

BOOK REVIEW

Tropical trees and forests. If any biologist did not read Hallé and Oldeman's work on the architecture and dynamics of growth of tropical trees or Oldeman's essay on the architecture of the Guianan forest, they now have no excuse (barring poverty, or, less probably, the inaccessibility of a library). *Tropical trees and forests**, subtitled *an architectural analysis*, is, however, more than these two books combined, and includes examples from temperate species and forests which suggest the wider application of the ideas discussed. Some points raised are treated in more detail in the recent *Tropical trees as living systems*, edited by P. B. Tomlinson & M. H. Zimmermann, which is also recommended reading.

The first two chapters include discussion of features like orthotropy, modular construction, etc., many of which are later used to characterize models. It is rightly emphasized that little is known about these characters, especially in tropical plants, and that this makes definitions difficult. Some of the many problems suggested need little more than patience and careful observation to solve, but it is a sad commentary on our knowledge that such basic questions can still be asked.

The next section deals with inherited tree architecture, "the visible, morphological expression of the genetic blueprint of a tree at any one time" (p. 74: elsewhere no time restriction is mentioned). This is done by describing models, "the growth programme that determines the successive architectural phases" (p. 75). The authors state that organizational diversity is greatest in the tropics, yet is not a continuum, and is less likely to be disturbed by exogenous, environmental factors in the understorey of the forest, and so is more accessible to the observer. The models are keyed out and described in detail; a section on the "strategy" of the model is usually added. The final sections of this part deal with vines, the connection between the architecture of trees and that of herbs, and fossil trees. The temptation to name new models has largely been resisted, although the variation within models like those of Troll and Tomlinson, and even Stone and Schoute, seem to be in characteristics that elsewhere define separate models.

The chapter on opportunistic architecture centres on reiteration, the modification of the tree's architecture not inherent in the definition of the model which results from environmental stimuli. This is important, since the shape of many mature trees is the result of reiteration superimposed on the basic architecture. Energetics and other aspects of the shape and size of crown and trunk are mentioned. The section on "strategy" treats a tree as a population of meristems. Trees of the future, present and past are defined and discussed. Although the tree is considered more from the point of view of its physiognomy and throughout its life cycle, the last section, curiously titled "a note on floristics", adopts a less flexible attitude.

The analysis of forest architecture begins with undisturbed forest, which is treated as horizontal sets of trees of the present (abundantly reiterated trees); the gradients of light, meristems, and humidity through the canopy are described. Discussion of the colonisation of gaps emphasises gaps of rather large size; colonisation proceeds through a series of homeostatic phases, each characterised by a set of trees of the present.

This outline does no justice to the diversity of topics covered. One can no longer consider a tree as a trunk, bundle of branches, and a rather larger bundle of twigs; as the authors happily put it, clouds of leaves, flowers and fruits, etc., do not hang in the air, but are parts of an organism. By examining the plant throughout its growth, they have clarified the action of some of the basic growth processes and shown that the way to understand pattern is through an appreciation of the process that produces it.

However, certain aspects of the argument, or lack of it, seem unsatisfactory, especially those concerning model delimitation and recognition, and these also affect other parts of the book. One can ask how the idea of tree growth conforming to a limited number of models might help us. Do models communicate the characters used to describe them? Do they show correlations with ecological or taxonomic patterns? Can concepts of tree architecture satisfactorily be integrated with ideas of forest growth?

To a considerable extent, of course, the answer to the first question determines the answers to the others, and I have had problems teaching tree architecture due to a number of interrelated reasons. The definitions of the characteristics used to recognize models are unsatisfactory and in some cases simply do not work; the problem is increased by

* *Tropical trees and forests* by F. Hallé, R. A. A. Oldeman and P. B. Tomlinson. Springer-Verlag, Berlin, Heidelberg, and New York. 1978. xvii + 441 pages. \$65.00 U.S.

their inconsistent application and by the all-too-brief discussion on the selection of these characters. The models themselves are delimited by a process of "definition" rather than "typification"; the former seems very typological in operation (p. 76). The definition of architecture encompasses everything from germination to death of the plant, whilst the model, in a canopy tree at least, may ignore both the sapling stage and the reaction of the plant to the conditions at the canopy surface. Hence to discuss the "strategy" of any but the simplest models seems unwise, the more so since little is known about the biology of the plants being discussed. The small numbers of the models which are thought to attest to their biological reality are as much, if not more, a reflection of the fact that many classes cannot be produced from a small number of two-state characters. Finally, it is clear that opportunistic and inherited tree architecture cannot easily be separated, perhaps especially in shrubby plants.

Apart from problems of character definition, the characters are too few to communicate more than a vague outline of the plant, and one must go beyond the characters used. Size *per se* may be architecturally unimportant, but it affects where a plant can grow. Some plants with compound leaves could biologically be considered as belonging to models with plagiotropic branches, although they are not placed in them (see the discussion on p. 210); conversely, one might question the wisdom of placing fossil trees, or even cycads, in models since it is difficult to homologise their organs with those of angiosperms. We know so little about what is adaptive, and when, that to focus on one stage may not tell us much. The crown shape of some taxa which reiterate is quite different from that of the unreiterated phase, and there may also be a prolonged juvenile stage, which may even be quite different from the model to which the flowering tree belongs (see the comments on *Syringa*, also the discussion on p. 614 in Tomlinson & Zimmermann's book). The authors are wise to avoid the physiognomic approach at first, but they oversimplify, and their efforts to redress this are not entirely successful. Both how the plant reacts to its environment and how it is constructed are important, and a system that takes only one of these, and that only partly, into account may well have serious limitations.

Some of these problems affect later sections of the book, since the recognition of trees of the past, present and future is connected with the recognition of their architecture. However, a number of points raised are thought-provoking, such as the correlation between the way in which conifers grow and their limited success, buttressing as being dependent on reiteration, the infrequency of reiteration in pioneer trees, and the idea that some forest giants are relics of an earlier forest phase. If reiteration seems to pervade these later pages, it is quite appropriate, since the circumstances under which reiteration takes place affect the success of the individual and the species.

The book is well produced, albeit lamentably expensive. The writing is generally clear, although somewhat repetitive owing to the organization of the book. There are separate indexes to subject and species, and a glossary; some entries in the glossary, e.g., biotype, epitrophy, are not indexed. Misprints are few.

In summary, Hallé, Oldeman, and Tomlinson's book is a useful contribution to the study of tree growth. I, for one, will never look at a tree or even an herbarium specimen in the same way again, and there is much of importance, both for systematists and ecologists, in the development of their ideas. In a way, however, the book is before its time, and will be improved by a stronger foundation; we may have to abandon the current approach to architectural models, or at least change it. The authors will be richly rewarded if their book stimulates these basic observations.

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