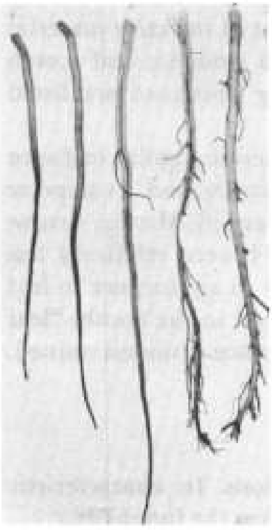


FIG. 21–3. *(left)* Red stele or brown core root-rot. The two roots to the left have dead ends and the centers are dead to the base where they joined the crown; the three on the right have dead rootlets and two have been sliced lengthwise to show the dark red-brown centers.

FIG. 21–4. *(above)* A root system severely affected by red stele root-rot. Note the dead root tips to the left.

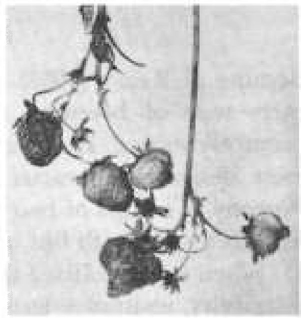


FIG. 21–5. Leaf spot, gray mold (botrytis), and leaf scorch may kill part or all of the caps or hulls, causing the berries to be small and unattractive and to ripen (if at all) without flavor or even with an offensive odor. The caps on all the berries shown are dead, and the later flowers have already dried up. These diseases may infect the flowers and kill them or develop later in green or ripening berries.

Leaf Disease Resistance

In general, damage to leaves is probably greatest by leaf spot, *Mycosphaerella fragariae* (*Figs. 21–5* and *21–6A*), next by leaf scorch, *Diplocarpon earliana* (*Fig. 21–6B*), and least by leaf blight, *Dendrophoma obscurans* (*Fig. 21–7*), although the latter disease is sometimes serious on Dunlap and Robinson, especially in Illinois, Indiana, and Michigan. One of the greatest factors for reduced loss has been the resistance of Howard 17 to all three leaf diseases, since Howard 17 composes such a large part of the ancestry of today's strawberry varieties. Blakemore and probably Fairfax inherit resistance from Howard 17 and have passed it on to their descendents. Plakidas (1948) of Louisiana and Bolton (1958) of Canada showed that there were races of the leaf spot fungus and that varieties differed in susceptibility to these races. Blakemore was severely affected by one race in Arkansas in 1957 and now is considered non-resistant there. No immunity to leaf spot has been found, although high resistance can be found. Propagation of virus-free stocks, if properly isolated, can reduce to a minimum the amount of infective material of leaf spots in fields. Leaf spot enters leaves through stomata; leaf scorch penetrates between epidermal cells. Varieties showing resistance are listed on page 391.

Kennedy and King (1962) have reported that a bacterial angular leaf spot is severe in humid weather in Minnesota. Robinson, Sparkle, and Trumpeter were most severely affected, while *F. vesca,* Grenedier, Catskill, Massey, Arrowhead, Earliness, Sioux, Vermilion, and Wisconsin 214 were relatively less affected. Other leaf spots are "purple leaf spot," similar in appearance to leaf scorch, with which it is usually confused, and widespread in the South, "leaf blotch," and *Cercospora* spots, whose economic importance is undetermined.

Powdery Mildew-Resistant Varieties

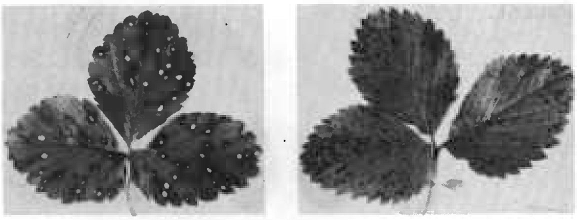
Mildew may affect strawberries in nearly all regions. Its characteristic appearance is an upward curling of the leaves (*Fig. 21–8*) as the fungus destroys the surface layers. As the disease progresses, the underside of the leaf reddens and affected parts die. Over half the leaves on a plant may be killed and flowers and green berries may not develop. The skin on ripening berries may be affected and not grow with the berry, so that the seeds are entirely on the surface and the skin may crack (*Fig. 21–9*). If the leaves are not affected more than in Midland, little loss of yield occurs, but the loss may be very serious with Armore. Catskill, Dunlap, Klondike, Marshall, and Sparkle have been notable resistant varieties. For others see page 391.

Verticillium-Resistant Varieties

Verticillium wilt affects strawberries in northern United States, in southern Florida, and along the Pacific Coast of California. It rarely causes damage from Maryland southward, including northern Florida. This fungus is present in nearly all soils of the United States but only builds up to the point of affecting strawberries following plantings of tomatoes, potatoes, and other solanaceous plants in northern and eastern states. The amount of inoculum from such plants is so great in northern states that susceptible varieties should not be grown for about two years after such crops. It persists for many years in the rocky soils of Dade County, Florida. The inoculum is so great along the Pacific Coast that for at least ten to fourteen years after such crops, as well as after cotton, melon, and many others, the disease may still be serious. However, since the disease is so serious, soil fumigation for Verticillium and other troubles is general for strawberries in California, consequently the problem is no longer acute.

FIG. 21–6. Two common leaf diseases of the strawberry. A *(left)* Leaf-spot disease; B *(middle)* Leaf-scorch disease. Note the large roundish transparent spots in leaf A in contrast to the smaller purplish irregular spots in leaf B that distinguish these two diseases.

FIG. 21–7. *(right)* Leaf blight *(Dendrophoma)*. Note the typical angular spot on the left leaflet and the wide purple margins of the spots with dead centers.



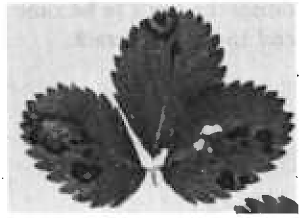


FIG. 21–8. Difference in mildew resistance of strawberries. Missionary (*left*), is very resistant; Midland (*right*), quite susceptible. Mildew can be so serious as in the Armore variety to reduce the crop by half or more.

Wilhelm (1955) has reported that many plants may be infected and survive and even show no injury, but no such tolerant seedlings were obtained from susceptible parents. Several varieties are resistant and have owed some of their popularity to this resistance, notably Howard 17, Catskill, Blakemore, Robinson, the Siletz in Oregon and Washington, and the Marshall. Sierra also is highly resistant. The Senga Sengana of Germany is also resistant, but many new varieties, such as Earlidawn, Dixieland, Jerseybelle, Northwest, Lassen, and Shasta are susceptible. The Florida Ninety, grown almost exclusively in Florida, is very susceptible. See page 391 for resistant varieties.

Breeding for resistant varieties is under way in California, New Jersey, and Florida in the United States, and has been successful in Oregon with the introduction of the Siletz. In British Columbia, Climax, Marshall, Northwest, Oberschlesien, Perle de Prague, Red Crop, Sierra, and Temple gave a high percentage of resistant seedlings. *Chiloensis* seedlings had the highest percentage of resistant seedlings of the species (Newton and Adrichem, 1958).

OTHER CROWN ROTS. Sclerotina crown and Rhizoctonia bud rot are serious under some conditions in the South, but no varietal differences in resistance are known. Brooks (1931) reported an anthracnose disease of strawberry runners and Horn and Carver (1963) reported that the same fungus, a *Colletotrichum,* caused a crown rot of the strawberry in Louisiana. Varietal differences in resistance may occur.

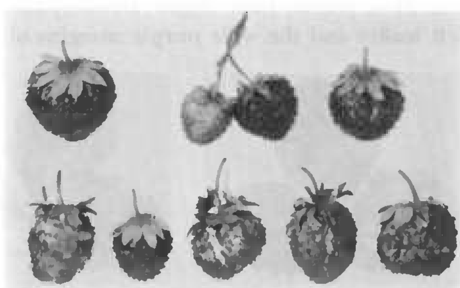


FIG. 21–9. Normal berry (*upper left*), and berries affected by mildew which causes the seeds to become prominent and the skin to crack.

Virus-Free and Virus-Tolerant Strawberries

In the United States in the 1920's, proof was obtained that strawberries were affected by virus diseases. By 1930 in Pacific Coast states and by 1940 in the East, it was discovered that viruses were serious there. By 1946 "virus-free" plants were found for three varieties in the East. By 1955 "virus-free" plants were found for the 42 varieties that represented 95 percent of the commercial production in the United States. Because virus-free plants propagate more freely than affected ones, the virus-free stocks were quickly propagated and have rapidly replaced diseased stocks. The greater part of the stocks in nurseries are now grown either under virus-free certification or have been grown from virus-free plants.

Because tests have shown that many wild plants have virus and could reinfect stocks in nurseries, regulations are in effect to ensure clean stocks by growing the plants in isolation from sources of reinfestation and by controlling insects, chiefly aphids and leaf hoppers, that spread the viruses.

We know that otherwise splendid varieties have been so weakened by viruses that they have disappeared and have been replaced by less affected varieties, and it is likely that many fine varieties of the past century have been replaced for the same reason.

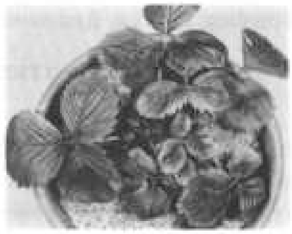
Symptoms vary with the variety, the particular virus or viruses present, with the stage of plant growth, and with weather conditions. Infected plants of some varieties show no obvious symptoms, though their yields may be greatly reduced by virus. Some varieties, like Marshall, show marked symptoms and are quickly weakened (*Figs. 21–10* and *21–11*). Others, like Ettersburg 80 (Huxley), Howard 17, and Blakemore, do not show symptoms plainly though they seem to be just as readily infected, and they are called tolerant varieties. It is considered best to originate tolerant varieties, for it is impossible for a grower in some areas to keep his planting virus-free for even one crop. Moreover, nontolerant varieties planted near infected stock of tolerant varieties can be severely injured by spread of virus from the tolerant ones. It is therefore desirable for nurseries to keep all varieties virus-free and for breeders to breed for tolerant varieties. On page 391 are listed some varieties showing marked tolerance.

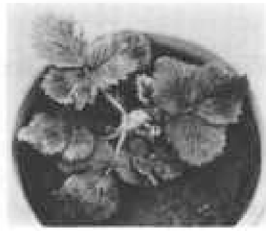
Variegation or June Yellows or Non-infectious Chlorosis

This trouble of the strawberry, the leaves becoming variegated or yellowed (*Fig. 21–12*), was noted as early as 1719 in *F. vesca,* the native woodland straw-

FIG. 21–10. *(right)* Yellows virus in the Marshall, one of the most sensitive of well-known varieties.

FIG. 21–11. *(far right)* Crinkle virus in the Marshall, to which it is also very sensitive.





berry of Europe, in 1778 in *F. virginiana* and *F. moschata,* and in 1832 in the cultivated strawberry. It has also been reported in native *F. ovalis* and *F. chiloensis* in Oregon. The greatest possible range of incidence of the trouble occurs, from tiny to large seedlings in their first year yellowing and dying outright; to varieties all of whose plants turn yellow, so that such varieties are lost many years after introduction; to varieties in which no plants ever turn yellow or to those in which only a few plants turn yellow through all the years that a variety may be grown. One phase of the trouble called June Yellows is temperature controlled. It appears in early spring but largely disappears in the hot summer. All runner plants from an affected one are variegated and no recovery is known (*Fig. 21–13*).

The seriousness of this trouble is evident today. The Auchincruive Climax variety raised in 1939 and introduced in 1947 quickly became the most important variety in Great Britain and other parts of northern Europe, supplanting many other varieties because of its many superior qualities. Variegation was first noted in it in 1950, and by 1954 this variety, which otherwise contained perhaps one of the finest combinations of desirable qualities yet known, had to be given up. Blakemore, for about twenty-five years the most important variety of the United States, was raised from seed in 1923 and introduced in 1929. In 1933 the major stocks of it were variegating. However, some stocks did not show variegation, and the variety is still extensively grown. Other varieties have been saved by such selection of non-variegating stocks. At present, Dixieland, introduced in 1953, the best shipping variety of eastern United States, is variegating and it is not known whether the variety can be saved by selecting non-variegating stocks. Many varieties have shown variegation and consequently have been lost.

Another serious, though indirect, loss due to variegation has been the elimination of seedlings and selections of certain crosses which incorporated high proportions of desirable genes. Thus, from the cross Blakemore x Dorsett many superior selections were made, but year after year additional selections became variegated and none was saved.

Because variegation has not been transmitted by grafting, it is not classed as a virus. A similar variegation has been obtained by irradiating seeds of the

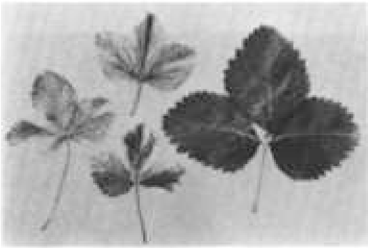


FIG. 21–12. Leaf variegation. Three leaves to left showing typical streaking. Healthy leaf to right. (See *Fig. 21–13.*)

diploid Alpine (*Fig. 21–14*). It is, therefore, classed as an inherited character due to an unstable gene. Different varieties have different rates of mutating to this variegated condition. No sure test to determine whether a variety will mutate, is known. Demaree and Darrow (1937) suggested that it might be helpful to grow a large population of selfed seedlings and observe whether variegation appears in the small seedlings. Fortunately it is possible to utilize variegating varieties in breeding; and most present varieties of the United States have Howard 17, which variegates, in their ancestry. Blakemore is also represented in many leading varieties. Variegation has never been found in Marshall, Klondike, and Lassen. Neither has it been found in Suwannee of the same parentage as Blakemore.

Variegation in any plant is thought to be due to a rogue plastid or plasmagene carried in the cytoplasm of the cells (Darlington, 1951). In breeding with a variegated plant, or with a plant of a variety subject to variegation, the variegational plant should always be used as the pollen parent. Morrow and Darrow (1952) obtained non-variegating varieties where varieties like Howard 17 and Blakemore were in their ancestry.

Fasciation of the Strawberry

This abnormal flattening and enlargement of the fruit stem and fruit and the witches-broom-like appearance (*Fig. 21–15*) of the plants is a trouble which is apparent in the Middle and South Atlantic States. Affected plants

FIG. 21–13. Leaf variegation (June yellows, genetic yellows) non-infectious chlorosis. All plants propagated from a variegated plant are variegated, as shown here, and are stunted as compared with those on either side. Though a major trouble and inherited, varieties affected have been successfully used as parents. (See also *Fig. 21–14.*)

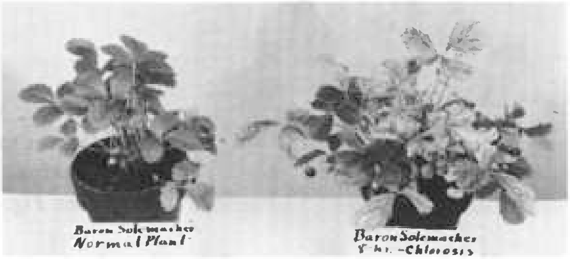


FIG. 21-14. Baron Solemacher, a seed propagated Alpine, showing to the right a plant with variegated leaf trouble induced by eight-hour irradiation of the seeds from which the plants were grown.

produce little marketable fruit and no runners. Because the principal varieties grown in the South are immune or highly resistant to fasciation, it usually is not considered important. However, when promising new varieties are tested, their culture may be limited, for many northern varieties are affected by fasciation when grown in the South, as is the case with Fairfax, Howard 17, Sparkle, and Catskill. For example, in Fairfax fasciation is serious in New Jersey and Maryland and rarely seen in New York and New England. Susceptibility to this trouble is inherited.

Fasciation has never been found in Blakemore and Missionary, and only in three plants of millions of Klondike; yet, at the end of one year, 100 percent of the mother, 29 percent of the June-rooted, and 8 percent of the August-rooted plants of Fairfax at Willard, North Carolina, were affected. Fasciation is initiated mostly in the fall when the days shorten and flower buds begin to develop. When tests were made by growing plants under different light periods, Howard 17 had no fasciated plants with twenty hours of light, 5 percent with seventeen hours, and 95 percent with fourteen, eleven, and eight hours (Darrow and Borthwick 1954). Missionary, Blakemore, and Massey had no fasciated plants under any day length. Thus, when growing conditions in the fall continue later than usual, fasciation can be serious farther north than usual. This happened with the Sparkle variety in New

FIG. 21-15. Fasciated plants of the Eleanor Roosevelt. None of these plants had marketable berries. Fasciation is an inherited response of most northern varieties when grown in the South or south of their region of best adaptation.

Jersey in the warm fall of 1952, during days which were as short as eleven hours.

Fruit Rots

Gray mold or botrytis rot (in all United States and in all the world), tan rot (in southern United States), hard rot (in all United States), leather rot (in Mississippi Valley, Maryland, and Virginia), and stem-end rot (in Michigan and surrounding area) are common field rots of the strawberry in the United States. No real resistance is known, although observation indicates that the Solana in California, Mollala in Oregon, Cascade & Columbia in Washington, Valentine in Sweden, and Tashkent in U.S.S.R. are less subject to gray mold than other varieties grown there. Firm-fruited varieties, like Blakemore and Dixieland, under some conditions, are much less injured than softer varieties. Because berries that stay moist are most affected, varieties that have dense leaf growth that prevents rapid drying after rain and dew are more likely to be affected than those with more open growth (*Fig. 21–16*). Gray mold may develop in frosted flowers and in injured green berries, so that frost-resistant varieties and varieties with flowers protected by leaves may have less rot than others (*Plate 20b*).

Running out of Strawberry Varieties

"Running out of strawberry varieties" to use the common expression, refers to the idea that varieties have a definite length of life or usefulness

FIG. 21–16. Missionary strawberry plant, before *(left)* and after *(right)* picking off leaves. Leaf protection of flowers against frost is important in some areas, but shaded berries are softer, more susceptible to rot, and have slightly lower vitamin C content than berries on longer flower stems.

after which they decrease in vigor and productiveness. Jucunda lasted for more than a hundred years as a major variety, but others last for only a few years. Research has shown that the loss of vigor in many varieties is due to several virus diseases, some of which are transmitted by aphids, while others are transmitted by nematodes and possibly still others by leaf hoppers. Still other viruses may be transmitted other ways. Plants free of known viruses have been far more vigorous and productive than ordinary stocks. Infestation of plants by nematodes, both bud and root, weaken them as do also root and leaf fungi, but stocks free of these pests can be obtained by heat treatment, or by rooting runners of plants infested with root nematodes in sterile soil.

When the strawberry is grown in subtropical regions, stocks of most varieties become weak and grow feebly, or not at all, the second year. Now we know that they need a cold rest period or chilling, as do most temperate climate plants. Thus, planting stocks may be obtained annually from the North to set in Florida, or Florida-grown plants may be refrigerated for a month and then reset. Varieties succeeding in such regions are those which require the least chilling. Varieties have been originated that are adapted to each particular length of day and chilling requirement. When grown continuously under shorter days, they are dwarfed and lack vigor; under longer days than where best adapted, they are usually too vegetative.

Plants freed of known viruses, fungi, and nematodes, and grown in the proper latitude for the variety, have for the most part been as vigorous and productive as when first fruited as seedlings. The question arises, do any varieties decrease in vigor just because the variety is older? It does not seem likely. In searching for causes for weak planting stock, *first,* winter injury to crowns and roots must be eliminated as a cause, for the variety must be hardy where grown; *second,* eliminate red stele root rot; *third,* eliminate bud and root nematodes; *fourth,* get stock free of all known viruses and keep them clean; *fifth,* get stock free of leaf and crown diseases and insects; and *sixth,* get stock that has had a cold rest period.

If all the above conditions are met most difficulties are eliminated. There are cases where it is not possible to explain the reason for loss of vigor, and unrecognized viruses may be the cause, but first the conditions listed above should be considered.

Through the past one hundred and fifty years there has been expressed a more or less decided opinion that some varieties are somewhat biennial: they fruit so heavily that they use up stored food reserves as well as current food supplies, and may die or may be severely weakened as a consequence; even without fungi and other pests that affect weakened plants, they do not recover enough to give a good crop the following year. The effect of breeding, especially the use of the hardy native Virginian strawberry, has probably largely eliminated this, were it ever really a factor. Before 1850 growers of the Virginian varieties were known to keep their bearing fields for as long as ten to twelve years; and present varieties protected against weeds, fungi, virus, and animal pests may, without replanting, still fruit well in a bearing field that long. Another factor in making some of the old varieties die after fruiting was their lack of resistance to high temperatures and to diseases after producing a heavy crop that weakened the plants.

22

Fun with Strawberry Breeding*

JAMES MERRICK, whose important work, *The Strawberry and Its Culture,* is reviewed in Chapter 5, described a phenomenon he observed in 1870 which is no less noteworthy today; that of the evident pleasure which accompanies the breeding of strawberries. Merrick writes, "The fascination that attends the raising of seedling fruits is well marked in the case of the strawberry. The abundance of seeds, the ease with which they germinate, the early age at which the new plants bear fruit, and the tolerable certainty of getting a very good variety from a hundred or two seedlings, all conspire to lead on the amateur, and induce him annually to increase the size of his seed-beds." Merrick goes on to say, "The careful hybridizer can plan in his mind what kind of a strawberry he will have, and by a skillful selection of parent plants he can realize his ideal."

During the past one hundred and fifty years many thousands of people from various backgrounds and positions of life have yielded to this fascination, and thereby found a source of interest and pleasure in growing strawberries from seed. These thousands have helped develop the wild strawberry into the magnificent fruit that we now enjoy, whether this help was the actual origination of new and better varieties, or whether it took the form of support and enthusiasm, providing the climate conducive to a springing up of interest, and the initiation of intensive work. For many, the reward of such interest has been an increase in knowledge, coming as a pleasurable familiarity with how plants are grown from seed, how the seed germinates and how

* By George Darrow and John Meader.

tiny plants develop size enough to set in the garden, where, encouraged by care yet almost mysteriously, they blossom, are visited by bees and set fruit. Then, following this, comes a more tangible reward for the "careful hybridizer": the sampling of ripe berries and a noting of the attributes of each —the mixing of acid, sugar, and astringency which when balanced go to make a good berry; the quality of flesh, whose smoothness determines a very good fruit; and the aroma, where a certain perfume adds the final cachet necessary to the delicate composition of what is presently termed the excellent berry. And through the months, from seed planting to ripe berry, a deeper understanding is gained of all living things.

Though it is possible to obtain good berries simply by growing seedlings, a good gardener soon learns many other things, along the lines of botany, as well as those of technique. For example, facts of sex in the strawberry were first learned in 1760 by Duchesne when he was thirteen. They were again discovered about 1808 by Keens, an English market gardener, whose variety Keens Seedling became the first great strawberry variety and an ancestor of most cultivated ones. In the United States these facts were again discovered by a market gardener of Philadelphia, named Abergust, and probably independently discovered and then forgotten by many others.

And one thing overlooked by many breeders even today is the importance of the source of the seed which they plant. If seed is taken from berries in the market, by far the most of them will not produce vigorous plants, for such berries come from large fields of one variety, and the seeds develop from self-pollinated flowers. If seed were obtained of the very large Fukuba of Japan, or of Madame Moutot, the large strawberry of Europe, or of the fine-flavored Royal Sovereign of England, most or all seedlings would be weak and give an entirely erroneous idea of the mother variety. This one point alone has discouraged many a promising hybridizer. Vigorous seedlings result only when actual crosses occur between two varieties or two different seedlings; a weak seedling of Fukuba, or Madame Moutot, or Royal Sovereign when crossed with another variety will give vigorous plants and may, in fact, give the very qualities of such varieties that are sought for.

It is also interesting to read about inbreeding and such things as hybrid corn, and then to attempt applying this method of breeding to the strawberry. Altogether too little is known about the results of inbreeding strawberries, and those who point their endeavours in this direction embark on a venture as interesting as a trip to the moon, for the possibilities are unlimited. In the case of inbreeding, however, it must be remembered that most seedlings of inbred strawberries are very dwarf and weak and more difficult to keep alive than hybrids, and only outcrossing or recrossing of inbred lines can recover the needed vigor.

Besides absorbing matters of botany, there are numerous other sources of interest and stimulus, for the strawberry breeder soon comes to know other breeders and thus can see how others do their work. There are breeders' conferences, such as the one held at Rutgers University in January 1963, where breeders, in this case from all over the United States and Canada, meet to study mutual problems. There are numerous articles available for study and for the developing of a better understanding of what has been done, and what might be done. And the problems that need to be tackled are legion! Some may be an after-office reason for having an intensely interesting small garden. Some problems for study can be combined with a search for the best strawberries for the table, and still others may lead to a part-time summer job, or one that lasts for a lifetime!

Here are some of the problems concerned with the Virginian and the western American wild strawberries: How common is mid-summer flowering in wild Virginian strawberries on the Blue Ridge of Virginia, or near your home, or in the meadows and pastures of all North America? Why do a large part of the wild strawberries of western America become summer- and fall-fruiting in Maryland and other parts of the East? How many generations of crossing and backcrossing wild strawberries with cultivated varieties will it take to recover full size, firmness, and yellow seeds on the berry surface? What crosses will do the job in one generation and what crosses will need two or more generations, and why? Can we ever get from summer-flowering wild plants the type of strawberries which will be two-crop varieties in the hot summers, like the two-crop raspberries that are fine garden plants in much of the United States? Interestingly, breeders are producing these fall-fruiting raspberries from selections having fall-fruiting wild plants as one parent.

And there are other problems: Hansen in South Dakota, Powers in Wyoming, and Georgeson in Alaska all succeeded in getting large-fruited strawberries hardy, to −40° and −50° F. without snow covering or mulch. But in the humid regions of the eastern United States all strawberries still have to be covered to protect them from the cold of winter. Our strawberry varieties still have non-hardy genes tracing back to their Chilean ancestry. Native wild strawberries, on the other hand, are hardy under the conditions of eastern United States. Mulching material is harder to obtain now and adds to the expense of strawberry growing. New varieties are needed that require no mulch.

While of less practical value for the present, a source of great enjoyment lies in trying to grow seedlings of strawberry crosses selected to give a great range of flavors, from apple, pineapple, apricot, raspberry, cherry and grape, to vinous and musky flavors. Merrick, a hundred years ago, called attention to such ranges of flavor in varieties of his time:

> There is really a much wider difference in the flavor of different strawberries than many inexperienced people will at first admit. Some have a distinct and delicate pineapple flavor, as Lenning's White—the White Pineapple and White Albion of some foreign lists—and River's Eliza. The Lucas, a fine seedling from La Constante, has a marked flavor of raspberries, while the Duc de Malakoff has a strong apricot, or, as some say, mulberry taste. The Hautbois strawberries are musky. A French berry, the Exposition de Chalons, has a marked taste of currants. Some foreign kinds have a decided cherry flavor. Our native wild strawberries have a delicious aroma, which is wholly absent in many of the largest kinds.

Such a range of flavors is still available in certain crosses, especially those which involve varieties not far removed from the Chilean. Selections with such flavors have not become major varieties in the past, but they are nonetheless delightful. Suwannee has the finest pure strawberry flavor (whatever that may mean) under most climatic conditions, but this flavor can be modified to involve less acidity, more sugar, less astringency, and any combination of the esters that make up the perfume of strawberries. Florida Ninety grown under some weather conditions can have a delightful perfume, even on arrival at a distant market. Perhaps new varieties can be bred to hold such a delightful flavor under a wider range of conditions.

Before the Wilson variety, the strawberry was chiefly a north temperate variety. Then it moved south to Louisiana and Florida, and with the Neunan and Hoffman, later the Klondike, and now the Florida Ninety, it is staying there. But the strawberry is extremely heterozygous; it has great numbers of genes that can be combined in an infinite variety of ways. It is possible that varieties can be produced which adapt to climates even closer to being tropical.

For that matter, why should we always stoop to pick strawberries from the ground? Why not pick them from a bush, or from plants not as low as our present ones? Staudt (1959) has what is called a bush strawberry where the flower stems are 18 inches long. Perhaps a variety can be bred where applications of gibberellic acid will extend the stems still higher.

Can plants be bred to such vigor that they can compete with weeds and need no protection against them, or with strong, thick root systems resistant to red-stele and capable of supporting plant beds for many fruiting seasons? Perhaps an everbearing variety can be bred whose energy for runner-production is channeled into root development, so that plants seldom need replacement and runner-production is unimportant. The variety might be seed-propagated. Can a variety be bred from the Chilean with thick leaves as protection against drought and cold, and perhaps against aphids? If a woody layer was extended over the roots, would they be less susceptible to root nematode damage? Can varieties be bred with fruit capable of ripening after harvest, as in the case of bananas, so the fruit could be harvested before full maturity, while less liable to damage? Machine harvesting might be facilitated if long, stiff flower stems held the fruit upright, and all berries ripened at once. Some of the wild *chiloensis* selected on the Pacific Coast display resistance to many diseases, including red-stele, Verticillium wilt, virus and mildew. How can these desirable characters be bred into the modern strawberry? Can these, or similar, characters be found in other wild strawberries? Do some possess immunity to leaf spot and leaf scorch?

While the questions are numerous and certainly could be multiplied, the possibilities of advance are far greater than any number of questions could ever imply. This, however, is not meant to intimidate the breeders of strawberries. On the contrary, such questions, problems, and suggestions should encourage breeding, for they show that the field is not a closed one, nor is the strawberry a finished fruit. There is room for further work with ample opportunity for amateurs, as well as for professionals, to make meaningful contributions. The strawberry is, after all, a plant, whose green foliage shelters shiny red fruit that is fragrant, sweet and juicy. The invitation is to enjoyment, both of work and its results.

23

Rating Systems for Strawberries and Sources of Superior Qualities

THE MATERIAL OF THIS CHAPTER is in two parts. One part describes systems for rating the various qualities of strawberries, both plant and fruit. The other part lists the sources of what are presently considered to be superior qualities. In effect, a possible method of evaluation is described, which is then followed by a list of qualities which experience suggests as deserving high valuation. This does not mean that those plants which are listed as sources of a certain highly rated quality were selected for the list by the rating system which is described. The method of rating is provided as a possible means of evaluation; it is not strictly referable to the sources of superior qualities which follow it.

Rating Systems for Strawberries

From ancient times fruit varieties have been compared with each other by growers, consumers, and writers. Comparisons gradually became more objective, and descriptive terms such as poor, fair, very good, and excellent, or small, medium, and large came to express more or less definite concepts. Nursery catalogues and popular descriptions commonly use such terms. But as science developed, still more accurate measures were needed. Some of the relatively accurate measurements that are often used now are: number of fruits per pound or bushel, weight of individual fruits, color names related to wave lengths of light, puncture pressure of epidermis and flesh as a measure of firmness, etc. For physical characters such measurements can often be made, but for some qualitative characters other measures are necessary.

In order to make comparisons as useful and as simple as possible, a numerical rating system has evolved with 1 indicating poorest and 10 indicating best (Morrow, 1949). Where rapid evaluations are necessary, all qualities may be so rated. Where one or more qualities, such as size or weight, are important enough to require a more or less exact figure, actual weights or sizes of samples may be taken, and such physical measurements may be integrated into the tables, or be translated into two numerical systems for use in tables.

In small-fruit research another fruitful approach in comparing varieties, and evaluating selections and seedlings, is the use of a score of 1 to 5 to indicate qualities too low to be commercially acceptable, with scores of 6 to 10 to indicate acceptable qualities. Hence, a score below 6 for any quality would make the variety or seedling unacceptable for commercial usage and those rating 6 or more for all qualities would be acceptable.

If a rating of 6 represents a measurable physical character, the numerical rating can be relatively exact over the years. If, however, a rating of 6 be given the flavor of a strawberry variety, it is based on the scorer's concept of an integration of acid to sugar ratio, tannin content and esters, taken in comparison with other varieties having acceptable flavors. In this case, as varieties with higher flavors are introduced, an acceptable rating of 6 may shift upward and a variety formerly rating 6 may have a rating of 5. There is little doubt that chemical measurements could be made of the components of flavor to establish relatively fixed standards but at present such are not available, at least for reference in the necessarily rapid evaluation of hundreds and thousands of seedlings during a short ripening season.

In the 1947 U.S. Department of Agriculture Yearbook a brief table was given to illustrate the great differences in qualities of strawberry varieties in one locality, as follows:

Variety	Size	Productiveness	Firmness	Flavor	Color	Resistance to spot	SEASON Earliest = 1 Latest = 10
Blakemore	7	8	8	7	9	7	2
Suwannee	7	8	5	10	8	7	3
Midland	10	10	7	9	7	9	2
Fairpeake	8	9	8	9	8	7	9
Redstar	8	7	7	7	8	9	10
Tennessee Shipper	5	8	10	5	7	7	3

These ratings were based on judgments of varieties grown in Maryland eighteen years ago. Our concept of size has changed and for this character each variety in that table would now be rated at least one point lower. For productiveness, too, each might drop one point. For firmness, our present judgment is that Blakemore should rate 9, Tennessee Shipper 9, and the others as given. Flavor, color, and spot resistance would not be changed. In season, Midland has proved to be earlier than Blakemore, perhaps enough to change its rating to 1. New standards based on new varieties are now available. Armore, Jerseybelle, and Midway are usually larger; and Armore, Pocahontas, Dixieland, and Earlidawn are more productive than Midland. Dixieland is as firm as Tennessee Shipper. No new varieties superior in flavor to Suwannee are available, no new variety for Maryland is more resistant to spot than Midland: Earlidawn may be slightly earlier than Midland, but the latter still rates 1.

In the same Yearbook article important differences between the same varieties grown in different areas were emphasized. Three varieties were rated for six characters, each variety in two locations as follows:

Variety	Location	Production	Firmness	Flavor	Color	RESISTANCE TO Spot	Scorch
Howard 17 (Premier)	Md.	9	4	6	7	9	9
"	Mass.	10	6	8	8	9	9
Missionary	Fla.	10	8	6–9	8	7	7
"	No. Car.	8	5	6–9	7	6	6
Marshall	Oreg.	9	6	9	8	7	9
"	Md.	1–3	3	3–5	5	3	7

Differences in climate in these different regions caused important differences in the varieties—berries of Howard 17 (Premier) were considerably firmer and higher flavored in Massachusetts as compared with those Howard 17 produced in Maryland, while Marshall showed even greater differences between Oregon and Maryland grown berries.

The strawberry in general has better flavor in northern parts of the United States, or at higher elevations, where the finer flavor is due to lower night temperatures and more sunshine (longer photoperiods with moderately warm days). However, the strawberry is an extremely heterozygous octoploid, and breeding in many localities has resulted in the selection of varieties with high flavor in many areas—Albritton in North Carolina, Midland from Maryland to Massachusetts, Suwannee from Mississippi to New York, and Sparkle from New Jersey to Maine. Florida Ninety is large-fruited in Florida, but small in Maryland. Weather and climate are important, but breeding for high flavor and other characters in any given section can give varieties with high ratings there.

The principal varieties of strawberries may be rated, for areas to which each is adapted, on the basis of eight characteristics considered commercially important, as follows:

Variety	1962% of Com. acreage	Size	Produc-tivity	Firm-ness	Flavor	Color	Res. to spot	Res. to Vertic.	SEASON 1 = Earliest 10 = Latest
Northwest	18	8	9	8	7	8	7	6	5
Blakemore	14	6	8	8	7	9	8	8	2
Robinson	8	8	9	5–6	6	8	5	9	7
Shasta	6	9	7	7	7	9	6	6	6
Headliner	5	–7	8	–	–	–	–	8	–
Tenn. Beauty	5	7	8	7	7	8	7	8	6
Dixieland	4	8+	8	10	6	9	7	1	2
Marshall	4	8	6	5	9	7	4	4	4
Sparkle	4	7	9	6	9	9+	7	5	6
Catskill	3	8	9	6	7	7+	8	10	5
Fla. Ninety	3	9	9	7	7	8	9	–	–
Lassen	3	8	10	5–6	6	9	–	7	6
Pocahontas	3	8+	9	7	8	9	6	4	3
Albritton	2	8	8	8	9	9	9	6	6
Earlidawn	2	7–8	10	7	8	8	8	1	1
Howard 17	2	6+	9	5–6	6	6+	9	9	2
Siletz	2	6	9	8	7	8	10	8 Or less	–8
Goldsmith	1	9	9	–	–	–	–	–	–
Jerseybelle	2	9	7	6	6	10	6	3	10
Surecrop	2	7	7	–	–	–	–	10	4
Armore	1	9	9–10	6	8+	7	6	4	6–7
Dabreak	1	8	8	–	–	–	–	–	–
Klonmore	1	6	7	8	7	8	10	–	–
Midland		7	8	7	9	7	8+	3	1
Fairfax		7	7	7	10	7	9	6	4
Klondike		6	6	7	7	6	7	?	3
Missionary		6	6	6	7	7	7	4	2
Senga Sengana (N.Y.)		8	8	6	7–8	9	–	–	6

This table gives individual values for each character. An overall score is often desired and is sometimes useful. It involves rating for other characters, or adjusting the values for the more important qualities. Earliness or lateness may sometimes have twice the importance of some other qualities. Size or flavor may be of unusual importance. Thus, for Glenn Dale, Maryland, the relative values for several qualities may be scored as follows:

Variety	Size (1–20)	Productiveness (1–20)	Firmness (1–10)	Flavor (1–10)	Color (1–10)	Resistance to spot (1–10)	SEASON 20 = Earliest 10 = Mid 20 = Latest	Total score
Earlidawn	15	19	7	8	8	8	20	85
Midland	15	16	7	9+	7	8+	19	81
Dixieland	15	17	10	7	9	7	16	81
Pocahontas	16	18	7	8	9	6	12	76
Armore	19	19	6	9	7	6	14	79
Vesper	19	17	7	6	8	4	20	81

The score indicates that Vesper may be of value if leaf spot can be controlled; if not, Vesper has no value at Glenn Dale. Its estimated productiveness, its size, and its lateness indicate that extra care and expense to control leaf spot may be warranted. Earlidawn may be the most profitable variety, especially on good soil where a good stand of plants can be obtained. Midland may be the third most profitable though its higher flavor may not return a higher price to compensate for lower yield. Ratings such as the above for a few qualities that are often important may have worth in showing potential values. However, the annual cycle of weather, soil fertility, insect and disease, weed or labor factors may have sufficient impact on many other genetic qualities to change the values by limiting plant stands, vigor, flower bud formation, fruit set and fruit development. For full evaluation of varieties, it would be necessary to interrelate number and time of runner production, leaf growth and flower-bud formation and development, response to temperature, to soil moisture, and to soil fertility, resistance to Verticillium, to mildew, to leaf scorch, to many kinds of nematodes and of root fungi, to fruit rots, to bud and root weevils, to spittle-bug and to other insects, as well as response to competition by various weeds and to cultural operations. For areas other than Glenn Dale, Maryland, other qualities will be rated as most important and the qualities in Maryland may be given different values.

Sources of Superior Qualities

Though the strawberry is a highly variable octoploid and most varieties may contain both desirable and undesirable characters, if a quality is represented by a single gene in a single chromosome, it may never or very rarely be expressed. But among the millions of seedlings that have been grown, some seedlings may have the desirable character in enough chromosomes for it to be apparent, and if these are used in breeding such qualities may be bred into cultivated varieties. Thus, tests in Illinois indicated that Aberdeen had resistance to the red stele root disease. Through breeding, this resistance is now in enough chromosomes in many varieties to be useful. In the same way the continuous fruiting of Nich Ohmer under the day length and cool temperatures along the coast of California has been utilized in obtaining Shasta, Lassen, Solana, Fresno, Torrey and Tioga. Recognition of such qualities and the recording of them for breeders is essential for the improvement of the strawberry. In the 1937 Yearbook of the U.S. Department of Agriculture, a listing of sources of many qualities was given and such a listing is continued here. When a certain quality, such as red stele resistance, becomes important an intensive search may indicate a surprising number of sources. Thus, resistance to some strains of the red stele fungus may be fairly common while resistance to other strains, rare in cultivated varieties, may yet be found in wild strawberries. Hence a listing of sources is to be used as a starting point, not as the sole source of a quality.

In some instances, listed varietal characters such as disease resistance may not hold true in certain regions, for strains of a disease may have developed that can affect an otherwise notably resistant variety. Such is the case of leaf spot resistance in Howard 17 and of red-stele resistance in all varieties. In like manner, Redcoat is firm enough in Canada to be the leading commercial variety, but it is not firm enough in the United States. Catskill and Sparkle are firm enough in New York and New England, but not in Maryland. Many characters must be so interpreted. In general, with an octoploid like the strawberry, if valuable qualities are noted in two varieties, then their desired combination can be obtained if enough seedlings are grown by the cross between the two varieties.

Disease Resistance—Plants

RED-STELE RESISTANCE TO ONE OR MORE RACES:

In the United States: Aberdeen, Temple, Sparkle, Stelemaster, Sunrise, Surecrop, Fairland, Redglow, Midway, Siletz, Mollala, Maine 55, Monmouth, Orland, Md-US-683, Vermilion, Columbia, Marshall, (slight). Resistant *Fragaria chiloensis* selections: Yaquina, Del Norte, Nelscott, Newport, and others; of *F. virginiana* selections: N-3953, Sheldon; of *F. ovalis:* Helmick.

In Great Britain: Frith, Auchincruive seedlings, Climax, Redgauntlet, Templar, Talisman, Cambridge Vigour, Oberschlesien (German), Cambridge Rival, Perle de Prague (French).

In Canada: Guardsman;

General resistance (lower level) may be in Little Scarlet and Marshall.

MILDEW RESISTANCE:

Columbia, Catskill, Dunlap (reported susceptible in Canada), Empire, Jerseybelle, Sunrise, Klondike, Konvoy, Solana, Puget Beauty, Siletz, Sparkle, Surecrop, Tennessee Shipper, Aroma, Marshall, Orland, Florida Ninety, Albritton; in *F. chiloensis, ovalis,* and *virginiana* species.

Europe: Merton Princess, Freya, Indra, Senga Sengana, Ettersburg 80 (Huxley), Cambridge Favourite, Gorella, Lassen, Valentine.

LEAF SPOT RESISTANCE:

Aroma, Howard 17, Fairfax, Midland, Blakemore, Surecrop, Redstar, Klonmore, Dorsett, Rockhill, Temple, Albritton, Headliner, Dabreak, British Sovereign, Dresden, Tennessee Beauty, Cyclone, Empire, Earlibelle.

Sweden: Lassen, Valentine.

LEAF SCORCH RESISTANCE:

Howard 17, Midland, Surecrop, Albritton, Dorsett, Blakemore, Fairfax, Rockhill, Suwannee, Redstar, Fairpeake, Aroma, Empire, Catskill, British Sovereign, Dixieland, Dabreak, Fletcher, Geneva, Trumpeter, Sunrise, Earlibelle, Valentine.

DENDROPHOMA RESISTANCE:

Earlidawn, Howard 17.

VERTICILLIUM RESISTANCE:

Vermilion, Catskill, Cavalier, Siletz, Surecrop, Sunrise, Sierra, Wiltguard, Robinson, Howard 17, Aberdeen, Marshall, Grenadier, Gem, Blakemore, (Aberdeen, Howard 17, and Temple have been reported both resistant and susceptible); in selections of *F. chiloensis* from North and South America.

Europe: Senga Sengana, Deutsch Evern (somewhat), Juspa, Talisman, Redgauntlet.

SALINE (ALKALINE) TOLERANCE:

Solana.

VIRUS TOLERANCE:

Northwest, Howard 17, Fairland, Blakemore, Tennessee Beauty, Siletz, Klondike, Missionary, Robinson, Columbia, Shasta, Lassen, Temple, Puget Beauty, Tioga, Mollala, *F. chiloensis* selections.

Europe: Madame Lafèbre

FREEDOM FROM FASCIATION:

Blakemore, Missionary, Klondike, and all other southern varieties.

FREEDOM FROM VARIEGATION:

Marshall, Klondike, Lassen, Suwannee.

RESISTANCE TO ROOT-KNOT NEMATODE:

F. ovalis (*platypetala,* Canada #5157), Fresno, Torrey.

RESISTANCE TO BLACK ROOT:

Siletz.

HARDINESS:

RESISTANCE TO VERY LOW TEMPERATURES:

F. ovalis, F. virginiana selections (No. Dak.) Cheyenne 1, 2, 3, Sioux, Radiance, Arapahoe, Ogallala, Sparta; Alaska selections; Dunlap, Glenmore, Glenheart, Jubilee, Parkland, Gem.

Europe: Senga Sengana, Abundance, Deutsch Evern (somewhat). (See under Russia)

RESISTANCE TO FROSTS (SPECIES):

F. virginiana "Sheldon," N. Dak., selections of *F. chiloensis* Chile.

RESISTANCE TO FROSTS (VARIETIES):

Earlidawn, Howard 17.

RESISTANCE TO HEAT:

Missionary, Florida Ninety, Klondike, Klonmore, Headliner, Dabreak, Blakemore, Ranger, Torrey, Lassen.

RESISTANCE TO DROUGHT:

F. ovalis, F. chiloensis, Blakemore, Marshall, Surecrop. (See under Russia, pp. 296, 298)

LOW CHILLING REQUIREMENT:

Dabreak, Headliner, Benizuru (Japan), Lassen, Klondike, Florida Ninety, Missionary, Torrey, Fresno, Tioga, Klonmore, Fukuba (Japan).

Photoperiods:

SHORT DAYS:

Ambato (Ecuador), Benizuru (Japan), Dabreak, Missionary, Florida Ninety, Fukuba (Japan), Cambridge Favourite.

FEW RUNNERS:

Earlidawn, Midland.

SUMMER FRUITING, COAST OF CALIFORNIA:

Tioga, Lassen, Goldsmith, Torrey, Fresno, Solana, Shasta, Marshall.

EVERBEARING:

Gem, Rockhill, Red Rich, Arapahoe, Radiance, Ogallala, Geneva, Ozark Beauty, Twentieth Century, Streamliner, Sparta (Canada).

Europe: Sans Rivale, Revada, Revita, Saint Claude, Saint Jean, Record, Profusion, selections of *F. ovalis, F. virginiana,* and the following varieties of *F. vesca semperflorens,* Montrueuse Caennaise, Belle de Meaux, Gaillons (rouge et blanc), Rugen, Baron Solemacher, Reine de Valles.

Germany: Macherauchs Dauerernte, Hertsbergs Triumph, Hummi Trisca, Ada Herzberg.

FALL CROPPING:

In favorable conditions; Redgauntlet, Talisman, Abundance, Precosa.

GOOD POLLEN PRODUCERS:

Fairfax, Empire, Midway, Puget Beauty.

Europe: Cambridge Prizewinner, Deutsch Evern, Georg Soltwedel, Marieva, Regina, Senga Gigana, Vola.

Fruit Characters:

EARLY:

Earlidawn, Midland, Cyclone, Redglow, Torrey, Wiltguard, Dabreak, Sunrise, Ogallala, Cavalier, Grenadier, Valentine; Fukuba and Benizuri (Japan); *F. virginiana* and *F. ovalis* selections.

Europe: Glasa, Senga Precosa, Macherauchs Frühernte, Deutsch Evern, Regina, Surprise des Halles, Lihama, Valentine.

LATE:

Redstar, Vesper, Mollala, Jerseybelle, Louise, *F. chiloensis.*

Europe: Talisman, Jucunda, Ydun, Tardive de Leopold, Souvenir de Charles Machiroux, Prof. Dr. Settegast, Dir. Paul Wallbaum, Mieze Shindler, Macherauchs Späternte.

FIRM:

Blakemore, Dixieland, Tennessee Shipper, Albritton, Fulton, Citation, Earlibelle, Earlidawn, Florida Ninety (in Florida in winter only); Fresno, Shasta and Goldsmith, Tioga (in California); Mollala.

Europe: Merveilleuse de Tihange, Gorella, Asieta, Vigerla, Senga 29, Senga Sengana.

LARGE:

Shasta, Goldsmith, Solana, Tioga, Florida Ninety (in Florida), Dabreak (in Louisiana), Jerseybelle, Robinson, Marshall, Cyclone, Albritton, Earlidawn, Armore, Vesper, Ambato, Trumpeter.

Japan: Fukuba.

Europe: Madame Moutot, Souvenir de Charles Machiroux, Sengana Gigana, Gorella, Merton Princess, Asieta, Finn.

LIGHT SCARLET:

Blakemore, Dixieland, Empire.

HIGH GLOSS:

Jerseybelle, Vesper, Albritton, Sparkle, Earlidawn, Tioga, Redcoat, Empire.

Europe: Glasa, Senga Gigana, Vola, Senga Precosa, Redgauntlet.

Superior for Freezing:

Northwest, Midland, Earlidawn, Blakemore, Pocahontas, Redcoat, Dixieland, Klondike, Fletcher.

Europe: Senga Sengana, Senga 29.

Excellent Flavor:

Fairfax, Suwannee, Midland, Dorsett, Marshall, Fletcher, Armore, Albritton, Solana.

Europe: Frau Mieze Schindler, Sieger, Macherauchs Marieva, Senga Precosa, Carolina Superba, Royal Sovereign, Cambridge Favourite, Talisman, Viscountesse Héricart de Thury, Regina, Cambridge Vigour, Deutsch Evern.

Resistance to Fruit Rots:

Possibly Solana, Cascade, Columbia, Mollala.

Europe: Possibly Jucunda, Juspa, and Senga Precosa, Taskent, Redgauntlet, Valentine, Xenion.

High Ascorbic Acid:

Catskill, Suwannee, Tennessee Beauty, Marshall, Sparkle, Fairpeake, Northwest.

Europe: Wädenswil 4, Georg Soltwedel, Valentine, Königin Luise, Senga 54, Record, Ambrosia Late, Purpuratka.

Easiest Capping:

Europe: Jucunda, Juspa, Gorella, Senga Precosa, Abundance.

Good Capping:

Tennessee Beauty, Fresno, Torrey, Tioga.

Europe: Cambridge Favourite, Regina, Senga Sengana, Wädensvil 4.

Processing:

Midland, Pocahontas, Earlidawn, Fresno, Tioga, Torrey, Mollala, Dixieland, Marshall, Tennessee Beauty, Sparkle, Catskill, Dabreak, Blakemore.

Europe: Marzcynka (Afrika), Abundance, Senga Sengana.

Concentrated Harvest:

Redglow, Dixieland, Pocahontas, Stelemaster, Fairland, Sunrise, Earlidawn, Surecrop.

Appendices

I

World List of Strawberry Breeders

Belgium

Linden, R., de Recherches de l' Etat pour l' Amélioration des Plantes Station Fruitière et Maraichères, Grand Manil, Gembloux

Canada

Aalders, L.E., Regional Research Station, Kentville, Nova Scotia
Craig, D.L., Regional Research Station, Kentville, Nova Scotia
Daubney, H.A., Experimental Farm, Agassiz, British Columbia
Evans, E.D., Ontario Agricultural College, Guelph, Ontario
Forest, B., Experimental Farm, Ste Anne de la Pocatiere, Quebec
Harris, J.H., Experimental Farm, Saanichton, British Columbia
Harris, R.E., Experimental Farm, Beaverlodge, Alberta
Quamme, H., Experimental Farm, Morden, Manitoba
Spangelo, L.P.S., Genetics & Plant Breeding Research Institute, Ottawa, Ontario
Weijer, J., University of Alberta, Edmonton, Alberta

Denmark

Jorgensen, M.B., Danish State Horticultural Research Station, Spangsbjerg, Madsen Esbjerg
Thuesen, A.

East Germany

Murawski, H., 1278 Macheberg (Mark) Wilhelm-Pieck Str. 72

Finland

Hardh, Prof. J.H., Univ. of Helsinki, Pautarkaneteen Laitos, Viik, Helsinki
Jaakho, Prof., Säkö, Piikkio

France

Drouzym, J.G., Vilmorin Andrieux, Verrières-le-Brisson, Seine-et-Oise
Pecaut, P., Station Centrale d'Amélioration des Plants, Versailles, Seine-et-Oise
Risser, Georgette C., Station d'Amélioration des Plantes, Maraichères, Montfavet, Vaucluse
Trébuchet, G.M., Verrières-le-Brisson

Germany

Bauer, R., Max-Planck-Institut für Züchtungsforschung, Köln-Vogelsang
Hondelmann, W.H.J., Sengana GmbH., Züchtung und Züchtungsforschung, Hamburg-Volksdorf, Waldredder 4
v. Sengbusch, R., Sengana GmbH., Forschungstelle der Kulturpflanzenzüchtung der Max-Planck-Gesellschaft, Hamburg-Volksdorf
Staudt, G., Institut für Vererbungs-und Züchtungsforschung, Berlin 33

Greece

Dendrinos, A.D., State Seed Testing Station, Halandrion

Italy

Baldini, E., Istituto di Coltivazioni Arboree, Bologna
Breviglieri, N., Univ. of Agraria, Florence
Branzanti, C., Istituto di Coltivazioni Arboree, Bologna
Cassini, E., Univ. of Agraria, Florence
Lalatta, E., Instuto di Frutticoltur et Electrogenetica, Roma

Japan

Honda, Fujio, Horticultural Research Station, Kurume, Fukuoka-ken
Ito, Junkichi, Experiment Station, Takarazuka, Hyogo-ken
Kakizaki, S., Yamagata-ken
Kamimura, Shaji, Horticultural Research Station, Shimökuriyagawa, Morioka, Iwate-ken
Kotani, Akira, Shimizu, Shizuoka-ken
Kuriyama, Takashi, Shimizu, Shizuoka-ken

Nakashizuka, Akira, Horticultural Research Station, Niitsu, Niigata-ken
Ninomiya, K., Shizuoka Expt. Station, Shizuoka, Shizuoka-ken
Serizawa, Yomei, Horticultural Research Station, Shiojiri, Nagano-ken
Sugawara, Y., Shimizu, Shizuoka-ken
Takai, Takatsuga, Horticultural Research Station, Morioka, Iwate-ken
Yamato, Shigehachi, Agricultural Research Station, Kurume, Fukuoka-ken

Netherlands

Kronenberg, H.G., Institute of Horticultural Plant Breeding, Wageningen
Wassenaar, L.M., Institute of Horticultural Plant Breeding, Wageningen

Sweden

Koch, Anne, Lige. Balsgård Fruit Breeding Institute, Fjalkestad
Olden, E.J., Balsgård Fruit Breeding Institute, Fjalkestad

Switzerland

Fritzsche, R., Wadenswil
Kobel, F., Wadenswil

Union South Africa

Evans, E.P., Horticultural Research Station, Pretoria, Transvaal
Steyn, P.A.L., Fruit and Food Technology Research Institute, Stellenbasch

United Kingdom

Boyes, D., Cambridge, England (retired)
Ellis, J.R., Galton Laboratory, University College, London, W.C.1
Harland, S.C., (retired), Department of Botany, University of Manchester, Manchester 13 (present address: Kilometer 22, Lima, Peru)
Jones, J.K., Department of Agricultural Botany, Reading University, Reading
Reid, R.D., Scottish Horticultural Research Institute, Auchincruive, Ayr, Scotland
Williams, H., John Innes Horticultural Institute, Hertford, England

United States of America

Anderson, R., Dept. Horticulture, University of Minnesota, St. Paul 1, Minn.
Blake, R.C., University of Southern Illinois, Carbondale, Illinois
Bowen, H.H., N. J. Agricultural Experiment Station, New Brunswick, N. J.
Bringhurst, R.S., California Agricultural Experiment Station, Davis, Calif.

Brooks, A.N., Strawberry Laboratory, Plant City, Florida
Chaplin, C.E., Kentucky Agricultural Experiment Station, Lexington, Ky.
Darrow, G.M., (retired) U.S.D.A., Plant Industry Station, Beltsville, Md.
Dearborn, C.H., Alaska Agricultural Experiment Station, Palmer, Alaska
Denisen, E.L., Iowa Agricultural Experiment Station, Ames, Iowa
Drain, B.D., Tenn. Agricultural Experiment Station, Knoxville, Tenn.
Felix, E.L., Tenn. Agricultural Experiment Station, Knoxville, Tenn.
Galletta, G., N. C. Agricultural Experiment Station, Raleigh, N. C.
Gilbert, F.A., Peninsula Horticultural Station, Sturgeon Bay, Wisc.
Haut, I.C., Maryland Agricultural Experiment Station, College Park, Md.
Hawthorne, F.L., La. Agricultural Experiment Station, Baton Rouge, La.
Hemphill, D.D., Missouri Agricultural Experiment Station, Columbia, Mo.
Hough, L.F., N. J. Agricultural Experiment Station, New Brunswick, N. J.
Howard, G.S., U.S. Horticultural Field Station, Cheyenne, Wyoming
Janick, J., Indiana Agricultural Experiment Station, Lafayette, Ind.
Johnson, H.A., Calif. Strawberry Institute, Morgan Hill, Calif.
Johnston, S., South Haven Experiment Station, South Haven, Michigan
Kalleo, A., University of Alaska, College, Alaska
Lawrence, F. J., Oregon Agricultural Experiment Station, Corvallis, Oregon
Meader, E.M., N. H. Agricultural Experiment Station, Durham, N. H.
Miller, J.C., La. Agricultural Experiment Station, Baton Rouge, La.
Moore, J.N., Arkansas Agricultural Experiment Station, Fayetteville, Ark.
Moulton, J.E., Mich. Agricultural Experiment Station, East Lansing, Mich.
Ourecky, D., N. Y. Agricultural Experiment Station, Geneva, New York
Overcash, J.P., Miss. Agricultural Experiment Station, State College, Miss.
Roever, W.E., Tenn. Agricultural Experiment Station, Knoxville, Tenn.
Schwartze, C.D., Western Washington Experiment Station, Puyallup, Wash.
Scott, D.H., U.S.D.A., Plant Industry Station, Beltsville, Md.
Slate, G.L., N. Y. Agricultural Experiment Station, Geneva, New York
Strobel, J.W., South Florida Agricultural Experiment Station, Homestead, Fla.
Thomas, H.E., Calif. Strawberry Institute, Morgan Hill, Calif.
Voth, V., University of California, 906 Grovement, Santa Ana, Calif.
Waldo, G.F., Oregon Agricultural Experiment Station, Corvallis, Oreg. (retired Dec. 31, 1965)
Watson, J.P., N. Y. Agricultural Experiment Station, Geneva, New York
Zych, C.C., Illinois Agricultural Experiment Station, Urbana, Illinois

II Chronology of Strawberry Varieties in the United States

Before 1800—Beginning about 1750, a few gardens had Early Hudson (a Virginian) and Hautbois, Wood and Chilean, all imported from Europe. In 1771 Large Hautbois, the Chili, the Redwood, and the Wood were offered for sale in Prince's (Long Island nurseryman) catalogue, and the first Pine and Large Early Scarlet about 1790.

1800 to 1840—First commercial culture beginning about 1812 near the larger cities—Boston, New York, Philadelphia, Baltimore; by 1830's a few hundred acres of native strawberry varieties (Early Hudson, Hudsons Bay, Large Early Scarlet, Old Scarlet, Methven Scarlet, and Crimson Cone) near large cities, a few Mulberry (a Pine) near Boston.

1840—Hovey, the first American variety put in trade.

1840 to 1858—By 1854 about 1500 acres, 95 percent native varieties; 600 acres, all Virginian varieties below Baltimore. In 1857 some Hovey around Boston.

1858—Wilson extensively planted.

1858 to 1880—By 1860 and through 1875 probably 90 percent of acreage Wilson, some Neunan beginning 1870 in South Atlantic States, by 1880 some Charles Downing, Crescent, Cumberland Triumph, Sharpless, and Miners Prolific.

1880 to 1900—Up to 1895 Wilson, Crescent, and Sharpless largest part of acreage in United States; Neunan to 1890 chief variety in South Atlantic States and as a pollinator for Cloud, replaced by Hoffman beginning about 1890; and Lady Thompson beginning about 1895; Gandy from 1890 chief late in North and Midwest; Aroma from 1895 a leading sort in Midwest; Warfield for early from 1890 in the North.

1900 to 1920—Hoffman in South Atlantic to 1905, then Klondike in entire South, except Missionary beginning about 1910 in south-central Florida and along Atlantic and Gulf Coasts; Aroma leader in entire Midwest; Dunlap and Warfield for North Midwest and to New England; Gandy for late from Virginia and Kentucky north; others important: Haverland, Sample, and Bubach pollinated by Parsons, Bederwood, Glen Mary, William Belt, Early Ozark, and Excelsior; Joe, Jessie, and Chesapeake in Del-Mar-Va peninsula; Marshall in central California, Oregon, and Washington; Klondike and Brandywine in southern California; some Gold Dollar, Clyde, and Jessie in central California; Clark in Hood River area of Oregon and Magoon in Oregon and Washington also.

1920 to 1940—Haverland, Warfield, Sample, Bubach, Wm. Belt, Glen Mary, Parsons, Bederwood, Early Ozark, Excelsior, and part of Dunlap replaced by Howard 17; Gandy replaced by Aroma except along Atlantic Coast States; Blakemore in 1930's replacing Klondike and part of Missionary in the South.

1940 to 1960—Blakemore leading variety in the South; Marshall in the Pacific Northwest; Shasta and Lassen replacing Marshall in California; Northwest replacing Marshall in Washington and Oregon; Massey replacing Blakemore and Klondike in North Carolina; and Albritton replacing Massey; Florida Ninety replacing Missionary in Florida; Klonmore replacing Klondike in Louisiana and Headliner replacing Klonmore; Armore replacing part of Blakemore in Missouri; Tennessee Beauty replacing part of Blakemore in Kentucky and Tennessee; Robinson replacing most of Howard 17 in Michigan and in part of Ohio, New York, and Pennsylvania; Sparkle and Catskill replacing part of Howard 17 in the Northeast; Midland, Pocahontas, and Dixieland replacing part of Blakemore and Howard 17.

1960 to 1965—Florida Ninety only variety grown in Florida; Dabreak replacing Headliner in Louisiana; Blakemore still major variety in Arkansas, Tennessee, Kentucky, and Missouri, but Pocahontas, Dixieland, and Tennessee Beauty grown also; Albritton only variety in North Carolina; Pocahontas, Midland, Dixieland, Surecrop grown in Maryland and Virginia to Missouri; Jerseybelle in New Jersey; Catskill and Sparkle in New England, New York, Pennsylvania, and Ohio; Robinson, Midway, and some Catskill in Michigan; Northwest grown chiefly but also some Siletz, in Oregon and Washington; Shasta and Lassen grown in California, but Lassen being replaced by Tioga, Fresno, Torrey, and Solana.

III

Howard 17 (Premier) as a Parent

Table 1
Thirty-nine varieties having Howard 17 as one parent

Variety	Parentage	Year introduced
Adirondack	Fairfax x Howard 17	1948
Beaver	Howard 17 x Burrill (probable)	1925
Bellmar	Missionary x Howard 17	1932
Blakemore	"	1929
Caledonia	Marshall x Howard 17	1929
Camden	"	1929
Cato	"	1929
Catskill	"	1929
Clermont	"	1929
Culver	"	1929
Dorsett	Howard 17 x Royal Sovereign	1933
Dresden	Beacon x Howard 17	1939
Dry Weather	Americus x Howard 17	1925
Earlee	Premier x un-named	1949
Earlimore	(Campbell inbred) x Howard 17	1958
Erie	Sparkle x Howard 17	1951
Essex	Howard 17 x Deutsch Evern	1951
Fairmore	Blakemore x Fairfax	1939
Howard Supreme	Howard 103 x Howard 17	1929
Jumbo	Bedarena x Howard 17	1950
Mackenzie	Excelsior x Howard 17	1941
Maine 55	Howard 17 x Aberdeen	1952

(Table 1, continued)

Variety	Parentage	Year introduced
Majestic	Howard 17 seedling	1940
Midland	Howard 17 x Redheart	1944
Monmouth	Aberdeen x Howard 17	1952
Narcissa	Howard 17 x Royal Sovereign	1933
Nectarena	Howard 17 x Bedarena	1947
Northstar	Howard 17 x Redheart	1939
O. A. C.	Parsons x Howard 17	1938
Orland	Aberdeen x Howard 17	1952
Pathfinder	Howard 17 x Aberdeen	1938
Red Gold	Howard 17 x everbearer	1925
Robinson	Howard 17 x Washington	1940
Southland	Ettersburg 80 x Howard 17	1932
Suwannee	Missionary x Howard 17	1945
Tennessee Beauty	"	1942
Tennessee Supreme	"	1940
Valentine	Howard 17 x Vanguard	1941
Wisconsin 537 (= Sharon)	Corvallis x Howard 17	1954

Table 2
Varieties (other than those in Table 1) having Howard 17 in their ancestry (H17 abbreviation for Howard 17)

Variety	Parentage	Year introduced
Agassiz	Pathfinder x British Sovereign	1957
Alamo	Blakemore x Ettersburg 80 (?)	1937
Albritton	Southland selfed x Massey selfed	1951
Arapahoe	Has Dorsett in ancestry	1954
Armore	Blakemore x Aroma	1950
Blaze	(Simco x Catskill) x (Tupper x Fairfax)	1952
Branford	(Kalicene x H17) x (Progressive x H17)	1939
Brightmore	Blakemore x Oregon 154	1942
Bristol	(Chesapeake x Marshall) x (Progressive x H17)	1939
Burgundy	SYS 3672-171 (Inbred H17)	1959
Cambridge Early Pine	Blakemore as one parent	1947
" Favourite	" " " "	1947
" Forerunner	Early Cambridge x Bellmar	1947
" Premier	Blakemore as one parent	1947
" Rival	Dorsett x Early Cambridge	1948
" Sentry	" " " "	1946
Campbell	US-634 & 543 & NY4626 (Marshall x H17) in ancestry	1949
Canall	Catskill x Golden Gate	1950
Cavalier	Valentine x Sparkle	1957

(Table 2, continued)

Variety	Parentage	Year introduced
Cheyenne 1	F_1 of Dorsett x *F. ovalis*	1942
Cupertino	US-634 in ancestry	1949
Cyclone	Iowa-1-3713 x Iowa-68-3702 (Beaver & Dorsett in ancestry)	1959
Dabreak	Howard 17 in ancestry	1961
Dixieland	Tennessee Shipper x Midland	1953
Donner	US-634 and Blakemore in ancestry	1945
Earle Felton	Howard 17 in ancestry	1951
Earlidawn	Midland x Tennessee Shipper	1956
Eden	Dresden x Fairfax	1951
Empire	Dresden x Sparkle	1951
Fletcher	Midland x Suwannee	1959
Fresno	Howard 17 in ancestry	1961
Frontenac	Erie x (Fairpeake x Dresden)	1959
Fulton	Starbright x Pathfinder	1959
Goldsmith (Z 5 A)	Howard 17 in ancestry	1962
Great Bay	Simcoe x Catskill	1949
Grenadier	Valentine x Fairfax	1958
Headliner	Suwannee & Klonmore in ancestry	1957
Hebron	Inbred Chesapeake x (F_1 inbred Progressive x H17)	1939
Howe	(Red Sugar x H17) x (Willard x Santiago de Chile)	1936
Institute X 2	Blakemore & US-634 in ancestry	1958
" Z 4	US-634 & 543 in ancestry	1958
" Z 5 A	US-634 & 543 in ancestry	1958
Jerseybelle	Pathfinder in ancestry	1955
July Morn	Redheart x NJ-5 (Mastodon x H17)	1938
Klonmore	Blakemore x Klondike	1940
Konvoy	Fairmore x Klondike	1942
Lassen	Blakemore & US-634 in ancestry	1945
Lustre	#3001 (H17 x Marvel) x #3700 (#3001 x Fairfax)	1949
Marion Bell	Fairmore x self	1946
Massey	US-634 (Royal Sovereign x H17) x Blakemore	1940
Midway	Dixieland x Temple	1959
Mildred Felton	Fairfax x #3001 (H17 x Marvel)	1947
Mr. Big	"May be seedling of Robinson"	1953
Mollala	Howard 17 in ancestry	1961
Northwest	Brightmore & Narcissa in ancestry	1949
Ogallala	Midland in ancestry	1958
Parker	Blakemore x Sparta	1953
Plentiful	Redstar x Pathfinder	1953
Pocahontas	Tennessee Shipper x Midland	1953
Puget Beauty	Howard 17 in ancestry	1956
Radiance	Dorsett in ancestry	1954
Redcoat	Sparkle x Valentine	1957
Redgauntlet	NJ-1051 (H17 in ancestry) x Auchincruive Climax	1957
Redglow	Fairland x Tennessee Shipper	1956

(Table 2, continued)

Variety	Parentage	Year introduced
Riogrande	Blakemore x Ettersburg 80 (?)	1937
Shasta	US-634 & 543 in ancestry	1945
Shelton	(Chesapeake x Marshall) x (inbred Progressive x H17)	1939
Sierra	US-634 & 543 in ancestry	1945
Simcoe	(Red Sugar x H17) x (Delecto x Cassandra)	1936
Siletz	Blakemore & Narcissa in parentage	1955
Solano	Howard 17 in ancestry	1957
Starkrimson	Midland x Fairpeake	1956
Strafford	(Simcoe x Catskill) x (Tupper x Fairfax)	1954
Surecrop	Fairland x Md-US-1972 (Md-US-683 x Blakemore)	1956
Tahoe	Narcissa in ancestry	1945
Talisman	NJ-1051 (H17 in ancestry) x Auchincruive Climax	1955
Tennessee Shipper	Missionary x Blakemore	1941
Tennessean	Tenn-230 (Missionary x H17) x Tenn-586	1950
Tioga	Howard 17 in ancestry	1963
Torrey	Howard 17 in ancestry	1961
Trumpeter	Burgundy x Howard 17 selfed	1960
Utah Shipper	Lindalicious x Catskill	1950
Vermilion	Redstar x Pathfinder	1950
Wiltguard	U.S. 634 in ancestry	1961
Wisconsin 214	Beaver & Premier in ancestry	1950
Wisconsin 261	Beaver & Howard 17 in ancestry	1951
Xenion	Deutsch Evern x Valentine	1959
Ydun	Culver in ancestry	1948

IV

Parentage of United States Strawberry Varieties

One way to illustrate the importance of varieties as parents is to list them as they appear in the parentage of the 23 varieties that constitute 1 percent or more of the acreage of strawberries in the United States. Howard 17 (Premier) is known to be in the ancestry of 20 of the 23 varieties and is probably in the ancestry of both Florida Ninety and Fairfax or in all except Marshall. Missionary is in the parentage of 15 of the 23 leading varieties. The composition of Howard 17 (Premier) is 62½ percent Crescent, 12½ percent Belmont, 6¼ percent Cumberland Triumph, 6¼ percent Sharpless (still grown in Poland), and 12½ percent unknown. Marshall, Fairfax, Aberdeen and Klondike follow Howard 17 and Missionary in importance as parents.

An example of the value of good ancestry is the steady building up of desirable qualities in the present California varieties by the California breeders.

Percentage of foundation varieties in present California varieties:

Foundation variety	Shasta	Lassen	Solana	Goldsmith	Torrey, Fresno, Tioga
Nich Ohmer	25.0	25.0	25.0	25.0	25.0
Howard 17 (Premier)	37.5	18.8	31.2	32.8	28.0
Royal Sovereign	31.3	6.2	18.8	18.8	14.1
Marshall (Banner)	6.2	18.8	9.35	16.4	14.1
Fendalcino	.0	18.7	.0	.0	9.4
Missionary	.0	12.5	3.1	3.1	9.4
Klondike	.0	.0	12.5	3.1	.0
Crescent*	.0	.0	3.15	0.8	.0

* Crescent is 5/8 of the ancestry of Howard 17, hence enters into the ancestry in a substantial way of every California variety.

This table indicates that the California breeders recognized the value of the qualities in these ancestors, or in varieties already bred from them. Thus, they obtained shipping quality and summer-fruiting from Nich Ohmer, great productiveness and disease resistance from Howard 17 (Premier), high flavor from Royal Sovereign, and large size and high flavor from Marshall.

Genealogy of United States Strawberry Varieties

(Listed according to importance 1962)
(The ancestry of a variety as a parent is given only once)

Variety and % of total acreage

Northwest 18%
- Brightmore
  - Blakemore (see below)
  - x
  - U.S-Oreg. 154
    - Ettersburg 121 (Unknown, probably *F. chiloensis* x unknown)
    - x
    - Marshall (unknown parentage)
- x
- US-Oreg. 456
  - US.-Oreg. 7
    - Ettersburg 121
    - x
    - Wilson (unknown)
  - x
  - Narcissa
    - Royal Sovereign
      - Noble
        - Excelsior (of England)
        - x
        - Sharpless (unknown) Possibly . .
          - Jucunda
          - x
          - Col. Cheney
      - x
      - King of the Earlies
    - x
    - Howard 17 (see below)

Blakemore 14%
- Missionary (unknown, probably
  - Hoffman
    - supposed Neunan
    - x
    - ?
  - x
  - ?
- x
- Howard 17 (see below)

Robinson 8%
- Howard 17 (see below)
- x
- Washington
  - Marshall (unknown)
  - x
  - *F. ovalis* (probably)

Genealogy of United States Strawberry Varieties (cont.)

Variety and % of total acreage

Shasta 6%
- Cal. 67.5
  - Nich Ohmer
    - Middlefield (unknown)
    - x
    - Unknown
  - x
  - USDA-634
    - Royal Sovereign (see above)
    - x
    - Howard 17 (see below)
- x
- Cal. 177.21
  - USDA-543
    - Royal Sovereign
    - x
    - Howard 17
  - x
  - Cal. 68.24
    - USDA-634
    - x
    - NY-4626
      - Marshall (unknown)
      - x
      - Howard 17

Headliner 5%
- L-7-27
  - Suwannee
    - Howard 17 (see below)
    - x
    - Missionary (see above)
  - x
  - L-6-30-45-7
    - Klonmore
      - Blakemore (see above)
      - x
      - Klondike (see below)
    - x
    - Self
- x
- L-7-42
  - Suwannee
  - x
  - Konvoy
    - Fairmore
      - Blakemore
      - x
      - Fairfax (see below)
    - x
    - Klondike (see below)

Tennessee Beauty 5%
- Howard 17 (see below)
- x
- Missionary (unknown parentage)

Genealogy of United States Strawberry Varieties (cont.)

Variety and % of total acreage

Dixieland 4%
- Tennessee Shipper
  - Missionary (see above)
  - x
  - Blakemore (see above)
- x
- Midland (see below)

Marshall 4%
- Unknown parentage, possibly Bubach or President Wilder as one parent

Sparkle 4%
- Fairfax (see below)
- x
- Aberdeen (unknown)

Catskill 3%
- Marshall (unknown)
- x
- Howard 17 (see below)

Florida Ninety 3%
- Missionary (see above)
- x
- Unknown

Lassen 3%
- Cal. 21.9
  - Blakemore (see above)
  - x
  - Cal. Z 9
    - Banner (= Marshall) (unknown)
    - x
    - Fendalcino
      - Fendall
        - William Belt (unknown)
        - x
        - Unknown
      - x
      - Ettersburg 121 (unknown)
- x
- Cal. 161.1
  - Nich Ohmer (see Shasta above)
  - x
  - Cal. 86.6
    - USDA-634 (see Shasta above)
    - x
    - Cal. Z11
      - Banner (= Marshall)
      - x
      - Fendalcino

Genealogy of United States Strawberry Varieties (cont.)

Variety and % of total acreage

Pocahontas 3%
- Tennessee Shipper (see Dixieland above)
- x
- Midland (see below)

Albritton 2%
- US-NC-1065
  - Southland
    - Ettersburg 80
      - Seedling
        - Rose Ettersburg
          - Seedling
            - Seedling
              - Sharpless (unknown)
                - Jersey Queen (unknown)
                - x
                - Unknown
              - x
              - Parry
            - x
            - Unknown
          - x
          - Chilean
        - x
        - Unknown
      - x
      - Ettersburg 20
        - Rose Ettersburg
          - Chilean
          - x
          - 3rd generation from Sharpless x Parry
        - x
        - *F. chiloensis*
    - x
    - Howard 17 (see below)
  - x
  - Self
- x
- US-NC-1053
  - Massey
    - USDA-634 (see under Shasta above)
    - x
    - Blakemore (see above)
  - x
  - Self

Earlidawn 2%
- Midland (see below)
- x
- Tennessee Shipper (See Dixieland above)

Genealogy of United States Strawberry Varieties (cont.)

Variety and % of total acreage

- **Howard 17** **2%**
  - Crescent
    - Hovey
      - Methven Scarlet
        - Hudson Bay (a Virginian)
        - x
        - Unknown
      - x
      - Keens Seedling
        - Keens Imperial
          - White Carolina
          - x
          - ?
        - x
        - Unknown
    - x
    - N.J. Scarlet (a Virginian)
  - x
  - Howard 1
    - Howard 4
      - Haverland
        - Crescent; probably
          - Hovey
          - x
          - N.J. Scarlet
            - a Virginian (? pure)
        - x
        - Sharpless (unknown)
      - x
      - Belmont (unknown)
    - x
    - Clyde
      - Cyclone
        - Crescent
        - x
        - Cumberland Triumph
          - Green Prolific
            - Hovey
            - x
            - Goliath
              - British Queen
              - x
              - Unknown
          - x
          - Jucunda
      - x
      - Unknown

- **Jerseybelle** **2%**
  - NJ-953
    - NJ-72
      - Lupton (unknown)
      - x
      - Aberdeen (unknown)
    - x
    - Fairfax (see below)
  - x
  - NJ-925
    - Pathfinder
      - Howard 17 (see above)
      - x
      - Fairfax
    - x
    - Fairfax

Genealogy of United States Strawberry Varieties (cont.)

Variety and % of total acreage

- **Siletz** **2%**
  - US-Oreg. 2012
    - US-Oreg. 1491
      - US-Oreg. 767
        - Corvallis
          - E-121 (see above)
          - x
          - Marshall (unknown)
        - x
        - US-836
          - Progressive (see below)
          - x
          - *F. chiloensis* (Ambato)
      - x
      - Narcissa
        - Royal Sovereign (see Northwest above)
        - x
        - Howard 17 (see above)
    - x
    - US-Oreg. 1509
      - US-Oreg. 305
        - Clark (supposed Wilson seedling)
        - x
        - Narcissa (see above)
      - x
      - US-Oreg. 812
        - *F. chiloensis*
        - x
        - Oregon selection
          - Marshall
          - x
          - Fairfax (see below)
  - x
  - US-Oreg. 1816
    - US-Oreg. 1579
      - US-Oreg. 834
        - Clark
        - x
        - *F. ovalis*
      - x
      - US-Oreg. 913
        - Blakemore (see above)
        - x
        - Marshall
    - x
    - US-Oreg. 319
      - Redheart (see Midland below)
      - x
      - Oreg. 46
        - Ettersburg 121 (see Northwest above)
        - x
        - Marshall (unknown)

Genealogy of United States Strawberry Varieties (cont.)

Variety and % of total acreage

Surecrop 2%
- Fairland
  - Aberdeen (unknown)
  - x
  - Fairfax (see below)
- x
- Md-US-1972
  - Blakemore (see above)
  - x
  - Md-US-683
    - Scotland BK-46 (probably Firth selfed)
    - x
    - Fairfax

Armore 1%
- Blakemore (see above)
- x
- Aroma
  - Cumberland Triumph (see Howard 17 above)
  - x
  - Unknown

Dabreak 1%
- Headliner (see above)
- x
- L-3-1169
  - Klonmore (see Headliner above)
  - x
  - L-0-242
    - L-7-42
      - Suwannee (see Headliner above)
      - x
      - Konvoy (see Headliner above)
    - x
    - L-117-1-45-3
      - Marion Bell
        - Fairmore (see Headliner above)
        - x
        - Self
      - x
      - Self

Dunlap 1%
- Crescent (see Howard 17 above)
- x
- Cumberland Triumph (see Howard 17 above)

Klonmore 1%
- Blakemore (see above)
- x
- Klondike (see below)

Genealogy of United States Strawberry Varieties (cont.)

Variety and % of total acreage

Goldsmith (Inst. Z5A) 1%
- Cal. 638.45
  - Cal. 337.2
    - Nich Ohmer (see Shasta above)
    - x
    - Cal. 68.25
      - NY-4626 (see Shasta above)
      - x
      - US-634 (see Shasta above)
  - x
  - Cal. 249.5
    - Cal. 68.24 (see Shasta above)
    - x
    - Cal. 32.50
      - Nich Ohmer (see Shasta above)
      - x
      - US-253
        - Howard Supreme
          - Howard 103
            - Crescent (see above)
            - x
            - Marshall (unknown)
          - x
          - Howard 17 (see above)
        - x
        - Klondike (see above)
- x
- Cal. 469.5
  - Cal. 177.21 (see Shasta above)
  - x
  - Cal. 222.4
    - Cal. 66.2
      - Marshall (unknown)
      - x
      - US-634 (see Shasta above)
    - x
    - Cal. 7.20
      - Blakemore (see above)
      - x
      - Nich Ohmer (see Shasta above)

Others

Fairfax (Probable cross)
- Ettersburg 450 (unknown)
- x
- Howard 17 (see above)

Genealogy of United States Strawberry Varieties (cont.)

Variety and % of total acreage

Klondike
- Pickerproof
  - Lulu
    - Crescent (see above)
    - x
    - Hoffman (supposed Neunan x ?)
  - x
  - Hoffman
- x
- Hoffman

Midland
- Howard 17 (see above)
- x
- Redheart
  - Portia
    - William Belt (unknown)
    - x
    - Unknown
  - x
  - Euresko
    - Chesapeake or Rose Ettersburg
    - x
    - Ettersburg 20 (see Albritton above)

Redstar
- Chesapeake (unknown)
- x
- Fairfax

Solana
- Cal. 177.19
  - US-543 (see Shasta above)
  - x
  - Cal. 68.24 (see Shasta above)
- x
- Cal. 103.22
  - Cal. AO8
    - US-253 (see Goldsmith above)
    - x
    - F_2 of US-253
  - x
  - Nich Ohmer

Genealogy of United States Strawberry Varieties (cont.)

Variety and % of total acreage

Progressive
- Pan American (sport of Bismarck)
  - Bubach (unknown)
  - x
  - Van Deman
    - Crescent (see Howard 17 above)
    - x
    - Capt. Jack (supposed Wilson seedling)
- x
- Dunlap (see above)

Fresno (Cal. 53.9–10)
Tioga (Cal. 53.9–2)
Torrey (Cal. 53.9–9)
- Lassen (see above)
- x
- Cal. 42.8–16
  - Sierra
    - Nich Ohmer (see Shasta above)
    - x
    - Cal. 177.21 (see Shasta above)
  - x
  - Cal. 752.23
    - Cal. 370.14
      - Cal. 720
        - Blakemore (see above)
        - x
        - Nich Ohmer
      - x
      - Cal. 177.21
    - x
    - Cal. 564.7
      - Cal. 144.2
        - Narcissa (see Northwest above)
        - x
        - Nich Ohmer
      - x
      - Cal. 68.25 (see Goldsmith above)

V

Parentage of German Strawberry Varieties*

A Important varieties

Senga Sengana 56%

- Markee (unknown U.S. variety or seedling from an U.S. variety, grown at the village Markee)
- x
- Sieger (see below)

Senga Precosa 10%

- Regina (see below)
- x
- S. 1260
  - Sparkle (American variety)
  - x
  - Eva Macherauch (see below)

Regina—6% and Macherauch's Frühernte—3%

- U.S. seedling (Geneva) (arising from unknown U.S. variety, introduced into Muncheberg in the thirties)
- x
- Deutsch Evern (see below)

Georg Soltwedel 2%

- Rotkäppchen
  - Deutsch Evern (see below)
  - x
  - Sieger (see below)
- x
- Hansa (see below)

Direktor Paul Wallbaum—1%

- Georg Soltwedel (see above)
- x
- Frau Mieze Schindler (see below)

Oberschlesien 8%

- Sharpless (unknown)
- x
- Jucunda (unknown)

* By W. H. J. Hondelmann

B Other varieties

Frau Mieze Schindler	Lucida Perfekta	Lucida x British Queen
	x	
	Johannes Müller	Wunder von Köthen x (unknown)
Sieger	Kaiser Samling	König von Sachsen x (unknown)
	x	
	Laxton's Noble	Excelsior x Sharpless (probable)
Deutsch Evern	Seedling	Helgoland (unknown) x King of the Earlies (unknown)
	x	
	Seedling	Garteninspektor Koch (unknown) x King of the Earlies (unknown)
Hansa	(Chance seedling of Laxton's Noble)	
Asieta	Madame Moutot (see p. 271) x Hansa (see above)	
Macherauch's Marieva	Hybrids 32/74 (unknown) x Georg Soltwedel (see above)	
Lihana	Unknown	
Macherauch's Dauerernte	Ada Herzberg (see below) x Prinz Julius Ernst (see below)	
Ada Herzberg	Deutsch Evern (see above) x Überreich (unknown)	
Herzberg's Triumph	Gartenbaudirektor Langer	Roter Elefant (unknown) x Überreich (unknown)
	x	
	Frau Mieze Schindler (see above)	
Hummi Trisca	Unknown	
Macherauch's Späternte	Frau Mieze Schindler (see above) x Georg Soltwedel (see above)	

C New introductions of 1963

Senga Gigana
- So. 341
  - Rotkäppchen
    - Deutsch Evern (see above)
    - x
    - Sieger (see above)
  - x
  - Hansa (see above)
- x
- Finn (chance seedling of Fairfax, at Alnarp, Sweden)

Vigerla
- Seedling of Deutsch Evern (see above)
- x
- Frau Mieze Schindler (see above)

D Other important varieties no longer on market

Senga 29, 54, 145, 146, 242
- Markee (see above)
- x
- Eva Macherauch (see below)

Senga 188
- Markee (see above)
- x
- Späte von Leopoldshall (see below)

Späte von Leopoldshall
- Comet (unknown)
- x
- Unknown

Eva Macherauch
- Königin Luise (unknown)
- x
- Laxton's Noble (unknown)

Prinz Julius Ernst
- Oberschlesien (see above)
- x
- Unknown

VI

The Literature of the Strawberry

In the preceding chapters of this book, Miss Lee has detailed early contributions to both the development of the modern strawberry and to knowledge about the strawberry in general. The contributions of Duchesne were notable in both instances. Later, the work of such men as Knight, Keens, and Laxton did much to further the strawberry's progress. The present chapter considers the more important books and articles on the strawberry which, with the contributions of many others referred to earlier, provide the literary background to the development of the modern strawberry.

As with most other crop plants, the literature of the strawberry is extensive and the contributions to our knowledge of it have been made by many. As a student of the strawberry and a writer about it, Duchesne set a high standard, and he has been followed by many dedicated students since. Each year reports of experiment stations, articles, and books add more to our knowledge and understanding. One of the more recent additions appeared in 1964, the work of Baldini and Brazanti which describes and beautifully illustrates in color 75 varieties tested or grown in Italy. Such contributions provide material and incentive for advance.

Not all of the important books and articles on the strawberry are presented in this chapter. Some, like the publications of East, Schiemann, Harland, and their students, are given separate treatment elsewhere (see Chap. 7), while others, especially articles resulting from experiment station work, are included with the material to which they are particularly appropriate. The literature described below marks special advances, or provides important collections of information.

Histoire Naturelle des Fraisiers, by A. Duchesne, 1766. 324 pp., Paris (see preceding chapters). A book of all that was known of the strawberry of the time.

"Upon the variations of the Scarlet Strawberry (*Fragaria virginiana*) when Propagated by Seeds," by T.A. Knight, 1818, in *Transactions of the Hort. Soc. of London,* published in 1820.

On August 4, 1818, Knight (*Fig. 5–1*) read this paper before the Horticultural Society of London and it was published in the Transactions of the Society in 1820. Knight had made actual crosses and he reported on selections from the following crosses:

White Chili x Black
Pine x Black
Scarlet (a Virginian) x Black

One of the selections (#7) was later named Downton and a color plate of it was published. It was a light scarlet and described as "exquisitely rich far excelling any other ever tasted." Selection #2 (White Chili x Black) bore the largest fruit Knight had ever seen (largest 274 grains = .6 oz., or 26 berries per pound). In 1819 he originated the Elton, long the standard of quality for preserving. Knight's articles were of importance not for their extent, but because they reported the first actual crosses ever made that resulted in named varieties. His success in breeding stimulated others to do systematic breeding, both in Europe and in America.

"An Account and Description of the Different Varieties of Strawberries which have been cultivated and examined in the garden of the Horticultural Society of London," by J. Barnet, 1824, in *Trans. of the Hort. Soc. of London,* published 1826.

When the Horticultural Society of London established a garden at Cheswick in the spring of 1822, the secretary wrote to members and others in an effort to obtain a collection, as complete as possible, of strawberries which grew in the gardens of Great Britain. He obtained 400 lots which James Barnet, an undergardener in the Fruit Department of the Garden, studied in 1823 and 1824. He reported on them at a meeting of the Society December 7, 1824, in a classic paper named above and published in their Transactions in 1826. For each variety he gave the history, so far as he could obtain it, along with the variety's synonyms and description, then classed the varieties with contrasting characters of each in mind. Of the 6 classes, he listed 26 varieties of the Scarlet (= Virginian), 5 of Black strawberries (= 1 type of Pine), 13 of Pine (= hybrids), the True Chili (= Chilean), Hautbois or Musky (= *F. moschata*), Green (= *F. viridis*), and Alpine and Wood (= *F. vesca*). His accuracy and breadth of view compares favorably with that of Duchesne.

"Recherches sur les caracteres de la vegetation du Fraisier," by M.J. Gay, 1857, in *Annales des Sciences Naturelles.*

M.J. Gay published his paper, in which he made detailed descriptions and gave the geographic distribution of those species considered good at that time. Duchesne was the first and Gay the second major botanist of the strawberry.

Le Fraisier in Le Jardin Fruitier du Museum, Vol. IX, by J. Decaisne and E. Vilmorin, Vols. published between 1862–1875.

In this series of volumes appearing from 1862 to 1875, volume 9 by Decaisne includes drawings of strawberry plants and colored illustrations of the fruit of the species and of important varieties. See *Plate 7–1*) These drawings and illustrations are by A. Piocreux, and nearly equal those prepared by Duchesne. This volume also contains detailed descriptions by Madame Eliza Vilmorin (Fig. 00) of both species and varieties of the time. The colored illustrations show us what the early strawberries were like and how present varieties compare with those of 100 years ago.

A Complete Manual for the Cultivation of the Strawberry, by R.G. Pardee, Third Edition, 1857, 157 pp. C.M. Saxton & Co., N.Y.

This early American treatise published before the Civil War gives specific directions for the cultivation of strawberries as well as for the selection of the best varieties, and includes descriptions of 24. Estimates of production for the year 1855 are given: about 1500 acres in the vicinity of New York and about 500 acres near each of Philadelphia, Boston and Cincinnati, producing an average of about fifty bushels per acre. Pardee stated that "one hundred and twenty-five bushels *ought* to be only an ordinary crop, and $1000 the product of any fair acre of land." He said that he often had plots of ground producing in a ratio of twice that amount and cited one case where 300 bushels per acre were realized.

Le Fraisier, sa Botanique, sou Histoire, sa Culture, by C. Lambertye, 1864, 392 pp.

This work by Lambertye is of major importance to the European strawberry. According to Bunyard (*Jour. Royal Hort. Soc.,* 39: 541–552, 1914) "This writer spent the years of his country retirement in growing all varieties of strawberries obtainable and in the study of their history and literature." No more complete work on this fruit has ever been published and for the history of strawberry development up to his day it stands unrivalled. Lambertye reviewed the species and their geographical distribution (115 pp.) and gives a chart of the origin of important varieties (pp. 68–69). The domestication of the strawberry is divided into 3 periods—from 1570 up to the book by Duchesne in 1766 (196 years), from 1760 to the second edition of "Fruits of France" by Comte Lelieur in 1842 (75 years), and from the "Fruits of France" to Lambertye's time, 1862 (20 years). A third part of this book is on the culture of the strawberry.

The Strawberry and Its Culture, by J.M. Merrick, Jr., 128 pp.

In 1870 J.M. Merrick, Jr., published this book, which was notable for its careful appraisal and description of 813 varieties. European as well as American strawberries were reviewed. Merrick, himself, had seedlings of the cross Hovey x Admiral Dundas not yet in fruiting and he gave details for crossing and for growing seedlings. For obtaining firmness of berry, he suggested using La Constante as a parent and described Underwoods Seedling from La Constante as wonderfully firm. He stated that all varieties of the native Virginian showed their parentage very strongly. The Brooklyn Scarlet was said to be so tender that a ripe berry laid on a dish would lose its shape by its own weight by morning. He stated, "What has been done merely shows us how great results we may hope for in the near future." He told of the many flavors of different varieties: pineapple in Lennings White and Rivers' Eliza, raspberry in Lucas, apricot in Duc de Malakoff, musky in Hautbois, currant in Exposition de Chalons, a cherry flavor in some foreign ones, and a delicious aroma in the native wild type, absent in many large varieties. He said further that the Chili varieties were of little value, being large, coarse, often hollow with soft poor-flavored flesh, and added that "Hautbois strawberries find very few admirers in this part of the country."

Das Buch der Erdbeeren, by F. Goeschke, 1874, 258 pp.

Franz Goeschke in 1874 did for Germany what Lambertye in 1864 had done for the French in publishing his authoritative book on the strawberry. Part 1 describes its culture in the field and in the greenhouse, and part 2 its history, botany, and varieties. Over 100 pages are used to describe and illustrate with fine drawings the varieties of 90 years ago.

Les Fraisiers, by A. Millet, 1898, 218 pp.

This book has 2 parts—the first, of 79 pages, on the origin and history of strawberries, and the second on their culture. It also includes a chapter on varieties of that day. Millet divides the development of large-fruited strawberries into seven periods: 1730 to 1766, 1766–1820, 1820–1845, 1845–1855, 1855–1870, 1870–1885, and 1885–1889. Each period he characterizes by the important varieties that advanced the strawberry industry.

The Strawberry in North America, by S.W. Fletcher, 1917, 215 pp., and *"Fragaria virginiana* in the evolution of the garden strawberry in North America," in *Society of Horticultural Science Proceedings,* 1915; 125–137; and "North American Varieties of the Strawberry," in *Technical Bulletin,* No. 11, of the Virgina Agricultural Experiment Station, 1916, 126 pp.

The works of S.W. Fletcher *(Fig. 12–7)*—(1) His two books, especially *The Strawberry in North America;* (2) his monograph on *"North American varieties of the strawberry,"* and (3) his article *"Fragaria virginiana* in the Evolution of the Garden Strawberry in North America," are possibly of greater value than the writings of Comte Lambertye, particularly for America. The importance of Fletcher's work is: (1) against the general opinion of the period in the United States he gave a new interpretation of the ancestry of the cultivated strawberry—that it was descended from the Pacific beach strawberry, the Chilean, crossed with the native meadow strawberry, the Virginian, and he gave his evidence in detail; (2) he described the important species and traced the origin of American varieties from those species, described the development of the commercial industry for each section, and evaluated the part played by the qualities of new varieties; and (3) he published in the Virginia Experiment Station *Bulletin* the record of the origin and a description of American varieties so far as could be found at that time. In all, it includes 1879 variety names.

Sturtevant's Notes on Edible Plants, ed. by U.P. Hedrick, publication of N. Y. Agric. Expt. Sta., 1919, pp. 273–282.

Sturtevant (1842–1887) was the first director of the New York Experiment Station and served from 1882 to 1887. In early life he planned a history of cultivated plants and by 1880 he was well along on its organization. He continued this work while director of the station and later. In this volume he discussed the origin of the word for strawberry and the early history of the strawberry, from Vergil, Ovid, and Pliny to its introduction as a cultivated plant. Of especial use are the references he made to the early literature and illustrations concerned with the strawberry. He also listed the number of cultivated varieties mentioned by garden writers from 1545 to 1887.

Strawberries, Part III of *Small Fruits of New York,* ed. by U.P. Hedrick et al., 1925. pp. 355–559.

This monograph, the seventh of a series on fruits, by U.P. Hedrick and associates, among whom was Geo. L. Slate (see pp. 205, 245), was published in 1925. Part III, on strawberries, includes 30 color illustrations of varieties of that time. It also has a 16-page discussion of the evolution of the cultivated strawberry and a 13-page description of the more common species. The references to species hybrids are helpful. Color illustrations of Aroma, Bubach, Chesapeake, Dunlap, Excelsior, Gandy, Haverland, Howard 17 (Premier), Joe, Klondike, Marshall (Banner), Progressive, Sample, Superb, Warfield, and Wilson, important varieties of the past, help to give an idea of the evolution of the strawberry.

Le Fraisier, ed. by F. Lesourd, 1943.

By F. Lesourd, editor-in-chief of *Revue Horticole* and of *Gazatte du Village.* This is the latest French book on the strawberry. Later editions are revisions by Simmen, assisted by Chouard, Dubois, and Verlott. The European species *vesca, viridis,* and *moschata,* and the American *virginiana* and *chiloensis* and hybrids are discussed, especially for France down to 1943. Included is a section on breeding, selection, propagation, and a chapter on varieties with their origin and characteristics.

Strawberry Improvement, by G. Darrow in *Yearbook of the U. S. Dept. Agriculture,* 1937, 445–495.

In this is given a summary of the history of the strawberry from its first crossing in 1766, its second crossing in 1819, and its subsequent improvement, by the origination of superior varieties, down to the present. Methods of breeding are discussed, the work being done at various places in the world is given, and the resulting varieties listed. The species of strawberries in each of the chromosome groups are given and their hybridizing discussed. A list of 65 citations to useful literature on strawberries is included. The sources of superior qualities in species and varieties are given. The most useful parts are the summaries of the breeding work of different institutions of the world, the discussion of breeding techniques, the cytology and relationship of the species, and the sources of superior germ plasm.

De Aardbei, H.G. Kronenberg, J.D. Gerritsen, C.H. Klinkenberg, M.A. Erkelens, and A.K. Zweede, 1949, 327 pp. W.E.J. Tjeenk Willink, Zwolle.

A thorough review of the strawberry—its morphology and physiology, varieties, its breeding, culture, and pests.

Important Horticultural Magazines

It is due to two horticultural periodicals, the *Gardener's Chronicle* of England and the *Revue Horticole* of France, that we not only have much information about the strawberry since its cultivation began, but growers were kept informed of the latest information about them. In addition, the Royal Horticultural Society of England has helped with its meetings, shows, and its authoritative articles over a period of more than 150 years. In more recent years, *Horticultural Abstracts,* including *Plant Breeding Abstracts,* has covered the literature of the world.

In the United States and Canada there are no periodicals with the continuity of *Revue Horticole* or *Gardener's Chronicle,* but in recent years (1903 to the present) the *Proceedings of the Society for Horticultural Science* have done a superb job of presenting research findings promptly. In addition, there are reports of State and Federal experiment stations of the United States and Canada (1926–today), the review publication, *Biological Abstracts* (1926–today), and *Fruit Varieties and Horticultural Digest* (1945–today) of the American Pomological Society.

VII

Literature Cited

Aalders, L.E., and Craig, D.L., "The Inbred-Line F_1 Hybrid Approach to Strawberry Breeding as Practiced at Kentville," *Can. J. Gen.* 6 (1964): p. 237.

Angelo, E., Iverson, V.E., *et al.*, "Studies on Some Factors Relating to Hardiness in the Strawberry," Univ. Minn. Agric. Sta., *Tech. Bul.* 135 (1939): pp. 5–36.

Anstey, T.H., and Wilcox, A.N., "The Breeding Value of Selected Inbred Clones of Strawberries with Respect to Their Vitamin C Content," *Scientific Agric.* 30 (1950): pp. 367–374.

Anthony, R.D., "Inheritance of Sex in Strawberries," N. Y. Agric. Expt. Sta., *Tech. Bul.* 63 (1917): pp. 10.

Austin, M.E., Shutak, V.G., and Christopher, E.P., "Color Changes in Harvested Strawberry Fruits," *Am. Soc. Hort. Sci.,* 73 (1960): pp. 382–386.

Averina, L.I., "Foreign Varieties of Strawberries," *Sadovodstvo* (Horticulture) 5 (1962): pp. 35–36.

Baldini, E., and Branzanti, E.C., "Monograph of the Principal Non-everbearing Varieties of Strawberries," *Univ. of Bologna* (1964): 237 pp.

Bogdanski, K., and Bogdanska, H., "The content of Ascorbic Acid in Strawberry as a Function of Variety and Year of Bearing," *Roczn. Nank. rol ser.* 81 (1960): pp. 421–439.

Bolton, A.F., Fitzpatrick, R.E., and Mellor, F.C., "Common Strawberry Diseases and Their Control," Bot. and Plant Path. Div., *Can. Dept. Agric. Pub.* 982 (1956): pp. 1–9.

Bolton, A.T., "Cultural Variation in *Mycosphaerella fragariae,*" *Can. J. Bot.* (1958): pp. 935–940.

———, "Pathogenic Variation in *Mycosphaerella fragariae,*" *Can. J. Bot.* 40 (1962): pp. 647–650.

Branzanti, E.C., "Everbearing Varieties," *L'Italia Agricola* 7 (1964): pp. 688–695.

———, "La Scelta della Cultivar," *L'Italia Agricola* 7 (1964): pp. 671–688.

Bringhurst, R.S., and Khan, D.A., "Natural Pentaploid *F. chiloensis—F. vesca* Hybrids in Coastal California and Their Significance in Polyploid *Fragaria* Evolution," *Am. J. Bot.* 50 (1963): pp. 658–661.

Bringhurst, R.S., and Voth, V., "Effect of Stratification on Strawberry Seed Germination," *Proc. Am. Soc. Hort. Sci.* 70 (1957): pp. 144–149.

———, "Solana Strawberry," *Cal. Agric.* (1958): p. 13.

———, "Fresno, Torrey, Wiltguard," *Cal. Agric.* (1961): p. 11.

———, "Tioga," *Cal. Agric.* (1964): pp. 12–13.

Brooks, A.N., "Anthracnose of Strawberry," *Phytopathology* 21 (1931): pp. 739–744.

Brooks, R.M., and Olmo, H.P., "Register of New Fruit and Nut Varieties," *Proc.*

Am. Soc. Hort. Sci. 76 (1960): pp. 725–757.

Brossier, J.O., "Non-everbearing Varieties of Strawberries Registered in the Catalogue of Species and Varieties. The Identification and Description," *Ann. Amelior. Pl.* 12 (1962): pp. 142.

Budd, J.L., "Hybrid Roses, Gooseberries, and Strawberries," *Iowa Sta. Bul.* 36 (1897): pp. 868–878.

Castle, R.L., "Pomology as a Study," *Trans. Royal Hort. Soc.* 29 (1904): pp. 146–160.

Cehmistrenko, P.E., and Papazova, N.G., "The Volgograd Strawberries," *Sadovodstov* (Hort.) No. 2 (1963): pp. 16–17.

Chen, T., and Rich, A.E., "The Role of *Pratylenchus penetrans* in the Development of Strawberry Black Root Rot," *Pl. Dis. Reptr.* 46, (1962): pp. 839–843.

Chouard, P. (F. Lesourd), "Recent Data on the Part Played by Light in Strawberry Forcing," *Rev. Hort.* (Paris) 115, (1943): p. 396.

Clarke, J.H., "Small Fruit Varieties," *N. J. Rept.* 1927 (1928): pp. 199–200.

———, "Length of the Fruit Development Period of the Strawberry Varieties," *Proc. Amer. Soc. Hort.* 28, (1931): pp. 211–215.

———, "Inheritance of the so-called everbearing tendency in the Strawberry," *Proc. Amer. Soc. Hort. Sci.* 35 (1938): pp. 67–70.

Clausen, R.E., "Ettersburg Strawberries," *Jour. Her.* 6 (1915): pp. 324–333.

Comstock, R.E., Kelleher, T., and Morrow, E.B., "Genetic Variation in an Asexual Species, the Garden Strawberry," *Genetics* 43 (1958): pp. 634–646.

Corbett, E.G., "The Breeding Behavior of the Non-stoloniferous Strawberry, *Fragaria X ananassa* Duch.," *Diss. Abstr.* (1962), No. 23.

Craig, D.L., Aalders, L.E., and Bishop, C.J., "The Genetic Improvement of Strawberry Progenies Through Recurrent Reciprocal Selection," *Can. J. of Gen. and Cytology* 5 1963): pp. 33–37.

Crandall, C.S., "The Vitality of Pollen," *Proc. Soc. Hort. Sci.* 12 (1912): pp. 121–130.

Culpepper, C.W., Caldwell, J.S., and Moon, H.H., "A Physiological Study of Development and Ripening in the Strawberry," *Jour. Agric. Res.* 50, (1935): pp. 645–696.

Cummings, M.B., and Jenkins, E.W., "Sterility of Strawberries; Strawberry Breeding," *Vermont Agri. Expt. Sta. Bul.* 232 (1923): pp. 3–61.

Darrow, George M., "Strawberry Varieties in the United States," *Farmers' Bul.* 1043 (and revisions to 1964) (1919).

———, "Progress in fruit breeding," *Jour. Hered.* 18 (1927): pp. 289–304.

———, "Sterility and Fertility in the Strawberry," *Jour. Agr. Res.* 34 (1927): pp. 393–411.

———, "Sterility in the Strawberry and its Solution," *Mem. Hort. Soc. N.Y.* 3 (1927): pp. 191–193.

———, "Development of Runners and Runner Plants in the Strawberry," *U.S.D.A. Tech. Bul.* 122 (1929): 28 pp.

———, "Inflorescence Types of Strawberry Varieties," *Am. Jour. Bot.* 16 (1929): pp. 571–585.

———, "New Ideas and Discoveries: Growers' Custom in North Carolina of Fertilizing Strawberries in Winter Seems to Have Scientific Warrant from the Fact that Root System Makes Large Growth During Winter," *Official Record* U.S.D.A., 2/28/1929: p. 5.

———, "Experimental Studies on the Growth and Development of Strawberry Plants," *Jour. Agr. Res.* 41 (1930): pp. 307–325.

———, "Strawberry Improvement," *U.S. Dept. Agr. Yearbk.* (1937): pp. 445–495.

———, "Finer Strawberries Ahead," *U.S. Dept. Agr. Yearbk.* (1943–47): pp. 293–299.

Darrow, George M., and Borthwick, H.G., "Fasciation in the Strawberry," *Jour. Hered.* 45 (1954): pp. 299–304.

Darrow, George M., and Scott, D.H., "Breeding for Cold Hardiness of Strawberry Flowers," *Proc. Amer. Soc. Hort. Sci.* 50 (1947): pp. 230–242.

Darrow, George M., and Sherwood, H., "Transpiration Studies on Strawberries," *Proc. Amer. Soc. Hort. Sci.* 28 (1931): pp. 225–231.

Darrow, George M., and Waldo, G.F., "The Practical Significance of Increasing the daily Light Period of Winter for Strawberry Breeding," *Sci.* 69 (1929): pp. 496–497.

———, "Effect of Fertilizers on Plant Growth, Yield, and Decay of Strawberries in North Carolina," *Proc. Amer. Soc. Hort. Sci.* 29 (1932): pp. 318–324.

———, "Response of Strawberry Varieties and Species to Duration of the Daily Light Period," *U.S.D.A. Tech. Bul.* 453 (1934): pp. 1–31.

———, "The Moisture Content of Strawberries as Influenced by Growing Conditions," *Proc. Amer. Soc. Hort. Sci.* 33 (1936): pp. 393–396.

Daubney, H.A., "Powdery Mildew Resistance in Strawberry Progenies," *Can. J. Pl. Sci.* 41 (1960): pp. 239–243.

———, "Effect of Parentage in Breeding for Red Stele Resistance of Strawberries in British Columbia," *Proc. Amer. Soc. Hort. Sci.* 84 (1964): pp. 281–294.

Davis, M.B., "Correlations in the Strawberry," *Proc. Amer. Soc. Hort. Sci.* 19 (1922): pp. 260–263.

Decaisne, J., and Vilmorin, M., "Le Fraisier," *Jardin Fruitier du Museum,* Paris, IX (1875): 59 pp.

Demaree, J.B., and Darrow, G.M., "Leaf Variegation in Strawberries not Considered a Virus Disease," *Pl. Dis. Reptr.* 31 (1937): pp. 400–403.

Denisen, E.L., "Cyclone—A New Strawberry for Your Garden," *Iowa Farm Sci.* 14 (1959): pp. 393–394.

Dermen, H., and Darrow, G.M. "Cholchicine-induced Tetraploid and 16-ploid Strawberries," *Proc. Amer. Soc. Hort. Sci.* 35 (1938): pp. 300–301.

Dogadkina, N.A., "A Contribution to the Question of Genome Relations in Some Species of *Fragaria,*" *Comptes Rendus Acad. Sc.* USSR 30 (1941): pp. 164–168.

Downs, R.J., and Piringer, A.A., "Differences in Photoperiodic Responses of Everbearing and June-bearing Strawberries," *Proc. Amer. Soc. Hort. Sci.* 66 (1955): pp. 234–236.

Drain, B.D., "Strawberry Improvement," *Tenn. Agr. Expt. Sta. Rpt.* (1934): p. 27.

Drain, B.D., and Fister, L.A., "Some Strawberry Breeding Progeny Data," *Proc. Amer. Soc. Hort. Sci.* 35 (1938): pp. 60–66.

Duschesne, A.N., *Histoire Naturelle du Fraisiers,* Paris (1768): 442 pp.

Duka, S., and Sokolovsky, I., "Reasons for Not Inbreeding," *Sci. Fruit Growing Mitchurinsk* 5 (1938): pp. 25–32.

East, E.M., "The Origin of the Plants of Maternal Type Which Occur in Connection with Interspecific Hybridizations," *Natl. Acad. Sci. Proc.* 16 (1930): pp. 377–380.

———, "A Novel Type of Hybridity in *Fragaria,*" *Genetics* 19 (1934): pp. 167–174.

Ellis, J.R., "Cytogenetic Studies in the Genera *Fragaria* and *Potentilla,*" *Doctor's Thesis* for Univ. College, London (1958): pp. 1–263.

———, "Intergeneric Hybridization Between *Fragaria* and *Potentilla,*" *International Gen. Congress Abs.* vol. II (1958): p. 74.

Ezell, B.D., *et al.* "Ascorbic Acid Content of Strawberries." *Food Res.* 12 (1947): pp. 510–526.

Fedorova, N.J., "Hybrids Between *Fragaria vesca* and *F. elatior,*" *Trudy Lab. Genet.* (*Akad. Nauk. S.S.S.R.*) *Bul.* 9 (1932): pp. 109–114.

———, "Polyploid Interspecific Hybrids in the genus *Fragaria,*" *Genetica* 16 (1934): pp. 524–541.

Fedorova, N.J., "Crossability and phylogenetic relations in the main European species of *Fragaria,*" *Compt. Rend. Acad. Sci.* USSR 53 (1946): pp. 545–547.

Filosofova, T.P., "Bridging species Method in Hybridization of the Garden Strawberry, *F. grandiflora,* with other *Fragaria* Species," *Akad. Nauk* (*Acad. Sci. USSR*) *Compt. Rend* (*Dok.*) 31 (1941): pp. 924–926.

Fletcher, S.W., "*Fragaria virginiana* in the Evolution of the Garden Strawberry of North America," *Proc. Amer. Soc. Hort. Sci.* 12 (1915): pp. 125–137.

———, "North American Varieties of the Strawberry," Va. Agric. Expt. Sta. *Tech. Bul.* 11 (1916): pp. 1–126.

———, *The Strawberry in North America,* (1917): 234 pp.

Franger, Wilhelm, *Das Tausendyarige Reich,* Coburg, 1947.

Fregoni, M., and Zioni, Emilio, "Non-everbearers of Torton: Magiostrina of Milan, Profumata of Torton," *L'Italia Agricola* 101 (1964): pp. 697–702.

Gardner, V.R., "Studies in the Nutrition of the Strawberry," Mo. Agr. Exp. Sta. *Res. Bul.* 57 (1923): 31 pp.

Gay, J.E., "Recherches sur les caracteres de la végétation du fraisier," *Ann. Sci. Nat. IV, Bot.* 8 (1857): pp. 185–208.

Georgeson, C.C., "Hybrid Strawberries," *Alaska Agr. Expt. Sta. Rept. for 1909* (1910): pp. 11–14.

———, "Production of Improved Hardy Strawberries for Alaska," *Bul.* 4 (1923): pp. 1–13.

Goeschke, F., *Das Buch der Erdbeeren,* Berlin (1874): 268 pp.

Gorustovic, N.I., "Pure Varieties and Yield of Strawberries," *Sadovodstvo* (Hort.) No. 7 (1963): pp. 18–19.

Hansen, N.E., "Elements of Prairie Horticulture," *So. Dak. Sta. Bul.* 81 (1903): pp. 67–110.

Hansen, N.E., and Haralson, Chas., "Breeding Hardy Strawberries," So. Dak. Sta. Bul. 103 (1907): pp. 224–265.

Harland, S.C., "Cytogenetical Investigations on Soft Fruit," *Progress Rept.,* Univ. Manch., Dept. Bot., for period ending 31st May, 1957. *Heredity* 11 (1957): p. 287.

Harland, S.C., and King, E.E., "Inheritance of Mildew Resistance in *Fragaria* with special reference to Cytoplasmic Effects," *Heredity* 11 (1957): p. 287.

Havis, A.L., "A Developmental Analysis of the Strawberry Fruit," *Jour. Bot.* 30 (1943): pp. 311–314.

Hedrick, U.P., *et al., The Small Fruits of New York,* (1925): 392–559.

Henry, E.M., "The Germination of Strawberry Seeds and the Technic of Handling the Seedlings," *Proc. Amer. Soc. Hort. Sci.* 31 (1934): pp. 431–433.

Hildreth, A.C., and Powers, L., "The Rocky Mountain Strawberry as a Source of Hardiness," *Proc. Amer. Soc. Hort. Sci.* 38 (1941): pp. 410–412.

Hill, H., and Davis, M.B., "Studies in Strawberry bud Differentiation," *Can. Dept. Agric. Bul.* 110 (1929): pp. 3–15.

Holbeche, J.A., and Cox, J.E., *Strawberry Culture,* New South Wales (1962): 31 pp.

Holbeche, J.A., "New Strawberry for Coastal Districts," *Agr. Gazatte* 72 (Dept. Expt. Sta.) (1961): p. 203.

Horn, N.L., and Carver, R.G., "Anthracnose and Powdery Mildew on Strawberry Plants in Louisiana," *Phytopath.* 53 (1963): pp. 768–770.

Hull, J.W., "Development of colchicine-induced 16-ploid Breeding Lines in *Fragaria,*" *Proc. Amer. Soc. Hort. Sci.* 75 (1960): pp. 354–359.

Hyams, E., *Strawberry Growing Complete,* London (1962): 159 pp.

Ichijima, K., "Cytological and Genetic Studies on *Fragaria,*" *Genetics* 11 (1926): pp. 590–604.

———, "Studies on the Genetics of *Fragaria,*" *Zeit. indukt. Abstamm. u. Vererb.-Lehre* 55 (1930): pp. 300–347.

Islam, A.S., "Possible Role of Unreduced Gametes in the Origin of Polyploid *Fragaria,*" *Biologia* 6 (1960): pp. 189–192.

Ivins, G.A., "Production of New Varieties," *Trans. Iowa Hort. Soc.* 38 (1903): pp. 345–348.

Jagurdina, S.I., "New Large-fruited Varieties of Strawberries for Uzbekistan," (Russian) *Trud. nanc-issled Inst. Sadovodstov., Uzbekistan. Akad. sel'skohozjajstv. Nauk.* 24 (1960): pp. 105–107.

Katinskaja, Ju. K., "New Varieties of Strawberries bred at the Institute of Plant Industry," (Russian) *Bjull. vsesojuzn. Inst. Rasten.* 2 (1956): pp. 35–36.

Katinskaja, Ju. K., "Strawberry Breeding in USSR," (Russian) *Agrobiology* (1963): pp. 943–949.

Kedrin, S.P., "Intervarietal Hybridization of the Strawberry," (Russian) *Agrobiology* (1963): pp. 876–879.

Kedrova, O.I., "New Strawberry Varieties of the Krasnodar Experiment Station," *Sad i Ogorod* 12 (1947): pp. 25–27.

Keffer, C.A., "Seedling Strawberries," *Mo. Agr. Expt. Sta. Bul.* 22 (1893): 11 pp.

Kennedy, B.W., and King, T.H., "Studies on Epidemiology of Bacterial angular Leafspot on Strawberry," *Pl. Dis. Reptr.* 46 (1962): pp. 360–363.

Kerner, A., and Oliver, F.W., *The Natural History of Plants,* (1895): pp. 663, 735, 767.

Kihara, H., "Karyologische Studies on *Fragaria* mit Besonderer Berücksichtigung der Geschlechtschromosomen," *Cytologia* 1 (1930): pp. 345–357.

Kluge, K., "Occurrence of Fertile Seedlings in progenies of Crosses of the Tetraploid Form of *F. vesca* var. *semperflorens* L. with varieties of *F. grandiflora* Ehrh. and of the Reciprocal Crosses," *Z. pflanzenz* 4 (1959): pp. 151–156.

Kronenberg, H.G., *et al., De Aardbei,* Netherlands (1949): 327 pp.

Kronenberg, H.G., "Breeding Work on Strawberries," *Hort. Pl. Breeding at Wageningen Inst. for Pl. Breeding* 39 (1952): pp. 522–535.

Kuhn, E., "Die Geschlechtsformen bei *Fragaria* und ihre Vererbung," *Züchter* 2 (1930): pp. 2–11.

Kuznecov, P.V., "New Strawberry Varieties for the Foothills of the Northern Caucasus," *Rep. Agric. Sci. Nauk* 1 (1963): pp. 51–55.

Lambertye, C., *Le Fraisier, sa Botanique, sou Histoire, sa Culture,* France (1864): 392 pp.

Lebedev, P.M., "A Hybrid Between a Cultivated and Wild strawberry (Variety Podmostovraja)," *Sad: Ogorod* 11 (1957): 56 pp.

Lesourd, F., "Le Fraisier," Paris, *Librairie Agricole de la Maison Rustique* (1945): 335 pp.

Lichovitzer, V.G., "Studies on the Karyotype of Fruit and Small Fruit Plants," *Scientific Fruit Growing* 3 (1934): 40 pp.

Lilienfeld, F.A., "Cytological and Genetical Studies in *Fragaria*. I. A Fertile Tetraploid Hybrid Between *F. nipponica* (n = 7) and *F. elatior* (n = 21)," *Japan. Jour. Bot.* 6 (1933): pp. 425–458.

———, "Karyologische und genetische Studien an *Fragaria*. II. Ist. *Fragaria elatior* eine autopolyploide Pflanze?" *Japan. Journ. Bot.* 8 (1936): pp. 119–149.

Lineberry, R.A., "Influence of Fertilizer on Winter Root Growth of Strawberries on Norfolk Fine Sandy Loam Soil in Eastern North Carolina," *Commercial Fertilizer* LXI (1940): pp. 7–10.

Lineberry, R.A., Burkhart, L., and Collins, E.R., "Fertilizer Requirements of Strawberries on New Land in North Carolina," *Proc. Amer. Soc. Hort. Sci.* 45 (1944): pp. 283–292.

Lippfert, Klementine, *Symbol-Fibel,* Standa-Verlag, Kassel, 1964.

Longley, A.E., "Chromosomes and Their Significance in Strawberry Classification," *Jour. Agr. Res.* 32 (1926): pp. 559–568.

Longworth, N., "Sexual Character of the Strawberry," *West. Hort. Rev.* 4 (1854): pp. 288–289.

Lord, W.J., "The induction of Parthenocarpy and possible Apomixis in the Strawberry by Treatment with Growth Regulators," *Ph. D. Thesis, Penna. State Univ.* (1955).

Mâle, Emile, *L'Art Religieux, Vol. III, Fin de Moyen Age,* Paris, 1925.

Mangelsdorf, A.J., and East, E.M., "Studies on the Genetics of *Fragaria*," *Genetics* 12 (1927): pp. 307–339.

Merrick, J.M., *The Strawberry and its Culture with a Descriptive Catalog,* Boston, J.E. Tilton & Co. (1870): 128 pp.

Millardet, A., "Note sur Hybridation sans Croisement ou Fausse Hybridation," *Mem. Soc. Sci. Phys. et Nat.,* Bordeaux 4 (1894): pp. 347–372.

Miller, J.C., "Methods of Strawberry Breeding in Louisiana," *Proc. Amer. Soc. Hort. Sci.* 34 (1936): pp. 339–340.

Millet, A., *Les Fraisiers,* Paris: 218 pp.

Moore, J.N., and Hough, L.F., "Relationships Between Auxin Levels, Time of Floral Induction, and Vegetative Growth of the Strawberry," *Proc. Amer. Soc. Hort. Sci.* 81 (1962): pp. 255–264.

Morrow, E.B., "Number and Length of Runners of Strawberry Varieties," *Proc. Amer. Soc. Hort. Sci.* 34 (1937): pp. 511–513.

Morrow, E.B., and Beaumont, J.H., "Effect of Age of Plant on Flower Production and Yield of Strawberries in North Carolina," *Proc. Amer. Soc. Hort. Sci.* 28 (1931): pp. 206–210.

Morrow, E.B., Comstock, R.E., and Kelleher, T., "Genetic Variances in Strawberries," *Proc. Amer. Soc. Hort. Sci.* 72 (1958): pp. 170–185.

Morrow, E.B., and Darrow, G.M., "Inheritance of some Characteristics in Strawberry Varieties," *Proc. Amer. Soc. Hort. Sci.* 39 (1941): pp. 262–268.

———, "Effects of Limited Inbreeding in Strawberries," *Proc. Amer. Soc. Hort. Sci.* 59 (1952): pp. 269–276.

Moulton, J.E., and Johnston, S., "The Breeding of 35 Strawberry Varieties Tested in Michigan," *Proc. Amer. Soc. Hort. Sci.* 66 (1955): pp. 246–253.

———, "Techniques Used in Strawberry Breeding In Michigan," *Proc. Amer. Soc. Hort. Sci.* 66 (1955): pp. 243–245.

Nelson, P.E., and Wilhelm, S., "Some Anatomic Aspects of the Strawberry Root," *Hilgardia* 26 (1957): pp. 631–692.

Newton, W., and Van Adrichem, M.C.J., "Resistance to *Verticillium* wilt in F_1 Generations of Self-Fertilized Species of *Fragaria*," *Can. J. Bot.* 36 (1958): pp. 297–299.

Nitsch, J., "Influence des Akenes sur la Croissance du Receptacle du Fraisier," *Compt. Rend. Acad. Sci.,* Paris, 228 (1949): pp. 120–122.

Nitsch, J.P., "Growth and Morphogenesis of the Strawberry as Related to Auxin," *Amer. Jour. Bot.* 37 (1950): pp. 211–215.

Nurnberg-Kruger, U., "Genetical Investigation on Diploid *Fragaria* Species. I. The Cross Between *F. vesca* and *F. nilgerrensis,* its Effect on the Morphology of the Plants and the Development of Sex," *Z. Vereb. Lehre* 89 (1958): pp. 747–773.

Overcash, J.P., Fister, L.A., and Drain, B.D., "Strawberry Breeding and the Inheritance

of Certain Characteristics," *Proc. Amer. Soc. Hort. Sci.* 43 (1942): pp. 435–440.
Peterson, R.M., "Breeding Behavior of the Strawberry with Respect to Time of Blooming, Time of Ripening, and Rate of Fruit Development," *Doctorial Series Publ.* 5366, (Minn. Expt. Sta.) (1953).
Petrov, D.F., Sankin, L.S., and Krylova, G.V., "A Polyploid Form of *F. orientalis* Los," *Nature* 193 (1962): p. 199.
Petrov, D.F., and Tukan, D.A., "On the Heterozygosity of the Male Sex in *Fragaria orientalis* Los," *Compt. Rend. (Doklady) Acad. Sci. USSR* 16 (1937): pp. 459–460.
Plakidas, A.G., "Strains of *Mycosphaerella Fragariae*," *Phytopath.* 38, (1948): pp. 988–992.
Pomazkov, Jn. N., and Mescerjakova, I.V., "Controlling Gray Mold," *Sadovodstovo* (Hort.) 7 (1963): pp. 18–19.
Popenoe, W., "The Frutilla, or Chilean Strawberry," *Jour. Hered.* 12 (1921): pp. 457–466.
Powers, L., "Meiotic Studies of Crosses Between *Fragaria ovalis* and *X. F. ananassa*," *Jour. Agr. Res.* 69 (1944): pp. 435–448.
———, "Strawberry Breeding Studies Involving Cross Between the Cultivated Varieties (*X. Fragaria ananassa*) and the Native Rocky Mountain Strawberry (*F. ovalis*)." *Jour. Agr. Res.* 70 (1945): pp. 95–122.
Queensland Ann. Rept., Dept. Agric. and Stock, 1961–2: p. 17.
Richardson, C.W., "A Preliminary Note on the Genetics of *Fragaria*," *Jour. Genetics* 3 (1914): pp. 171–178.
———, "A Further Note on the Genetics of *Fragaria*," *Jour. Genetics* 7 (1918): pp. 167–170.
———, "Some Notes on *Fragaria*," *Jour. Genetics* 10 (1920): pp. 39–46.
———, "Notes on *Fragaria*," *Jour. Genetics* 13 (1923): pp. 147–152.
Risser, G., "Comparative Trial of Six Strawberry Varieties Grown in Forcing Frames," *Rev. Hort.*, Paris, 135 (1963): pp. 572–573.
———, "Description of Some Varieties of Strawberry," *Ann. Amelior. Pl.: Hors. Ser. II* (1963): pp. 38.
Rudloff, C.F., "Entwicklungsphysiologische Studies in der Gattung *Fragaria* L.," *Gartenbauwiss.* 3 (1930): pp. 79–100.
Saks, A.I., "Comparative Salinity Tolerance of Strawberry Species and Varieties," *News Siber. Sect. USSR Acad. Sci.* 7 (1961): pp. 98–110.
———, "Comparative Frost Resistance of Strawberry Species and Varieties," *News Siber. Acad. Sci. Ser. Biol. Med. Sci.* 2 (1962): pp. 97–104.
———, "Characteristics of the Water Requirement of Strawberry Species and Varieties," *News Siber. Sect. USSR Acad. Sci.* 6 (1960): pp. 72–85.
Sargin-Berezousky, G.N., "Distant Hybridization in the Strawberry," *Trud. Inst. Genet.* (Trans. Inst. Genet.) 30 (1963): pp. 321–356.
Sbitnev, N., "The Variety Neiscerpaemaja," *Sadovodstvo* (Hort.) 7 (1960).
Schiemann, E., "Über Geschlechts-und Artkreuzungsfragen bei *Fragaria*," *Ber. Deutsche Bot. Ges.* 48 (1930): pp. 211–222.
———, "Geschlechts und Artkreuzungsfragen bei *Fragaria*," *Bot. Abh.* 18 (1931): pp. 1–112.
———, "Entstehung der Kulturpflanzen," *Hdb. Vererb. ungewiss. III.* L. 377/S. Verl. Borntrager-Berlin (1932): pp. 319–329.
———, "Artkreuzungen bei *Fragaria*. II.," *Zeitschr. Indukt. Abstamm. u. Vererbungsl.* 73 (1937): pp. 375–390.
———, "Entstehung der Kulturpflanzen," *Ergebnisse Biol.* 19 (1943): pp. 409–553.
———, "Artkreuzungen bei *Fragaria*. III," Die *vesca*-bastarde," *Flora* (Jena) 37 (1944): pp. 166–192.
———, "Artbildung in der Gattung *Fragaria*," *Proc. VII, Intern. Cong. Bot.* (1950): pp. 180–181.
———, "Open Questions in the genus *Fragaria*," *Pflanzenzüchtung* 30 (1951): pp. 464–472.
———, "Observations on a Subfertile *Fragaria* Clone," *Planta* 52 (1958): pp. 77–95.
Schutz, F., and Kobel, F., "Wadenswil 7—a new Strawberry," *Obst und Weinbau* 73 (1964): pp. 420–421.
Scott, D.H., "Cytological Studies on Polyploids Derived from Tetraploid *F. vesca* and Cultivated Strawberries," *Genetics* 36 (1951): pp. 311–331.
Scott, D.H., and Ink, D.P., "Germination of Strawberry Seed as Affected by Scarification Treatment with Sulfuric Acid," *Proc. Amer. Soc. Hort. Sci.* 51 (1948): pp. 299–300.
———, "Treatments to Hasten the Emergence of Seedlings of Blueberry and Strawberry," *Proc. Amer. Soc. Hort. Sci.* 66 (1955): pp. 237–242.
Shoemaker, J.S., "The Strawberry," *Ohio*

Agr. Expt. Sta. Bul. 444 (1929): p. 50.
Shipler, E.E., "New Early Varieties of Strawberries for the South of Ukrainian USSR," *Sad i Ogorod* 12 (1947): pp. 21–24.
Sistrunk, W.A., *et al.* "Relationship of Field and Processing Factors to the Quality of Frozen Strawberries," *Oreg. Agr. Exp. Sta. Spec. Rept.* (1962): pp. 1–23.
Skvortzov, B.V., "Contributions to the Knowledge of the Wild Growing Fruit Plants of Far East Asia," *Trudy Prikl. Bot., Gen. i Selek.* 22 (1929): 213–239.
Slate, G.L., "The Best Parents in Strawberry Breeding," *Proc. Amer. Soc. Hort. Sci.* 28 (1931): pp. 107–111.
———, "A Second Report on the Best Parents in Strawberry Breeding," *Proc. Amer. Soc. Hort. Sci.* 43 (1943): pp. 175–179.
Smith, W.L., and Heinze, P.H., "Effect of Color Development at Harvest on Quality of Post-Harvest Ripened Strawberries," *Proc. Amer. Soc. Hort. Sci.* 72 (1958): 207–211.
Smoljaninova, N.K., "Hybrids of Wild and Garden Strawberries," (Russian) *Agrobiologija* 5–6 (1946): pp. 96–101.
Solms-Laubach, H., "Ueberunsere Erdbeeren und ihre Geschichta," *Bot. Zeitib* 5 (1907): pp. 45–76.
Spangelo, L.P.S., "Combining Ability in Strawberries," *Univ. Minn. Ph.D. Thesis,* (1963).
Spangelo, L.P.S., and Bolton, A.T., "Suggested Infection Scales for Roguing Strawberry Seedlings Susceptible to *M. fragariae* and *D. earliana," Phytopath.* 43 (1953): pp. 345–347.
Sproat, B.B., Darrow, G.M., and Beaumont, J.H., "Relation of Leaf Area to Berry Production in the Strawberry," *Proc. Amer. Soc. Hort. Sci.* 33 (1935); pp. 389–392.
Staudt, G., "Cytotaxonomy and Phytogenetic Relationships in the Genus *Fragaria," Proc. 9th International Botanical Congress, Montreal,* 2 (1959): p. 377.
———, "A Tall Mutation which Arose Spontaneously in *F. vesca* L.," *Naturwissenschaften* 46 (1959): pp. 23–24.
———, "The Origin and History of the Large-Fruited Garden Strawberry in Germany," *Züchter* 31 (1961): pp. 216–218.
———, "Taxonomic studies in the Genus *Fragaria," Can. J. Bot.* 40 (1962): pp. 869–886.
Strasburger, E., "Zeitpunkt der Bestimmung des Geschlechts, Apogamie, Parthenogenesis und Reduktionsteilung," *Jena* (1909): pp. 41–47.
Sturtevant, E.L. (Edited by Hedrick), "Sturtevant's Notes on Edible Plants," *N. Y. Agri. Expt. Sta.* ("Fragaria") (1919): pp. 273–282.
Tataurova, A.S., "New Strawberry Varieties Selected at the Central Asiatic Branch of the Institute of Plant Industry," *Trudy nauc.-issled. Inst. Sadovodstvo., Uzbekistan. Akad. sel'skohozjajstv. Nauk.* 24 (1960): pp. 109–112.
Thompson, P.A., "The Development of Embryo, Endosperm and Nucellus Tissues in Relation to Receptacle Growth in the Strawberry," *Ann. Bot.* 27 (1963): pp. 589–605.
———, "Reversal of Photoperiodic Induction of Strawberries with Maleic Hydrazide," *Nature* 200 (1963): pp. 146–148.
———, "The Effect of Applied Growth Substances on Development of the Strawberry Fruit. I. Induction of Parthenocarpy, *Jour. Expt. Bot.* 5 (1964): pp. 347–358.
Teranishi, R., et al., "Volatiles from Strawberries. 1. Mass Spectral Identification of the More Volatile Components," *Jour. Food Sci.* 28 (1963), 478–483.
Tschierske, P., "Anatomy of Fruits of *Dryadeae," Zeitschr. fur Naturwissenschaften* 5 (1886): pp. 594–600.
Tukey, R.B., Some Physiological Factors Influencing the Growth and Development of Strawberry Fruits," *Ph.D. Thesis, Cornell Univ. 1952.*
Valleau, W.D., "Sterility in the Strawberry," *Jour. Agric. Res.* 12 (1918): pp. 613–669.
———, "How the Strawberry Sets its Fruit," *Minn. Hort.* 46 (1918): pp. 449–454.
———, "Inheritance of Flower Types and Fertility in the Strawberry," *Am. Jour. Bot.* 10 (1923): pp. 259–274.
Van Tieghem, P., and Douliot, H., "Researches Comparatives sur l'origine des Membres Engodenes dans les Plantes vasculaires," *Ann. Sci. Nat., Bot.* 8 (1888): pp. 1–660.
Vilmorin, H.L., "Perpetual Strawberries," *Jour. Roy. Hort. Soc.* 22 (1899): pp. 311–326.
Waldo, G.F., "Fruit-bud Development in Strawberry Varieties and Species," *Jour. Agr. Res.* 40 (1930): pp. 393–407.

Waldo, G.F., and Darrow, G.M., "Strawberry-bud Formation is Favorably Influenced by Temperature and Light," *U.S.D.A. Yearb.* (1932): pp. 357–359.

Went, F.W., "The Experimental Control of Plant Growth," pub. by *Chronica Botanica,* chap. 9 (1957).

White, P.R., "Studies of the Physiological Anatomy of the Strawberry," *Jour. Agr. Res.* 35 (1927): pp. 481–492.

White, P., "Mychorhiza as a Possible Determining Factor in the Distribution of the Strawberry," *Ann. Bot.* 43 (1929): pp. 535–544.

Wilhelm, S., "Verticillium Wilt of the Strawberry with Special Reference to Resistance," *Phytopath.* 45 (1955): pp. 387–391.

Williams, H., "June yellows: A Genetic Disease of the Strawberry," *Jour. Gen.* 53 (1955): pp. 232–243.

Wills, A.B., "Non-chromosomal Inheritance of Strawberry June Yellows," *Hered.* 17 (1962): p. 302.

Wilson, W.F., and Giamalva, M.J., "Days from Bloom to Harvest of Louisiana Strawberries," *Proc. Amer. Soc. Hort. Sci.* 63 (1954): pp. 201–204.

Winter, M., and Wilhelm, B., "Flavors x Flavor of Fresh Strawberries, Analysis of Carbonyl Compounds, esters and Volatile Alcohols," *Helv. Chim. Acta* 47 (1964): pp. 1215–1227.

Winton, A.L., "The Anatomy of edible berries," *Conn. Exp. Sta. Rept.* (1902): pp. 288–325.

Yarnell, S.H., "Meiosis in a Triploid *Fragaria,*" *Proc. Natl. Acad. Sci.* 15 (1929): pp. 843–844.

———, "Notes on the Somatic Chromosomes of the Seven-chromosome group of *Fragaria,*" *Genetics* 14 (1929): pp. 78–84.

———, "Genetic and Cytological Studies on *Fragaria,*" *Genetics* 16 (1931): pp. 442–454.

———, "A Study of Certain Polyploid and Aneuploid Forms in *Fragaria,*" *Genetics* 16 (1931): pp. 454–489.

Zeilinski, Q.B., and Garren, R., "Effects of Beta-naphthoxyacetic acid on Fruit Size in the Marshall Strawberry," *Botanical Gazette* 114 (1952): pp. 134–139.

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