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Seasonal activity of cambium in some tropical trees. III. *Salvadora persica* L.

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Abstract

Seasonal activity of cambium has been investigated in *Salvadora persica* L., one of the commonest evergrenn tree of northern India, from March, 1974 to February, 1975 in the main stem and the branch. Secondary vascular cambium behaves abnormally on the xylem side, by producing xylem and phloem in succession, resulting in the formation of interxylary phloem. It has a storied (stratified) cambium organization, comprising short fusiform and isodiametric ray initials. The fusiform initials show characteristically beaded cell walls due to the presence of primary pit fields and are uninucleate. These are highly vacuolate during the active period.

The cambial activity starts in the month of March, reaches the peak in August and finally slows down in the main stem. In an young branch, however, it is initiated in March-April and reaches the peak in July and then declines till November. It once again showed an upward trend gradually. It appears that the initiation of the combial activity in this tree takes place by a hormone produced in the newly formed leaves, coupled with the high rainfall, enhanced relative humidity, optimum temperature, and short-day conditions. Size measurements for the fusiform initials showed considerable variations during the span of a year. A comparision of the organization of three types of phloem 'normal', 'included' and 'internal' occurring in this plant has also bean presented.

INTRODUCTION

Cambial activity has been investigated in detail in the trees of temperate regions of the globe by several workers. As is well known these trees show definite growth rings due to marked climatic change in the seasons. There are, however, conflicting reports about the periodicity of wood formation in tropical trees. For example, Antevs (1917) has reported that some trees in the tropics never form distinct growth rings, even when the cambium shows periods of peak activity alternating with quiescent ones. On the other hand, Koriba (1958) reported that in Malaysia, where growth conditions are ideal and nearly uniform throughout the year, only about 15 per cent of the species show continuous radial growth, although the majority are evergreen. For the Amazon rainforest trees, however, Alvim (1964) estimated that only 43 per cent show growth rings. Chowdhury (1961) recorded growth rings in 75 per cent of the indigenous rain-forest trees of India. More recently, Paliwal and Prasad (1970) have reported the occurrence of distinct growth rings in *Dalbergia sissoo,* a common deciduous tropical tree of India.

The aim of the present communication is to elaborate the relationship between the various factors vis-a-vis cambial activity in *Salvadora persica* L. a common evergreen tropical tree.

MATERIAL AND METHODS

The material was collected from a tree, growing at the old Delhi ridge. Monthly colections were made from March, 1975 to February, 1975. Small portions of bark, intact with wood (measuring 6 × 10 cms), were peeled off from the main stem with the help of an axe, hammer, and chisel. Simultaneously, pieces of young branches (measuring 1 cm in diameter) were also collected. By using an electric saw these large pieces were cut into smaller ones. These were then fixed in Craf III mixture for 24 hrs. After washing thoroughly in running water these were preserved in 70 per cent alcohol.

For the detailed study, sections of the main stem pieces were cut in transverse, tangential and radial longitudinal planes with a Reichert Sliding Microtome, at 20—30 μm. In order to compare the cambial activity in the main stem and twigs, sections of the latter were cut only in transverse plane at 20 μm. The sections were placed serially in a mixture of 70 per cent alcohol and glycerine (1 : 1) over a slide, and tied to the slide with a fine sewing thread. They were then passed through tannic acid-ferric chloride-locmoid triple stain as outlined by Cheadle et al. (1953). Sections were left in the stain for 12—18 hrs, passed through ethyl alcohol-xylene series, and the thread was removed after these had been cleared through xylene. Mounting was done in Eukitt. Mercuric bromophenol blue staining combination of Mazia et al. (1953) was employed for the test of P-proteins.

Cambial activity was determined by counting the number of undifferentiated layers in transverse sections, lying between the secondary xylem and normal secondary phloem. Measurements of cell dimensions were taken with ocular and stage micrometers. Percentage of cambial initials was calculated from the camera lucida drawings drawn on the graph paper.

Meterological data of temperature, rainfall, relative humidity, and duration of sunshine were obtained from the Indian Meterological Department, New Delhi (Safdarjung).

Black and white photomicrographs were taken with an Exakta camera using ORWO NP 22 film, Ernst Leitz Wetzlar microscope, and Agfa normal photographic paper.

OBSERVATIONS

General description of the stem. In a young stem, the epidermis is cutinized and some of the epidermal cells contain tannin. Lenticels are common. The cortex is occupied by chlorenchymatous cells. Pericycle is represented by isolated groups of sclerenchymatous cells, connected by flattened thick-walled cells with pitted thickenings.

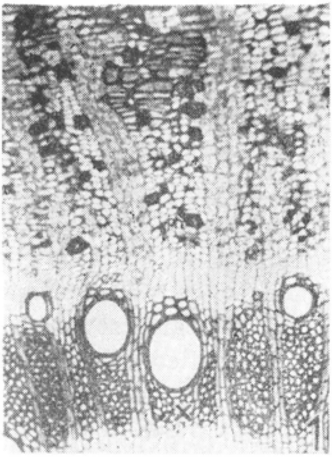
The cork comprises several layers of dead cells in the mature stem. Druses are present in the cortical cells. In this region some of the phloem elements as well as the ray cells become lignified. The normal phloem consists of sieve tubes, companion cells, parenchyma, and fibers (Fig. 1). Next to the phloem is the cambium which behaves in an abnormal manner and produces xylem and phloem successively, towards the pith (Fig. 1). Soon after the xylem formation, the cambium cuts off periclinally some thinwalled cells centripetally, which remain unlignified and become differentiated into sieve elements in the centre. The same arc of the cambium again resumes its normal activity and produces xylem. In this manner, the phloem patches get embedded in xylem resulting in the formation of 'phloem islands'.

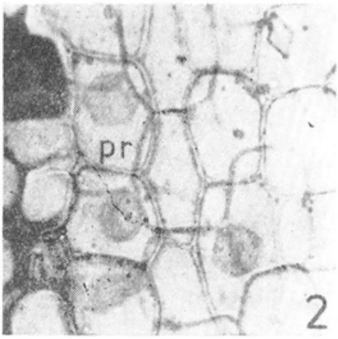
The wood forms the major part (78.3 per cent) of the secodary tissues. It consists of vessels, fibers, and parenchyma (Fig. 1). The vessel are comparatively smaller in length and wider in diameter, having pitted thickening on the walls. The diameter of the vessels varies markedly. These occur either isolated or in groups of 2 to 9. Xylem parenchyma is of vescicentric type and its cells store starch. The vascular rays are 1 to 6 cells wide and consist of elongated, thick-walled and pitted cells. These cells are thin-walled in the zone of normal and included phloem. In this region these cells contain starch and rhomboidal to cubical crystals (Fig. 2). Fibers constitute the major bulk of the xylem and are much elongated as compared to the vessel members.

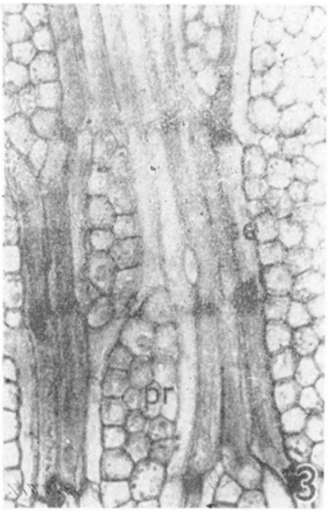
In the young stem protoxylem vessels located near the pith get crushed due to the meristematic activity of the cells surrounding them (Fig. 6). As a result, some new cells are formed and they start enlarging. These stain rather feebly like the ordinary parenchyma cells of the cortical region.

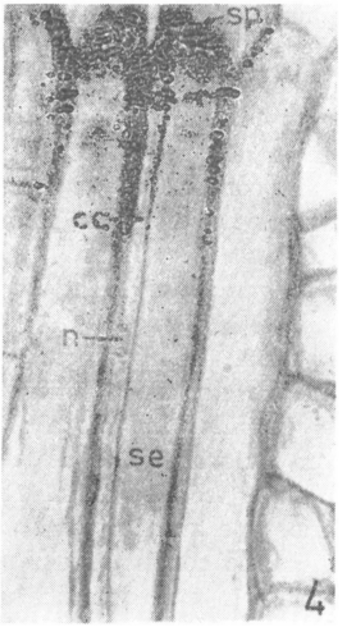
Normal, included, and internal phloem. As stated earlier, the normal and included phloem have their origin as a result of the activity of the vascular cambium. The internal phloem, on the other hand, seems to originate from the pith cells which become meristematic. The number of sieve elements, companion cells, and parenchyma cells is less in the

Plate I









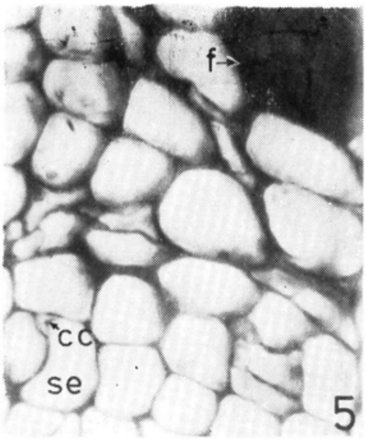
Figs. 1—2. Transections of a stem of *Salvadora persica*

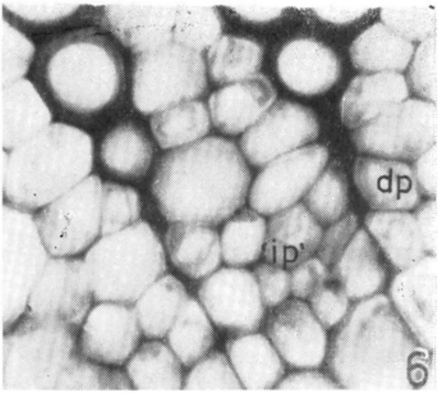
Fig. 1. Stem in the regions of normal secondary pholoem, xylem and part of included phloem below the xylem. *cz* — cambial zone, *ph* — phloem. *x* — xylem; × 300. Fig. 2, Cubical and rhomboidal crystals seen in phloem rays. *pr* — phloem ray; × 500.

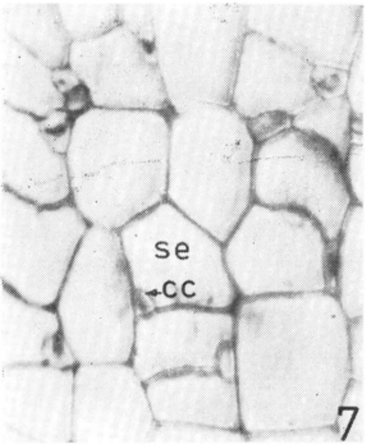
Figs. 3—4. Tangential longitudinal sections of phloem

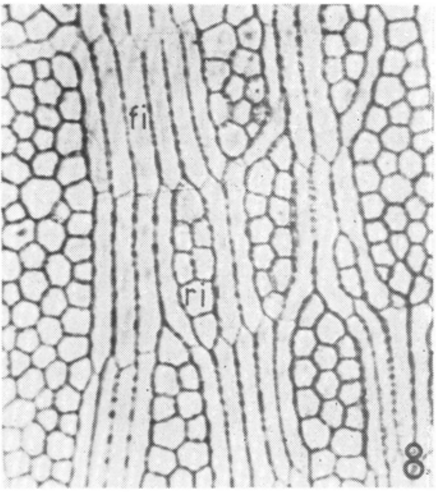
Fig. 3. Storied sieve elements and crystal containing rays, *pr* — pholoem ray, *se* — sieve element; × 200. Fig. 4. Enlarged portion of the phloem showing a companion cell with dense cytoplasmic content and nucleus and almost empty sieve tubes with oblique sieve plate. *cc* — companion cell, *se* — sieve element, *sp* — sieve plate, *n* — nucleus × 1050.

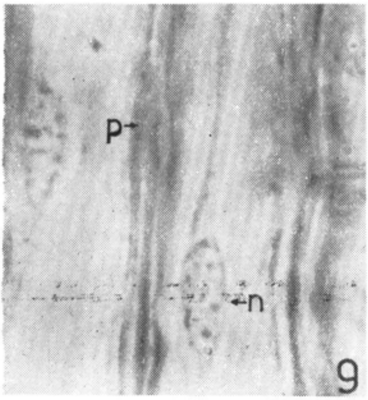
Plate II

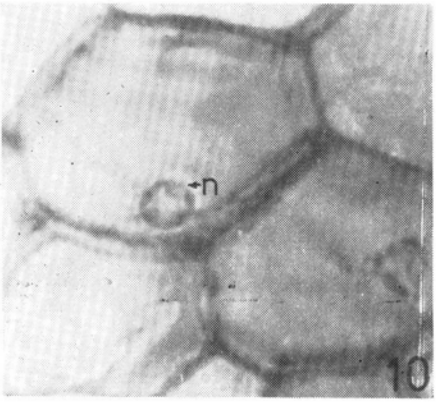










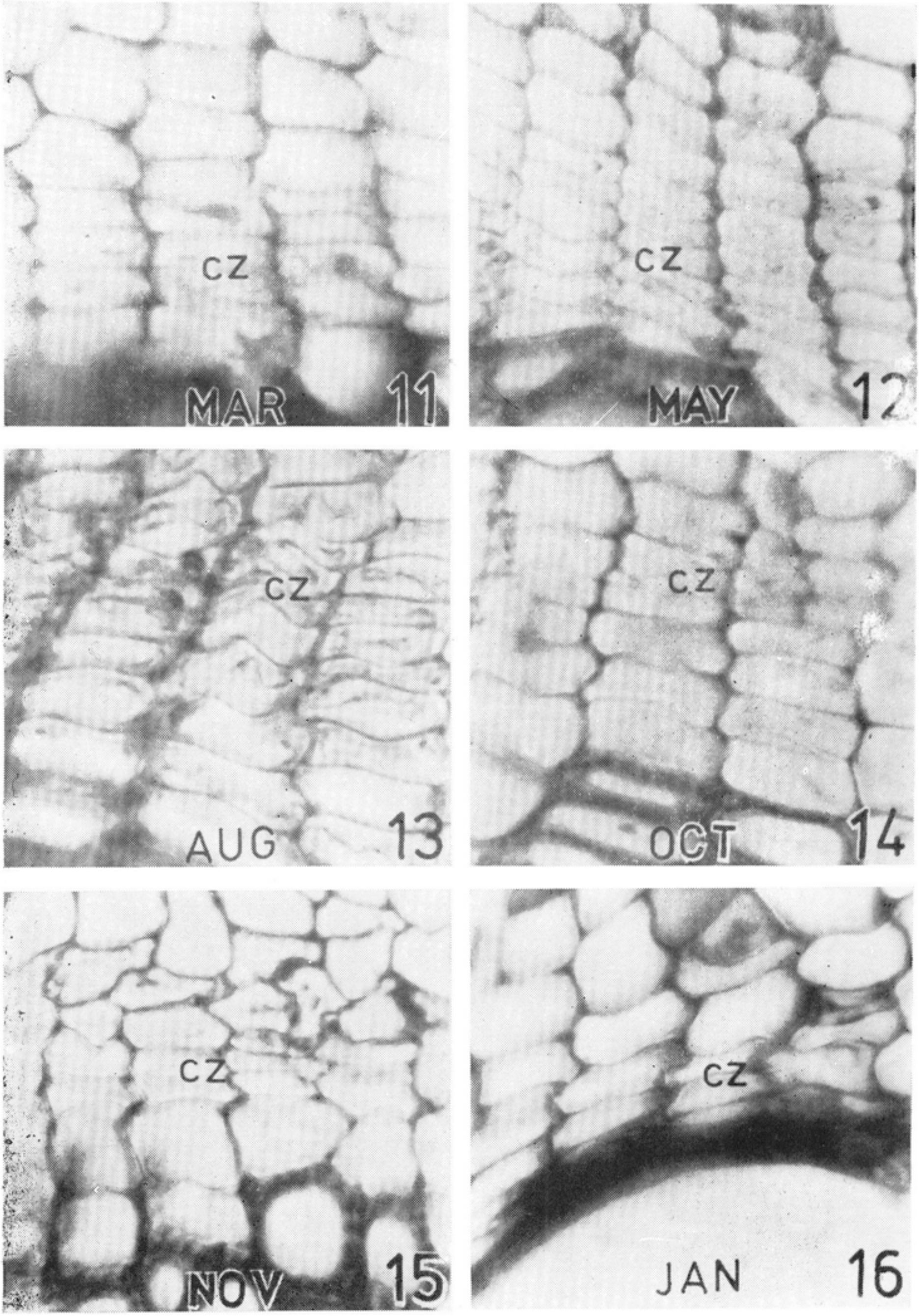


Figs. 5—7. Transections of normal, internal, and included phloem
Figs. 8—10. Tangential longitudinal sections of cambium

Fig. 5. Normal secondary phloem showing fibers, sieve elements, companion cells, and parenchyma, *cc* — companion cell, *f* — fiber. *se* — sieve element; × 560. Fig. 6. Distorted protoxylem surrounded by thin-walled and nucleated parenchymatous cells (internal phloem). *dp* — distorted phloem, *ip* — internal phloem; × 966. Fig. 7. Included phloem with abundant companion cells, sieve elements, and parenchyma cells, *cc* — companion cell, *se* — sieve element; × 560.

Fig. 8. Storied arramgement of fusiform initials showing beaded cell walls. *fi* — fusiform initial, *ri* — ray initial; × 225. Fig. 9. Two fusiform initials enlarged showing primary pits on the radial walls and elongated nuclei, *n* — nucleus, *p* — pit; × 1435. Fig. 10. Ray initials with rounded nucleus and cell walls devoid of pits. *n* — nucleus; × 1435

Plate III



Figs. 11—16. Variations in the cambial zone dimension during different periods of an year. × 735

cz — cambial zone

normal phloem and more in the included phloem (Figs. 5 and 7). Phloem fibers are present exclusively in the former. However, the internal phloem does not possess any of the features of the phloem for example, sieve plate, callose, companion cell, etc. In our opinion, therefore, there seems little justification to label these patches as 'phloem'.

It is the most recently formed phloem which appears to be functional. The older one seems to lose its activity very soon as judged by the depositon of callose plugs. The sieve plates are storied, simple and slightly oblique (Figs. 3 and 4). Each sieve tube is accompanied by a single companion cell. P-protein is present in the sieve elements.

Cambium structure. The cambium is storied or stratified, comprising short, hexagonal fusiform initials and isodiametric ray initials. The fusiform initials are arranged in regular tiers lying one above the other (Fig. 8). The ray initials rarely occur in regular tiers lying one above the other and are uni- to multiseriate. The cell walls in the dormant initials are slightly thick-walled with a characteristic beaded appearance due to the presence of primary pit fields (Fig. 9). They have dense cytoplasm. In the active cambium, however, the cell walls are comparatively thin and the ctyoplasm is higly vacuolate. Fusiform initials are uninucleate (Fig. 9). The nucleus is elongated and contains several nucleolei. The ray initials are also uninucleate with round nucleus (Fig. 10). The fusiform initials constitute 62.12 per cent of the total cambial tissue.

Cambial activity. The cambial activity is initiated in *S. persica* in the month of March and resumes the peak in July; it then declines till November and finally again increases till January in the young shoot. In the main stem, however, it starts in March-April and reaches the maximum in August and stops in September and then shows upward and down ward trends. During the active period, the cambium becomes 8—10-layered, which are reduced to 2 in the dormant season (Figs. 11—16). Fusiform initials multiply by radial longitudinal divisions. A graphic representation of the activity, as indicated by the count of cambial layers in t.s., in relation to the various climatic factors is shown in Fig. 17.

Measurements of the dimensions of the cambial initials show variations during the span of a year. The length varies from 120.3 μm — 156.2 μm and the breadth of the ray initials varies from 14.5 μm — 20.3 μm. During the active period, the fusiform initials first become elongated and later as a result of divisions their length declines. Breadth of the fusiform and ray initials tends to decline during the active period (Fig. 18).

Leaf fall and arrival of new shoots. Under the climatic conditions of Delhi, new shoot buds arise on the tree in the month of March. Being an evergreen tree there was little leaf fall during the year March 1974 to February 1975.

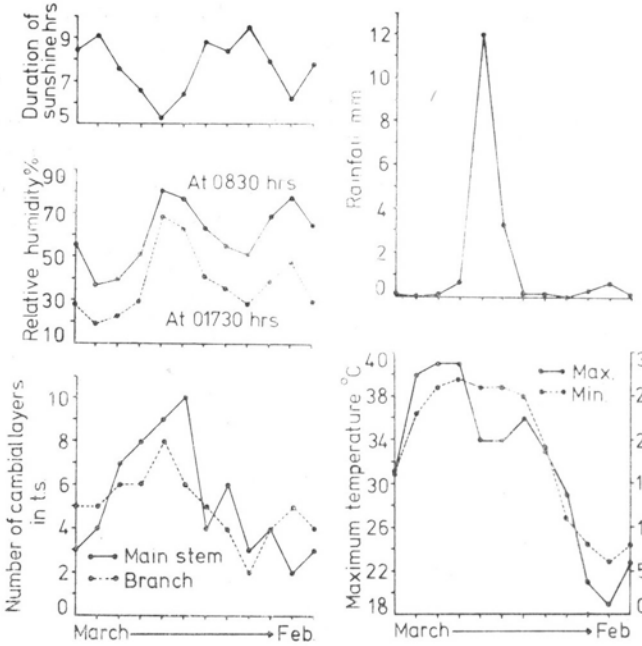


Fig. 17. Comparative analysis of cambial activity in relation to the various climatic factors

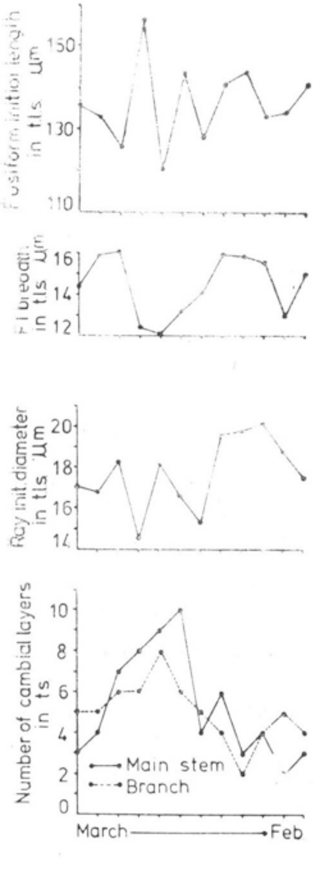


Fig. 18. Seasonal variations in the size of cambial initials (Average of 50 values)

(t. s. — transverse section; t. l. s. —tangential section)

DISCUSSION

The vascular cambium in *S. persica* behaves in an abnormal fashion soon after it initiates production of secondary tissues and forms a complete ring. The organization of the combium in this plant is not like most of the other common trees. Phylogenetically, the stratified cambium is considered to be advanced and is found only in a few dicotyledonous taxa. From this standpoint, it can be considered as an advanced taxon, having storied cambium, coupled with short vessel members.

Bailey (1923) reported that in *Pinus sylvestris* the fusiform initials constitute about 87.5 per cent to the total area of cambial zone. Later, Wilson (1963) recorded 90.0 per cent fusiform initials in the cambial zone of *Abies concolor*. Recently, Butterfield (1972) found that the fusiform initials occupy 95.0 per cent area of the combium in *Aeschynomene hispida*. However, Ghouse and Yunus (1974) observed that in a fully grown tree of *Dalbergia sissoo,* the fusiform initials do not constitute more than 60.0 per cent of the cambium. In the young twigs, however, their magnitude may go up to 80.0 per cent. Our observations in *S. persica* indicate that cambium constitutes 62.1 per cent fusiform initials and 37.9 per cent ray initials. It is evident that in plants having multiseriate ray initials, the percentage of fusiform initials tends to be low.

Singh (1943) studied the anatomy of young stem of *S. persica* and reported that the included phloem is differentiated from the thin-walled parenchymatous cells cut off by the cambium on its inner side and become embedded in the wood when the cambium resumes its normal activity. According to him these islands are surrounded by cambial like cells and due to their meristematic activity phloem elements get crushed. Our observations indicate that these cells resemble the cambial cells in shape and structure, i.e. layered appearance in transverse section and fusiform in tangential longitudinal section with beaded cell walls.

Simon (1914) and Coster (1927—28) recorded that the cambial activity did not occur during the leafless period and that it has a bearing on the formation of new leaves. Amobi (1973) studied the periodicity of wood formation in some trees of lowland rain-forest in Nigeria and found that cambial activity is closely related to the formamtion of new leaves. In *S. persica* it is initiated in March, when the new shoot buds make their appearance. This is evident from the early initiation of cambial activity in the young twigs. In the main stem it reaches the peak after the cambial activity in the young twig had reached the maximum level. In the young twigs the cambium becomes dormant in November and resumes its activity in December-January. It is probable that at this stage young buds might have made their appearance inside the stem which are the source of hormone for the initiation of cambial activity. Activity of the cambium does not reach the peak simultaneously in the twigs and the main stem. Digby and Wareing (1966) reported that initiation of cambial activity starts simultaneously in the ring-porous (*Ulmus glabra*) and not in diffuse-porous (*Populus trichocarpa*). The present observations substantiate this viewpoint for *S. persica.*

It is well known that various climatic factors influence the cambial activity in many ways. Investigations by Waisel, Niliphschitz and Fahn (1970) revealed that in *Zygophyllum dumosum,* a mediterranean medium-sized tree, the activity of the young plants seems to be markedly affected by water supply, whereas it is endogenously controlled in the older specimens. Waisel and Fahn (1965) observed that in *Robinia pseudoacacia,* activity of the cambium is increased by high temperature whereas low temperature induces dormancy. Wareing and Roberts (1956) reported that dormancy can be induced in the cambium by short--day treatment and its reactivation can be achieved by long-day conditions in *R. pseudoacacia* and *Pinus sylvestris.* Recently, Aljaro et al., (1972) observed that *Proustia cunefolia,* a drought deciduous shrub, shows a typical desert correlated cambium rhythm, highly sensitive to rainfall. The cambium remains active during the period of adequate moisture. Earlier, Tsuda and Shimaji (1971) recorded that in *Pinus densiflora* the cambial activity is maximum in the trees during April-May (period of comparative higher temperature), but that of seedlings do not vary much throughout the year.

The present study on *S. persica* seems to indicate that short-day conditions, high rainfall, and increased relative humidity coupled with the arrival of new shoots are conducive for the initiation and furtherance of the cambial activity, which is maximum in July-August. It is important to mention here, that in spite of the seasonal variation in the activity of the cambium, no growth rings are formed in this tree. This may perhaps be due to non-continuous xylem formation (patches of phloem occurring in between xylem elements).

A study which deserves to be mentioned here is that of Dobbins (1971) who investigated the anomalous cambial activity in *Doxantha unguis-cati.* He propounded that anomaly is brought due to the appearance of first four unidirectional cambial arches, which are near the major vascular strands. Since all the leaves and traces are connected to these strands, he proposed a working hypothesis that the metabolic products transported by the vascular system may be influential in the control and regulation of unidirectional cambial activity.

In the present study we are unable to give emphasis on anatomical features which are responsible for morphogenetic manipulation in controlling the cambial activity due to the diffused nature of the factors causing this abnormal behaviour.

Acknowledgements

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Sezonowa aktywność kambium niektórych drzew tropikalnych. III. Salvadora persica L.

Streszczenie

Badano aktywność kombium wiecznozielonego gatunku *Salvadora persica* L. z płn. Indii w okresie od marca 1974 do lutego 1975 — w pniu głównym i konarach.

Wtórne naczyniowe kambium zachowuje się nienormalnie od strony ksylemu wytwarzając sukcesywnie ksylem i floem. Kambium ma strukturę piętrową (warstwową) i zawiera krótkie, wrzecionowate, izodiametryczne komórki inicjalne promieni. Aktywność kambium w pniu głównym zaczyna się w marcu, osiąga maksimum w sierpniu i stopniowo zanika. W młodej gałęzi zaczyna się w marcu do kwietnia, osiąga szczyt w lipcu i opada aż do listopada.