



## Cambial periodicity and wood production in *Acacia ehrenbergiana* Hayne growing on dry sites of Saudi Arabia

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### Publication Info

Paper received:  
25 February 213

Revised received:  
19 March 2013

Re-Revised received:  
10 July 2013

Accepted:  
19 August 2013

### Abstract

This study aimed at elucidating the process of cambial activity and wood formation in *Acacia ehrenbergiana* Hayne growing in the Al-Baha region of Saudi Arabia, has revealed that the vascular cambium was active for almost the whole year, producing phloem in two flushes (February-March and August-October), and xylem for about 11 months, with varying pace of cell division and differentiation. A close relationship existed between emergence of new leaves and initiation/acceleration of cambial activity and tissue differentiation. Monthly average of the maximum and mean daily temperature showed negative correlation with cambial-zone width. Relative humidity showed positive relationship with xylem differentiation. Leaf water deficit had an adverse effect on the cambial activity ( $r = -0.94$ ,  $p < 0.01$ ), xylem production ( $r = -0.93$ ,  $p < 0.01$ ) and phloem production ( $r = -0.97$ ,  $p < 0.01$ ). On the whole, moderate temperature, low water deficit and high relative humidity and rainfall favored cambial activity and vascular tissue formation. Annual production of xylem was about five times that of phloem. *A. ehrenbergiana* appears to be a drought-tolerant species by having narrow, dense and thick-walled vessels, thick-walled fibers, high wood density ( $0.9273 \text{ g cm}^{-3}$ ), low vulnerability factor (4.20) and the capacity of thriving well at 35 to 47% water-saturation deficit.

### Key words

Cambial activity, Drought tolerance, Phenology, Water deficit, Xylem production

### Introduction

In a three-dimensional view, vascular cambium exists as a continuous cylindrical sheath about the xylem, and is normally characterized by the presence of vertically elongated fusiform initials and more or less isodiametric or radially expanded ray initials (Iqbal and Ghouse, 1990). The cambium normally undergoes successive active and dormant phases during a growth year in most of the species, except for few arid zone tropical evergreen species that exhibit cambial activity all the year round (Fahn, 1982). Performance of vascular cambium in woody plants is regulated by the genetic make-up, physiological phenomena and environmental conditions of the habitat (Creber and Chaloner, 1990; Pozgaj *et al.*, 1996; Begum *et al.*, 2012). The local environment and the foliage-based type (deciduous or evergreen) of species have a decisive role in regulating the cambial behavior. The timing of cambial reactivation is controlled

primarily by temperature and the maximum daily temperature may have a decisive role in modulating the cambial behavior (Begum *et al.*, 2012). Day length and temperature have been the main environmental factors affecting the cambial activity in the tropical and sub-tropical regions (Yanez-Espinosa *et al.*, 2006; Venugopal and Liangkuwang, 2007; Oliveira *et al.*, 2009).

Fourteen species of *Acacia* are widely distributed in the arid and semi-arid regions of the kingdom (Chaudhary, 1999; Aref *et al.*, 2003). Currently, the genus *Acacia* is catching attention due to its drought-resistance abilities (Oba *et al.*, 2001), capacity to fertilize soil through nitrogen fixation, and use as fodder and as a source of shade and live fencing (Chaudhary, 1999). With their wide distribution in the kingdom, great inherent potential for survival, perpetuation and biomass production in extreme adverse environments, *Acacia* spp. provides interesting material for growth studies. In Saudi kingdom, they are threatened due to

human and environmental pressure, narrow genetic diversity, small population size and low population density. No study has yet been undertaken on the growth behavior of *Acacia* species in the kingdom. It was, therefore, planned to investigate the influence of climatic variations on the activity of cambium and the differentiation of secondary vascular tissues in a widely distributed species, *Acacia ehrenbergiana* Hayne, which has low osmotic potential, narrow vessels and a reduced transpiration rate to resist the xylem embolism in severe drought conditions (Kalapos, 1994). It is a large shrub or small tree, having equally strong branches coming up from the base. It is deciduous in nature and develops purplish red to reddish-grey branches bearing glabrous, stipular spines, yellow globular heads as inflorescence, and greenish-red to purplish-red pods (Chaudhary, 1999).

### Materials and Methods

Saudi Arabia, with an area of 2.5 million km<sup>2</sup>, located between 15°45' N and 34°34' N latitude and 34°40' E and 55°45' E longitude, comprises mainly of desert and semi-desert regions besides the mountains in the southwest region, scattered valleys and the western and eastern coasts (Aref and El-Juhany, 2000).

Five *A. ehrenbergiana* trees of comparable size, vigour and age (about 30-year old), growing wild in Mikhwa in the Al-Baha region of Saudi Arabia (Fig. 1), were selected and tagged for the present study. This region, between 19°40' N latitude and 41°26' E longitude at an elevation of 407 m a. s. l., is a lowland coastal area with hot and humid weather condition. During the study years (2009 and 2010), monthly average of (a) maximum daily



**Fig. 1 :** Map of the Kingdom of Saudi Arabia showing its 13 provinces including Al-Baha (marked in black): In the southwest of Al-Baha lies Al-Mikhwa, the collection site

temperature and (b) the mean daily temperature ranged from 31 to 48 °C and 29 to 42 °C, respectively, with lowest value in January and the highest in June. Relative humidity was maximum in January (67%), declined gradually till June, remained low up to September (52 – 55%), and then increased from October till December (66.2%). The mean monthly rainfall varied between 2.1 to 12.5 mm, with the minimum recorded in June and maximum in March. Mikhwa received more rain during winter and spring than in summer and autumn, with an annual mean rainfall of about 100 mm. The mean values of the weather data collected from the local meteorological station, for the years 2009 and 2010, are presented in Fig. 2.

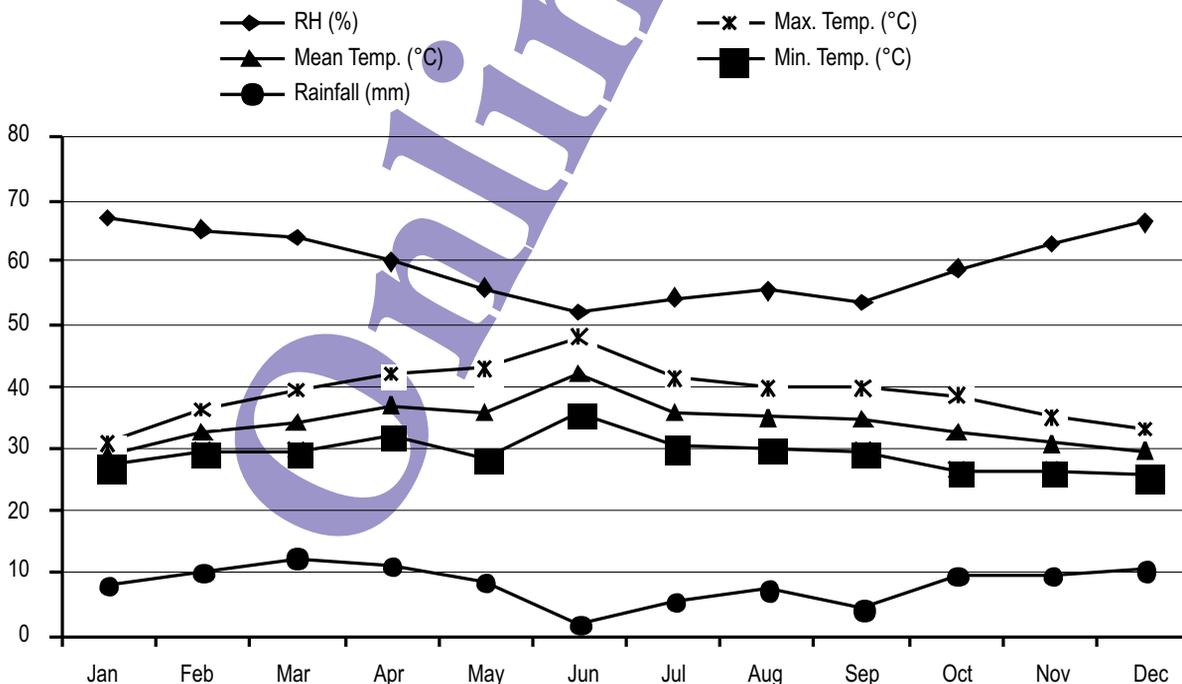
**Collection and processing of samples:** Fortnightly collection of 2cm x 2cm tissue blocks (containing the bark, intact cambium and some portion of wood) was made from the breast-height level of mature branch axes (about 17 cm in diameter) of five tagged trees of *A. ehrenbergiana* Hayne, in early hours of the day, for two consecutive years (2009 and 2010). The blocks were fixed on the spot in FAA (formalin: acetic acid: alcohol)-50. After a week, these were trimmed to a size suitable for microtomy and transferred to alcohol-glycerol solution (50% Ethanol + 50% Glycerol, V:V) for softening and preservation.

**Sectioning and staining :** Permanent slides were prepared for 10 µm thick transverse, tangential and radial sections obtained on a sliding microtome (AO-860, NY, USA). These sections were

stained in haematoxylin-safranin, haematoxylin-Bismarck brown (Johansen, 1940) and tannic-acid ferric-chloride lacmoid (Cheadle *et al.*, 1953) combinations, and dehydrated in ethanol series before mounting on glass slides in Canada balsam. The slides so prepared for all monthly collections were studied thoroughly to determine the periodicity of cambial activity, differentiation of cambial derivatives and the structural features of the secondary tissues produced.

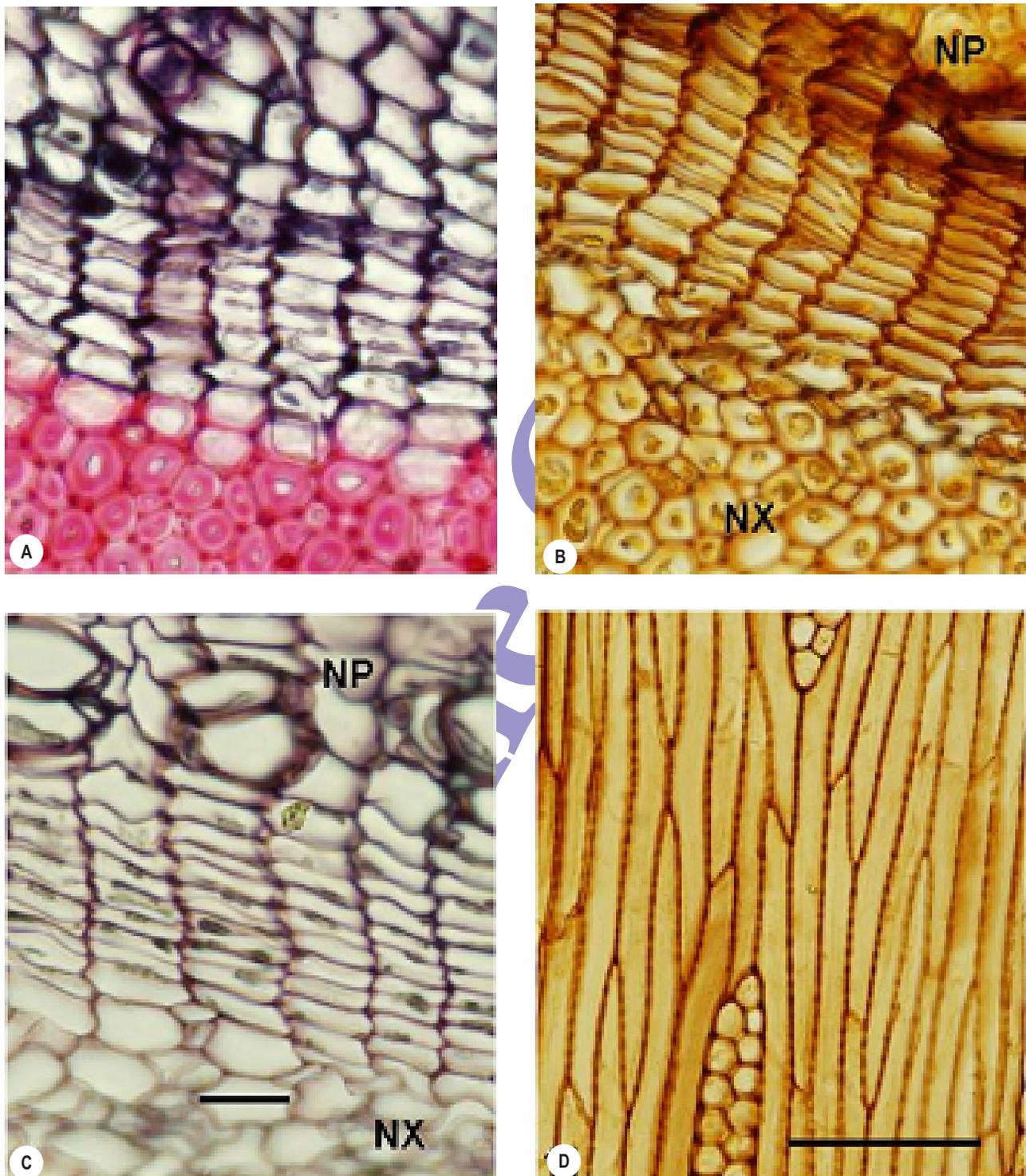
**Maceration technique:** Wood samples were macerated following the modified method of Franklin (1945) to obtain measurements of macerated xylem fibres. Match-stick-sized specimens were heated in a test tube containing solution of equal amounts of glacial acetic acid and hydrogen peroxide (35%), at 70°C in a water-filled beaker for 48h or more, until the specimens became white (due to decomposing of wood resins). The treated specimens were then washed thoroughly in tap water and shaken gently in a test tube to separate the macerated fibres. Fifty fibers from each of the five trees sampled were then measured with micrometer scale attached to a light microscope (Olympus CX41, Japan).

**Area analysis:** Relative proportions of fusiform initials and ray initials on the cambial surface were determined from tangential sections, while those of wood components (vessels, fibers, axial parenchyma and rays) from transverse sections, exposed to digital camera (Olympus DP 72) attached with Olympus BX 51



**Fig. 2:** Graphic presentation of monthly averages of the minimum, maximum and mean daily temperatures (°C), relative humidity (%) and rainfall (mm) recorded at Mikhwa, Al-Baha. Values represent the mean of monthly averages obtained for two years (2009 and 2010)





**Fig. 4 :** The transverse (A-C) and tangential longitudinal (D) sections of cambium from the stem of *A. ehrenbergiana* during a growth year: (A) Dormant cambial zone (5-6 layers) flanked with almost mature cells of secondary phloem (on the upper side) and secondary xylem (on the lower side) around the end of December; (B) Active cambial zone (10-12 layers) with differentiating derivative cells adding new phloem (NP) and new xylem (NX) during February; (C) A wide cambial zone in April with differentiating xylem tissue on the lower side and fully developed, mature sieve-tube elements with associated companion cells on the upper side; and (D) Non-storeyed arrangement of the fusiform cambial initials, showing portions of biseriate rays and thin-walled fusiform initials. Scale bars at C and D = 100  $\mu$ m; scale at C applies to A and B also

microscopic fields (each of 1.608mm<sup>2</sup>) from five slides per tree. The data were subjected to SAS 9.1.3 (updated July 2008) for statistical analysis. Relationships among climatic factors, WSD and growth variables were analyzed using the SAS package for obtaining correlation coefficient.

All measurements of cambial cells were obtained from tangential longitudinal sections, while the data on diameter, wall thickness and density of vessel elements were generated from transverse sections. The measurements of lengths of fibres and vessel elements were obtained from the macerated xylem tissue.

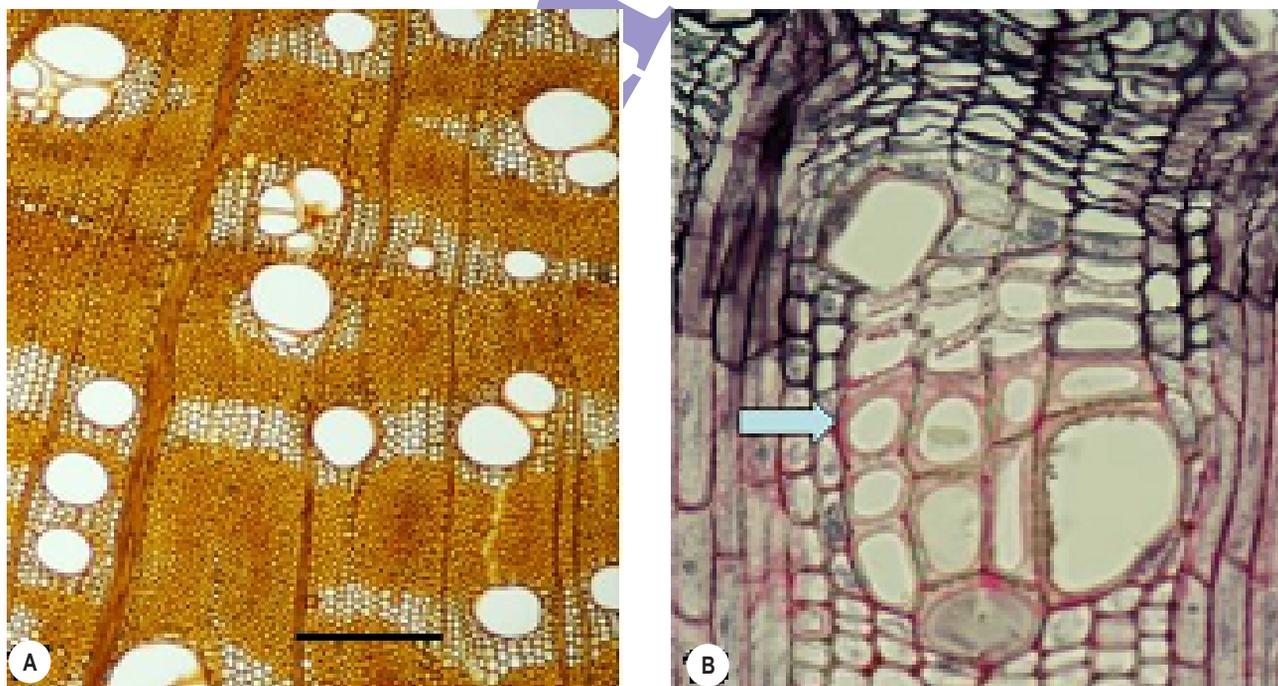
### Results and Discussion

Mature leaves of *A. ehrenbergiana* turned yellow in December followed by onset of defoliation and within 30 days the trees became completely leafless. Sprouting of new leaves started immediately (first week of January), and trees were in full foliage again within a month. Floral buds began to develop in February, followed by heavy flowering and immediate fruit setting. Fruit maturation took two months and dispersal occurred in May-June (Fig. 3). In the mean time, leaves produced in January turned yellow and dropped. New leaves developed in July, followed by flowering and fruiting once again (Fig. 3), but the numbers of flowers and fruits produced this time were relatively less.

Water saturation deficit in *A. ehrenbergiana* leaves ranged between 35% to 47% during the calendar year. It was the

maximum (47%) in summer, followed by a decline (41%) in autumn, and touching the lowest (35%) in winter. It increased again (44.73%) during the spring with the increase in atmospheric temperature. The annual mean WSD was 41.73%. However, the tree is capable to withstand water scarcity by developing some special anti-drought strategies (Aref et al., 2013).

The available literature indicates that the meristematic activity of vascular cambium is periodic and regulated by interaction of several internal and external factors (Rajput et al., 2008; Iqbal et al., 2010a; Begum et al., 2012). In tropical/sub-tropical trees, the cambium becomes active during spring or summer, when temperature is moderately high. Increase in temperature accelerates cambial cell division and tissue differentiation, which slow down or stop during winter months, when temperature goes down (Iqbal, 1994, 1995; Begum et al., 2008). The present study also shows a positive correlation with the climatic data. Temperature affects cambial reactivation, mainly through its impact on bud break, and subsequent foliation (Iqbal and Ghouse, 1985; Volland-Voight et al., 2011). Increase in temperature and/or photoperiod favours cambial growth, if water is not a limiting factor (Fahn and Werker, 1990; Iqbal et al., 2005). Tree size also has a role in regulating the timing, duration and pace of cambial activity. The active phase was longer in dominant than in intermediate or suppressed trees in a population of silver fir (*Abies alba*) in France; growth duration correlated best with tree height, as did growth rate with crown size (Rathgeber et al.,



**Fig. 5 :** Transverse sections of secondary xylem from the stem of *A. ehrenbergiana*: (A) Mature wood showing density and distribution of vessels, broad tangential bands of fibers, and the aliform-confluent axial parenchyma around vessels; (B) Formation of a cluster of vessels (arrow) in differentiating xylem in the month of October; Scale bar = 250 µm for A and 100 µm for B

2011). Cambial activity and xylem differentiation in *A. ehrenbergiana* continued for major part of the year except for a brief spell of dormancy around the late December and early January. Nonetheless, cambial activity of some mangrove trees in Thailand was not driven by climatic factors, but showed strong correlation with sea-water level (Buajan and Pumijumong, 2012).

Active cambium exhibited features like : thin cell walls with shallow primary pit fields; enlarged nucleus with reduced chromaticity; incidence of periclinal and then anticlinal division and proliferation of cambial cell layers as seen in transverse view. Dormant cambium in the stem (late December to early January) comprised of 5-9 cell layers (Fig. 4A). Signs of activity appeared around the end of January after the emergence of new leaves. The activity was low during April to July, which was the time of fruit formation, and gained momentum in August, after the second flush of leaf emergence in July (Fig. 3). Width of the cambial zone increased (10-12 cell layers) gradually from January to March (Fig. 4B), followed by a gradual decline in the number of cambial-cell layers till July, making the cambial zone as thin as it was during its dormant phase, possibly due to a fast differentiation of young derivative cells. Periclinal cell division was on its full swing during August to October, resulting in a broader (10-12 layered) cambial zone. The activity declined in November and stopped by the middle of December (Fig. 3).

The periclinal cell divisions observed in the cambial zone during January to March, when atmospheric temperature and leaf-water deficit were relatively low, resulted in simultaneous differentiation of phloem and xylem (Fig. 3). Subsequently, phloem production stopped in April (Fig. 4C), and mature sieve elements were seen in contact with the cambial zone. Periclinal divisions were low from April to July with little development of xylem alone (Fig. 3), when temperature and leaf-water deficit were quite high and reproductive growth events (fruit formation and maturation) were in progress. After re-emergence of new leaves (second flush) in July, cell division became vigorous, giving rise to phloem and xylem simultaneously. Phloem production stopped in October, whereas xylem formation continued till December (Fig. 3), having its peak during August-October.

Thus, the cambial activity in *A. ehrenbergiana* stem continued almost all the year round, forming secondary phloem in two separate flushes of 2 and 3 months and secondary xylem in a continuous spell of 11 months. The pace of cell division and cell differentiation varied during the active phase of cambium, depending on seasonal climatic conditions. The cambial-zone width declined when differentiation of derivative cells went faster than their production by periclinal division.

Width of the cambium in *Tectona grandis* trees growing in Ivory Coast was strongly correlated to monthly rainfall, and

**Table 1 :** Structural details about the cambium and wood of *A. ehrenbergiana* growing wild at Mikhwa in the Al-Baha region of Saudi Arabia. Values represent an average of readings obtained every month of the year during the course of study

Cambium		Wood	
Fusiform initial length (µm)	247.0 ± 14.82	Vessel element length (µm)	149.2 ± 7.46
Fusiform initial width (µm)	14.2 ± 0.85	Vessel radial diameter (µm)	89.8 ± 4.49
Cambial ray height(µm)	337.8 ± 23.64	Vessel tangential diameter (µm)	96.0 ± 5.37
Cambial ray width(µm)	49.7 ± 2.98	Vessel wall thickness (µm)	6.24 ± 0.37
Fusiform Initial area fraction (%)	81.1 ± 4.46	Vessel density mm <sup>-2</sup> wood	22.30 ± 1.56
Cambial ray area fraction (%)	18.9 ± 1.04	Fiber length (µm)	943.0 ± 47.15
Ray cell initial diameter (H) (µm)	13.8 ± 0.68	Average annual wood increment (mm)	2.61 ± 0.42
Ray cell initial diameter (V) (µm)	13.5 ± 0.62	Wood density (g cm <sup>-3</sup> )	0.9273 ± 0.064

**Table 2 :** Correlations of secondary growth events with climatic factors and leaf-water deficit

Growth variables		Climatic factors				Water Saturation deficit (%)
		Monthly mean of maximum daily temperature (°C)	Monthly mean of average daily temperature (°C)	Monthly mean of relative humidity (%)	Monthly mean of rainfall (mm)	
Average cell layers in cambial zone	r	-0.676	-0.653	0.510	0.375	-0.940
	d	45.69	42.64	26.03	14.07	88.36
	t	<b>2.903*</b>	<b>2.724*</b>	1.875 <sup>NS</sup>	1.279 <sup>NS</sup>	<b>8.714**</b>
Average depth of current-year xylem (µm)	r	-0.708	-0.611	0.792	0.469	-0.930
	d	50.12	37.33	62.72	22.01	86.60
	t	<b>3.174**</b>	<b>2.442*</b>	<b>4.102**</b>	1.680 <sup>NS</sup>	<b>8.042**</b>

R = correlation coefficient, d = coefficient of determination, t = observed 't' value; \* = Significant at p<0.05, \*\* = Significant at p<0.01

special “xylem-growth zones” developed within the annual growth rings, corresponding to emergence of new foliage (Die et al., 2012). Fahn (1958, 1959) and Fahn et al. (1968) reported a continuous cambial activity and radial growth in the stem of *A. raddiana*, *A. tortilis* and four species of *Tamarix* growing in the desert of Israel. Reactivation of cambium leading to the first flush of simultaneous differentiation of xylem and phloem in *A. ehrenbergiana* was preceded by the emergence of new leaves in January. However, there was a gap of 3-4 weeks between the second flush of leaf emergence (in July) and the second phase of simultaneous production of phloem and xylem (in August). Thus, the radial growth in the present study is linked to extension growth, as noticed earlier in various woody species (Ajmal and Iqbal, 1987a,b; Rao and Rajput, 1999; Marcati et al., 2008).

Flowering and fruiting in *A. ehrenbergiana* do not seem to suppress cambial activity and tissue differentiation, as both the phenomena progressed together. In species like *Prosopis spicigera* (Iqbal and Ghouse, 1982) and *Streblus asper* (Ajmal and Iqbal, 1987a), the long time gap detected between leaf emergence and cambial activation was ascribed to a probable diversion of growth hormones, produced in expanding young leaves, to the site of emergence of floral buds. In the present study, cambial activity and xylem production were slow, while phloem production stopped during April-July marked with sufficiently high atmospheric temperature and leaf-water deficit. Phloem production in two flushes was interesting; cambial reactivation twice a year, corresponding to the biannual occurrence of flowering and fruiting, was observed earlier in *Psidium guajava* (Khan, 1977).

Simultaneous differentiation of secondary phloem and secondary xylem, as in *A. ehrenbergiana*, has been observed mostly in ring-porous species and rarely in diffuse-porous ones (Ghouse and Hashmi, 1982, 1983). On the contrary, phloem formation preceding xylem formation is common in majority of the tropical and sub-tropical species (Iqbal and Ghouse, 1985; Ajmal and Iqbal, 1987b; Iqbal, 1995; Iqbal et al., 2010b). The ratio between the annual productions of the xylem and the phloem was over 5:1 in *A. ehrenbergiana*, which is not uncommon. On the contrary, Khan (1977) found the extent of phloem production to be at least twice that of xylem in *Psidium guajava*.

We were able to demarcate the annual production of wood on the basis of tangential layers of border (marginal) parenchyma in the diffuse porous wood of *A. ehrenbergiana*. Patterns of vessel morphology also helped, as solitary vessels dominated the early wood, whereas radial multiples and clusters of vessels were more frequent in the late wood. Continuity of xylem production (February to December) ensured formation of a single xylem ring per year, despite that leaf emergence occurred in two separate flushes. Many tropical trees display multiple-ring formation or intra-annual xylem development in correspondence with the number of bud breaks within a year (Amobi, 1974; Die et al., 2012).

The cambial zone of *A. ehrenbergiana* carried 5-12 cell layers in different months of a calendar year. The cambium was non-storied, composed of elongated fusiform initials (with average length of 247 μm and average width of 14.2 μm) and clusters of more or less isodiametric ray initials (Fig. 4D). Cambial rays measured about 338 μm in height and 50 μm in width (Table 1) and were uni- to multiseriate (up to 8-cells wide) and homocellular. They occupied about 19% of the cambial surface in tangential view, the rest being covered by the fusiform initials.

The diffuse-porous secondary xylem showed faintly visible annual-growth marks in the form of layers of marginal parenchyma. The average annual wood production, calculated on the basis of annual wood increments during the last five years, was 2.61 mm. The vessels formed early in the growth year were predominantly solitary, while those produced late in the year were either in radial multiples of 2-3 or in clusters of 4-28 (Fig. 5A-B). They occupied about 12% of the wood area in transverse view. Dimensional details of vessel elements and xylem fibres are given in Table 1. Xylem fibers, constituting about 54% of the transverse wood surface, formed broad tangential bands alternating with axial parenchyma, which exhibited the aliform or aliform-confluent type of distribution pattern (Fig. 5A). Axial parenchyma occupied 22% of the transverse wood-surface area. Some of the axial-parenchyma cells were crystalliferous. Rays were uni- to multiseriate (1-8 cell wide), occupying about 12% area fraction in transverse view. They were homogeneous, comprising of procumbent cells only, as seen in longitudinal views. Wood density was calculated to be 0.9273 g cm<sup>-3</sup> and vulnerability factor of the wood, was only 4.20, showing that the xylem was reasonably resistant against water stress. Vessel elements of *A. ehrenbergiana* also showed tannin deposition on pits as an adaptive feature against drought stress, as reported by Aref et al. (2013) for *A. tortilis* subsp. *raddiana* growing in Saudi Arabia.

The vessel-element length is considered as a sensitive indicator of ecological conditions. Narrow vessels are positively correlated with xeromorphism in dicotyledons (Carlquist, 1966). Further, the small-diameter latewood vessels and the narrow vascentric tracheids near the large vessels help in conduction of water during the air embolism (Carlquist, 1985; Hargrave et al., 1994; Cochard et al., 1997). *Acacia ehrenbergiana* exhibited a high frequency of narrow thick-walled vessels, which offer a high degree of safety under water-stress conditions (Tyree and Zimmermann, 2002; Al-Khalifah et al., 2006). The success of *A. ehrenbergiana* in the harsh environmental conditions of Mikhwa, Al-Baha could possibly involve all these factors.

Of the six *Eucalyptus* species introduced in the hot Riyadh region of Saudi Arabia, *Eucalyptus sideroxylon* (with Vf 16.58) faced dieback problem at merely 20-32% WSD (Al-Zught, 1997; Al-Khalifah and Khan, 2006); nonetheless, *Acacia ehrenbergiana* was able to thrive in conditions with a much higher

(up to 47%) water-deficit level. Rainfall often shows a close correlation with cambial growth and wood development (Volland-Voight *et al.*, 2011). Non-availability of water during long dry season caused a prolonged (5-7 month long) dormancy in different tree forms in Ethiopia (Krepkowski *et al.*, 2011).

Width of the cambial zone (in cell layers) showed a significant negative correlation with monthly average of the maximum ( $r = -0.676$ ;  $p < 0.05$ ), and the mean ( $r = -0.653$ ;  $p < 0.05$ ) daily temperatures and leaf WSD ( $r = -0.940$ ;  $p < 0.01$ ), and a non-significant positive correlation with the monthly mean rainfall ( $r = 0.375$ ) and relative humidity ( $r = 0.510$ ). However, humidity together with the monthly maximum and mean temperatures showed a strong positive correlation with xylem formation, whereas water deficit had a strong negative correlation with it (Table 2). A moderate temperature and low water deficit could sustain cambial activity; a high rainfall and relative humidity, further enhanced the cambial activity and the consequent xylem formation.

Climatic factors have a joint effect on the cambial activity and tissue differentiation, and may not be assessed in isolation. As expected, water deficit heavily affected the growth activities of *A. ehrenbergiana*, with leaf WSD showing a negative correlation with xylem production ( $r = -0.93$ ,  $p < 0.01$ ). Heavy drought stress resulted in the production of high-density wood ( $0.9273 \text{ g cm}^{-3}$ ), thick-walled fibers, high fiber transverse-wall-area fraction, thick-walled narrow vessels, and low xylem vulnerability factor (Vf 4.20), rendering *A. ehrenbergiana* a drought-tolerant species. Al-Khalifah *et al.* (2006) reported similar effects of drought on *Calligonum comosum*, a shrub growing wild on Saudi sand dunes.

### Acknowledgments

The authors gratefully acknowledge funding of this research by the Deanship of Scientific Research at the King Saud University of Riyadh through the Research Group Project #VPP 226.

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