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Seasonal Anatomy of Secondary Phloem of Teak (*Tectona grandis* L. *Verbenaceae*) Growing in Dry and Moist Deciduous Forests

By

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With 3 Figures

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Summary

RAJPUT K. S. & RAO K. S. 1998. Seasonal anatomy of secondary phloem of teak (*Tectona grandis* L., *Verbenaceae*) growing in dry and moist deciduous forests. – *Phyton* (Horn, Austria) 38 (2): 251–258, 3 figures. – English with German summary.

Seasonal development of secondary phloem in samples of bark collected from *Tectona grandis* growing in the moist and dry deciduous forests of Gujarat state in Western India was studied anatomically. In both forests active cambial cell division and differentiation of phloem began in June when the dormant shoot buds opened. Phloem development continued until October in moist deciduous forest and November in dry deciduous forest. Phloem function began to decrease in December in the trees of moist deciduous forest and in January in the dry deciduous forest. All the sieve elements became nonfunctional by May in both forests. In the moist deciduous forest, phloem developed more rapidly than xylem in the beginning of growth season. The phloem elements produced in the preceding season just prior to dormancy were imposed to resume function in the following growing season as the older elements died. The structure and development of secondary phloem are discussed with other developmental phenomena occurring within the tree.

Zusammenfassung

RAJPUT K. S. & RAO K. S. 1998. Die jahreszeitliche Anatomie des sekundären Phloems von Teak (*Tectona grandis* L. *Verbenaceae*) aus trockenen und feuchten

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laubabwerfenden Wäldern. – *Phyton* (Horn, Austria) 38 (2): 251–258, 3 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Es wurde die jahreszeitliche Entwicklung der Anatomie des sekundären Phloems von *Tectona grandis*-Bäumen, welche in feuchten und trockenen laubabwerfenden Wäldern des westindischen Staates Gujarat wuchsen, an Borkenproben untersucht. In beiden Wäldern begann die Zellteilung des aktiven Cambiums und die Differenzierung des Phloems im Juni, sobald sich die Knospen zu öffnen begannen. Die Phloementwicklung hielt bis Oktober im feuchten Wald an, im trockenen hingegen bis November. Im feuchten Wald begann die Funktion des Phloems im Dezember abzunehmen, im trockenen Wald erst im Jänner. Alle Siebelemente wurden gegen Mai in beiden Wäldern funktionslos. Zu Beginn der Wachstumsperiode entwickelte sich im feuchten Wald das Phloem viel stärker als das Xylem. Die Phloemelemente, welche in der Jahreszeit gerade vor der Ruheperiode gebildet wurden, sind dazu vorgesehen, die Tätigkeit in der folgenden Wachstumsperiode zu übernehmen, wenn die alten Elemente absterben. Die Struktur und die Entwicklung des sekundären Phloems wurde in Zusammenhang mit anderen Entwicklungsphänomen anderer Bäume diskutiert.

Introduction

Plants growing in temperate climatic regions show annual rhythms in the development of secondary phloem parallel with the succession of the seasons (DAVIS & EVERT 1968, ALFIERI & EVERT 1968, 1973, ESAU 1969, KOZLOWSKI 1971). On the other hand, in tropical trees the periodicity of the phloem production has not been fully understood (LAWTON & LAWTON 1971, GHOUSE & HASHMI 1983, DESHPANDE & RAJENDRABABU 1985, VENUGOPAL & KRISHNAMURTHY 1987, VISHWAKARMA 1991). Although studies on the seasonal development of phloem of *Tectona* are made (LAWTON 1972, VENUGOPAL & KRISHNAMURTHY 1987), comparative studies in trees growing in different forest types are lacking. The present investigation was, therefore, aimed to compare and analyse the development, structure and longevity of phloem in *Tectona grandis* growing in moist deciduous and dry deciduous forests.

Materials and Methods

Bark samples along with outer xylem and inner phloem measuring 60 mm × 20 mm × 20 mm were collected from the main trunks of 15 to 20 years old trees of *Tectona grandis* growing in a moist deciduous forest (MDF) at Waghai of Dangs region and a dry deciduous forest (DDF) at Pavagadh of Gujarat State, Western India. Samples were collected at monthly intervals from January to December 1994 from trees of similar trunk diameter and fixed immediately in FAA (BERLYN & MIKSCH 1976). Each time four blocks were obtained from two trees and no tree being sampled more than once. Transverse, radial and tangential longitudinal sections of 12–15 µm thickness were obtained with a sliding microtome. After staining with tannic acid-ferric chloride-lacmoide (CHEADLE & al. 1953) the sections were dehydrated and mounted in DPX. The mean lengths of sieve tube elements and fusiform cambial cells were measured from tangential longitudinal sections with the help of

an ocular micrometer. To obtain a mean value, 100 random measurements were taken for each element.

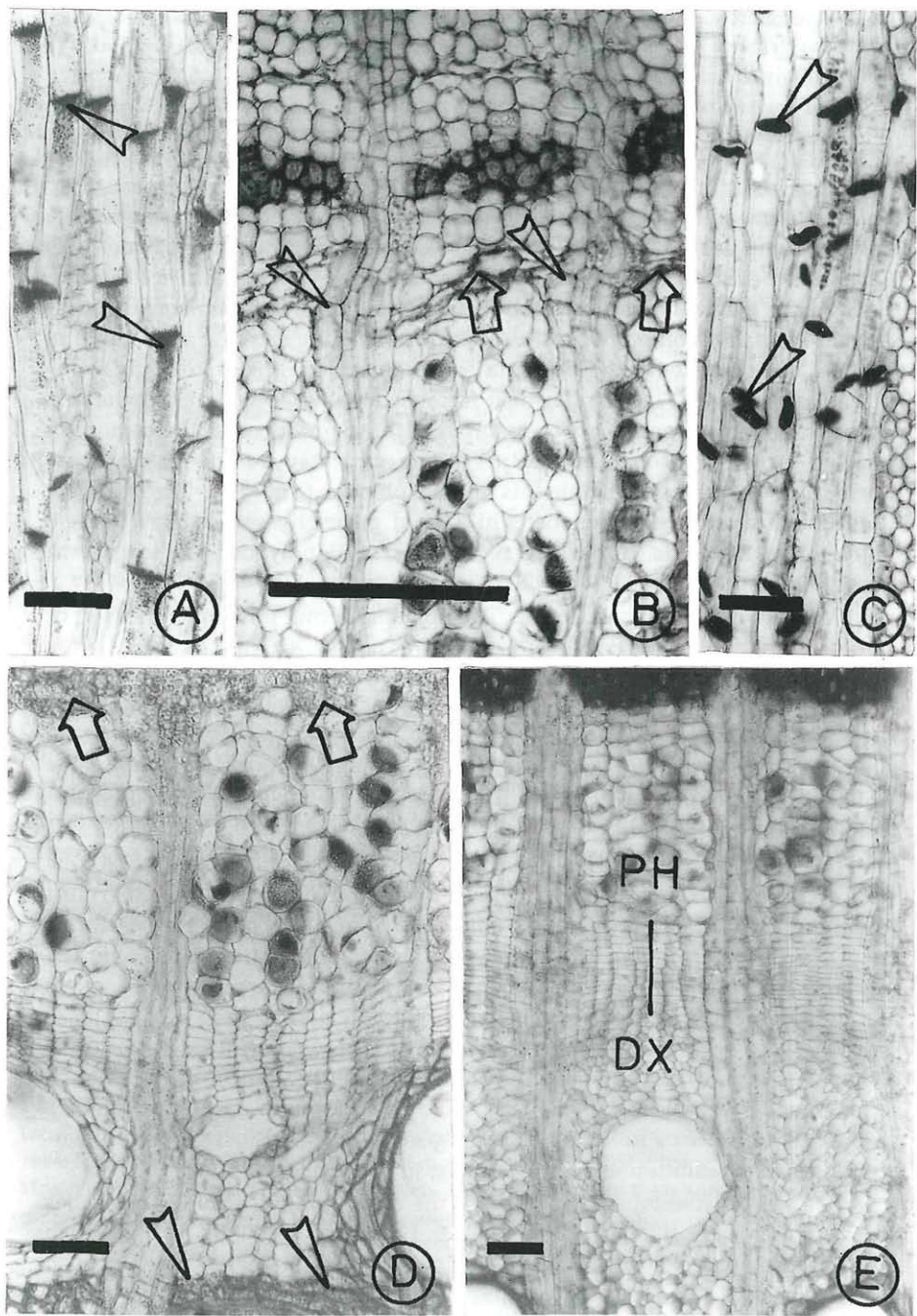
Results

Phloem structure: The secondary phloem of *Tectona grandis* is nonstoried with sieve tube members, companion cells, fibres, axial and ray parenchyma cells. Sieve tube members are the largest cells in a transverse section whereas companion cells are the smallest. The parenchyma cells are intermediate in size. Tangential bands of 3–4 rows of fibres alternate with sieve elements and axial parenchyma. Each sieve tube member is associated with a companion cell. A variable amount of slime and starch is found associated with the sieve plates which are transverse to slightly oblique and simple (Fig. 1A). The last formed sieve tubes or parenchyma in a growth increment are narrow compared to those produced in the beginning of the growth season. This feature along with ray nodding pattern discriminate the annual increments in the phloem (Fig. 1B). The rays are multiseriate and heterogenous. while axial parenchyma occur as verticle strands of 2–3 cells, appearing rectangular and polygonal in transverse sections.

Nonconducting phloem: The nonconducting phloem is the part of phloem in which the sieve elements are no longer functional. As the phloem approaches cessation of function, sieve elements accumulate callose on the sieve plates (Fig. 1B, C) and undergo partial collapse. With continued secondary growth, more and more sieve elements collapse followed by radial and tangential enlargement of phloem parenchyma cells. Complete collapse and obliteration of sieve elements occur in the outermost nonconducting phloem.

Seasonal cycle of secondary phloem development: A few differentiating xylem elements have been noticed from the innermost cambial zone of March samples collected from a moist deciduous forest (MDF). However, phloem differentiation is not noticeable in the samples. In both the forest types cambial cell divisions and differentiation of xylem and phloem start after the sprouting of young leaves in June (Fig. 2A). Although new xylem and phloem increment begins together differentiation of the latter is found to be rapid in MDF. As a result about $\frac{3}{4}$ of the phloem increment is produced by July (Fig. 1D). Then the development of phloem declines and ceases in October. The season's first and last cells to differentiate from cambium are always found to be sieve elements.

In a dry deciduous forest (DDF), the development of phloem reaches peak along with that of xylem in August–September (Fig. 1E) and then ceases in November (Fig. 2B.). The first and last elements of phloem to differentiate from cambium are parenchyma and sieve tube elements respectively.



The division of phloem mother cells are not necessarily synchronous during the differentiation of sieve elements. A mother cell may undergo periclinal division followed by an anticlinal division or two subsequent divisions are periclinal leading to the production of 3–4 sieve tube members. A single companion cell, presumably by transverse division, produces a strand of 2–4 companion cells. Two to four bands of phloem fibres are produced between July and November. The cessation of the current year's phloem function begins in December with the yellowing of leaves in MDF. In DDF phloem becomes nonfunctional with the initiation of leaf shedding in January. Cessation of phloem function as a conducting tissue is characterised by accumulation of callose on the sieve areas of the first formed sieve elements of the growth season and spreads gradually towards the last formed sieve elements. However, most of the phloem becomes nonfunctional by March except a few elements close to the cambium when the trees are completely leafless in both forest types. By May all the elements close to the cambium also become nonfunctional by massive deposition of callose (Fig. 2C). These elements regain their function in June with the sprouting of young leaves and remain functional until late July or early August (Fig. 2D). The nonfunctional sieve elements undergo collapse followed by an enlargement of associated axial parenchyma cells.

In MDF, the length of sieve tube members increases from May to August and decreases from October to December, whereas in DDF, the length decreases from January to May, July to September and October to December. The length and width of sieve tube members vary from 210–290 μm and 23–25 μm in MDF and 213–295 μm and 22–36 μm in DDF respectively (Fig. 3).

Discussion

In temperate regions, differentiation and senescence of phloem are periodic events and sieve elements may remain nonfunctional during the leafless phase of the trees (ESAU 1969, PHILIPSON & al. 1971, CATTESSON 1974). The annual cycle of phloem development in *Tectona* is similar to that of temperate tree species. In both forest types, phloem development

Fig. 1 A, C: Tangential sections, B, D, E: Transverse sections

A: Functional sieve tube elements in September. Note the slime bodies (arrow heads) along with starch grains near the sieve plate. – B: Growth ring boundary between last year's and current year's phloem increment (arrows). Note the ray nodding at the boundary (arrow heads). – C: Nonfunctional sieve elements in May. Note the massive deposition of callose on sieve plate (arrow heads). – D: Development of relatively more amount of phloem in July in moist deciduous forest. Arrows and arrowheads indicate growth ring boundary in phloem and xylem respectively. – E: Xylem and phloem development in dry deciduous forest in July. Note the relatively more differentiating xylem. Scale bar = 100 μm .

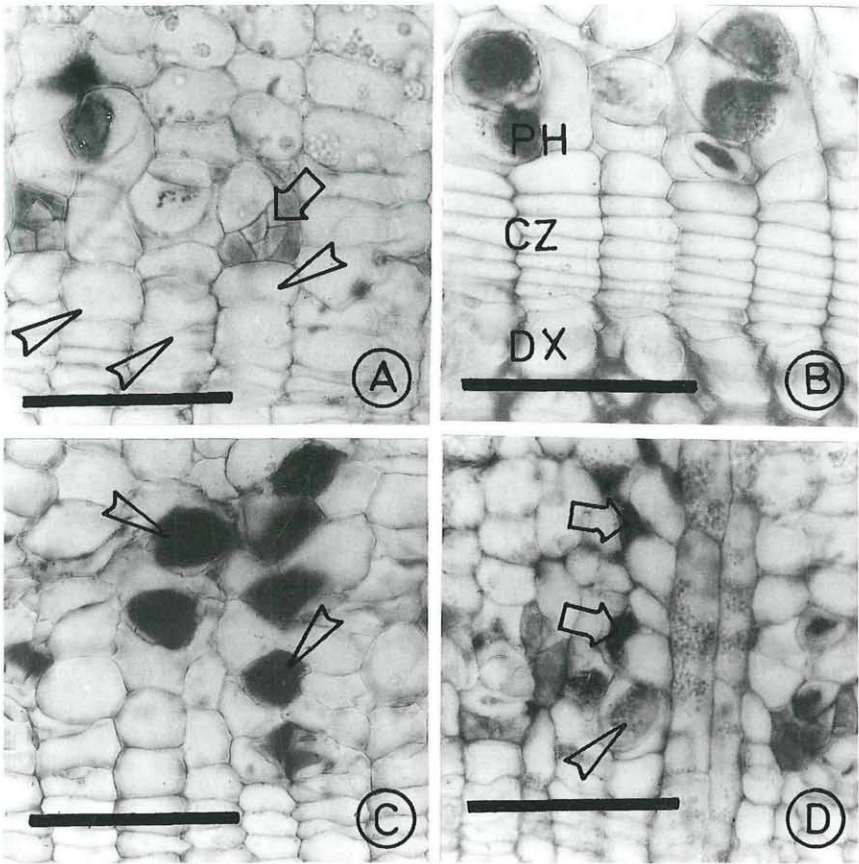


Fig. 2. A-D : Transverse Sections

A: Initiation of phloem development (arrowheads) in June. Arrow shows narrow sieve tube elements formed at the end of cambial growth. – B: Cessation of cambial cell division and phloem development in November. – C: Massive deposition of callose on sieve plates of elements (arrowheads) close to the cambial zone in May. – D: Sieve tube elements close to the cambial zone showing dissolution of callose (arrowhead). Note the nonfunctional sieve tube elements with callose little away from cambium (arrows). Scale bar = 100 µm. (PH: Phloem, CZ: Cambial Zone, DX: Differentiating Xylem)

begins with the sprouting of young leaves in June. The time of phloem and xylem differentiation is not necessarily synchronised, phloem development may begin before, after or together, with xylem formation and ceases later or simultaneously (PHILIPSON & al. 1971). Although both the vascular tissues differentiate simultaneously in both forest types, phloem development ceases first followed by that of xylem. LAWTON 1972 reported, phloem development in *Tectona grandis* growing in Nigeria occurs in two phases.

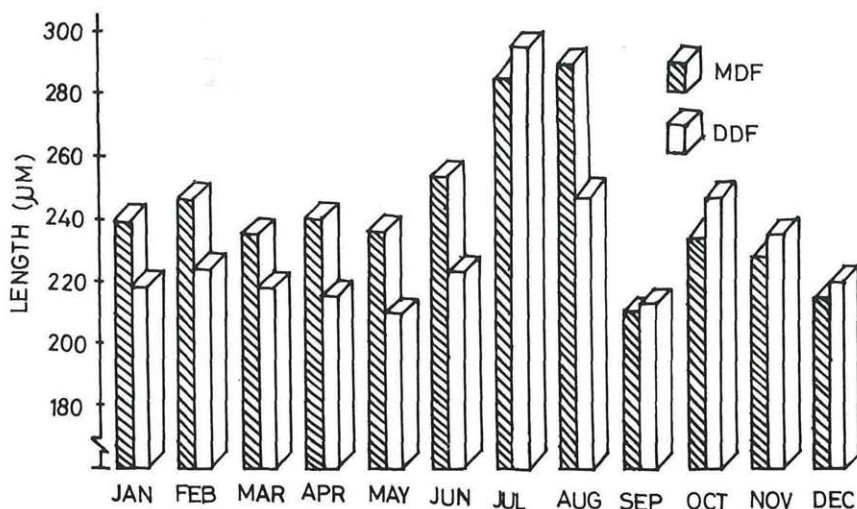


Fig. 3 : Histogram showing variations in the length of sieve tube elements in the phloem of *Tectona* growing in moist and dry deciduous forests.

However, such different flushes of phloem production has not been encountered in the present study. The development of phloem culminates first in July resulting in $\frac{3}{4}$ of the season's phloem production in MDF. The early cambial growth resulting in relatively more phloem production may be related to the active translocation of photosynthates to the developing foliage in the beginning of the season. More phloem production in *Ficus rumphii* is considered to be due to low temperature and high humidity (AJMAL & IQBAL 1987). In DDF, development of phloem reaches peak along with that of xylem in August when the trees are with full foliage. Although phloem development starts simultaneously in both forest types it ceases in MDF about one month earlier.

Accumulation of callose and cessation of phloem function begin with the yellowing of mature leaves and initiation of leaf-shedding in December and January in MDF and DDF, respectively. Although the time of callose deposition and cessation of phloem function differ, all the sieve elements except a few close to the cambial zone become nonfunctional by March in both forest types. During this period trees shed all the leaves and remain leafless until May. The sieve elements next to the cambial zone also become nonfunctional by May following massive deposition of callose on the sieve plates. A similar pattern of phloem behaviour has been reported for *Grewia*, a tropical deciduous tree (DESHPANDE & RAJENDRABABU 1985). Development of callose on sieve plates and lateral sieve areas is regarded as a sign of inactivation of sieve elements in temperate (EVERT 1984) as well as tropical trees (LAWTON & LAWTON 1971, VISHWAKARMA 1991). With the

sprouting of leaves in June, sieve elements close to the cambial zone lose callose and regain their function in both the forests. From the study it appears that the structure and the seasonal course of development of phloem are more or less similar in the trees of MDF and DDF.

Acknowledgement

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