

Dating branch growth units in a tropical tree using morphological and anatomical markers: the case of *Parkia velutina* Benoist (Mimosoïdeae)

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Abstract

• **Context** In tropical areas, studies based on the retrospective analysis of tree development have focused principally on growth ring research. The interpretation of primary growth markers is overlooked although it opens perspectives to provide long time-series on tree-crown development.
• **Aims** This study focused on *Parkia velutina*, an emergent tree of neotropical rain forests. Our objectives were (1) to characterize the phenological cycle of this species, and (2) to identify temporally interpretable morphological and anatomical markers.

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Contribution of the co-authors E.N. and P.H. designed the study; E. N. supervised the work and coordinated the project; E.N., B.L. and T. M. carried out the tree census; B.L., E.N. J.B. and J.R. collected field samples; E.N. and B.L. studied tree morphology; J.R., J.B. and E.N. studied tree anatomy; T.M. analyzed climate typology; E.N., P.H. and J.R. wrote the paper; all the authors discussed the results and commented on the manuscript.

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• **Methods** We collected dominant branches in 14 adult trees and identified growth markers that limit longitudinal and radial increments. We coupled this approach with a 2-year phenological survey of 20 trees.

• **Results** Leaf shedding, growth unit elongation and growth ring formation define the phenological cycle. At tree scale, this cycle is synchronous and affects all axes. At population scale, trees can be desynchronized. This cycle is annual despite some slight variability. Successive growth units and growth rings are easily identifiable.

• **Conclusion** Dating a branch by counting the number of growth units or growth rings is possible in many years with a reasonable error. Nevertheless, estimating their precise month of formation in order to study climatic influences remains difficult.

Keywords Crown development · Deciduousness · Dendrochronology · French Guiana · Growth ring · Phenology · Tree architecture · Wood anatomy

1 Introduction

Plant phenology can be defined as the study of the timing of recurring biological events, their causes with regard to biotic and abiotic forces, and the relationship between phases in the same or in different species (Leith 1974). In temperate areas, winter influences the growth phenology of trees by imposing an annual rest period and a rhythmic annual growth period for both deciduous and evergreen species. However, yearly growth may occur in one or more longitudinal increments depending on the species, on the ontogenetical age of the individual, and on axis position in the crown (Barthélémy and Caraglio 2007). Consequently, the axis length portion extended in any one year can be made up

of a variable number of longitudinal increments of growth units (GUs; Hallé and Martin 1968). The different GUs are generally easy to identify on the stem (Barthélémy and Caraglio 2007). When several successive GUs are formed in the same annual vegetative cycle, they most often present distinctive features: it is often easy to distinguish between spring shoots and summer or additional shoots (Nicolini 2000; Heuret et al. 2003; 2006). While the annual cycle of primary growth can be broken down into intra-annual sub-cycles, only one period of thickening generally occurs in a year, giving rise to a single growth ring (GR) per year. These morphological and anatomical markers make it possible to interpret retrospectively the growth of the tree in each successive past year, determine tree age (Heuret et al. 2000; Passo et al. 2002), and understand the temporal expression of growth, branching and flowering processes (Heuret et al. 2006).

In less seasonal wet tropical forests, environmental cues (T°C, light and rainfall) are not so restrictive. Highly diverse phenological patterns reflect the huge diversity of trees present in these ecosystems. Tropical phenological studies have focused primarily on leaf shedding patterns, flowering/fruiting patterns (Reich 1995; Newstrom et al. 1994; Sakai 2001; Kushwaha et al. 2010) and the identification of annual rings in wood (Worbes 1995, Rozendaal and Zuidema 2011). We hold that research in tropical plant phenology could be improved considerably by considering three main points that are generally not taken into account in scientific studies. First, the temporal interpretation of growth by means of a retrospective analysis of plant structure is restricted generally to the counting of annual rings, and markers of primary growth or flowering processes are not considered (but see Heuret et al. 2003; Zalamea et al. 2008). Second, the entire tree is most often considered, and organization inside the crown (e.g., synchronism of the different axes) is overlooked. Third, primary and secondary growths, and flowering, are often considered separately, with no coordinated vision of the trade-off and dependencies between these processes (but see Loubry 1994 and O'Brien et al. 2008). Our knowledge of the spatial/temporal distribution of longitudinal increments in the crown, and the spatial/temporal pattern of radial increments in tropical trees, is still limited.

A better understanding of how growth (elongation, thickening), branching and flowering processes are coordinated over time inside the crown, and of associated morpho-anatomy, is essential for the long-term retrospective analysis of tree development and any analysis of the causes of the variations observed. Faced with the necessity to characterize plant responses to climate change, these retrospective analyses, which provide access to long-term growth series, will be essential as complements to data from permanent plots.

In this paper we attempt to fill the gaps in our knowledge of growth, branching and flowering coordination by means

of a novel approach coupling (1) a retrospective analysis of longitudinal/radial increments in both crown and trunk, and (2) a phenological crown survey over 33 months. We focused our work on a well known tree of neotropical wet forests, *Parkia velutina* Benoist (Leguminosae: Mimosoïdeae), for several reasons: (1) it is an emergent tree that is distributed widely but discontinuously across Amazonian Brazil and Peru, French Guiana, eastern Venezuela and Colombia west of the Andes (Hopkins 1986); (2) it is deciduous with a “resting” period between two growth cycles; (3) leaf drop seems to be mainly annual and synchronous for part of the population in French Guiana (Loubry 1994); (4) the relative simplicity of the mature crown, with only a few axes, makes it relatively easy to capture a large part of growth variability at an individual scale; (5) the genus *Parkia* has anatomical features (Détienne 1995) suited to the counting of annual rings; (6) finally, it has unusual morphological features suitable for determining GU (including height growth), making this species particularly attractive for retrospective growth investigations in a neotropical tree species.

This study was aimed at establishing the phenological cycle of this tropical wet forest tree species and its variability, a pre-requisite to a future retrospective analysis of the long-term longitudinal/radial growth of this species.

2 Materials and methods

2.1 Study area and climate typology

The study was conducted in a lowland tropical rainforest at the Paracou experimental site (5° 18' N, 52° 55' W), in French Guiana. The site consisted of a stand of old-growth forest. The most common soils are shallow and ferrallitic, limited in depth by a more-or-less transformed loamy saprolite (Boulet and Brunet 1983).

Climate parameters (precipitation, temperature, solar irradiance, day length) had been measured over the previous 18 years (1989–2008; see Fig. 1) at an on-site weather station in Pointe Combi (5° 18' 25" N, 52° 55' 26.3" W), maintained by CIRAD. After a principal component analysis of these parameters, it was possible to subdivide the year into four climatic units (T1, T2, T3 and T4) that are significantly different and organized mainly around the precipitation parameter. T1 corresponds to a short rainy season (Dec–Jan: 638 mm) and T3 to a long rainy season (April–June: 1,290 mm). These alternate with a short dry season T2 (Feb–March: 487 mm) and a long dry season T4 (July–Nov: 551 mm).

2.2 Trees and field samples

We located 84 individuals constituting a balanced population distributed throughout the Paracou field station (Table 1). In

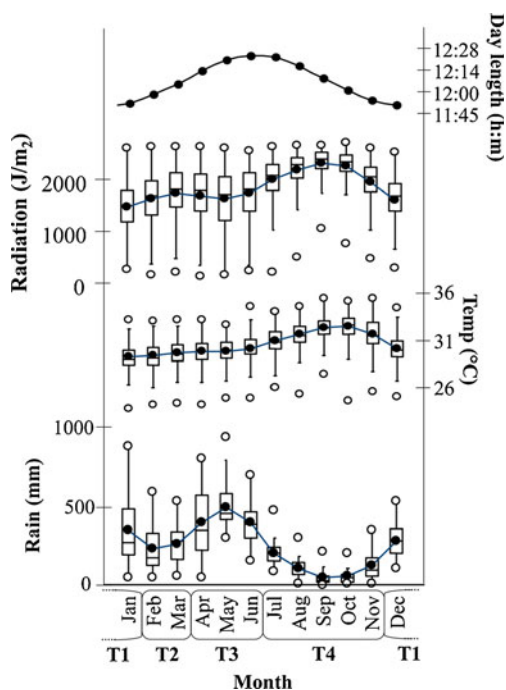


Fig. 1 Variations over a calendar year of day length [h:min(m)], radiation (J/m^2), temperature (1984–2007; °C) and rainfall (1980–2008; mm). Box plots are presented for radiation, temperature and rainfall (1980–2008; mm); white dots minimum and maximum values, black dots mean, box 25th and 75th percentiles, line inside the box: 50th percentile (median). The year can be subdivided into four climatic units (T1, T2, T3 and T4). The statistical significance of this subdivision was tested using a principal component analysis (PCA) based on the four climatic variables collected monthly over the previous 18 years, followed by a between-class analysis (Dolédéc and Chessel 1987). This quantified the proportion of the PCA's inertia explained by a variation across the months gathered by a qualitative variable, in this case, climatic typology (Lebreton et al. 1991). In our case, 53.25 % of PCA inertia is explained by the qualitative variables (climatic units: T1, T2, T3 and T4). We then tested the significant differences between climatic units using a permutation test (999 permutations for estimating the *P*-value with significance set at 1%). A preliminary test pointed to a significant variation in climate across the climatic units ($P < 0.001^{***}$), underscoring the reliability of this climatic typology

Table 1 Number of trees studied and diameter at breast height (DBH). DBH classes are presented in the first column. *A* All individuals found at the Paracou experimental site, *B* individuals designated for the study

DBH (cm)	A	B
0–9 cm	9	
10–19 cm	33	2
20–29 cm	11	1
30–39 cm	5	
40–49 cm	9	3
50–59 cm	6	5
60–69 cm	3	5
70–79 cm	6	5
80–89 cm	2	2
Tree number	84	23

this study, we focused on 23 of these trees (Table 2): 21 adult trees (including two senescent trees) and 2 juveniles (based on the reiterated status of the crown, Barthélémy and Caraglio 2007).

Among these 23 trees, 20 were selected for the phenological survey (from January 2009 to September 2011). With the exception of one juvenile tree, these were mainly of adult classes (Table 1). All selected trees had an emergent crown (full overhead and side light) or were in the upper canopy layer (full overhead light) in order to minimize the effects of shading on phenology. Inside the crown of 14 of these trees (including the juvenile one), we collected one vertical and dominant branch for a retrospective description of the longitudinal/radial growth. We took this branch to be representative of the past height growth of the trees (Fig. 2).

Two other adult trees were felled to study radial growth in all parts of the tree, including the trunk. One or two dominant branches were sampled in the crown of the remaining trees and full disks of wood were collected every 2 m from the base of the trunk to the basal parts of the crown (Fig. 2a).

One juvenile tree was felled and described on the basis of the same protocol. Juvenile trees—which here represented an unbalanced sample compared to the number of adult trees—were used to provide preliminary results in terms of ontogenetic effect.

The morphological/anatomical analysis of tree branches on the one hand, and tree surveys on the other, are complementary approaches. Structural regularities can give rise to hypotheses about the expression of developmental processes over time (Heuret et al. 2003; Zalamea et al. 2008) and such studies pave the way to establishing pertinent protocols for field surveys that may be used, within a reasonably short period, to validate these hypotheses.

2.3 Retrospective descriptions

2.3.1 Structure and measurement of GUs

The limits of the GUs that make up the axes were located by recognizing markers that result from the rhythmic activity of the primary meristems, and which persist for several years in the bark and pith (Barthélémy and Caraglio 2007; Heuret et al. 2000, 2006; Nicolini et al. 2001; Longuetaud and Caraglio 2009). The literature contains no information about the morphology of this species, and thus the attempt made in this section to illustrate the different expressions of primary growth in the species may be considered as original results. In *P. velutina*, each living axis in the crown has a pseudo-whorl of large composite leaves during the leafy period (Fig. 3A, B). In the youngest parts of the branch, the most recent GU (Fig. 3C), which is covered with a dense red-brown pubescence, bears small basal cataphyll (c) and large composite petiolated leaves (p). When leafless, this last

Table 2 Trees studied and summary of the results. *Ind* Tree identifier. Data sampling reports on the different samplings for each tree. Growth synchrony refers to the different behaviors noted at different scales (“Individual” and/or “Branch”) for each tree by different methods (“survey” and/or “retrospective analysis”): for the different scales

(“Branch” or “Individual”), see Fig. 5 (a–e) and Fig. 10 (A–C). The third column in growth synchrony presents individuals for which we checked and confirmed growth synchrony (S) between longitudinal growth (I) and radial growth (II)

Ind: ou Tree identifier (Ind)	DBH (cm)	Stage ^a	Data sampling ^b			Growth synchrony			No. leafless events per year	
			P	B	F	Individual (survey)	Branch (retrospective analysis)	I/II	2009	2010
16	15	Juvenile	X	1		A	b	S	1	1
11	16	Juvenile		1	X	— ^c	e	S	—	—
625	22	Adult	X			A	—	—	1	1
4	42	Adult		2	X	—	a	S	—	—
5	43	Adult	X	1		A	a	S	1	1
8	47	Adult	X	1		A	a	S	1	1
2	50	Adult	X	1		A	a	S	1	1
9	50	Adult		2	X	A	a	S	1	1
709	53	Adult	X			A	—	—	1	1
18	57	Adult	X			A	—	—	1	1
3	58	Adult	X	1		A	a	—	1	1
113	62	Adult	X			A	—	—	1	1
PV6	63	Adult	X			A	—	—	1	1
15	66	Adult	X			A	—	—	1	1
PV9	67	Adult	X			A	—	—	1	1
14	69	Adult	X	2		A	a	—	1	1
1	71	Adult	X	3		A	a	—	1	1
906	72	Adult	X			A	—	—	1	1
13	75	Senescent	X			B	—	—	1	2
12	78	Adult	X	2		C	c	—	1	2
190	79	Adult	X	2		B	a	—	1	1
6	80	Adult	X	1		A	d	S	1	2
7	85	Senescent	X	1		B	d	—	1	2

^a Developmental stage of each tree: *juvenile* a tree with a non reiterated crown, *adult* tree with a reiterated crown and sometimes reproductive, *senescent* a reproductive tree with a fragmented crown due to axis mortality

^b *P* Phenological survey, *B* one or more branches were collected (number), *F* the individual was felled

^c No data

increment (Fig. 3D) shows thin basal cataphyll scars (cs), whereas larger scales (ls) are observed in the place of the composite leaves. Sometimes, a pseudo-whorl of dried unexpanded small leaves is observed at the apex and remains in place for several months before breaking off and leaving an apical scar (X). Longitudinal cuttings show pith discontinuity between two successive GUs at the apical scar. In *P. velutina*, the apical meristem dies after each GU elongation, and the new GU is provided by the delayed (proleptic) branching of a lateral meristem located close to the apical scar. Growth is then determinate and the remaining structure is identified as a “sympodial growth unit” (SGU). Similar SGUs may be identified in the older parts of the branches (Fig. 3E).

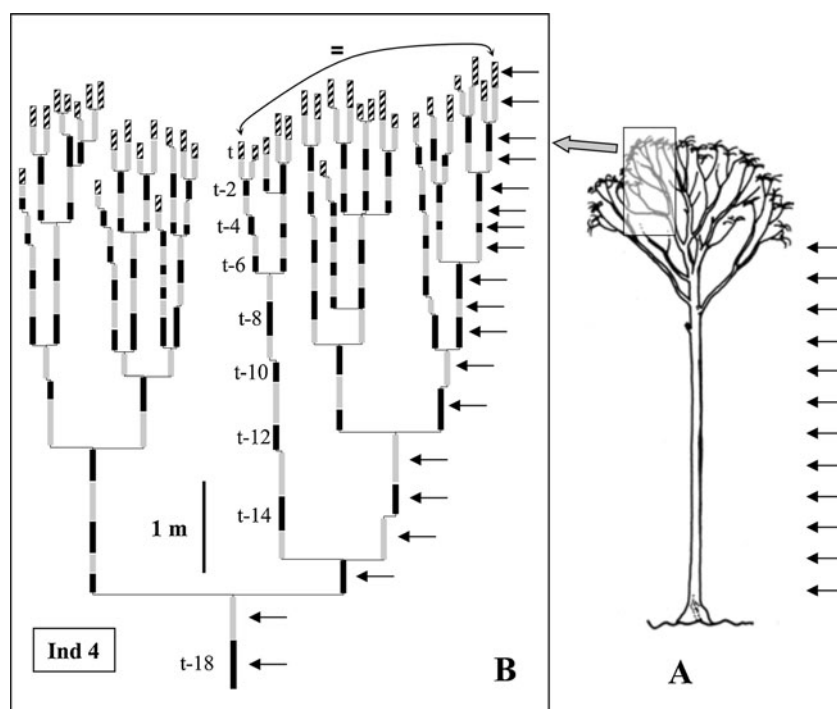
In our study, once the SGU structure had been recognized, we conducted retrospective investigations on the sampled

branches by identifying all the successive SGUs making up the axes. SGU ranks and the relationships between axes were recorded. Finally, we measured the length of all the SGUs making up all the dominant or dominated axes in the branches. Once the retrospective investigation had been completed, we designated a dominant axis in each branch and collected one full disc of wood from the base of each previously identified SGU (Fig. 2A) in order to compare radial and longitudinal growths in the crown.

2.3.2 Structure and measurement of GRs

Parkia velutina shows clearly distinct GRs edged by a thin line of axial parenchyma (one row of cells), both in trunk (Fig. 4A) and branches (Fig. 4B, C). The wood structure of

Fig. 2 **A, B** Samples taken within the tree's architecture. In some individuals, such as that presented in **A**, we collected one main branch that provided access to the height growth of the tree in **B**. After retrospectively describing the branch and identifying the limits to successive sympodial growth units (SGUs; alternately coloured in gray, black or with stripes for visual effect), we sampled one disc of wood in the middle of each SGU (arrows in **B**). SGUs with stripes were bearing leaves when indicated with *t*. In the particular case of felled trees, we also sampled one disc of wood every 2 m from the base of the trunk to the remaining parts of the crown (arrows in **A**)



Parkia rings can be classified as a marginal-parenchyma-bands type in the trunk, combined with a vessel-distribution type in branches, according to the classification of Coster (1927), adapted by Worbes (1995). In the branches, indeed, the lines of axial parenchyma were combined with vessel elements due to the anastomoses of axial aliform-confluent parenchyma, showing furthermore different degrees of alignment. This arrangement, which resembles a porous zone (Fig. 4C), is particularly evident near the pith and in the first GRs (2nd or 3rd from the pith). The vessel elements had a mean diameter of about 150–200 μm at the start of the GR, whereas they were far smaller (<100 μm) in the final part of the GR. A thin line of xylem densification was observed near the marginal parenchyma band in both trunk and branches. Four of the trees studied showed wedging or completely missing rings in their branches. We detected these anomalous and relatively rare rings successfully by checking ring continuity over the entire stem disc.

Once the GR structure had been fully characterized, we conducted retrospective investigations on the sampled axes by identifying all the successive GRs in their composition. GR measurements were made along two radii in a straight line, and perpendicular to ring boundaries. The number of annual GRs was counted and the width of each ring was measured on each of the radii.

2.4 Phenological survey

Leaf phenology was assessed monthly for 33 months (years 2009, 2010 and 2011) in the 20 designated trees by visual

inspection using binoculars. Leaf shedding pattern was assessed at the tree scale by considering different foliation stages as defined by Loubrý (1994): (1) axes are leafless, (2) axes are growing and young red/light-green leaves are expanding, and (3) growth of axes is finished and mature leaves are dark green. Flowering was also assessed by recording successive stages from inflorescence elongation to fruit formation. For simplification, we focused on one stage: capitula at anthesis with red flowers.

3 Results

3.1 Retrospective analysis

3.1.1 Longitudinal growth of branches

We identified the successive SGUs that made up the different axes of the branches sampled in 14 trees (see also Fig. 2B). In this way, we accessed past growth for 15 to 42 successive vegetative SGUs depending on the individual. All the trees bore leaves at the time the study was conducted, but these were located only on the last SGU of each living axis, as seen in Ind 4 (“t” rank, SGUs with stripes, Fig. 2B). In 9 of the 14 sampled trees (64%), we found that whatever the path followed on the different axes constituting the sampled branch, the number of SGUs was the same (Fig. 5a). In addition, a similar pattern of successive SGUs length was found when comparing the different paths in the same sampled branch. This was also validated when

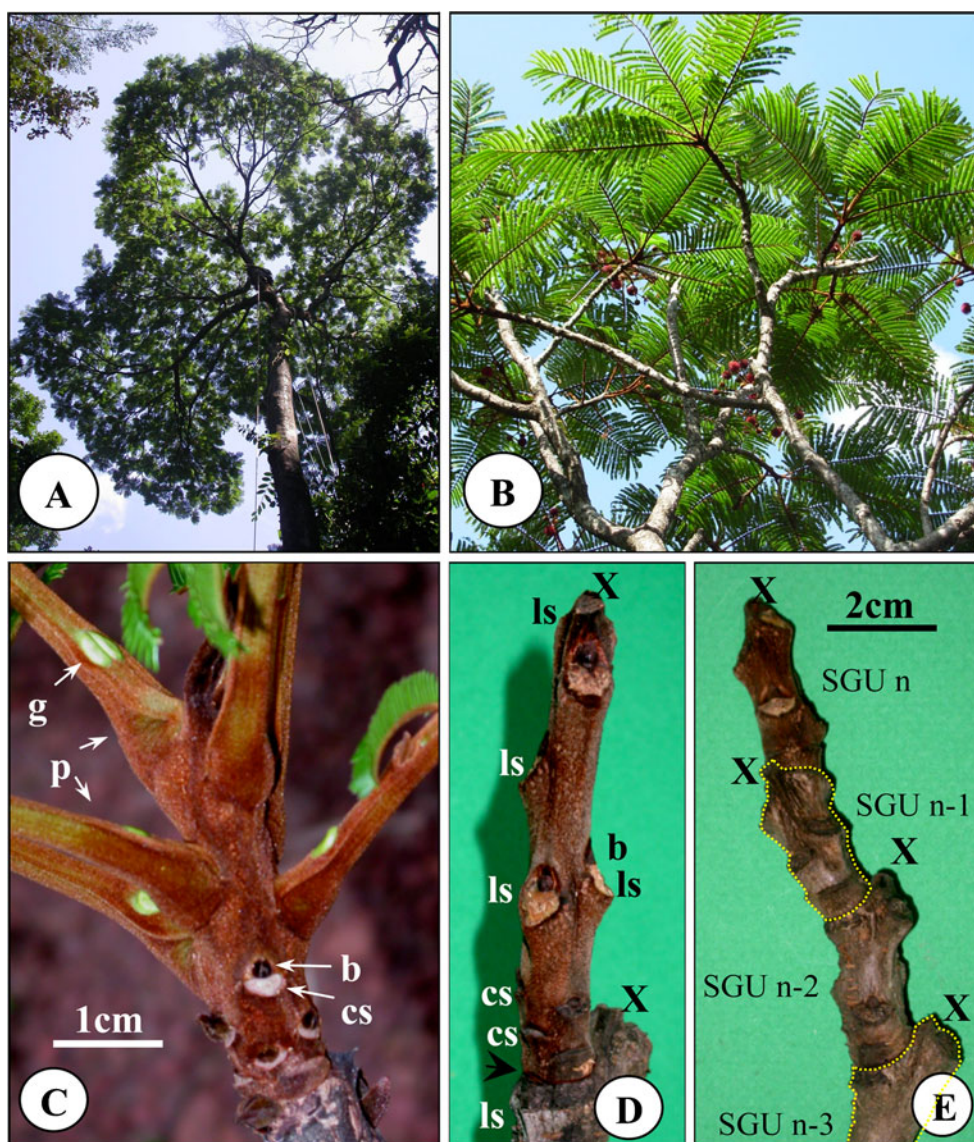


Fig. 3 A–E Situation and structure of the sympodial growth units (SGUs) in the tree *Parkia velutina*. **A** *P. velutina* tree. **B** Growing parts in the crown. **C** Leafy sympodial growth unit (SGU) at the distal part of an axis. **D** SGU after leaf shedding. **E** Axis made up of four

successive SGUs; the last SGU formed is “n”, the SGU previously formed is “n–1”, and so on. *Cs* Cataphyll scar, *b* bud, *g* gland, *ls* leaf scar, *p* leaf petiole, *X* apical scar

comparing different branches sampled on opposite sides of the crown (Fig. 6, see also Ind 9).

Irregularities were nevertheless noted in the number of SGUs formed in the five remaining trees. In one juvenile tree (Ind 16, Table 2), one lateral leafed axis in the crown formed an additional SGU (two successive leafed SGUs; Fig. 5b), whereas the other axes in the crown did not. In another juvenile tree (Ind 11), we found that several lateral axes did not form the expected number of SGUs: these axes, made up of three SGUs and usually borne by SGU_{t-3} , were also found on older SGUs (SGU_{t-4} , SGU_{t-5} and SGU_{t-7}). Longitudinal cuttings indicated that they were epicormic branches (Fig. 5e). We also observed that several SGUs were missing in some suppressed axes of the sampled

branches in two large adult trees (Ind 6 and Ind 7), as these axes did not grow for several years (Fig. 5d). Finally, several axes had formed additional SGUs in Ind 12, a senescent tree, but we never found two successive leafed SGUs as in Ind 16 (Fig. 5c).

3.1.2 Radial growth of axes

GR width was very variable from the pith to the bark but a similar pattern of successive GR widths was found when comparing the full discs of wood sampled at different heights in the tree (Fig. 7, Ind 4). For example, the thinnest GR had the same rank (n–5) from the bark at various levels in Ind 4, showing that this GR

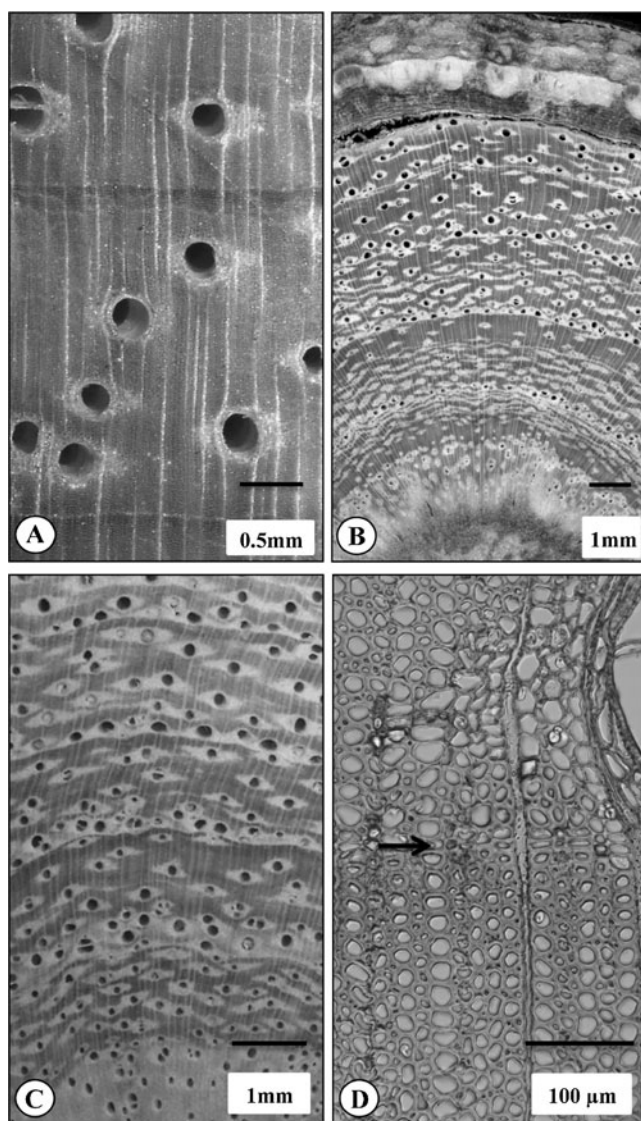


Fig. 4 Structure of the growth rings in *P. velutina*. Growth rings (GRs) were observed from full disks of wood sampled from adult trees. **A** Detail of a disk sampled from a trunk. **B** Detail of a disk sampled from a branch. **C** Detail of a disk sampled from a branch, with a notable initial porous zone. **D** Detail of a transversal cross section from a branch, showing cell wall thickening near the ring boundary, indicated by the *black arrow*

had been formed at the same time in the different parts of the tree. Finally, we counted the GRs present inside the successive SGUs on the branches. We found that the number of GRs perfectly matched SGU rank, i.e., we found six GRs inside the sixth SGU (Fig. 8).

3.2 Phenological survey

3.2.1 Leaf shedding and flowering at the population scale

Leaf shedding occurred every year and the leafless period lasted about 4 weeks. Leafless trees were seen from January

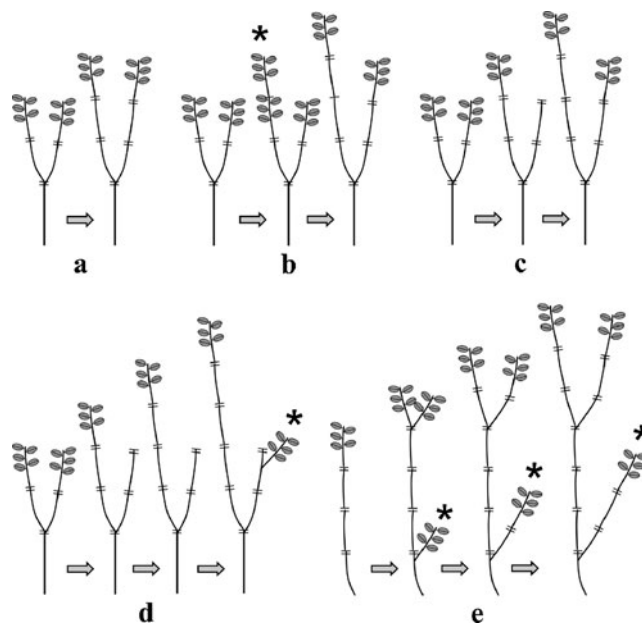


Fig. 5 a–e Modalities of longitudinal growth observed in branches sampled in *P. velutina*. Schemes show growing axes and grey symbols are leaves borne by SGU. The symbol “=” indicates that a new SGU is formed after leaf shedding on the previous SGU, whereas symbol “—” indicates that a new SGU is formed without leaf shedding on the previous SGU. Sequences **a**, **b** and **c** take place over approximately 1 year, whereas sequences **d** and **e** take place over several years (here ca. 3 years)

to November (Fig. 9), but most of them dropped their leaves in concert during July (2009 and 2010) or August (2011). Conversely, five trees dropped their leaves in concert during January 2010, and from January to March in 2011.

Eighteen trees flowered during the phenological survey and anthesis was highly dependent upon the leaf shedding month (Figs. 9 and 10), occurring in most cases 3 months after the end of the leafless period.

3.2.2 Leaf shedding and flushing at the tree scale

Despite the variability noted for the leaf-shedding time, 17 trees (85%) were leafless only once a year (Fig. 10A–C), while 3 trees (15 %) were leafless twice a year in 2010 (Fig. 10D). Longitudinal growth occurred only once between two leafless periods. Ind 12, previously mentioned, behaved in a particular manner (Fig. 10E): half of the crown (Part A) was leafless during April 2010, but the other half (B) was leafless during July 2010. Some axes in Part A were growing as the other axes were shedding their leaves. After the leafless period, Part A developed new leaves in May–June, while Part B developed new leaves at the end of July. The tree was fully foliated during August 2010. Part A was again leafless in February 2011. This behavior, expressed by a large tree (78 cm DBH; Table 2), contrasted markedly with the trees that shed all their leaves at the same time and those

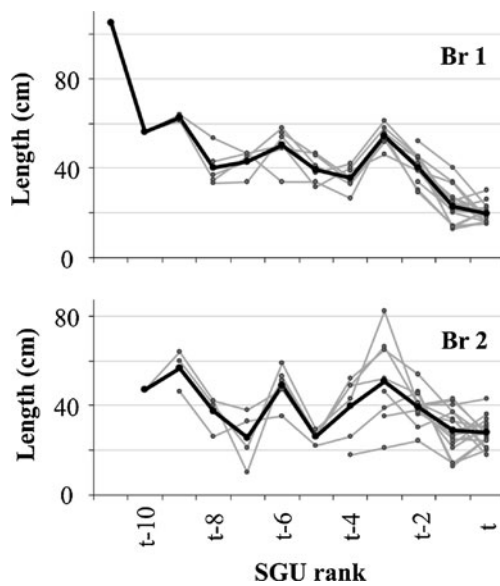


Fig. 6 Length (in cm) of the successive sympodial growth units (SGUs) making up the different axes of two branches (Br 1 and Br 2) sampled on opposite sides in the crown of an adult tree, Ind 9. SGU are labelled from the top. The "t" SGUs were the last formed. Grey lines SGU length for different axes, black line mean length

where leaf-shedding occurred gradually, generally starting in the most elevated parts.

3.2.3 Duration of the leafy period

The leafy period lasted for 8–14 months with two main modes centred on months 10 and 13 (Table 3). Group 1: Most (12) of the trees were leafless every year during July at the transition point between the long rainy season (T3) and the long dry season (T4) (Fig. 10A); Group 2: two trees were leafless every year during January (Fig. 10B) at the transition point between the short rainy season and the short dry season. Consequently, the leafy period in those trees with these two behaviors lasted for around 12 months, although their leaf shedding occurred in different months. Group 3: Six trees lost their leaves during indeterminate periods from T1 to T4 and showed shorter

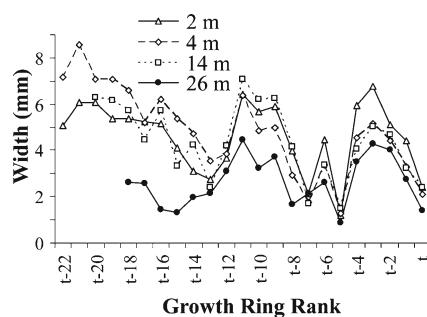


Fig. 7 Width of successive growth rings (GRs) described at various levels in the trunk (2, 4 and 14 m) and inside the crown (26 m) of Ind 4. Growth ring "t" is the last one formed

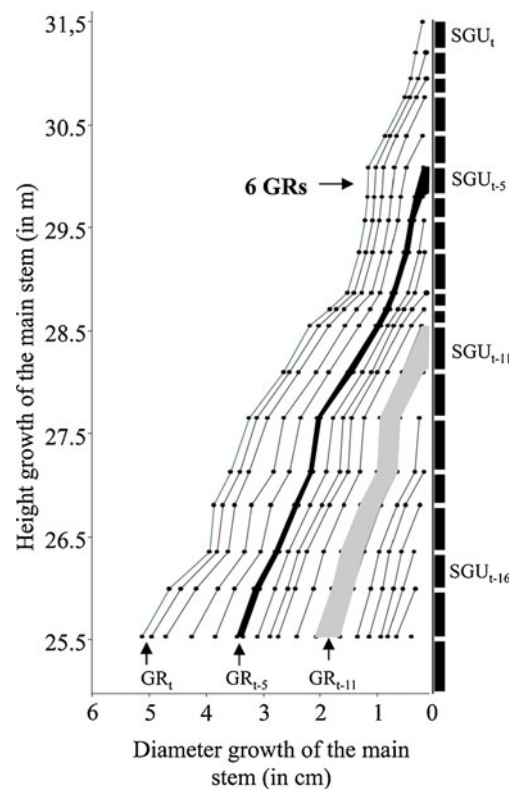


Fig. 8 Stem profile of a dominant axis in an adult tree crown. Black rectangles (right) symbolize successively formed SGU with different lengths (tree height growth); SGU_{t-n} is the last SGU formed; the y-axis symbolizes the tree cumulative height growth. Curves limit the successive radial increments of the main stem; GR_{t-n} is the last growth ring (GR) formed; the x-axis symbolizes tree cumulative radial growth

cycles ranging from 8 to 11 months (Fig. 10C, D). The trees could be leafless at any of the four periods in the year (T1–T4). Some were leafless twice a year in 2010 (Fig. 10D). One tree (ID 12) was desynchronized and the different parts of its crown shed leaves and grew in alternation (Fig. 10E).

3.2.4 Flowering at the tree scale

Nine trees flowered in only one of the two years (2009 or 2010), whereas 10 trees flowered in both years. We also observed one tree that flowered four times over the 33-month survey period and was also leafless four times during the survey (Fig. 10D, first line).

4 Discussion

In this study we analyzed the growth pattern of *P. velutina* and its variability based on a retrospective analysis of SGUs and GRs coupled with a phenological crown survey. We established the limits of successive SGUs and identified relatively long series of longitudinal growth (up to 40) based on evident morphological (e.g., cataphyll scars) and macro-

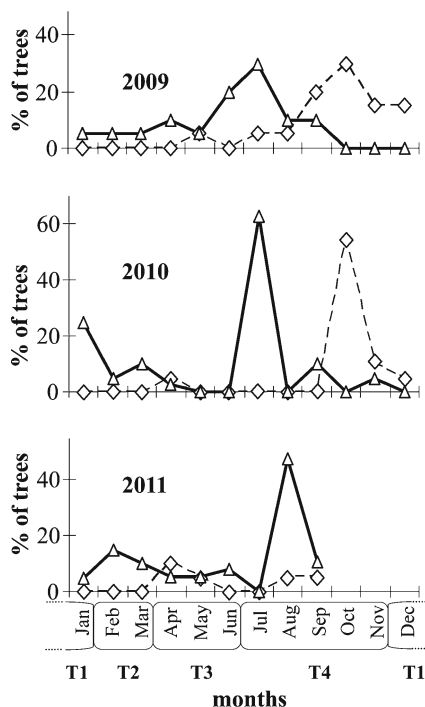


Fig. 9 Percentage of leafless (triangles and continuous line) and flowered trees (diamonds and dashed line) per month in three successive calendar years (2009–2011)

anatomical (pith) markers. We also showed that GRs are observable on *P. velutina* as on *P. nitida* (Détienne 1995) and we validated that one ring corresponds to one SGU. These morpho-anatomical markers open up perspectives for further dendroecological studies. However, if this topological scale (rings, succession of SGUs) is to be converted into a temporal scale, then the temporal pattern of the phenological cycle needs to be identified.

4.1 Topological synchronisms in primary and secondary growth

We observed systematically in the tree crowns that only the most recently formed SGU on each living axis bore leaves. This suggests that each living axis forms only one SGU between two successive leaf-shedding events. Is this behavior the general rule, or is it particular to the time period embraced by this study? In deciduous temperate species, polycyclism refers to a growth pattern in which the annual length growth of an axis (between two successive leaf-shedding events) involves more than one bout of elongation (Barthélémy and Caraglio 2007). The formation of several SGUs during the same vegetative cycle is frequently associated with a topological asynchrony in crowns (Sabatier and Barthélémy 1999), as only some axes in the crown grow twice during the same vegetative growth cycle. Our retrospective analysis demonstrated that, in 9 of the 14 trees sampled, the number of SGUs was the same whatever the path followed on the different axes

constituting the branch sampled (Fig. 5, behavior a). Additionally, we found a similar pattern in the successive SGUs length when comparing the different axes constituting the sampled branch of Ind 9 (Fig. 4). This could be interpreted as a common response to environmental factors. These different properties support the notion that growth occurs once between two successive leaf-shedding events on all parts of the tree. This conclusion, based on tree morphology, is supported by our tree-scale observations made during the 33-month survey.

Irregularities were nevertheless reported for five trees, therefore corresponding to different behaviors. (1) One juvenile tree showed two bouts of elongation between two successive leaf-shedding events. This phenomenon was observed directly during the phenological survey, and it is noteworthy that only one ring was formed on these two successive SGUs. It is possible that this behavior occurs only in juvenile trees, as a form a polycyclism. Further studies at the youngest stages will be required to investigate such ontogenetical effects. (2) Growth of epicormic shoots (sprouting, Fig. 5e) was observed in another juvenile tree that was suddenly exposed to high light levels. Epicormic shoots were also observed in two senescent trees that exhibited an ageing behavior (Fig. 5d). These structures were easily identifiable and did not compromise the possibility of a retrospective growth reconstruction. (3) Finally, the most serious irregularities were expressed by only one senescent tree (Ind 12, see also Table 2) that showed a truly “desynchronized” behavior (Fig. 5c). Here we were not able to interpret its structure retrospectively. It may therefore be concluded that primary markers can be used in most cases to rank SGUs that have formed over a given period inside the crown.

Retrospective examination of GRs also throws light on growth behavior. Annual GRs are more often found in deciduous species (Worbes 2009; Borchert 1999), as they slow their radial growth during leafless periods (*D. panamensis* and *L. ampla*, O’Brien et al. 2008). In *P. velutina* we found that a line of parenchyma marked each GR limit in the full disk. This was often associated with large vessels in a ring-porous arrangement in branches, a phenomenon observed frequently in some temperate (Zimmerman and Brown 1977) and tropical (Détienne 1995; Worbes 2009) tree species. In accordance with Dünisch et al. (2002), we assume that the parenchyma limit in *P. velutina* may correspond to the end of cambial activity, whereas the initial porous area (early-wood vessels) indicates the initial phase of cambial growth. As the number of GRs perfectly matched the SGU rank in branches, we believe that each GR is formed during one vegetative cycle, which corresponds to one SGU in adult trees. We assume that a new GR is also formed simultaneously in the entire plant body as we observed similar radial growth patterns in the higher and lower parts of the tree.

Consequently, the phenological cycle can be defined by the following succession of events: leaf shedding (lasting nearly 4 weeks), elongation of one SGU associated with one

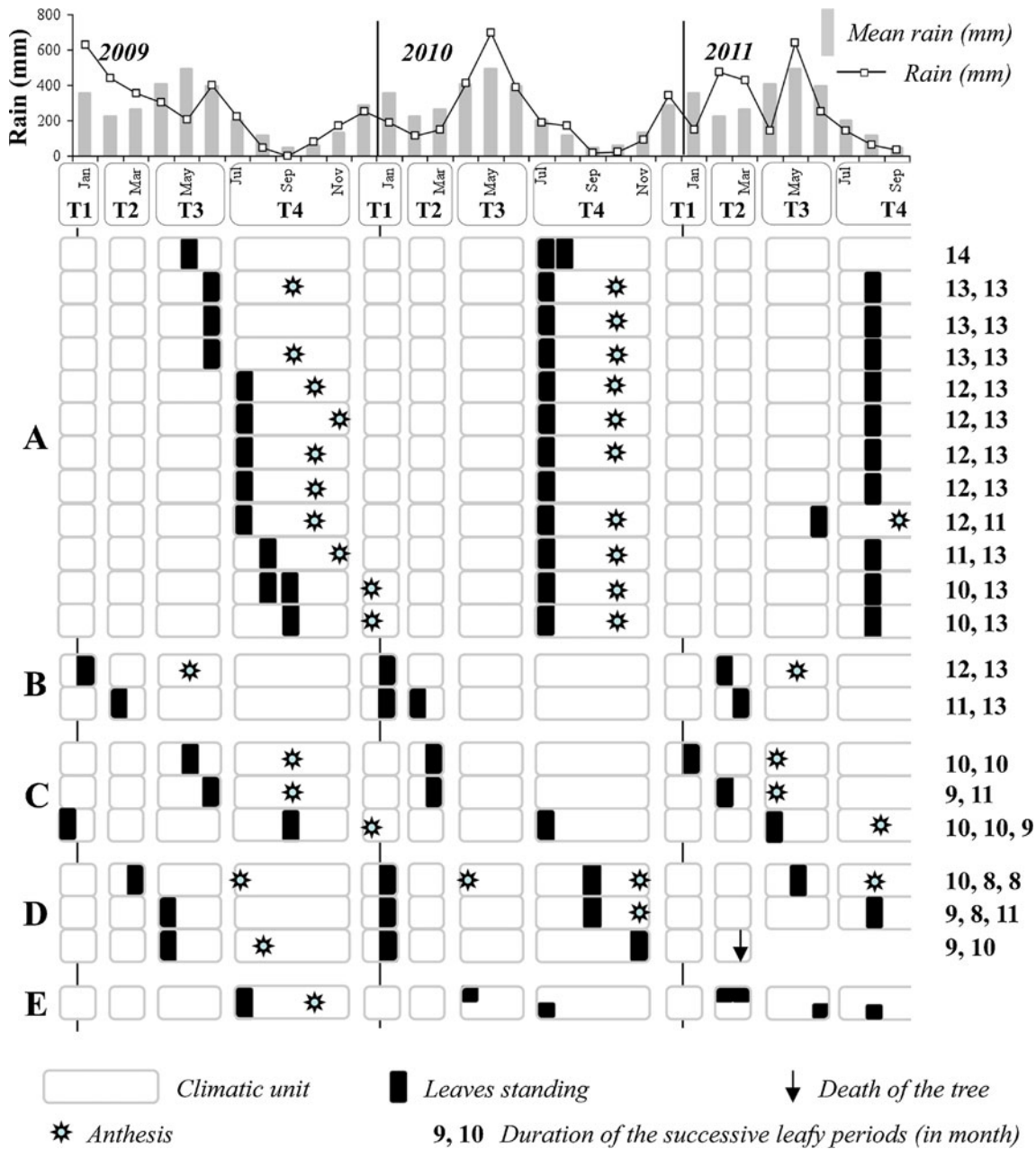


Fig. 10 Leaf shedding patterns at the population scale. Groups A–E present the different leaf shedding patterns found in the trees. In each group, each row corresponds to a single tree. Numbers to the right of the lines indicate the duration (in months) of the leafy period between two leafless periods. For clarity, we divided the year into four main seasonal periods: short rainy season (T1), short dry season (T2), long

rainy season (T3) and long dry season (T4). Black rectangles Months in which a tree was observed to be leafless; ↓ death of the tree; vertical grey bars mean rainfall per month (in mm) for the last 29 years (1980–2008); open squares and lines total rainfall per month (in mm) in years 2009, 2010 and part of year 2011

GR, and flowering, which occurs on average 3 months after the end of the leafless period. We are therefore able to advance the hypothesis that cambial reactivation is not disconnected in time from flushing in *P. velutina* since cambial growth is induced by the growth of the crown apical buds in some tropical species (Creber and Chaloner 1990; Borchert 1999; Yañez-Espinosa et al. 2010; Iqbal 1995; Little and Pharis 1995).

4.2 Periodicity of SGU/GR formation

In any time-series analysis, “recurrence time” refers to the number of indices (e.g., months) starting from a given event until its subsequent occurrence (Heuret et al. 2003). For any set of sequences, this characteristic takes the form of a frequency distribution. In temperate deciduous species, the recurrence time for the leaf-shedding event is 12 months and

Table 3 Recurrence time for the leaf-shedding event for each group of trees. In *Parkia velutina*, recurrence time for the leaf-shedding event (from the flushing time to a new leaf-shedding event) lasted for 8–14 months. A, B, C and D are the different tree groups (see also Fig. 10); *All ind.* All individuals; for each case, the number of trees is given, with the percentage of trees in parentheses (%)

	Recurrence times (in months)						
	8	9	10	11	12	13	14
A					5 (26%)	12 (64%)	2 (10%)
B				1 (25%)	1 (25%)	2 (50%)	
C		2 (29%)	4 (57%)	1 (14%)			
D	3 (37%)	2 (25%)	2 (25%)	1 (13%)			
All ind.	3 (8%)	4 (10%)	6 (16%)	3 (8%)	6 (16%)	14 (37%)	2 (5%)

is practically invariable. In our case, this frequency distribution included values ranging from 8 to 14 months. Two main tree behaviors were noted in this distribution:

- (1) Trees that lost their leaves every 12 months correspond to trees with a leaf-shedding event occurring (a) around January (2 trees), or (b) in July and August (12 trees). This is partially consistent with Loubry (1994) who, for this species, reported leafless trees in July (1990; 78% of trees) or August (1991; 67% of trees).
- (2) On the other hand, some trees lost their leaves during indeterminate periods from T1 to T4 and showed shorter cycles ranging from 8 to 11 months. Loubry (1994) reported similar cases in *P. velutina*. Two hypotheses can be put forward to explain these shorter 8- to 11-month cycles. First, these trees may be viewed as a transition from behavior (a) to behavior (b), and so give rise to a shorter leafy period (Fig. 10C). On the other hand, some of the trees with short cycles, which developed SGUs twice a year in 2010, were the largest emergent or pre-senescent trees forming the shortest SGUs (< 5 cm long), and showing a marked dieback in their crown. One of these fell in late February 2011 (Fig. 10D; ↓). A second hypothesis is that these trees have shorter phenological cycles as a result of their advanced stage of development. This conflict between the two main leaf shedding periods (T1–T2 or T4) is clearly expressed by Ind 12 (Fig. 10E), which shed leaves in one part of its crown in T2 and those in the other part in T4.

4.3 How can a topological series be converted into a temporal series?

The study described here shows that *P. velutina* has an annual rhythm that includes one bout of elongation at the adult stage. As a result of the variability observed in recurrence time between the two flushing events, the number of SGUs corresponds closely, but not exactly, to the age of the structure. When we adjusted the distribution to the recurrence time

distribution for the leaf shedding event (mean=11.37 months) and convoluted this 40 times, the resulting distribution ranged from 434 to 479 months with a 95% confidence interval. In other words, when 40 SGUs are identified, this corresponds to 36.2 to 39.9 years of growth (37.9 on average). In consequence, it is conceivable to estimate the age of a structure by counting GUs or GR. However, attributing a precise date (year or month) to a SGU, with the aim of comparing trees or understanding the correlation with environmental variables cannot be achieved accurately. In fact, trees that show an annual behavior are able to express an annual resting period at different times: around January or around July. Therefore, the correlation between SGU length or ring width and climatic variables must not be studied by considering a particular fixed month as explanatory variable.

4.4 Conclusions and perspectives

This study on *P. velutina* provides evidence of (1) variability in leaf shedding time, and (2) synchronicity between longitudinal and radial growths. We showed that it is possible to analyze retrospectively both height and diameter growth (which provides access to wood volume produced) through the observation of morpho-anatomical markers. We demonstrated that the growth of *P. velutina* is globally annual and synchronized inside the crown of adult trees even though the time between two successive leaf-shedding events is slightly variable.

The next step is to understand the causes of the variation observed in (1) the timing and recurrence time of the leaf-shedding event, and (2) the amplitude of the growth, branching and flowering processes (e.g., SGU length or GR width). It is noteworthy that branching and flowering are still difficult to analyze retrospectively over long periods due to the self-pruning process that renders the analyzed structure incomplete when old parts of the branch are observed. All these processes must be analyzed conjointly if we are to understand the trade-off in biomass allocation that takes place inside the tree to maintain vital functions (e.g., exploration, conduction, reproduction, etc.).

The cause of variations in the timing, frequency and amplitude of such processes can be found in ontogenetical effects. For example, we suspect that (1) juvenile trees are able to exhibit several events of axis length growth between two annual leaf-shedding events, and (2) senescent trees have a shorter cycle with more than one leaf-shedding event per year. These hypotheses will need to be tested. Finally, these variations may also be due to the influence of environmental factors (irradiance, rain, soil moisture; see also Yañez-Espinosa et al. 2006; Borchert 2004). A study conducted on adult, dominant trees (to avoid ontogenetical effects), where the number of SGUs is closest to the number of years (to avoid the discrepancy between SGU rank and calendar year) would reduce the complexity of this task.

Little information is available concerning the height growth of adult tropical trees. Establishing long-term records takes time before interpretable results are available, and such studies have the disadvantage of being restricted to one particular situation. Moreover, tree height measurement may also be subject to errors that can easily be larger than the actual height growth between two censuses. Another way to gain access to height growth is based on stem analysis (Rozendaal and Zuidema 2011) but this approach requires the presence of annual rings and its precision is dependent upon the distance between the wood-disk samples. With our study, we have shown that analyzing morphological primary growth markers can provide a very precise quantification of height growth and this warrants further exploration in other species.

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