THE PERIODICITY OF GROWTH IN TROPICAL TREES WITH SPECIAL REFERENCE TO DIPTEROCARPACEAE – A REVIEW

by

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SUMMARY

The periodicity of leaf change and flowering and fruiting of tropical trees is discussed. Cambial activity patterns in tropical trees are reviewed. Emphasis is put on research undertaken in South-East Asia on the most important timber tree family in that region, the Dipterocarpaceae. There is an urgent need for more information on the effects of rainfall patterns and phenological periodicity on cambial activity and ring formation in this family

Key words: Tropical trees, periodicity, phenology, dipterocarps.

INTRODUCTION

The understanding of periodicity of growth in tropical trees is an important prerequisite for the timing of silvicultural measures both in natural and plantation forests in the tropics.

A workshop on this subject was held in April 1980 in Petersham (Bormann & Berlyn 1981). The present paper reviews further research conducted in this field with emphasis being given to research conducted in South-East Asia.

PHENOLOGICAL RHYTHMS

Phenology is the study of recurrent phenomena like leaf change, flowering and fruiting which can be visually detected (Ng 1988). The phenology of meranti tembaga (*Shorea leprosula*), kapur (*Dryobalanops sumatrensis*, earlier *D. aromatica*) and chengal (*Neobalanocarpus heimii*) and species from other families in Peninsular Malaysia is discussed below.

Vertical growth

Continuous and intermittent growth dependent on species have been observed. These growth patterns occur irrespective of temperature and precipitation (Ng 1979), and may even change during the lifetime of trees.

In many dipterocarps, juvenile and mature stages can be distinguished by their crown form (Ng 1981), in which apical dominance is shown during the early years (up to

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18 m tree height). The leader shoot controls side branch development, resulting in a tapered crown. Later, the crowns become sympodial. Lateral shoots then compete with the leader and crowns become round and flat. Branches would develop their own 'crowns', a process called 'reiteration' (Hallé & Ng 1981). Ng (1981) assumes this phenomenon to be more influenced by quantity and intensity of light rather than by the age of the tree. With increasing age, leaves of some dipterocarps (e.g. kapur) become intolerant to shade.

Leaf change

In tropical trees, shoot extension may be annual, bi-annual, or irregular (Tomlinson & Longman 1980). Hill dipterocarp forests (Medway 1972) as well as lowland dipterocarp forests (Ogawa 1978; Ng & Loh 1974) in Peninsular Malaysia show two flush periods coinciding with heavy rainfalls after a dry season, namely in the months of March/April and September/October. Deciduous trees in the tropics can be found in zones with markedly seasonal climate (e.g. monsoon climate).

A common feature for trees in the humid tropics is the synchronous occurrence of leaf flush and leaf fall. For this semi-deciduous behaviour the term leaf exchange or leaf change has been coined (Coster 1927; Longman & Jenik 1974). Characteristically these trees are never truly deciduous, but always carry old and young leaves at the same time. Only a small number of tree species in the humid tropics are truly deciduous, e.g. rubberwood (*Hevea brasiliensis*). Young *Hevea* flushes several times per year; however, its leaves discolour and shed over a period of two months as soon as trees are older than 15 years (Edgar 1960). This 'wintering' period happens in Peninsular Malaysia during the months of March and April.

On the Malayan peninsula the rainfall pattern shows two peaks, namely during the months of May and October. Minima occur in January/February and in June/August. The semi-annual occurrence of flushing of several tree species ties in with this rainfall pattern (Medway 1972; Ng 1981).

Flowering

Most trees in the humid tropics show irregular flowering and fruiting (Barnard 1954; Ng & Loh 1974). This irregularity occurs within a species as well as between different species. While some species flower and fruit regularly (e.g., *Hevea brasiliensis, Acacia mangium*), some twice a year (*Durio zibethinus*) (Ng 1988), others reproduce only at longer intervals. Ridley (1901) had observed that, e.g., *Shorea leprosula* only flowers every six years, *Dryobalanops sumatrensis*, however, in shorter, more regular intervals of about two years (Ashton et al. 1988). Some species flower synchronously, i.e. the entire stand is in flower (e.g., *Neobalanocarpus heimii*).

The flowering and fruiting for one species can differ within a short distance depending on the site. Ashton et al. (1988) observed marked differences between the flowering periods for *Dryobalanops sumatrensis* over a distance of 20 km, for instance between Kepong and Kanching.

There is a distinction between sporadic and mass or gregarious flowering (Ng 1981). During sporadic flowering only some individuals of one species flower, during mass flowering nearly all individuals of one or several species in a given stand would flower. The latter was reported in Peninsular Malaysia for the years 1957, 1958, 1963, 1968, 1970, and 1976 (Ng 1981). Both flowerings might be triggered by sudden, short dry spells at the end of a prolonged rainy period, as Holttum (1940) observed in Singapore. Yap (1982) observed flowering after a rainy period in February for Kepong, Peninsular Malaysia, others reported *Dryobalanops sumatrensis* flowering in March/April (Hahn-Schilling 1987), April/May 1989 and 1991 (own observations) and May (Burgess 1972). *Shorea leprosula* was observed to flower in 1981 in Pasoh (150 km south of Kepong) during October/November (Mohd. Ghazali & Abd. Rahim 1985).

Ng (1988) thinks that the annually recurring change of cloudy, overcast to clear sky in February and with it the available light induce flowering in the Kepong area, a view which is questioned by Palmer (1979). Ashton et al. (1988) observed a close correlation between flowering and a drop of 2°C in minimum temperature for several nights. This temperature change can be a result of clear, cloudless skies after the rainy season. Ashton et al. (1988) also reported mass flowering in Peninsular Malaysia induced by a dry spell as a result of the El Niño phenomenon.

Fruiting

Weather affects the ripening of fruits. During dry spells, fruits tend to be small and of low quality, while fruits during humid periods are usually bigger and of better quality (Foxworthy 1932). In general, fruits need 3–6 months to ripen (Ng 1988). During mass flowering, first fruits fall about 18 weeks after the first flowers have appeared (Wood 1956; Chan 1980). If the fruits mature during dry weather, fruitfall is retarded. With many tropical trees, leaf change, flowering, and fruiting can occur simultaneously, as is known for *Neobalanocarpus heimii* (Barnard 1954) and observed for *Intsia palembanica*.

CAMBIAL ACTIVITY

A review of past efforts in measuring age and annual growth in tropical trees was given by Mariaux (1981). Hence, older publications are only briefly discussed. Research results from South-East Asia will be emphasized here.

There are fewer investigations on cambial growth of tropical trees than of trees from temperate climates. The earliest results were reported by Brandis in 1856 (Mariaux 1981), who studied the growth of teak (*Tectona grandis*) in India by measuring annual ring width. Chowdhury (1939) assessed the cambial activity of nine Indian tree species with the help of xylem and bark samples taken at different times throughout a year.

Paliwal and Prasad (1970) observed increased cambial activity for the months of February to May in the deciduous shisham (*Dalbergia sissoo*) collected near Delhi. *Dalbergia sissoo* was also studied by Venugopal and Krishnamurti (1987), together with *Tectona grandis, Albizzia lebbek, Terminalia crenulata, Calophyllum inophyllum, Mangifera indica* and *Morinda tinctoria.* They identified growth zones, as well as changes in starch content in the adjacent parenchymatic tissues before and after the period of cambial activity.

Cambial growth in *Swietenia macrophylla*, as well as in *Cordia alliodora* and *Prioria copaifera* in Central America has been studied by, e.g., Tschinkel (1966) and McKenzie (1972). Tomlinson and Craighead (1972) observed annual rings in a number of tropical trees from Florida. Worbes (1989) reported annual rings in trees from Venezuela.

Worbes (1985) assessed the cambial activity in various species of the families Leguminosae–Caesalpiniaceae, Bombacaceae and Euphorbiaceae from inundation forests along the Amazon river in Brazil. He showed that a period of cambial rest triggered by annual inundations is reflected in periodically returning cambial patterns (growth zones).

Considerable work in this field has been reported from West Africa. Hummel (1946) studied xylem and bark samples of *Entandophragma angolense* and *Khaya grandifolia* taken over a one-year period. Lowe (1961) worked with *Triplochiton scleroxylon*, and Bryant (1968) with *Pterocarpus angolense* from Tanzania. Amobi (1973) proved the existence of an annual growth rhythm for 11 tree species from Nigeria.

Mariaux wounded the cambia of different West African tree species over several years in order to assess their cambial activity with the application of 'Mariaux's window'. He also measured the diameter increment with the help of dendrometers. He succeeded in establishing growth zones for *Aucoumea klaineana* (Mariaux 1970), *Terminalia superba* (Mariaux 1969), and for some Meliaceae (*Entandophragma angolense, E. candollei, E. utile, E. cylindricum*, *Guarea cedrata*, as well as for the introduced *Cedrela mexicana*) (Mariaux 1977). In *Lovoa trichiloides* no growth zones could be observed (Mariaux 1977). In *Acacia raddiana*, originating from the Sahel zone growth zones occurred only at very irregular intervals (Mariaux 1975).

Geiger (1915) studied cambial growth in South-East Asian tree species (*Tectona grandis*). Coster (1927, 1928) sampled more than 200 autochthonous and introduced tree species on Java from three different climatic zones (humid tropics, semi arid, and arid tropics) during rainy and dry seasons with the help of a Pressler borer. He made phenological observations, but no dipterocarps were included.

Research on dipterocarps was first reported by Nakamura et al. (1987) applying the radiocarbon method for age determination. Shiokura (1989) studied different *Shorea* species, *Dipterocarpus* spp., *Sindora* spp., and *Palaquium* spp. from East Kalimantan, Indonesia.

Toma (pers.comm.) conducted three years of dendrometrical measurements on *Shorea leprosula*, *Dipterocarpus sublamellatus*, and *Endospermum malaccense* in the low-land dipterocarp forest of Pasoh in Peninsular Malaysia. He observed a correlation between cambial growth and rainfall. During periods of low precipitation (e.g. February/March) less xylem was built than during rainy periods.

Killmann (unpubl.) applied 'Mariaux's window' for four years (1988–1991) at twomonth intervals to eight trees each of the dipterocarps *Shorea leprosula*, *Dryobalanops sumatrensis*, and *Neobalanocarpus heimii* planted about fifty years ago in Kepong, Peninsular Malaysia, as well as to individuals of plantation-grown *Acacia mangium* and *Hevea brasiliensis*. First results are published by Sass et al. (1995a, b).

Further methods for the assessment of cambial growth in tropical trees are described by Vetter (1995) and Worbes (1995).

CONCLUSIONS

Shoot extension and flowering of trees in the humid tropics (whether seasonal or aseasonal climate) follow inherited as well as climatic patterns. Although it is still a matter of debate whether the flowering is triggered by the absence of rain during dry weather, available light, or temperature changes, there is much indication for the first factor.

While most trees in seasonal tropical climates show periodically recurring intervals of rest, which are reflected in the dormancy of the cambium and the leaf-fall behaviour, periodicity of cambial growth of trees in an aseasonal tropical environment has long been disputed. However, there are indications that even under these climatic conditions trees show rhythmic growth possibly as a function of varying amount of precipitation. More research is needed to confirm this assumption.

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