The contribution of Italian wheat geneticists: From Nazareno Strampelli to Francesco D'Amato

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Abstract

This paper is a synthesis – in the global frame of the Green Revolution – of the history of the progress and results of wheat science and breeding in Italy during the last century. New varieties came forward suitable not only to the Italian agroecosystems, but, through new gene combinations, largely introduced in other national and international programmes. N. Strampelli's (1866-1942) work allowed Italy to become almost self-sufficient in bread wheat production, going from an average yield of 1.0 t/ha at the beginning of the 20th century to about 1.5 t/ha in the 1930s. The main innovative elements of the Strampelli's model of wheat improvement were: intraspecific hybridization between varieties genetically distant; interspecific hybridization between wheat and species – even wild – of the Triticeae subtribe; realization of more than 800 cross and backcross combinations; phenotypic selection of about one million plants and of tens of thousands "fixed" lines for several morphological (e.g. reduction of plant height and increased culm elasticity or stiffness to improve lodging tolerance), physiological (photoperiod insensitivity, heading earliness) and agronomic characters, related to productivity, adaptation, resistance to biotic and abiotic stresses, and grain quality. Strampelli was also able to establish a large network of experimental field stations, selective analysis procedures under different agroecological conditions, efficient extension services, and facilities for multiplication and distribution of certified seeds of high yielding varieties. The cultivation of new varieties was extended in South and East Europe, in the Mediterranean basin, in South America and China, and their germplasm was extensively used in cross-combinations in many national and international programs, so that Strampelli's work can be considered as the first example of "Green Revolution". Genetic and breeding work on bread wheat was continued in the second half of the 20th century in the Experimental Agricultural Research Institute founded by Strampelli, in Faculties of Agriculture of many Italian Universities and by experts working in private enterprises. Equally outstanding are the results of the genetic and breeding programmes on durum wheat, a species

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that, at the end of the 1950s, could be considered as "orphan" of scientific research. The great leap forward took place in two research centres. In one of them, the Italian National Committee for Nuclear Energy, a mutagenesis programme, using durum wheat for basic genetic studies and applied mutation breeding, was started by F. D'Amato (1916-1998) and co-workers. Remarkable results were obtained in radiogenetics, cytology and cytogenetics, genetics and breeding. The direct use of selected mutants as varieties, or of varieties from crosses of mutant lines with durum wheats, have had a great impact on durum production, both in Italy, in the Balcans and in Mediterranean and Near East Countries, where Italian mutants have been successfully used also in cross-breeding programmes. Almost at the same time, new opportunities were created at the Italian Institute for Cereal Research, and its regional sub-stations, providing a strong impetus in basic studies, for an intensification of the breeding activities on durum wheat and for the release of high yielding varieties. Genotypes with high and stable yield, tolerant to biotic and abiotic stresses, with special attention to earliness at tillering stage and to tolerance to thermic and water stress at the end of the plant cycle, have also been the goals of the research activities carried out at the Agricultural Faculties of Italian Universities and by private enterprises. Profitable cooperation among research centres has been carried out in building genetic linkage maps and in the introgression, by chromosomal engineering, of useful genes (resistance to diseases, grain quality, etc.) from wild species of *Triticum, Agropyron* and *Dasypyrum*. In this respect, special attention has been given to the genetics of seed storage proteins and allele variability at loci coding for gliadin and glutenin subunits in durum and in wild relatives. Finally, it must be stated that the improvement of technological quality of durum wheat semolina for pasta making – taking into account traits like: protein content, gluten viscoelastic properties, semolina colour, kernel vitreousness and red colour, cooking strength, firmness and stickiness of pasta – remains one of the main goals of the Italian studies on durum wheat.

Introduction

My lecture today deals with the history of wheat science in Italy which I believe reflects, in a paradigmatic way, the title of this international conference.

The history of wheat science can be traced back to more than 20 centuries ago: famous writers of ancient Rome (Columella, Varrone, Virgil, Pliny the Elder) wrote that a fundamental agricultural food product in the Mediterranean region was wheat, obviously integrated, in the diet, by grain legumes. Historical events, traffic and trade throughout the Mediterranean basin underlined the predominance of cereals, particularly wheat, as a staple food of primary economic importance. Climate and nutritional needs of the human populations have made wheat one of the most symbolic agricultural plants, with a high adaptation to different agroecosystems in the Mediterranean region, and obviously in its center: Italy.

In Italy, studies and scientific observations on natural phenomena also related to agriculture were carried out at the beginning of the 1600s by the Academy of Lincei, the first scientific Academy in the world. Studies on the plant kingdom were also extended to crop plants. In 1752, the Academy of Georgofili was established in Florence, mainly dedicated to the development of agricultural technologies through scientific and applied research.

In the 19th century, much work was carried out in Europe (in France, e.g. by Vilmorin), and also in Italy in the first State Agricultural Experimental Stations, and in Agrarian Academies founded in various cities and mainly dedicated to improve cultivation techniques, but also to increase productivity of the best local landraces of many crops.

Bread wheat *(Triticum aestivum)*

At the end of 19th century a large, improved and adapted primary wheat gene-pool was available for cultivation in Italy and several other countries of Western Europe. Based on this germplasm, research on wheat breeding in Italy was successfully developed especially in Bologna, thanks to the activity of the private company "Produttori Sementi" and to the scientist who promoted the pedigree selection of wheat, professor F. Todaro.

Todaro personified the Italian scientific tradition and sustained, from the beginning of the 20th century up until the 1930s, the superiority of the method of genealogical selection, the only method which, "integrated if necessary by artificial crosses", could guarantee the solution to the problems of seed purity in wheat cultivation, preserving also quality and bread making quality. "Selection means choice", affirmed Todaro, attributing to "fashion" and to "advertising", through the media, the appearance and diffusion in Italian agriculture of varieties selected after hybridization applying the principles of Mendelian genetics: Strampelli's wheats.

Strampelli's wheats

Up until the 1920s, "conservatism" and "localism", political attitudes for defending the quality of typical traditional local wheat populations, were opposing the introduction of Strampelli's varieties and the application of genetic discoveries. This was occurring despite the critical Italian economy, burdened by a heavy yearly import of 2.5 million tons of wheat grain. It seems that, after a century, the same story is true also today, regarding molecular genetics engineering as an advanced breeding method.

But let us go back to the topic of the Green Revolution. The successful management of wheat genetic resources, genetic laws and breeding methodologies was started by Nazareno Strampelli (Figure 1) one century ago, and remained silent for about 15 years.

If the Green Revolution in agriculture means an impressive improvement of the most important crops, like cereals, the pioneering wheat breeding, the program and the right management of the new genetic lines, the spreading circulation of such

Figure 1. Nazareno Strampelli (1866-1942) at the turning of the 20th century.

scientific and technical outcome for the general prosperity, then there is no doubt that research activity of prominent Italian wheat breeders and scientists were the first example of Green Revolution (Lorenzetti 2000).

Strampelli's work (degree in Agricultural Sciences from Pisa University, 1891) started, developed and achieved fundamental results in the first 20 years of the last century. The sequence of the principal events is the following: 1900: N. Strampelli performed the first hybridization, Noè × Rieti (Noè was a French selection of a Russian variety), while he was appointed at the University of Camerino; 1903: chaired the "Special chair for wheat cultivation" in Rieti, renamed in 1907, "Royal Experimental Station for grain crops of the Ministry of Agriculture"; 1914: released the first variety Carlotta Strampelli; 1919: founded in Rome the "National Institute of Cereal Crops Genetics"; 1923: at the "Exhibition of Agriculture, Industry and Applied Arts" in Rome, presented 35 new varieties of bread and durum wheat; 1939: the "National Registry of Selected Varieties" lists 50 varieties of wheats, 32 of which had been released by Strampelli; 1941: the year of his death: by then he had already released 65 varieties of cereals.

The undeniable value of the lines selected by N. Strampelli and the impressive series of elite varieties developed from them were accepted by farmers and allowed Italy to become self-sufficient, going from an average annual wheat production in the years 1910-13 of 4.9 million tons (average yield 1.04 t/ha) to 7.0 million tons per year (average yield 1.42 t/ha) in the years 1930-33.

N. Strampelli reached these goals thanks to a program, the best at that time, in which he clearly conjugated technical-scientific methodologies with productive and economic objectives. The principal innovative elements of the Strampelli model of wheat improvement were: intraspecific hybridization between varieties genetically "distant"; interspecific hybridization of wheat and species – even wild – of the Triticeae subtribe; high number (more than 800) of cross-combinations and backcrosses; phenotypic selection of about one million plants and of tens of thousands "fixed" lines, for several morphological (e.g. reduction of plant height and increased culm elasticity or stiffness to improve lodging tolerance), physiological (heading earliness) and agronomic characters, connected to productivity, adaptation, resistance to biotic and abiotic stresses and grain quality.

Of no less importance was Strampelli's ability to promote a large network of experimental field stations, the selective analysis under different agro-ecological conditions, efficient extension services, timely availability for farmers of seeds of high yielding varieties, thanks to a system of facilities for multiplication and distribution of certified seeds. Also of great importance was Strampelli's unique ability to transmit to his collaborators enthusiasm, cohesion and a team spirit.

A basic characteristic of Strampelli's program was the exploitation of a large amount of genetic resources. The first group of crosses involved the Italian landrace Rieti with germplasm introduced from other European regions: varieties Massy from France, and Wilhelmina Tarwe from the Netherlands, which originated from Squaredhead UK 1882 × Zealand white.

His first success was the cv Carlotta Strampelli, named after his wife and first coworker (Figure 2). It was a cross made in 1905 between the local landrace Rieti, a famous rust-resistant variety successfully grown since long time in Central and Northern Italy, with the French variety Massy, characterized by culm elasticity. Carlotta Strampelli, a rust-resistant variety with an average yield gain of 0.5-0.7 t/ha over the best varieties at that time, suitable for cool areas of Central Italy and sufficiently lodging resistant, was released in 1914, together with cv Gregorio Mendel; both gave fame to N. Strampelli.

As a scientist, N. Strampelli published, from 1906 to 1919, in the Proceedings of the Academy of Lincei, his studies on the inheritance of some wheat charac-

Figure 2. Nazareno Strampelli and Mrs Strampelli engaged in wheat hybridization.

ters and the Academy awarded him with the "Santoro Prize" (1919). Strampelli reported data on the dominance-recessiveness relations of 27 pairs of characters, 17 of which had scientific priority. Nevertheless, Strampelli was very reluctant in writing scientific papers because, as he said, "my scientific achievements are my wheat varieties".

Carlotta Strampelli, after some years of good performance, showed the same flaw of other wheat varieties of the time: late heading time, which caused the grain filling to occur mainly during hot days. Sometimes an exceptionally hot wind ("favonio") caused sudden soil dryness and compactness around the wheat plant-crown surface ("stretta") and consequent collapse of water and nutrient flow to the grain, which, at maturity, showed a severe shrivelling. This pushed Strampelli to pursue the breeding objective of a 2-3 weeks earlier heading to escape "stretta". This idea, coupled with the aim of realizing an ideotype with short straw, lodging resistance, high spikelet fertility and high yield potential, led to a big leap in the yield performance of the lines selected from 1913 and of the derived varieties. It was at that moment that we can say that the first Green Revolution was born (Bianchi 1995).

The real boost was the cross, made in 1913, between two lines of the cross Whilhelmina Tarve × Rieti with a very early but agronomically poor Japanese wheat strain called Akakomughi. One of the selected lines, characterized by earliness (15-20 days earlier), short straw (80-100 cm), cold and rust resistance, with high spikelet fertility, low tillering ability, relatively low seed weight and high yield potential, was called Ardito and was released in 1920. Ardito gave a first, clear demonstration that earliness and short straw were not antagonistic, neither to high yield potential, which could be largely expressed thanks to the improvement of agronomic techniques and use of fertilizer allowed by lodging resistance, nor to the technological quality, as was demonstrated by an *ad hoc* national scientific commission.

Among the progenies from Rieti germplasm crossed with Akakomughi, Strampelli selected four varieties: Ardito, Mentana, Villa Glori and Damiano Chiesa, (Strampelli 1937), which later on would be called "the varieties of victory" because the success of the "wheat battle" attributed to them was launched by the Fascist government in 1925. Strampelli's breeding programs were able to resolve the above-mentioned fundamental problem in the Italian economy, and importation of wheat was reduced from an average of 2.5 million t/year to 0.8 million t/year in the 1930s. This was an increase in production of about two million tons yearly, an upgrade of the unitary production without expanding the wheat area, and outputs of up to 8 t/ha. Before World War II, Strampelli's wheats spread over more than 90% of the area covered by elite varieties in continental Italy, allowing the country to approach self sufficiency.

The contribution of other geneticists and breeders to bread wheat improvement

Looking at the contribution of Italian geneticists and breeders to wheat improvement, other scientists deserve to be mentioned (for more details see D'Amato 1989).

Professor E. Avanzi (Pisa University), started wheat breeding work in 1916, paying attention at first to select Tuscan local races (Gentil Rosso and Gentil Bianco) and later (1919) carrying out intervarietal crosses aiming at varieties suitable for hilly and low-mountain areas. The same goal was also pursued by A. Oliva and M. Gasparini, professors at Florence University, while Professor M. Bonvicini, from the Agriculture Institute for Cereal Breeding in Bologna, following the intercrossing of Strampelli's varieties, released, in the middle of the last century, varieties with a great range of adaptation to difficult as well as to fertile soils; for instance, varieties Funo and Fortunato were able to yield up to 7 t/ha.

The validity of Strampelli's pioneering decision to improve wheat by searching and using earliness sources is confirmed by the success of another Italian wheat breeding project. In early 1930s, C. Orlandi and G. Venturoli, of the Società Produttori Sementi (SPS) in Bologna, started crosses between an old Japanese short-straw lodging resistant and early variety, Saitama 27, and lines from Ardito crossed to Inallettabile 95. The first variety derived from the SPS program, Orlandi, was released in 1947 and was followed by cvs Produttore in 1953 and Argelato in 1959. The latter two varieties were very successful in Northern Italy, the Balkans and Poland, and were widely used for breeding programs.

R. Forlani and A. Trentin, working in the northern Italian substations of the Strampelli's Institute, continued the breeding projects of their old Director (Forlani 1945). For example, they expanded the Strampelli program of interspecific and intergeneric crosses producing pathogen-resistant amphiploids types: e.g. variety S. Martino from Mentana × *Aegilops ovata*, and variety Forlani from Villa Glori × *T. turgidum* (the so-called "miracle wheat" for its very fertile spike) were extensively grown also in the Balkans and Turkey. Trentin's varieties (Leone, Leonardo, Libellula), highly productive and cold resistant, were also introduced in the Balkan countries, in China and also used for breeding projects.

Among the private breeders, we should also mention Michaelles who, starting in the 1920s, by mass and genealogical selection of the Tuscan land race Gentil Rosso, produced the variety Frassineto, widely cultivated in Central Italy. Crossing Frassineto with Strampelli's varieties (Mentana and Villa Glori), Michaelles was able to release, between 1950 and 1970, through his Seed Company Michaelles-Samoggia in Bologna, outstanding varieties (Mara, Abbondanza, Marzotto, Generoso, etc.) combining the rusticity of Gentil Rosso and Frassineto with the high-yielding potential and the quality of North America varieties of Strampelli's germplasm.

In the last decades, characterized by a decrease of the bread wheat area due to the fall of international prices, a large work of coordination of the wheat breeding programs, outlined by the evaluation of behaviour in different agroecological areas and under advanced agronomic techniques, by increased resistance to abiotic stresses and to diseases and by research on the factors related to the technological properties, was carried out by the Rome Headquarter of the National Institute for Cereal Breeding, under the direction of Professor U. De Cillis, and from 1971, by Professor A. Bianchi and coworkers A. Alessandroni, G. Boggini, B. Borghi, B.M. Mariani, N.E. Pogna, M.C. Scalfati and others.

In recent years, molecular marker technology for assessing the genetic variation and for cultivar identification has been used by B. Borghi and collaborators working in the S. Angelo Lodigiano substation of the National Institute for Cereal Breeding. Bread making quality is also a long-standing area of intensive research in Italy. Research groups working at the Universities of Bari and Viterbo and in the National Institute for Cereal Breeding have been particularly involved in the identification at the molecular level of those genes encoding for gliadin and glutenin subunits capable of conferring superior bread making properties to wheat flour (Porceddu et al. 1983; Lafiandra et al. 1990). Nevertheless, no genetic engineering programs at a sufficient level are now in progress on bread wheat in Italy.

The genes that expanded the Italian wheat revolution

The superior performance of these varieties and others with the same pedigree, was quickly confirmed in many other parts of the world (Central and Southern America, Southern and Eastern Europe, the Mediterranean region, China, etc.) where they were used in direct crop systems and, even more, in breeding programs.

Mentana and Ardito, for instance, after the 1920s were cultivated in Latin America. They were used in wheat breeding programs in Argentina and gave rise to the rust resistant varieties Klein (30, 31, 32) and Acero. According to J. Vallega (Vallega et al. 1974), those varieties helped to overcome the problems of rust diseases due to *Puccinia graminis*, *P. striiformis* and *P. recondita*. Mentana was noted for its great adaptability, and the related genes were introduced into breeding programs in Brazil, Mexico, USA and Canada. In the 1940s, Mentana was one of the three key varieties in the "Mexican Wheat Research and Production Programme" (Borlaug 1968). Furthermore, the world-wide cultivated Russian wheat Bezostaja has Ardito and Klein-33 in its pedigree.

Among all the varieties, cv Mentana was a real masterpiece. Besides its good adaptation in Italy from the Po Valley to Sicily, Mentana performed very well in many other countries of the world. It was also important for the genetic factors providing disease resistance and technological quality. One of the latest varieties bred by N. Strampelli, S. Pastore (Balilla × Villa Glori), was for decades very successful in Italy and in several other countries.

Genetic analyses of the factors which characterized the Italian bread wheat programs were carried out in the 1980s and 1990s especially at the John Innes

Research Center (UK), by Worland (1999), Law and coworkers, who studied the two genes responsible for the novel genetic variation introduced by Strampelli: *Rht8*, for reduced height, and *Ppd1*, for photoperiod insensitivity. Such combination permits earlier flowering and consequently early grain to set and fill before the hot and dry weather conditions. The close linkage of *Rht8* and *Ppd1* explains the good performance of Strampelli's varieties Ardito, Villa Glori, Damiano and Mentana, as well as of the cultivars derived from this Italian germplasm and spread to virtually all modern wheat varieties of Southern and Eastern Europe, the Mediterranean basin, South America and China. In conclusion, the introduction into Italian wheat breeding programs of genes for early flowering and photoperiod insensitiveness, lodging resistance and semidwarfism, made by Strampelli and coworkers during the first decades of the 20th century, favoured an extraordinary progress in Italian cereal production, and led us to acknowledge the relevance of the Italian wheat breeding in domestic but also in the worldwide wheat revolution.

Durum wheat (*Triticum turgidum* spp. *durum*)

Strampelli's archievements

The other wheat species of great importance for Italian agriculture, and therefore a commitment for Italian agricultural genetics, is durum wheat. Advantages of durum wheat are: tolerance, during growing seasons, to relatively dry climates, with hot days and cool nights; grain quality and good semolina as the basic product for good pasta production.

Even though – as we have seen – he concentrated all his efforts on the genetic improvement of bread wheat, N. Strampelli, up to early 1910 set up a durum wheat program based on pure line selection of local races grown in Southern Italy, the Italian islands and the Mediterranean area. In the fall of 1907, senator Raffaele Cappelli (Minister of Agriculture) lent N. Strampelli a field near Foggia (in the Apulian Plain) where he sowed lines from landraces and a composite cross obtained from intercrossing several bread wheat × durum wheat lines. The following summer was extremely dry but he was able to select 63 drought-resistant lines from which he released in 1914 the bread wheat variety Luigia and the first four durum wheat varieties with the common name Dauno. In 1915, he selected the variety Senatore Cappelli (from a late-maturing pure line selected from the North African landrace Jean Retifah), released in 1923. Afterwards, he released the durum wheat varieties Milazzo (from a line selected in 1917 in a bread wheat × durum wheat composite cross), Aziziah 17-45 and Tripolino (from early maturing pure lines selected from Syro-Palestinian durum wheat landraces), and Volturno and Sapri.

Among these varieties, Cappelli had the greatest success because of its wide adaptability, rusticity and semolina quality, although it was tall, late and susceptible to lodging. The introduction of Cappelli raised the average yield from 0.9 t/ha in 1920 to 1.2 t/ha at the end of the 1930s. For several decades Cappelli covered the largest fraction (up to 60%) of the durum-wheat grown area in Italy, and was extensively cultivated in all Mediterranean countries, including Turkey and Spain. Cappelli is present in the pedigree of almost all durum wheat varieties bred in Italy and elsewhere, starting with Garigliano (Tripolino × Cappelli) in 1926, up to the latest releases. After almost one century, it is still cultivated in regions of Southern Italy (Basilicata) as source of semolina for outstanding pasta industries.

As time passed, N. Strampelli realized that hybridization would have been the real method for improving durum wheat. Also, from 1926 up to 1932 he carried out progeny testing from 73 crosses, including common wheat varieties and involving Cappelli in almost half of them. Probably, the basic idea was to transfer some key characters from common to durum wheat and vice-versa, but probably non-valid recombinants were identified.

Achievements by Strampelli's coworkers

Strampelli's research project was continued (after his death in 1941) in his Institute and Regional Sections by researchers who by exploiting a large pool of genetic variability also outside the tetraploid level, released new varieties around the middle of the century. F. Casale released Patrizio and Capeiti 8, selected from the cross Cappelli × palestinian Eiti: Capeiti 8 is earlier and shorter than Cappelli, but with poor pasta-making qualities. De Cillis (1964) released three varieties under the Timilia name. Forlani, whose farsightedness showed the need to enlarge the genetic variability within the Italian durum wheats by interspecific crosses. Conti, also working at the Bari Agricultural Experimental Station, was able to select interesting lines from Azizia, and, from the famous Russian durum wheat Taganrog, the series of varieties Russello which were largely grown in Sicily and Southern Italy. Grifoni selected, among others, the varieties Grifoni 234 and 235 which, in the Apulian Plain, showed better yield and lodging resistance than the variety Cappelli.

The work of F. D'Amato and G.T. Scarascia Mugnozza at the Casaccia Research Center of the National Committee for Nuclear Energy (CNEN)

At the beginning of the 1960s, the durum wheat yield, although around 1.8-2.0 t/ha, due also to improved agronomic practices, was far lower than bread wheat yield. Although durum wheat grains had a better price for their pasta-making quality, the crop was unprofitable even for farmers of Southern Italy, mainly for the low grain yield per hectare and insufficient response to fertilizers. This caused a steady decrease in the cultivated area and a lack of attention from plant geneticists and physiologists. Durum wheat could be defined as a species “orphan” of scientific research on genetics, crop physiology, technological quality and so on. The crossing among progenies between varieties phylogenetically very close, which had brought great progress, was no longer enough.

A “revolution” was needed to promote the knowledge of the genetics of the species, theoretical as well as finalized to the expression of functions influencing productivity and adaptability also in difficult agroecological conditions. This knowledge would be used in breeding programs from which to obtain varieties most suitable for cultivation, assuring a fair income to farmers and to the pasta industries and advantages to market and consumers. The great leap forward took place in two research centres. In 1958, in the newly established Laboratory for Plant Genetics and Mutagenesis at the Research Centre in Rome (Casaccia) of the National Committee for Nuclear Energy (CNEN), a project by F. D’Amato (Figure 3), scientific consultant, and by the director of the Laboratory, G. T. Scarascia Mugnozza, took shape and materialized.

The commitment to support Italian agriculture in the new European Common Market (1958), addressing also the improvement of durum wheat, created the conditions that favoured the acceptance of the research programs devised by D’Amato and Scarascia Mugnozza. Almost at the same time opportunities were developed at the National Institute for Cereal Research, founded by N. Strampelli, for providing a strong impetus in research and basic studies for intensifying the breeding activities on durum wheat.

Figure 3. Prof. Francesco D’Amato (1916-1998).

F. D'Amato (1916-1998), a scientist of great international value in natural and botanical sciences, a cytogenetist and researcher in developmental biology, started his scientific interest in mutagenesis after participating in research on radiogenetics and chemical mutagenesis of the diploid species *Hordeum vulgare*, in the Laboratory of the Swedish Seed Association, in Svalöf, directed by Prof. A. Gustafsson.

The D'Amato-Scarascia project had two objectives: the first, to use durum wheat as a model plant for studies in genetics, cytogenetics and mutagenesis, both natural and induced (D'Amato 1992). The second, to increase the variability of the species through induction and selection of useful mutations. Those objectives aimed to develop research and methods for practical applications, through large field experiments on genotypes that, in laboratory analysis, appeared to be of value for the genetic improvement of durum wheat. Seeds (caryopses) of the durum wheat cultivars Cappelli, Aziziah, Capeiti, Garigliano, Russello, Grifoni and others, were irradiated with different doses of x-rays, thermal neutrons, fast neutrons or treated with different concentrations of chemical mutagens. Five out of 1,024 induced chlorophyll mutations were shown to be dominant or semidominant, with a range of mutation frequencies from 1 to 24%. The inheritance of 126 independently obtained chlorophyll, morphological and physiological mutations was analysed; most mutants behaved as monogenic recessive, a few as semidominant and very few as dominant. Interestingly, a new monogenic recessive dwarf-twisted mutant was identified after both physical (X-rays, thermal and fast neutrons) and chemical (DSE, EMS) mutagenic treatments. Those mutants carried alleles for correcting defects like long culm, susceptibility to lodging and heading lateness and were used to release varieties possessing higher-yielding ability and good agro-environment adaptability. Interesting results have been obtained by studying the hereditary basis of quantitative characters related to grain yielding ability such as: heading date, number of spikelets per main ear, spike length, kernel weight, number of culms, culm length and duration of the developmental phases of the life cycle (Bagnara and Scarascia Mugnozza 1973).

D'Amato used to say: "During the 15 years (1958-1973) as scientific consultant in that laboratory, I was a researcher among researchers. I learned that fundamental research in some crop plants could be used as a basis for developing possible applications, and this is highly gratifying". So, durum wheat (*Triticum durum* Desf. 2n = 4x = 28; AABB genomes), at that time considered the "Cinderella" of the *Triticum* in the international literature, proved to be, beyond prediction, excellent material for the acquisition of knowledge of a general nature. Hundreds of chlorophyll mutations and of vital mutations, morphological and physiological, were isolated after several mutagenic experiments with radiation and chemical agents: they made up the material for extensive genetic, cytogenetic, biochemical and physiological research at the Casaccia Center and elsewhere. Mutants, and the segregating generations after crossing mutants with cultivars, were subjected to multi-year agronomic tests and new varieties of wheat were isolated. They improved the production in Italy and in various other countries (Scarascia Mugnozza et al. 1993), where some varieties were used as parental lines in pedigree programs to produce short-strawed durum wheat cultivars, e.g. in France, in Austria (cv Gandur and Unidur), in Greece, in Bulgaria (cv Lozen, Sredets, etc.) and also in the USA as a parent, for example, of cultivars of the synthetic crop species *Triticale*.

A few of the new varieties were tested in the FAO-IAEA-CNEN Program on "Evaluation of mutant durum wheat lines in the Mediterranean basin". Trials were carried out for five years (1966-1970), in 35 locations (from Morocco to Pakistan and India), on 13 varieties: nine mutant lines, four control varieties (two local and two widely-cultivated Italian varieties), and examined 15 characters: date of planting, date of emergence, date of heading, date of maturity, plant height, net plot area, grain yield, volume weight, kernel weight and percentage of yellow-berry. Although it was impossible to keep this scheme for every year and location, more than 3,300 experimental plots were evaluated (Bogyo et al. 1974). The mutant line Casteldelmonte - GRA-145 was the overall best yielder and with good environmental adaptability, closely followed by the mutant line GAR-25 and the Italian control cv Capeiti. The differences in period of ripening (no. of days from heading to maturity) among entries, and its correlations with other characteristics, appeared to be very significant. Besides the interest to use the most promising lines also for cross-breeding programs, the highly-significant "variety × location × year" interaction showed the importance to test, over years, an increasing number of entries in the specific environment of the cooperating institutions. In this program on evaluation of mutant lines in the Mediterranean region, those mainly involved were: the CNEN Laboratory (Casaccia-Roma) with G.T. Scarascia Mugnozza, D. Bagnara, A. Bozzini, C. Mosconi; IAEA (Vienna) with B. Sigurbjörnsson, P.T. Bogyo.; FAO (Rome) with J. Tessi.

From the Casaccia Center, in which brilliant and capable scientists (geneticists, agronomists, biologists and chemists) worked in a spirit of vivid, sympathetic interdisciplinary integration, some of the best mutants were registered as new cultivars: Castelporziano and Castelfusano from Cappelli, Casteldelmonte from Grifoni, Castelnuovo from Garigliano. Professor Francesco D'Amato was appointed full professor at the University of Pisa in 1959, i.e. the first professor in Plant Genetics in an Italian Faculty of Agriculture. He is credited for having founded the Italian School of Plant Genetics. He has lectured to three generations of students supervising their studies in cytogenetics, cytophysiology, developmental genetics and cytogenetics of both spontaneous and induced mutants. He also laid the basis for the genetic and cytological interpretation of the somaclonal variation occurring during plant cell and tissue *in vitro* culture. These studies were instrumental to the development of the basic biological tools and knowledge for plant regeneration after plant genetic transformation and genetic engineering experiments. His pioneering work must be regarded as a factor of promotion of the present Italian research Centers of plant genetics and breeding in the Universities of Pisa, Bari, Viterbo, Napoli and Potenza, in CNEN-ENEA and in the National Research Council (CNR). In these Institutions, among the many plants cultivated and studied by brilliant researchers, much attention was given to the study of genetics and breeding of durum wheat.

Further breeding activities at CNRN-ENEA and at the National Institute for Cereal Crops

A program for ascertaining the behaviour of the new induced genetic variability in the germplasm of wheat was also developed, and progenies from crosses with tetraploid and hexaploid wheats were deeply investigated for increasing general knowledge and for breeding purposes (Blanco et al. 1988; Bozzini 1988). For example, it has been assessed that the mutant cv Castelporziano has the GA sensitive *Rht14* semidominant gene for semidwarfism (Börner et al. 1996). From the progeny of a cross between a Cappelli short-straw mutant CpB144 and the CIMMYT short-straw line [(Yt54, N10-B) Cp-63] Tc^2 (recombinant from a cross between a standard durum line and a short-straw bread wheat), the Creso variety was released in 1974 by the Laboratory of Agriculture of the Casaccia Research Center (Bozzini and Bagnara 1974). The Creso ideotype had immediate success, and this variety represented for Italian durum wheat breeding the highest point of genetic effort turned to fill up the gap between durum and bread wheat yield potential. In fact, the yield potential of Creso has reached, several times, levels of up to 10 t/ha, preserving, at the same time, good grain quality for pasta making and resistance to *Fusarium graminearum* and to several races of brown rust. In the same laboratory, investigations on biochemical and technological characteristics of quality in induced durum wheat mutants were also carried out by Cervigni and Giacomelli.

A review of both basic genetic studies and applied mutation breeding work carried out at the Casaccia Research Center in its first 20 years of activity is summarized by Scarascia Mugnozza et al. (1993). It shows that, out of ca. 1,000 mutants obtained from mutagenic treatments, 262 could be regarded as worthy of further investigation for breeding purpose. The extensive selection and hybridization work resulted finally in the release of 22 registered varieties. Of these, six resulted from direct selection of induced mutants, the rest being the result of cross breeding.

A great contribution was made by the National Institute for Cereal Research, directed by Professor U. De Cillis from 1948 to 1971, and then by Professor A. Bianchi up to 1996. De Cillis and coworkers (F. Casale, A. Dionigi, G.T. Grifoni and P. Jannelli) selected varieties, as: Sincape 9 (obtained by Casale from Sinai × Capelli), Camar 7 (obtained by P. Jannelli from B.52-Grifoni × Cappelli) with agronomical and yield characters superior to the cv Cappelli and Isa-1 (obtained by A. Dionigi), very early. Optimal grain quality and yield were achieved in Southern Italy by growing the cv Appulo, released by R. Grifoni in 1964 after a pedigree selection of progenies obtained from the triparental hybrid [(Cappelli × Grifoni

235) × Capeiti]. Alessandroni et al. (1976) and Mariani et al. (1995), following a research line developed by Forlani, have carefully exploited the possibility of improving durum wheat by means of interspecific crosses. Clear improvements have been achieved with respect to disease, cold and lodging resistance and reduction of yellow berry percentage. Spike fertility has been increased by utilizing crosses with *T. dicoccum, T. turgidum, T. sphaerococcum, T. vulgare*, etc.. Vallega and Zitelli (1973) developed a fruitful breeding program incorporating genes for resistance to diseases (namely rust, powdery mildew and *Septoria*), present in *Triticum dicoccum, Aegilops umbellulata, Agropyron elongatum*, *A. glaucum*, *T. timopheevi* and *T. spelta*, into the Italian varieties via crosses with North Dakota durum wheats: Yuma, Wells and Lakota. At the beginning of the 1970s they released varieties: Valgerardo, Valgiorgio, Valselva, etc., not only highly resistant to diseases, but very valuable for high yield potential, good adaptability to several environments and with good or sufficient quality.

During the last two decades, the programs of the Section in Foggia of the National Experimental Institute for Cereal Crop Research, located in the Apulian Plain (characterized by good soils and semiarid environment with cool winter, irregular rainfall in spring and dry and hot summers, that can negatively influence the heading time and the grain filling phase) and of the Section in Fiorenzuola D'Arda (in the Po Valley with more regular rainfall in spring and summer) were focused on genetics and physiology of *T. durum* as well as on breeding high-yielding varieties selected according to the methodology of quantitative genetics and in relation to their performance in the critical phases of the plant cycle when productivity (Spano et al. 2003) and qualitative features (Lamacchia et al. 2001) are becoming determinant (Cattivelli et al. 2002). From a large cross-breeding program, the Institute in the 1990s released the varieties: Ofanto, Lesina, Gargano, Venosa, etc., whose pedigrees include many of the best varieties selected in the previous Italian programs: e.g. Capeiti 8, Trinakria, Appulo, Valforte and Creso. Among the physiological parameters, attention was paid to the increase in photosynthetic activity and its persistance, the number of sinks, the translocation and accumulation of photosyntesis in the sinks (seeds). Therefore, particular attention was paid to the flag leaf, with a wide but not long lamina, to the spike, longer with a high number of spikelets, large size glumes and elongated and persisting green awns. Finally, chemical mutagenesis, using sodium azide, has been included in the programs of the Foggia Section, together with first attempts of genetic transformation (cv Ofanto) by particle gun approach (Lamacchia et al. 2002).

Durum wheat genetics and breeding performed at Italian Universities and by the private sector

Durum wheat breeding has always been one of the goals of the research activities carried out at the Agricultural Faculties of the Universities in Southern Italy. After the pioneering work carried out at Palermo University by G.P. Ballatore, who released the cv Trinakria in 1973, and in Sassari and Naples by R. Barbieri, who selected Maristella and Ichnusa (Biancale × Capeiti), a large contribution to durum wheat breeding was given by Bari University. During the first half of the 1980s the cvs Messapia, Salentino and Salizia were selected by G.T. Scarascia Mugnozza, A. Blanco and coworkers. Messapia, derived from a cross between cv Tito and the CIMMYT line Mex × Crane S, is 9-11 days earlier and 5-10% more productive than Creso. Interested in finding more rapid and efficient alternatives to conventional breeding procedures, a genetic linkage map of durum wheat was built by Blanco et al. working at the Universities of Bari and Viterbo (1998). Additional AFLP markers were subsequently added by Lotti et al. (2000). Extensive work deploying SSRs to characterize the genetic distances among durum accessions is being carried out at DISTA, University of Bologna (Maccaferri et al. 2003, 2004, 2005). The final objective of this SSR-based investigation is to identify a large panel of genotypes suitable for association mapping of genes/QTLs influencing agronomic traits.

Gene transfers for desirable characters from wild *Triticinae* species to *T. durum* (Simeone et al. 2001a, b) were studied from cytogenetic and genetic viewpoints, evaluating the procedures usable in order to reach positive results. Remarkable research projects are being carried out at Viterbo University by Giorgi and coworkers (Giorgi et al. 2003) on the genetic analysis of *Aegilops* species; and by De Pace et al. (2001), in collaboration with C. Qualset (California University), on the hybridization of *Triticum turgidum* var. *durum* × *Dasypyrum villosum* (2n = 14). Information is collected on crossability and seed fertility between parental species, and on the time span for the appearance of important domestication-syndrome related traits in fertile hybrid progenies. Those data indirectly quantify early genetic events during wheat domestication, especially for the transition from tetraploid to hexaploid wheat domestication. In addition, hexaploid amphiploids with good agronomic performance have been produced.

In the private sector, remarkable work has been done by C. Maliani using interspecific crosses, mainly with hexaploid wheats. By crossing durum wheats with the hexaploid variety R. Forlani, he obtained high-yielding and high-protein durum varieties, as it was the case of C. Jucci (Forlani × Russello), G. Raineri and V. Montanari. In the seed company Società Produttori Sementi in Bologna, the main durum wheat breeding targets were yield, resistance to diseases (mainly leaf rust and powdery mildew) and pasta-making qualitiy, also in cooperation with the firm Barilla, the leading pasta producer. Società Produttori Sementi has released in the 1990s the cv Lira, the first Italian cultivar selected using gliadin electrophoresis as a quality marker; the cv Zena, the first Italian variety having a high yellow index semolina and cv Svevo (Sel. CIMMYT × Zenit sib), very early and with an exceptionally high pasta-making quality. The programs of the Società Italiana Sementi (S.I.S.) are mainly addressed to obtain genotypes with high and stable yield, tolerant to biotic and abiotic stresses, with special attention to heat stress at the end of the plant cycle. In a profitable cooperation between private and public research, resistance genes from wild species (*Agropyron* and others) have been transferred into S.I.S. durum lines by chromosomal engineering at the University of Viterbo by Ceoloni et al. (1996, 2005). The recent breeding work performed by Calcagno in Sicily, must also be mentioned. He obtained a series of cvs (Simeto, Platani, Colosseo, Ciccio and Cannizzo) now largely grown in Italy, Spain, Greece, Portugal and North Africa.

Studies on grain quality of durum wheat varieties

Since the pioneering investigations of De Cillis (1942), the technological quality of durum wheat semolina has been one of the most important goals of the studies for the genetic and biochemical improvements for pasta making and, more recently, of bread-making qualities in Italy. Apart from the influence of agroecological factors, such as nitrogen fertilization, water supply, environmental conditions during seed ripening, etc., breeders have to also take into account other traits like protein content, gluten viscoelastic properties, semolina colour, kernel vitreousness, cooking strength, firmness and stickiness of pasta, and bread volume. Protein content (which in durum can vary from 9 to 18%, but poor in essential aminoacids) and gluten quality have been the focus in Italy of the majority of the studies due to their role in determining the technological value of durum wheats. The genetics of seed storage proteins and allele variability at loci coding for gliadin and glutenin subunits in durum and in wild relatives (*T. monococcum, T. dicoccum, T. dicoccoides* and *T. tauschii*) and the introgression of loci for high protein content from wild relatives, have been studied since the 1980s by many scientists: E. Porceddu, D. Lafiandra, M. Ciaffi, R. D'Ovidio, M.A. Pagnotta, L. Montebove, A. Blanco, R. Simeone, N.E. Pogna and others. Genes coding for gliadin subunits and for several prolamin subunits, with electrophoretic mobilities corresponding to those of omega- and gamma-gliadins of wheat, where localized in a chromosome (IV) of *Dasypyrum villosum,* in the frame of the already mentioned extensive wheat cross-breeding work carried out in the 1990s at the Universities of Bari and Viterbo. The already-mentioned work carried out by C. De Pace (Viterbo University) and C. Qualset (California University) provides opportunities for pre-breeding and preparing primary mapping populations for chromosomal location of *D. villosum* genes controlling Mendelian as well as complex genetic traits in wheat such as gluten strength, red caryopses, immunity to powdery mildew and leaf rust, and earliness at tillering stage.

In genetic and breeding programs (Viterbo University) aimed at improving gluten quality, the complex loci controlling the gliadin and glutenin subunits, and the consequent effects on gluten quality, have also been studied using molecular marker techniques. The homologous genes encoding protein disulfide isomerase (PDI), an important enzyme involved in disulfide bond formation and affecting quality and their promoters, have been cloned and characterized (Ciaffi et al. 2003). The cloning and molecular characterization of gene sequences controlling flowering and flower morphogenesis is in progress. Blanco et al. (2002), working on lines from a cross between Messapia (low protein content) and the wild tetraploid *T. dicoccoides* (high protein content), used molecular and morphological markers to detect and compare in different environments the significance of quantitative trait loci (QTLs) involved in the expression of complex traits such as grain protein content, sedimentation volume, semolina color and grain yield. The conclusion was that the number of QTLs which influence a trait cannot be rightly estimated in a single environment. Moreover, since the success of every breeding program largely depends on the efficiency of selection, a number of methods have been suggested and applied to evaluate novel genotypes in durum wheat. Among other parameters influencing pasta making quality, yellow colour is a characteristic which, although of secondary importance in the past, is now of increasing value also in Italy. The yellow colour of pasta is determined by the carotenoid content of semolina and by the lipoxigenase activity, both characters being controlled by a few major genes with additive effects and significantly affected by environmental conditions. With a molecular analysis (Borrelli et al. 2003) of the expression of lipoxygenase, an enzyme causing the oxidative degradation of the carotenoid pigments of seeds, genotypic variation due to different transcriptional levels of the relative genes has been demonstrated. Consequently, breeding for low lipoxygenase levels in durum semolina through the genotypic control of this character might be planned, aiming also at increasing the carotenoid content. A remarkable increase of the carotenoid content of semolina was obtained by chromosome engineering (Ceoloni et al. 2005) with the introgression into durum wheat of the *Yp* (yellow pigment) gene from *Agropyron elongatum*.

Other characteristics of increasing importance in Italy are: (1) a high extraction rate of semolina, being the semolina yield obtained milling wheat kernels of evident importance for the milling industries; and (2) the use of durum wheat for bread production, due also to the high protein content and long shelf-life of bread from durum as compared to the bread obtained from common wheat (Pogna et al. 1996, 2002). Among the research for developing durum cultivars of superior bread-making quality, the use of chromosome engineering for the introgression of genes encoding for suitable glutenin subunits should be mentioned.

Looking at the future strategy for improving the basic factors influencing durum quality, the selection assisted by molecular markers, to identify durum wheat genotypes having QTLs correlated, over space and time, with yield and quality traits (Blanco et al. 2002), may be an interesting goal in order to accelerate the procedures and times for superior genotypes identification. Very scanty, on the contrary, is in Italy the use of genetic engineering methodologies for opening new avenues in quality improvement, except for an already quoted (Lamacchia et al. 2001) research carried out at Foggia, on cv Ofanto, in cooperation with the Agricultural Experimental Station in Bristol (U.K.; Lamacchia et al. 2002).

Quite recently (2004), a cooperative research project (M. Motto, E. Porceddu, G.T. Scarascia Mugnozza. et al.) on durum wheat, fostered by the Ministry of Agriculture, aims at understanding the functional genomics of durum wheat in relationship to tolerance to environmental stresses (water shortage, high temperatures and salinity), so as to develop new strategies and methodologies for the improvement of this crop.

Other research projects funded by the European Union in the Vth FP have recently been started at DiSTA, University of Bologna, by R. Tuberosa and coworkers and in collaboration with Società Produttori Sementi. The project IDuWUE (2003-2006; Improving water-use efficiency and sustainability of durum wheat in the Mediterranean basin; for details see the website http://137.204.42.130/iduwue/html) aims at identifying QTLs for yield and protein content; a mapping population developed by Società Produttori Sementi and a large panel of accessions are being evaluated under a wide range of water availability in field trials carried out in the Mediterranean basin. A similar project (TRITIMED, 2004-2008: Improving drought tolerance and nitrogen-use efficiency of durum wheat in the Mediterranean basin) will deploy microarrays to identify candidate genes for QTLs influencing water- and nitrogen-use efficiency in durum wheat. DiSTA and Società Produttori Sementi are also involved in a FP6 project (BIOEXPLOIT, 2005-2009) aimed at exploiting marker-assisted selection to improve resistance of durum wheat to fungal diseases.

Finally, it seems appropriate to point out that the commitment by Italian researchers to make the cultivation of durum wheat profitable and competitive is shown by the fact that, at the end of the 20th century, 50% of the area cultivated with durum wheat in the European Union (15 Countries) was in Italy, making the Italian production equal to 52% of Europe and 13% of the rest of the world production.

Conclusions

I have tried to present, in the global picture of the Green Revolution, the contribution made by Italian geneticists and breeders, throughout the 20th century, to the worldwide increase in wheat production, through new varieties suitable not only to the Italian agroecosystems, and through new gene combinations vastly introduced in other national and international programs. The Green Revolution was, and still is, a fundamental and essential component of the social, economic and cultural evolution, and revolution of humankind. It will continue to be, together with the latest Gene Revolution, one of the major factors in solidarity worldwide, necessary and urgent in the 21st century.

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