The Classification of Tropical American Vegetation-Types

J. S. Beard

Ecology is currently published by Ecological Society of America.

———. 1929. The oecology of British land mollusca, with special reference to those of ill-defined habitat. Proc. Mal. Soc. London, **18**: 213-224.

———. 1934. The habitats of land mollusca in Britain. J. Ecology, **22**: 1-38.

Brown, A. P. 1911. Variation in some Jamaican species of Pleurodonte. Proc. Acad. Nat. Sci. Philadelphia, **1911**: 117-164.

Clench, W. J. 1937. Notes on three rare American *Polygyra*. Nautilus, **51**: 17-18.

Cockerell, T. D. A. 1903. Variation in the snail genus Ashmunella. Proc. Acad. Nat. Sci. Philadelphia, **1903**: 615-616.

Ferriss, J. H. 1900. The Great Smoky Mountains. Nautilus, **14**: 49-59.

Foster, T. D. 1936a. Biology of a land snail, *Polygyra thyroidus* (Say). Thesis Abs., U. of Illinois.

———. 1936b. Size of shell in land snails of the genus *Polygyra* with particular reference to major and minor varieties. Amer. Midland Nat., **17**: 978-982.

———. 1937. Productivity of a land snail, *Polygryra thyroidus* (Say). Ecology, **18**: 545-546.

Mayr, Ernst, E. Gorton Linsley and Robert L. Usinger. 1953. Methods and principles of systematic zoology. New York.

Pilsbry, H. A. 1897. *Polygyra ferrissi,* n. sp. Nautilus, **11**: 92.

———. 1900. Mollusca of the Great Smoky Mountains. Proc. Acad. Nat. Sci. Philadelphia, **1900**: 110-150.

———. 1939. Land Mollusca of North America (north of Mexico). ANSP Monograph **3**, vol. I, part 1.

———. 1940. *Ibid.,* vol. I, part 2.

Walker, Bryant. 1910. Variation of *Polygyra albolabris* in Michigan. Proc. Acad. Nat. Sci. Philadelphia, **1910**: 21-40.

THE CLASSIFICATION OF TROPICAL AMERICAN VEGETATION-TYPES

J. S. Beard

P.O. Box 39, Pietermaritzburg, Natal, South Africa

In 1944, in a paper entitled "Climax Vegetation in Tropical America," the writer proposed a system of classification for the plant formations of the American tropics. In the decade since this paper was written, further experience has been acquired and our knowledge of this vegetation widened by the work of numbers of different authors. The writer has himself used the system in studies of the vegetation of Tobago (1944b), Trinidad (1946b), and the Windward and Leeward Islands (1949a). It has been put into use by Beebe and Crane (1947) in Venezuela, by Curtis (1947) in Haiti, and Wadsworth (1951) in Puerto Rico and, recently, (1952) has been followed by Fanshawe in his Preliminary Review of the Vegetation of British Guiana which constitutes its first application by another ecologist than its author on a large scale. Sundry interesting problems have been raised in the course of all this; definitions given and views expressed may require modification, and new plant formations can now be recognized. At this juncture, therefore, it is appropriate to make a review of the subject.

The broad principles of the original classification were laid down in the original paper and have been restated on two occasions (1945, 1949b). Briefly they are as follows. The basic unit is the plant association which is a floristic grouping, being the largest possible group with consistent dominants either of the same or closely allied species. Associations may be divided into minor floristic groups, to which it was proposed to apply the Clementsian terminology. Also, they may be termed consociations if they are single-dominant communities. Climax associations, that is, communities apparently mature, stable and integrated, may be further grouped together according to their structure and physiognomy into formations. The formation is a physiognomic group and is independent of flora. Communities which are situated in widely scattered parts of tropical America and for that reason are quite differently constituted may thus be classified into a single formation if of similar structure and physiognamy. The properties of the community express the habitat: the consistent dominance which defines the association expresses a constant local habitat within the regional flora and the consistent physiognomy which defines the formation expresses a constant essential habitat within the tropical zone. Types of habitat which are in general similar permit us further to group formations together into formation-series. There is thus a grouping at three levels: a floristic grouping—the association, a physiognomic grouping—the formation, and a habitat grouping—the formation-series. The association must bear a floristic name such as *"Eschweilera-Licania* association," the formation a physiognomic name such as "deciduous seasonal forest" and the formation-series a habitat name such as "montane formations." This rule may however be broken for formations in order to draw into the
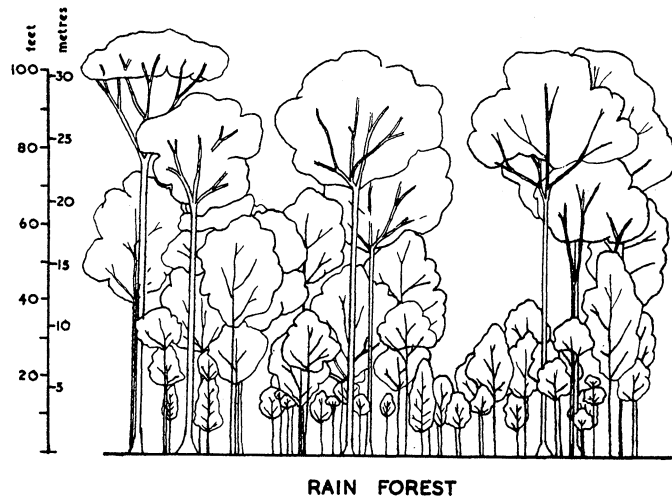
J. S. BEARD

RAIN FOREST

FIG. 1. "Type Specimen" of Rain Forest: the *Eschweilera-Licania* association of British Guiana, from the original diagram by Davis and Richards (1933).

classification well-established and understood names.

Twenty-six formations were described and defined in the original paper of 1944. One more, named "montane thicket" in English, was added to the Spanish translation published at Medellín in 1946. Another, "evergreen bushland," was defined in 1949 as a member of the dry evergreen formation-series. In the meantime also, it had appeared that one of the original formations, "palm-brake" might have to be dropped on the ground that it is a disturbance climax and not a natural climax of the same order as the other montane formations, work in the Lesser Antilles (Beard 1945b, 1949a) having led to this conclusion. To the twenty-seven climax types thus defined, Fanshawe (1952) has now added ten more, four in the dry evergreen, two in the seasonal-swamp and four in the swamp formation-series. A change of name in the seasonal-swamp series was also proposed. The discussion which follows below aims at consolidation of the classification to date.

An essential concept of the system is that rain forest (Fig. 1) stands alone, having both formation and formation-series rank, in the center, and that from it radiate the habitat groups in descending order from optimum to pessimum. The formation-series which has been best know hitherto is the seasonal group. A full series of five formations (six if "desert" is also illustrated) was defined and shown diagrammatically in the 1944 paper, repeated in 1946 and taken up by Richards (1952). This series is shown in Figure 2 herewith. It is envisaged that there is in reality one long unbroken series, in which the formations

are artificially delimited stages. Each stage shows a regular stepping-down of structure. Rain forest has three tree stories, the uppermost one continuous. Evergreen seasonal forest also has three stories but the uppermost is discontinuous and canopy is formed by the second layer. In semi-evergreen seasonal forest only two stories remain, of which the upper is closed, and in deciduous seasonal forest this upper layer becomes discontinuous. Thorn woodland has only one tree story left, and in cactus scrub we have only the bushes and succulents. Desert retains nothing but a ground layer. Other physiognomic changes of course accompany the reductions of structure throughout.

We ought also to look for a similar regularly descending series of types in the other formation-series: not necessarily, perhaps, in the inundated swamp and seasonal-swamp series owing to their greater specialization, but certainly in the dry evergreen and montane series. In 1944, the writer did not have the data to substantiate this, and could illustrate the structure of only one dry evergreen formation and three montane ones. Now, however, more can be done.

Fanshawe (1952) has recognized six dry evergreen formations in British Guiana: Wallaba forest, xeromorphic rain forest, xeromorphic woodland, xeromorphic scrub, heath and littoral woodland. The choice of the name "Wallaba forest" was unfortunate, since wallaba is the vernacular name for the *Eperua* spp. which dominate the local association, and it is not desirable to give a floristic name to a formation. Supposing that forests of similar structure and physiognomy but not constituted by *Eperua* spp. are now described
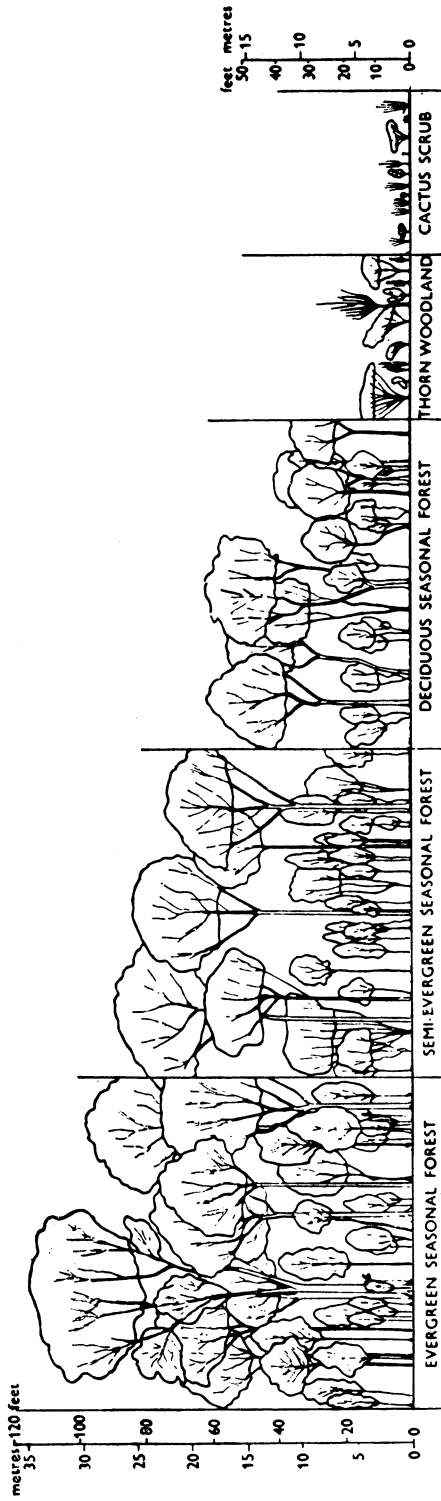
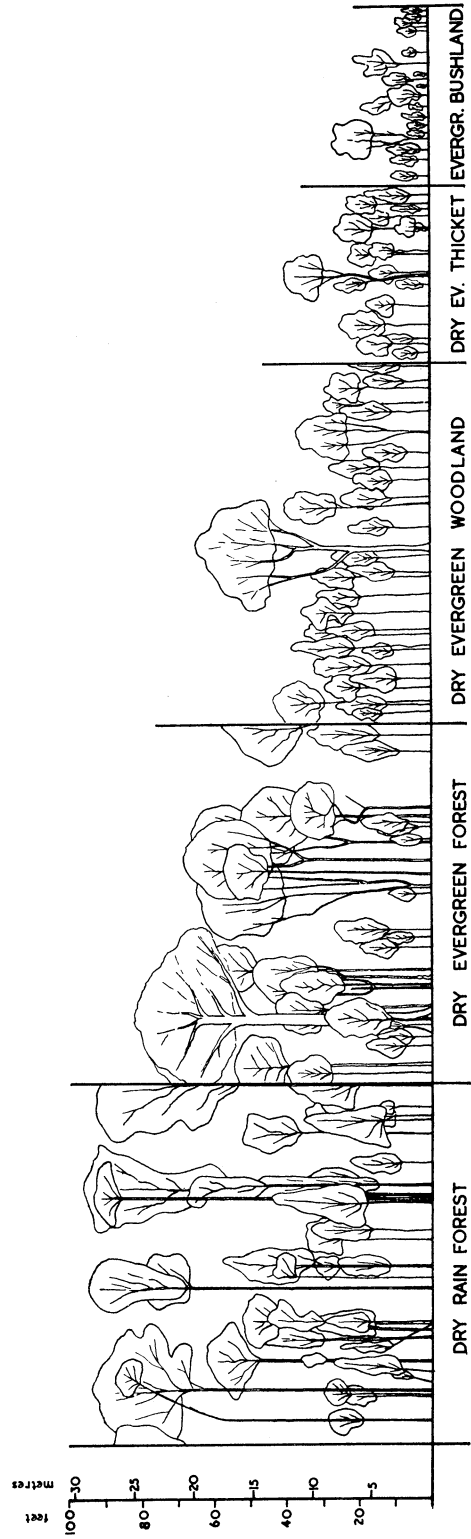Fig. 2. The Seasonal Formation-Series, after Beard (1944a) as redrawn in Richards (1952).

Fig. 3. The Dry Evergreen Formation-Series. Dry Rain Forest redrawn from Fanshawe's diagram of "Wallaba Forest" (1952), Dry Evergreen Forest from Beard's Xerophytic Rain Forest in 1944b, the remainder imaginary, from descriptions.

elsewhere, we cannot justifiably call them wallaba forests and some other term will have to be found. "Dry rain forest" is proposed as the most convenient term, since this formation lies very close to the true rain forest but is differentiated therefrom by the underlying white sands which are unretentive of moisture and cause a paradoxical dryness of the habitat. Xeromorphic rain forest is stated to be the same as Beard's xerophytic rain forest, with a minor change of terminology that has much to commend it, but the structure does not agree with Beard's definition. Xeromorphic woodland is a new formation. Xeromorphic scrub is the same as the evergreen bushland which had already been brought into the terminology (Beard 1949a). Fanshawe's use of "heath" here for an "herbaceous vegetation of "xerophytic lily-like plants" is surely inadmissible as there is no resemblance to the true heath of temperate climates. The writer suggests "rock pavement vegetation" as a substitute.

In attempting to consolidate the dry evergreen formations, the writer suggests first the elimination of the awkward terms "xerophytic" and "xeromorphic" in favor of "dry evergreen." We can next proceed to delimit our formations structurally with the aid of Figure 3. Nearest to the optimum comes the *Dry Rain Forest,* Fanshawe's "Wallaba forest," characterized as follows (adapted from Fanshawe) :

A three-storied forest with the canopy more or less closed between 25-35 meters, a discontinuous understory between 12-20 meters and a dense not very well-defined undergrowth from 6-12 meters. Illumination within the forest is relatively intense and the atmosphere dry. Stocking density is high and the trees are slender in relation to height. True under-growth species are few and the herb layers are poorly represented. Lianes are few and small. Epiphytes, especially sun epiphytes, are plentiful and descend low on the trees. Heavy buttressing is very rare. The proportion of semi-deciduous species is higher than in true rain forest. Leaves are mesophyllous, mostly compound in the canopy and simple in the understory.

Second in line of descent comes what we will now term *Dry Evergreen Forest,* equivalent to Beard's xerophytic rain forest but not to Fanshawe's xeromorphic rain forest. Reduction in structure now sees the canopy formed by a layer of crowded, slender trees reaching 12 to 20 meters in height above which an occasional emergent reaches 30 meters. Leaves are simple and ever-green, the majority being stiff and fleshy, a high proportion with latex or essential oil. Bark-shedding may be a conspicuous feature. The shrub and herb layers are poorly represented.

Thirdly, we have Fanshawe's xeormorphic rain forest, which we must now term *Dry Evergreen Woodland.* The understory of 6-12 meters is now the canopy-former, with emergents reaching 20 meters. Fanshawe describes this as:

"A 2 storied forest with the canopy formed of densely packed, attenuated trees, now larger than 18-20 in. diameter (45-50 cm.) and about 20-40 ft. high (6-12 meters). There is a discontinuous emergent layer between 60-80 ft. high, made up of larger trees. The forest is almost entirely evergreen."

Fanshawe's xeromorphic woodland, which it is preferred to term *Dry Evergreen Thicket,* is to be considered as a valid new formation, characterized as follows :

A 2 storied forest with a low, open, or dense canopy and a dense or sparse undergrowth. The canopy is between 20 and 40 ft. high (6-12 meters), and trees have slender stems not larger than 6-8 inches. (15-20 cms) diameter. There is an occasional, larger emergent.

Most reduced of all the woody formations is the *Evergreen Bushland,* Fanshawe's xeromorphic scrub, colloquially known as muri or moeri-moeri in the Guianas. This formation was detailed by Beard in 1949a.

Rock Pavement Vegetation takes the form of an irregular and open growth of herbaceous and woody plants less than two meters in height, growing in crevices or in mats of humus upon sheet rock, usually with much bare rock between. Such vegetation is frequently associated with outcrops of hard sandstone and granite bosses.

The 1944 formation *Littoral Woodland* must now be considered as identical with dry evergreen woodland, and the *Littoral Thicket* and *Littoral Hedge* (Beard 1949a) as dry evergreen thicket and bushland respectively. It may still be convenient to retain the names for particular studies, to differentiate dry evergreen vegetation under the influence of the sea, just as it is convenient to separate mangrove from freshwater swamp: but although the littoral habitat may be very different from that of inland sites carrying dry evergreen communities, we must recognize the essential physiognomic identity of these types. Differences such as the predominance of thickly cutinized salt-spray resistant leaves in littoral types must be regarded as of minor significance.
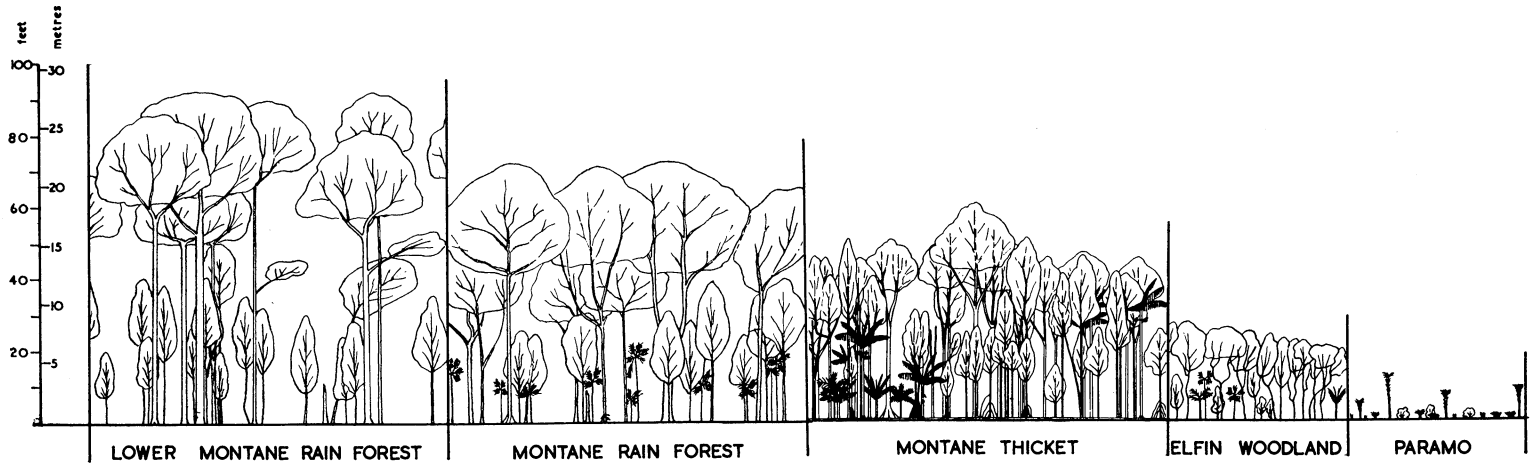
FIG. 4. The Montane Formation-Series, redrawn from Beard (1944a) with inclusion of Montane Thicket from 1949a and Paramo (sketched).
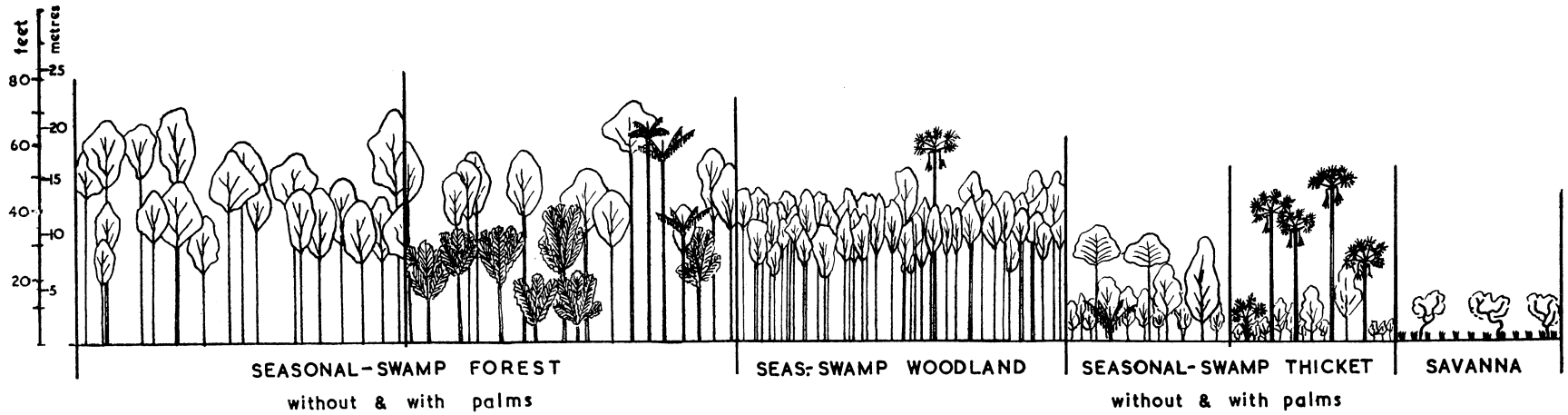

FIG. 6. The Seasonal-Swamp Formation-Series. Seasonal-Swamp Forests and Woodland redrawn from Fanshawe's diagrams (1952). Seasonal-Swamp Thickets after the Palm Marsh of Beard 1944a, Savanna diagrammatic.

It will be seen that the dry evergreen formations "step down" as their structure is reduced but not quite in the same way as the seasonal formations where successive strata become first discontinuous and then absent. In this way we seem always to have a canopy layer with emergent trees standing above it and little or no understory. As we descend the series, the height of these two layers is reduced.

We are now able to characterize the montane series of formations more fully than in 1944 (see Figure 4) and it will be seen that in this case the reduction of structure proceeds again somewhat differently. All forest-like montane formations present a continuous canopy layer without emergent trees and as we proceed through the series we find that the canopy layer is gradually lowered until finally it coalesces with the understory. On low mountains which do not rise above the upper limit of the mist belt ($\pm$ 2,500 meters) the zonation is as shown in Figure 4. First and at lowest altitude, the *Lower Montane Rain Forest,* with two tree strata at 3-15 meters and 20-30 meters. Secondly, as the cloud belt is fully entered, comes the *Montaine Rain Forest* or *Cloud Forest* with the two strata reaching about 10 and 20 meters respectively (higher under favorable conditions). The above two formations featured in the 1944 account and there was an obvious discontinuity between the montaine rain forest and the elfin woodland, a gap which was filled in 1946a and 1949a by the inclusion of *Montane Thicket.* In this formation, the canopy layer is down to 10-15 meters and the understory is suppressed to the point of disappearance. Finally growth descends to the *Elfin Woodland* or *Mossy Forest,* a single-storied, impenetrable tangle, whose height varies from 10 meters down to one meter. Our terminology is not too good here, as we should correctly speak of montane woodland and elfin thicket; "elfin woodland" is however an old established name.

From studies undertaken (Beard 1945b, 1949a), it must appear that the palm brake (Fig. 5), although it may often appear stable, is a disturbance climax at an equivalent level to the montane

thicket. In the Lesser Antilles, there can be no doubt that it is a successional stage on areas bared by wind, landslides, or volcanic eruptions. Wadsworth (1951) supports this view for Puerto Rico. Cuatrecasas (1934) has described a "palmetum" of *Ceroxylon andicola* in the Andes of Colombia occurring as a society in the "Clethrion" which appears to be montane thicket. No opinion is expressed as to its status. In view of the fact that the physiognomy of the palm brake is at variance with that of the other members of the montane series, it seems very probable that it never does constitute a true climax.

On mountains rising to some extent above the mist belt, the elfin woodland gives place to the paramo. Closer acquaintance with this formation shows that it is in no sense comparable to an alpine meadow, as was suggested in 1944. It is much more similar to heath. The paramo finally gives way to the tundra at highest elevations. Where mountains rise so far above the mist belt as to carry a forest zone above it, we shall find a formation described as "frost woodland" in 1944 but which it is now preferred to call *High Mountain Forest.* *Mountain Pine Forest* is apparently a fire-climax derived from the latter and like the palm-brake must therefore be excluded from full rank in our classification. The writer has no structural data for high mountain forest. In zonation, it stands between cloud forest and elfin woodland. Further information on the *Bamboo Brake* proposed in 1944 indicates that *Chusquea* communities in the Andes are only of societal rank in the elfin woodland. There are *Guadua* societies also but these are riverain and at low altitude. It does not appear that we have any equivalent of the bamboo forest of East Africa and the Himalayas. The valid montane formations are thus reduced to seven.

The original four seasonal-swamp or "marsh" formations have been expanded to six by Fanshawe, who applies the name marsh to them. It is however highly debatable whether we should try to perpetuate the artificial distinction between "marsh" and "swamp" suggested by the present writer in 1944, in view of the fact that this distinction does not exist in common usage. While both represent inundated habitats, "swamp" is defined as having a perpetually waterlogged soil deprived of oxygen, whereas in "marsh" there is a fluctuating watertable permitting seasonal aeration of the topsoil. It seems generally preferable to substitute the term "seasonal-swamp" firmly for "marsh."

Four of his "marsh" formations are said by Fanshawe to occur in a regular zonation across the interfluves of the main rivers in the North-

FIG. 5. Palm Brake, from Beard, 1949a.

west District, in this order : palm marsh forest →
marsh forest → palm marsh woodland → palm
marsh. The first named of these is at the river
bank, which in a delta region stands higher than
the ground level further away between the main
channels. Away from these, seasonal rise and
fall of the watertable gradually decreases and the
vegetation is reduced. Actually, the true order
of progression of the marsh series is not exactly
in the order of this zonation, since the marsh
forest is clearly the least reduced type of all and
should stand at the head of the series. Evidently
conditions are at the most favorable not in the
palm marsh forest nearest to the creek but in the
marsh forest belt slightly further away.

Our knowledge of the seasonal-swamp series
has been greatly extended by Fanshawe but cer-
tain comments must be made. It does not now ap-
pear to the writer that the presence and absence
of palms is such an important diagnostic feature
as was previously suggested. There is little struc-
tural difference, apart from the palm question, be-
tween Fanshawe's marsh forest and palm marsh
forest, nor between marsh woodland and palm
marsh. As Fanshawe states that there are also
palm-dominated variants of rain forest, seasonal
forest and swamp communities in British Guiana,
and there is a palm type of savanna as well, it
seems that we should regard the seasonal-swamp
communities with palms as merely variants also.

Figure 6 illustrates some of the variants but
the main classification is consolidated to seasonal-
swamp forest, woodland and thicket followed by
savanna. There is in this case a considerable dis-
crepancy between the head of the series and the
optimum, within which no intermediates are
known. The forest-like seasonal swamp forma-
tions are characterized by highly irregular canopy.
It may be possible to define strata, but they are
erratic and the forest canopy is now high, now
low as growth varies from short to tall, dense to
open. Passage through the series witnesses a
progressive reduction in the stature of this
jumbled assemblage.

Seasonal-Swamp Forest (without palms) is
somewhat similar to dry evergreen forest and is
defined by Fanshawe as follows for his "marsh
forest" :

"A 2-3 storied forest in which palms only
account for 5% of the stand. There is a
low canopy of trees between 30-50 ft. (9-15
meters) and an emergent layer between 50-
80 ft. (15-25 meters). Shrubs are more
or less absent, but ground cover may be
dense or sparse. Lianes are few, epiphytes
fairly frequent. Buttresses are not marked.

Leaves are evergreen, mesophyllous, 75%
simple."

Seasonal-Swamp Forest with Palms is the orig-
inal marsh forest of Beard. Palms here enter
the assemblage in great numbers and become
dominant, providing 40-60% of all trees and 60-
75% of the lower story forms the canopy at 5-10
meters, and emergents, both trees and palms
reach heights up to 25 meters.

Seasonal-Swamp Woodland is, after Fanshawe :
"A low woodland of small-stemmed, regu-
larly spaced trees with scattered emergent
palms or trees of peculiar habit. The can-
opy lies between 30-50 ft. (9-15 meters) with
emergent palms to 60 ft. (18 m.). The shrub
layer is virtually absent ; the ground cover
sparse or dense. The mean tree diameter
is 4 in. (10 cm.) ; emergents are from 16-
36 in. (40-90 cm.) in diameter. The stock-
ing is high—between 300-400 stems per acre,
4 in. diameter and over—but the flora is re-
stricted to about 20 tree species. Lianes are
few, epiphytes rare and these mostly hemi-
epiphytes. Leaves are evergreen, mesophyl-
lous, simple. Stilt roots are a common fea-
ture."

It is now clear that the *Amanoa* consociation
described by Beard on the central plateau of
Dominica (1949a) and tentatively classified as a
"swamp phase of montane thicket" belongs to this
formation.

The marsh woodland and palm marsh of both
Beard and Fanshawe are now to be consolidated
as seasonal-swamp thicket, without and with
palms respectively. Savanna has been very fully
dealt with by Beard in a recent paper (1953).

The original four swamp formations (swamp
forest, palm swamp, herbaceous swamp, and man-
grove woodland) have been expanded to nine by
Fanshawe by the addition of four new formations
and the recognition as full formations of the two
former subdivisions of herbaceous swamp, now
termed herbaceous swamp and semi-aquatic
swamp. Not all of Fanshawe's treatment is, how-
ever, acceptable. At the pessimum he gives us
aquatic swamp, "submerged trailing vegetation,
attached to rocks in the shallow, fast running parts
of the rivers." This would presumably include
also the aquatic communities of lakes and ponds.
All these are to be regarded as seral and unworthy
of formation rank. We might very well, however,
take up Fanshawe's term aquatic swamp for that
division of herbaceous swamp which, at the true
pessimum, consists of mats of grass rooted at the
bottom but floating and rising up and down with

the water level. This was rather inaptly termed swamp savanna in 1944.

Between herbaceous swamp and swamp forest, Fanshawe has given us two useful new formations, *Arborescent Swamp* and *Swamp Woodland*. *Arborescent Swamp,* which for the sake of uniform terminology it is preferred to call *Swamp Thicket*, stands in shallower water, marks the appearance of woody growth and "consists of a dense growth of shrubby vegetation, on sand banks or stretches of silt, submerged at high tide or at high water. Woody species are restricted, but gregarious; shrubs, perennial herbs and lianes are occasionally associated" (Fanshawe).

Swamp Woodland is defined by Fanshawe as follows:

> "This term is proposed to connote the riparian fresh water fringe of low, spreading trees. Swamp woodland is remarkably homogeneous, comprises one or very few species and has a simple structure. There is one tree stratum 10-40 ft. high (3-12 meters) and the canopy is loose and open. A shrubby or herbaceous undergrowth may be present."

Swamp Forest and *Mangrove Forest* need no new definition are are the equivalents in fresh and brackish water respectively. They are to be regarded as fresh and brackish water phases of one and the same formation.

The above five formations constitute a harmonious series in reduction of structure. Neither of the remaining two types that we have to consider, Beard's palm swamp and Fanshawe's Mora forest, stands in a very satisfactory relation to the others and may have to be discarded. Palm swamp was not found by Fanshawe in British Guiana and in view of the probable modification by fire of the Trinidad swamps from which it was described, it is possible that it represents a fire climax, and is degradation of swamp forest or woodland, or of swampy normal forest. There may also be a confusion with seasonal-swamp types in some cases. Alternatively, as we have suggested that the presence of palms in seasonal-swamp types may not be diagnostic, "palm swamp" may be only swamp woodland or arborescent swamp in which palms happen to be present. Further data on this question are desirable.

Fanshawe's Mora forest is not a welcome member of this series. Apart from the nomenclature, which draws the same criticism as Wallaba forest, we cannot recognize it as a separate formation because the structure differs little if at all from rain forest and there is little or no other difference in physiognomy. The Mora may indeed be associated with wet riverain sites, but it should be regarded properly as a type of rain forest. It is true that the formation swamp forest is far removed from the optimum in structure so that we might expect to find other types to fill the gap. Mora does not fill any gap, however, because in structure it *is* optimum. This same hiatus occurs also as we have seen with seasonal-swamp types and is probably due to their specialization. There is less room here for intermediate stages, because the site is either inundated or not and the distinction tends to be clear cut. In the Trinidad forests, there are societies of species tolerant of wet ground, tending to resemble swamp forest, on low-lying sites but there is always an abrupt change to true swamp where permanent waterlogging occurs (see Beard 1946b: 67).

The classification of American tropical vegetation types is thus consolidated as follows. For reasons to be discussed, the montane series is now placed before the dry evergreen and we follow Fanshawe in taking seasonal-swamp before swamp. On balance, the consolidation has only added two formations to the previous total of twenty-six.

A. Optimum Formation.
   Rain Forest.
B. Seasonal Formations.
   1. Evergreen Seasonal Forest.
   2. Semi-Evergreen Seasonal Forest.
   3. Deciduous Seasonal Forest.
   4. Thorn Woodland.
   5. Cactus Scrub.
   6. Desert.
C. Montane Formations.
   1. Lower Montane Rain Forest.
   2. Montaine Rain Forest or Cloud Forest.
   3. Montane Thicket.
   3a. High Mountain Forest.
   4. Elfin Woodland or Mossy Forest.
   5. Paramo.
   6. Tundra.
D. Dry Evergreen Formations.
   1. Dry Rain Forest.
   2. Dry Evergreen Forest.
   3. Dry Evergreen Woodland and Littoral Woodland.
   4. Dry Evergreen Thicket and Littoral Thicket.
   5. Evergreen Bushland and Littoral Hedge.
   6. Rock Pavement Vegetation.
E. Seasonal-Swamp Formations.
   1. Seasonal-Swamp Forest.
   2. Seasonal-Swamp Woodland.
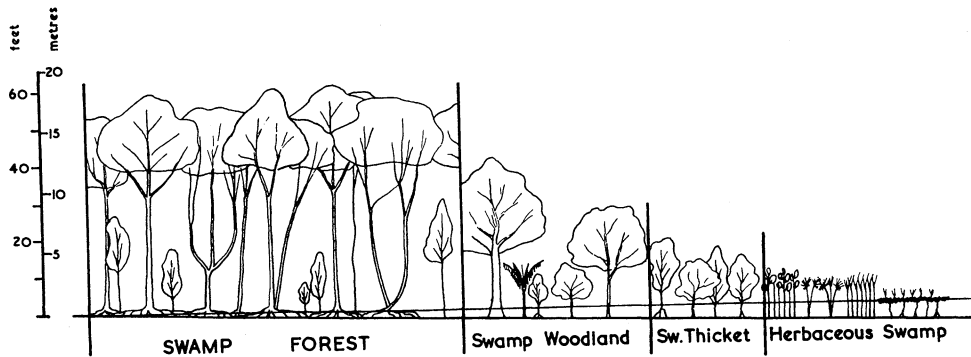   3. Seasonal-Swamp Thicket.
   4. Savanna.

FIG. 7. The Swamp Formation-Series. Swamp Forest after Beard, 1944a, the remainder imaginary and diagrammatic.

F. Swamp Formations.
  1. Swamp Forest and Mangrove Forest.
  2. Swamp Woodland.
  3. Swamp Thicket.
  4. Herbaceous Swamp.

Space does not permit a recapitulation here of the physiognomic details of these formations and it is assumed that students of the question will be familiar with the earlier papers cited. The twenty-eight formations characterized should now be adequate to include all the possible types of vegetation in tropical America apart from "atypical formations" as envisaged in 1944a. Caution must be exercised in attempting to apply the system. It will not fit secondary or damaged forests, seral communities nor local societies, some of which, like the riverain *Guadua* bamboo groves of Colombia, may differ strongly from the climax association.

Certain observations on the habitat of the formations will now be made, since some of the original conceptions have to be modified. Fanshawe's work emphasizes in strong measure the overwhelming importance of soil drainage in controlling the vegetation of high rainfall areas. In dry and moderately dry areas, the most important character of the soil is its moisture-supplying ability, in which the drainage factor assumes a smaller and smaller role as the dryness of the climate increases. In wet areas, however, as the wetness increases only sites of increasingly favorable relief and physical structure of the soil are able to dispose of surplus water by run-off or infiltration and continue to support unspecialized vegetation. Even here, paradoxically, we can also find soils whose drainage is at the other extreme and too free. The climatic climax, in its narrow sense, can only exist on sites where drainage is optimum and neither too free nor impeded. In British Guiana, climate differentiates the rain forest from the seasonal forests of the eastern border

and from the montane forests of higher altitudes in the Pakaraimas. It is drainage which separates from these the enormous areas of dry evergreen, seasonal-swamp and swamp.

There is nothing to be added at this stage to our knowledge of rain forest and seasonal forests. These can only occur on well-drained sites and are invariably predominantly controlled by climate. Locally, sites of poor moisture supplying ability will carry vegetation of a drier type than the regional climax, and unusually favorable sites vegetation of a more luxuriant type. In such cases seasonal formations are still present and show only a move up or down in the formation-series.

Montane formations likewise reflect essentially the climatic zonation associated with altitude and have for this reason been placed next in the classification, rather than the dry evergreen formations which are less clearly climate-controlled. Generally speaking, rainfall and humidity increase progressively up to a level of some 2,500 meters, above which there is again a progressive decrease. Temperature falls steadily with altitude, but only becomes critical above about 3,000 meters. At this level and upward it must be responsible for the zonation of high mountain forest, elfin, woodland, paramo, and tundra below the snow line at about 4,500 meters. In different regions rainfalls vary widely within this zone without changing the essential character of the vegetation. There are both wet and dry paramos. Lower down in the cloud belt exposure becomes a factor of great importance and is responsible for alternations of lower montane and montane rain forest with montane thicket and elfin woodland. The more reduced formations are found to come in on ridge tops, very steep slopes or areas particularly exposed to the prevailing wind. Below 2,500 meters, the vegetation is still essentially tropical and it seems unlikely that temperature has any effect on

zonation which is primarily due to the exposure factor. In previous papers the writer suggested that the exposure could result in excessive transpiration on clear days and that this was largely responsible for the reduction in stature and leaf size. It now seeems that this view is not tenable. "Exposure" is compounded of numerous effects. Most important of these is probably the mechanical effect of wind, which could break or blow down large trees on exposed ridges and slopes with shallow soil. The exposed situations in the mist belt are those where fog forms most consistently and where humidity and precipitation are highest. This may reduce transpiration to the point of stunting growth of the trees. A further limitation will be imposed by lack of root-room on steep slopes: however high the rainfall, shallow soil is bound to mean a lower forest. Again, in certain cases, the perpetual wetness of the climate sets up impeded drainage conditions even on mountain slopes, accentuated by pan-formation and the accumulation of a saturated surface peaty layer, with resultant reduction of the vegetation. This was found to be the cause differentiating montane thicket from lower montane rain forest in Puerto Rico by Wadsworth and Bonnet (1951). In such a case the montane thicket becomes close to marsh woodland.

Of the remaining three formation series, seasonal-swamp and swamp are clearly edaphic formations while the dry evergreen occupy a somewhat intermediate position and may be termed edapho-climatic. The swamp types are the most specialized, growing in permanently or more or less permanently inundated ground. The seasonal-swamp formations are in a sense intermediate between true swamp and dry evergreen, being periodically inundated on the one hand and associated with soils of obstructed internal drainage on the other, while the dry evergreen formations stand between seasonal-swamp and the truly climatic seasonal and montane types. These affinities between the habitat groups are shown by the certain degree of floristic interchange which takes place in a horizontal direction between them. Certain trees such as *Symphonia globulifera* are at home in both seasonal-swamp and swamp, while *Clusia fockeana* may be a dominant in both seasonal-swamp woodland and dry evergreen woodland in British Guiana.

Seasonal-swamp and swamp formations are in a true sense edaphic. Entirely under the influence of ground water, they will appear in substantially the same form under any climate where the edaphic conditions are similar. They stand moreover in a clear developmental relationship

to the climatic climax, occupying sites which are capable of evolving towards an optimum or have already devolved away from it. The dry evergreen formations are more difficult. Where littoral types are concerned they are controlled by climate, but it is a local and not the regional climate Dry evergreen forest which seems formerly to have existed in the Lesser Antilles at low altitude (Beard 1949a) would have been controlled by climate and climate induced soil conditions in "terras" and "shoal" soils which had developed drainage impedance. Dry evergreen formations in the interior of British Guiana are all differentiated from the climatic optimum by soil conditions, but these vary widely. In the white sands, we have a peculiar soil type of excessive drainage, which is not a climate-induced development, nor will it be capable of developing in any direction except by topographic senilty: there is no developmental relationship, therefore, between dry rain forest and the climatic climax. On the Kaieteurean sandstones, the dry evergreen vegetation occupies immature soils, where the rock has not yet decayed deeply: as it does so, there is presumably a development towards the climatic climax. Yet again, we find dry evergreen on ridges of lateritic ironstone, senile soils that have developed gradually the lateritic horizon: as they did so, there was presumably a development away from the climatic climax. Unlike seasonal-swamp and swamp formations, dry evergreen are always to some extent controlled by climate. Seasonal-swamp and swamp will be the same under any climate if groundwater conditions are constant whereas dry evergreen vegetation on a given soil type will vary according to the prevailing climate. The ecological status of dry evergreen formations may frequently appear to vary widely, but they are united by their essential habitat. An essential similarity of moisture relationships accounts for .the fact that the same formation may appear on such widely different soil types, now deep white sands, now shallow sandstone, and now rocky laterite ridges.

There is little difficulty in assessing the habitat of swamp formations which are in general differentiated by the depth and duration of inundation, with salinity and aeration of the water and nature of the rooting medium as subsidiary factors. Seasonal-swamp vegetation is always associated with impeded drainage of the type which will lead to stagnation of the ground water and deprivation of oxygen, occurring on flat areas having a pan or impermeable subsoil or simply a high water table and deficient means of lateral drainage. In true swamps, water-logging is always present and

the ground can never dry out. In seasonal-swamp there is at least a fall in the water table, allowing seasonal aeration of the topsoil. It is this factor which appears to control the segregation of these two major groups of edaphic communities. Under a strongly seasonal climate, waterlogging and stagnation of ground water take place on ill-drained sites during the rainy season while in the dry due to the nature of the soil there comes a period of desiccation. This acute alternation of moisture conditions is too severe for tree growth and is the commonest cause of the appearance of savanna. In higher rainfall areas, such severe seasonal desiccation may never occur, but there will be a relatively dry period of more favorable conditions in sites of bad drainage and stagnant ground water, giving us the woody seasonal-swamp formations, which are differentiated by the drainage factor into the series of formations, seasonal-swamp forest occurring where the drainage conditions are least severe and at the other extreme seasonal-swamp thicket standing for long periods in relatively deep stagnant water.

It is drainage variations which determine the zonation in and around savannas. With rainfalls of upwards of 2000 mm. a year, sedge savannas are most often found and occur typically as relatively small patches surrounded by a zonation of seasonal-swamp types from thicket to forest, these woody formations being enabled to appear due to the preponderance of the waterlogging factor. With rainfalls between 1000 and 2000 mm. a year, conditions on flats with impeded drainage are ideal for savanna, there being sufficient seasonal periodicity in the rainfall to maintain an intense alternation of the water conditions. This is the niche of tall bunch grass savanna which occupies wide areas, including sites which under higher rainfall would be constantly wet and carry woody seasonal-swamp vegetation. The transition to adjoining climatic forest is now usually abrupt, without ecotones or intermediate communities. An intermediate stage can however, sometimes be found where the rainfall is about 1500 mm. or less and the savanna is surrounded by semi-evergreen or deciduous seasonal forest. In such a case there may be a belt, called *cerradão* on the Brazilian plateau (Waibel 1948) and which we may perhaps term savanna woodland, constituted by a closing-up of the savanna trees to form a dense woodland 10-15 meters high. As the flora is still essentially that of the savanna, this must be considered as properly a type of savanna rather than as a separate formation. Under rainfalls below 1000 mm. a year, the waterlogging factor begins to fade out and is only now severe in depressions.

The low rainfall accentuates relief, so that the climatic climax—thorn woodland and cactus scrub—comes in on all the slight rises to form an intricate mosaic with short-bunch grass savanna which occurs as small patches in the slight depressions.

Dry evergreen communities not infrequently associate with savannas, appearing on reefs of white sand where rooting depth becomes very great, or on rock outcrops where rooting depth is greatly reduced: drainage is however good in both cases.

Summary

The classification of plant formations in tropical America proposed by the writer in 1944 is reviewed in the light of subsequent work, particularly of Fanshawe's "Vegetation of British Guiana" (1952). The original twenty-six formations are expanded to twenty-eight, listed in the text on p. 96. The physiognomy and habitat of these formations are discussed.

References

Beard, J. S. 1944a. Climax vegetation in tropical America. Ecology 25: 127-158.

———. 1944b. The natural vegetation of Tobago. Ecological Monog. 14: 135-163.

———. 1945a. Some ecological work in the Caribbean. Empire For. Jour. 24: 40-46.

———. 1945b. The progress of plant succession on the Soufriere of St. Vincent. Jour. Ecology 33: 1-9.

———. 1946a. Los climax de vegetación en la América tropical. Rev. Fac. Nal. de Agronomía, Medellín, 6: 225-293. (Spanish translation of "Climax vegetation in tropical America.")

———. 1946b. The natural vegetation of Trinidad. Oxford Forestry Memoir No. 20.

———. 1949a. The natural vegetation of the Windward and Leeward Is. Oxford Forestry Memoir No. 21.

———. 1949b. Ecological studies upon a physiognomic basis. Actas del 2°. Congreso Sudamericano de Botánica, Lilloa 20: 45-53.

———. 1953. The savanna vegetation of northern tropical America. Ecological Monog. 23: 149-215.

Beebe, W., and J. Crane. 1947. Ecology of Rancho Grande, a subtropical cloud forest in northern Venezuela. Zoologica 32: 43-60.

Cuatrecasas, J. 1934. Observaciones geobotánicas en Colombia. Madrid.

Curtis, J. T. 1947. The palo verde forest type near Gonaives, Haiti, and its relation to the surrounding vegetation. Carib. Forester 8: 1-12.

Davies, T. A. W., and P. W. Richards. 1933. The vegetation of Moraballi Creek, British Guiana. Jour. Ecology, 21: 350-384.

Fanshawe, D. B. 1952. The vegetation of British Guiana. A preliminary review. Imp. For. Inst. Paper No. 29, Oxford.

Richards, P. W. 1952. The tropical rain forest. Cambridge.

Schomburgk, R. 1847. Travels in British Guiana. Leipzig (in German). English translation by W. E. Roth, Georgetown, British Guiana, 1922. 2 vols.

Stehlé, H. 1945. Forest types of the Caribbean Islands, Part. I. Carib. Forester Suppl. to Vol. 6.

Wadsworth, F. H. 1951. Forest management in the Luquillo Mountains, I. Carib. Forester **12**: 93-114.

Wadsworth, F. H., and J. A. Bonnet. 1951. Soil as a factor in the occurrence of two types of montane forest in Puerto Rico. Carib. Forester **12**: 67-69.

Waibel, L. 1948. Vegetation and land use in the Planalto Central of Brazil. Geog. Rev. **38**: 529-554.

THE RELATIONSHIP OF WATER ECONOMY TO TERRESTRIALISM IN AMPHIBIANS[1]

THOMAS B. THORSON

Entomology-Zoology Department, South Dakota State College, Brookings, South Dakota

INTRODUCTION

One of the most essential requirements for life on land is the ability to avoid excessive loss of water from the body tissues. Among the terrestrial vertebrates, reptiles, birds, and mammals have met this requirement more or less effectively by the acquisition of an impermeable integument or integumentary modifications such as scales, feathers, and hair, and by the ability to excrete waste products not accompanied by large quantities of water. Amphibians, on the other hand, have no extensively developed integumentary modifications that tend to conserve body water. Even in the most terrestrial species, the integument itself offers little resistance to water loss, but on the contrary, loses water freely by evaporation. Furthermore, as far as is known, amphibians always excrete hypotonic urine. Perhaps largely because of their failure to meet the requirement of water conservation effectively, amphibians are in general confined to water, the vicinity of water, or at least to moist places or moist soil. As a terrestrial vertebrate group, they have not been markedly successful.

Despite the apparent lack of a highly effective water-conserving mechanism in amphibians as a group, marked differences exist between species in their degree of dependence on water. Some species are restricted to water throughout life, a few have been completely emanicipated from open water even in their embryogeny, while the remaining species are distributed between the two extremes.

Because of their diversity as regards independence of water, and since they are a group showing transition from the aquatic to the terrestrial

environment both historically and developmentally, amphibians are peculiarly appropriate subjects for investigations concerning the role of water economy in the development of terrestrialism.

In the amphibian body there are several sites of water exchange where water may be introduced into the system or lost to the environment, and on which water-conserving mechanisms could therefore conceivably act: (1) Throughout the body, wherever oxidation takes place, metabolic water is produced. This is added directly to the watery medium of the protoplasm and is subject to loss from the body only indirectly as any excess water of whatever source is subject to elimination. In any case, the production of metabolic water in amphibians amounts to less than 0.01% of the body weight per 24 hrs. at 20° C (Adolph 1943) and thus scarcely needs be considered. (2) In mammals, birds, and other animals that take water into the body by mouth, the absorption of ingested water into the system through the lining of the digestive tract is an extremely important consideration in any study of water metabolism. However, among amphibians, although about one half of the total water uptake of tadpoles is by mouth (Rey 1937), adults do not drink except under certain abnormal conditions as following dehydration due to immersion in salt solutions of relatively high concentration (Overton 1904). Thus the alimentary canal is not an important site of water exchange except in the degree to which water is ingested as a component of the food and egested with fecal matter. Since the animals used in the following experiments were kept in a fasting condition, intestinal exchange of water has not been a problem. (3) In air-breathing forms, the lungs dissipate a small and probably fairly constant quantity of water into the atmosphere. In the saturated or nearly saturated atmosphere above the surface of a body of water or in other moist surroundings fre-