

THE PROBABLE GROWTH HABIT OF THE EARLIEST FLOWERING PLANTS

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About a hundred years ago, Charles Darwin referred to the origin of the Angiosperms as an "abominable mystery." Modern research, although it has shed light on many of the problems which in Darwin's day were mysterious and unsolved, has done little to clarify this problem. It still occupies the thoughts of many botanists interested in evolution, to their bewilderment and frustration.

The reasons for this difficulty are manifold, but lie chiefly in the imperfection of the fossil record. Clear evidence regarding the origin and early evolutionary history of angiosperms would need to consist of a series of well preserved reproductive structures connecting the most primitive angiosperms with non-angiospermous seed plants, comparable to the fossil series which Florin (1951) has used so brilliantly to interpret the origin and evolution of the conifers. We do not have even the beginnings of such a series. Instead, we have only detached leaves, fragments of wood, and pollen grains. All of these kinds of fossils are clearly unreliable for tracing evolutionary phylogenies. Typical angiosperm leaves are simulated by the leaves of *Gnetum*, which most botanists, including the present writer, regard as a highly specialized side line, far from the ancestry of the angiosperms. On the other hand, some angiosperms, such as *Kingdonia* and *Circeaster* (Foster, 1959, 1963), have leaves with such an anomalous venation pattern that if they were found as fossils, unaccompanied by reproductive structures, they would not be recognized as angiosperms at all. The degree of specialization in wood structure, as Bailey (1944, 1953, 1957) has pointed out, is very poorly correlated with the degree of advancement in respect to reproductive parts. The wood of primitive, vesselless angiosperms is hard to distinguish from that of Pteridosperms and other non-angiospermous seed plants. In respect to pollen, identification is relatively easy and definite if one is dealing with close relatives of modern forms, but would be hopelessly uncertain if we were dealing with forms very different from any of those living today, which I believe must have been the nature of the common ancestors of monocotyledons and dicotyledons. Consequently, none of these frequently preserved parts, even if present in a complete sequence connecting angiosperms with their presumed ancestors, would by themselves provide evidence regarding angiosperm phylogeny, unless they were accompanied by macrofossils of reproductive parts.

Faced with this virtual absence of clearly recognizable fossils, many botanists have abandoned as hopeless any attempts to solve the problem of angiosperm origins. Such an attitude is in many ways justified. Nevertheless, this problem is of such importance for understanding the evolution of higher plants that many hypotheses and speculations about angiosperm origins have been and are still being

put forward. Such speculations should be critically reviewed in the light of our increasing knowledge about the processes of evolution.

One such speculation, offered by Melville (1960), is that the earliest angiosperms may have looked so different from the conceptions about them which are held by most contemporary botanists that we would not recognize these forms as related to flowering plants even if we did find them as fossils. I shall not attempt in this article to review the revolutionary ideas about the nature of the angiosperm flower which form the basis of Melville's speculations. I shall, rather, review some current ideas another characteristic of primitive angiosperms, their habit of growth.

THE BASIS FOR THE BELIEF THAT ANGIOSPERMS WERE ORIGINALLY WOODY

Plant anatomists are now nearly unanimous in their belief that the original angiosperms were woody, and that the herbaceous growth habit is in all instances derived from an ancestral woody condition (Metcalf & Chalk, 1950). The general acceptance of this hypothesis followed the publication and wide popularity of E. C. Jeffrey's (1916) "Anatomy of Woody Plants" and the nearly contemporary work of Eames (1911) as well as Bailey & Sinnott (1914). Jeffrey advanced the hypothesis that the herbaceous condition was derived from woodiness through an increase in the amount of ray parenchyma tissue surrounding the bases of the leaves. In this way, the originally continuous woody cylinder became broken up into separate vascular bundles. This type of change probably accompanied the origin of many herbaceous forms, including the ancestors of the monocotyledons. Nevertheless, many herbs belonging to both primitive and relatively advanced families possess continuous vascular cylinders, containing rays no wider than are those of typical woody stems. Bailey & Sinnott, therefore, rejected Jeffrey's hypothesis as a general explanation for the origin of the herbaceous condition, and their verdict is now generally accepted (Metcalf & Chalk, 1950).

Bailey & Sinnott gave the following reasons for believing that herbs are derived from woody forms:

1. Reduction in cambial activity, by means of which the amount of woody tissue in the stem becomes reduced relative to pith and cortical tissue, can be traced in many phylogenetic lines constructed through comparisons between modern forms, and is a part of the general tendency for reduction which exists throughout the higher plants.
2. All of the non-angiospermous seed plants (conifers, *Gnetales*, *Ginkgoales*, cycads) are basically woody, in that their stems possess a continuous vascular cylinder.
3. The earliest known fossil angiosperms all belong to woody families.
4. In floras which on the basis of their present geographic distribution appear to be ancient, woody forms predominate.

In my opinion, none of these arguments can be regarded as general and irrefutable, and even when all four are taken together, they by no means constitute proof that the trend from the woody to the herbaceous condition is always in one

direction. The possibility that some woody plants are secondarily derived from herbs should not be disregarded.

REVERSIBILITY OF TRENDS IN GROWTH HABIT

The validity of the first argument depends upon the degree to which one accepts the so-called "Principle of Irreversibility" in evolution, sometimes designated "Dollo's Law." This principle has been critically reviewed by Simpson (1953, pp. 310-312) largely on the basis of his wide knowledge of the fossil sequences in molluscs and particularly vertebrates, which include the most complete sequences known to us. He points out that reverse mutation for most, if not all, individual characteristics is a well known fact of genetics. Moreover, reversals of direction in respect to single characteristics are recorded in many fossil sequences. An example is body size in the evolution of horses.

Whatever validity exists for the principle of irreversibility is based upon the fact that evolutionary advances consist of parallel and integrated changes in a large number of characteristics controlled by different genes which are capable of segregating independently from each other. The integration of these gene complexes is produced by the action of natural selection, which builds up successions of adaptive gene complexes in response to progressively changing environments. If the direction of environmental change becomes reversed, the evolutionary line of organisms is much more likely to develop superficially similar but fundamentally different adaptations to such reversals than it is to retrace the complex path by which it originally evolved, and revert to an adaptive complex like those of its remote ancestors. When terrestrial vertebrates, such as reptiles or mammals, became readapted to aquatic life, they became fishlike in appearance; but whales are fundamentally no more like fishes than are elephants or lions. When they re-entered the water, the Podostemaceae took on an alga-like appearance, but fundamentally they are vascular plants and no closer to algae than are roses or saxifrages.

Applied to the evolution of growth habit, the principle of irreversibility as presently understood can tell us the following. Many plants have evolved a complex system of woody tissues, such as those of the more advanced angiosperms, in which many kinds of cells are differently adapted by their shape, wall structure, pitting, and cytoplasmic contents to perform separate functions of conduction, support, and storage. The growth and functioning of the stem depends upon a proper balance and integration between these different kinds of cells. Hence, we cannot expect such plants to reverse the numerous, integrated trends of specialization which produced this condition, and to evolve backwards toward a more generalized wood structure such as that found in gymnosperms. On the other hand, there is no reason to doubt that the genes controlling the amount of cambial activity could mutate either toward an increase or a reduction of this activity. Consequently, increase of woodiness is as much to be expected, given an environment in which it has an adaptive advantage, as is reduction of cambial activity and evolution toward the herbaceous condition. Furthermore, increase of "woodiness" through the development of a new kind of tissue is exactly the means by which one would

expect an ancestral herbaceous stock to give rise secondarily to woody derivatives. The secondary cambium which occurs between the vascular bundles of arborescent *Liliales* such as *Dracaena*, the sclerenchymatous cortical tissue of bamboos, and probably the interxylary phloem of many woody forms in the *Centrospermae* are cases in point. Sinnott & Bailey, in fact, recognize that in the monocotyledons shrubby and arboreal forms are derived secondarily from herbs.

If, therefore, we are to assume that all modern herbs are recent derivatives from ancestral woody stocks, we must reply on evidence other than the so-called principle of irreversibility. The second argument, that vascular tissue of herbs is more specialized than that of woody plants, is true in large part but by no means universally. Some strictly woody families, such as the *Bombacaceae*, *Burseraceae*, and *Meliaceae*, have relatively specialized xylem and phloem, while herbs such as *Paeonia* (Kumazawa, 1935) and many groups of vesselless monocotyledons (Cheadle, 1953) have vascular tissues which are more primitive than are those of most woody angiosperms.

RATES OF EVOLUTIONARY SPECIALIZATION IN WOODY PLANTS AND HERBS

Since the correlation between the herbaceous condition and specialization of woody tissue is imperfect, we must ask ourselves whether it could be based at least in part upon some other cause than that of unidirectional phylogenetic trends. Is it possible that the herbaceous condition is in itself a condition which increases the adaptive value of specialized vascular tissues? There is some basis for such an hypothesis. Herbs, particularly those growing in temperate climates or in the more arid portions of tropical regions, are usually adapted to undergoing regular cycles of rapid growth under favorable conditions, slower growth when conditions become worse, and dormancy during the cold or dry season. Furthermore, they often possess underground storage organs which help them to survive during unfavorable periods. Hence, we might expect them to evolve more efficient mechanisms for translocation and storage of food materials than would conifers or evergreen woody angiosperms, which maintain a slower but more continuous activity of metabolism and growth throughout most of the year.

Consequently, evolution in the direction of specialized vascular tissues could progress more rapidly in a line which was evolving the herbaceous growth habit than in a related line which remained woody. This would mean that families which acquired the herbaceous growth habit at an early stage in the evolution of angiosperms would even at this early period of time have evolved more specialized vascular tissues than their contemporary woody relatives. This seems to be the best way of resolving an apparently paradoxical situation. Many groups of herbaceous angiosperms, such as genera of *Ranunculaceae*, *Berberidaceae*, *Saxifragaceae*, and some families of monocotyledons, have relatively primitive reproductive structures as well as patterns of geographic distribution which suggest that they are very old. At the same time, their anatomical structure and vascular tissues are highly specialized. In my opinion, these groups are as old or older than many families of

woody angiosperms. At an early stage in angiosperm evolution they evolved a high degree of vegetative specialization, which they have retained ever since then.

EVIDENCE FROM THE FOSSIL RECORD AND FROM GEOGRAPHICAL DISTRIBUTION

The third kind of evidence which has led people to believe that the earliest angiosperms were trees is that from the fossil record. The fossil leaves and pollen which occur in the strata of lower to middle Cretaceous age, the earliest unquestionable angiosperms, resemble modern forms which are trees. This is also true of much more recent fossils, even those of early Tertiary age. Does this mean that herbs did not exist when the earliest angiosperms appeared?

Such an assumption would make extremely difficult the interpretation of disjunct distribution patterns in many modern herbaceous genera. Bailey & Sinnott correctly maintained that woody forms predominate among those species which have modern patterns of geographic distribution indicating that they are very old. Nevertheless, there are many examples of herbaceous groups which have similar relictual distribution patterns. As pointed out many years ago by Fernald (1931), and reaffirmed by many other plant geographers including the present writer (Stebbins, 1940), the presence of vicarious species in eastern North America and eastern Asia, as well as in such remote regions as subtropical Africa and South America, can be explained only by assuming that the common ancestors of these species became widely dispersed not later than the beginning of the Tertiary Period. Many of these species are herbs belonging to such specialized families as *Compositae*, *Gramineae*, and *Orchidaceae*, which must have had a long period of evolution at the level of herbs or shrubs before the common ancestors of the vicarious species in question evolved. The occasional presence in fossil beds of Cretaceous age of fragmentary remains belonging to grass-like plants, or to plants resembling water lilies and other herbs is further evidence that herbaceous forms were already developed in the Cretaceous Period.

The absence or scarcity of herbaceous and shrubby forms in the older fossil record is, therefore, best ascribed to the imperfection of this record. There are two reasons why the record should be biased in favor of trees. In the first place, leaves and pollen of trees are much more abundant in any forest than are those of shrubs and herbs. Secondly, the most favorable sites for deposition of fossils are lowland areas—stream banks, lake shores, and coastal plains (Axelrod, 1952, 1961). Even in regions with a relatively dry climate, such sites are likely to be occupied by well developed forests. The upland areas and steep mountainsides which are most favorable for the growth of shrubs and herbs are by their very nature particularly unfavorable for the preservation of fossils.

One feature of the fossil record points definitely to the conclusion that the absence or scarcity of shrubs and herbs in it is due to its imperfection and the biased character of the sample preserved. On the basis of the principles of modern genetics the belief that any major groups of organisms arose through the occurrence and establishment of a single "macromutation" is now untenable (Grant,

1963; Mayr, 1963). If, therefore, the earliest angiosperms were trees, then their immediate ancestors must also have been arboreal. But, as Axelrod (1961) has pointed out, if these pre-angiospermous seed plants were large trees, then they should have been abundant in the widespread forests of the Jurassic Period. Consequently, they would have been preserved along with the remains of the conifers and other trees which are known as fossils of Jurassic age. If the evolutionary line of seed plants which finally gave rise to angiosperms consisted of a long series of progressively more specialized forest trees, it should be as well preserved in the fossil record as that of the conifers, and the presence of Darwin's "abominable mystery" is incomprehensible. On the other hand, if the non-angiospermous seed plants which were the immediate ancestors of the earliest angiosperms were small plants, and particularly if they were insect pollinated, so that they shed very little of their pollen into the air, then their virtual absence from the fossil record could be explained.

ECOLOGICAL CONSIDERATIONS

If we recognize natural selection as the principle guiding force of evolution, we have another reason for believing that the earliest angiosperms were relatively small, short lived plants rather than large trees. Angiosperms are distinguished from other plants chiefly by various features of their reproductive biology, such as the carpel, the double integument of the ovule, the reduced number of mitoses in the male gametophyte, the fusion of the polar nuclei in the female gametophyte, and double fertilization. Collectively, these new features must have evolved through coordinated changes in a large number of genes. Such coordination could have been achieved only through relatively strong pressures of natural selection.

Populations of long lived trees living in an equable climate would not be subject to strong selective pressures for greater efficiency of their reproductive system. Each individual tree can, during its life time, produce millions of seeds. In a stable forest, replacement occurs only when an old tree dies, permitting one or a few younger ones to occupy its place. Under such conditions, species can survive even though their reproductive systems are relatively inefficient, provided that they have sufficient vegetative vigor and are well adapted to their habitat. It is certainly no accident that all of the modern conifers, cycads, and other non-angiospermous seed plants are long lived and live in relatively stable habitats. They can compete well with angiosperms under conditions which place a greater premium upon a highly efficient vegetative system than upon reproductive efficiency, but they have not been able to give rise to short-lived derivatives, in which efficiency of the reproductive system is necessary for survival and evolutionary success.

If by some miracle of reincarnation a botanist could be given a glimpse of the of the entire plant world of the Mesozoic era, he would probably recognize the early angiosperms or their immediate ancestors as having the greatest degree of reproductive efficiency possessed by any plants existing at that time. Moreover, they must have been members of a variety of structured plant communities which occupied various habitats, just as different kinds of plants do today. Since the forces of mutation, genetic recombination, and natural selection must have been acting in ways

very similar to their action in modern times, we might expect that the plants with the greatest reproductive efficiency would have occupied habitats similar to those occupied by the most reproductively efficient plants of modern times. Consequently, we can obtain the best idea of the habitats which saw the first evolution of angiosperms by inquiring, what are the ecological sites which today support plants with the highest degree of reproductive efficiency? Since these primitive angiosperms were almost certainly woody, we can, perhaps, obtain the best impression of this habitat by directing our attention to the shrubby representatives of the most advanced families of dicotyledons, such as the *Labiatae* and *Compositae*.

There is no doubt that such plants are most abundant and highly developed in semi-arid hilly or mountainous regions, such as coastal California, the Mediterranean region, the Mexican plateau, parts of the Andes mountains in South America, and the coastal hills and mountains of South Africa. They are, moreover, predominantly low shrubs rather than trees. On the basis of this reasoning, we would expect to find that the initial evolution of the new level of reproductive efficiency which characterizes angiosperms took place in such semi-arid, hilly or mountainous pioneer habitats.

The argument which has been presented in this discussion up to the present point can be summarized as follows. Several lines of evidence indicate that herbaceous angiosperms evolved almost or quite as soon as the flowering plants appeared, and that they have existed throughout the evolutionary history of the class. Due to the more equable conditions which prevailed during the Cretaceous and the first half of the Tertiary Period, which resulted in a much more widespread distribution of forests, the proportion of herbs in the floras of those more ancient times was almost certainly lower than it is now. Many woody groups must have given rise to modern herbaceous types as recently as the middle portion of the Tertiary Period. Nevertheless, the virtual absence of herbs from the older fossil record of angiosperms is much better explained as an artefact of the record than as an indication of the actual situation. There are, moreover, good reasons for believing that the earliest angiosperms and their immediate ancestors could not have been large trees.

On the other hand, one irrefutable argument exists in favor of the hypothesis that the earliest angiosperms, as well as their immediate ancestors, had the anatomical structure of woody plants. This is the fact that, so far as we know them, all known non-angiospermous seed plants, both living and fossil, are basically woody.

The logical reconciliation between these two lines of evidence, which appear at first sight to point in different directions, is the hypothesis which will be developed in the remainder of this article. This is that the earliest angiosperms, as well as their immediate ancestors, were low shrubs or subshrubs which occupied semi-arid pioneer habitats such as mountainsides and talus slopes. They might be visualized as similar in growth form to many species of *Polygonum*, *Eriogonum*, *Thymus*, and various genera of *Ericales* and *Compositae*. From such plants, evolution in the form of adaptive radiation gave rise in one direction to taller shrubs and trees, and in the other direction to various kinds of herbs, including monocotyledons. Evidence in support of this hypothesis will be presented from three major groups of

dicotyledons. They have been chosen from numerous possibilities because of their diversity, and because they include some of the most widespread trees of moist tropical forests.

SOME RELATIONSHIPS OF INDIVIDUAL FAMILIES

The first example is the order "*Gruinales*" of Wettstein, including *Rutaceae*, *Simarubaceae*, *Burseraceae*, *Meliaceae*, and *Sapindaceae*. Heimsch (1942) pointed out the cohesiveness of this group based upon their close resemblances in woody anatomy. In respect to floral structure, the most generalized family of this group is unquestionably the *Rutaceae* (Engler, 1931). In many genera of this family the flowers are completely regular, with all parts present and free from each other. In some genera the carpels are only partly united and at maturity form dehiscent follicles. In these groups, the embryo in the mature seed is surrounded by a copious endosperm. The groups in which these generalized floral characteristics are commonest are all in the subfamily *Rutoideae* and consist of the *Xanthoxyleae* subtr. *Choisyinae*, *Ruteae* subtr. *Rutinae*, and the tribe *Boroniae*.

In the *Rutaceae* as a whole, shrubby forms outnumber trees by about two to one, and the three groups mentioned above consist almost entirely of shrubs. The groups of *Rutaceae* containing the highest proportion of trees are in the subfamily *Flindersoideae*, in which the flowers have a trend of specialization toward zygomorphy; and the *Aurantoideae*, characterized by completely united carpels which form usually fleshy, indehiscent fruits. In both of these subfamilies, the mature seeds lack endosperm.

The family most nearly related to the *Rutaceae* is the *Simarubaceae*. Their flowers are in some ways more specialized than those of the generalized groups of *Rutaceae*, particularly in the reduction of the seeds per mature carpel to one, the prevalence of indehiscent, often winged fruits, and the reduction or disappearance of endosperm from the mature seeds. Their flowers are, moreover, much reduced in size, and are aggregated into compound inflorescences. In this family, the ratio of trees to shrubs is reversed as compared to the *Rutaceae*; trees outnumber shrubs about two to one.

In the *Burseraceae*, the floral specializations characteristic of the *Simarubaceae* occur to an even greater degree. The carpels are always completely united, the ovules are reduced to one or two per carpel, and the fruits are indehiscent. The flowers are small, in complex inflorescences, and the seeds lack endosperm. The pinnate or bipinnately compound leaves which characterize the family are probably also a specialization. The *Burseraceae* consist almost entirely of trees.

In the *Anacardiaceae*, *Meliaceae*, and *Sapindaceae*, trees outnumber shrubs by more than two to one. These families possess the same trends toward floral specialization as those of the *Simarubaceae* and *Burseraceae*. In addition, the *Meliaceae* have various strong specializations of their androecium, while the *Sapindaceae* tend to have zygomorphic flowers. In this group of families as a whole, therefore, the most generalized floral structure, in the *Rutaceae*, is associated with a predominance of the shrubby habit of growth, while the groups which are predominantly arboreal possess various specializations of their flowers, fruits, and seeds.

In the second group of families to be considered, those forming the order *Malvales*, the same trends are evident. The most generalized family of this order is the *Tiliaceae*. Within this family, the least specialized in floral characteristics are a group of six genera in the tribe *Tilieae* which have completely dehiscent fruits (Schumann, 1895). Two of these contain shrubs as well as trees, two are shrubs, one (*Corchorus*) contains shrubs and herbs, while the sixth, *Entelea*, is arboreal and monotypic. The genera of the *Tilieae* which have indehiscent fruits, including *Tilia* itself, are all trees. Of the other tribes, the *Apeibae* consist of three genera, all of which contain shrubs. The *Brownlowieae*, which are strictly arboreal, are specialized in their calyx consisting of united sepals, their fruits, with ovules reduced to one or two per carpel, and their frequent reduction of endosperm. The tribe *Grewieae* is specialized in possessing an androgynophore, with filaments adnate to the bases of the carpels. In this tribe, nearly all of the arboreal genera have indehiscent fruits, which in some instances are winged, and some genera have, in addition, unisexual flowers.

Nearest to the *Tiliaceae* are the *Sterculiaceae*. The tribes of this family which have the most generalized flowers, with all parts present and separate, are the *Dombeyae* and *Hermannieae*. Of the eleven genera in these two tribes, seven are entirely shrubby, two contain both trees and shrubs, one is a tree, and one an herb. In the neighboring tribe *Buettnerieae*, all of the genera contain shrubs except for *Theobroma* and *Guazuma*. *Theobroma* is highly specialized in its cauliflory and indehiscent, pulpy fruits. The *Helicteraeae*, which are specialized in possessing an androgynophore, contain three strictly arboreal genera, and two which include both trees and shrubs. Finally the most specialized tribe of the family is the *Sterculieae*, in which the flowers are unisexual, apetalous, and possess a well developed androgynophore. This tribe consists entirely of trees.

The next family, the *Malvaceae*, consists almost entirely of shrubs and herbs. The most generalized flowers in this family are in the tribe *Hibisceae*, possessing capsular fruits. The genera of this tribe are predominantly shrubby, and many lines of evidence indicate that in this family herbs have been derived from shrubs. The final family of the order, the *Bombacaceae*, is in some ways the most interesting of all. Although very closely related to the *Malvaceae*, the *Bombacaceae* consist almost entirely of trees. Their capsular fruits and woody habit of growth, indicate a closer relationship with the tribe *Hibisceae*. According to Metcalfe & Chalk (1950), their wood is highly specialized, and in all features agrees closely with that of the *Hibisceae*. Another very interesting feature of the *Bombacaceae* is their series of chromosome numbers, which have now been counted in several genera (Baker, 1960, and unpubl.). All of them are high polyploids, apparently on a base of $x = 9$. The commonest somatic number is $2n = 72$. This basic number of $x = 9$ is found in most sections of *Hibiscus*, in which genus the number $2n = 72$ is also common (Menzel & Wilson, 1963). It seems likely, therefore, that the arboreal *Bombacaceae* have been derived from primitive shrubby members of the *Malvaceae*, tribe *Hibisceae*, or their immediate ancestors by a course of evolution which involved extensive polyploidy.

The third group to be considered, the family *Polygonaceae*, differs from the

others in being predominantly herbaceous and temperate in distribution. Although its relationships to other families are somewhat obscure, it certainly belongs to the order *Centrospermae*, which are predominantly temperate and herbaceous. The most generalized flowers of this family are in the genus *Polygonum*. Among these, the sections *Avicularia* and *Duravia*, both of which contain suffrutescent species, are probably the most generalized in habit of growth. Furthermore, personal observations on one species of this group, *Polygonum Bolanderi* Brew., indicate that it has a relatively primitive nodal anatomy. In this species, three leaf traces emerge from three gaps, while in most species of the family, including other species of *Polygonum*, five or more leaf traces are found.

From a primitive suffrutescent condition, genera and species in this family radiated along numerous lines of evolution to growth habits of various types: caulescent perennial and annuals, rhizomatous perennials, rosette perennials, and vines. Trees are found only in the subfamily *Coccoloboideae*, which is strictly tropical, and has the specialized characteristic of a furrowed endosperm, as well as the specializations of nodal anatomy which characterize most of the family. Three genera are predominantly or entirely arboreal: *Coccoloba*, *Ruprechtia*, and *Triplaris*. In its calyx of united sepals, which become fleshy at maturity to produce a berry-like fruit, *Coccoloba* is decidedly specialized. *Ruprechtia* and *Triplaris* are both dioecious, and in *Triplaris* the difference between staminate and pistillate flowers is very pronounced. These genera of tropical trees almost certainly are end points of lines of specialization which probably began with shrubs adapted to a warm, temperate climate.

GENERAL CONCLUSIONS REGARDING THE EVOLUTION OF GROWTH HABIT

The three examples selected here for detailed treatment are by no means the only ones which could have been chosen. Equally good cases could be made for the derivation of trees from shrubs in the *Dilleniaceae*, *Rosaceae*, *Leguminosae*, *Myrtaceae*, *Oleaceae*, *Ericales*, and many other groups.

A logical question which might be asked is: does this kind of evidence really indicate that trees have been derived from shrubs, or is it more likely that in each of the groups concerned there existed ancestral forms which were trees, but which had generalized floral characteristics similar to those now found chiefly in shrubs? Two reasons can be given for a negative answer to this question. In the first place, as pointed out earlier in this article, the selective pressures which might lead to modification or extinction would be expected to act less strongly on trees living in stable forest communities than on shrubs which are generally found in less permanent habitats. Hence, if the ancestors of these groups were trees, some of them should have survived as long as their shrubby relatives. Secondly, the kinds of specializations which are found in the various lines described above are those which are generally characteristic of trees, and which are developed to their highest degree in such trees of temperate climates as the *Fagaceae*, *Juglandaceae*, *Ulmaceae*, and *Betulaceae*. These are unisexual flowers, reduction in flower size, development

of complex inflorescences, reduction in number of seeds per carpel and of carpels per gynaecium, evolution of indehiscent fruits, and reduction in the amount of endosperm in the seed. In various combinations, these characteristics probably make up character complexes which have a particular high adaptive value in association with the arboreal habit of growth.

The fact must, of course, be recognized that trees are more common than shrubs in the most primitive angiosperms, the woody *Ranales*. These ancient types are, however, relicts of much larger groups, and the numerous forms which must once have connected the various isolated families of the group are now completely extinct (Bailey & Nast, 1945). In view of the probability that arboreal forms can, in general, outlast their shrubby relatives through a course of environmental changes over a long term period of evolution, the writer is inclined to believe that some, and perhaps most of the common ancestors of the contemporary families of woody *Ranales* were shrubs rather than trees.

The conclusions reached in this discussion should by no means be interpreted as meaning that the trend from shrubs to trees is an irreversible one. As stated at the beginning of the article, general trends such as those in growth habit might be expected to reverse themselves from time to time. Among modern, highly specialized woody families of temperate regions, such as the *Salicaceae*, *Betulaceae*, and *Fagaceae*, the reduction of growth habit from trees to shrubs and subshrubs has undoubtedly taken place many times. This has been in response to the exposure of members of these families to increasing drought and cold.

Lack of space prevents further exploration of the conclusions which have been reached. The relationships between dicotyledons and monocotyledons, the probable age of the angiosperms, and many similar questions deserve consideration and will be treated in future publications. The writer hopes that this brief new look at an old problem will stimulate other botanists to take a similar new look, and that some of them may likewise arrive at new conclusions.

SUMMARY

The hypothesis is advanced that the original angiosperms were woody shrubs or subshrubs, rather than trees as some authors have maintained. The trend from shrubs to trees is considered to be reversible, and evolution has progressed in either direction, depending upon the relationships between populations and their environment. The relatively high degree of specialization found in herbs is regarded as a result of stronger selection pressure for this condition rather than as evidence that herbs are necessarily more recent in their evolution than are woody plants. The geographic distribution patterns of many herbaceous groups of species suggest that they are very old. Their absence from the fossil record is, therefore, regarded as the effect of an expected bias in the record rather than as evidence that herbs did not exist during the earliest period of angiosperm evolution. Reasons are given for believing that the selective pressures which brought about the angiospermous reproductive condition would have acted more strongly on smaller, short lived plants inhabiting pioneer or relatively temporary habitats than on the trees of stable mesic



Stebbins, G Ledyard. 1965. "The Probable Growth Habit of the Earliest Flowering Plants." *Annals of the Missouri Botanical Garden* 52, 457–468.
<https://doi.org/10.2307/2394810>.

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DOI: <https://doi.org/10.2307/2394810>

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