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Cambial Periodicity and Formation of Wood in *Ailanthus excelsa* Growing Under the Influence of Combined Air Pollutants

By

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With 3 Figures

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Summary

RAJPUT K.S. & RAO K.S. 2005. Cambial periodicity and formation of wood in *Ailanthus excelsa* growing under the influence of combined air pollutants. – *Phyton* (Horn, Austria) 45 (1): 51–64, 3 figures. – English with German summary.

The seasonal behaviour of cambium and formation of secondary xylem was compared between the trees of *Ailanthus excelsa* ROXB. (*Simaroubaceae*) growing under the influence of combined air pollutants (affected trees) and in relatively unpolluted (normal trees) regions. Radial growth in the main stem occurred throughout the year in both normal and affected trees, but the development of secondary xylem was reduced significantly in the latter. In normal trees rapid cambial cell division activity started in June with the arrival of rains and the activity reached peak from July to September. In the succeeding months the intensity of cell division and differentiation declined with the maturation of the leaves. Cambial growth was sluggish from April to June during the drier part of the year. On the other hand, in affected trees cambium activity attained first peak in October when the trees shed their mature leaves and a second peak was observed in January when the development of floral buds and fruit setting was in progress. The differentiation of xylem elements declined in the succeeding months and radial growth became sluggish from March to July. The xylem of *Ailanthus* is diffuse porous with indistinct growth rings in both

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normal and affected trees. In affected trees, the annual radial increment was relatively less and the vessels were arranged in radial or tangential multiples.

Zusammenfassung

RAJPUT K.S. & RAO K.S. 2005. Das periodische Verhalten des Kambiums und die Holzbildung bei *Ailanthus excelsa* unter Einfluss kombinierter Luftverunreinigungen. – Phytion (Horn, Austria) 45 (1): 51–64, 3 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Es wurde das jahreszeitliche Verhalten des Kambiums und die Bildung des sekundären Xylems zwischen Bäumen von *Ailanthus excelsa* ROXB., (*Simaroubaceae*) welche in Gegenden mit kombinierten Luftverunreinigungen (beeinflusste Bäume) und solchen mit relativ sauberer Luft (normale Bäume) wuchsen, verglichen. Das Radialwachstum des Hauptstammes konnte das ganze Jahr über sowohl in beeinflussten als auch normalen Bäumen beobachtet werden, aber die Entwicklung des sekundären Xylems war in den beeinflussten signifikant vermindert. In normalen Bäumen begann mit Einsetzen des Regens eine rasche Zellteilungsaktivität im Juni und die Aktivität erreichte ihren Spitzenwert von Juli bis September. In den darauf folgenden Monaten sank mit der Ausreifung der Blätter die Häufigkeit der Zellteilungen. Das Kambialwachstum war während der trockeneren Zeit des Jahres von April bis Juni langsamer. Andererseits erreichte bei den beeinflussten Bäumen die Aktivität des Kambiums ihre erste Spitze im Oktober als die Bäume ihre reifen Blätter abwarfen und eine zweite konnte im Jänner beobachtet werden als die Entwicklung der Blütenknospen und die Fruchtbildung einsetzten. Die Bildung der Xylemelemente verminderte sich in den Folgemonaten und das Radialwachstum wurde von März bis Juli langsamer. Das Xylem von *Ailanthus* ist sowohl bei beeinflussten als auch bei normalen Bäumen zerstreutporig und mit undeutlichen Jahresringen. In beeinflussten Bäumen war der jährliche Radialzuwachs relativ gering und die Gefäße waren in radiären oder tangentialen Gruppen angeordnet.

Introduction

Much of the data available on climatic control of tree growth and cambial activity is based on observations made on temperate trees where seasonal variation in temperature constitutes the principal climatic driving variable. In the tropical climate, however, rainfall seasonality constitutes the primary climatic determinant of the phenology (BORCHERT 1999). Therefore, cambium activity and radial growth in tropical trees continue either throughout the year (e.g. FAHN 1982, DAVE & RAO 1982, SRINIVAS 1996, RAJPUT & RAO 2002) or for the major part of the year (DAVE & RAO 1982, AJMAL & IQBAL 1987, SRINIVAS 1996, RAJPUT & RAO 2002).

The response of the plants has been studied for morphological, biochemical and anatomical variations brought about by the gaseous pollutants under natural or experimental conditions (e.g. MUDD & KOZLOWSKI 1975, SAX & MURALI 1989, RAO & DUBEY 1990, SCHULZ & al. 1990, SANDERS

& al. 1992) mostly outside the tropical areas. Much work has also been carried out to assess the role of air pollutants on forest decline, wood production, structure, density, moisture content of wood and width of growth rings of affected trees in temperate regions (e.g. KELLER 1980, BAUCH 1986, FENDEL & SCHULZ 1986, FINK 1986, JACUKS & BABOS 1988, SHYAMAL & al. 1991). Similar studies on Indian tropical trees are very limited (e.g. GHOUSE & al. 1984, AHMED & KALLIMULLAH 1986). Apart from these studies, no information is available on the influence of combined air pollutants on the seasonal behaviour of the vascular cambium and the formation of wood in Indian tropical trees. The reduction in cambial activity in species growing under the influence of combined air pollutants may be due to the oxides of sulphur, nitrogen, and ammonia etc. in tropical (AHMMAD & KALLIMULLAH 1986, 1988, GHOUSE & al. 1984, PALIWAL & PALIWAL 1990) and temperate trees (JACUKS & BABOS 1988, SHORTLE & BAUCH 1986). Thus, there is an urgent call for such studies on more tropical trees growing under pollution stress to understand the seasonal behaviour and adjustment of cambium to the changing environment.

Baroda is one of the most polluted cities in Western India because of major industries like Gujarat State Fertilisation Corporation (GSFC), Indian Petrochemical Ltd. (IPCL), Gujarat Industrial Development Corporation (GIDC) and several other chemical factories surrounding it. Therefore, the present study is aimed to elucidate the cambial periodicity, structure and formation of wood in *Ailanthus excelsa* growing under the influence of combined air pollutants.

Materials and Methods

Cambial tissues along with outer xylem and inner phloem of 15–20 year old trees of *Ailanthus excelsa* with a trunk diameter of about 30–35 cm were sampled in the second week of every month for two years from April 1996 to April 1998. Four samples measuring 60 mm X 20 mm in length and width were excised from the main trunk at breast height of ten trees growing close to Gujarat State Fertiliser Corporation (GSFC), Baroda. These trees were considered as affected trees since they show symptoms of air pollution along with the other vegetation. For comparison, samples were also collected from the trees growing in University Botanical Garden and Arboretum. These trees were considered as normal or control trees as they grow in a less polluted area 15 km away from the GSFC. Soon after collection, the samples were fixed in FAA (BERLYN & MIKSCH 1976) and aspirated to remove air from the tissues. Transverse and longitudinal sections of 12–15 µm thickness were cut with a sliding microtome and stained with a combination of tannic acid–ferric chloride–lacmoid (CHEADLE & al. 1953). After dehydration in an ethanol–xylene series the sections were mounted in DPX. The air emission from the fertilizer complex is a combination of various pollutants such as sulphur dioxide, oxides of nitrogen, ammonia and suspended particulate matter. The composition of these pollutants as monitored by the Central Pollution Control Board is given in Table 1.

Table 1.

Ambient air quality monitoring data (average of one week) of the GSFC area, Baroda

| | Pollutants | Concentration in $\mu\text{g}/\text{m}^3$ |
|----|------------------------------|---|
| 1. | Sulphur dioxide | 41 |
| 2. | Oxides of Nitrogen | 24 |
| 3. | Ammonia | 04 |
| 4. | Suspended Particulate Matter | 346 |

The terms cambial zone and cambium have been used to include the entire population of ray and fusiform cambial cells between the xylem and phloem. The cambial activity was determined by counting the number of undifferentiated layers between xylem and phloem in transverse sections. A small portion of xylem adjacent to the cambium was macerated with Jeffery's fluid (BERLYN & MIKSCH 1976) at 60 °C for 24–36 hrs to measure the length and width of vessel elements and of fibres. The vessel lumen diameter and the vessel frequency per mm^2 cross sectional area were obtained directly from transverse sections with a projection microscope. One hundred random measurements were taken to obtain the mean and standard deviation.

Seasonal phenological changes of the trees were recorded at the time of each sample collection. Data on air temperature and rainfall were obtained from the meteorological section of the Physics Department, M. S. University of Baroda.

Results

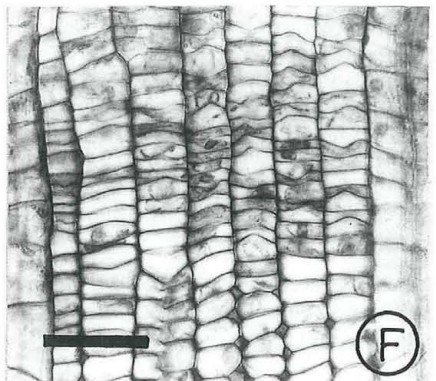
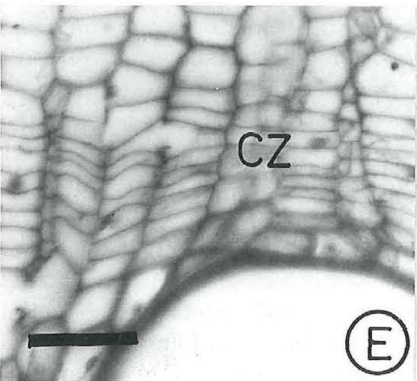
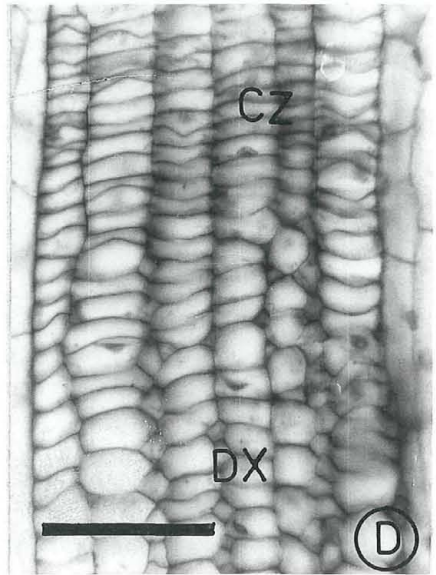
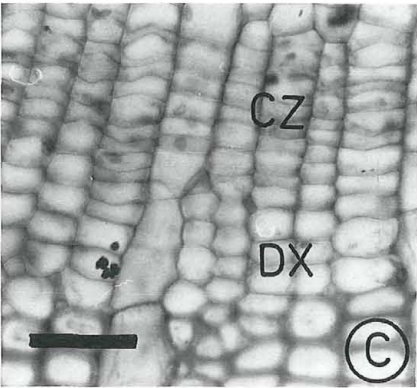
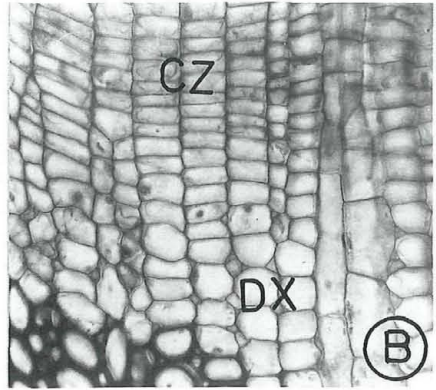
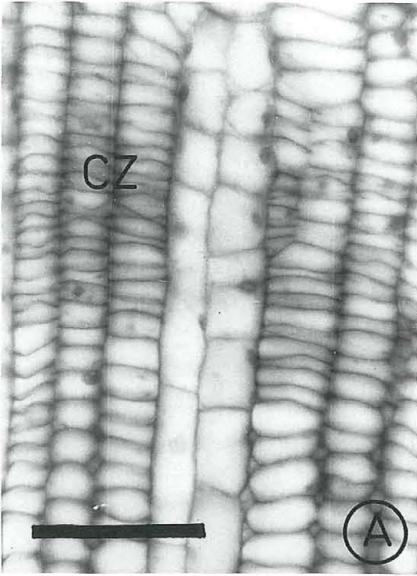
Structure of Cambium

The cambium in *Ailanthus* is non-storied with vertically elongated fusiform initials and more or less isodiametric ray initials. The rays are uni- to multiseriate and heterogeneous. The cambial zone remains narrow with 5–7 layers of cells in each radial file when the cambium growth is sluggish and it is wider with 10–16 layers of cells during the period of peak activity.

Cambial Activity

Cambial cell division and differentiation of xylem occur throughout the year in both the normal and affected trees. In normal trees cambial cells undergo rapid mitotic cell divisions followed by differentiation in June; the activity reaches its peak from July to September with 12 to 16 cells in each radial file (Fig. 1A). In the following months the intensity of

Fig. 1. Transverse view of cambium and differentiating xylem of normal (A–C) and affected (D–F) trees of *Ailanthus excelsa*. A: Peak activity of cambium in August. B: Narrow cambial zone showing declined activity in November. Note the small number of differentiating xylem elements. C: Declined cambial activity in April. Note the relatively narrow cambial zone with very few differentiating xylem elements. D: Peak activity of cambium in August. E: Declined cambial activity in November. Note the narrow cambial zone with very few differentiating xylem elements in left corner. F: Cambium showing peak activity in January. CZ = Cambial Zone; DX = Differentiating Xylem, V = Vessel. Scale Bar = 100 μm .



cell division and differentiation declines gradually (Fig. 1B) and cambial growth remains sluggish during April–May (Fig. 1C).

Although, cambium remains active throughout the year, radial growth in affected trees occurs in two distinct flushes. The first flush of cambial activity reaches its peak in October with 11 to 15 cells in each radial file (Fig. 1D). In November, the cambial cell division and differentiation declines (Fig. 1E) but a second peak of activity is noted in January with 12 to 14 cells in each radial file (Fig. 1F). In the succeeding months, the differentiation of xylem elements is declined and the divisions become sluggish from March to July with 6 to 9 cambial cells in each radial file.

Structure and Development of Xylem

The xylem is diffuse porous with indistinct growth rings in both normal and affected trees (Fig. 2C–D). It is composed of vessels, fibres, tracheids, axial and ray parenchyma cells. The axial parenchyma is aliform to confluent and vascicentric. In normal trees the vessels are mostly solitary but radial multiples of 2–3 cells are encountered occasionally (Fig. 2C) and their lumen diameter is maximal in August ($280 \pm 1.39 \mu\text{m}$) and minimal in February ($212 \pm 2.13 \mu\text{m}$). There is a relation between increase and decrease in vessel lumen diameter with decrease or increase in vessel frequency. Interestingly vessel frequency is maximal in wood formed in February (i.e. 22 ± 1.63 vessels per mm^2) when the lumen diameter is less and it is minimal in August (i.e. 14 ± 1.27 vessels per mm^2) when the lumen diameter is maximal. The annual radial increment in 1996 and 1997 is about 12.7 mm and 12.9 mm, respectively.

Xylem in the affected trees does not show significant variation in its structure except in vessel lumen diameter and vessel frequency. Vessels are mostly in radial or in tangential multiples of 2–6 elements while solitary vessels are encountered rarely (Fig. 2D). Compared to normal trees, vessel lumen diameter is less. However, it is larger in the wood formed in January ($220 \pm 1.42 \mu\text{m}$) and less in the wood formed in April and November ($180 \pm 1.87 \mu\text{m}$). The vessel frequency shows a positive correlation with vessel diameter, the frequency is higher (i.e. 32 ± 1.89 vessels per mm^2) in April and November when the diameter is less and the frequency is less in January (20 ± 1.77 vessels per mm^2) when the diameter is larger. The annual radial increment of the xylem of affected trees for two successive years, i.e. in 1996 and 1997, is about 7.8 mm and 8.3 mm, respectively.

In normal trees, maximal increase of wood biomass occurs from July to September with 17 to 30 differentiating xylem elements in each radial file (Fig. 2A). The development of xylem declines in the following months with 8 to 15 differentiating elements from February to June. Compared to

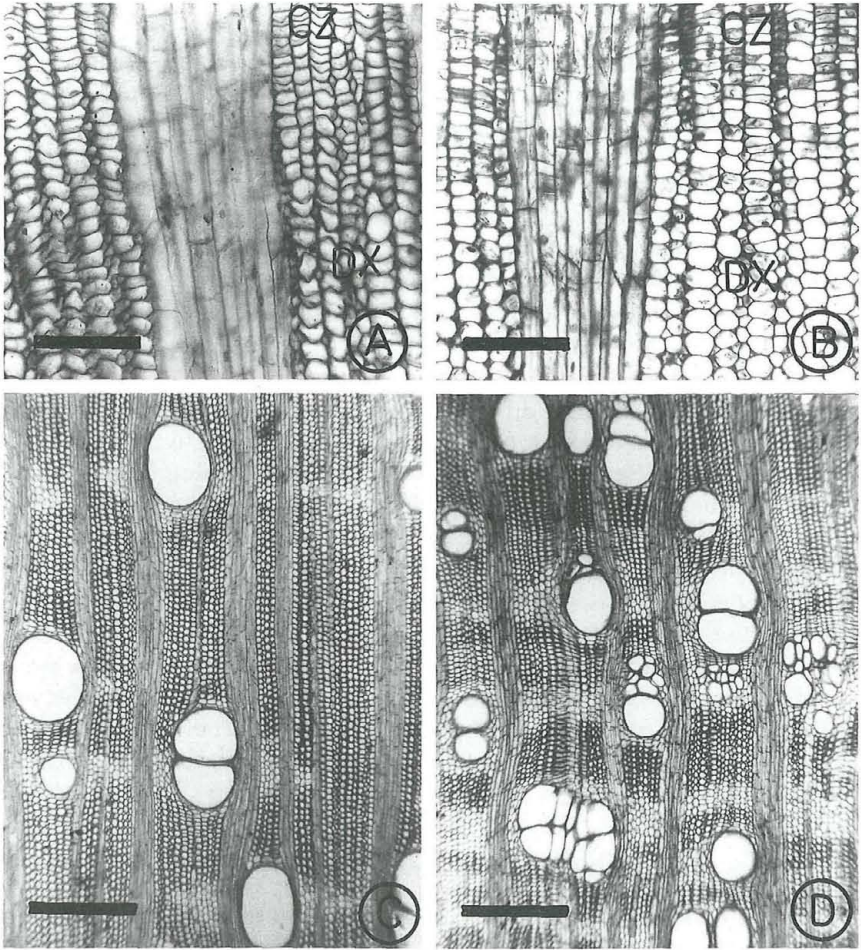


Fig. 2. Transverse view of cambium and differentiating xylem of normal (A & C) and affected (B & D) trees of *Ailanthus excelsa*. A: Differentiating xylem elements in August during the main period of cambial activity. B: Development of xylem culminates in August when the activity attains a peak. C: Structure of xylem in trees growing in an unpolluted area. Note that vessels are mostly solitary. D: Xylem showing distribution pattern of vessels in affected trees. Note that vessels are mostly in groups. CZ = Cambial Zone; DX = Differentiating Xylem, V = Vessel. 2A-B: Scale Bar = 150 μm . 2C-D: Scale Bar = 600 μm .

normal trees the annual xylem increment in affected trees is considerably less. In affected trees the number differentiating elements reach maximum both in October and January (Fig. 2B) while in the remaining months the differentiation is slow with 6–9 elements.

Phenology of the Trees

The trees of *Ailanthus* are leafless for a short period. Sprouting of new leaves starts in March and by May the entire old crown is replaced by a new leaves and the extension growth continues till September. The phenological changes always commence first with the leaves produced in the beginning of growth and spread to those produced later. Yellowing of the leaves starts in October followed by defoliation in November and the trees become completely leafless in February. As the defoliation progresses further floral bud development commences in December. Fruit setting and maturation occur in February and March, respectively, followed by fruit dispersal in the following months.

Cambial activity and phenology of the trees go hand in hand. Rapid cambial cell divisions and differentiation of xylem elements occur from June when the trees are with new foliage. Cell division activity reaches its peak from July to September when the trees bear maturing foliage and it declines in the succeeding months with the yellowing of the leaves. Radial growth becomes sluggish when the trees are completely leafless and the development of floral buds and fruit setting is in progress.

The phenological events in normal and affected trees coincide entirely, but cell division activity and development of xylem elements show considerable variation. However, in affected trees cambium reaches a peak twice within a year. The first peak occurs in October when the trees are with mature and yellowing of the leaves (Table 2). The second peak in January coincides with the leafless condition and the development of floral buds.

Climatic Conditions and Cambial Activity

Rapid division and differentiation of cells in normal trees occur in June with the arrival of rains and the activity culminates between July to September when the rains are heavy. Cambial activity declines and a sluggish growth is observed during the drier part of the year. In affected trees cambial activity reaches a peak at the end of monsoon. A second peak of activity is noticed in January when the temperature is minimum of the year.

Discussion

Trees outside the tropical belt do not grow continuously but rather periods of active growth alternate with periods of inactivity and dormancy. Dormancy of buds and cambium and leaf shedding are responses to environmental pulsation representing a temporary level of adjustment (HALLE & al. 1978). However, in tropical climates the cambium may remain

Table 2.

Periodic changes in the number of cambial layers and differentiating xylem elements in relation to phenology in *Ailanthus excelsa* growing in relatively unpolluted and polluted regions of Baroda.

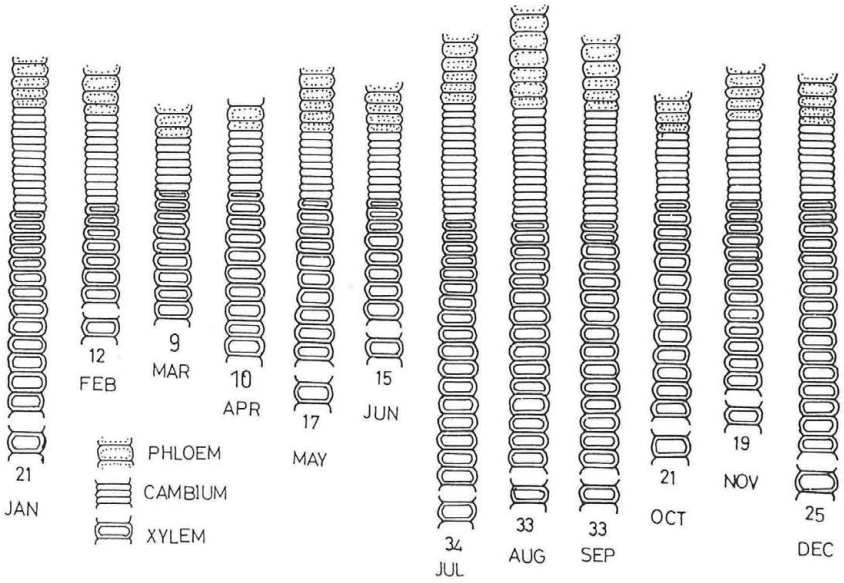
| MON | Phenology of normal trees | Cambial layers | Differentiating xylem | Phenology of the affected trees | Cambial layers | Differentiating xylem |
|-----|---|----------------|-----------------------|---|----------------|-----------------------|
| JAN | Defoliation, flowering and fruit setting | 11 ± 1.38 | 13 ± 2.64 | Defoliation, flowering and fruit setting | 15 ± 1.55 | 17 ± 2.42 |
| FEB | Complete defoliation, flowering, fruit setting and fruit maturation | 12 ± 1.59 | 10 V 2.06 | Complete defoliation, flowering, fruit setting and fruit maturation | 9 ± 2.42 | 16 ± 1.76 |
| MAR | Sprouting of new leaves, fruit maturation and fruit drying | 7 ± 1.53 | 14 V 1.49 | Sprouting of new leaves, fruit maturation and fruit drying | 7 ± 1.28 | 9 ± 1.46 |
| APR | Sprouting of young leaves, fruit drying and dispersal | 9 ± 0.79 | 9 ± 1.87 | Sprouting of young leaves, fruit drying and dispersal | 6 ± 2.25 | 6 ± 1.58 |
| MAY | Full foliage with young leaves and fruit dispersal | 8 ± 1.00 | 10 ± 1.37 | Full foliage with young leaves and fruit dispersal | 6 ± 0.87 | 7 ± 1.72 |
| JUN | Full foliage with young leaves, terminal bud active | 12 ± 1.67 | 9 ± 1.57 | Full foliage with young leaves and terminal bud active | 7 ± 0.77 | 5 ± 1.29 |
| JUL | Full foliage with young leaves, terminal bud active | 14 ± 2.40 | 17 ± 2.12 | Full foliage with young leaves and terminal bud active | 9 ± 1.24 | 6 ± 1.58 |
| AUG | Full foliage with young leaves, terminal bud active | 15 ± 2.84 | 21 ± 2.53 | Full foliage with young leaves and terminal bud active | 12 ± 1.73 | 10 ± 1.31 |
| SEP | Full foliage, leaf maturation, terminal bud active | 15 ± 2.45 | 29 ± 2.16 | Full foliage, leaf maturation, terminal bud active | 11 ± 1.60 | 12 ± 1.72 |
| OCT | Maturation and yellowing of leaves, terminal bud dormant | 11 ± 1.92 | 27 ± 2.51 | Maturation and yellowing of leaves, terminal bud dormant | 13 ± 1.53 | 15 ± 1.24 |
| NOV | Maturation and yellowing of leaves and initiation of defoliation | 10 ± 1.95 | 19 ± 2.09 | Maturation and yellowing of leaves and initiation of defoliation | 9 ± 1.07 | 17 ± 2.21 |
| DEC | Yellowing of leaves defoliation and development of floral buds | 10 ± 1.38 | 16 ± 1.92 | Yellowing of leaves, defoliation and development of floral buds | 12 ± 1.31 | 12 ± 2.12 |

active throughout (DAVE & RAO 1982, FAHN 1982, RAJPUT & RAO 2002) or for the major part of the year (FAHN & SARNET 1963, DAVE & RAO 1982).

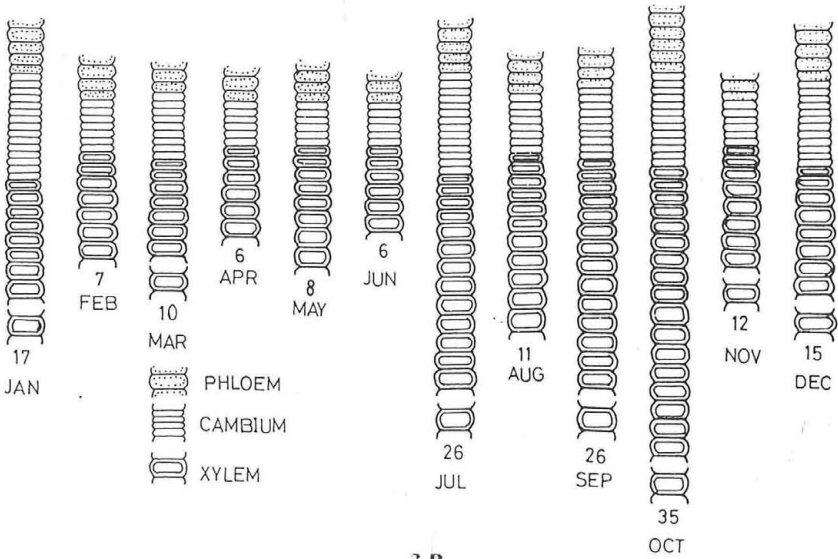
Available literature shows that the cambial growth is greatly influenced by leaf initiation and development (WAREING & al. 1964, KRAMER & KOZLOWSKI 1979, FAHN 1982, PALIWAL & PALIWAL 1990, RAJPUT & RAO 2002). Cambial growth is regulated by the physiological activity of the crown and specifically by translocated substances produced in the shoots (KRAMER & KOZLOWSKI 1979). In evergreen species the correlation between extension growth and radial growth is not clear (WAISEL & al. 1970, FAHN & al. 1968, DAVE & RAO 1982, RAJPUT & RAO 2000). Unlike in other deciduous trees, in *Ailanthus* cambial growth continues when the plants are experiencing yellowing of leaves and defoliation. Although the defoliation is in progress in both normal and affected trees, the cambium remains active throughout the year. Radial growth during defoliation from December to February in both normal and affected trees may be associated with the development of floral buds and the availability of reserve carbohydrates. However, it appears that growth hormones produced for flower development may be sufficient enough for radial as well as reproductive growth. The peak cambial activity in January in affected trees is strange and needs further studies on *Ailanthus*.

Cambial periodicity and xylem production is controlled by various environmental and physiological factors. Among them the effect of temperature is considered to be of primary importance for the reactivation of cambium following its effect on bud break and subsequent shoot growth of trees in temperate climate (KRAMER & KOZLOWSKI 1979). In the present study the cambium remains active throughout the year and it seems there is no correlation with higher (39 °C) and lower temperature (11.4 °C). Besides temperature, rainfall has a direct effect on the enhancement of cambial activity and xylem production (KRAMER & KOZLOWSKI 1979, PALIWAL & PALIWAL 1990, RAJPUT & RAO 2000). However, it has been found that water stress directly inhibits cambial activity by reducing the turgor pressure of the cells and indirectly inhibits it by reducing the growth of leaves and apical meristem thereby reducing the supply of hormones and assimilates (LITTLE 1975). According to LIPHSCHITZ & YADUN 1985 the periodicity of cambium is endogenously determined, whereas external factors like temperature and water supply may advance and/or prolong the growing phase but do not prevent alterations between growing and resting phase.

Fig. 3. Schematic representation of cambial activity and differentiation of xylem and phloem in normal (A) and affected (B) trees. Numbers given bellow each radial row of xylem elements represent the average number (of one hundred counts) of differentiating xylem cells.



3 A



3 B

Though climatic variations are negligible in the present study, much alteration in cambial behaviour is found between normal and affected trees. Although the cambium remains active throughout the year, the number of differentiating xylem cells is less in affected trees. Similar observations are made in our earlier study (SRINIVAS & al. 1998). The reduction in cambial activity of affected trees of *Acacia* may be due to a mixture of air pollutants (RAJPUT 1998). These pollutants may have an influence on the photosynthetic activity of the foliage, thus reducing the supply of food material and growth hormones necessary for cambial growth and differentiation. The reduction of the photosynthetic area by reducing the leaf size in pollution-affected trees is reported for a few tropical trees (VIJAYAN 1987).

The distribution of vessels per mm² area of xylem differs in both normal and affected plants of *Ailanthus*. It has been considered that in extreme habitats a high density of narrow vessels occurs in contrast to low density of wider vessels in mesomorphic environment (ALONI 1987, RAJPUT & RAO 2000). Xylem shows considerable variation in vessel lumen diameter and frequency in affected trees. Compared to normal trees, vessel frequency is higher and lumen diameter is less. A decrease in the cross sectional area of tracheids in pollution affected European spruce and fir (BAUCH 1986) and vessel lumen diameter has been reported for *Holoptelea*, *Acacia* and *Ailanthus* (RAJPUT 1998). It is well known that pollution causes a reduction in growth of the leaves (LITTLE 1975, RAJPUT & RAO 2002, SANDERS & al. 1992, SAX & MURALI 1989, SCHULZ & al. 1990), which indirectly results in the development of vessels with narrow diameter by reducing the supply of growth hormones and assimilates. Therefore, increase in vessel frequency may be the possible cause to compensate the required water supply in affected trees to mitigate the physiological stress on water conduction caused by air pollutants.

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