SEASONAL ACTIVITY OF THE CAMBIUM IN THE YOUNG BRANCH OF *SWIETENIA MACROPHYLLA* KING

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SARI

Keragaman musim dalam aktivitas kambium pembuluh pada *Swietenia macrophylla* King telah diteliti mulai bulan Agustus 1983 sampai dengan Juli 1984. Di bulan Agustus aktivitas tersebut lambat dan di bulan September tampak sifat-sifat dorman. Setelah bulan-bulan kering itu aktivitas kambium kembali tampak di bulan Oktober saat curah hujan tinggi. Aktivitas terus berlangsung di bulan-bulan berikutnya dan mereda di bulan Maret. Aktivitas kambium paling tinggi berlangsung di bulan April sewaktu terjadi puncak kedua dalam curah hujan di musim hujan. Aktivitas yang tinggi itu terjadi bersamaan dengan munculnya daun baru yang didahului oleh suatu periode gugur daun yang singkat. Aktivitas kambium mereda di bulan-bulan berikutnya.

ABSTRACT

Seasonal variation in the activity of the vascular cambium of *Swietenia macrophylla* King has been investigated from August 1983 to July 1984. Cambial activity is slow in August, and in September dormant features are seen. After the preceding dry months the cambium shows activity again in October when heavy rainfall occurs. The activity continues during the following months and slows down in March. The cambium is most active in April when a second peak of rainfall occurs in the rainy season. This grand activity of the cambium coincides with the emergence of a new crop of leaves which is preceded by a brief period of defoliation. Cambial activity slows down again in the following months.

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1. Introduction

It is often thought that the uniform climate in the tropics would allow continuous growth of the tree and consequently of its cambial activity. Only a few trees, however, show continuous cambial activity (Alvim, 1964. Fahn, 1977). Most trees show a sharp periodic activity of the cambium. The seasonal activity of the cambium in tropical trees has not often been investigated unlike those of temperate species, in spite of its importance in understanding tree physiology. There have been several efforts to investigate factors controlling the activity of the cambium in tropical and subtropical climates (Amobi, 1974; Paliwal and Prasad, 1975; Ghouse and Hashmi, 1983). The present work aims to study seasonal activity of the cambium in *Swietenia macrophylla* King which grows in the Bandung area and views its relationship with some climatic factors.

2. Materials and methods

Four *Swietenia macrophylla* or mahoni trees at the Bandung Institute of Technology campus, each about 15 years old and 15 meters tall, were selected for similar phenological behaviour to be used as source material. Portions of side branches in their second year of growth were collected in the morning at forthnight intervals from August 1983 to July 1984, fixed in FAA (formaline, acetic acid and ethyl alcohol), and then aspirated. Ten twigs were used at each collection date. They were later sectioned with a sliding microtome at 25–40 microns and stained with safranin and fast green (Johansen, 1940). Seasonal changes with regard to external morphology were also recorded. Climatic data were obtained from the local meteorological station in Bandung which is geographically located at 6°55″ S. latitude, 107°36″ E. longitude, and 791 m above mean sea level.

3. Observations

3.1 Cambial activity

In spite of the precautions taken to ensure uniformity of the material by selecting trees of similar phenological behaviour there were differences in growth of different branches which were reflected in the activity of the cambium.

It was found that periclinally dividing cambial cells were not always found in complete tangential layers but may occur at different times in cells within the radial series produced by the cambium. Therefore the cambial initials and their immediate derivates which have not yet expanded radially are referred as the cambial zone in this work. Figure 1 shows a 4–5 layered cambial zone in August 1983. Tangential layers of tannin filled cells in the phloem often mark

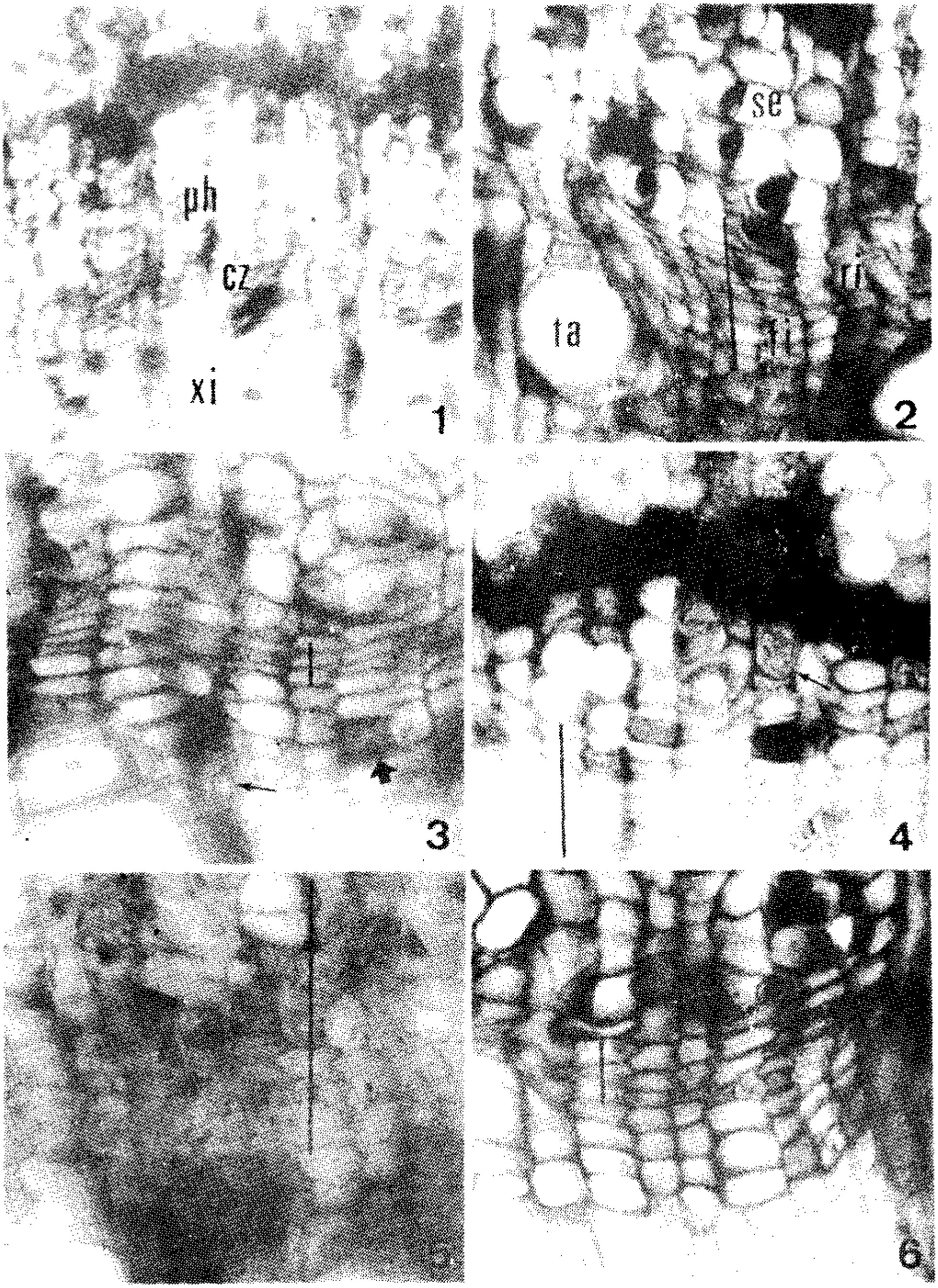

Figure 1—6 Transverse sections of the cambium of *Swietenia macrophylla.*

Figure 1 Overall view showing cambial zone (cz) in the area between phloem (ph) and xylem (xi). A tangential row of tannin filled cells is indicated by an arrow. August 1983 collection. x 200.

Figure 2 Part of figure 1 enlarged showing fusiform initial (fi), ray initial (ri), trachea (ta), and sieve element (se). The vertical line indicates width of cambial zone, as in all other figures where it appears. x 400.

Figure 3 Dormant cambium in September 1983 consisting of tangentially flattened cells with thick walls. Arrow points to a prismatic type of crystal. x 400.

Figure 4 Cell layers in the cambial zone have increased in number in December. Arrow points to druse filled cell. x 375.

Figure 5 Delicate radial walls of the cambial cells are widening radially. January collection. x 400.

Figure 6 Narrow cambial zone in March 1984 collection. x 400.

the boundary of a growth increment. Immature xylem elements are shown abutting the lignified xylem cells which constitute the diffuse porous wood. One to two layers of immature phloem cells are present at the outer side of the cambium (figure 2). In September a dormant cambium is seen consisting of 1–3 layers of tangentially flattened cells with thickened walls (figure 3). Immature vascular cells are found at both sides of the cambium. Tannin filled cells are found scattered but more pronounced in rays. Crystals of druse or prismatic type are often found, mostly in the phloem cells. Starch grains are found in the last formed lignified xylem cells. In the months that follow, the cambial zone consists of cells which are of more rectangular shape and is many layered, indicating increased activity. In December 3–7 layers of cells form the cambial zone with several of them in pairs (figure 4). Those newly formed cells will differentiate as shown in figure 5 where cells with wavy radial walls are seen due to the still inadequate rigidity of their walls (figure 5).

Starch grains in lignified xylem tend to dissolve with increased cambial activity. Crystals and tannin are found less frequently. The cambial activity slows down again in March where it shows a 3–4 cell layered zone with more layers of unlignified xylem elements (figure 6). In April, some cambium cells have swollen radially and periclinal divisions occured followed by other cells in the tangential layer of cambium which then divide more frequently producing many layers in this grand period of cambial activity (figure 7 and 8). More cells are formed to the xylem than to the phloem side. Most of the vessels of a growth increment are formed at this time. In July cambial activity has declined while earlier formed xylem elements are in the process of differentiation (figure 9). Phloem cells seem to have matured earlier. Divisions in the cambial zone concerns mostly fusiform initials while ray initials usually only lengthen radially. Periclinal division in the ray initials also occur but much less frequently. Such a division is shown in figure 10.

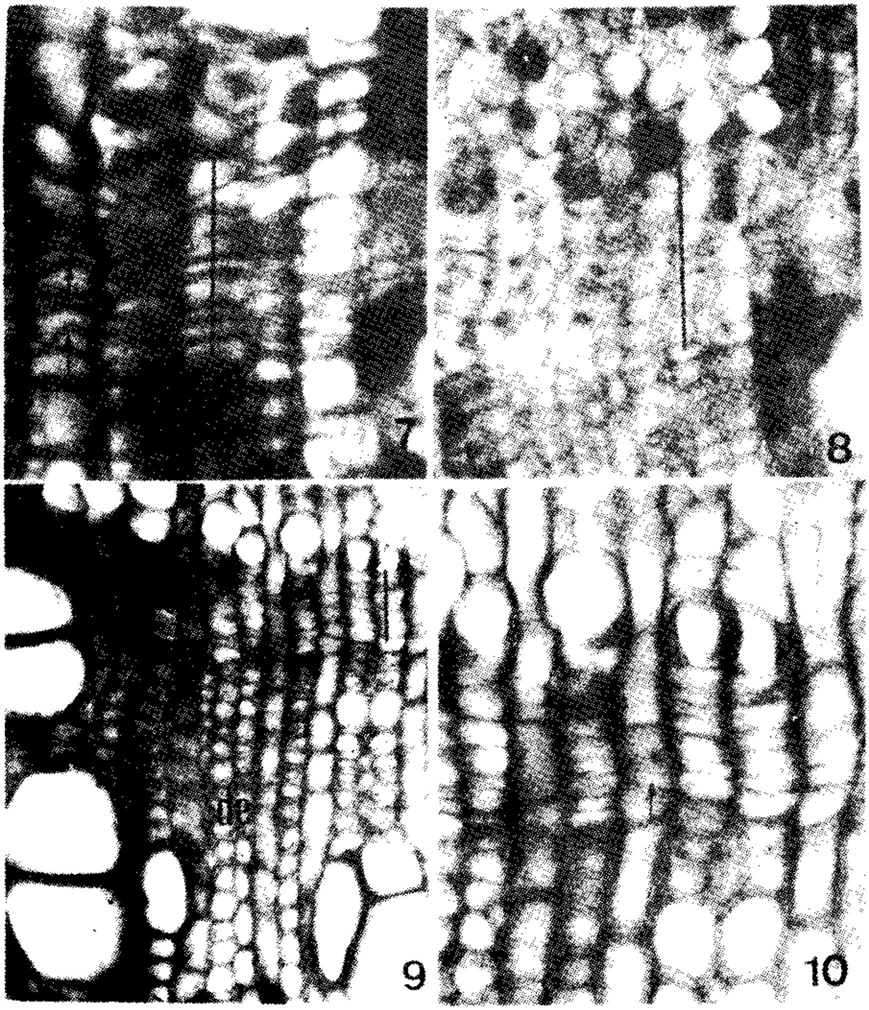

Figure 7–10 Transverse sections of the cambial zone of *Swietenia macrophylla.*
Figure 7 Active cambial zone in April 1984. Arrows point to swelling of cambial cells. x 400.
Figure 8 Radial widening of delicate cambial cells in May. x 400.
Figure 9 Declined activity of the cambium in July with a large number of differentiating elements (de) in the xylem. x 225.
Figure 10 Part of figure 9 enlarged to show dividing ray initial (arrow). x 400.

3.2 Cambial activity in relation to phenology

Swietenia macrophylla is a deciduous tree which sheds its leaves entirely or partially. In the Bandung area, during August 1983 through March 1984 the trees under observation did not form new leaves. The leaves instead became dark green and tended to droop at the end of the period. Meanwhile the shoot apex showed many bud scales covering the apical meristem resulting in a distal end with a diameter of about 8 mm. In April 1984, bud scales start to grow in height indicated by the pale yellow scale bases. Drop of the now yellowish brown coloured old leaves takes place while young leaves emerge. The new shoot axis produces a new crop of leaves and most of the extension growth of the axis is finished in May. Meanwhile the colour of the new leaves changes from red to light green and during the following months will turn dark green. Cambial activity is resumed in April after a decline in March. The grand period of cambial activity in April coincides with the formation of a new crop of leaves. The relation between cambial activity and phenology is presented in table 1.

Table 1 Relation between cambial activity and phenology

Month	Phenology	Cambial layers
August 1983	Full foliage	3 – 5
September	Full foliage	1 – 3
October	Full foliage	3 – 5
November	Full foliage	3 – 5
December	Full foliage	3 – 7
January 1984	Full foliage	3 – 5
February	Full foliage	3 – 5
March	Full foliage	3 – 4
April	Leaf fall followed by development of new leaves and flowers	8 –12
May	New leaves have reached full size	4 – 8
June	Full foliage	4 – 7
July	Full foliage	3 – 6

3.3 Cambial activity in relation to climatic factors

Rainfall during the period of investigation showed a peak in October and in April (figure 11). Relative humidity was high during those two occasions. The number of sunshine hours also showed some relationship with rainfall, being higher when rain was meagre such as in August 1983 or July 1984. The minimum temperature fluctuated around 18°C while the maximum was around 30°C with an average of about 24°C. Dormant cambium was seen in the dry September month. Resumption of activity occurred in October and the following months when rain was plentiful. Decline of cambial activity was seen in March, when rainfall was relatively less. The cambium was most active in April, coinciding with the second peak of rainfall. Thereafter cambial activity declined while the rainfall also decreased.

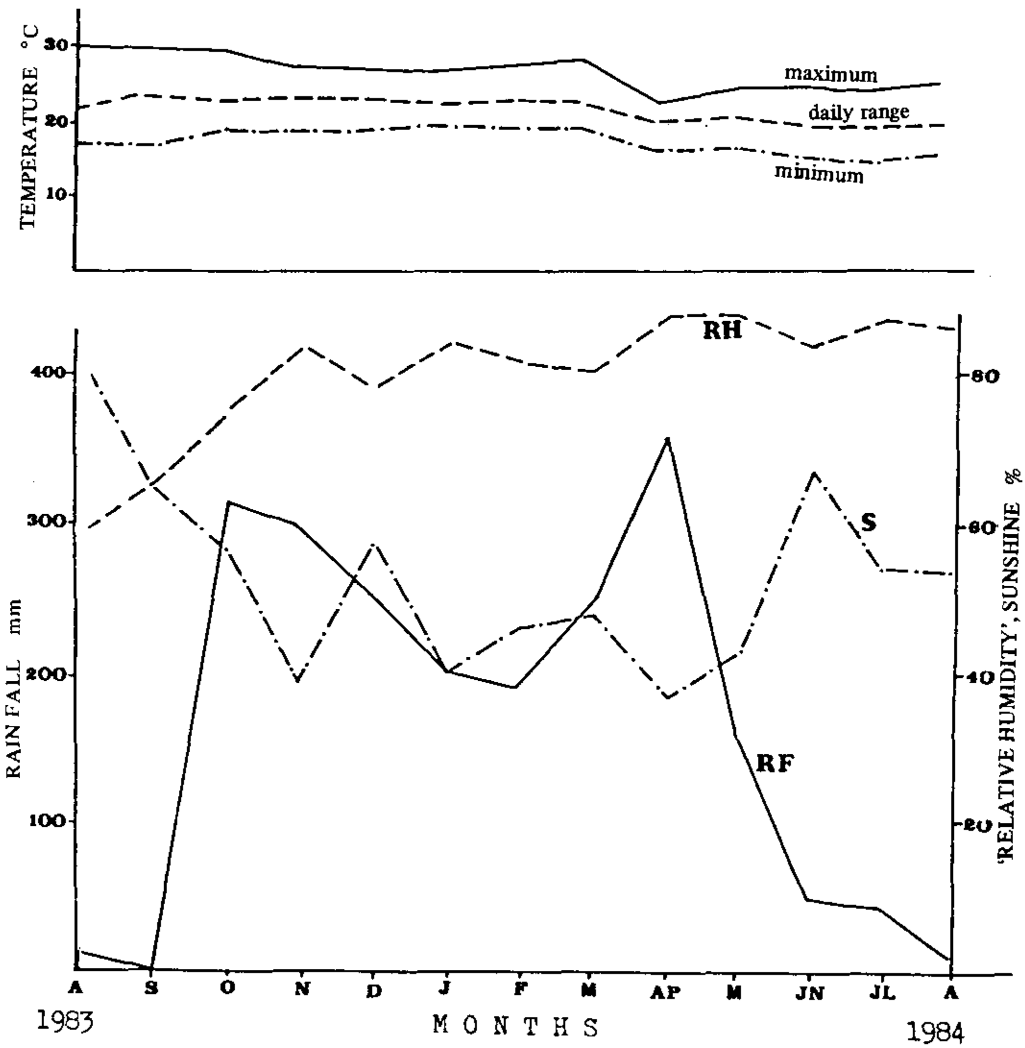

Figure 11 A graphic representation of meteorological data of Bandung from August 1983 to August 1984. Above : Temperature. Below : Rainfall (RF), Relative humidity (RH), and Duration of sunshine (S).

4. Discussion

In the nearly ideal and uniform climate of Bandung, West Java, *Swietenia macrophylla* shows a long period of cambial activity. A cambium with dormant features in September resumes activity in the following months and declines it in March before the grand active period occurs in April. A long period of activity was reported for *Psidium guajava* in Taiwan (Chou and Chiang, 1973), for *Gmelina arborea* in India (Dave and Rao, 1982), and was found to be the case in many tropical species (Philipson *et al.* 1971). Some species may have a shorter period of activity such as 5½ months for *Mimusops elengi* in India (Ghouse and Hashmi, 1983). Dormant features of the cambium such as tangentially flattened cells with relatively thicker walls as shown for *Swietenia macrophylla* in the present work has been reported also for other species. Only some cells show dense cytoplasm such as mentioned for dormant cambium (Philipson *et al.* 1971). Swelling of cells at resumed activity could be observed only in some cells in *Swietenia macrophylla* but slipping of the bark was evident. This swelling is taken as an indication of the first sign of cambium reactivation and is also found in *Polyalthia longifolia* (Ghouse and Hashmi, 1979a) and *Gmelina arborea* (Dave and Rao, 1982).

The pattern of radial growth is paralleled by the width of the cambial zone which increases and then declined according to the rate of cell production (Philipson *et al.* 1971). During the most active or grand period of cambial activity in *Swietenia macrophylla* most of the wood vessels of the increment are produced from the xylem mother cells. This was reported also for twigs of *Swietenia mahagoni* but was not the case in the trunk (Coster, 1927, 1928). Others reported that the young branch showed similar behaviour of growth as the trunk, although not with the same intensity (Dave and Rao, 1982). More studies are needed to show whether the twigs would reflect similarity of behaviour with the trunk, since using twig samples would be more feasible with regard to the tree under investigation.

It is known that the environment plays a controlling part in cambial development through the production of auxin by developing buds and leaves (Romberger, 1961). In *Swietenia macrophylla* there is a close association between emergence of new leaves and the grand activity of the cambium. Cambial activity, however, was detected as scales elongate just before the young leaves emerge while the old leaves are shedding. Reactivation of cambium at the time of leaf fall was also reported for *Dalbergia sissoo* in New Delhi (Paliwal and Prasad, 1970). On the other hand, increased cambial activity long before leaf emergence was reported for *Psidium guajava* (Chou and Chiang, 1973) while in *Mimusops elengi* the cambial activity commenced 4 weeks after new leaf emergence (Ghouse and Hashmi, 1983). Correlation of budbreak and the initiation of cambial activities was found in twigs of *Drepanocarpus lunatus* and *Ormecarpum serrucosum* (Amobi, 1974). More studies are needed before a general conclusion can be reached.

Among the climatic factors observed, it seems likely that in *Swietenia macrophylla* the peak of rainfall, in October and in the following months, influences cambial activity even though no new leaves were formed. *Gmelina arborea* also showed maximum cambial activity while new leaves were at full maturity and rainfall was high (Dave and Rao, 1982). An additional activity of cambium of *Swietenia macrophylla* after a period of moisture stress was found in the dry months of August and September 1983. This phenomenon was also reported for cacao (Alvim and Alvim, 1978). The renewed activity associated with leaf fall and emergence of new leaves which occurs in April and May 1984 for *Swietenia macrophylla* investigated here may be explained by the existence of an individual cycle of the tree and perhaps the short drier period in the rainy season in February and March 1984. It could be a trigger mechanism as for cacao (Alvim and Alvim, 1978). From casual observations on other individuals, it was noted that many trees show emergence of new leaves in October 1983 which also is the month of heavy rainfall following a dry period in the Bandung area. Such different times of flushing was also noted for *Swietenia mahagoni* in Bogor (Coster, 1927, 1928). Temperature does not seem to influence cambial activity in the material used. This was also true for *Gmelina arborea* (Dave and Rao, 1982).

In view of the discussion above, it seems likely that differences in genetic constitution and differences in the environmental condition of the individuals each by itself will influence cambial activity in *Swietenia macrophylla* aside from the availability of moisture.

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