SIZE-DENSITY RELATIONS IN TROPICAL FORESTS: A ROLE FOR RESEARCH

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Textbooks on silviculture refer to two key principles: size-density relations and growth-growing stock relations (Daniel *et al.* 1979, Smith 1997). Langsaeter's curve (from Langsaeter 1941, in Daniel *et al.* 1979, Jack & Long 1996) illustrates the trade-off between individual tree growth (size-density) and stand growth (growing stock), or between annual growth increment and total cubic-foot volume stocking. According to silvicultural theory, individual tree height and height growth are relatively unaffected by density, but tree diameter growth decreases with increasing density for both intraspecific and interspecific competition (see Knowe and Hibbs 1995 for review). Silvicultural systems are based on these assumptions (Jack & Long 1996), yet there is considerable debate about them, particularly the relations between size and density (e.g. Weller 1987, Lonsdale 1990).

Theoretically, an upper limit, or maximum density, bounds the number of plants of a specific mean size that can live in any given area (Harper 1977). This relation between maximum average size and maximum density is linear when plotted on a log-log scale and is referred to as the "self-thinning rule." A generalised form of the self-thinning rule is:

$$\ln B = C - X \ln \text{density} \qquad \text{(equation 1)}$$

where
B = measure of average tree size,
C and X = constants and
density = stocking density.

Yoda *et al.* (1963) calculated a value of - 1.5 for the slope, X, when B was equal to total aboveground biomass of the average individual in a population (this form of equation 1 is known as the - 3/2 power law of self-thinning). The size of the average individual could be expressed, for example, by diameter, weight or volume. Diameter is commonly used in forestry because it is easy to measure and because early research in temperate forests established a relation among diameter, density and volume (Reineke 1933). The slope of the self-thinning line varies with parameters of different sizes (Jack & Long 1996), yet the upper limit has long been assumed independent of site quality and species (Hibbs 1987). This assumption of independence is fundamental to silviculture. Recent research has questioned the validity of this and related assumptions: if, for example, maximum density differs among species, if it is independent of site (Sterba 1987, DeBell *et al.* 1989), and if it also applies in mixed species stands (Puettmann *et al.* 1992).

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Evidence now suggests that the slope of equation 1 differs among–but not within–species and that the intercept also differs among species. Such variation in the slope and intercept of the self-thinning line may be random, or it may be systematic and indicate that, biologically, different species use space differently (Zeide 1991). For example, the slope of the self-thinning line could be a function of the volume that a tree occupies at a given stocking density and the way in which photosynthetic efficiency changes with available resources. Studies that investigate a biological basis for slope and intercept variation have focused on effects associated with shade tolerance (Harper 1977, Lonsdale 1990) and with analysis of plant parts such as stems and branches (White & Harper 1970) rather than whole tree analysis.

The slope and intercept values influence the placement and interpretation of the self-thinning line. The variation reported for these values has raised questions about the validity and application of the maximum density concept. Indeed, Weller (1987) rejected the subjective nature of maximum density estimates and concluded that it is wrong to call the -3/2 self-thinning line a "rule" or "law" because the slope is not consistent for both interspecific and intraspecific relations. Responses to this analysis noted pseudoreplication in Weller's (1987) statistical analyses (Lonsdale 1990) and argued that variations in the self-thinning line should provide a basis for further investigation (and refinement) rather than for rejection of the concept. Subsequent research has focused on identifying patterns in observed variation (Jack & Long 1996), on correcting flaws in statistical analyses (Sterba & Monserud 1993) and on designing experiments to investigate interspecific and intraspecific competition-density relations (Cole & Newton 1987, Hummel 2000).

The self-thinning rule is being refined rather than rejected. Key questions about size-density relations remain: does the upper limit of the self-thinning line describe a maximum density for interspecific populations (Lonsdale 1990), for single species undergoing density-dependent mortality (the focus of Yoda *et al.* 1963), or does it instead illustrate the growth trajectory of an individual stand during stand development (Jack & Long 1996)? To what extent does observed variation in slope and intercept occur within a species? What are the silvicultural implications of variation? As the debate continues about how to best fit and interpret the self-thinning line, data sets to be used should include forests of different latitudes and biomass measures for whole plants rather than just aboveground stems.

An understanding of how individual tree species responds to density is essential for forest management. One way in which research has extended the principle of size-density relations to forest management is through the development of relative density indices (e.g. Drew & Flewelling 1979). These indices seek to avoid the subjectivity and site-dependent nature of absolute measures of density (e.g. trees per unit area) and instead use mean size parameters such as quadratic mean diameter (see Jack & Long 1996 for a summary of commonly used relative density indices). The indices, based on theories of self-thinning populations and forest production (Newton 1997), have been constructed for dozens of temperate species in Japan and North America (see lists in Jack & Long 1996, Newton 1997) and a handful of tropical and boreal ones (e.g. Hummel 1997, Kumar *et al.* 1995, Newton 1997). Such diagrams illustrate volume and diameters associated with different levels of trees per area and help managers recognise how a stand is stocked relative to a maximum density. Thinning schedules can then be designed to achieve desired objectives, such as timber production or habitat structure, e.g. for elk (*Cervus elaphus*) (Smith & Long 1987, McTague & Patton 1989) and martens (*Martus* sp.) (Sturdevant *et al.* 1996). Newton (1997) reviewed the historical development and utility of stand density management diagrams and provides a list of useful references.

Imagine a simple matrix of stand conditions, ranging from single-species to mixed-species with no single dominant and from low to high density. It may be appropriate to add a third dimension, perhaps latitude or soil characteristics (Figure 1). The majority of previous research on size-density relations has been in the temperate, single-species, high-density cell. However, studies in other cells are extending results of the single-species work, thus raising questions for further research. This matrix can be a framework for organising and integrating the results of research on size-density relations. Much is known about the response of individual tree growth to variable levels of tree density in even-aged stands of temperate forest trees. A task now is to use this information to design experiments that investigate how the general response differs at different latitudes and in mixed-species forests. One place to start is with essentially even-aged single-species stands of tropical trees that fit the assumptions of temperate mensurational methods. The difficulties of obtaining age estimates could be addressed, for example, by working in plantations with a known establishment date (e.g. Kumar *et al.* 1995) or by selecting trees that exhibit seasonal growth rings (e.g. Hummel 1997).

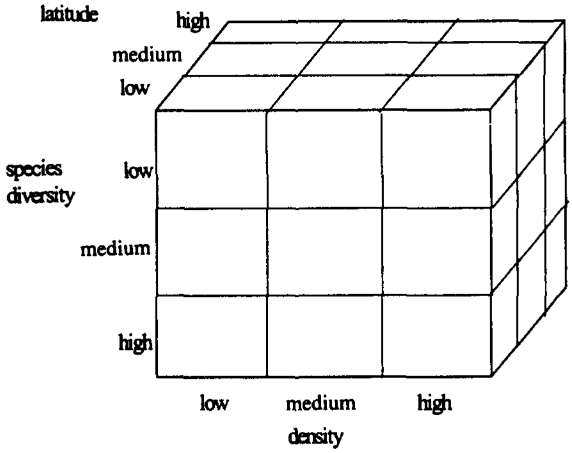

Figure 1 A conceptual framework for synthesising silvicultural research

This framework suggests that results generated from decades of studies in temperate forests can be used as hypotheses for studies in tropical and boreal forests. The implications of extending size-density theory to, for example, tropical trees encompass more than species-specific management. Combined with the difficulties of obtaining height measurements in tropical forests, a lack of height-diameter equations has led to growth models that use only diameter as a predictive variable (e.g. Condit *et al.* 1993). Vanclay (1995) provides a detailed and useful summary of the approaches used to model growth in tropical forests and concedes that height measurements are so "difficult and inaccurate" as to be unsuitable for prediction. Diameter is only one dimension of growth, however, and research that relates diameter and height over a range of densities would clarify how biomass in low-latitude forests changes over time. As the simpler cases are clarified, complexity could be increased by moving from single-species, even-aged stands to mixed-species, multi-aged stands. This will necessarily involve adapting or developing experimental methods appropriate to the system of study. For example, crown-competition methods or leaf area indices may have the potential of measuring the density of uneven-aged stands (Daniel *et al.* 1979) or tropical species (Morataya & Galloway 1998) more reliably than the basal-area methods now in use.

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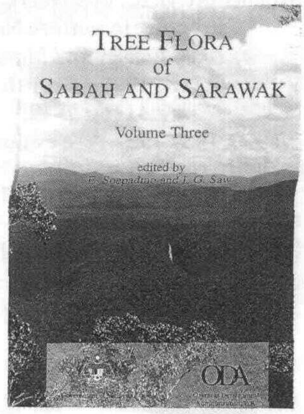
BOOK REVIEW

SOEPADMO, E. & SAW, L. G. 2000. **Tree Flora of Sabah and Sarawak. Volume III.** Forest Research Institute Malaysia (FRIM), Sabah Forestry Department, Malaysia and Sarawak Forestry Department, Malaysia. xvi+511 pp. US$100. ISBN 983-2181-06-2



Volume I of the *Tree Flora of Sabah and Sarawak* describes the background and objectives to The Tree Flora of Sabah and Sarawak Project. The objectives include documenting and updating the taxonomic status of the native trees of Sabah and Sarawak (Malaysia's two largest states situated in north and western Borneo), and publishing within 10 years eight volumes to describe this flora. Further objectives are to upgrade Malaysian capability and expertise in plant taxonomic research and strengthen the management capability of Malaysian herbaria and their data bases. This project was launched in November 1991.

Volume I (published 1995) contains three fascinating introductory chapters on the background to the project, a history of botanical collecting in Borneo, and the biogeography and ecology of the tree flora. Thirty-one plant families are covered, most of which contain a rather small number of tree species, with Burseraceae and Rutaceae the largest families. Volume II (published 1996) covers 23 more families, again with only two large groups, Anacardiaceae and Sapindaceae.

Volume III appeared in 2000. It covers just three large families (Fagaceae, Moraceae and Myristicaceae) and the subfamily Caesalpinioideae (Leguminosae). Coverage of these particular families is significant for those interested in the flora and forest of Borneo. Fagaceae is a common family in Borneo's hill and lower montane forests (100 species are described in volume III), while Myristicaceae accounts for a rather high proportion of understorey trees in most Borneo dipterocarp forests (110 species are described in volume III). The inclusion of Moraceae is also particularly welcome. Seventy species of tree *Ficus* are described, while about 75 species of stranglers, climbers and epiphytes are included in an excellent key based on vegetative characters.

Following the format of the previous volumes, for each family there is an introductory description along with notes on the family distribution, ecology, uses and taxonomy. For each family there are keys to the genera, and for each genus keys to the species. For each species described there are concise notes on major references, derivation of the genus and species name and typification, followed by detailed botanical description with notes on distribution and ecology. Vernacular names, notes on taxonomic controversies and uses of the trees are provided for some species.

The quality of Volume III in terms of content and presentation equals that of the earlier volumes, and all three fulfil admirably the original intention of this project. The number of line drawings has declined from 98 in Volume I to 87 in Volume II, to 63 in Volume III, presumably reflecting the decreasing numbers of families in each volume. In general, format and style are consistent throughout all the volumes. A slight inconsistency which I noted is that the Distribution section for most species refers only to 'Kalimantan' (the Indonesian part of Borneo, which encompasses about 70% of the island) while for a few species there is somewhat greater precision as to which parts of Kalimantan. In view of the purpose of this project I cannot fault the authors and editors but, as a user based in Kalimantan, a little more detail where possible on Borneo-wide distribution would be welcome.

Volume III contains a Dedication by the editors to K. M. Kochummen who died in March 1999 and who was Malaysia's most experienced forest botanist. The dedication includes a list of 53 publications authored and co-authored by Kochummen, who was senior botanist to the Tree Flora of Sabah and Sarawak with a special task of revising large and difficult families. Kochummen was senior author for the treatment of Moraceae.

The Foreword to Volume III (by the Director-General of the Forest Research Institute Malaysia and the directors of the Sabah and Sarawak forestry departments) and Acknowledgements both note that publication of this volume was made possible by financial support from the Malaysian Government, the Malaysian Forestry Research and Development Board, and the Overseas Development Administration of the United Kingdom. I hope very much that funding limitations will not be a constraint to continuation of the Tree Flora of Sabah and Sarawak Project.

I rate this project as one of the most significant in the Southeast Asian region in relation to conservation of rain forest biodiversity. Most tropical rain forest will be lost. If we wish to save some of it, we should devote effort to identifying and arguing for preservation of specific areas, which together capture most of the original species diversity of the region. To argue for a good selection of specific areas (both protected areas and timber production forests) we first need to know what exists in as many areas as possible. I believe that tree species composition is a good indicator of both biological endemism and diversity in a particular forest area. Describing and evaluating tree species composition requires, at minimum, an experienced botanist, or a keen biologist or ecologist armed with high quality books. Even now, there are perhaps only 25 of so people in the world who can go into any bit of forest in Borneo and immediately name to genus level the first five trees that they see. In short, projects which help to produce more good botanist and comprehensive tree identification aids are a prerequisite for identifying focal areas of high biological diversity.

The four volumes of *Tree Flora of Malaya* (Longman, 1972–1989) remain invaluable, but there are so many Bornean taxa absent from Malaya, and quite a few revisions of classification and naming. *The Manual of the Larger and More Important Non-Dipterocarp Trees of Central Kalimantan Indonesia* (Forest Research Institute Samarinda, Indonesia/ODA, 1999) provides a welcome addition for Borneo island, but inevitably leaves so many gaps. A comprehensive tree flora of Borneo would be ideal but is clearly beyond the realm of reality.

The issues of comprehensiveness and consistent reliability are of great importance in rating the quality of tree flora books. On this basis, the Tree Flora of Sabah and Sarawak project is of extraordinarily high value. People with a sound background in botany or zoology tend to forget how careless others are in using books for plant identification. In general, foresters and other professionals in the forest conservation field have only a vague interest in tree identification. Commonly, trees will be given a name based on using any old tree-related book that happens to be at hand, or on "translating" a local name given by someone of unknown competence. Accordingly, many documents which should be of importance in managing or conserving forests, such as timber production forest management plans and environmental impact assessments, are full of nonsense.

The *Tree Flora of Sabah and Sarawak* volumes are of such a high standard and the features of their content must have gone through some serious discussion and decision-making years ago, that I hesitate to make any comments on additions that would help users such as myself. Often, the initial problem in trying to identify a Malaysian forest tree (in the absence of help from a professional botanist) is to decide the family to which the tree belongs, rather than the genus or species. I would love to have included in a future volume, a practical combined guide to identifying trees to family and genus level in the forests of Sabah and Sarawak, using features relating mainly to bark and leaves. Also, if authors know any features of particular genera or species that are helpful towards identification in the field, they should include them in the descriptions. Features relating to bark slashes (texture, colour, odour, exudate, etc.) are helpful to field-workers.

In practice, only a small number of readers are likely to make use of the *Tree Flora of Sabah and Sarawak* books for the purpose of identifying trees in their work or study area, but this does not detract from their value. They are a fine reference work for anyone whose work requires knowledge of the tree flora of Borneo. For example, people who conduct environmental impact assessments should read all the sections on "Distribution" to obtain a better picture of the regions where species endemism is likely to be high. I would like to see the Tree Flora volumes as obligatory reading in Malaysian degree courses in biological sciences. In the long run, students with potential will get more out of repeatedly browsing them than any amount of books which consist of pre-selected case studies on environment or ecology. It would also be nice to seek ways to distribute the Tree Flora to the field operations of logging companies, which often employ one or two staff who have the potential to learn, but no source of encouragement or information.

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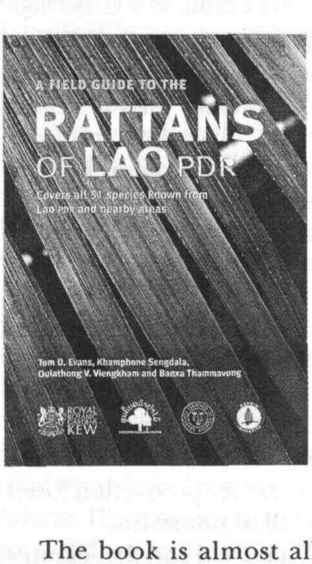

EVANS, T. D., SENGDALA, K., VIENGKHAM, O. V. & THAMMAVONG, B. 2001. **A Field Guide to the Rattans of Lao PDR.** Royal Botanic Gardens, Kew. 96 pp. £15.00. ISBN 1-84246-009-9

Rattan is important for the socio-economy of Lao People's Democratic Republic (PDR). Efforts have been devoted to further develop this industry and improve the management of the resource. These efforts are expressed by the publication of this book. The Oxford Forest Institute, the Royal Botanic Gardens at Kew, and the National Agriculture and Forestry Research Institute of Lao PDR produced the book collaboratively through a project "Diversity and Sustainable Use of Rattans in Lao PDR". The Darwin Initiative for the Survival of Species funded the project.

The book is almost all that one needs to know about rattans in Lao PDR. The colourful book was printed using high quality paper. The small format of the book makes it easy to carry and convenient to use in the field. The content was carefully organised and arranged to minimise complications and thus making this book a precious tool even for those who do not have any knowledge on rattan.

The book gives the background on the structure of rattans, general information on the ecology, flowering, cultivation and uses, and explains some ideas and terms that one needs to know about rattan. There are field keys that guide the process of identification of unfamiliar species. One can check and compare a species with closely related species. The two-page account of individual species provides enough information for confirmation of the identity of a species. Colourful photos and simplified illustrations of rattan plants and parts are helpful to readers in the identification process.

There are 31 main species of rattan in Lao PDR. A total of 20 allied species found outside Lao or with little information are also described briefly. During the research of the book eight species were discovered: four species from the genus *Calamus* were named, while four other species (two each from *Calamus* and *Daemonorops*) are yet to be named. One of the newly named species is *C. laoensis*, a large-diameter species known from central Lao. Another species endemic to Lao is the short-stemmed species *C. harmandii*, only found in south Lao. Species that are widely distributed are *C. viminalis*, *C. palustris* and *D. jenkinsiana*. Commercially important species are *C. solitarius*, *C. gracilis*, *C. tetradactylus* (all small-diameter canes) and *C. poilanei* (large-diameter cane). *Calamus tenuis* is the main species planted for commercial shoot production.

The handbook is superb for those who need to identify rattans for forestry, agroforestry, agriculture, conservation or for scientific purposes. It is written in a straightforward manner with guidelines suitable for a layman. It comes in English and Lao, to cater the Laotian and those from neighbouring countries.

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