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Structure of Cambium and its Derivatives in the Compressed Stem of *Canavalia ensiformis* (L.) DC. (*Fabaceae*)

By

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With 3 figures

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Summary

RAJPUT K. S. 2003. Structure of cambium and its derivatives in the compressed stem of *Canavalia ensiformis* (L.) DC. (*Fabaceae*). – *Phyton* (Horn, Austria) 43 (1): 135–146, with 3 figures. – English with German summary.

Variations in the structure of cambium, xylem and phloem were studied in the stem of *Canavalia ensiformis* (L.) DC. (a woody twiner) caused by external pressure developed due to radial growth in the stem of supporting tree. The radial increment in the main stem of supporting as well as twinning plant exerted a pressure on their contact sides, which led to the deformation of cambial structure and inhibition of its cell division and differentiation. The stem became flat and additional cambial arcs developed from the cortical parenchyma cells on both adjacent lateral sides of the stem. Fusiform cambial cells lost their storied arrangement on the opposite side of the stem and showed inconsistent intrusive growth while on the adjacent side fusiform cambial cells underwent divisions resulting into short, isodiametric, ray-like cells. With the gradual increase in pressure on the stem; completely differentiated vessel elements became oval to oblong and finally lost their characteristic shape. Whereas, newly differentiating vessel elements became deformed and irregular in outline. When the pressure increases the vessels are very narrow and the xylem fibres showed rhomboid crystals in their lumen. In the normal stem, cambium was storied with compound (tall) and heterocellular cambial rays. Xylem was diffuse-porous with indistinct growth rings and characterized by the presence of included phloem.

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Occurrence of included phloem is discussed in relation to habit and ecological condition of the plants. Vessels were mostly solitary and possessed simple perforation plates on their transverse end walls.

Zusammenfassung

RAJPUT K. S. 2003. Der Aufbau des Kambiums und seiner Abkömmlinge im zusammengedrückten Stamm von *Canavalia ensiformis* (L.) DC. (Fabaceae). – Phytion (Horn, Austria) 43 (1): 135–146, 3 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die Veränderungen in der Struktur des Kambiums, Xylems und Phloems wurde am Stamm von *Canavalia ensiformis* (L.) DC. (einer holzigen windenden Pflanze) untersucht. Solche Änderungen werden durch den von außen wirkenden Druck verursacht, welcher durch das radiale Dickenwachstum des Baumes entsteht, um den sich die Pflanze windet. Der radiale Zuwachs sowohl des Stützbaumes als auch der windenden Pflanze übt einen Druck auf die Kontaktflächen aus, welcher zu einer Deformation der Kambialstruktur und Verminderung der Zellteilung und Differenzierung führt. Der Stamm wird flach und zusätzliche Kambialbögen entwickeln sich aus den Rindenparenchymzellen auf beiden seitlich angrenzenden Bereichen des Stammes. Die faserförmigen Kambialzellen verlieren ihre regelmäßige Anordnung auf der gegenüberliegenden Seite des Stammes und zeigen ein unregelmäßiges gedrängtes Wachstum, während auf der angrenzenden Seite faserförmige Kambialzellen Teilungen unterliegen, die in kurzen, isodiametrischen markstrahlenähnlichen Zellen münden. Mit dem zunehmenden Druck auf den Stamm werden die ausdifferenzierten Gefäßelemente oval bis rechteckig und schließlich verlieren sie ihre charakteristische Form. Dagegen werden neu gebildete Gefäßelemente unregelmäßig geformt. Sobald der Druck weiter zunimmt, werden die Gefäße eng und die Holzfasern zeigen rhomboidale Kristalle in ihrem Lumen. Im normalen Stamm ist das Kambium aus großen Elementen und heterogenen Strahlen aufgebaut. Das Xylem ist zerstreutporig, mit undeutlichen Jahrringen und das Vorhandensein von eingeschlossenem Phloem ist charakteristisch. Das Auftreten von umschlossenem Phloem wird in Bezug auf die Art des Wachstums und die ökologischen Bedingungen dieser Pflanzen diskutiert. Die Gefäße sind meistens einzeln und besitzen einfache Porenplatten auf ihren abgeschrägten Wänden der Zellenden.

Introduction

Canavalia (Fabaceae) as a perennial woody twiner coils around any object for support. The present study is carried out with *Canavalia ensiformis* growing on *Guazuma tomentosa* a medium sized tree for its support. The radial growth in the main stems of both, *Canavalia* and supporting tree, exerted a pressure on their contact sides which resulted in the compression of and flattening of the *Canavalia* stem, while the supporting stem does not show much variation may be due to the relatively hard bark. In the forests, it is often observed that the perennial weak-stem plants (climbers) are seeking support from the neighbouring trees. After a period of time, due to the increase in their trunk diameter, they are tightly coiled with each other, blocking the photosynthate transport through the phloem

and ultimately resulting in a swelling of bark like in a girdling experiment. In some extreme cases both, supporting as well as climbing stems, get merged with each other while in other cases the supporting plant becomes killed may be due to complete inhibition of photosynthate translocation.

Experimental studies like girdling, reorientation of cambium, artificial external pressure etc. on cambium revealed that the structure of the cambium and its derivatives undergoes various changes in accordance with the availability of growth hormones (BROWN & SAX 1962, KURODA & SHIMAJI 1984, LEV-YADUN & ALONI 1991, 1992). However, in experimental studies the phloem is either completely removed by girdling or artificial pressure is directly given constantly on a particular area on the stem. On the other hand, in the present investigation the pressure is continuous in spiral fashion throughout the stems of both climbing and supporting species and does not bring sudden change in the physiology of the species as it happens in experimental cases due to injury. Thus, the present investigation is aimed at understanding the structural changes induced by gradually increasing pressure on cambium and its derivatives of *Canavalia* and also to report the occurrence of included phloem, although, structure and development of xylem in *Canavalia* was studied earlier (CUMBIE 1967).

Materials and Methods

Samples of eight to ten plants of compressed and normal stems of *Canavalia ensiformis* growing in M. S. University campus of Baroda, Vadodara were collected. Eight to ten pieces of each stem measuring about one to three cm in diameter and four to five cm in length were immediately fixed in FAA (BERLYN & MIKSCH 1976). Transverse, tangential and radial longitudinal sections of 12–15 μm thickness were obtained with a sliding microtome and stained with tannic acid–ferric chloride–lacmoid combination (CHEADLE & al. 1953). In affected stems tangential longitudinal sections were cut in three different directions viz. adjacent, adjacent lateral and opposite sides.

Length and width of fusiform cambial cells, ray height and width were measured directly from tangential longitudinal sections. To obtain length and width of vessel elements and xylem fibers, a one mm portion of the xylem adjacent to the cambium was macerated with Jeffrey's fluid (BERLYN & MIKSCH 1976). One hundred measurements were chosen randomly to obtain mean and standard deviation. The circular and compressed stems are referred in the text as normal and affected stems respectively.

Results

Morphology of stem

The normal stem of *Canavalia* is long, cylindrical and in transverse view it appears circular with a soft bark. In compressed stem, the outline of the stem changes from circular to oval-elliptic due to the development of pressure on the contact side of *Canavalia*. The secondary growth on contact side gradually decreases and ultimately the cambium ceases to divide

and differentiate. On the other hand, the cambium located on the opposite and adjacent lateral sides of the stem divides freely giving an elliptical shape. However, cell division activity and the structure of cambium and its derivatives differ on all the sides of the stem. Thus, to avoid confusion, all the three sides of the stem are termed as adjacent (side of the stem facing the supporting stem), opposite side (opposite to contact side of the stem) and adjacent lateral side (the portion of the stem close to contact side) is used in the text.

Structure of cambium

In the normal stem the cambium is storied with vertically elongated fusiform initials and horizontally arranged isodiametric, cuboidal clusters of ray initials. Cambial rays are mostly multiseriate, compound (tall) and heterocellular (Fig. 1A) but unicellular rays are also seen occasionally. The length and width of the fusiform cambial cells vary from 288–310 μm and 13–24 μm , respectively. The cambial rays are uni-multiseriate and 140–584 μm in height and 22–450 μm in width. In compressed stems, the fusiform cambial cells lost its storied arrangement and show significant variation in its structure and dimensional details. On the adjacent lateral side, the fusiform and ray cambial cells are more or less uniform in shape and size, making it indistinct from the cambial rays (Fig. 1B). On the opposite side divisions in the fusiform cambial cells are not synchronous resulting in a loss of storied arrangement and become zigzag (Fig. 1C). As compared with the normal stem, the fusiform cambial cells are relatively short on the opposite side ranging from 74–217 μm (Fig. 1C). In this region cambial rays are mostly uni-biseriate while multiseriate rays are observed rarely.

Development of cambial variant

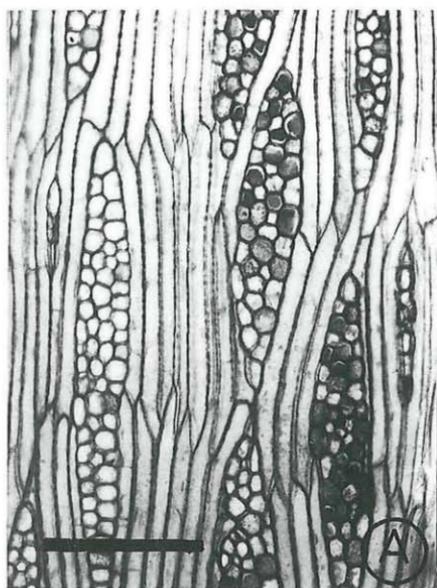
In normal stems a single cambium ring divides throughout the life span. In affected stem, some of the cortical parenchyma cells of the ad-

Fig. 1. Tangential longitudinal (A–C) and transverse (D) view of cambium and xylem of *Canavalia ensiformis* (L.) DC.

- A: Storied arrangement of fusiform cambial cells in normal stem. Note the compound (tall) heterocellular cambial rays.
- B: Loss of storied arrangement of fusiform cambial cells on the adjacent lateral side of the stem. Note that fusiform (arrows) and ray cambial (arrowhead) cells are more or less isodiametric in shape and size.
- C: Deformed fusiform cambial cells on the opposite side of stem. Note that rays are uni-biseriate (arrows).
- D: Origin of new cambium from the cortical parenchyma cells (arrow) on adjacent lateral side of the stem. Arrowhead indicates few differentiated lignified elements.

Fig. 1. A, B, D Scale bar = 250 μm .

Fig. 1. C Scale bar = 100 μm .



adjacent lateral sides undergo swelling followed by periclinal divisions resulting in the development of "C" shaped arcs of the meristematic cells. Like normal cambium it divides bidirectionally producing xylem centripetally and phloem centrifugally (Fig. 1D). The stem becomes flat due to the addition of xylem and phloem elements on the adjacent lateral sides from these cambial arcs. (Fig. 2A).

Structure of xylem

Xylem in the normal stem is diffuse-porous with indistinct growth rings. It is composed of fibers, vessels, and included phloem and unlignified axial and ray parenchyma cells. These parenchyma cells form the ground tissue of the stem in which lignified elements (xylem fibers and vessels) are present in pockets (Fig. 2A, B). These lignified elements range from small pockets solely of vessels surrounded by strengthening fibers or islands of fibers. The non-septated fibers with simple pits vary in their length from 1800–2500 μm .

The vessels are dimorphic in nature with exceptionally large (348–389 μm) and small (85–138 μm) lumen diameter while some of them are intermediate (158–248 μm) in size. The length of the larger vessel elements remains always shorter than its width. The average length of vessel elements varies from 68–217 μm . Perforation plates are simple on their slightly oblique end walls to transverse end walls. Vessels are mostly solitary but radial multiples of 2–3 vessels are also observed occasionally.

Structural and dimensional changes occurring in the xylem derivatives of affected stem vary in accordance with their position on different sides of the stem. In the initial stages of increasing pressure, the xylem derivatives from the adjacent side lose their vertical alignment and become irregularly arranged. After a definite period when the pressure is sufficient enough to inhibit the expansion of xylem mother cells, cambium ceases to divide. Moreover, increasing pressure also result in a crushing of vessel elements (Fig. 2C). On the adjacent lateral side of the stem, axial parenchyma forms narrow and continuous tangential bands and each band is lined with marginal crystaliferous fibers. However, the occurrence of such crystaliferous fibers is not seen in normal stem. The length of xylem fibers decreases drastically compared to that of normal stems, measuring about 560–835 μm . Some of the vessel members are also arranged either in tangential or in zigzag manner (Fig. 2D) and some fail to achieve its characteristic shape (Fig. 3A). The occurrence of vessels either in clusters of 4–12 or in radial multiples of 2–8 is a common feature. Compared to a normal stem, lumen diameter decreases significantly (208–267 μm) while its frequency increases. Xylem structure on opposite side does not show much variation.

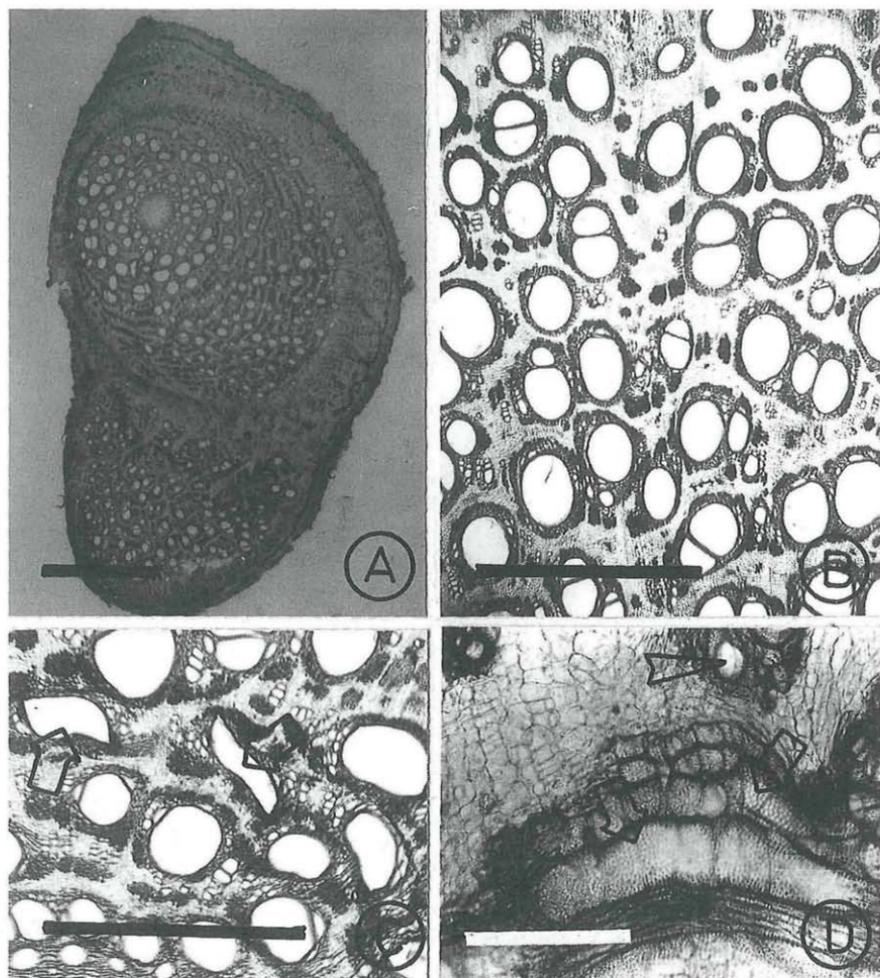


Fig. 2. Transverse (A-D) view of stem showing xylem structure of *Canavalia ensiformis* (L.) DC.

A: Structure of compressed stem. Note that eccentric growth on adjacent lateral and opposite side of the stem while no xylem development on adjacent side.

B: Structure of xylem in normal stem. Note the ensheathing-lignified element restricted only to the vessel elements.

C: Compressed portion of xylem showing crushed vessel elements (arrows) and gradual lose of its characteristic shape.

D: Horizontally arranged vessel elements (arrows) on the adjacent lateral side of the stem. Arrowhead indicates vertically aligned vessel elements and axial parenchyma.

Fig. 2. A-D Scale bar = 500 μ m.

Structure and development of included phloem

Development of included phloem is a bit delayed in both normal and affected stems and no sieve tube elements are observed near the cambium as well as in recently formed xylem. Some of the xylem parenchyma situated deep inside (2–3 mm away from the cambium) the xylem undergoes periclinal divisions resulting into small and large cells. Among them one of the cells differentiates into a sieve tube member and another into a companion cell. Thus, the islands of included phloem are always either in the form of isolated sieve elements or in a group of 2–3 sieve tube members (Fig. 3B).

In both, normal and affected stems, a group of 2–3 sieve elements are observed intermixed with the axial parenchyma of the xylem (Fig. 3B). Sieve tube elements are characterized by simple sieve plates with well-developed sieve areas on their lateral walls. Each sieve element is accompanied by a single companion cell. The lengths of the sieve tube elements vary from 270–295 μm . Functional sieve elements possess slime (P-protein), starch grains and callose around the sieve areas.

Similar to vessels, sieve elements in affected stems also lose their vertical alignment and become irregularly arranged. As compared to normal stems, the length of the sieve tube members decreases significantly in the affected stem ranging from 75–210 μm . However, the frequency of phloem islands in the ground tissues of the xylem is relatively small. Structure and behaviour of sieve elements from both, adjacent lateral and opposite side of the stem remains more or less similar to that of normal ones.

In both, the normal and affected stem the included phloem islands begin to cease its function by loss of cell content and heavy accumulation of callose followed by obliteration of sieve elements. With the initiation of obliteration, adjacent parenchyma of the phloem islands enlarges in both radial and tangential direction and undergoes periclinal divisions (Fig. 3C, D). This results in the development of additional parenchyma, which compensates the space formed by obliteration of nonfunctional sieve elements.

Discussion

The vascular cambium of *Canavalia* is storied (CUMBIE 1967) but in affected stems it undergoes irregular (pseudotransverse) division and lose its storied arrangement. This may be attributed due to the imbalance of hormones, nutrients and water supply. There is small but convincing body of evidence that the orientation of vascular cambium is influenced by the lines of nutrients and water in the plants and can be altered if the lines of flow are changed (THAIR & STEEVES 1976). On the adjacent lateral side, fusiform cambial cells undergo divisions forming cambial ray-like cells. However, change in the orientation of vascular elements depends on the

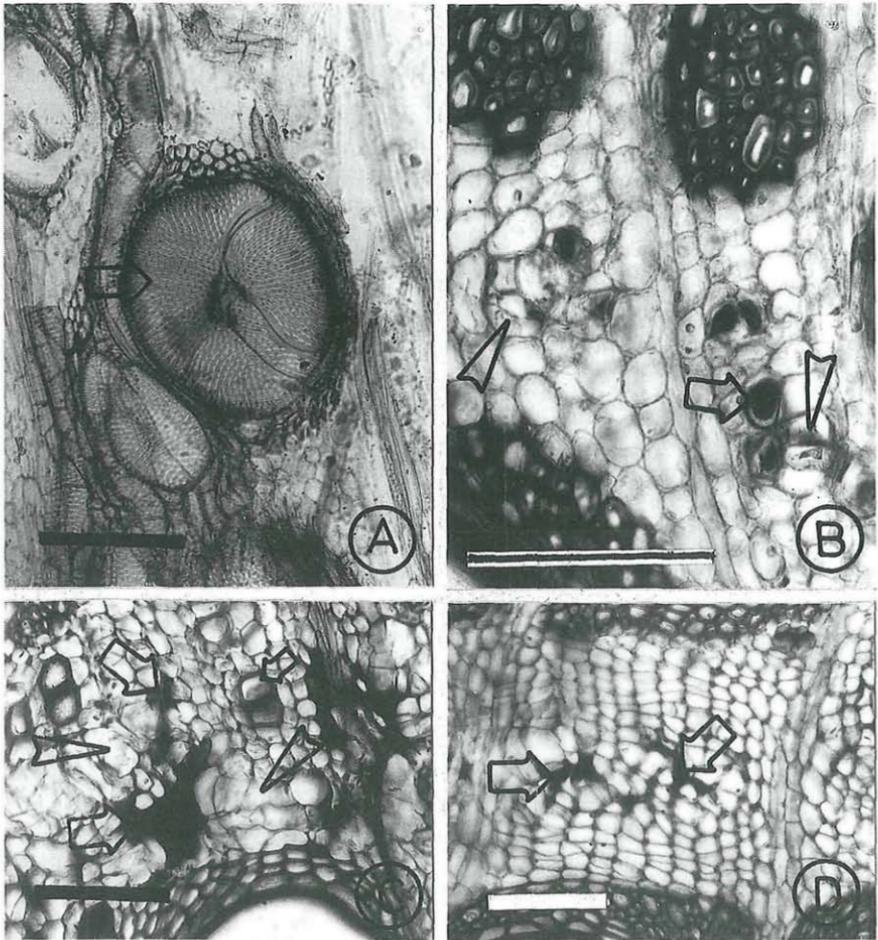


Fig. 3. Tangential (A) and transverse (B–D) view of xylem and included phloem in the stem of *Canavalia ensiformis* (L.) DC.

A: Deformed xylem on the adjacent lateral side of the stem showing circular vessel element (arrow).

B: Isolated bands of included phloem in the normal stem (arrow). Arrowheads indicate newly differentiating sieve tube elements.

C: Heavy accumulation of callose on non-functional sieve elements (arrow) followed by radial and tangential expansion of surrounding parenchyma cells (arrowheads). Small arrow indicates functional sieve element.

D: Complete obliteration of sieve elements (arrows) while repeated divisions in the surrounding parenchyma resulted into radial arrangement of newly formed parenchyma.

Fig. 3. A, B Scale bar = 100 μ m.

Fig. 3. C, D Scale bar = 150 μ m.

change in direction of polar flow of auxin and may-be also on other developmental signals (SACHS & COHEN 1982) and it results in the development of rays (SACHS 1981, LEV-YADUN & ALONI 1991, 1992).

In the present study, the inhibition of cambial growth on the adjacent sides suggests that development of additional cambial arcs on adjacent lateral side may be associated with the shifting of polar flow of auxin from adjacent side to the adjacent lateral side of the stem.

The ground tissue of *Canavalia* consists of unligified thin walled parenchyma in which lignified elements are distributed in small pockets solely or vessels surrounded by fibers or isolated islands of fibers. A function in enhancing stem flexibility has been ascribed to the presence of parenchyma, especially in those stems in which anomalous cambial activity results (CARLQUIST 1985, BAMBER & WELLE 1994) such parenchyma distribution permits vessel bearing segments to twist without fracture, and minimize the damage to the phloem (CARLQUIST 1975, SIEBER & KUCERA 1980). It seems true in the case of *Canavalia* as it bears exceptionally large diameter vessels and included phloem.

The structure and development of xylem in *Canavalia ensiformis* has already been studied earlier (CUMBIE 1967) but no report is made about the occurrence of included phloem. This may be due to the fact that differentiation of sieve tube members is delayed and it is observed only 2-3 mm away from the cambium. In transverse view, strands of interxylary or included phloem appear to be either scattered in their distribution or they may be arranged in concentric circles. According to METCALF & CHALK 1983 the concentric type is initiated from a succession of cambia, each of which repeats a structure of young stem while in the scattered type there is a single permanent cambium which is normal in its behaviour except in producing sporadic strands of phloem which becomes embedded in the surrounding xylem. PHILIPSON & al. 1971 considered such phloem development as *Combretum* type. According to *Combretum* type the internal derivatives of small arcs of normal cambium may for short time differentiate as phloem instead of xylem. However, in the present study the case is different, instead of producing phloem, some of the phloem (sieve tube) mother cells are transferred as it is along with the xylem parenchyma and after a period of time they differentiate into sieve tube elements. These phloem mother cells are difficult to distinguish from xylem parenchyma cells and can be discerned only when these cells begin to differentiate into sieve tube members.

Included phloem tends to occur in those genera and species in which growth and flowering occurs suddenly and seasonally (CARLQUIST 1982). Sprouting of new leaves in *Canavalia* starts in June with the arrival of rain followed by massive flowering and fruit setting in subsequent months. Being a woody twinner, it achieves great height while proportionately re-

mains narrow. Moreover, flowering and fruiting represents presumptively large energy expenditure. Therefore, the presence of included phloem in *Canavalia* may be associated with its limited translocational area of the stem and to compensate large energy expenditure during the period of flowering and fruit setting.

In tropical deciduous trees accumulation of callose and cessation of phloem function begins with yellowing of mature leaves and initiation of leaf shedding during the dry period. Being a tropical deciduous species in *Canavalia* normal phloem ceases its function with the yellowing and defoliation and entire phloem becomes nonfunctional by March while included phloem remains functional throughout the dry period of the year and nonfunctional included phloem is observed only in the innermost xylem. Here it appears that the xylem surrounding the phloem acts as an insulating layer that protects the included phloem from high temperature during summer and may be playing an important role in the supply of photosynthate at the time of sprouting of new leaves in June when the normal phloem is nonfunctional. The development of callose on sieve plates and lateral sieve areas is regarded as sign of inactivation of sieve elements in temperate (EVERT 1984) as well as tropical trees (LAWTON & LAWTON 1971, DESHPANDE & RAJENDRABABU 1985, VISHWAKARMA 1991). A similar pattern of phloem behaviour is also reported for *Tectona grandis* (RAJPUT & RAO 1998).

Any change in the cambial structure ultimately reflects the quality and quantity of wood. In affected stems, xylem formed towards opposite and adjacent sides of the stem lose its vertical alignment. While on the adjacent lateral sides length of xylem fibers is reduced significantly. Although, the ground tissue of xylem in *Canavalia* is composed of parenchyma, which functions as a mechanical shock absorption, exerting pressure on xylem shows considerable damage to the vessel elements. It has been inferred (CARLQUIST 1975, 1988) that wide vessels offer low friction and conduct large volume of water per unit time but are vulnerable to air embolism and such vessels represent substantial loss of hydrosystem. Therefore, increase in vessel frequency per unit area and its lumen diameter may help to compensate the damaged hydrosystem.

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