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Polycyclism, a fundamental tree growth process, decline with recent climate change. The example of *Pinus halepensis* Mill. in Mediterranean France

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Abstract

Polycyclism, the ability for a plant to produce several flushes in the same growing season, is a key process of plant development. Polycyclism frequency is likely to change with the anticipated climate trend, expected to impact plant growth over the next century. However, polycyclism processes are not well-described in the literature and an important lack of knowledge prevents any possible prediction for the 21st century. Aleppo pine is a good model to study polycyclism: it is known to produce up to four annual flushes in one growing season. In this study, we used architectural analysis to describe and reconstruct polycyclism processes, periodicity and frequency on Aleppo pine in a Mediterranean site for the last 15 years. We also assessed relationships between polycyclism frequency and climate. Since 1995, climate was far hotter and drier than normal in South-eastern France: polycyclism was significantly reduced, particularly after 2003 heat-wave, which delayed effect remains till 2008, exacerbated by repeated droughts. Morphologically, polycyclism is primarily influenced by twig vigour, status (principal / secondary and strong axes) and position (low, middle or top crown). Climatically, it depends on summer temperatures of the current and preceding year, rainfall of the first half of preceding year and winter rainfall. Previous year abundant rainfall combined with colder temperatures and high rainfall in spring or at the end of summer of the current year increase polycyclism frequency. Polycyclism is likely to decrease significantly in the 21st century due to a hotter and drier climate.

Introduction

The Mediterranean climate is characterized by high temperatures associated with low rainfall in summer, drought being the main environmental constraint for vegetation growth (Le Houerou 2005). For the 21st century, climatic models forecast that the Mediterranean basin will be prone to a faster warming than most other continental areas over the world (Gibelin and Deque 2003; Hesselbjerg-Christiansen and Hewitson 2007). This warming will also be associated with a significant rainfall decrease during the growing season. In Southeastern France, abnormally low rainfall levels (40 to 60% below the average for the growing season) were successively observed from 2003 to 2007 (Vennetier and Ripert 2009). Moreover, ten of the twelve hottest years since 1850 were recorded between years 1997 and 2009 (MétéoFrance 2009). Mean annual temperature and mean summer temperature of years 1995-2009 were 0.9°C and 1.3°C above the 30 years-average. Finally, the 2003 heat wave significantly impacted French Mediterranean forests as well as most of Europe (Zaitchik et al. 2006). Scorching heat had direct and delayed negative effects on tree growth, especially on pine species (Vennetier et al. 2007). Unfortunately, such extreme climatic events are likely to be recurrent in the next decades with global warming (Houghton et al. 2007; Deque 2007). The resulting increase in summer water stress will reduce tree growth in Mediterranean areas (Rathgeber et al. 2000; Borghetti et al. 2004; Ogaya et al. 2003; Sardans and Peñuelas 2007). Raising temperature may also lead to phenological lags (Kramer et al. 2000), particularly in the beginning and end of the growing season.

Formation of several growth units (flushes) in the same growing season, a process called polycyclism (Barthelemy and Caraglio 2007), confers to a tree a significant advantage in contrast to monocyclic species, particularly in the Mediterranean area where the growing season is split in two parts by drought. Polycyclism increases branching rate and total photosynthetic area and plays an important role in total annual growth. Polycyclism rate decreases with tree and twig age and vigour (Sabatier et al. 2003), and varies according to species (Barthelemy and Caraglio 2007). Anatomical and morphogenetic bases of polycyclism are described in details for a few species or families (Kremer and Roussel 1986); (Weinstein 1989). Underlying processes are primarily driven by climatic conditions of the previous and the current year (Sabatier et al. 2003; Verdu and Climent 2007). Thus, they should be greatly impacted by climate change. Actually, no paper deals with the relationship between climate and polycyclism. Potential number of flushes per growing season was quantified on some species (Kremer and Roussel 1986; Weinstein 1989) and for trees in irrigated conditions (Pardos et al. 2003), but the real polycyclism rate (quantification on annual bases and variations in the medium or long term) in natural stands and on adult trees is unknown in scientific literature. Gathering such information is compulsory to improve models of tree growth, architectural development, and functioning in a climate change context.

Aleppo pine (*Pinus halepensis* Mill.) is a polycyclic tree species that typically grows in the dry mild areas of the Mediterranean region (Nahal 1962; Farjon 2005). Its natural range distribution around the Mediterranean basin extends from Morocco to Syria in North Africa and from Portugal to Greece on the northern shore. It is normally replaced by *Pinus brutia* Ten. in the eastern basin where it has been extensively planted. Aleppo pine is generally found at low altitudes, from sea level to 600 m in its northern range, but it also grows at an altitude up to 1000 m in southern Spain, and up to 1700 m in Morocco and Algeria (Richardson 1988). Aleppo pine is characterized by an exceptional plasticity; heliophilous and thermophilous, it tolerates drought and disfavours high humidity, frost, and snow (Rushforth 1999). Its pioneer reputation is explained by a high fructification rate, easy seed dissemination, and by its capacity to grow in very hot sites and on any type of non-hydromorphic soil including on limestone. Consequently, Aleppo pine is one major component of Mediterranean forest dynamics (Rushforth 1999). Aleppo pine is a good model to characterize polycyclism: when adult, it is known to produce up to four annual growth units in the growing season, one or two, more rarely three, from late winter to the beginning of summer and sometimes one after summer drought (Debazac 1963; Serre 1976). In an irrigated seed orchard, up to seven successive annual flushes were recorded for grafted Aleppo pine (Pardos et al. 2003). Polycyclism rate also depends on the location within the tree architecture (i.e. trunk *versus* branches, (Caraglio et al. 2007).

Many other pine species are polycyclic: in Europe, *Pinus brutia*, *Pinus edulis* Engelm. *Pinus palustris* P. Mill. *Pinus pinaster* Ait (Kremer and Roussel 1986; Weinstein 1989). For *Pinus brutia*, the number of summer shoots depends on local summer rainfall (Isik et al. 2002). In North America, *Pinus banksiana* Lamb. is polycyclic under favourable climate conditions, and up to three growth units are produced per year (growing season from June to September) (Plourde 2007). At fall, polycyclic growth is ended by shortened photoperiod and cold temperatures (Pardos et al. 2003). Occasionally, mild weather in late fall induces buds that normally would not flush until the following spring. Late polycyclism delays the beginning of the next growing season (Sabatier et al. 2003) or may even continue to grow till next spring if winter climate is temperate enough.

Plant architecture is commonly neglected in climate change impact studies. In terms of photosynthetic biomass, primary growth (i.e. lateral and principal twig growth) and leaf production are far more important than secondary growth (i.e. radial growth) (Lopez-Serrano et al. 2005). Our goals in this study were (i) to describe polycyclism periodicity and frequency on Aleppo pine in the Mediterranean region and (ii) to assess interrelationships between polycyclism frequency, twig status, twig growth, and climate. We hypothesized that polycyclic shoots represent a high percentage of total annual growth on Aleppo pine and that climate change may significantly alter polycyclism frequency in the 21st century.

Methods

Study area

The study site was located on a flat plateau (slope <5%) in the Departmental Forest of Font Blanche (43° 14' 25'' N, 5° 40' 40'' E, altitude 425m a.s.l.) in Provence, Southeastern France (Figure 1).

Figure 1, Location of the study area in southern France. Grayscale colors represent altitude whereas black zones represent main towns.

Its Mediterranean climate is characterized by a severe drought lasting two to four months in summer, mild and humid winters, and very low cloudiness. At this site, mean annual temperature (1979-2008) was 13.2°C and mean annual precipitation (1979-2008) was 690 mm. They were respectively 12.7°C and 745 mm for the

period 1961-94 (Figure 2). Climatic data were interpolated as a function of altitude (0.6°C/100 m) and distance from four stations of the National Meteorological Survey Network (MétéoFrance 2009) located near the experimental site (5-10 km, altitude difference less than 200 m). An on-site station exists since 2008. The limestone-based shallow soil (10-30 cm) is characterized by pH close to seven, high nutrient content, a high percentage of coarse elements, and rock outcrops. Stand productivity depends mainly on penetrability of superficial bedrock for root extension. The Font Blanche forest is dominated by Aleppo pine uneven-aged stands from 35 to 115 years (dominant and sampled class = 55 years), 12-14 m high, mixed with six meters-high *Quercus ilex* L. coppice by patches (Lookingbill and Zavala 2000). The understory is composed principally by *Quercus coccifera* L. and *Phyllirea latifolia* L.

Figure 2, Average annual precipitation and temperature in Font Blanche since 1995 showing also 1961-2008 average.

Sampling and growth reconstruction

Pairs of dominant branches (exposition in the crown: north and south) were cut at three crown positions (top, intermediate and low-level when alive, aged respectively 15, 25 and 35 years) on 35 dominant Aleppo pines at Font Blanche. Successive branch sampling from 2005 to 2009 (seven trees per year) was made to consider branch and axes autocorrelation and expand the studied time span. Morphological markers like size and density of scales at the base of the growth units, lateral axes, and position of cones (Figure 3) were used to reconstruct tree primary growth for the last 10 to 15 years on each branch, following methods described by Sabatier et al. (2006) and Pardos et al. (2003) which proved to be relevant for Aleppo pine.

Figure 3, Schematic illustration of Aleppo pine polycyclism according to morphological markers used for twig datation. All flushes start by sterile scales, small and clustered on the first one, larger and spaced out on the following ones. Male flowering (left): male flowers appear at the base of the first flush over sterile scales and give hooked scales. Shoots with male flowers are rarely polycyclic. Female flowering (right): cones (with very few exceptions) appear at the top of the first annual flush. The presence of one branch or of a whorl indicates the top of a flush. Nb. A twig never bears male and female flowers the same year.

In addition to measurements on branch principal axis, two pairs of secondary axes (Figure 4) (one strong and one weak in each pair) were sampled: one pair 10 years-old and the other pair 5 years-old. Twig markers crossdatation was made by comparing ages of annual shoots on main axis with first

shoots of basic whorls. At first, twigs were classified within each branch as function of their status: principal (P) (main axis), strong secondary axis (S-Strong) and weak secondary axis (S-Weak). The status is based on relative diameter and growth on each branch and not related to absolute vigour. Then, we classified twigs independently of their status and position: according to their vigour. To do so, twig length of years 2003-2005 (period common to all samples) was calculated and sampling was split into three groups (Figure 5C): frail twigs (annual growth ≤ 70 mm), medium vigour (71-140 mm) and vigorous (≥ 141 mm). Although twig vigour generally decreased with its position from the top to the base of the crown, and from principal to S-Weak axis, it was highly variable due to the variability of the competition with neighbouring branches and trees. Indeed, high standard deviation was found in twig vigour for each exposition, position and status (Figure 5). Finally, shoot length and polycyclism

chronologies of the period 1995-2008 were computed for each exposition, position, status and vigour. The 14 years retrospective analysis period (1995-2008) was chosen because structural information disappears with time due to (1) the natural fading of morphological markers and (2) the natural self-pruning of twigs. Too few data were available for 1994 and previous years. Length of flushes was measured using an electronic ruler (± 0.1 mm).

Figure 4, Schematic representation of the sampling. Principal axis, S-Weak and S-Strong axes of five years-old and those of 10 years-old are represented.

Figure 5, Classification of twigs as function of their shoot length and their A) status (S-Weak, S-Strong and Principal), B) position (low, middle, top canopy) and C) vigour (frail, medium, vigorous). Lower and upper quartiles are respectively 25th and 75th percentiles as the middle line represents the median.

Phenological observations

In this station, 9m-high scaffolds were installed in 2007 and 2008 to reach the top-level foliage of 17 mature Aleppo pines of the same generation (55 ± 1 years). On each pine, three to six branches close to the scaffold were chosen for weekly phenologic observations, with the same protocol as for polycyclism sampling. Phenological stages (phenological phases or phenophases) were identified using a procedure proposed by (DuMerle and Mazet 1983). Budburst, leafing-out, flowering, and fruiting processes were scaled over several stages ranging from stage A (winter stage) when the bud was completely closed to stage E (maturation) when the new leaves were fully developed and mature (table 1). The onset of twigs was checked by visual observations of the apical buds. Flush length was measured to the nearest millimeter with a ruler, every week or 15 days from February 12th to November 15th 2008 and from January 28th to December 15th 2009.

Statistical analysis

Relationships between polycyclism frequency and climate were investigated using a partial least square (PLS) regression. PLS regression was chosen because it handles many variables with relatively

few observations (Cramer et al. 1988) and deals with correlated variables (Wold 1995). The number of components was chosen by a permutation test (Good 1994) with a 5% threshold for the explained variance. Variables were tested with a 1000-step cross-validation test (Amato and Vinzi 2003), and they were accepted only if zero did not belong to the confidence interval ($p < 0.05$) for their partial correlation coefficient. Climatic parameters tested for the regression were rainfall (P), maximum temperature (MaxT), minimum temperatures (MinT), and mean temperatures (MT) from January of year (n-1) to November of year (n) over the period 1995–2008, according to the phenology of this species in Southeastern France (Serre 1976); (Orshan 1989). In order to test which factor among twig exposition, position, status, and vigour had the greatest influence on polycyclism frequency, mean values between classes were compared with an ANOVA and contrasts were computed. Statistical analyses were computed with ADE4 (Thioulouse et al. 1997) and R software (R Development Core Team 2004).

Table 1, Aleppo pine phenological stages: winter stage, budburst, young leaves opening, lengthening, mature.

Winter stage	Budburst	Young leaves opening	Lengthening	Mature

Results

Polycyclism frequency

Variance analysis for twig classes is displayed in Table 2. Higher branches were more polycyclic than lower branches ($p < 0.0001$), principal axes were more polycyclic than S-Weak axes and twigs of higher vigour were more polycyclic than frail twigs. Exposition (North-South) was not significant ($p = 0.14$). PLS regression was used to calculate the contribution of each factor to polycyclism frequency. According to their partial correlation coefficients, respectively 0.51, 0.38 and 0.26, twig vigour was the greatest contributing factor followed by twig status (P, S-Strong, S-Weak) and position (low, middle, top crown) ($p < 0.001$). Branch exposition was not statistically significant ($p = 0.06$) and was removed from the PLS regression.

From 1995 to 2008, a significant decline ($p < 0.05$) of polycyclism frequency was observed for all series except S-Weak and S-Strong axes. Generally, this trend was driven by the sharp decrease following 2003. Also, polycyclism frequency (both bi- and tricyclism) was low (generally $< 35\%$) since 1995 on S-Weak and frail axes and became rare (generally $< 20\%$) on low branches after 1997 (Figure 6). Then, no tricyclism was observed on frail axes during the period 2003–2007. Whatever their status, position and vigour, all twigs followed a common pattern of polycyclism: two waves with maximal values in 1996–97 and in 2001–03, an intermediate frequency trough between 1998 and 2000 and a generally abrupt fall after 2003 with a minimum in 2005. After a slight increase in 2006, polycyclism frequency remained constant for the higher class of status, position, and vigour, and decreased rapidly for the two lower classes.

Table 2, ANOVA results showing importance of branch position (low, middle, top crown), exposition (north, south), axis status (S-Weak, S-Strong, Principal) and vigour (frail, medium, vigorous) to explain polycyclism frequency.

Source	Sum of squares	Df	Mean square	F	Probability
<i>Effects</i>					
Branch exposition	0.08	1	0.08	2.21	0.1385
Branch position	0.87	2	0.43	12.27	<0.0001
Twig status	2.91	2	1.46	41.17	<0.0001
Twig vigour	4.37	2	2.19	61.87	<0.0001
Residuals	9.75	276	0.04		
Total	28.46	283			

In the PLS regression, low number of observations (16) and high inter-annual variability of climate made grouping monthly climatic parameters necessary to obtain significant results. We grouped successive months having same signs for their individual correlation coefficients (sum of precipitations, average temperature). Figure 7 shows the relationships between polycyclism frequency and climatic variables for principal axes. Vigorous and top axes showed similar R^2 values for the same climatic variables. Other classes of vigour, position and status were also investigated and showed similar patterns but at slightly lower R^2 values. The role of the previous year's climatic conditions [n - 1], rainfall as well as temperature, seemed to be dominant in Aleppo pine monocyclism and at least as important as current year [n] conditions for tricyclism. Monocyclism was primarily favoured by low levels of precipitation from January to August [n-1], from November [n-1] to February [n], and in August [n], in addition to high summer [n-1] and spring [n] temperatures. By contrast, tricyclism frequency was mainly linked with abundant precipitations from January to August [n-1], as well as in spring, August and fall of year [n], and low temperatures in summer [n-1] and September [n].

Polycyclism and shoot length

Since 1995, Aleppo pine monocyclic shoots were 53% shorter than bicyclic ($p < 0.05$ except in 2000) and 77% shorter than tricyclic shoots ($p < 0.01$) (Figure 8a). In comparison, tricyclic growth was almost twice the bicyclic growth ($p < 0.05$). Significant decrease of mono-, bi- and tricyclic shoot length was observed since 1995 ($R^2 = 0.74, 0.70$ and 0.83 respectively, $p < 0.01$). First, second and third flush length decreased with twig vigour, from vigorous to medium and frail twigs (fig 8 b, c and d) so that annual shoot elongation was not entirely linked with the number of growth cycles but also with branch status.

Percentage of shoot elongation per flush

Second and following cycles represented an important percentage of total annual growth for vigorous and medium axes, respectively close to 47 and 30% on average over the studied period (Table 3). On frail axes which are mainly monocyclic, they counted for only 10%. Those percentages significantly decreased since 2004, from respectively 25, 50 and 80%. Whatever the number of cycles and the flush order, annual shoot length and each flush length displayed similar relative variations in time, with low values in 1997, 1999, 2001 and 2004, peaks in 1996, 1998, 2000 and 2003, and generally a small increase in 2007 (Figure 8a, b, c and d). This general trend was common to all flushes order. For vigorous and medium axes, it was mainly due to the break following 2003. This trend started earlier for frail axes, which did not recover completely after years like 1997, 1999 and 2001.

Statistical analysis

Relationships between polycyclism frequency and climate were investigated using a partial least square (PLS) regression. PLS regression was chosen because it handles many variables with relatively few observations (Cramer et al. 1988) and deals with correlated variables (Wold 1995). The number of

components was chosen by a permutation test (Good 1994) with a 5% threshold for the explained variance. Variables were tested with a 1000-step cross-validation test (Amato and Vinzi 2003), and they were accepted only if zero did not belong to the confidence interval ($p < 0.05$) for their partial correlation coefficient. Climatic parameters tested for the regression were rainfall (P), maximum temperature (MaxT), minimum temperatures (MinT), and mean temperatures (MT) from January of year (n-1) to November of year (n) over the period 1995–2008, according to the phenology of this species in Southeastern France (Serre 1976); (Orshan 1989). In order to test which factor among twig exposition, position, status, and vigour had the greatest influence on polycyclism frequency, mean values between classes were compared with an ANOVA and contrasts were computed. Statistical analyses were computed with ADE4 (Thioulouse et al. 1997) and R software (R Development Core Team 2004).

Table 3, *Percentage of each flush length in total annual growth in relation with twig vigour. Pearson coefficient (r) and probability (p) are shown.*

Table 3

Years	Frail first flush	Medium first flush	Vigorous first flush	Frail second flush	Medium second flush	Vigorous second flush	Frail third flush	Medium third flush	Vigorous third flush
1995	0.83	0.70	0.44	0.16	0.28	0.44	0.01	0.02	0.12
1996	0.73	0.55	0.50	0.26	0.40	0.40	0.01	0.05	0.10
1997	0.75	0.61	0.45	0.23	0.37	0.40	0.02	0.03	0.15
1998	0.89	0.67	0.51	0.11	0.270	0.40	0.00	0.07	0.09
1999	0.91	0.69	0.54	0.09	0.28	0.38	0.00	0.03	0.08
2000	0.89	0.62	0.51	0.11	0.359	0.40	0.00	0.02	0.09
2001	0.90	0.67	0.55	0.10	0.32	0.41	0.00	0.00	0.04
2002	0.90	0.64	0.49	0.10	0.35	0.42	0.00	0.02	0.10
2003	0.89	0.63	0.45	0.11	0.35	0.46	0.00	0.02	0.09
2004	0.95	0.70	0.57	0.05	0.30	0.41	0.00	0.00	0.02
2005	0.99	0.85	0.64	0.01	0.15	0.35	0.00	0.00	0.01
2006	0.96	0.81	0.62	0.04	0.18	0.36	0.00	0.00	0.03
2007	0.97	0.84	0.62	0.03	0.15	0.33	0.00	0.01	0.05
2008	0.99	0.91	0.62	0.01	0.08	0.30	0.00	0.01	0.08
Mean	0.90	0.71	0.54	0.10	0.28	0.39	0.00	0.02	0.08
Std. Err.	0.08	0.11	0.07	0.08	0.10	0.04	0.00	0.02	0.04
r	0.86	0.79	0.80	-0.85	-0.73	-0.66	-0.62	-0.70	-0.70
R ²	0.73	0.62	0.64	0.73	0.53	0.43	0.38	0.49	0.48
p	0.000	0.001	0.001	0.000	0.003	0.011	0.019	0.005	0.006

Growth rhythms of monocyclic and polycyclic shoots

The 2008 and 2009 growth period began in winter and finished in November in Font Blanche forest (Figure 9). Monocyclic shoots had relative constant growth between initiation (winter) and the end of June, interrupted by a plateau between the end of February and the beginning of April where flush length remained nearly unchanged. This plateau coincided with the initiation of male flower buds on some twigs and of a second flush on some others (bicyclism). Between the beginning (2009) or the end (2008) of April and late-June, high-speed elongation of second growth units was observed followed by a stagnation during the dry season in summer and up to mid October. A late polycyclism was initiated at the end of October 2008 and 2009 on many shoots of the top and middle of crowns and on main and S-Strong axes resulting in an exceptionally high frequency of tricyclism on the most vigorous twigs in 2008-09. This new cycle was immediately interrupted by frost in November and remained needless and very short

(5-20 mm). However, our surveys showed that shoot elongation occurred between December 2008 and mid-February 2009, when very mild climate and abundant precipitations were recorded at Font Blanche. It was difficult to attribute this winter cycle to the preceding [n-1] or current [n] year: some of these winter growth units are similar to those initiated in October. Also, they stopped elongating till February and growth re-started as the first flush of 2009 without new ramification. Exceptional up to 2002, these very short needleless growth units became frequent since 2003.

Figure 6, Annual polycyclism frequency as function of A) twig status (S-Weak, S-Strong and principal), B) branch position (low, middle, top canopy) and C) twig vigour (frail, medium, vigorous).

Figure 7, Significant climate parameters for the relationship between polycyclism frequency and climatic variables. R^2 and p values for the PLS regression are presented. P_i = precipitation at month i ; MT_i : mean temperature at month i ; P_{-i} : previous year precipitation at month i ; MT_{-i} : previous year mean temperature at month i .

Figure 9, Growth rhythms of monocyclic and polycyclic shoots during the 2008 and 2009 growing season in Font Blanche.

Figure 8, Growth evolution of mono-, bi- and tricyclic shoots (A), length of frail, medium and vigorous for each flush (first: B, second: C and third: D) since 1995 in Font Blanche.

Discussion

Polycyclism versus axes vigour and architecture

Polycyclism is primarily a developmental phenomenon associated with the search for better light conditions (Kaya et al. 1994). In the Mediterranean climate context, polycyclism allows trees to take advantage of the second part of the growing season after summer drought. Monocyclic species are particularly held back in this climate by early summers or late winters and unable to compensate immediately for the loss of leaf area after a scorching heat like the one that happened in 2003 (Thabeet et al. 2009). Conversely, Aleppo pine frequently develops a fall cycle on vigorous twigs in the top canopy (nearly 66% in 2009, 1995-2008 average is 28%), and every good year on main axes whatever their position in the crown (27% in 2009, 1995-2008 average is 16%). This late cycle may also be recorded in trunk growth as a large latewood and even a complete or partial false ring (Serre 1976).

Polycyclism proved to be mainly, but not strictly, correlated with axis vigour (Pardos et al. 2003). Branch position in the crown and axes status also influences polycyclism frequency independently from their vigour. Moreover, our results showed that when annual shoot length was decreasing, the length of all flushes was decreasing nearly proportionally. So that symmetrically, shoot length is not strictly related to polycyclism. Some monocyclic shoots can be longer than polycyclic ones (Bugnon and Bugnon 1951; Debazac 1963; Kremer and Roussel 1982; Kremer et al. 1990; Alia and Durel 1998). Thus, polycyclism appears as an important basic process in Aleppo pine growth which is expressed according to architecture (Caraglio et al. 2007) and disappears on frail twigs, in very unfavourable periods and through axis ageing. One advantage of multiple growth units is the increase in branching rate (Heuret et al. 2006); (Caraglio and Barthelemy 1997; Pardos et al. 2003), as lateral twigs may appear at the top of each growth unit. In fact, spring bicyclism, when present, is already scheduled in the terminal bud of the previous year and the resulting elongation of both preformed growth units will depend on twig vigour, controlled by its position, tree global vigour and status and finally by the prevailing climatic conditions during the fall and winter that precede shoot expansion in the spring.

Polycyclism vs meteorology

Groups of significant climate parameters selected by the PLS regression are considered as representative of five ecologically critical periods for bud induction and development. 1 - High total rainfall preceding or accompanying terminal bud formation before summer drought of year $[n - 1]$ favour good health conditions for trees (Opler et al. 1975; Serre 1976; Borchert 1994) and the induction of several potential growth units in these buds. 2 - High temperatures at the end of spring and in summer $[n-1]$ have the opposite impact, increasing water stress and limiting the resources that trees allocate directly to bud formation (before summer drought) or store for next year (August, September). The same months were significant for crown development and ramification rate of *Pinus silvestris* L. in the same region (Thabeet et al. 2009), where growth units are also predetermined in the buds of year $[n-1]$. 3 - High winter precipitations between years $[n-1]$ and $[n]$ decrease monocyclism. Plentiful soil water reserve sustains the early development of the first flush in spring (Serre 1976; Schiller and Cohen 1995) decreasing the probability of an early drought which would prevent the induction or elongation of following cycles. However, these winter rains have no influence on tricyclism frequency. 4 - High precipitations at the end of spring of year $[n]$ improve tricyclism. Good water availability at this period helps the induction or development of the second and sometimes the third spring flush and at the same time improves tree health and vigour, preparing a potential late flush in fall. High temperatures during this period have the opposite effects and favour monocyclism. 5 - Abundant rainfall in August $[n]$ both increase tricyclism and decrease monocyclism. The earlier the summer water stress is released, the faster the later cycle develops (Serre 1976; Schiller and Cohen 1995). When rainfall arrives too late in autumn, no flush develops or the late cycle cannot be seen through successfully and remains short and needleless.

Monocyclism is mainly linked with climate of year $[n-1]$, probably because it depends primarily on the induction of a single growth unit in the terminal bud during this previous year and only secondarily of

the absence of the initiation or development of a new flush in year [n]. However, the development of a late polycyclism on shoots which were monocyclic in spring was observed in our phenological surveys due to exceptionally warm falls in the last years (2008-2009). Tricyclism depends at the same level on the rain and temperatures of year [n-1] for the induction of a bicyclic bud, and on climate of year [n] for the induction or development of a third cycle in the end of spring or in autumn. Our phenologic surveys confirm the PLS model outputs. The very dry 2007-2008 winter (1/3 of average rainfall from October to March) led to a one month delay in flush elongation after bud burst, seriously shortening the growing season. A very mild and rainy winter 2008-2009 led to late polycyclism and high polycyclism frequency the next year. Tetracyclism which occurred exceptionally before 2007 (<1%) counted for 4% in late 2008 and 2009 due to longer growing season extended to December.

Polycyclism vs medium and long term climate variability

The decreasing trend in polycyclism frequency between 1995 and 2008 was mainly due to the break observed after 2003. As natural polycyclism frequency remains unknown in literature, lack of measurements before 1995 prevents any possible speculation about the 'standard' frequency of polycyclism. High values in 1996 can be attributed to the climate of 1995, an exceptionally good year for trees with moderate temperatures and no summer drought. Such years are rare in Southeastern France. However, 1995-2000 climate can be considered as very close to the average climate over the 30 previous years, except for a slight increase in temperature. The fact that polycyclism is not far from 100% for vigorous twigs in these first years of the study indicates that branch development was probably near its optimum. This confirms previous studies on Aleppo pine height growth trend in the 20th century showing an acceleration and maximum in the 90's (Vennetier et al. 2007). A weak tendency to polycyclism reduction with time, at least on low and intermediate position in the crown, corresponds to the normal ageing of branches and the progressive decline with increased competition by the top crown and neighbouring trees. This natural trend is described in literature (Caraglio et al. 2007; Barthelemy and Caraglio 2007; Masotti et al. 1995) and can be assessed thanks to the successive branch sampling (2005-2009). As middle crown branches were chosen to be 10 years older than top branches, we can compare the growth of shoots of the extremity of top branches with 10 years older shoots of middle branches: they were, with a ten years interval, exactly in the same relative position in tree crown. The same reasoning allows comparing the extremity of middle crown branches (25 years old) and 10 years older shoots of low crown branches (35 years old). As Aleppo pine height growth models for Southern France (Vennetier and Herve 1999) indicate a linear trend and no change in tree architecture between 35 and 55 years, one can consider that the same position in the crown should lead to the same growth rate and polycyclism frequency. Lower value for the branch end compared to the branch middle of the lower level in canopy indicates a faster decrease than the natural trend. Figure 8 D shows that the observed decrease was faster than expected, mainly after 2003. Direct competition with neighbours can be considered as only a secondary factor as no suppressed or strongly shaded branch was selected. Our 2008 and 2009 phenologic surveys showed an increasing polycyclism frequency, a good index of tree recovery (Leuschner et al. 2001) after two years of normal annual rainfall without excessive heat.

Scorching heat of 2003 significantly impacted tree growth in Southeastern France (Ciais et al. 2005); (Thabeet et al. 2009). The delayed effect of 2003 combined with dry years had drained the majority of tree reserves and primary growth suffered (Breda et al. 2006; Fensham and Fairfax 2007). After summer 2003, trees lost more than half of their needles in our plots; but they made new growth units early in fall with new needles (personal observations). The post-2003 period was also a dry period with rainfall levels lower than the last 40 years average and a significant drop of polycyclism frequency was observed. Indeed, polycyclism occurs generally when tree health and climate conditions are optimal (Caraglio and Barthelemy 1997). The precipitation decrease observed between 2003 and 2007 in Southeastern France was 9, 39, 27, 28 and 61% (respectively) below the average (MétéoFrance 2009). In the Mediterranean Basin, a significant decrease of 30% of spring and summer precipitations is expected within the next 50 years (Hesselbjerg-Christiansen and Hewitson 2007). Thus, the 2003-2007 period gave us a good idea of the expected climate and how Aleppo pine will react. As summer average precipitation is less than 80mm (June, July and August) at Font Blanche,

fewer precipitations will have negative effects on this ecosystem, noticeably on tree growth (Borghetti et al. 1998; Zavala et al. 2000; Rathgeber et al. 2005) and architecture.

Our phenological survey showed that twig growth stopped in mid-November 2008 but re-started in late-December 2008 or early-January 2009. Over the 21st century, with warmer temperatures during autumn and winter, very late polycyclism is prone to occur frequently. Growth can be initiated in a period where frost is likely to destroy apical buds and also cambium superficial layers, reducing subsequent twig and tree vigour. Such an accident was documented in 1956 (Monange 1961): budburst and elongation happened in January and a deep frost in February wiped out a majority of buds, killed many trees, and stopped diameter growth for one to three years. Moreover, since 2003, fungus attacks were frequently observed on insufficiently lignified late flushes at the end of winter, leading to high abortion rates (data not shown).

Conclusion

Our results show that Aleppo pine polycyclism processes decline as a result of a warmer climate and longer drought, particularly in spring and at the end of summer. As demonstrated in (Pardos et al. 2003), Aleppo pine polycyclism frequency, shoot length, and flowering were high in a watered seed orchard. Indeed, up to seven annual flushes were observed in Guadalajara (Central Spain, Mediterranean climate), but tetracyclism is unlikely in a natural forest. If the actual climate change tendency continues, polycyclism frequency may decrease on vigorous axes and disappear on less vigorous branches (middle, low, S-Strong and S-Weak axes). Additionally, unusual events (as the 2003 heat wave or winter 1956) are likely to be recurrent. Delayed effect of extreme events may significantly reduce polycyclism frequency and thus Aleppo pine primary growth and productivity. Finally, our three hypotheses were verified. 1) On Aleppo pine, polycyclic shoots represent between 10 and 45% of total annual growth on medium vigour twigs and reach more than 60% on vigorous twigs. 2) Vigorous axes are prone to be more polycyclic than the frail ones, but position in the crown and twig status within a branch also play an important role. 3) Polycyclism frequency had significantly decreased in the last decade following several dry and very hot years in southern France.

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