PHYTON

ANNALES REI BOTANICAE

VOL. 41, FASC. 1 PAG. 1–160 29. 6. 2001

Phyton (Horn, Austria)	**Vol. 41**	Fasc. 1	1–12	29. 6. 2001

Xylem Structure and Annual Rhythm of Development in the Twigs of *Acacia nilotica* (L.) DEL. growing in Different Forests of Gujarat State (India)

K. S. RAO*) K. S. RAJPUT*)

With 5 figures

Received June 8, 2000

Accepted July 4, 2000

Key words: Cambium, phloem, xylem, *Acacia nilotica, Mimosaceae.*

Summary

RAO K. S. & RAJPUT K. S. 2001. Xylem structure and annual rhythm of development in the twigs of *Acacia nilotica* (L.) DEL. growing in different forests of Gujarat state (India). – Phyton (Horn, Austria) 41 (1): 1–12, with 5 figures. – English with German summary.

Periodicity of vascular cambium and development of secondary xylem was studied in the two-three year old branches of *Acacia nilotica* (L.) DEL. growing in moist deciduous (MDF), dry deciduous (DDF) and scrubland (SF) forests of Gujarat State. Xylem development was continued for ten months in MDF and SF and nine months in DDF. Cambial cells began to divide with the sprouting of new leaves in January and culminated in April and May during the drier part of the year in MDF and DDF respectively. The activity then declined gradually and ceased in October in MDF and September in DDF. Compared to other two forests, initiation

*) K. S. RAO, K. S. RAJPUT, Department of Biosciences, Sardar Patel University, Vallabh Vidyanagar 388 120, India.

of cambial cell division and xylem production was delayed by two months in SF. Inception of cambial activity was seen in March with maximal radial growth in July. Xylem production was then ceased in December with the yellowing of leaves. Xylem was diffuse porous with indistinct growth rings in all the three forests. In MDF axial parenchyma cells were vasicentric and aliform to confluent but this pattern was not regularly maintained in other two forests. Considerable variations were also observed in the xylem structure of trees growing in SF. Cambial activity and xylem production in branch was correlated with local climatic conditions and phenology of the trees.

Zusammenfassung

RAO K. S. & RAJPUT K. S. 2001. Die Xylemstruktur und der jahreszeitliche Rhythmus in Zweigen von *Acacia nilotica* (L.) DEL. aus verschiedenen Wäldern des Staates Gujarat (Indien). – Phyton (Horn, Austria) 41 (1): 1–12, mit 5 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die Perodizität des vasculären Kambiums und die Entwicklung des sekundären Xylems wurde in zwei – drei Jahren alten Zweigen von *Acacia nilotica* (L.) DEL. untersucht. Diese wachsen in feuchten laubabwerfenden (MDF), trockenen laubabwerfenden (DDF) und Buschwäldern (SF) des Staates Gujarat. Die Xylementwicklung erfolgte zehn Monate lang in MDF und SF, neun Monate jedoch in DDF. Die Kambialzellen begannen sich gleichzeitig mit dem Austreiben der jungen Blätter im Jänner zu teilen und waren besonders aktiv während der trockenen Zeit des Jahres im April und Mai im MDF und DDF. Die Aktivität sank allmählich und endete im Oktober im MDF und September im DDF. Im Vergleich zu den beiden anderen Wäldern war der Beginn der Zellteilungen und die Xylemproduktion in SF um 2 Monate verzögert. Die Kambialaktivität begann im März und zeigte den maximalen Radialzuwachs im Juli. Die Xylemproduktion endete im Dezember mit dem Vergilben der Blätter. Das Xylem ist zerstreut porig mit undeutlichen Zuwachsringen in allen drei Wäldern. Die Kambialaktivität und die Xylemproduktion in den Ästen waren mit den klimatischen Bedingungen und dem physiologischen Zustand der Bäume korreliert.

Introduction

The phenological variations and environmental changes play an important role in the initiation, peak and cessation of cambial activity (VENUGOPAL & KRISHNAMURTHY 1987, PALIWAL & PALIWAL 1990, IQBAL 1990, LARSON 1994, RAO & al. 1996a, b, RAO & RAJPUT 1999). Moreover, experimental studies carried under controlled environmental conditions also showed considerable variations in the periodicity of cambium (LIPHSCHITZ & al. 1981, 1984, 1985, LIPHSCHITZ & LEV-YADUN 1986). However, there is no information on the species growing naturally under different local climatic conditions (RAO & RAJPUT 1999, RAJPUT & RAO 2000). Our previous studies in some tropical trees on cambial activity and xylem structure have shown significant variations (RAJPUT 1997, RAJPUT & RAO 2000, RAO & RAJPUT 1999). In the main trunk of *Acacia nilotica*, cambial growth occurs for major part of the year in MDF, throughout the year in DDF and in two growth flushes (i.e. in January-May and October-December) in SF (RAJPUT & RAO 2000). Similarly xylem structure remained more or less similar in MDF and DDF but showed significant variations in the distribution of vessels in and axial parenchyma in SF. Although, the samples were collected from the trees having straight trunk and no leaning habit, occurrence of gelatinous fibres was a constant feature in the trees growing in SF. Gujarat State is famous for its varying climatic conditions ranging from moist deciduous to pure desert conditions. The present paper deals with the cambial periodicity and development of xylem in the young branches of *Acacia nilotica* growing in different forests of Gujarat State.

Materials and Methods

Periodic collection of two to three year old branches measuring from 1.5 to 2 cm in diameter were made from six to eight branches of two different trees of *Acacia nilotica* growing in moist deciduous forest (MDF) at Waghai, dry deciduous forest (DDF) at Pavagadh and scrubland forest (SF) at Nakhatrana from Kutch. Samples were collected from January to December 1994 in the second week of every month. Sections of 12-15 μm thick were obtained with the help of sliding microtome and stained them with tannic acid-ferric chloride-Lacmoid combination (CHEADLE & al. 1953). After passing through ethanol-xylene series, sections were mounted in DPX. The procedure used for sectioning, staining and study of the material was same as described in details earlier (RAO & RAJPUT 1999).

Seasonal changes in phenology were recorded at the time of each sample collection. Data on air temperature and rainfall were obtained from the Indian Meteorological Department, Ahmedabad.

Results

Structure and activity of cambium

Cambium was nonstoried with axially elongated fusiform cambial cells and more or less isodiametric ray cambial cells. Cambial rays were predominantly multiseriate but uni-biseriate rays were also noticed occasionally (Fig. 1 A). During the dormant period, cambial zone was narrow with relatively thick radial walls and surrounded by mature xylem and phloem. It was wider with thin radial walls and surrounded by differentiating xylem and phloem elements during active period of growth. Prior to the initiation of cell division, cambial cells underwent swelling and followed by periclinal divisions in all the three forests (Fig. 2A).

Cambial cells began to divide in January in MDF and DDF, reached peak in April and May respectively with 7–10 cells in each radial file (Fig. 1B, C). Activity was then declined in the succeeding months and ceased to divide in October and September in MDF and DDF respectively (Fig. 1D). In SF, periclinal divisions in the cambial zone commenced in

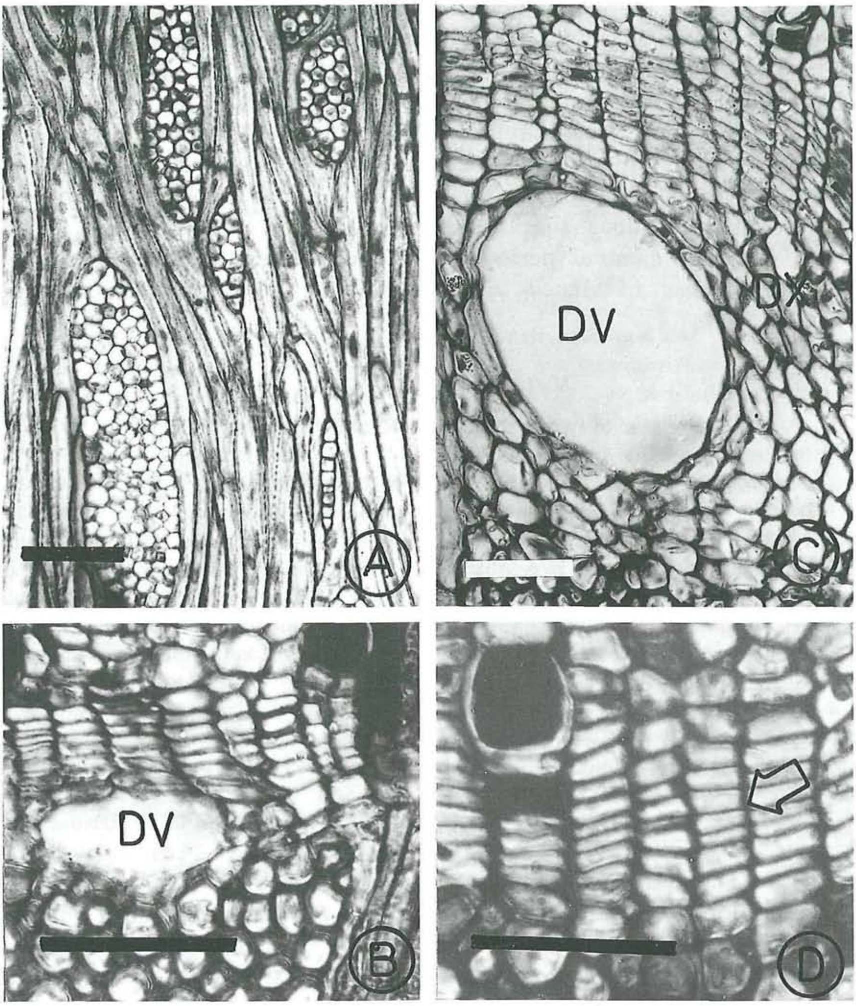


Fig. 1. Tangential longitudinal (A) and transverse (B-D) view of cambium and adjacent xylem and phloem of *Acacia nilotica*. A: Nonstoried arrangement of cells during peak cambial activity. B: Initiation of cambial cell division in January in MDF. Note the differentiating vessel element. C: Wider cambial zone with differentiating xylem elements in May in DDF. D: Dormant cambium surrounded by mature xylem and phloem elements in MDF. Note the thick radial walls (arrow). DV = Differentiating Vessel, DX = Differentiating Xylem. Fig. 1A-D: Scale bar = 75 µm.

March (Fig. 2A) with peak activity in July (Fig. 2B) and the divisions ceased in December. Details regarding the timing of initiation, peak and cessation of cambial activity as well as its duration are illustrated in Figures 3, 4 and 5.

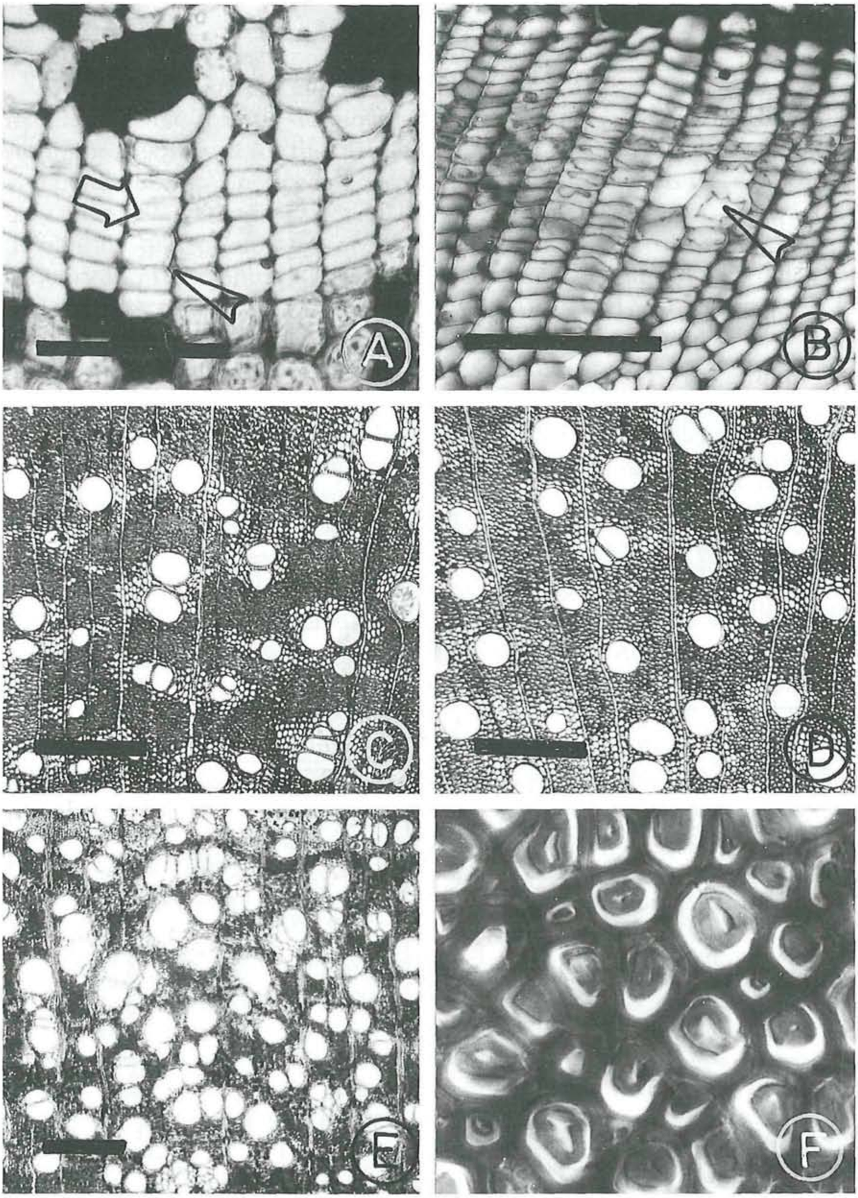


Fig. 2. Transverse view of cambium (A & B) and xylem (C-F) of *Acacia nilotica*. A: Swelling of fusiform cambial cells prior to the inception of cambial activity in February in SF. B: Peak activity of cambium in July in SF. Arrowhead indicates enlarging xylem derivative to differentiate into a vessel element. C: Xylem structure of trees growing in MDF. Note the aliform to confluent type of parenchyma distribution. D: Xylem structure of trees growing in DDF. Pattern of parenchyma distribution is not regularly maintained. E: Distribution of vessels in SF. Note the large lumen diameter of the vessels. F: Xylem with fibers showing gelatinous layer in their lumen. Fig. 2A-B: Scale bar = 75 µm, C-E: Scale bar = 350 µm and F: Scale bar = 30 µm.

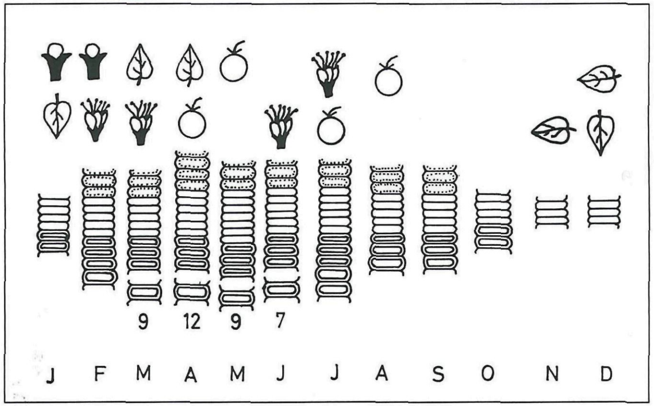


Fig. 3. Schematic representation of cambial activity and differentiating xylem and phloem in moist deciduous forest. Numbers given bellow each radial row of xylem elements in some of the months represent the average number of differentiating xylem derivatives.

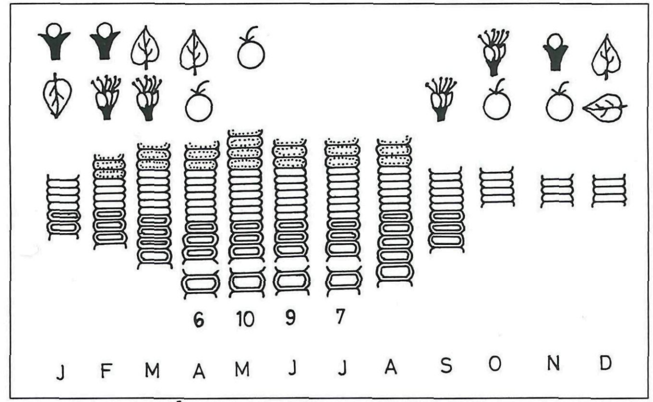


Fig. 4. Schematic representation of cambial activity and differentiating xylem and phloem in dry deciduous forest. Numbers given bellow each radial row of xylem elements in some of the months represent the average number of differentiating xylem derivatives.

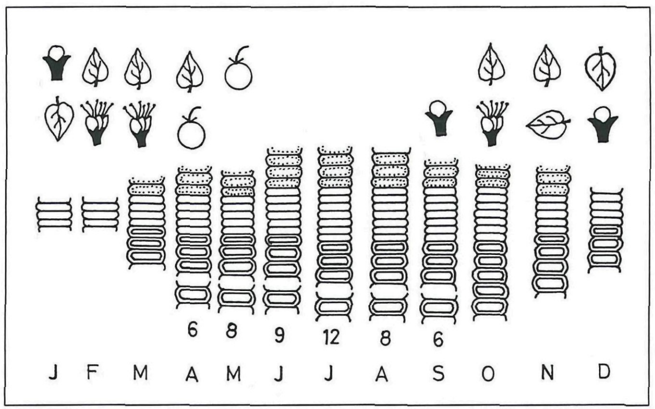
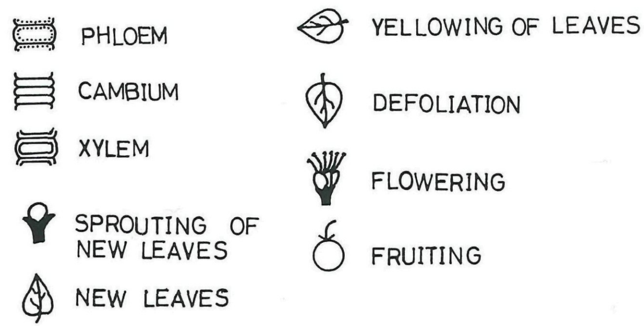


Fig. 5. Schematic representation of cambial activity and differentiating xylem and phloem in scrubland forest. Numbers given bellow each radial row of xylem elements in some of the months represent the average number of differentiating xylem derivatives.



Phenology of the trees

Being an evergreen tree, *Acacia* does not shed all the leaves at a time. In all the three forests, development of new shoots, flowering and fruit setting was observed for the major part of the year but yellowing of leaves and defoliation was noticed once in a year. New shoot buds were produced only once in MDF and twice in DDF and SF (Figs. 3, 4 and 5). Initiation of defoliation and production of vegetative buds were seen in December–January in MDF, January in DDF and December–January in SF. The second flush was seen in October-November in DDF and September in SF. In all the three forests, vegetative bud initiation between December–February was most productive, resulting in the development of several leaves and young shoots.

There was only one period of leaf shedding in all the three forests. In MDF leaf yellowing and defoliation started in November and December respectively followed by sprouting of new leaves in January. In DDF, yellowing of leaves started in December whereas, defoliation and sprouting of new leaves were noticed simultaneously in January. Similarly, yellowing of leaves was observed in November followed by defoliation and sprouting of new leaves in December–January in SF. Although, yellowing of leaves, defoliation and sprouting of new leaves differed in all the three forests but the entire crown of old leaves was replaced by young ones before the second week of March.

Two periods of flowering within a year were seen in all the three forests. Floral buds began to develop in January in all the three forests followed by flowering and fruit setting in the succeeding months (Figs. 3 to 5). Dispersal of matured fruits was started in April and continued up to June. A second set of flowering was differed in all the forests. Floral buds were begun to develop in June–July in MDF followed by fruit setting and fruit dispersal in the succeeding months. In DDF, development of floral buds was seen in September. In SF development of floral buds was seen in October but not followed by fruiting.

Climatic conditions

The state of Gujarat is famous for its varying climatic conditions ranging from moist deciduous (southern part) to pure desert conditions (Kutch). As the tropic of cancer passes through the northern border of the state, winters are severe and summers are oppressively hot with wide range of diurnal temperature. The hottest months of the year are April-May throughout the state. The maximum temperature is varying in different parts of the state being lowest in southern part (37 °C) than the central and northern parts (40.5 °C). State experiences winter from November to February with December–January being coldest months (12–14 °C). The monsoon months are June to September with maximum rains are in July closely followed by August and few light showers some times in the first week of October. November to May are rainless months. In general rain fall is more in southern part (1252–3162 mm) than other parts of the state and lowest in Kutch (80–153 mm).

Development of vascular tissues

The secondary xylem of *Acacia nilotica* consisted of xylem fibres, vessels axial and ray parenchyma. Details regarding the timing of initiation, peak development, cessation of xylem of production and their duration is illustrated in Figures 3, 4 and 5. Xylem production was noticed for period of ten months in MDF and SF whereas nine months in DDF. Development of xylem started before that of phloem and phloem development ceased first followed by the xylem in all the three forests. Xylem production began in January in both MDF and DDF (Fig. 1C) with maximal radial growth in April and May respectively. Then it declined gradually and the cambial zone was seen surrounded by mature xylem and phloem in November in MDF and October in DDF (Fig. 1D). Xylem production commenced in March in SF and culminated in July with maximal number of differentiating xylem derivatives. Development of xylem declined in the succeeding months and ceased in December. Cambial zone was seen surrounded with mature xylem and phloem in January.

Structure of xylem

Xylem was diffuse porous with indistinct growth rings in all the three forests. It was composed of vessel elements, tracheids, libriform fibres and parenchyma cells. However, during the early part of secondary growth xylem possessed uni-triseriate rays (Fig. 2C, D) while they became multiseriate and compound during the latter part of the growth. Annual amount of xylem can be discerned by the development of crystaliferous fibres and abruptly narrow xylem elements produced at the end of cambial activity. Structurally the xylem was more or less similar in MDF and DDF. Vessels were mostly solitary (Fig. 2C, D) but radial multiples of 2-3 cells were also seen. In MDF axial parenchyma were vascicentric and aliform to confluent (Fig. 2C) but this pattern of parenchyma distribution was not regularly maintained in DDF (Fig. 2D). Vessel frequency per 0.5 mm^2 area of xylem in transverse view of xylem was seen about 8–12 in MDF and 9–16 in DDF. Vessel lumen diameter was measured about 56–83 μm in MDF and 54–93 μm in DDF and 65–113 μm in SF.

Compared to other two forests, in SF vessels was either solitary or in tangential multiples of 3–5 cells (Fig. 2E) and their frequency was more ranging from 12–18 vessels per 0.5 mm^2 area of xylem in transverse view. Axial parenchyma were vascicentric and aliform to confluent (Fig. 2E). Occurrence of gelatinous fibres is a common feature in all the three forests (Fig. 2F).

Discussion

The timing of vegetative bud break, initiation of cambial activity and production of xylem tissues in the young branches of *Acacia* growing in all the three forests is shown in figure 3, 4 and 5. It is evident from the figures that in MDF and DDF cambial reactivation and xylem differentiation started simultaneously with the sprouting of new leaves in January while in SF there was two months gap between these two phenomenons. However, reactivation of cambium and differentiation of xylem took place simultaneously with the sprouting of new leaves in *Dalbergia*, *Terminalia* (deciduous) and *Morinda* an evergreen diffuse porous species (VENUGOPAL & KRISHNAMURTHY 1987). Whereas, reactivation and xylem differentiation, commenced about one and half month before the formation of vegetative buds during the second peak of cambial activity in the same plants (VENUGOPAL & KRISHNAMURTHY 1987). In the present investigation, although, sprouting of new leaves occurred in the same months in all the three forests but reactivation of cambium was delayed by two months in SF. Reactivation of the cambium in different months of the same species growing under the different local climatic conditions are reported in some evergreen ring porous species (ZIMMERMANN & BROWN 1979) but such comparative studies are lacking on tropical diffuse porous species. In the main trunk of *Acacia nilotica*, cambium was found active for the major part of the year in MDF, throughout the year in DDF and in two growth instalments in SF (RAJPUT & RAO 2000). Radial growth of branch cambium occurred in single growth flush in all the three forests. Unlike main stem cambium was found dormant from October to December in DDF and such instalments in the cambial growth were observed in SF.

In MDF and DDF maturation of leaves is correlated with the cambial dormancy and cessation of xylem development while in SF cambial cells ceased to divide in December when defoliation and sprouting of new leaves were experienced by the trees. AMOBI 1974 recorded that inflorescence induced wood formation in *Hildegardia barteri*. Similar observation was made in *Bombax cieba*, a deciduous tree (RAO & al. 1996a). But in the present study, cambial cells ceased to divide in September when the second set of flowering occurred in DDF and xylem production remained suspended in the succeeding months when the flowering and fruiting was in the progress. In MDF also xylem production declined when the second set of flowering and fruit setting was noticed. It seems that flowering does not have any effect on cambial activity and xylem production in *Acacia nilotica*.

In mediterranian climate active growth occurs during mild and wet winters and spring, and there is a period of dormancy during the drier and warmer season (LIPHSCHITZ & LEV-YADUN 1986). However, in the tropical climate the cambium remains active throughout (DAVE & RAO 1982a, FAHN

1982) or for the major part of the year (FAHN & SARNET 1963, DAVE & RAO 1982b, RAO & al. 1996b). *Acacia nilotica* being an evergreen tropical tree, undergo radial growth for most part of the year in all the three forests (RAJPUT & RAO 2000).

Periodicity of cambium and xylem production is controlled by various environmental and physiological factors (KRAMER & KOZLOWSKI 1979, AJMAL & IQBAL 1987, LARSON 1994, RAO & RAJPUT 1999). The effect of temperature is considered as a factor of primary importance for reactivation of cambium following its effect on bud break and subsequent shoot growth (KRAMER & KOZLOWSKI 1979). But in MDF and DDF, sprouting of new leaves and reactivation of cambium start in January although maximum temperature is reported lowest for the year. Similar observations are also made on *Acacia raddiana* growing on Negave Mountain (FAHN & al. 1968) and in *Azadirechta indica* (RAJPUT 1997). Thus, though, low temperature play a major role in controlling the cambial activity it does not appear to be only important factor in controlling the activity of cambium in *Acacia*.

Besides temperature, rainfall has also a direct bearing on the enhancement of cambial activity (KRAMER & KOZLOWSKI 1979, RAO & al. 1996a, b, RAO & RAJPUT 1999). However, in MDF and DDF, cambial activity and xylem production culminated in April and May respectively at the end of dry season and it declines with the arrival of rains in June. In MDF and DDF cambial activity and xylem production ceased in October and September respectively when the rains are over, whereas, in SF, cambial activity and xylem development culminated in July when the rains are heavy. Occurrence of peak activity in July in SF may be associated with the availability of ground water, as the annual precipitation is very less and that may not be sufficient enough for maximal growth during the drier part of the year like other two forest types.

Xylem and phloem development is not necessarily synchronised, xylem formation may begin before, after or simultaneously with phloem production and cease earlier, later or together (PHILIPSON & al. 1971). In the present study, xylem development precedes that of phloem and phloem development ceases first in all the three forests. There are some data in the literature regarding duration and rate of xylem differentiation, both these being subject to variation even within the same plants but depending on the environmental conditions (FAHN & al. 1968, VENUGOPAL & KRISHNAMURTHY 1987). However, VENUGOPAL & KRISHNAMURTHY 1987 reported the variations in the differentiation of individual wood elements during the development of xylem. But no such variation in wood elements is observed in the present study.

The distribution of vessels per 0.5 mm^2 area of xylem differs in the plants of all the three forests. It has been considered that plants grown in extreme habitats usually have high density of very narrow vessels in contrast to low density of wider vessels in plants grown in mesomorphic environment (ALONI 1987). This appears true in case of *Acacia* growing in SF. Compared to other two forests, trees growing in SF show more density of vessels in 0.5 mm^2 area of xylem in transverse view but lumen diameter is relatively more.

Acknowledgement

Authors are thankful to the University Grants Commission, New Delhi for the financial support.

References

ALONI R. 1987. Differentiation of vascular tissues. – Ann. Rev. Plt. Physiol. 38: 179–204.

AJMAL S. & IQBAL M. 1987. Seasonal rhythm of structure and behaviour of vascular cambium in *Ficus rumphii*. – Ann. Bot. 60: 649–656.

AMOBI C. C. 1974. Periodicity of wood formation in twigs of some tropical trees in Nigeria. – Ann. Bot. 38: 931–936.

CHEADLE V. I., GIFFORD E. M. & ESAU K. 1953. A staining combination for phloem and contiguous tissues. – Stain Technol. 28: 49–53.

DAVE Y. S. & RAO K. S. 1982a. Cambial activity in *Mangifera indica* L. – Acta Bot. Acad. Sci. Hung. 28: 73–79.

— & — 1982b. Seasonal activity of vascular cambium in *Gmelina arborea* ROXB. – IAWA Bull. n.s. 3: 59–65.

FAHN A. 1982. Plant anatomy (Ed. 3rd). – Pergamon Press, Oxford.

— & SARNET C. 1963. Xylem structure and annual rhythm of development in trees and shrubs of the desert. IV Shrubs. – Bull. Res. Counc. Israel 11D: 198–201.

— , WAISEL Y. & BENJAMINI L. 1968. Cambial activity in *Acacia raddiana* SAVI. – Ann. Bot. 32: 677–686.

IQBAL M. 1990. The vascular cambium. – Research Studies Press Ltd. Tunton, Somerset, England.

KRAMER P. J. & KOZLOWSKI T. T. 1979. Physiology of woody plants. – Acad. Press New York.

LARSON P. R. 1994. The vascular cambium, development and structure. – Springer Verlag, Berlin, Heidelberg, New York.

LIPHSCHITZ N. & LEV-YADUN S. 1986. Cambial activity of evergreen and seasonal dimorphics around the Mediterranean. – IAWA Bull. n.s. 7: 145–153.

— , — & WAISEL Y. 1981. The annual rhythm of activity of the lateral meristem (cambium and phellogen) in *Cupressus sempervirens* L. – Ann. Bot. 47: 485–496.

— , — & — 1984. The annual rhythm of activity of the lateral meristem (cambium and phellogen) in *Pinus halepensis* Mill. and *Pinus pinea* L. – IAWA Bull. n.s.5: 263–274.

— , — & — 1985. The annual rhythm of activity of the lateral meristem (cambium and phellogen) in *Pistacia lentiscus*. – IAWA Bull. n.s. 6: 239–244.

PALIWAL S. P. & PALIWAL G. S. 1990. Influence of climatic variations on the seasonal behaviour of vascular cambium in some Himalayan trees. III *Rhododendron arboreum* SMITH. – Phytomorphology 40: 257–271.

PHILIPSON W. R, WARD J. M. & BUTTERFIELD B. G. 1971. The vascular cambium, its development and activity. – Chapman & Hall. – London.

RAJPUT K. S. 1997. Seasonal cambial activity and wood development in some timber trees growing in three different forest regions of Gujarat State. – Ph. D. Thesis M. S. University of Baroda, Vadodara, India.

— & RAO K. S. 2000. Cambial activity and development of wood in *Acacia nilotica* (L) Del. growing in different forests of Gujarat State. – Flora 195: 165–171.

RAO K. S. & RAJPUT K. S. 1999. Seasonal behaviour of vascular cambium in teak (*Tectona grandis* L.f.) growing in moist deciduous and dry deciduous forests of Gujarat State. – IAWA J. 20: 85–93.

— , SRINIVAS T. & RAJPUT K. S. 1996a. Seasonal anatomy of vascular cambium in young branches of *Bombax ceiba* Burm. – Acta Bot. Indica 24: 17–20.

— , & — 1996b. Seasonal anatomy of cambium in young branches of cannon ball tree (*Couroupita guianensis* AUBL.). – J. Tree Sci. 15: 70–75.

VENUGOPAL V. & KRISHNAMURTHY K. V. 1987. Seasonal production of secondary xylem in the twigs of certain tropical trees. – IAWA Bull. n.s. 8: 31–40.

ZIMMERMANN M. H. & BROWN C. L. 1979. Trees, structure and function. – Springer-Verlag, New York.