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Seasonal variations in phenological traits: leaf shedding and cambial activity in *Parkia nitida* Miq. and *Parkia velutina* Benoist (Fabaceae) in tropical rainforest

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Abstract

Key message In French Guiana, the leaf and cambium phenologies should not be considered only as exogenous-driven processes, as the dry season, but also as endogenous-driven, as tree development stage.

Abstract Studies of the periodicity of wood formation provide essential data on tree age and on factors that control tree growth. The aim of this work was to investigate cambial phenology and its relation with leaf phenology and climatic seasonality in two briefly deciduous tropical rainforest species belonging to the genus *Parkia*. Wood microcores were collected every 15 days from April 2009 to February 2012 from five trees of each species. The microcores were stained with cresyl violet acetate to facilitate counting the number of cells in the cambial zone, in

the radial enlargement zone and wall-thickening zone. At the same time, we observed leaf shedding pattern in the crown of the same trees. In both species, cambial activity was significantly reduced during the leafless period. In *P. nitida*, these two concomitant events were observed during the dry season whereas in *P. velutina* they can occur anytime in the year with no apparent link with seasonality. In conclusion, the period of reduced cambial activity in some tropical rainforest trees may be independent of rainfall seasonality and not necessarily follow an annual cycle. It appears that leaf phenology is a good proxy to estimate cambial activity.

Keywords Cambial activity · Tropical rainforest · Climate · Leaf shedding pattern · French Guiana

Introduction

Studies of the periodicity of wood formation provide key data that constitute the basis of dendrochronological

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studies (Boninsegna et al. 2009; Pumijumnong 2013). These data are therefore very important to estimate tree age (Worbes et al. 2003; Brienen 2005), to study wood properties (Bouriaud et al. 2005; Franceschini et al. 2013), or more generally, to study forest dynamics (Rozendaal and Zuidema 2011) and carbon storage (Worbes and Raschke 2012).

Tree growth is controlled by both endogenous factors, such as plant genotype or physiological processes (Schrader et al. 2003, 2004), and by exogenous factors, such as rainfalls and light availability (Deslauriers and Morin 2005; Gricar et al. 2007), and these factors affect tree growth in an interrelated way.

In temperate regions, winter conditions influence tree phenology through a synchronized annual period of rest for both primary and secondary growth, which, in deciduous species, is associated with leaf shedding. In this case, climatic conditions are the main factor that controls tree growth dynamics and the long winter-induced rest period leaves markers in the wood and on the stems.

In tropical rainforest, climatic parameters (temperature, light, and rainfall) are less restrictive, and fluctuations in primary and secondary growth can be caused by various environmental factors: rainfall variations (Bullock and Solismagallanes 1990; Wright and Cornejo 1990; Pumijumnong et al. 1995; Worbes 1995; Bullock 1997; Borchert 1999; Worbes 1999; Oliveira et al. 2011; Grogan and Schulze 2012), annual floods (Callado et al. 2001; Schöngart et al. 2002, 2005; Dezzeo et al. 2003), variations in day length (Borchert and Rivera 2001; Williams et al. 2008), variations in peaks of irradiance (ter Steege and Persaud 1991; van Schaik et al. 1993; Wright and van Schaik 1994), and by internal rhythms (Alvim and Alvim 1978). According to these various sources of growth fluctuation, tropical tree species display more diverse growth patterns than temperate ones, from trees exhibiting a continuous growth to trees with intermittent growth (Osada et al. 2012; Zalamea et al. 2013). Thus, the macro-anatomical or morphological growth markers may not correspond to an annual rhythm, or to any period of fixed time, and may even be absent from the wood or stems (Jacoby 1989; Wils et al. 2009; Nicolini et al. 2012). This can be an issue in dendrochronological studies, and it highlights the importance of a better understanding of tropical tree growth periodicity.

Despite many studies, our knowledge on leaf and cambium phenologies of tropical trees remains sparse and there is still no coordinated vision of how these processes interact with each other and with the environment. In South American tropical forests, 15 studies on cambial seasonal activity have been conducted using histological approaches (Callado et al. 2013). Although a period of cambial dormancy appeared to occur during the dry season

(Krepkowski et al. 2011; Die et al. 2012), the cambial activity sometimes appears to be independent of seasonality (Trouet et al. 2012; Pumijumnong and Buajan 2013). Concerning leaf phenology, both large-scale continental studies using satellite data (Caldararu et al. 2012; Pennec et al. 2011) and field studies (Loubry 1994; Nicolini et al. 2012) showed that new flush of leaves appeared shortly after leaf fall at the beginning of the dry season, but some species also appeared to have a non-seasonal leaf phenology (Nicolini et al. 2012; Borchert 1999). Finally, the few studies on the relationship between leaf phenology, cambial activity, and environmental variables, showed that cambial activity was reduced during the dry season when the trees were leafless (Callado et al. 2001; Marcati et al. 2006; Venugopal and Liangkuwang 2007; Lisi et al. 2008; Marcati et al. 2008; Yañez-Espinosa et al. 2010; Singh and Venugopal 2011). However, they rarely focused on species in which the leafless period and the dry season were disconnected in time, which is a necessary condition to disentangle the effect of the dry season and the effect of leaf fall on cambial activity.

In the present study, we thus investigated seasonal variations in cambial activity in tropical trees in relation with their leaf shedding pattern and climatic factors. We focused on two emergent neotropical species: *Parkia nitida* Miq. (Fabaceae) and *Parkia velutina* Benoist (Fabaceae). Both are deciduous and have easily identifiable successive growth rings (Détienne 1989; Nicolini et al. 2012; Morel 2013). *P. nitida* trees exhibit a stable annual and seasonal defoliation pattern (Loubry 1994; Manganet 2013). In contrast, some *P. velutina* trees also have a stable annual and seasonal defoliation pattern while others showed a stable but infra-annual defoliation pattern, with leaf shedding every 7–10 month, leading to non-seasonal defoliation from year to year (census 1990–1991 in Loubry 1994; census 2009–2011 in Nicolini et al. 2012).

Using these two different species, we attempted to clarify the relationship between cambial activity and leaf phenology to answer the three following questions: (1) is cambial activity seasonal?, (2) are cambial activity and leaf phenology linked?, and (3) are the two processes linked to climate seasonality?

Materials and methods

Study site and tree selection

The study was conducted in the lowland tropical rainforest of the Paracou experimental site at 5°18'N, 52°55'W, French Guiana (Gourlet-Fleury et al. 2004). The site is a stand of old-growth forest dominated by Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae, and Burseraceae

(Sabatier and Prévost 1989). The most common soils are shallow and ferrallitic, limited in depth by a more or less transformed loamy saprolite (Boulet and Brunet 1983).

The site receives nearly two-thirds of the annual 3041 mm of precipitation between mid-March and mid-June, and less than 50 mm per month in September and October (Wagner et al. 2011). The daily mean temperature of 25.8 °C is almost constant over the year.

We studied five trees of each of the two species, distributed throughout the Paracou field station. Tree diameters at breast height (DBH) ranged from 45 to 100 cm (Table 1a). Only trees with an emergent crown (full overhead and side light) or that were in the upper canopy layer (full overhead light) were selected to minimize the effects of competition for light on tree growth.

Wood formation monitoring

Wood formation was monitored every 15 days by sampling microcores (15 mm in length and 2 mm in diameter) from the stem of the selected trees. The survey lasted 24 months (February 2010–February 2012) for *P. nitida* and 34 months (April 2009–February 2012) for *P. velutina*. Microcores were collected at breast height using a Trephor tool (Rossi et al. 2006a). Samples were taken in a spiral up the stem from 30 cm below to 30 cm above DBH, 2–8 cm apart (Deslauriers et al. 2003). This spacing is necessary because traumatic tissues may form where previous cores have been

removed (Forster et al. 2000). Once sampled, the microcores were conserved in an ethanol solution (50 % in water) in Eppendorf microtubes and stored at 5 °C to avoid tissue deterioration. Some samples were not exploitable (10 % of the microcore data) due to the extreme fragility of microcores, which break easily when handled.

To allow microscopic observation of cambial activity and wood formation, transverse sections were prepared from every microcore. Each sample was oriented by making a pencil mark on the transversal side under a microscope at 12× magnification. The samples were then dehydrated before being embedded in paraffin. Next, 5 µm transverse sections were cut with a rotary microtome (Leica, RM 2255). Finally, sections were stained with cresyl violet acetate (0.16 % in water) and observed with visible and polarized light at 100× magnification (Rossi et al. 2006a).

We distinguished three distinct cell zones in the sections: (1) a cambial zone (cz) with cells with thin cell walls and small radial diameters, (2) a zone in which the cells were enlarging (ez) where the cells were larger than those in the cambial zone and had thin walls, and (3) a zone in which the cell walls were thickening (wz) where the cells exhibiting birefringence were developing secondary walls under polarized light and appeared violet and blue under white light after staining with cresyl violet acetate (Samuels et al. 2006). The Wiesner reaction was performed on additional sections by pouring a few drops of 2 % phloroglucinol ethanol solution onto the section mounted on a glass slide, adding one drop of 35 % HCl and covering the section with a cover slip. The Wiesner reagent reacts with coniferyl (G) and sinapyl (S) aldehyde units in lignin. The higher the Klason lignin content, the more intense the red color (Yoshizawa et al. 2000). The difference in color makes it possible to differentiate cells with thickening walls from the first mature cells.

To determine cambial activity, we recorded the radial number of cells along three continuous cellular files in each cell zone (Figs. 1, 2; Skene 1969; Antonova et al. 1995; Deslauriers et al. 2003; Rossi et al. 2006b). Despite the fact that these two species are known to have distinct growth rings (Nicolini et al. 2012 for *P. velutina* and Morel 2013 for *P. nitida*), we did not observe growth ring limits in the microcore sections and were thus unable to include mature cells in our counts.

Phenological survey

In addition to wood formation monitoring in the same trees, we used binoculars to assess the vegetative state according to the four following categories: leafless (>80 % crown without leaves), young (>80 % crown with light-green expanded leaves), mature (>80 % crown with dark-

Table 1 (a) Diameters at breast height (DBH) and heights (*H*) of the sampled trees of *Parkia nitida* and *Parkia velutina* and (b) periodicity of leaf fall and cambial activity

	(a)		(b)	
	DBH (cm)	H (m)	Leaf fall periodicity (months)	Cambial activity periodicity (months)
<i>Parkia nitida</i>				
PN1	85.9	30.0	12	11.5
PN2	105.0	27.0	12	9.5
PN3	76.4	26.6	11	13
PN4	47.8	19.5	13	12
PN5	70.0	28.5	12	–
<i>Parkia velutina</i>				
PV1	93.9	34.0	8, 9	7.5
PV2	89.1	32.5	9, 8, 7, 10	14.5
PV3	70.0	31.5	8, 10, 10	10.5
PV4	47.7	31.0	11, 13	12.5
PV5	45.8	31.0	10, 10, 9	11

Leaf fall periodicity is expressed as the length (in months) of the leafy period between two successive leaf falls

For PN5, “–” for cambial activity means no seasonal pattern observed

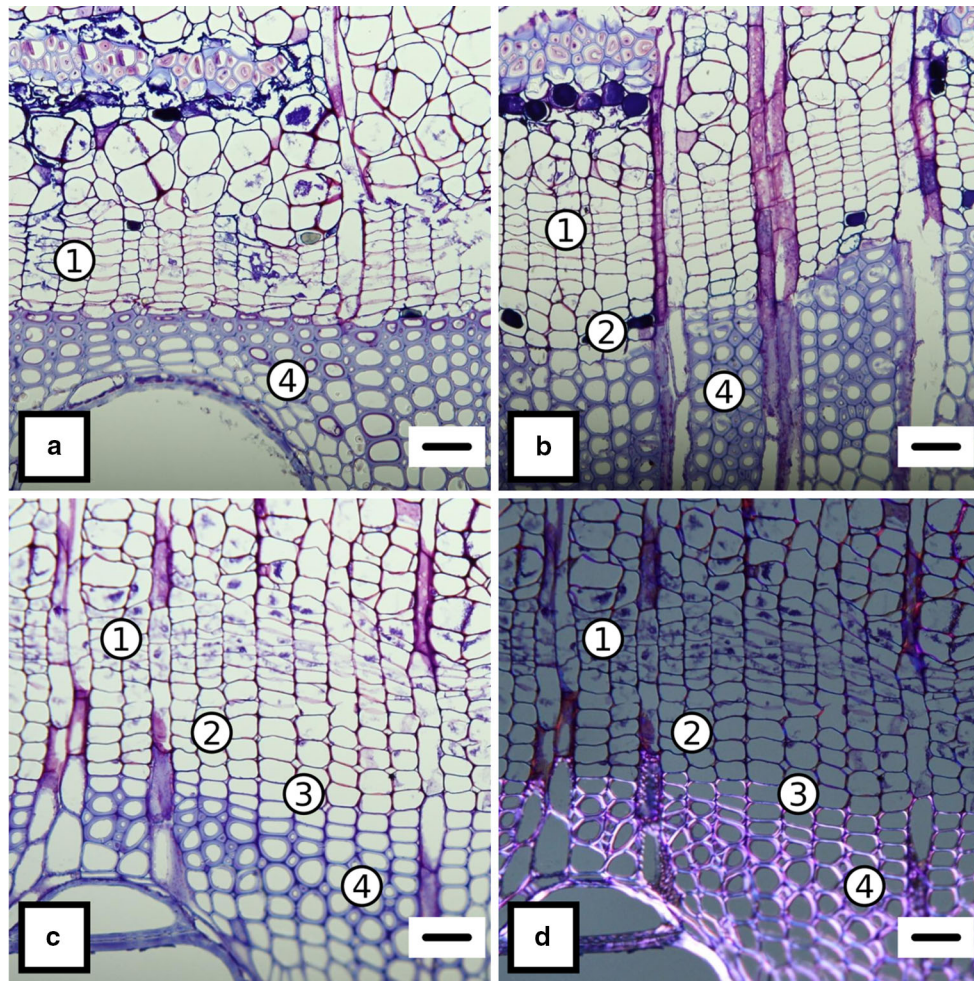


Fig. 1 Cross sections of a *Parkia nitida* stem, **a** period of low cambial activity (May 4, 2010), **b** transition period (July 13, 2010), **c** strong cambial activity, and **d** strong cambial activity in polarized

light (December 26, 2011). 1 Cambial zone (cz), 2 zone with enlarging cells (ez), 3 zone with cells with thickening walls (wz), and 4 mature cells. Scale bars 25 μ m

green leaves), and senescent (>80 % crown with yellow-brown leaves). All observations were made by the same researcher (T.M.), thus minimizing subjective estimation variability.

Data analysis

Concerning climatic variables, after a preliminary analysis (see online supplementary materials for details, Fig. A1), we extracted the four following climatic parameters from each 15-day time window preceding each sampling data: (1) sum precipitation, (2) mean temperature, (3) mean relative humidity, and (4) mean solar radiation. Because climatic parameters were highly interrelated, we chose to summarize the climatic information using a principal component analysis (PCA). The first axis of the PCA explained up to 77 % of the inertia. We used the first axis score as a summary climatic variable because of its significant correlation with each of the climatic parameters

(Fig. 3). In this way, we obtained an easy way to interpret climate variable centered on zero in which negative values represented hot dry periods and positive values represented cool moist periods (Fig. 3).

Concerning leaf phenology, the skewed bell-shaped patterns of photosynthetic capacity through a leaf's lifetime (Kuo et al. 2013), along with the fact that the durations of the senescent, defoliation, and young leaf stages were very short when considered separately compared with the duration of the mature leaf stage, lead us to focus on mature leaves versus other stages of leaf phenology in our analysis.

Concerning cambial phenology, we tested periodicity using Spearman's linear correlation coefficient (for more details see online supplementary materials, Fig. B1).

We then explored the relationships between cambial activity, leaf phenology, and climate seasonality using linear mixed models. We chose to explore these relationships separately because both cambial activity and leaf phenology were likely to be sensitive to climate. If we used leaf

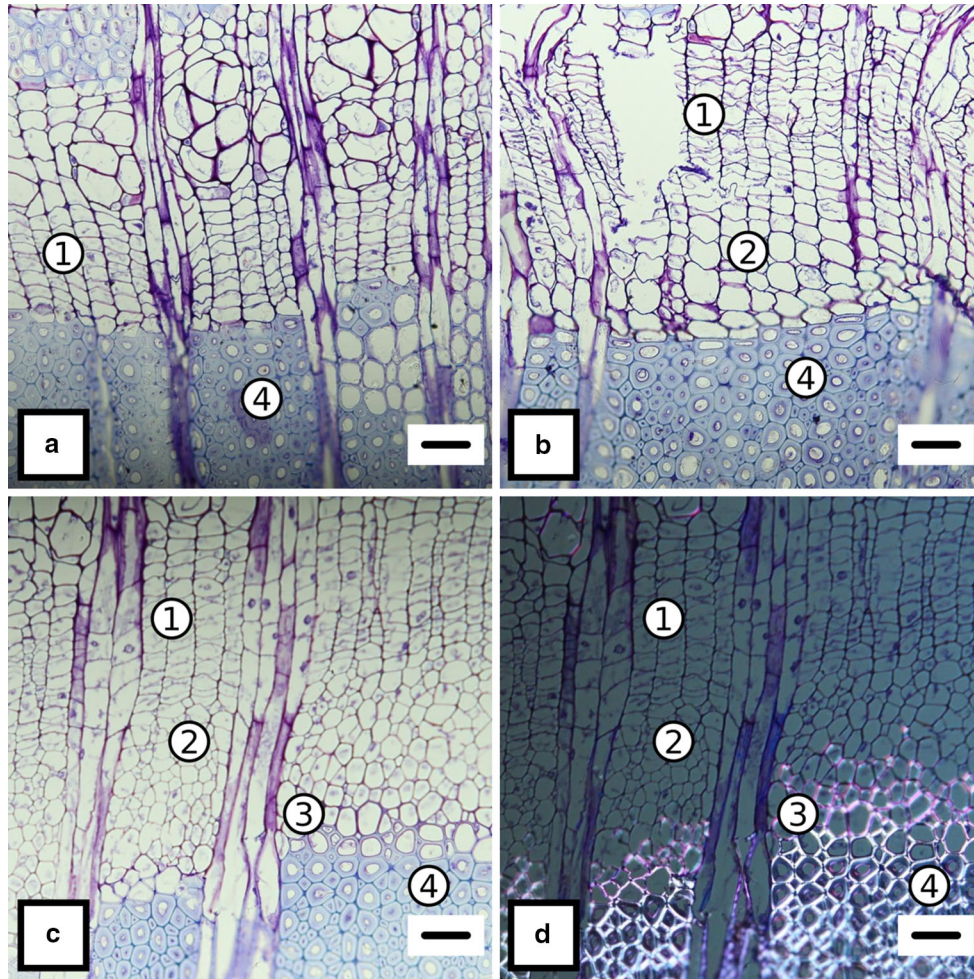


Fig. 2 Cross sections of a *Parkia velutina* stem, **a** reduced cambial activity period (May 4, 2010), **b** transition period (July 27, 2010), **c** high cambial activity, and **d** high cambial activity in polarized light

(December 2, 2010). 1 Cambial zone (cz), 2 zone with enlarging cells (ez), 3 zone with cells with thickening walls (wz), and 4 mature cells. Scale bars 25 μ m

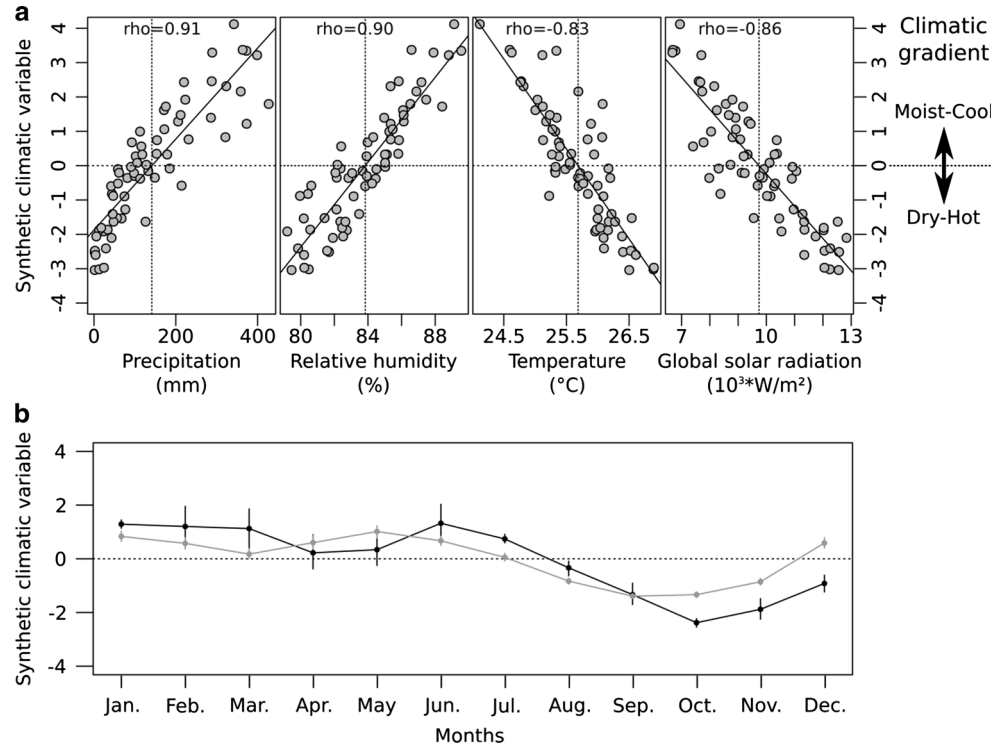
phenology and climate simultaneously in a model to explain variations in cambial activity, we would not be able to distinguish real climatic effects from indirect effects. In order to take into account the inter-individual variability, we integrated in each model an individual random effect on both intercept and slope. Thus, we first explored the relation between cambial activity and climate with a linear mixed model in which we set climate as a fixed variable and individual ranking as random effect on both intercept and slope: (1) cambial activity \sim climate + (1 + climate | individual). We then explored the relation between cambial activity and leaf phenology using a linear mixed model in which we set leaf phenology as a fixed variable and individual ranking as a random effect on both intercept and slope: (2) cambial activity \sim leaf phenology + (1 + leaf phenology | individual). Finally, we explored the relation between leaf phenology and climate using a mixed logistic regression analysis in which we set climate as a fixed variable and

individual ranking as a random effect on both intercept and slope: (3) leaf phenology \sim climate + (1 + climate | individual). We log10-transformed cambial activity in models (1) and (2) to obtain more symmetric distributions.

Due to the absence of standard statistical procedures to assess the significance of fixed explicative variables in mixed models, we used a parametric bootstrap approach to compute 95 % confidence intervals for each estimated parameters and we could then infer on the significance of the fixed explicative variables.

For models (1) and (2), we expressed the goodness-of-fit with the marginal R^2 (R_m^2), which gives the variance explained by the fixed variables, and with the conditional R^2 (R_c^2), which gives the variance explained by both fixed and random variables (Nakagawa and Schielzeth 2013). For model (3), we expressed the goodness-of-fit with the area under the receiver operating characteristic (ROC) curve (expressed thereafter as AUC), which represents the

Fig. 3 a Correlations between climatic parameters (precipitation, relative humidity, temperature, and global solar radiation) and the summary climate variable. **b** Monthly variation in summary climatic variable during the survey (black line) and during the 2004–2012 period (gray line). The summary variable is centered on zero. *Negative values* represented dry and hot periods while *positive values* represented rather moist and cool periods. *Bars* represent 95 % bootstrapped confidence intervals. *Rho* Spearman's rank correlation coefficient. Significance levels associated with the Spearman's rank correlation coefficient was $P < 0.001$ in all cases



discriminative ability of the model, i.e.. in our case, the ability of the model to predict tree phenology according to climatic data. AUC can be seen as the proportion of true predictions made by the model, and range from 0.5 (null prediction ability) to 1 (excellent prediction ability).

All analyses were performed using the R statistical platform (R Development Core Team 2011) and the lme4 package (Bates et al. 2014).

Results

Leaf shedding pattern

In 2010 and 2011, all *P. nitida* trees lost their leaves at the same time during the long dry season, at intervals of 11–13 months (Fig. 4; Table 1b). The leafless period lasted 15–30 days.

During the 3 years of the survey, individual *P. velutina* trees went through three to five leafless periods (Fig. 4; Table 1b), implying that some trees lost their leaves twice a year. The leafless period was slightly synchronous between trees, but could occur at any time of the year (Fig. 4). Most trees lost their leaves at sub-annual scale, at intervals from 7 to 10 months (PV1, PV2, PV3, and PV5) and only one tree showed annual defoliation behavior (PV4, Table 1b). Like *P. nitida*, the leafless period lasted 15–30 days.

Cambial activity pattern

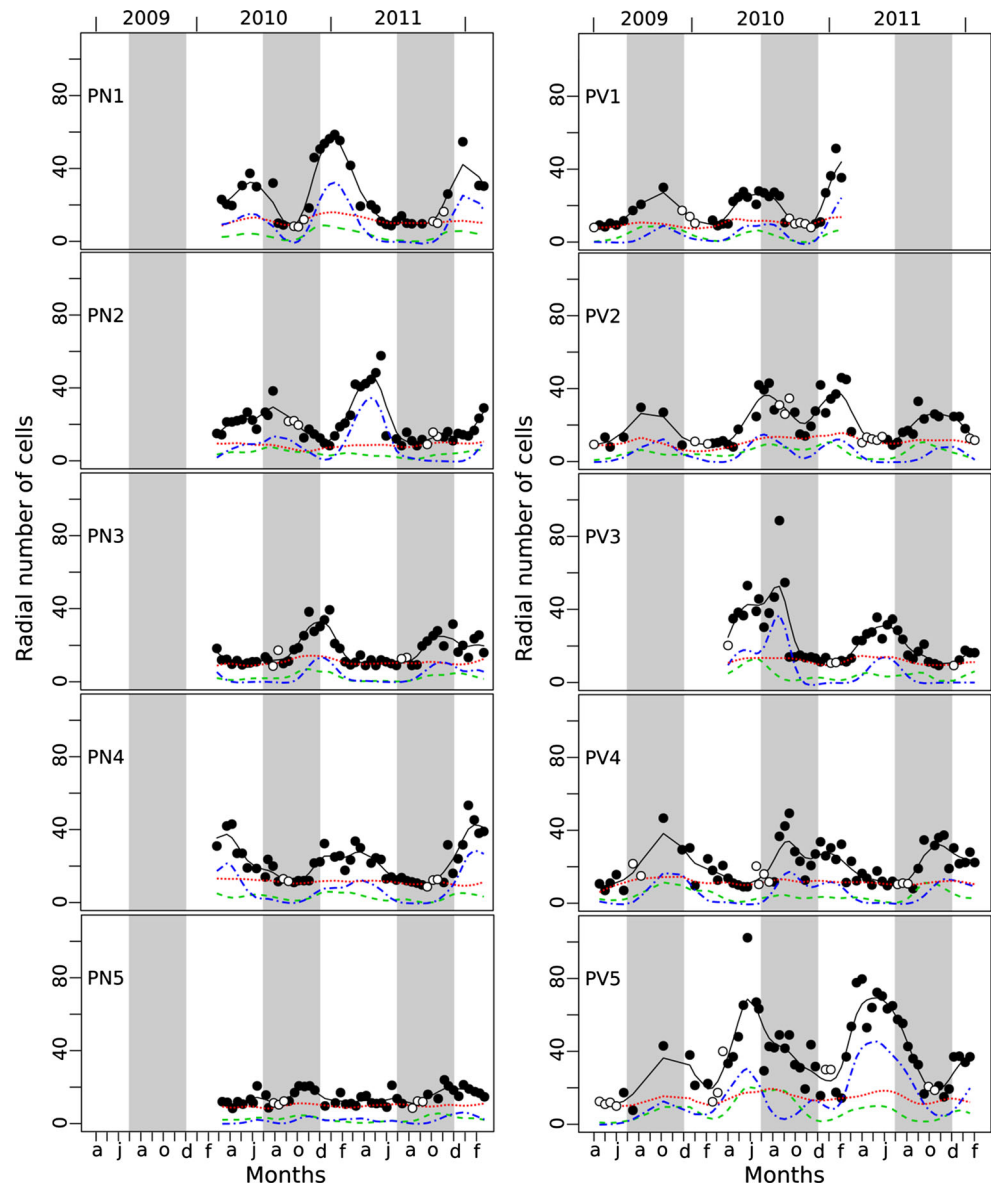
Cambial activity varied between the two species and among trees, with each tree alternating in the periods of low and high cambial activity during the survey (Fig. 4). In *P. nitida*, the periodicity of cambial activity was close to annual in PN1, PN3, and PN4, but less than annual in PN2 (Fig. 4; Table 1b). We did not observe any periodicity in PN5, probably due to its very weak cambial activity. In *P. velutina*, cambial activity periodicity ranged from 7.5 to 14.5 months.

In both species, the variation in cambial activity was mainly the result of changes in the number of enlarging cells (ez) and wall-thickening cells (wz) (Fig. 4, green-dashed lines and blue dash-dotted lines), whereas the number of cells in the cambial zone (cz) remained more or less constant over time (Fig. 4, red-dotted lines).

Relationships between cambial activity, leaf phenology, and climate

In both species, cambial activity at the population scale tended to increase from hot and dry periods to moist and cool periods, but this trend was not significant (Table 2; Fig. 5a, b). The result was reinforced by the fact that we observed individual trees showing an opposite trend in the relationship between cambial activity and climate in both species (Fig. 5a, b).

Fig. 4 Cambial activity and leaf shedding patterns of the five *Parkia nitida* (on the left) and of the five *P. velutina* trees (on the right) from April 2009 to February 2012. The red-dotted, green-dashed, and the blue dash-dotted lines represent, respectively the number of cell layers of the cambial zone (cz), of the zone with enlarging cells (ez) and of the zone with cells with thickening walls (wz), while the circles represent the sum of these three measurements ($\Sigma_{cz_ez_wz}$) and the local fitting is represented by the solid line. The color of the circles indicates the phenological stage of the tree at the time of the microcore sampling: black for “mature leaves” and white for “senescent leaves”, “leafless”, and “young leaves”. The long dry season (July–November) is symbolized by the gray stripes in the background



On the other hand, we found a positive and statistically significant increase of cambial associated with the presence of mature leaves at the population scale in both species (Table 2; Fig. 5b, c), and this increase in cambial activity was observed in all individuals. Cambial activity tended to decrease before leaf fall and to increase again immediately or with a lag of a few months after canopy leafing (Fig. 4).

Finally, while the presence of mature leaves was significantly related to cool moist periods in *P. nitida*, no significant link between climate and leaf phenology at the population scale was observed for *P. velutina*. In only one tree out of the five of this species, the probability of observing mature leaves increased significantly from the hot and dry to the moist and cool periods.

Discussion

The present work is original, in that it is among the very few studies on tropical trees to explore cambial activity through regular sampling of microcores at a bi-monthly scale (see Callado et al. 2013 for a review of studies in South America). Importantly, we included leaf phenology as an additional biological covariable because it reflected the functioning of the primary meristems while most other studies focused only on cambial activity and its links with environmental factors, sometimes on the radial increment alone (Callado et al. 2013). In our opinion, cambial activity plus leaf phenology definitely offer a larger insight on the growth regulation occurring inside the growing plant and

Table 2 Summaries of the linear mixed model analyses of relationships between cambial activity and climate (model 1), and cambial activity and leaf phenology (model 2), the mixed logistic regression

model analyses of relationships between phenology and climate (model 3) for *Parkia nitida* and *Parkia velutina*

<i>Parkia nitida</i>		<i>Parkia velutina</i>	
Model (1) ln(cambial activity) ~ intercept + climate + (intercept + climate individual)			
<i>Fixed effects</i>	Coefficient [95 % CI]	<i>Fixed effects</i>	Coefficient [95 % CI]
Intercept β_0	2.85 [2.70; 2.99]	Intercept β_0	3.02 [2.77; 3.27]
Climate β_1	0.04 [-0.04; 0.12]	Climate β_1	0.04 [-0.04; 0.11]
<i>Individual random effects</i>	SD	<i>Individual random effects</i>	SD
Intercept β_0	0.16	Intercept β_0	0.26
Climate β_1	0.08	Climate β_1	0.08
<i>Goodness-of-fit</i>		<i>Goodness-of-fit</i>	
Marginal R^2	0.02	Marginal R^2	0.01
Conditional R^2	0.21	Conditional R^2	0.24
Model (2) ln(cambial activity) ~ intercept + phenology + (intercept + phenology individual)			
<i>Fixed effects</i>	Coefficient [95 % CI]	<i>Fixed effects</i>	Coefficient [95 % CI]
Intercept β_0	2.51 [2.33; 2.68]	Intercept β_0	2.61 [2.42; 2.81]
Phenology β_1	0.38 [0.14; 0.34]	Phenology β_1	0.49 [0.30; 0.71]
<i>Individual random effects</i>	SD	<i>Individual random effects</i>	SD
Intercept β_0	0.01	Intercept β_0	0.15
Phenology β_1	0.19	Phenology β_1	0.13
<i>Goodness-of-fit</i>		<i>Goodness-of-fit</i>	
Marginal R^2	0.06	Marginal R^2	0.10
Conditional R^2	0.17	Conditional R^2	0.29
Model (3) phenology ~ intercept + climate + (intercept + climate individual)			
<i>Fixed effects</i>	Coefficient [95 % CI]	<i>Fixed effects</i>	Coefficient [95 % CI]
Intercept β_0	2.87 [2.21; 4.34]	Intercept β_0	1.54 [1.21; 1.98]
Climate β_1	0.80 [0.31; 1.51]	Climate β_1	0.06 [-0.16; 0.31]
<i>Individual random effects</i>	SD	<i>Individual random effects</i>	SD
Intercept β_0	0.47	Intercept β_0	0.20
Climate β_1	0.43	Climate β_1	0.16
<i>Goodness-of-fit</i>		<i>Goodness-of-fit</i>	
AUC	0.82	AUC	0.63

Cambial activity was log10-transformed in model (1) and (2). Fixed effects indicate the model estimated parameters at the population scale while taking into account the inter-individual variability. Random effects provide information concerning the inter-individual source of variability (expressed as standard deviation) of the model estimated parameters. The significance of relationships can be inferred from the 95 % parametric bootstrap confidence intervals. The marginal R^2 gives the variance explained by the fixed effects and the conditional R^2 gives the variance explained by both fixed and random effects. *AUC* represent the ability of the model to predict tree phenology according to climatic data and range from 0.5 (null prediction ability) to 1 (perfect prediction ability). See the data analysis section for more details

on the possible interactions with exogenous parameters like temperature or precipitation.

In both species, the variation in cambial activity was mainly the result of changes in the number of enlarging and wall-thickening cells rather than changes in the number of cells in the cambial zone. While the majority of studies on cambial activity in both temperate and tropical trees only focused on the number of cells in the cambial zone to explain cambial activity (temperate studies: Bäucker et al. 1998; Frankenstein et al. 2005; Marion et al. 2007, tropical studies: Pumijumnong and Wanyaphet 2006; Marcati et al. 2008; Krepkowski et al. 2011; Die et al. 2012; Pumijumnong and

Buajan 2013); our results show that the other types of cells should also be taken into account in the analysis of cambial activity in tropical trees. Indeed, variations in the number of cells in the cambial zone can be significantly smaller than variations in the number of other cell types.

Despite the fact these two species are known to have distinct growth rings (Nicolini et al. 2012 for *P. velutina*, Morel 2013 for *P. nitida*), we were unable to distinguish the limits of the growth rings in the microcores due to (1) the small size of the core and (2) the confusion between the bands of axial parenchyma lines located within the ring and the continuous band of axial parenchyma corresponding to

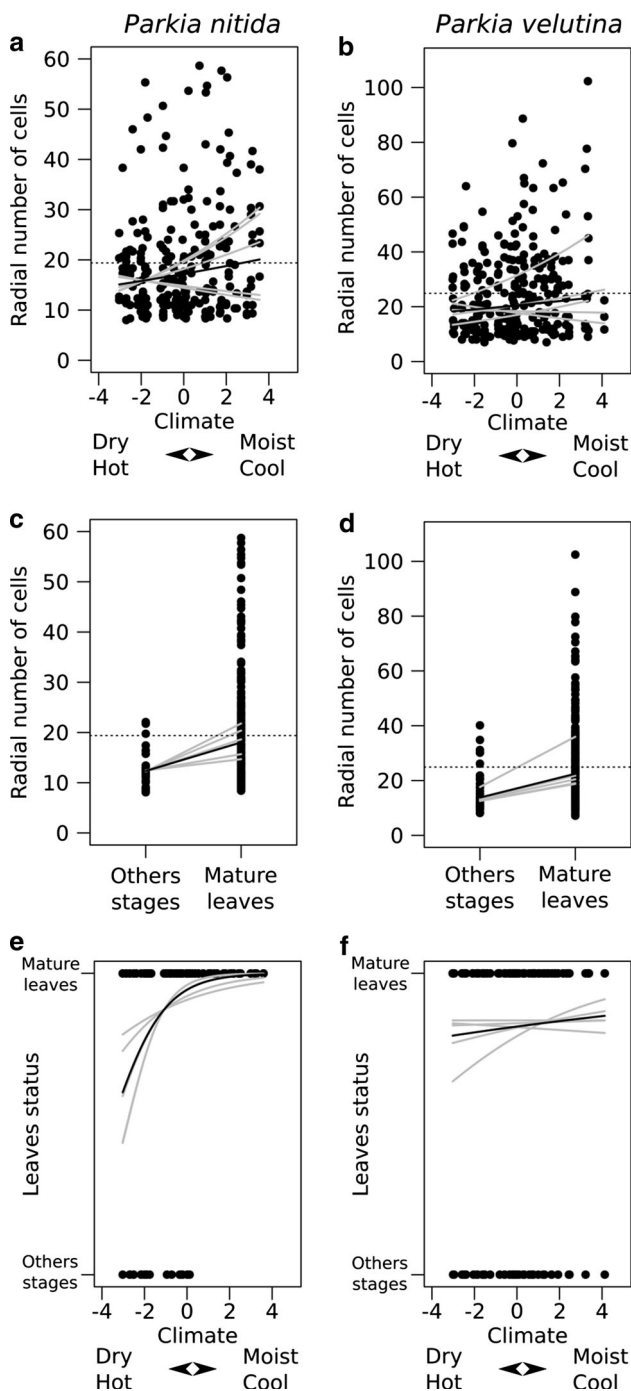


Fig. 5 Relationships between leaf phenology, cambial activity and climate seasonality at population scale in *Parkia nitida* (a, c, and e) and *Parkia velutina* (b, d, and f). The black curves represent the mixed model predictions for the fixed effect at the population scale and the gray curves represent the mixed model individual predictions. The circles represent the actual observations. In a, b, c, and d, the horizontal striped line corresponds to the mean cambial activity during the survey at population scale. In a, b, e, and f, the x-axis corresponded to synthetic climate variable centered on zero (obtained with a PCA on climatic variables). Negative values represented hot dry periods and positive values represented cool moist period

the end of the current ring. Consequently, we were unable to take the mature cells into account in our counting and thus, to obtain other cambial activity parameters like the speed of differentiation of the cells, a parameter indicative of tree growth status was introduced. Future studies should include longer cores but at a monthly scale to prevent disease entrance.

The main result of this study was that periods of low cambial activity significantly matched with leaf fall and leafless periods in both species, and this result was reported in several others studies in deciduous and semi-deciduous tree species (Callado et al. 2001; Venugopal and Liangkuwang 2007; Marcati et al. 2008; Cardoso et al. 2012). Leaf phenology is known to be an important factor influencing the activity of the vascular cambium and leaf fall generally has a significant and direct effect on cambial activity, as reported by Callado et al. (2001) where the period of leaf abscission was correlated with the formation of latewood in three deciduous and semi-deciduous species. Thus, it's clear that the radial growth cannot be considered and interpreted in deciduous and semi-deciduous species without taking into account the leaf phenology in studies about effects of climate on tree radial growth.

Leaf shedding patterns are largely determined by the seasonality of rainfall in tropical regions (Frankie et al. 1974; Lieberman 1982; Reich and Borchert 1982, 1984; van Schaik et al. 1993; Lisi et al. 2008). To avoid hydric stress, deciduous trees that shed their leaves at the beginning of the dry season, remain leafless throughout the dry season and only grow new leaves when the first rains fall at the end of the dry season. Conversely, in the Paracou experimental site, *P. nitida* trees change their leaves early in the dry season, just before depletion of soil water reserves (Wagner et al. 2011), and end the dry season with new leaves (see also trees observed by Loubry 1994, Pennec et al. 2011 and Mangenet 2013). The dry season is characterized by a minimum cloud cover and high solar irradiation, a situation that probably allows trees to optimize their photosynthetic activity (Wright and van Schaik 1994; Huete et al. 2006; Xiao et al. 2006).

However, Mangenet (2013) reports that some *P. nitida* trees (3 of 14 trees) changed their leaves during other periods than long dry season, suggesting that sensibility to climate could be unequal between individuals, a well-observed point for *P. velutina*. Thus, the variability of the leaf life span we observed in *P. velutina*, combined with its apparent non-seasonal and non-annual leaf fall behavior, suggest that they were not only influenced by climate factors (e.g., occurrence of the dry season which is supposed to influence all trees equally). This hypothesis is supported by similar observations in other tropical studies (Lieberman 1982; Reich and Borchert 1982; van Schaik et al. 1993; Do

et al. 2005; Singh and Kushwaha 2005; Elliott et al. 2006; Yañez-Espinosa et al. 2006; Williams et al. 2008; Valdez-Hernández et al. 2010; Mendez-Alonzo et al. 2013).

Contrary to *P. nitida* and even if trees grew in the same conditions, both leaf fall periodicity and cambial activity were variable in *P. velutina* in our study. However, we can also observe in *P. nitida* leaf fall pattern variability as shown by Nicolini et al. (2012) and Mangenet (2013). So, this variability necessarily involves the influence of other factors than the seasonality of the precipitation alone, such as soil and microclimatic conditions (Reich and Borchert 1982; Singh and Kushwaha 2005; Valdez-Hernández et al. 2010; Cardoso et al. 2012) or physiological factors like internal clock (Yañez-Espinosa et al. 2006; Williams et al. 2008; Lüttge and Hertel 2009; Seyoum et al. 2012). For example, Brousseau et al. (2013) showed the existence of an individual variability of the leaves' photosynthetic efficiency that could allow the faster realization of the foliar phenological cycle which could be a rational explanatory factor of the variation of the length cycle.

In conclusion, this study highlighted the interrelations between leaf phenology, cambium phenology, and climate in two closely related tropical tree species in French Guiana. For *P. nitida*, the cambial activity pattern was seasonal, annual, and synchronous at the population scale whereas it was non-seasonal, non-annual, and asynchronous in *P. velutina* but periodic at the tree scale. In spite of these differences, we found that the periods of cambial inactivity were significantly associated with leaf fall and leafless stages in both species. Further studies will be necessary to examine possible connections between plant ontogeny and patterns of leaf phenology and cambial activity and disentangle their interrelated relationships.

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Conflict of interest The authors declare that they have no conflict of interest.

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