IAWA Journal, Vol. 31 (3), 2010: 293–307

PHENOLOGY AND RADIAL STEM GROWTH PERIODICITY IN EVERGREEN SUBTROPICAL RAINFOREST TREES

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SUMMARY

A close relationship between leafing, flowering, fruiting and radial growth has been conjectured to occur in tropical and subtropical rainforest trees. Radial stem growth, in particular, has been associated with the activity of the two secondary meristems, the vascular cambium and, to a lesser degree, the phellogen. In tropical trees vascular cambium activity may occur either virtually year-round, or it may be restricted to a short season. Phellogen and vascular cambium activities may or may not correspond to each other. In subtropical environments, even evergreens may demonstrate seasonal phenology in leaf initiation, flowering and seed set. In the present study, phenological events were analyzed in the evergreen species *Aphananthe monoica*, *Pleuranthodendron lindenii* and *Psychotria costivenia*. A correlation analysis showed that more than half of the variation is shared by phenological event variables (leafing, flowering and fruiting) and radial growth variables (vascular cambium and phellogen activity, and vascular tissue differentiation). Leaf initiation, flowering and vascular cambium activation were the most closely-related simultaneous events during the summer; whereas fruiting, phellogen activity and vascular tissue differentiation were the most closely-related simultaneous events during the summer and fall. This could explain why the leaf initiation and expansion stages, which produce growth regulators, are directly involved in radial growth.

Key words: Radial growth, vascular cambium, phenology, evergreen trees, Mexico.

INTRODUCTION

Phenological events related to tree leaf renewal, flowering and fruiting, as well as cambium activity may have periodic rhythms (Frankie *et al.* 1974; Breitsprecher & Bethel 1990). In some tropical tree species, phenological events may also be simultaneous

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Associate Editor: Steven Jansen

(Lieth 1974; Killmann & Hong 1995) and are related to radial growth (Borchert 1994; Iqbal 1995; Schöngart *et al.* 2002; Marcati *et al.* 2008). Worbes (1995) suggests that phenological events provide a starting signal for growth in an individual population or a plant community. Flushing is usually associated with shoot extension, while flowering may or may not be (Schöngart *et al.* 2002).

The radial growth of stems and branches in most woody plants is primarily the result of vascular cambium activity and, to a lesser extent, of phellogen activity (Philipson *et al.* 1971; Kozlowski *et al.* 1991; Catesson 1994). Although the structure and function of vascular cambium has been exhaustively studied in various temperate species and a few tropical ones, studies on periodicity of the cambial activity of tropical trees are still scarce (Hallé *et al.* 1978; Catesson 1994; Marcati *et al.* 2008) as are those of phellogen activity (Waisel 1995).

It is known that vascular cambium is not active all year round; the activity is periodic and seasonal (Philipson *et al.* 1971; Iqbal 1994; Rao & Rajput 1999; Chowdhury *et al.* 2008), and apparently, the annual rhythm of phellogen activity is independent of that in vascular cambium (Waisel 1995). In tropical trees, the vascular cambium and phellogen may remain active either year-round, or the active period may be as short as in temperate species (Iqbal 1995; Waisel 1995). The seasonal behavior is affected by a variety of factors, including the genetic constitution of the plant, physiological processes within the plant, and environmental factors. Genetic factors rather than environmental factors may explain why different species, and also individuals of the same species, growing in the same site under similar environmental conditions, could have different patterns (Philipson *et al.* 1971; Waisel 1995).

In temperate-zone tree species, periodic growth in height and diameter is related to the production of hormones. However, no such relationship is known to occur in tropical trees (Hallé *et al.* 1978). Some authors suggest that the reactivation of the vascular cambium is closely related to leaf-flushing, as auxins, which are produced by the expanding buds and leaves, stimulate cell division in the cambium zone (Iqbal 1995; Little & Pharis 1995).

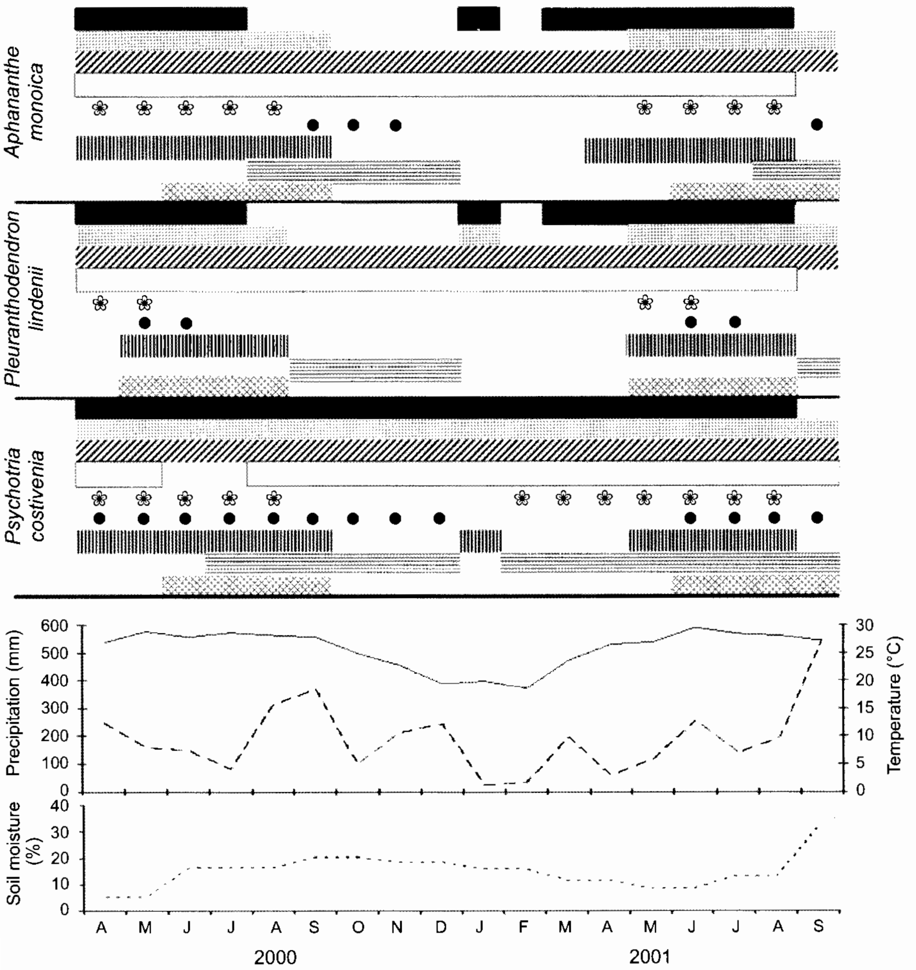
Studies of phenological patterns, and their relationship with environmental variables, have been carried out for several species in different forests in Mexico (Bullock & Solís-Magallanes 1990; Williams-Linera 1997; Ochoa-Gaona & Domínguez-Vázquez 2000). There are, however, few studies that examine the association of phenology with the radial growth of trees and with environmental variables (Makocki 2000; Yáñez-Espinosa *et al.* 2006; Marcati *et al.* 2006; Venugopal & Liangkuwang 2007; Marcati *et al.* 2008).

The climatic variables in both tropical and subtropical forests are not homogeneous throughout the year (Borchert 1999), but rather they exhibit fluctuations and exhibit some degree of seasonality. In the north-central part of the state of Veracruz in Mexico (Gómez-Pompa 1973), there is a subtropical rainforest that has been well-defined, floristically and ecologically.

Since seasonality was observed in the phenology of *Aphananthe monoica*, *Pleuranthodendron lindenii* and *Psychotria costivenia* (Yáñez-Espinosa *et al.* 2006), we hypothesized that radial growth would also show seasonality and that interdependence between these variables would probably be observed. Accordingly, in this study, we analyzed phenology and radial growth in the three species and determined their correlation.

MATERIALS AND METHODS

The study was conducted on a 1-ha, long-term research plot in a subtropical rain-forest located in central Veracruz, Mexico (from 19° 49' to 19° 51' N, and from 96° 32' to 96° 37' W, 420–640 m asl). The average annual temperature along a two-year period



Fgure 1. Phenology and radial growth rhythms of the tree species studied, and climate data of the study site (April 2000 to September 2001).

■ leaf initiation ▨ leaf expansion ▨ leaf mature ☐ leaf fall
❀ flowering ● fruiting ||||| vascular cambium activity
▤ vascular tissue differentiation ▩ phellogen activity
— temperature --- precipitation .... soil moisture utilization

of continuous recording at the site was 22.4 °C; with a minimum of 9.4 °C and a maximum of 34 °C. Rainfall data were taken from the nearest weather station, located in Misantla, 15 km from the study area. The total average annual precipitation was 2217 mm, with a four-month rainy season lasting from June to September (Fig. 1). A total of 15 % of total precipitation falls during the winter, and there is a short period in March and April with average monthly precipitation of 88 mm. The soil is rich in organic matter and calcium.

Three tree species that are native to this forest are *Aphananthe monoica* (Hemsl.) Leroy (Ulmaceae), *Pleuranthodendron lindenii* (Turcz.) Sleumer (Malvaceae), and *Psychotria costivenia* Griseb. (Rubiaceae). All three are evergreen species. However, *A. monoica* and *P. lindenii* have an intermediate shade tolerance, a trait that is characteristic of dominant tree species in late succession, distributed in the intermediate and upper canopy strata, while *P. costivenia* is a shade-tolerant species that is characteristic of the understory (Yáñez-Espinosa *et al.* 2003).

A sample of 20–33 trees per species was selected from a census of trees that had a breast height diameter (DBH) ≥ 1 cm (Table 1). The sample was divided into categories based on the diameter of the trees. Observations for each tree in the sampled categories were recorded bimonthly, during 18 months from April 2000 to September 2001, including two complete growth periods.

Table 1. The number of specimens per tree species and size range of the tree species included in the sample.

Species	Trees (number)	DBH (m)	Height (m)
Aphananthe monoica	30	0.02–1.16	3.0–30.0
Pleuranthodendron lindenii	33	0.03–0.23	2.8–20.0
Psychotria costivenia	20	0.03–0.10	3.0–6.0

Phenological observations were made bimonthly in all sampled trees of each species, either directly or aided by binoculars, recording the presence or absence of leaf flushing, expansion, maturity and fall, and the flowering and fruiting of each individual. Leaf expansion was determined by labeling, immediately after leaf flushing, 10 leaves of three individuals per species, and measuring bimonthly the length and width increment of the blade. Leaf maturity was reached when blade length and width remained unchanged. Ten 0.5-m^2 traps were placed beneath the crowns of the tallest trees to confirm the presence of fruits.

Cambium activity, vascular tissue growth, and phellogen activity were observed bimonthly by collecting branches from only three trees per species, which were cut in 1–2 cm long segments, and fixed in glutaraldehyde (Ruzin 1999). In the laboratory, the segments were washed with phosphate buffer solution (pH = 7.4) and stored in 70 % ethanol. The samples were then cut into 0.5–1 cm thick pieces and dehydrated with ethanol. They were infiltrated by immersion in stepped concentrations of 2-hydroxyethyl methacrylate (Aldrich Chemical Company) in ethanol until they could be inserted into gelatine capsules filled with 100 % 2-hydroxyethyl methacrylate. The samples were then polymerized at 45 °C for 24 h. Transverse sections 2 μm thick were then prepared with a rotary microtome and stained with toluidine blue (Ruzin 1999). Wounds were made in the vascular cambium of the trees using wooden skewers 5 mm in diameter. At the end of the first growing season, five trees of each species were selected, and a section of stem was removed where the wound had been made. The samples were fixed in formalin-ethanol-glacial acetic acid, and stored in 1 : 1 : 1 glycerine-ethanol-water until they were sectioned. They were then washed in running water, and 40-μm transverse sections were cut using a sliding microtome. The sections were stained with safranin-fast green (Ruzin 1999) and mounted in synthetic resin. The samples were examined using an image analyzer (Media Cybernetics, Image-Pro Plus v.3.1).

Diametric frequency classes were used to summarize the phenological events and radial growth data. Spearman's Rank correlation coefficient (r_S) was calculated, in order to determine the association between the phenological events (leaf initiation and expansion, flowering, and fruiting) and timing of radial growth (cambium activity, vascular tissue growth, phellogen activity) for each species because they are discrete variables. The three species that were studied are evergreen and, therefore, there were always some trees that had completely expanded mature leaves, and leaf fall was registered almost all year round; these leaves were not included in the analysis. Statistical analyses were carried out using the MYSTAT software (SYSTAT software Inc.).

RESULTS

Phenology

While all three species showed seasonal phenology, the initiation and length of the phenophases differed among species (Fig. 1). The leaf initiation phase is synchronous in the majority of trees for the three species studied. However, *Psychotria costivenia* had a continuous leaf initiation throughout the year, except for September 2001, while in *Aphananthe monoica* and *Pleuranthodendron lindenii* leaf initiation occurred during only three months (April–June 2000; May–July 2001). Moreover, *A. monoica* and *P. lindenii* had an additional one-month-long leaf initiation period in January, for approximately 50 % and 70 % of the individuals, respectively (Fig. 1). More than 70 % of *P. costivenia* trees remained in the leaf expansion phase for nine months, from March to November. This was four months more than for 70 % of *A. monoica,* and 80 % of *P. lindenii* individuals (May–September, Fig. 1). During the additional one-month period (January, Fig. 1), 60 % of *P. costivenia* trees were in leaf expansion. Mature leaves were present year-round for all individuals sampled. The leaf-fall phase lasted year-round in *A. monoica* and *P. lindenii*, with some exceptions. For example, one exception was in *A. monoica* for a one-month period during the second growth season (in September, although more than 50 % of the trees had falling leaves for nine months from September to May). In *P. lindenii,* leaf fall also lasted year round, but more than 50 % of the trees were in this stage for five months from January to May. In *P. costivenia*, more than 50 % of the trees were in the leaf-fall stage for five months from January to May (Fig. 1). Although *P. costivenia* displayed a long flowering phase, only during 1–2 months were 80 % of individuals in flower at the same time (April–May). In *A. monoica* flowering

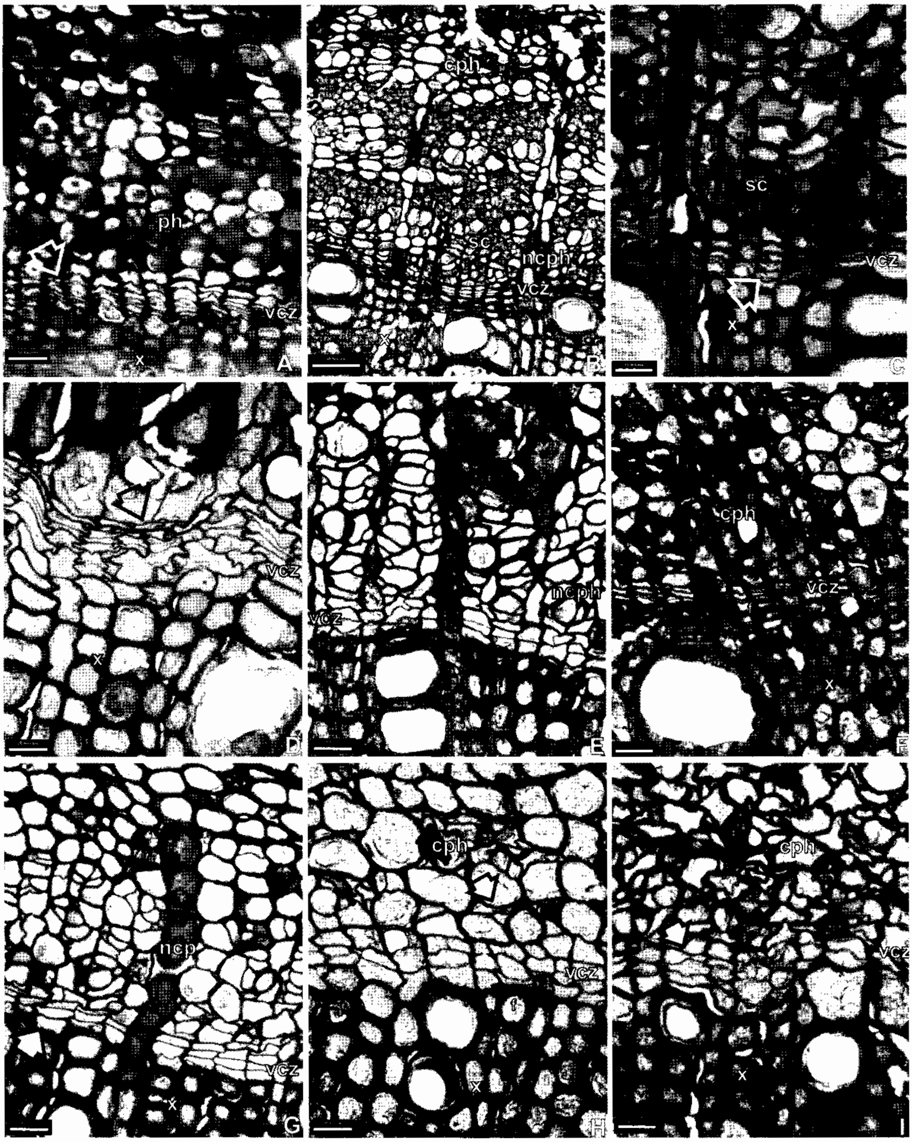


Figure 2. Vascular cambium activity and vascular tissue differentiation rhythm in the three species studied. Transverse sections. — *Aphananthe monoica*: A: cambial zone with periclinal divisions (July) (arrow). – B: cambial zone without divisions, fiber wall deposition in xylem (arrow) and sclereid groups in non-collapsed phloem (November). – C: cambial zone without divisions, thick-walled fibers in xylem (arrow) and collapsed phloem with sclereid bands (January). — *Pleuranthodendron lindenii*: D: cambial zone with periclinal and anticlinal divisions (June) (arrow). – E: cambial zone without divisions, secondary wall deposition in fibers and few collapsed sieve tubes and companion cells (November). – F: cambial zone without divisions, thick fiber walls in the xylem (arrow) and the secondary phloem totally collapsed (January). — *Psychotria costivenia*: G: cambial zone with periclinal divisions (June) (arrow). – H: cambial

lasted 3–4 months, with 60% of the trees in this phase from April to July 2000, and from May to July 2001 (Fig. 1). *Pleuranthodendron lindenii* had the shortest flowering phase, 1–2 months, during which more than 80% of individuals were in flower (April–May). The shorter fruiting phase lasted 1–2 months in *P. lindenii* (June–July) followed by *A. monoica*, which had a 4-month fruiting phase (August–November), and *P. costivenia*, which had an 8-month fruiting phase (April–November). In *Psychotria costivenia,* however, more than 50% of the trees were fruiting during a 3-month interval (July–September, Fig. 1).

Radial growth

All three species showed seasonal rhythms in vascular cambium activity, vascular tissue differentiation and phellogen activity (Fig. 1). In *Aphananthe monoica,* the period of vascular cambium activity lasted five months (April–August), although, during the first year of the study, activity in 33% of individuals extended into September (Fig. 1), and the activity of the phellogen lasted four months, from June to September. Periclinal divisions were observed at the beginning of the period (Fig. 2A), while both the periclinal and anticlinal divisions into xylem and phloem were seen later. The cambial zone was observed to be active in July, with periclinal and anticlinal divisions. Differentiated thin-walled fibers and wide vessels were present near the cambial zone. Non-collapsed phloem was wider than the collapsed phloem because the new phellogen differentiated from inner parenchyma strata in this collapsed phloem region, and therefore the phellogen was actively dividing (Fig. 3A). In September, there were no divisions in the vascular cambial zone, but secondary-wall accumulation was detected in all xylem cells. This secondary-wall accumulation continued to November. Functional sieve tubes and companion cells could be seen in the non-collapsed secondary phloem, together with discrete sclereid groups, which did not merge into bands until November (Fig. 2B). By January, no more divisions were taking place in the vascular cambium. Xylem fiber walls were thick, and the secondary phloem had collapsed into a continuous sclereid band (Fig. 2C).

In *Pleuranthodendron lindenii,* the vascular cambium and phellogen remained active for four months, and were synchronous from May to August (Fig. 1). Periclinal divisions were observed, as well as very few anticlinal divisions, when vascular cambium activity began (Fig. 2D), and the phellogen differentiating into phellem cells with thin walls and phelloderm cells that had thick walls and abundant dark-staining contents (Fig. 3C). Later in June, periclinal and anticlinal divisions into xylem and phloem were observed. The periderm was active, with more phellem divisions. By September, no divisions were seen in the vascular cambial zone and the phellogen. Accumulations of the secondary walls in xylem fibers and the contents of the phloem parenchyma

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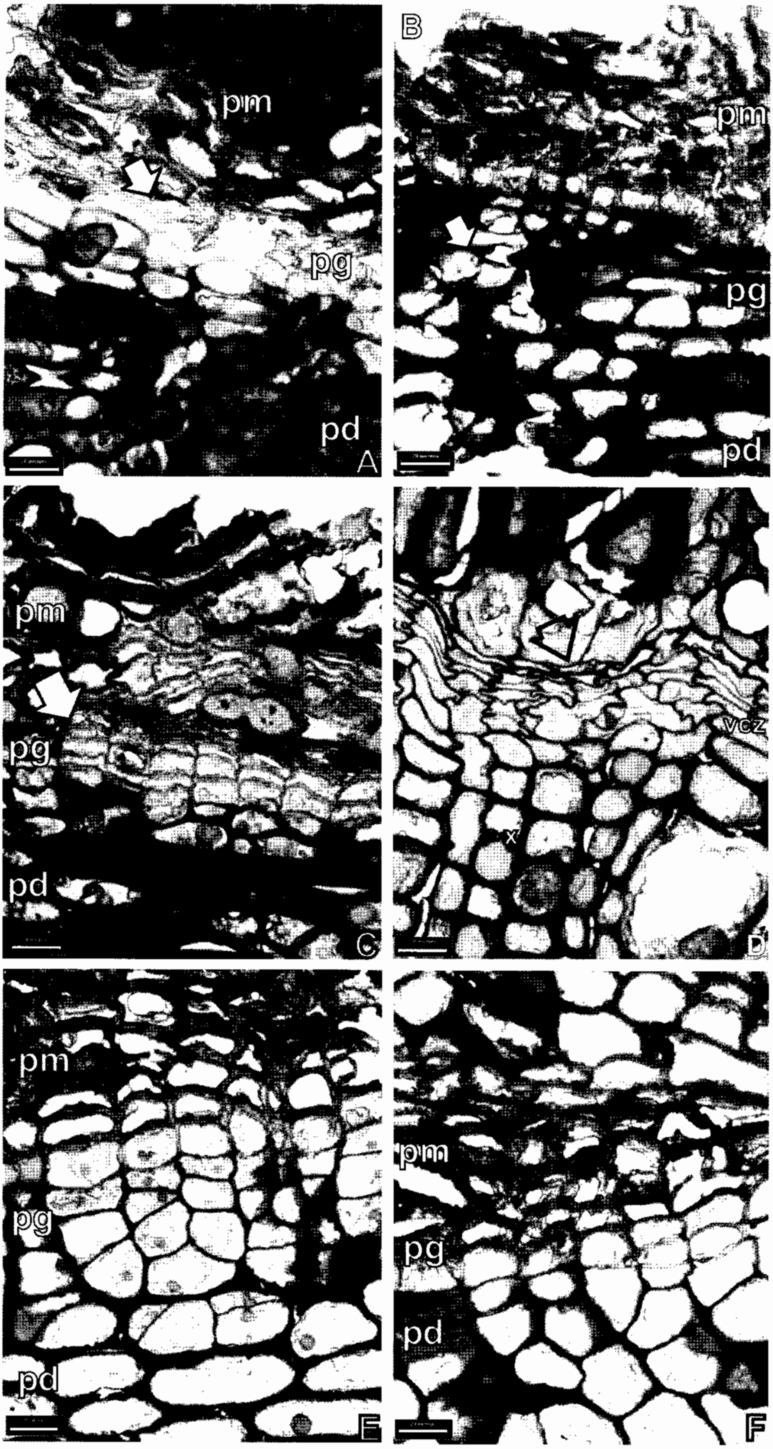
zone without divisions, secondary wall deposition in fibers and in collapsed sieve tubes (arrow) (November). – I: cambial zone with periclinal divisions (January) (arrow). — ncph = non-collapsed phloem; cph = collapsed phloem; ph= phloem; vcz = vascular cambium zone; x = xylem; f = fiber; sc = sclereid. — Scale bars all 20 µm except for B, which is 50 µm.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continued through November (Fig. 2E). In the periderm, the walls of the most recently differentiated phellem cells were slightly thicker and with dark-staining contents (Fig. 3D). By January, no more divisions were taking place in the vascular cambium, the xylem fiber walls were thick, and the secondary phloem was totally collapsed, with abundant dark-staining contents in the parenchyma cells (Fig. 2F).

In *Psychotria costivenia,* vascular cambium activity lasted, in general, for five months (April to August), but for six months (April–September) during the first year of the study, in 33 % of individuals. Notably, a second period of cambium activity was observed during the winter (January). Phellogen activity lasted four months, June to September, with activity also observed during the winter. Periclinal, and a few anticlinal divisions in the developing xylem and phloem, were observed at the beginning of the period, in April (Fig. 2G). Phellogen presented periclinal divisions; the phellem had slightly thick cells, and the phelloderm thin-walled cells (Fig. 3E). In September, there were no divisions in the vascular cambium zone, but, in the periderm, the phellem cells continued their differentiation. Secondary-wall accumulation continued through November in the xylem fibers, and discontinuous regions of collapsed secondary phloem with parenchyma cells that contained abundant prismatic crystals were observed during this month (Fig. 2H). In November, the phellogen was inactive, and in the phellem the last differentiating cells were of narrow radial diameter and had thick walls (Fig. 3F). Periclinal, and a few anticlinal divisions, were also seen in the vascular cambium region during January (Fig. 2I). Divisions in the vascular cambium region were not seen in March, but secondary fiber wall deposition continued in the discontinuous regions of non-collapsed secondary phloem.

Phenology – radial growth

Radial growth and phenology relationships for the three species are summarized in Table 2. The phenological variables that were more correlated with the cambial activity in *Aphananthe monoica* were flowering, leaf initiation and expansion. The correlation was positive for the three variables (Table 2). The association between vascular tissue differentiation and fruiting was positive and was negatively correlated with expansion of the leaves and with flowering. Phellogen activity was positively associated with expansion of the leaves (Table 2). Cambial and phellogen activity were positively cor-

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Figure 3. Phellogen activity, phellem and the rhythm of phelloderm differentiation in the three species that were studied. Transverse sections. — *Aphananthe monoica*: A: phellogen with periclinal and anticlinal divisions (July) (arrow). – B: phellogen with scanty periclinal divisions (arrow), phellem and phelloderm cells next to the phellogen with thinner walls and dark contents (November). — *Pleuranthodendron lindenii*: C: phellogen initial divisions (arrow) with differentiating phellem cells with thin walls, and phelloderm cells with thick walls and abundant dark contents (May). – D: phellogen without divisions (September) (arrow). — *Psychotria costivenia*: E: phellogen with periclinal divisions (arrow), the phellem cell walls slightly thickened, and the phelloderm with parenchymatous cells (June). – F: phellogen without divisions, differentiating phellem cells with reduced radial diameter and thick walls, and phelloderm cells with thick walls (November). — pg = phellogen; pd = phelloderm; pm = phellem. — Scale bars all 20 µm.

Table 2. Correlation matrix for the radial growth and phenology variables of the three species.

Species Radial growth phenology	Cambial activity	Vascular tissue differentiation	Phellogen activity
Aphananthe monoica			
Leaf initiation	0.48**	-0.69**	-0.07
Leaf expansion	0.47**	-0.11	0.46**
Flowering	0.49**	-0.44**	0.07
Fruiting	-0.23*	0.74**	0.24*
Pleuranthodendron lindenii			
Leaf initiation	0.72**	-0.73**	0.72**
Leaf expansion	0.52**	-0.17	0.52**
Flowering	0.19	-0.38*	0.19
Fruiting	0.75**	-0.37*	0.75**
Psychotria costivenia			
Leaf initiation	0.22	-0.22	-0.15
Leaf expansion	0.13	-0.13	-0.13
Flowering	0.17	-0.17	-0.40
Fruiting	-0.02	0.02	0.77**

* P<0.05, ** P<0.0001

related with leaf initiation and expansion and fruiting in *Pleuranthodendron lindenii*; but there was a negative relationship between the differentiation of the vascular tissue and all phenological variables. There was a positive association between phellogen activity and fruiting for *Psychotria costivenia* alone (Table 2).

DISCUSSION

Vascular cambium activity

Phenology and vascular cambial activity were seasonal in *Aphananthe monoica* and *Pleuranthodendron lindenii*. *Aphananthe monoica* and *P. lindenii* undergo a simultaneous 4- to 5-month period of vegetative and radial growth. In contrast, *Psychotria costivenia* exhibits continuous vegetative growth, lasting from winter to summer, and two radial growth periods per year. This can be explained as, when new leaves are periodically produced in tropical evergreen species, the cambial activity is also periodical (Fahn & Werker 1990). Moreover, there are differences in the period of activity of the vascular cambium and the phellogen for each species.

All three species can be classified as evergreen, given that these species are in leaf throughout the year, continuously producing new leaves and dropping senescent leaves. Leaf initiation occurs during the warm season when seasonal temperature variations are moderate, but the relationship between the season and moisture levels is weak. This set of environmental conditions favors continuous periods of leaf initiation and fall, as moisture stress does not influence the timing of old leaf fall. Rather, leaves do not fall until the optimum temperature for leaf replacement has been reached (Jackson 1978). This is a likely explanation for the extensive leaf initiation period in *P. costivenia* and *A. monoica* and the winter period in *P. lindenii*, as the winter soil moisture content averages 17–18% (Yáñez-Espinosa *et al.* 2006), due to the percentage of clay (27%) and organic matter content (7%) of the soil (Yáñez-Espinosa, unpubl. data).

Leaf initiation is, in general, associated mostly with cambium activity, indicating that these events are concurrent, except in *P. costivenia*. The association between cambium activity and new leaf formation has also been recorded in other tropical and subtropical forest trees (Iqbal 1994; Rao & Rajput 1999; Marcati *et al.* 2008). Kozlowski *et al.* (1991) stated that normal vascular cambium growth is the end result of the equilibrium between several growth regulators, including both stimulators and inhibitors, and the synergetic effects among them. In trees like *A. monoica*, *P. lindenii* and *P. costivenia*, auxins (IAA), abscisic acid and gibberellins are probably synthesized in mature leaves, and transported with the photoassimilates to sink tissues such as the apical and lateral meristems through the phloem, as in other species (Baker 2000). IAA stimulates cell division in the cambium cells and in the developing leaves. In species with diffuse porosity, cambium activity continues even after the end of leaf initiation, due to IAA production in both expanding and mature leaves (Kozlowski *et al.* 1991). In *A. monoica* and *P. lindenii*, however, the growth of the vascular cambium was not reactivated during the short winter leaf-initiation period. This may be due to the low levels of IAA present; it has been demonstrated that some species do not produce auxins in their mature leaves when the day lengths are short (Kozlowski *et al.* 1991). If the high soil moisture content in fall triggered leaf initiation, then low temperatures may limit leaf growth. It is evident that in winter the light conditions that prevail in the microenvironment on the understory are favorable for *P. costivenia*, as the canopy is thinned by deciduous leaf fall of the upper tree species. This explains how leaf initiation and subsequent auxin production stimulate a second period of cambium growth in January.

In all three species studied, cell differentiation in vascular tissue and the leaf initiation and expansion were found to be simultaneous. Although the differentiation of both the vessels and the sieve tubes is induced by IAA, a major hormone produced mainly by young leaves (Aloni 2004), cellular differentiation among the secondary xylem elements is controlled by another supply, which is produced by expanding new leaf buds. This source gradually increases the starch content during the growth period, and latewood differentiation is probably associated with an abundant supply of stored carbohydrates (Wilcox 1962). During expansion of the leaves, the rate of photosynthesis increases, generally peaking before the expansion is completed, and then decreasing steadily until the leaf reaches the senescent stage, reducing the carbon uptake (Dengler 1994; Morecroft *et al.* 2003). It has also been suggested that gibberellins that are produced in the mature leaf, induce the differentiation of fibers in the secondary xylem (Aloni 1991), and this may explain the thickening of the fiber walls in the species studied.

Phellogen activity

Activity in the phellogen lasts for four months in the three species studied. Nevertheless, in *P. lindenii*, the phellogen was active simultaneously with the cambial division period, but, in the other two species, it was displaced by two months. It has been reported that phellogen activity is continuous or periodical in many species and, apparently, their annual rhythm may or may not correspond to vascular cambium activity (Waisel 1995). In *Cupressus sempervirens* L., cambial and phellogen activity were not coincident. The phellogen was only active during one month, at the end of the period of cambial activity (Liphschitz *et al.* 1981). Seasonal changes in phellogen activity were similar to other species that have been studied (Philipson *et al.* 1971; Catesson 1990, 1994; Larson 1994; Iqbal 1994, 1995; Chaffey *et al.* 1998).

The occurrence of phellem cells with thick walls characterized the phellogen dormancy, as observed in the three species and the production of phellem cells and thin-walled square phelloderm cells characterize the phellogen activity period (Waisel 1995) and correspond with the observations that we made in the three species studied.

Radial growth

Several factors can affect the stem diameter, and the most important of these is probably variations in the tissue water content, which may mask the cambium activity (Breitsprecher & Bethel 1990). Trees generally rehydrate and increase the diameter of their stems before the beginning of leaf or flower bud development (Borchert 1994), and this is also suggested by the increase of the geophytoelectrical current during June, July, and January in the three species studied (Yáñez-Espinosa *et al.* 2007).

Flowering and fruiting in the three species studied showed different relationships with radial growth. This indicates that they could be associated with the climate, the microclimate, or by plant-animal interactions. In *A. monoica*, a positive association was observed between the flowering phase and cambium activity, suggesting that flower bud opening is related to the production of auxins, and also to cambium activity. Rao and Rajput (1999) mentioned that maximal cambium activity occurred at the same time as flowering in a deciduous species. Iqbal (1994) stated that vascular cambium activity was stimulated during flowering. During the fruiting phase, in contrast, cambium activity generally decreases to the point of ceasing (Iqbal 1994), as in *A. monoica*, while in *P. lindenii* and *P. costivenia*, the fruiting phase overlaps with cambium or phellogen activity respectively, perhaps due to the relative lengths of both periods.

Previous studies have suggested a close relationship between leaf phenology and radial growth (Worbes 1995; Schöngart *et al.* 2002), and, in fact, such a relationship has been recognized for several tropical and subtropical forest tree species (Iqbal 1994; Makocki 2000; Venugopal & Liangkuwang 2007; Marcati *et al.* 2008). In this study, however, the correlation analysis confirmed that the magnitudes and direction of the relationships were different for each species (Yáñez-Espinosa *et al.* 2006). This could be related to their different positions in and below the forest canopy .

Radial growth periodicity in *Aphananthe monoica*, *Pleuranthodendron lindenii* and *Psychotria costivenia* is correlated with the seasonal reaction of the vascular cambium and, to a lesser extent, with the seasonal response of the phellogen. Both lateral meristems did not show a long cambial activity period, probably because they are growing on the northern limits of the intertropical region (19° 50' N). Microclimate conditions and species-intrinsic factors could lead to differences in the length of the cambial and phellogen activity and in the time of xylem initiation and phloem production. However, it is unknown if this reaction is common to other species that grow at the northern limits of the tropical region, since the activity of vascular and cork cambia have been poorly studied at intermediate latitudes.

ACKNOWLEDGEMENTS

This research was supported by a grant from the Consejo Nacional de Ciencia y Tecnología (CONACYT) to L. López-Mata (0443P-N). The senior author thanks CONACYT for a scholarship (141818) to conduct doctoral studies. The Colegio de Postgraduados provided additional support. We thank Bernardo Vega-Hernández, the owner of the Santa Gertrudis land, for providing facilities to conduct this research. Oliva Godínez-Ibarra and Segundo Zárate provided assistance in the field. L. López-Mata acknowledges CONACYT support for a one-year sabbatical leave, which made it possible to finish this paper.

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