
Tree Architecture: New approaches help to define the elusive biological property of tree form
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Source: *American Scientist*, Vol. 71, No. 2 (March-April 1983), pp. 141-149
Published by: Sigma Xi, The Scientific Research Society
Stable URL: http://www.jstor.org/stable/27851897
Accessed: 25/08/2011 13:58

Tree Architecture

P. B. Tomlinson

New approaches help to define the elusive biological property of tree form

The form of trees is perhaps their most distinctive feature as a biological group, yet we have only recently understood quite elementary features of their construction. In this article I will describe advances in three rather different fields, using different approaches, which collectively have contributed to a better comprehension of tree form. One method is descriptive, another is theoretical, and the third is largely experimental.

First, in the realm of descriptive and qualitative morphology, investigation that takes into consideration the diversity of tropical tree species has revealed general principles of construction which show how the shape of the tree crown is established by a combination of deterministic and opportunistic processes. Second, in the field of theoretical and quantitative biology, simulation of crown shape through computer programs has provided insights into the developmental control of tree form. This approach has a further advantage in that its methods are applicable to treelike forms that occur in quite unrelated disciplines. Third, experimental research on water transport in trees has suggested the presence of structural constraints that control water movement to the hydraulic advantage of major axes as opposed to minor ones, a mechanism that allows trees to grow tall, since the upper branches and especially the trunk are favored in times of water stress. Although research in all these areas is still in its infancy, it points the way to interesting new developments in the discipline of plant morphology.

These three seemingly different topics are all related to a central concept of tree architecture formulated around the more abstract notion of "architectural model" by two European botanists who worked initially in the tropics: Francis Hallé and Roelof Oldeman. Their method, which is based on a broad comparative survey of trees with emphasis on tropical species (Hallé and Oldeman 1970), has recently been expanded, refined, and applied to the analysis of total forest composition (Hallé et al. 1978). Such a step is a logical one, since it seems inherently reasonable to approach an understanding of how forests are made by finding out how the individual units of the forest—the trees themselves—develop.

Hallé and Oldeman conceived of the architectural model as an abstraction of the genetic ground plan upon which the construction of the tree is based. The concept is dynamic, and development is strongly emphasized (Fig. 1). The visible expression of this model or ground plan at any one moment in time is the architecture of the tree. In this sense *architecture* is different from such widely used terms as growth habit, life form, and especially crown shape, all of which refer to the ultimate expression of tree form—its form as an end product. Moreover, size is not a factor in architectural analysis; plants of different final stature, such as herbs and trees, can have the same architectural model. The system is quite empirical and was arrived at by recording a few relatively easily observed growth parameters for a great diversity of tree species. Since tropical species are emphasized, the resulting concept of tree is a very broad one, including such plants as tree-ferns, palms, pandans, cycads, bamboos, and even bananas, as well as dicotyledonous trees that botanists of the temperate zone would recognize as having a more conventional construction. Indeed, an appreciation of tropical diversification enormously broadens the concept of conventional tree form.

That each tree has a precisely determined genetic growth plan was established by observing the development of many different species grown from seed, either as cultivated specimens in nurseries and plantations or—preferably—as populations established naturally in natural ecosystems. The features observed included such factors as whether the tree branches or remains unbranched (as in some palms), whether or not branching is restricted to the base of the trunk, whether shoot extension is continuous (a tropical feature) or rhythmic, whether or not there is branch differentiation, with some branches orthotropic (i.e., erect and with radial symmetry) and others plagiotropic (i.e., horizontal and with dorsiventral symmetry), whether flowers are terminal or lateral, and whether or not crown form involves late changes in the orientation of branches. Some of these possibilities represent clear-cut alternatives; for example, flowers are either terminal or lateral. In other cases the alternatives are less sharply contrasted (as with methods of shoot extension) or represent a continuum of possibilities (as with the orientation of axes). Obviously there is considerable subjectivity in the selection of features and even in the interpretation of the observations, but the value of the approach lies in the comparative analysis it permits, in its ordering of biological

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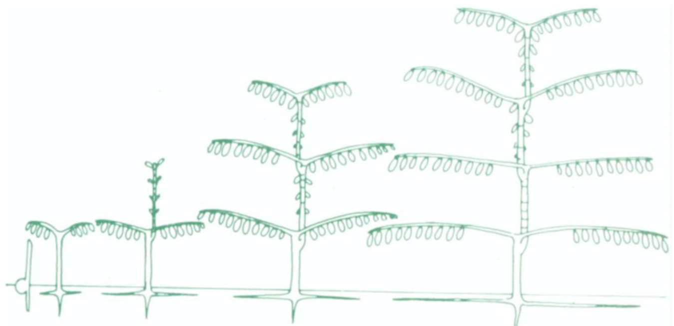
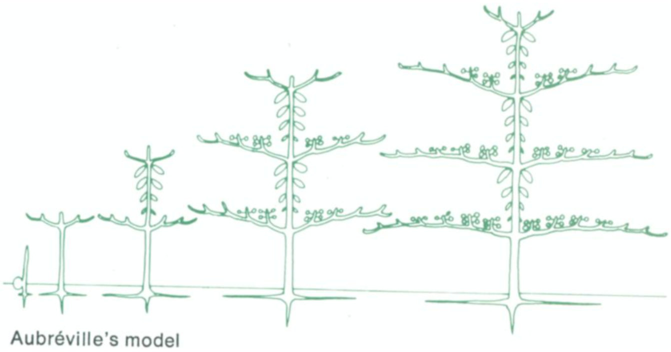


Nozeran's model



Aubréville's model

Troll's model

Figure 1. In Hallé and Oldeman's dynamic concept of tree architecture, trees develop according to a precise genetic ground plan – the architecture model – that determines the form of the tree. In Nozeran's model, for example, the apex of the seedling axis produces a tier of horizontally oriented branches; a new erect axis then arises below the tier and repeats the process, and additional tiers are formed in the same fashion. The trunk axis is therefore sympodial, or made of numerous separate segments. By contrast, Aubréville's model is monopodial, characterized by a single trunk axis with rhythmic growth. Each cycle of growth produces a new tier of horizontally oriented branches, which themselves develop as sympodial complexes that support leafy rosettes with flowers. Troll's model, a common form, develops by superposition of a succession of horizontally oriented branches, each overtopped in turn by a younger branch. The trunk is again sympodial. The dynamic approach to analysis of tree form has important consequences when the changing response of the tree to both competitive and environmental influences is examined. (After Hallé et al. 1978.)

diversity, and most of all in the insight it has offered into the basic adaptive process of opportunistic development.

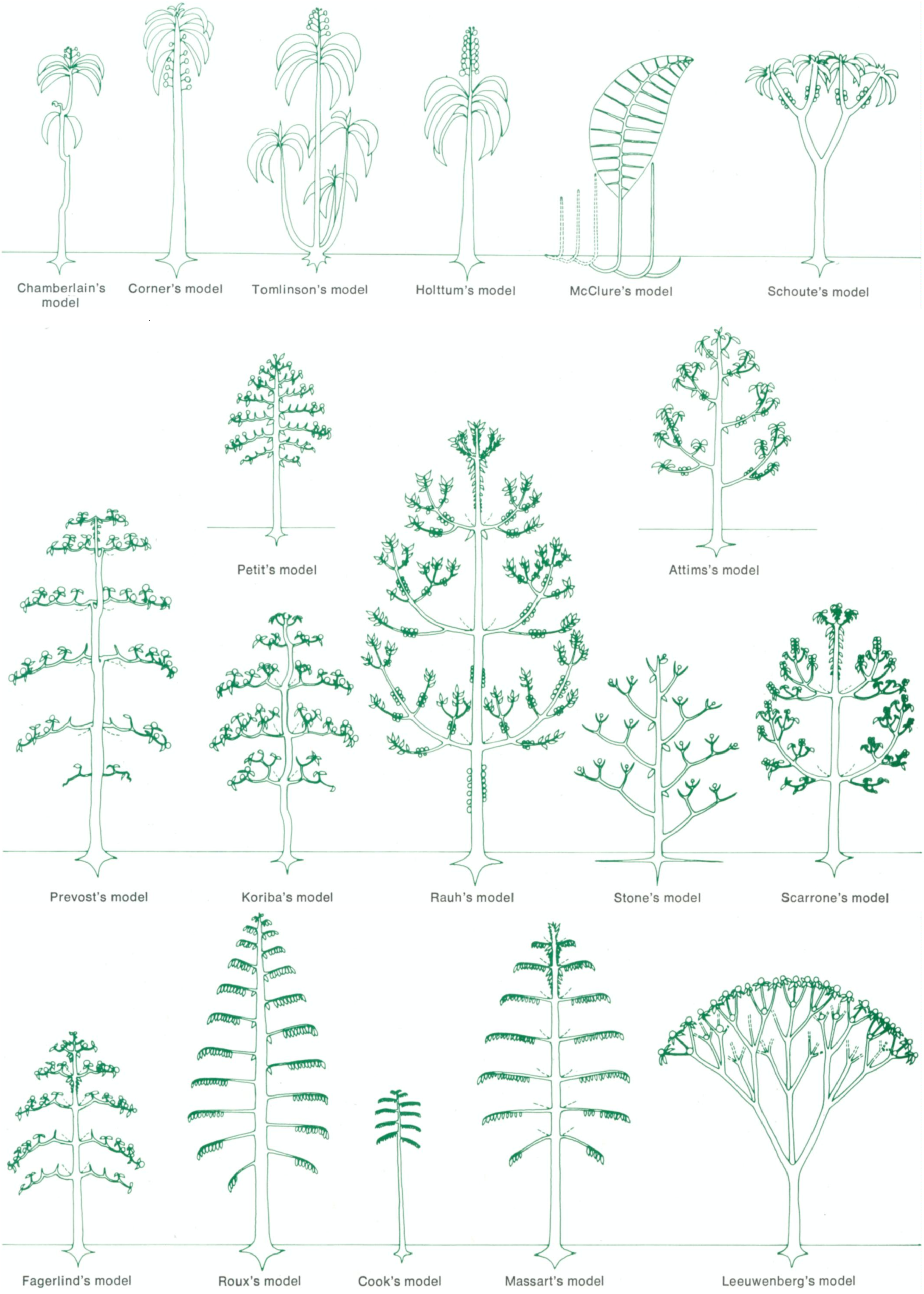
Using the simple method of analysis outlined above, Hallé and Oldeman reduced the total diversity of tree forms to 23 developmental modes or architectural models (Fig. 2)—a remarkable achievement which provides a universally applicable set of reference points. The intellectual step thus taken is comparable to the development of the binary system of nomenclature by Linnaeus. A neutral system of labeling for these models was devised by using the names of botanists who had contributed information about the development of appropriate species. Chamberlain's model, for example, refers to plants with a single sympodial trunk, a common feature of the cycads, whose construction Chamberlain did much to elucidate. This system of nomenclature eliminates the evolutionary connotations of a typological system using named plant examples, and avoids problems which arise because botanists can only be familiar with a limited number of species. Although the rubber tree *Hevea brasiliensis* is a good example of the widely distributed Rauh's model in the tropics, a more familiar example such as an oak (*Quercus rubra*) would have to be used for the temperate zone.

This is not to imply that every tree can be precisely ascribed to one of the named tree models, because there is in effect a continuum of architectural possibilities. Some trees are intermediate between particular architectural models, while others, such as the hemlock (*Tusga*) (Hibbs 1981), share features of more than one model. Moreover, only trees of either very precise or very simple organization—for example, palms and many conifers—grow in such a way that they always conform to a described tree model. Most trees conform to their model for a limited period as saplings, their continued development being the result of crown modification related to accidental events, as described in more detail below.

Application of architectural analysis

Although Hallé and Oldeman's convenient terminology describes the form of trees in a developmental framework, it has also led to several useful generalizations, some of which relate to the functional significance of tree form. First, the survey confirms that the greatest variety of tree form occurs in the tropics, where representatives of all 23 models exist. The fact that tropical rain forests include a greater variety of tree species than do temperate forests is well appreciated by systematic botanists. For example, Poore (1968) identified 374 species of trees in a 23-hectare plot in lowland West Malaysia—almost as many trees as occur in the whole of the continental United States. Southern Florida is a microcosm of this tropical diversity, with a particularly rich representation of species; out of a total of 120 native

Figure 2. By examining a few relatively easily observed features in a wide variety of tree species, Hallé and Oldeman were able to reduce the diversity of tree form to 23 models, a number of which are illustrated at the right. In each case the form is stylized and only one developmental stage is shown, representing the fully expressed architecture of each model; the root systems, which are unknown, are merely indicated schematically. The examples represent commonly expressed forms in what is a continuum of architectural models, and thus a tree may be intermediate between two models or may share features of more than one model. Most trees conform to their models for a limited time as seedlings; their continued development is usually modified by accidental events. (After Hallé et al. 1978.)


Chamberlain's model
Corner's model
Tomlinson's model
Holttum's model
McClure's model
Schoute's model
Petit's model
Attims's model
Prevost's model
Koriba's model
Rauh's model
Stone's model
Scarrone's model
Fagerlind's model
Roux's model
Cook's model
Massart's model
Leeuwenberg's model

species, about 100 are tropical (Tomlinson 1980). The evolutionary explanation for this tropical profusion is not readily apparent, but may be sought in the relative uniformity of climate found in many lowland tropical areas. Adaptations for survival, then, are related to biotic rather than climatic factors. In principle, tropical conditions are uniformly favorable for plant growth, and strategic success for a species is related to competitive interactions with other plants or with animals. These interactions seem to allow a greater range of possibilities than is the case where interaction between plant and climate is the overriding factor. A more precise explanation, however, is still lacking.

Many of the 23 models are in fact restricted to the tropics, and there are a number of reasons for this. In some cases, as with Attims's and Petit's models, the definition of the model includes continuous shoot extension, which is not possible in temperate or seasonal climates. In other cases, for example, Holttum's and Corner's models, the models are largely represented by monocotyledons, which seem to be restricted to the tropics because they have no dormancy mechanisms that allow them to overwinter, even though they can survive dry seasons. Particularly complex tree models restricted to the tropics are those with highly specialized systems of branch axes, such as Nozeran's model, represented by cocoa (*Theobroma cacao*), and Aubréville's model, represented by sea almond (*Terminalia catappa*). A distinctive feature of both these models is their dependence on syllepsis, the growth of lateral buds without previous rest in a dormant stage, which is primarily a tropical phenomenon.

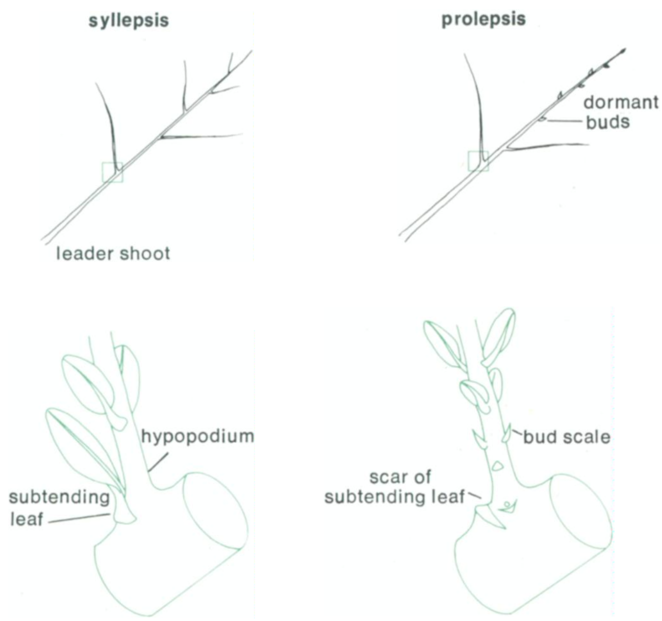


Figure 3. The existence of two different modes of branching in woody plants offers important clues to the chronology of development. In syllepsis, the bud develops immediately into a branch that grows simultaneously with its parent trunk, producing a hypopodium without basal bud-scales; the first leaves are of nearly normal size. By contrast, in prolepsis the branch develops after a period of rest as a lateral bud – in the case of temperate trees, in the second year. A series of bud-scale leaves is present, together with a scar from the subtending leaf, and there is a gradual transition to normally developed foliage leaves. Recognition of these features allows some assessment of the tree's earlier branching history. (After Tomlinson 1980.)

A second generalization is that there is no necessary correlation between architecture and broad systematic position (Hallé et al. 1978). Species within a genus or within closely related genera can have the same architecture, but there are frequent exceptions. The same distinctive tree form can occur in quite unrelated families. Nozeran's model, found in the Sterculiaceae, also occurs in 4 other families which are widely separated systematically. Aubréville's model occurs in at least 19 families. Some dicotyledonous families are architecturally rich out of proportion to their size. For example, the relatively small tropical family Icacinaceae, which contains 300 species, includes at least 7 models (Hallé 1974); conversely, some large families are architecturally poor, with a preponderance of one architectural type. Troll's model, for instance, is very common in the extremely large family Leguminosae (12,000 species), demonstrating that ecological success is not dependent on architectural diversity. By contrast, the conifers are architecturally poor, with only 4 recognized architectural models; gymnosperms in general are not very diversified architecturally.

Sometimes inherent structural constraints limit developmental modes. Plants without secondary thickening, a process in which the diameter of the trunk increases as the tree grows taller and the crown becomes larger, have an obvious restriction on their ability to branch. Most woody monocotyledons conform to this pattern. Branching of major axes is then either restricted to the base of the trunk, as in McClure's (bamboos) and Tomlinson's (for example, many palms) models, or follows a fixed pattern, as in Schoute's (for example, the palm *Hyphaene*) or Stone's (some *Pandanus* species) models. Nevertheless, analysis at this elementary level shows that tree monocotyledons are architecturally *more* diverse than gymnosperms, even though the latter have the ability to develop thicker trunks as they grow. This again demonstrates the greater adaptive radiation of angiosperms as compared to gymnosperms, and further accounts for the competitive success of flowering plants.

Third, the emphasis of the models on the dynamics of growth has revealed previously unappreciated correlations between modes of branching and the chronology of development. It has been stressed (Tomlinson and Gill 1973) that there are two opposed developmental possibilities for lateral buds in woody plants: an axillary bud can grow by syllepsis, i.e., without previous rest, or by prolepsis, i.e., after a period of dormancy (Fig. 3). Although these processes can occur in a single individual, they are normally quite sharply contrasted and result in appreciable morphological differences. Thus sylleptic and proleptic branches can usually be recognized even if the development of the tree has not been observed over a long period of time. This is an instructive example of the way in which a dynamic interpretation of the architecture of a tree can be made without long-term observation once the correlation between growth and structure is established.

In most temperate trees branching is entirely by prolepsis, and the lateral buds for the current year remain unextended—that is, the ends of major branches (i.e., leader shoots) remain unbranched. Syllepsis is very common in tropical trees; here lateral buds extend contemporaneously with their parent axis—that is, leader shoots can be branched. This means that the phenomenon of apical dominance, or suppression of the lateral buds by growth substances emanating from the terminal bud, is not universal, as plant physiologists working with temperate species have tended to assume. The value of comparative analysis is particularly well demonstrated by this point, which shows that valid generalizations cannot be made without reference to tropical plants.

Of special interest are those trees in which these two contrasted methods of branching occur in sequence as essential architectural features and are precisely correlated with contrasted types of branch orientation. In Nozeran's model, for example (Fig. 1), the horizontally oriented axes that form each tier of branches are produced by syllepsis, whereas the vertical axes that initiate each new tier are produced by prolepsis. The causal mechanisms for these two different responses are not known. The more general question of why syllepsis should be an essentially tropical phenomenon also remains unanswered; it may have something to do with the hydraulic factors discussed below. For the present it should be emphasized that the distinction between syllepsis and prolepsis has been largely overlooked by morphologists and plant physiologists until recent years. One reason for this is obvious: since syllepsis is predominantly a tropical feature, relatively few botanists have had the opportunity to observe it as a normal growth process.

The process of reiteration

Perhaps the most important insight that the study of tree architecture has produced is related to the recognition of the way in which the majority of tree species repair a damaged crown. Most trees respond to environmental damage by the process of reiteration, that is, by a replication of the original architectural model from one or more active or inactive buds. Reiteration can be interpreted as an adaptive response to certain kinds of environmental stress. Saplings in the forest understory may be broken by branches falling from taller trees, by animal predators, or by wind damage. Indeed, since undamaged specimens are rare in some natural environments, it may be difficult to make a developmental analysis based on a growth model alone.

Each such event results in a "reiterative complex" within the crown, essentially a repetition of the architectural model of the tree. In symmetrical trees, the reiterated complex may appear as a miniature version of the tree perched in the existing crown (Fig. 4). Usually the replication is complete, but it may be partial, so that only branches, not trunks, are produced, as in the genus *Araucaria*. In many instances the reiterated complex originates from a reserve bud—a dormant bud that has played no previous part in crown development. However, reiteration can also occur through branch reorientation—for example, when a horizontally oriented branch reverts to a vertical orientation and the vertical shoot then establishes a new reiterative complex. This process accounts for the massive J-shaped limbs that are seen on many trees growing in open spaces: a branch has in effect become a trunk. Some tropical trees such as the common *Rhizophora* reiterate exclusively by this means.

Reiteration takes many forms, and includes several phenomena familiar to foresters: the development of stump or trunk sprouts, the emergence of root suckers, and the release of buds on leaning trunks (Fig. 4). Propagation from cuttings is a form of artifically stimulated reiteration. In architectural terms these processes indicate the repetition of the growth plan of the tree. The value of architectural analysis then becomes apparent: it is only when the basic branching pattern of the tree has been clearly perceived that the extent to which crown construction is the result of reiteration can be appreciated. Crown shape in trees is determined entirely by the twin processes of architecture (a deterministic process) and reiteration (an opportunistic process). Thus the shape of the mature tree crown is the result of *all* the collective deterministic and opportunistic events which the individual has experienced during its lifetime. We cannot speak of the "adaptive value" of a crown shape, since the shape is largely determined by chance events.

The opportunistic nature of much crown development suggests that the tree's ability to produce reserve buds is part of its adaptive response. The success of angiosperms may therefore be related to this ability as much as to their ability to express a diversity of architectural models. It is revealing that one of the most common tree models—Troll's model (Fig. 1)—is characterized by architectural plasticity. Although easily recognized, it is a difficult model to define, as if the

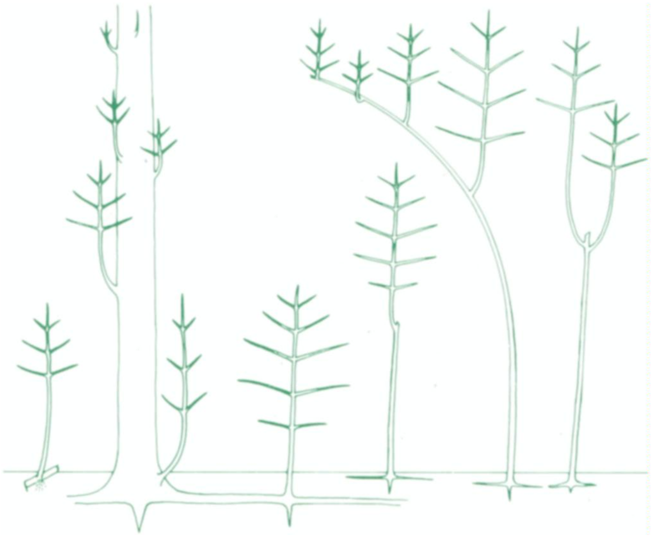


Figure 4. Most trees respond to damage through reiteration, or the replication of their original architectural model. Shown here from left to right are a number of examples of this process: propagation from a detached stem, the development of new shoots on the trunk, the emergence of root suckers, the creation of the "bayonet joint" characteristic of broken saplings, the growth of reiterated complexes (miniature trees repeating the basic architecture) on a leaning trunk, and the development of a forked axis with two shoots reiterating the original model. In this kind of reiteration, the source of the repeated architecture is a previously dormant bud known as a reserve bud; reiteration can also result from reorientation of branches. (After Hallé et al. 1978.)

randomness of environmental hazards is anticipated in the very lack of precision of the growth model itself, since neither the position of branches nor their orientation is very predictable.

Quantification and simulation

Studies of tree architecture such as those discussed above are almost entirely qualitative. A different but parallel approach to the study of tree form emphasizes quantification, reducing crown shape to a series of simple parameters and thus allowing computer simulation of crown development. This approach reflects only one specialized aspect of the current interest in the "tree" as a mathematical model, defined as a branching system with only one possible pathway between any two points. Trees, then, are no longer the exclusive domain of botanists but can be recognized in a number of quite unrelated fields such as geomorphology (river systems), neurology (nerve pathways), physiology (lungs), zoology (corals), and even cybernetics (certain kinds of communication networks). The dichotomous key that is commonly used by systematists to identify unknown organisms from a set of contrasted characters is another such tree.

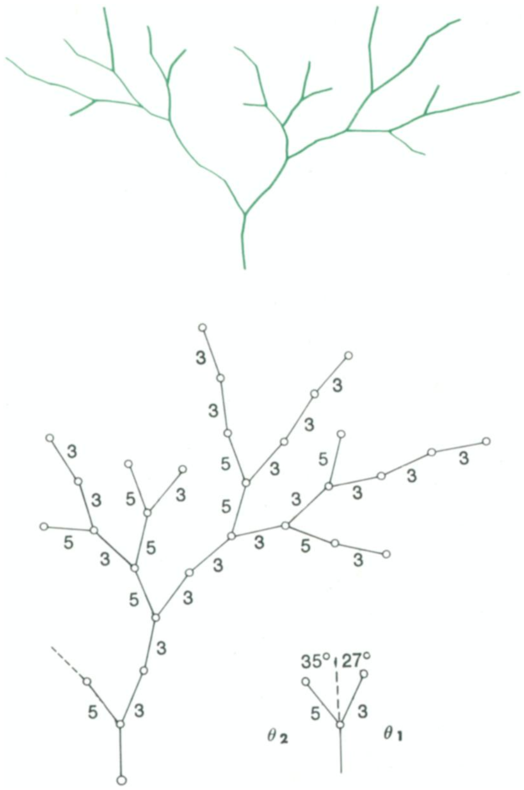


Figure 5. By measuring the angles in actual branch complexes of the sea almond (*Terminalia catappa*), rules of branching were established that allowed the creation of a theoretical branch system for use in computer simulation. The example at the top shows an actual branch complex viewed from above (see Aubréville's model in Figure 1 for a schematic side view). In the theoretical system at the bottom the branches alternate from axils of leaves 3 and 5 (numbered in order of initiation on the segment), with the average angles at forks θ_1 and θ_2 indicated in the inset. The frequency of branching is established randomly, so that sometimes only one, otherwise two branches develop at the links represented by open circles. In the real tree these links are the location of leafy rosettes. (After Fisher 1978.)

Honda (1971) first showed that relatively few parameters are needed to generate simple treelike shapes on a computer with a display output, using stereological images to create three-dimensional forms. The effect on simulated tree shape of changes in these parameters could easily be demonstrated, opening the way for synthetic manipulation of crown shapes.

Fisher and Honda (1977) next used values derived from direct measurements of *T. catappa* (Aubréville's model) to simulate its very regular branch morphology (Fisher 1978). In this tree the leaves in each horizontally oriented branch complex grow in such a way that they are arranged in a series of rosettes located at the interstices of a network of axes which have an essentially hexagonal geometry. In addition to minimizing the total length of axes in the complex, the regular geometry facilitates simulation, since "rules" of branching can easily be established by measuring real trees (Fig. 5). By varying the angle of branching within a simulated branch complex, a multitude of patterns were produced. Further calculations showed that the pattern in which the theoretical angle coincided most closely with the real angle corresponded to one in which mutual shading by rosettes within the same complex was minimal (Honda and Fisher 1978). In other words, the interception of light was maximized and photosynthesis was made most efficient (Fig. 6). This is not a surprising conclusion, but it is a good example of a precise demonstration of the presumed ability of a tree to maximize photosynthetic activity by the method of leaf display.

More complex programs have now been developed. One such program (Honda et al. 1981) simulates competitive interaction both within a single branch system and between adjacent branch systems (Fig. 7)—a step toward the simulation of interaction among tree crowns as forest canopies develop. In another program (Honda et al. 1982), simple rules have been generated which progressively restrict branching in progressively higher branch orders. This phenomenon certainly occurs in nature; if it did not, branch ends would soon intertwine. Where branch systems in nature correspond closely to simulated ones, it is possible that the artificial rules of development correspond in some way to real developmental rules, validating the use of theoretical information. Certainly theoretical research brings with it the enormous benefit of simple experimental design; it would require many years to carry out comparable experiments on real trees. The situation is complex: botanical trees are three-dimensional systems of great diversity, but the recognition of the limits of this diversity provided by architectural analysis can make the selection of computer models a realistic one. Continual reference to living examples is needed to balance theoretical analysis, but the economy of research effort which simulation permits can be readily appreciated.

Hydraulic architecture

The study of the ability of different parts of the plant to control its water supply has also contributed to a new understanding of tree structure. The integrated nature of the hydraulic system of the tree is readily verified by simple experiments in which dye is injected and its path is traced. But since the movement of water from root to crown in a transpiring tree is ultimately controlled by physical forces, structural modifications are necessary to regulate the flow along the various axes of the tree. For example, if a tree is to grow tall, its upper axes must be favored in the distribution of the water supply, even though they are at a hydrostatic disadvantage in being remote from root sources. This principle is expressed in all plants by the simple fact that lower branches and lateral appendages such as leaves may wilt first in times of water stress. How is this achieved? Whatever the mechanism, it is likely to have evolved very early in the history of vascular plants. The early replacement of equal dichotomy, a primitive feature of geologically ancient trees, by some kind of controlled lateral branching may well be the first morphological manifestation of this simple physiological requirement.

Working at Harvard Forest, Zimmermann (1978a, b) recently demonstrated experimentally that there is a hydraulic constriction at the point at which branches join the trunk. This was done by measuring the rate of water flow on both sides of branch-trunk unions by means of a simple gravimetric method and relating the values thus obtained to the weight of leaves above each portion of the axis, a measure of the transpiration capability and transport requirement of the shoot. Values are always lower in branches than in their parent axes and are minimal at the base of branches, suggesting that flow is restricted (Fig. 8). This restriction is in part due to a reduction in vessel diameter, which decreases with distance up the tree (Zimmermann and Potter 1982), but could also indicate a reduced number of conducting vessels or a combination of these two factors. An analogous constriction zone has been found in dicotyledonous plants (Larson and Isebrands 1978), where resistance to flow across the junction between stem and leafstalk has been clearly demonstrated.

A further possibility is that conducting vessels are shorter in the region of branch-trunk unions, although this would appear to be very difficult to measure. However, Zimmermann and Jeje (1981) have devised an ingenious but elegantly simple method for measuring the distribution of vessel lengths in axes by injecting very dilute latex paint. We thus have the capability to establish the structural basis for the total hydraulic ar-

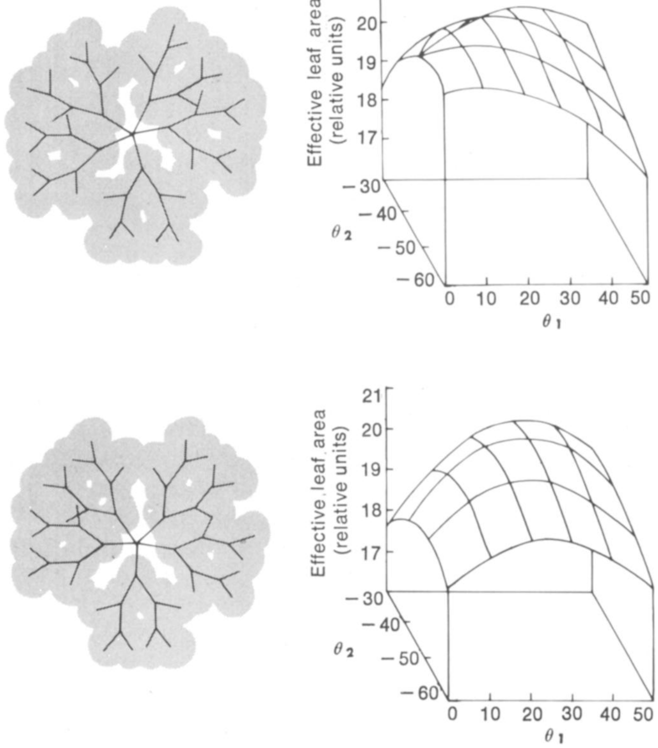


Figure 6. Computer simulations of a single tier of *T. catappa* based on the rules established in Figure 5 are illustrated. Normally each tier contains five branch complexes, as shown here. The leafy rosettes at each link are represented by overlapping disc-like shapes; the projected outline of these discs, indicated here, is the effective leaf area. This may be compared with the total leaf area, which is the sum of the area of all the discs. The most efficient system photosynthetically is the one in which the effective leaf area is maximized, with a minimum area of openings in the leafy canopy. Two different systems are simulated: at the top the system is uniform, with the smaller branch angle (θ_1) always on the same side of the first fork; at the bottom the system is mixed, with the smaller angle on different sides of the first fork, as in real trees. The graphs at the right plot values for branch angles at the forks (θ_1 and θ_2) against the projected effective leaf area relative to total leaf area in arbitrary units. The maximum effective leaf area for a given combination of angles is indicated by the highest point of the curved surface. Measured values correspond closely to maximum theoretical values, suggesting that the tree can itself measure and control branch angle very precisely. (After Fisher and Honda 1977.)

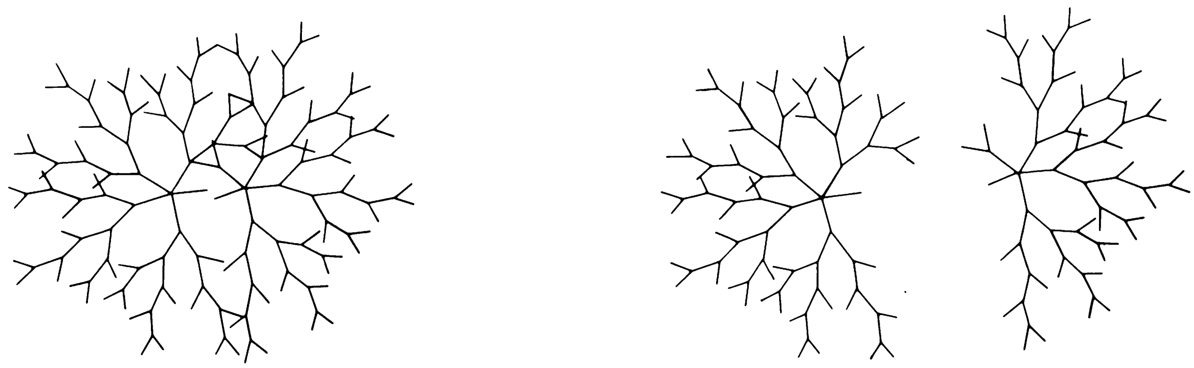


Figure 7. Simulation of interaction between adjacent branch complexes of two trees in a single plane can provide a simple model for interaction among tree crowns in a developing forest canopy. At the left the tiers are shown separated by a distance of 2.2 units, where 1 unit is the length of the first lateral branch. At the right the tiers are shown disengaged, to indicate the extent of branch loss where impinging axes are destroyed. The rules of branching are basically the same as those used in Figure 6, with the addition of a factor for loss through interaction. (After Honda et al. 1981.)

chitecture of the tree. The vista for future work is exciting, and the research itself is of considerable practical importance in view of the number of diseases of woody plants in which a pathogen disrupts normal vascular flow. The Dutch elm disease is, of course, an all too familiar example.

At a more basic level, the emerging relation between form and function may put us in a position to elucidate some of the correlative peculiarities already discussed. Prolepsis may establish a different kind of vascular connection than syllepsis does, either a more efficient one or a safer one, in that vascular failure through embolism of functional vessels is minimized. John Sperry, a graduate student at Harvard, has recently compared the conductivity values of proleptic and sylleptic branches within a given tree and found that such values are lower in young proleptic attachments than in young sylleptic ones. The situation is reversed as the union thickens, suggesting that young proleptic unions are less efficient but safer, whereas mature proleptic unions are more efficient but less safe. Temperate trees may thus have evolved to favor the safest union, i.e., that produced by prolepsis. Although the sylleptic union favored by tropical trees is less safe, it may also be less disadvantageous given the less stressful climates.

Architecture and ecology

The several aspects of tree form discussed so far can all be related to the central problem of the ability to survive in the competitive environment of the forest. Having abstracted the tree from the forest in order to investigate how its form is developed, expressed, and controlled, it seems appropriate to reinsert it in its natural environment and try to account for its success. However, the ecological success of a tree does not seem to be correlated with architecture alone, since trees conforming to contrasted architectural models can be found in close association (Ashton 1978). In part this is presumably because some trees are adapted to grow in the understory of the forest, i.e., in the shade of other trees. This may be the status of cocoa. Its sympodial trunk form (Nozeran's model, Fig. 1) may allow it to take advantage of small, irregular openings in the canopy above. On the other hand, the crown form of *T. catappa*, a tree of sunny, open sites, seems adapted to maximize the interception of light within a tier and to minimize shading between tiers, which are developed at optimal distances.

The fact that reiteration is a major component in crown development also suggests that architecture alone cannot be the key to the survival of the tree in the forest in competition with individuals of its own as well as other species. The forces working against this survival are highly unpredictable, and thus opportunistic as well as deterministic processes play a role. Much of the refinement of crown development depends on the ability of the tree to control shoot development so that reserve buds are produced. Progressive evolution of tree form in geological time may, then, be related to progressive refinement of the reiterative process. The features to which I have drawn attention demonstrate the remarkable organizational ability of modern trees, which in turn has produced the tremendous complexity of the species-rich tropical forest.

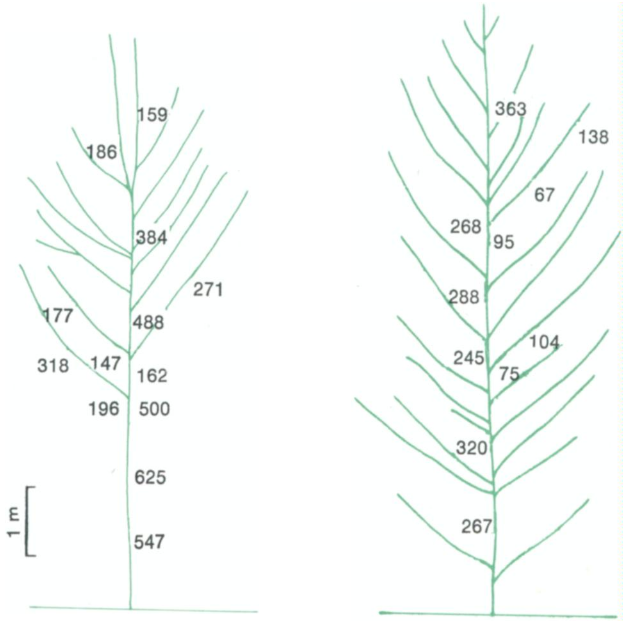


Figure 8. Measurements of conductivity values in a birch, *Betula papyrifera* (*left*), and a poplar, *Populus grandidentata* (*right*), show that in general conductivity is greatest in the trunk, particularly the lower part, and lower in the branches, with the point at which the branch joins the trunk being a region of hydraulic constriction. The experiments were carried out by allowing a dilute solution of potassium chloride to flow by gravity through detached segments of various parts of the tree. The values shown for each level represent microliters per hour of the solution conducted per gram of leaves above the segment of the system being tested. (After Zimmermann 1978a.)

Attempts to define the elusive biological property of tree form have resulted in remarkable advances at the empirical, theoretical, and experimental levels in the last decade. As a biological class, trees are cosmopolitan in their distribution, so it seems appropriate that a cosmopolitan approach has been beneficial in increasing our understanding. Similarly, trees are highly integrated organisms, and it is also appropriate that studies of apparently unrelated aspects, when integrated, have revealed fundamental biological processes. Our appreciation of why trees are such successful organisms is still quite imperfect, but the findings described here show that major breakthroughs have been achieved by quite elementary approaches. In spite of its long history as a discipline, plant morphology is currently a much neglected area of inquiry. The existence of these breakthroughs augurs well for a revitalization of morphological research.

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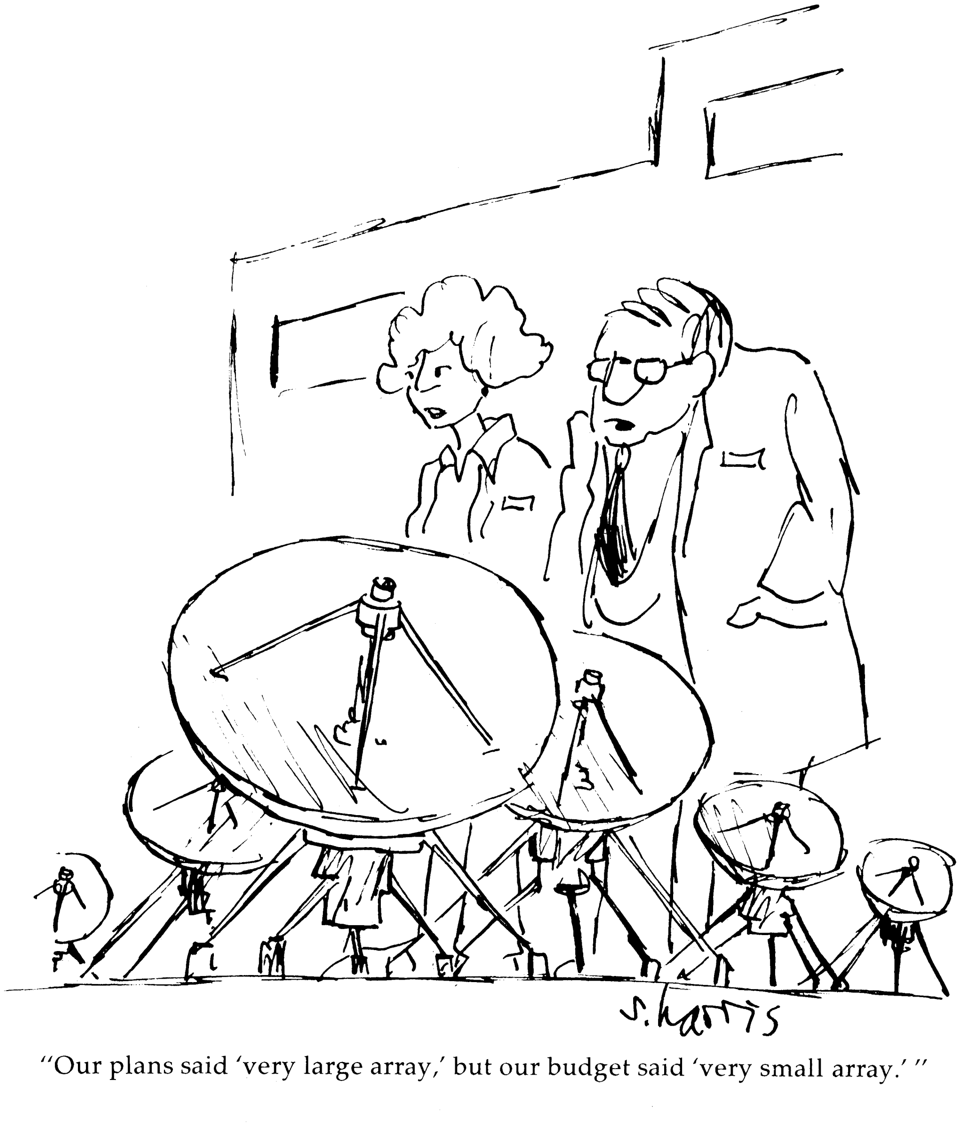

"Our plans said 'very large array,' but our budget said 'very small array.' "