

## CLIMATIC PERIODICITY, PHENOLOGY, AND CAMBIUM ACTIVITY IN TROPICAL DRY FOREST TREES

by

**Rolf Borchert**

Biology Division, University of Kansas, Lawrence, KS 66045-2106, USA

### SUMMARY

The seasonal time course of vegetative phenology and cambium growth is compared for tree species from Central America and Asia growing in tropical climates with a long, severe dry season. Although the inhibition of plant growth by water stress is well established, responses to seasonal drought vary widely among such trees, and their annual development is not well synchronized by climatic seasonality. In deciduous trees growing at microsites with low soil moisture storage, phenology and cambium growth are well correlated with each other and with seasonal rainfall, and most trees have distinct annual rings. Phenology and cambium growth are progressively uncoupled from climatic seasonality in brevideciduous and evergreen trees growing at microsites with large soil water reserves which buffer trees against seasonal drought and thus may prevent the formation of distinct annual rings. There is some experimental evidence concerning the control of growth initiation in apical meristems and the cambium, but little is known about the mechanisms which arrest growth and determine qualitative changes in organ development and cambium cell differentiation.

**Key words:** Tropical trees, periodicity, climate, phenology, cambium activity.

### INTRODUCTION

Most widely held concepts concerning climatic control of tree development and of cambium activity, the basis of dendrochronology, are based on observations in temperate climates, where seasonal variation in temperature constitutes the principal climatic driving variable. In contrast, in tropical climates with a long and severe dry season, rainfall seasonality constitutes the primary climatic determinant of tree phenology. The effects of temperature vs. rainfall seasonality will be therefore compared.

## CLIMATE AND SEASONAL DEVELOPMENT OF BROAD-LEAVED TREES

*Cold-temperate climates* (Fig. 1A)

Each cycle of seasonal development starts with shoot growth and flowering and ends with leaf shedding. Cambium activity is triggered by bud break in spring and ends prior to leaf shedding in fall. Consecutive cycles are separated by rest periods imposed by winter cold. Phenological changes are highly correlated with environmental changes (temperature, photoperiod). Because of strong climatic control, the phenology of all species in a forest is highly synchronous and peaks of phenophases are narrow.

*Control of tree development by tree water status* (Fig. 2)

All processes involving cell expansion, such as shoot growth, flowering, and cambium activity are well known to be strongly inhibited by water stress (Borchert 1994a, b), which also enhances leaf shedding. Tree water status thus constitutes the principal physiological driving variable controlling phenology and cambium activity in seasonally dry tropical forests (Fig. 2 left). Tree water status, in turn, is a function of the balance between water absorption by roots and transpirational water loss (Fig. 2 center), both of which depend on a variety of organismic variables and environmental inputs (Fig. 2 right). Rainfall, the principal climatic variable in tropical dry forests, constitutes only one among many variables that determine tree water status and thus affects phenology and cambium activity only indirectly. It remains to be established whether good correlations between climatic input and cambium activity, as sought in dendrochronology (Fig. 2 bottom), are common among trees of seasonally dry forests.

*Phenology in seasonally dry tropical forests* (Fig. 1B, C)

Both monsoon forests and neotropical dry forests are characterized by a long, severe dry season. In contrast to temperate forests, peaks of phenophases are broad, and

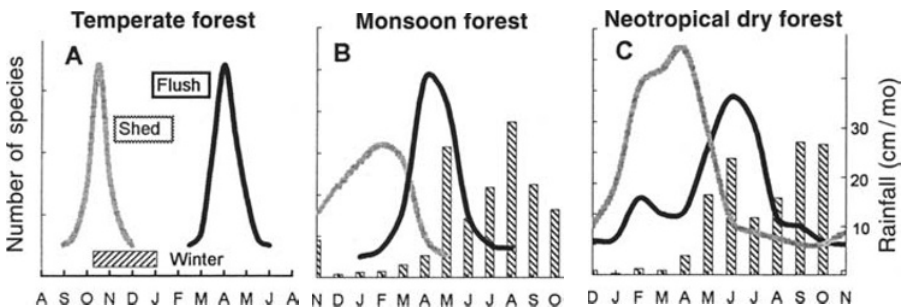


Fig. 1. Phenology of shoot growth (flushing) and leaf shedding of broad-leaved trees in a cold-temperate forest (A) and two tropical forests with a long and severe dry season: B: monsoon forest in India (Troup 1921); C: dry semideciduous forest in Costa Rica (Frankie et al. 1974).

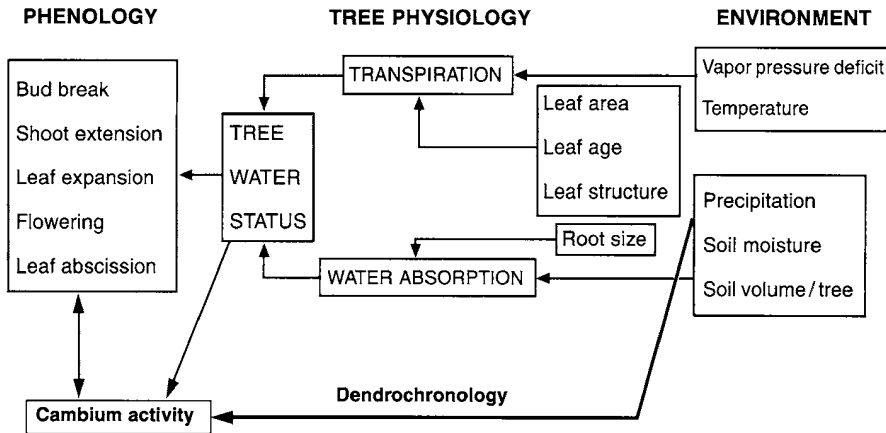


Fig. 2. Causal relations between environmental inputs (right), tree water status and its organismic determinants (center) and seasonal development in tropical dry forest trees (phenology and cambium activity, left); redrawn from Borchert (1991).

leaf fall and flushing are not separated by seasonal drought. Based on the known effects of seasonal water stress on tree phenology (Fig. 2), leaves should be shed during the early dry season, and flushing and flowering should occur after the onset of the rainy season. Actually, a broad peak of leaf shedding extends long into the dry season, i. e., many trees retain their leaves for months after the last rainfall. In clear contradiction to predictions, most tree species in monsoon forests flush during the dry season, months before the monsoon rains (Fig. 1B; Thailand: Rundel & Boonpragob 1995: Fig. 5.7) and flushing is strongly asynchronous. In neotropical dry forests some species flush during the dry season, most do so after the first rains (Fig. 1C).

In conclusion, temporal correlations between climate and phenology are poor in seasonally dry tropical forests. This raises the question why seasonal drought does not synchronize tree phenology as strongly as seasonal cold does in temperate trees.

#### LEAF EXCHANGE DURING THE DRY SEASON

Flushing or flowering during climatic drought contradict predictions based on ecophysiological theory. Both phenological events are always preceded by leaf shedding (Fig. 3B–E; Williams et al. 1997). This suggests that flushing is caused by leaf shedding and the resulting changes in tree water status, not by climatic inputs such as rainfall. Analysis of the temporal relations between climate, tree water status and phenology in a dry forest in Costa Rica revealed the following events after the cessation of rains in November (Borchert 1994 a, b). *Deciduous hardwood species* growing at dry upland sites with minimal soil water storage desiccate strongly before shedding their leaves (Fig. 3A; very negative stem water potential  $\psi$ ) and do not rehydrate and flush until the next rainy season. In trees with access to stored soil water the reduction

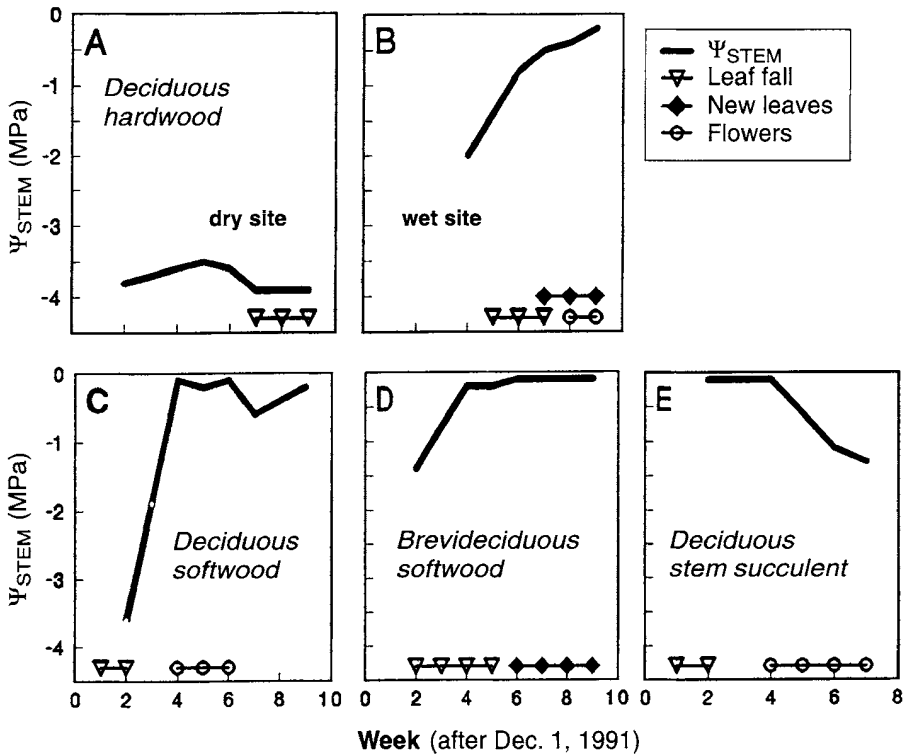


Fig. 3. Temporal relations between tree water status and phenology in several functional tree types during the early dry season in a semideciduous forest in Costa Rica (see Fig. 1C). Stem water potential ( $\Psi_{STEM}$ ), a measure of tree water status, was measured in terminal twigs using a pressure chamber; redrawn from Borchert (1998).

in transpirational water loss caused by leaf shedding always results in rehydration (Fig. 3B–D; water potential  $\psi$  increases to values near 0 MPa) and subsequent flushing or flowering. Tree species in which leaf flushing always follows leaf shedding during the dry season (leaf exchange) are referred to as *brevideciduous* or semi-deciduous (Williams et al. 1997). In contrast to ‘normal’ hardwood species (Fig. 3A), *stem-succulent tree species* growing at very dry sites remain well hydrated during the dry season and flower soon after leaf shedding (Fig. 3E). Similarly, the distribution of major monsoon forest types in Thailand varies with moisture availability and along altitudinal gradients in evapotranspiration stress (Rundel & Boonpragob 1995: Fig. 5.3).

Many trees of tropical dry forests are thus well buffered against the impact of seasonal climatic drought by access to water stored in the soil or in stem tissues. Stored water enables rehydration after leaf shedding and subsequent flushing or flowering during severe climatic drought (Fig. 1B, C; Borchert 1994a, b, 1998).

## CLIMATE, PHENOLOGY, AND CAMBIUM ACTIVITY

Temporal correlations between phenology and cambium activity of tropical and subtropical trees have been described earlier by Coster (1927/28) in Indonesia, Chowdhury (1939/40) in India, Fahn (1959) in Israel, and in several later studies, summarized by Iqbal (1994).

In a neotropical dry forest in Costa Rica, simultaneous observation of environmental variables (rainfall, soil moisture, evaporation), seasonal changes in girth (dendrometer bands), and phenology revealed the following causal relations in *deciduous trees* growing at dry sites (Fig. 4 left; Reich & Borchert 1984): a: the first heavy rains cause rapid rehydration of trunks (rapid increase in girth); b: trunk rehydration causes flushing; c: flushing induces resumption of cambium activity; d–f: cessation of rainfall causes a decline in soil moisture (d), stem shrinkage indicating arrest of cambium activity and tree water stress (e), and leaf shedding (f). In deciduous trees at dry sites water status, phenology, and cambium activity are thus directly determined by rainfall seasonality. The annual tree rings of such trees are likely to indicate interannual variation in rainfall.

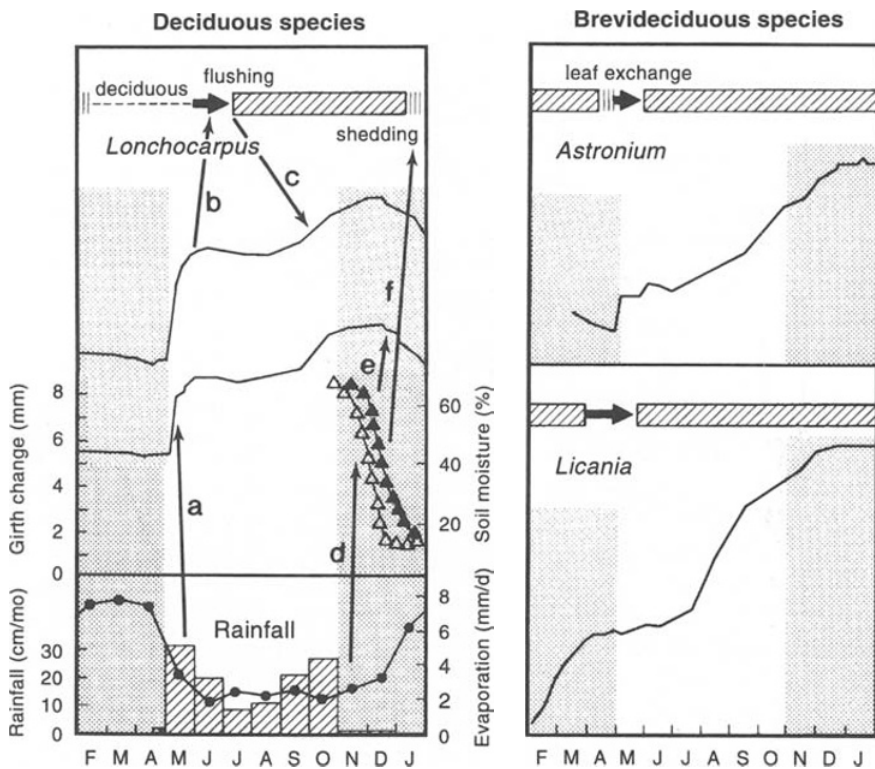


Fig. 4. Temporal relations between climate (rainfall, evaporation), soil moisture, phenology and growth in girth (measured using dendrometer bands) in a deciduous and two brevideciduous trees of a semideciduous tropical forest in Costa Rica (see Fig. 1C). For explanation see text; redrawn from Reich & Borchert (1984).

*Brevideciduous species* (Fig. 4 right) are confined to microsites with adequate soil water availability (Borchert 1994a; Nepstad et al. 1994). They experience at best moderate water stress during the dry season (no stem shrinkage; high water potential in Fig. 3D) and exchange leaves during seasonal drought. Cambium activity may continue well into the dry season (Fig. 4 *Astronium*). Phenology and cambium activity of such species are thus well buffered against seasonal drought by soil water storage, and climatic variation is unlikely to be recorded in tree rings.

#### CAMBIUM ACTIVITY AND TREE-RING FORMATION

A review of the literature (for references, see Bormann & Berlyn 1981 and Iqbal 1994) suggests that – as in temperate broad-leaved trees – cambium activity in tropical trees is generally induced by flushing and terminates some time before leaf shed-

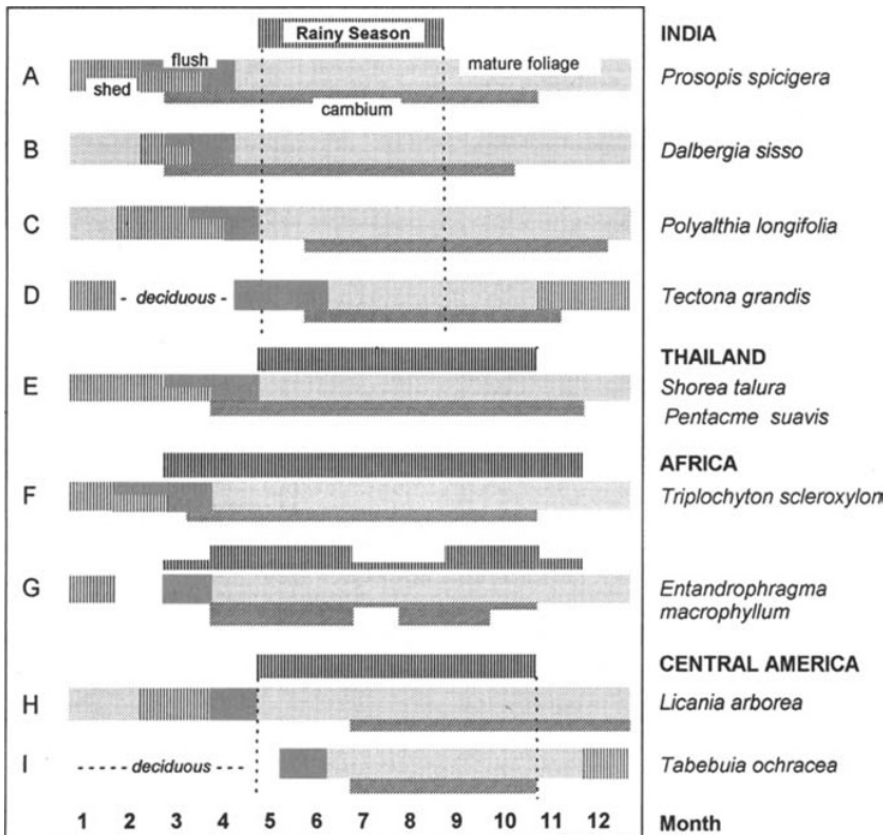


Fig. 5. Time course of phenology and cambium activity in brevideciduous and deciduous tropical species from seasonally dry forests in Asia, Africa and Central America. Data from Reich & Borchert (1984) and various sources cited in Bormann & Berlyn (1981).

ding (Fig. 5). In *brevideciduous* species both flushing and the resumption of cambium activity may occur during seasonal drought (Fig. 5A, B, E, F). Cambium activity may temporarily decline during dry spells interrupting the rainy season (Fig. 5G). In keeping with the role of tree water status in controlling plant cell growth (Fig. 2), cambium activity of teak growing in monsoon forests varies strongly with interannual rainfall variation during the low-rainfall months preceding and following the heavy monsoon rains (Pumijumnong et al. 1995).

In marked contrast to temperate trees, periodic cambium activity in tropical trees does not always result in observable periodic changes in xylem structure, which are macroscopically manifest as tree rings. A review of the literature (Bormann & Berlyn 1981; Malavassi 1995) leads to the following tentative conclusions. In *brevideciduous species* tree-ring formation is the exception and existing rings are often not annual because trees are rarely exposed to the regular and severe seasonal water stress apparently required to induce annual rings (compare Fig. 3D & 4 right). Most *deciduous hardwood species* form tree rings at dry sites (Worbes 1995), but rings may be indistinct or non-annual in trees growing at moist sites, as has been long known for teak (Geiger 1915). Many deciduous *stem succulent species* (e.g., *Bombax*, *Bursera*, etc.) form tree rings that are visible macroscopically but not microscopically (Borchert, unpubl.; Malavassi 1995; Worbes, unpubl.).

#### MODIFICATION OF PHENOLOGY AND CAMBIUM ACTIVITY BY ABNORMAL DROUGHT

The 1997 El-Niño event caused severe drought during the normal rainy season (Fig. 6 top) in the neotropical dry forest discussed above (Fig. 1C, 3, 4). Heavy rainfall in early June, causing normal flushing in deciduous species, was followed by 10 weeks of very low rainfall (Fig. 6 bottom), during which newly expanded leaves of many trees at dry sites remained severely wilted and leaf water potentials declined to values below -7 MPa (Borchert, Rivera & Hagnauer, in preparation). During the rainy September these trees shed their leaves much earlier than normal and had an abnormal second annual flush of shoot growth in October (Fig. 6d, f). Trees at moist sites and a few trees at dry sites displayed a near normal phenology, but shed their leaves earlier than normal during the regular dry season beginning in December (Fig 6c, e).

This well documented modification of normal phenology by abnormal drought in 1997, which was preceded by two abnormally wet years (> 2000 mm rainfall/year), will enable the detailed analysis of the relations between climate, phenology, and tree-ring formation and the testing of predictions such as the following which are based on the above conclusions. 1) Deciduous trees at dry sites which exchanged leaves in September 1997 (Fig. 6f), should have formed two narrow rings in 1997 preceded by two wide rings in 1995/6 (Fig. 6g, h). 2) In contrast, trees without abnormal leaf exchange in 1997 should form a single ring for this year. 3) *Brevideciduous species* and deciduous trees growing at moist sites should have less distinct ring patterns than

deciduous trees at dry sites. The planned experimental testing of these predictions will significantly enhance our understanding of the relations between climate, topography, phenology and cambium activity of tropical dry forest trees.

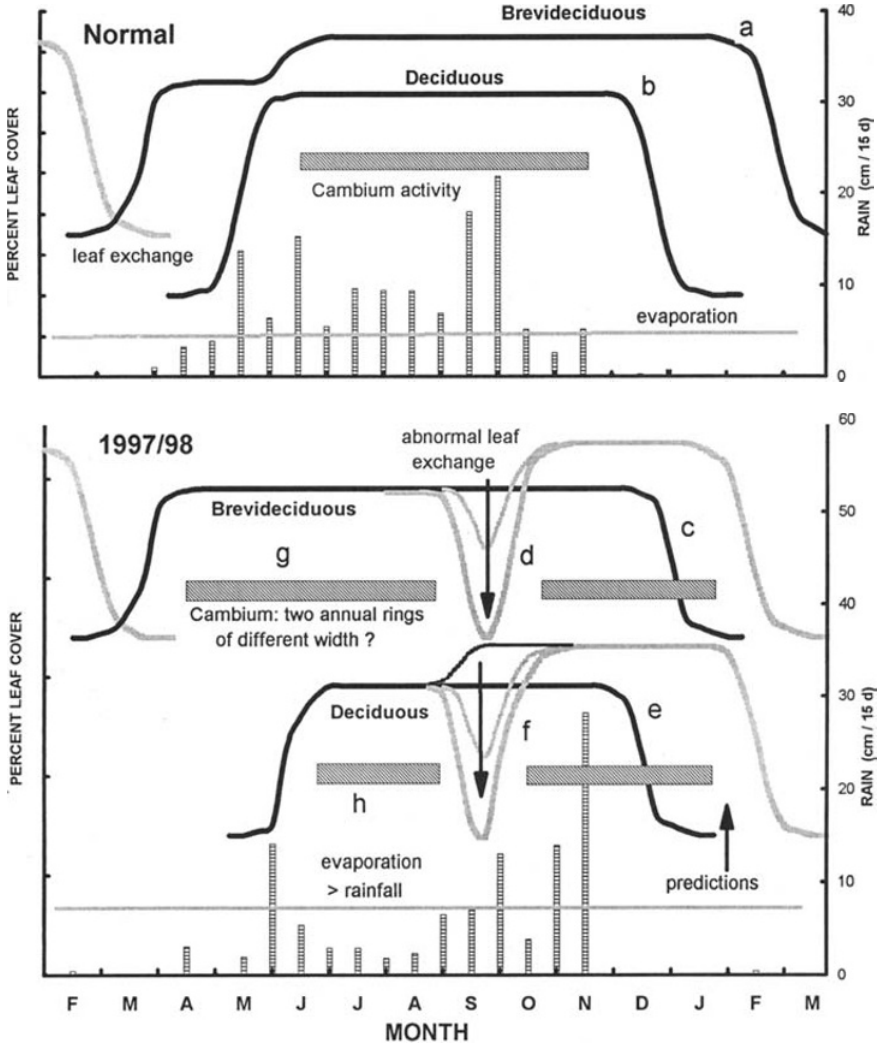


Fig. 6. Modification (c–f) of normal phenology (a, b) in deciduous and brevideciduous trees in a tropical semideciduous forest (Fig. 1C) as caused by abnormal drought induced by the 1997 El-Niño event. Postulated modification of cambium activity is also shown (g, h) (Borchert, Rivera & Hagnauer, in preparation).

ACKNOWLEDGEMENTS

Current field work described in Figure 6 is supported by the Andrew Mellon Foundation’s Program of Terrestrial Ecology.



## REFERENCES

- Borchert, R. 1991. Growth periodicity and dormancy. In: A. S. Raghavendra (ed.), *Physiology of trees*: 221–245. John Wiley, New York.
- Borchert, R. 1994a. Water storage in soil or tree stems determines phenology and distribution of tropical dry forest trees. *Ecology* 75: 1437–1449.
- Borchert, R. 1994b. Water status and development of tropical trees during seasonal drought. *Trees* 8: 115–125.
- Borchert, R. 1998. Responses of tropical trees to rainfall seasonality and its long-term changes. *Climatic Change* 39: 381–393.
- Bormann, F.H. & G. Berlyn (eds.). 1981. *Age and growth rate of tropical trees: new directions for research*. Yale University Press, New Haven.
- Chowdhury, K.A. 1939/40. The formation of growth rings in Indian trees. II/III. *Indian Forest Records (NS) Utilization* 2 (2): 41–75.
- Coster, C. 1927/28. Zur Anatomie und Physiologie der Zuwachszonen- und Jahresringbildung in den Tropen. I/II. *Ann. Jard. Bot. Buitenzorg* 37/38: 49–161; 1–114.
- Fahn, A. 1959. Xylem structure and annual rhythm of development in trees and shrubs of the desert. *Bull. Res. Council. Israel* 7D: 25–38; 122–131.
- Frankie G.W., H.G. Baker & P.A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 881–919.
- Geiger, F. 1915. Anatomische Untersuchungen über die Jahresringbildung von *Tectona grandis*. *Jahrb. Wiss. Bot.* 55: 521–607.
- Iqbal, M. 1994. Structural and operational specializations of the vascular cambium of seed plants. In: M. Iqbal (ed.), *Growth patterns in vascular plants*: 211–271. Dioscorides Press, Portland, Oregon.
- Malavassi, F. 1995. *Maderas forestales de Costa Rica*. Universidad de Costa Rica, San José, Costa Rica.
- Nepstad, D.C., C.R. de Carvalho, E.A. Davidson, P.H. Jipp, P.A. Lefebvre, G.H. Negreiros, S.E. Trumbore & S. Vieira. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372: 666–669.
- Pumijumnong, N., D. Eckstein & U. Sass. 1995. Tree-ring research on *Tectona grandis* in Northern Thailand. *IAWA J.* 16: 385–392.
- Reich, P.B. & R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *J. Ecol.* 72: 61–74.
- Rundel, P.W. & K. Boonpragob. 1995. Dry forest ecosystems of Thailand. In: S.H. Bullock, H.A. Mooney. & E. Medina (eds.), *Seasonally dry tropical forests*: 93–123. Cambridge University Press.
- Troup, R. S. 1921. *The silviculture of Indian trees*. Clarendon Press, Oxford.
- Williams, R.J., B.A. Myers, W.J. Muller, G.A. Duff & D. Eamus. 1997. Leaf phenology of woody species in a Northern Australian tropical savanna. *Ecology* 78: 2542–2558.
- Worbes, M. 1995. How to measure growth dynamics in tropical trees – A review. *IAWA J.* 16: 337–351.