ORIGINAL ARTICLE

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Shoot growth components and flowering phenology in grafted *Pinus halepensis* Mill.

Abstract Shoot elongation and flowering were assessed for a season (January–November) in 25 grafts from five clones of *Pinus halepensis* growing in a seed orchard. A co-dominant shoot from the upper crown and a dominated, low shoot were measured from each ramet. Upper shoots elongated continuously from a variable onset date between January and March and followed a logistic function against Julian day and a Gompertz function against heat sum above 0°C. Three to seven (averaging five) successive cycles were formed through the growing season; usually, two of them were preformed in the terminal bud (spring cycles) and one to four were neoformed, summer cycles. The number of summer cycles and their contribution to the annual shoot growth were the only variables with a significant clonal influence. Ovulate strobili appeared from February to April and in October. Some ramets showing two female flowering cycles in the same shoot were observed. Lower shoots, bearing pollinate strobili always displayed a single spring cycle preformed in the winter bud.

Keywords Aleppo pine · Polycyclism · Multiple flowering · Clone · Developmental plasticity

Introduction

Shoot elongation patterns are considered essential in forest species to improve predictions of genetic and environmental influence on growth traits (Cannell et al.

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1976; Kremer and Roussel 1986; Isik et al. 2002). At a first level of subdivision, the annual height increment is divided into successive flushes or cycles (Cannell 1978). A wide diversity of shoot growth patterns has been described within the genus *Pinus* after observations of the number of flushes and the lapse between the formation of stem units and their elongation. Lanner (1976) considered three general modes (free growth, fixed growth or a combination of both) which are divided into ten different patterns for pines growing in cold and temperate regions. A similar criterion had been formerly given by Debazac (1963).

Development patterns have been shown to vary within a given species due to age, intraspecific genetic variation and environmental characteristics (Lanner 1976). Differences in shoot behaviour between juvenile, mature and old individuals are a general trait in plants (Poethig 1990) and are evident in various conifers (Ritchie and Keeley 1994; Greenwood 1995). Typically, these differences are related to the proportion of free and fixed growth, and of monocyclic and polycyclic shoot growth. Genetic differences among families or provenances in individuals of the same age have been reported in several species, such as *Pinus banksiana* (Kremer and Larson 1983), *P. taeda* (Williams 1987), *P. pinaster* (Kremer and Roussel 1986; Alia et al. 1997), *P. brutia* (Isik et al. 2002) and also in other conifers such as *Pseudotsuga menziessi* (Kaya et al. 1993). Branch position in the crown is another major factor affecting growth and flowering behaviour in many woody plants. In pines, vigorous upper branches tend to produce seed strobili while pollen cones appear predominantly in lower or secondary branches with little vegetative vigour (Mirov 1967; Farjon and Styles 1997).
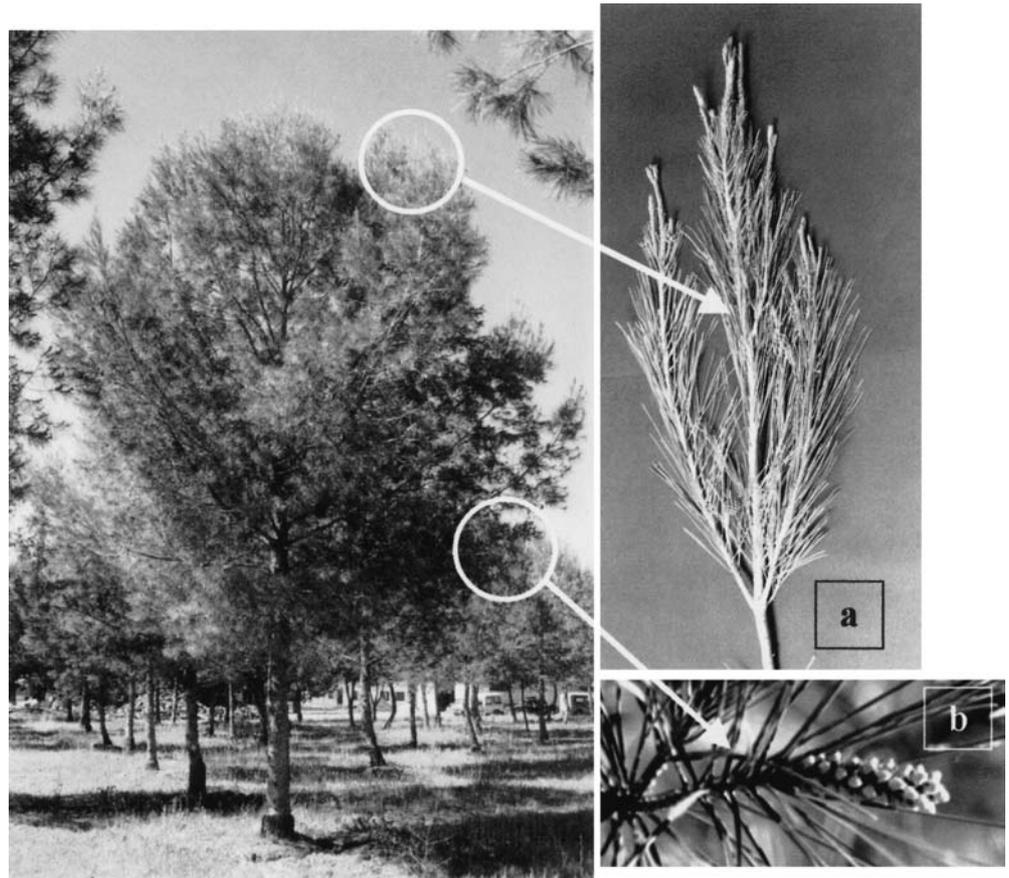
Pinus halepensis Mill. has a wide natural distribution throughout the Mediterranean basin with important stands (about 806,000 ha) in the eastern Iberian peninsula. In addition, it is widely used in afforestation programs in Spain, representing more than 30% of all planting stock produced. Its great resistance to drought along with its high plasticity make this species valuable for prevention and recovery from erosion in arid environments (Gil et al.

Fig. 1a, b View of a sampled graft of *Pinus halepensis* indicating the two types of shoots studied. **a** Upper shoot corresponding to a codominant leading branch; **b** lower shoot corresponding to a dominated branch

1996). These characteristics make *Pinus halepensis* a key species for Mediterranean countries, justifying the interest in significant physiological and ecological issues, such as water relations (Grunwald and Schiller 1988; Tognetti et al. 1996; Schiller and Cohen 1998), the behaviour of planting stock (Royo et al. 2001) or the mechanisms of seed release and natural recruitment (Nathan et al. 1999; Tapias et al. 2001).

The analysis of different molecular markers revealed low levels of genetic diversity in Spanish stands of this species compared to other pines, although significant differences were found among populations (Agundez et al. 1997). The comparison between diversity parameters (evaluated through neutral molecular markers) and various quantitative traits related to seed germination and seedling growth showed different levels of natural selection for each trait (Alia et al. 2001). Moreover, progeny trials showed high levels of phenotypic variation in height growth and growth components, resulting in low heritabilities for height growth (Prada 1999).

These aspects heighten the interest in acquiring more information on phenotypical markers in *P. halepensis* such as shoot elongation patterns and flowering phenology, and their adaptive significance under Mediterranean conditions in Spain. Although there is some information on shoot growth and flowering phenology in seedlings and saplings of this species (Debazac 1963; Weinstein 1989a; Prada 1999) little is yet known about grafted

individuals. Apart from their relevance in seed orchards (Roldán et al. 1992; Matziris 1997), grafted plants are valuable for assessing the adult behaviour at an attainable height in forest tree species due to cyclophysis and topophysis, i.e. the memory of the mature condition and position of the propagule (Ahuja and Libby 1993).

Many diverse patterns of shoot behaviour have already been observed in seedlings and grafts of *P. halepensis*. The research presented here aims to further the available knowledge on shoot behaviour in this species. As a first step, shoots of grafted plants were measured for a growing season to test for any clonal and individual effects in (1) the onset and evolution of shoot elongation and its relationship with heat sums, (2) the number of cycles (both floral and vegetative), and (3) the contribution of preformed cycles (spring growth) and of neoformed cycles (summer growth) to the annual elongation.

Materials and methods

Plant material

Observations were carried out on a *Pinus halepensis* clonal seed orchard located in Guadalajara, Spain (3°10'W, 40°38'N, 640 m a.s.l.). The climate is mesomediterranean with continental influence (Rivas-Martínez 1983); the annual rainfall is 457 mm and the annual average temperature is 15.4°C with wide daily and yearly oscillations. The orchard consists of 49 clones selected in natural

stands from the interior of the Iberian peninsula (provinces of Guadalajara, Teruel, Cuenca and inland Valencia). Scions (collected from upper branches of selected mother trees 30–40 years old) were tip-grafted on 2-year-old rootstocks of the same species and provenance, and planted out the following year in 17 completely randomised blocks and one-tree plots at 5×5 m spacing. The soil is deep and clayey on limestone bedrock. The orchard was watered regularly during the dry summer months; thus, soil water availability was constant.

Experimental design and data collection

Five ramets of five clones were randomly chosen for the observations. All ramets studied were 8 years old and had not been top-pruned until the year of study. Two trees died during the experiment so data concerning these individuals are incomplete. One shoot from the upper quarter of the crown and another from the lower half were chosen in each ramet from the sunny half of the crown (Fig. 1). Upper shoots were randomly chosen among first order co-dominants. A distinct top leader was normally absent in these ramets but, if present, was avoided with the intention of homogenising the sample. Low shoots were randomly chosen among second order shoots. Male strobili primordia were visible in all the low shoots studied at the beginning of the experiment.

Shoot length was measured to the nearest millimetre with a tape measure, approximately every 15 days from 13 January to 22 November. A black mark was made at the first measurement as a datum point. The following parts were considered in the elongation of upper branches (Fig. 2): a basal sterile scale zone and a fertile scale zone which included a dwarf-shoot zone with insertion of female strobili, lateral buds and long shoot terminal bud (LSTB). Low branches exhibited male strobili at the basal portion of the fertile scale zone. In the upper branches studied, a whorl of lateral branches was not always present at the base of a new cycle, thus the initiation of a new flush was determined by the presence of a new basal sterile scale zone (Cannell et al. 1976) (Fig. 2). This lack of lateral branching between some flushes makes whorl back-counting, frequently carried out in other related species (e.g. Isik et al. 2002) in order to reconstruct past shoot growth, meaningless in *P. halepensis*. Annual shoot growth (AG) was divided into three parts: growth deriving from preformed, spring cycles (SPG), growth deriving from neo-formed, summer cycles (SMG), and terminal bud. Flowering phenology was followed during the same period and measuring dates. The diameter at the base of the graft was also measured in all 25 ramets on 13 January. Branch diameter at the base of the first cycle was measured at the end of the growing period. The measured and derived traits are shown in Table 1.

Data of rainfall and daily maximum and minimum temperatures were gathered 200 m away at a nearby meteorological station. Cumulative heat sums above 0° in degree-days were calculated from 1 January. An approximation was made through a triangular function (Mutke et al. 2003), which modified the concept of the thermic integral. This modification allows heat units to be calculated when the mean temperature does not reach t_0, but the maximum does. This makes heat sum calculations closer to the real thermic integral in contrasted temperature conditions.

$$dd = \frac{(M - t_0)^2}{2(M - m)} \quad \text{if } m < t_0 < M \tag{1}$$

$$dd = \frac{M + m}{2} - t_0 \quad \text{if } t_0 < m \tag{2}$$

$$dd = 0 \quad \text{if } M < t_0 \tag{3}$$

where dd is day degrees sum, M is daily maximum temperature, m is daily minimum temperature and t_0 is the threshold temperature.
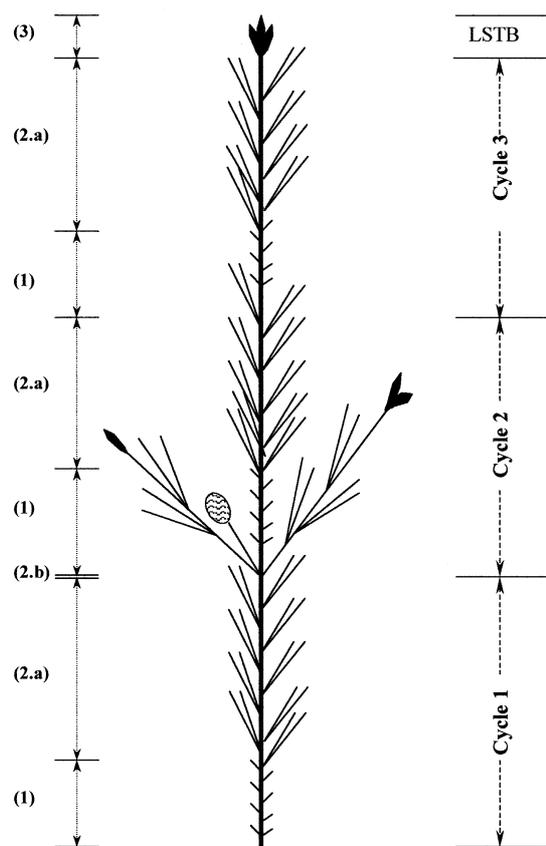
Fig. 2 Diagrammatic representation of annual growth in a theoretical upper shoot of *Pinus halepensis*. The following parts can be distinguished in each cycle: (*1*) basal sterile scale zone; (*2.a*) dwarf-shoot zone; (*2.b*) insertion of female strobili and lateral buds; (*3*) long shoot terminal bud, LSTB. As a whorl of lateral branches is not always present at the base of a new cycle (e.g. cycle 3), the initiation of a new flush is determined by the presence of a new basal sterile scale zone

Table 1 Abbreviations and description of the traits studied for the *Pinus halepensis* grafts

Abbreviation	Description	Unit
AG	Annual shoot growth	mm
HS	Heat sum	degrees×day
SPG	Growth due to preformed (spring) cycles	mm
SMG	Growth due to neo-formed (summer) cycles	mm
%SPG	Contribution of spring cycles to AG	%
%SMG	Contribution of summer cycles to AG	%
NC	Total number of cycles	
NSMC	Number of summer cycles	
a, b, k	Coefficients of Gompertz function	Various
a', b', k'	Coefficients of logistic function	Various

Statistical analysis

The statistical analysis was performed as a block design. Statistical analysis of branch elongation was based on standardised, percentage values to allow comparison between individuals. Clone and block effect on measured variables were tested using analysis of

variance of individual tree data. Graft diameter and branch diameter were introduced as covariates of shoot growth. Non-linear regression models were used to predict total shoot growth, with heat sum and Julian days as independent variables. Differences of the coefficients of the regression models for each shoot among clones and blocks were also tested through ANOVA.

Results

Relationship between upper shoot growth, Julian days and heat sums

Logistic regression models were highly significant ($P<0.001$) when upper shoot growth was regressed against Julian day (Fig. 3). In contrast, the relationship to heat sum was better explained by a Gompertz function (double exponential, Fig. 4) since heat sum also followed a logistic function of Julian days. Neither clone nor block significantly affected ($P>0.05$) the parameters in both regressions even when branch diameter was introduced into the model as a covariate. Hence, elongation behaviour must be considered and described separately for each shoot.

AG was not affected by clone or by ramet within clone ($P>0.05$). Elongation of upper shoots was initiated in four early growing ramets when heat sum was 57.2 degrees×day. Ten ramets restarted elongation when heat sum was between 132.8 and 287.6 degrees×day without any change in minimum or maximum temperature values. The other seven ramets started to grow coincident with a release night frosts occurring on day 42 and day 70. The last date of shoot growth initiation (day 70) coincided with the end of the period of continuous night frosts. Shoot growth almost ceased by day 293 (20 October, 4,020.5 degrees×day).

Polycyclic shoot growth

Clones differed significantly in the growth proportion attributable to SPG and SMG (Tables 2 and 3). Obviously, the ranking among clones based on winter-spring

$$\%SG = a + \frac{c}{1 + e^{-b*(Day-m)}}$$
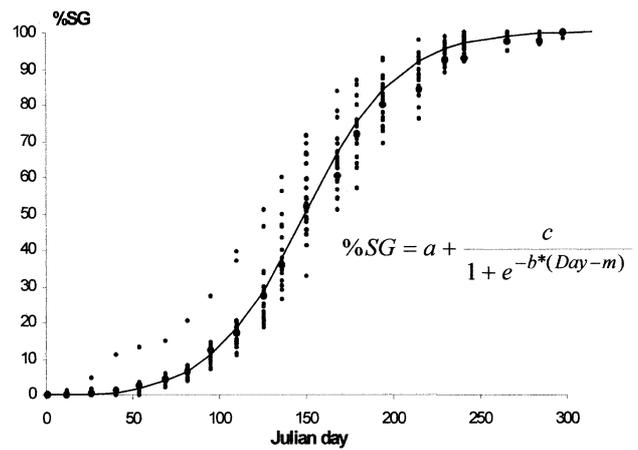
Fig. 3 Annual shoot growth (%) versus time in the studied *Pinus halepensis* grafts. Points represent individual data for each graft ($n=23$). Mean shoot growth over time is adjusted to a logistic regression (*continuous line*, $a=1.300241$; $b=0.036887$; $c=101.3984$; 148.65). Julian day 0= January 1
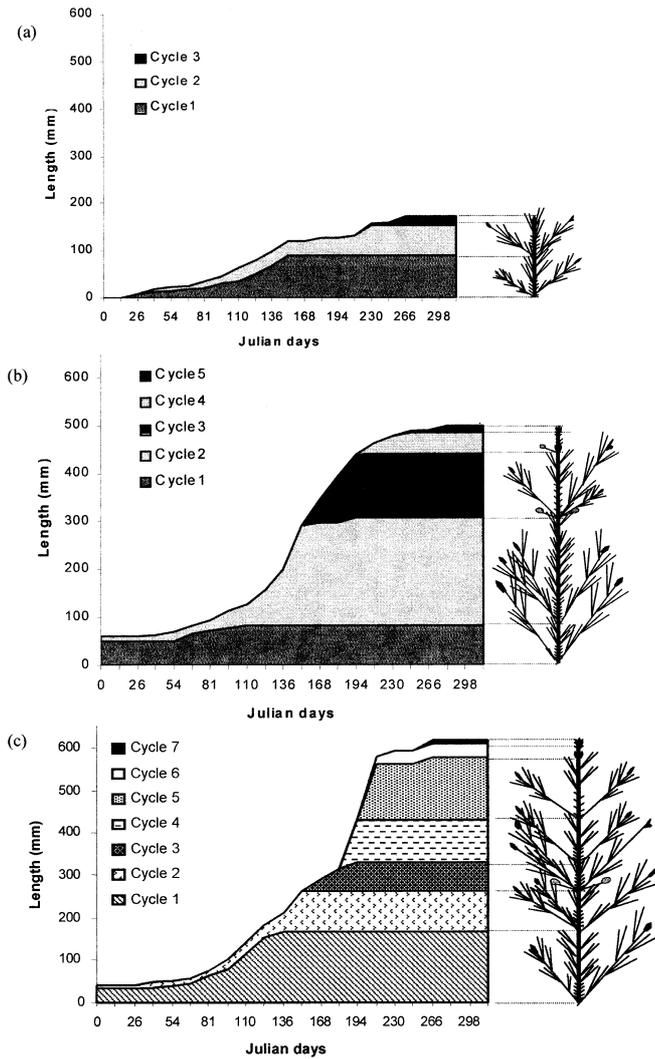

$$\%SG = a*e^{-b*e^{-k*HS}}$$
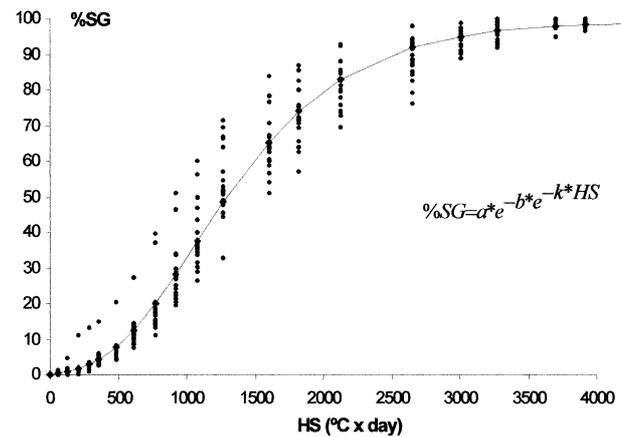
Fig. 4 Annual shoot growth (%) versus cumulative heat sums (degrees×day) in the studied *Pinus halepensis* grafts. *Points* represent individual data for each graft ($n=23$). Mean shoot growth vs cumulative heat sums is adjusted to an exponential (Gompertz) regression (*continuous line*, $a=99.16$; $b=5.58$; $k=0.001613$)

Table 2 Analysis of variance for the traits studied in *Pinus halepensis* grafts. Grafts diameter and branch diameter were included as covariates, but only branch diameter was significant. a, b, k, coefficients of Gompertz function and a', b', k', coefficients of Logistic function
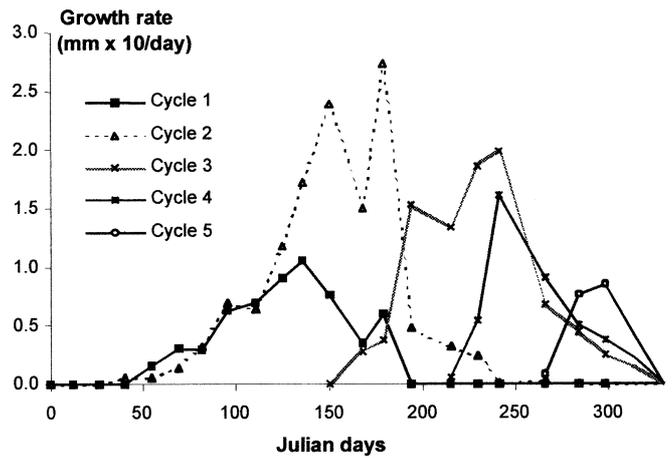
Traits	Clone		Block		Branch diameter	
	MS	$F<P$	MS	$F<P$	MS	$F<P$
AG		n.s.		n.s.		n.s.
SPG	5,330.61	0.0016	1,991.25	n.s.	54,183.0	0.0000
SMG	5,619.8	0.0010	2,216.9	0.0345	91,007.6	0.0000
%SPG	226.34	0.0013	109.78	0.0223	177.18	0.0226
%SMG	182.57	0.0046	79.13	n.s.	313.00	0.0057
NC		n.s.		n.s.		n.s.
NSMC	0.50995	0.0281	0.28399	n.s.	1.58079	0.0043
A		n.s.		n.s.		n.s.
B		n.s.		n.s.		n.s.
K		n.s.		n.s.		n.s.
a'		n.s.		n.s.		n.s.
b'		n.s.		n.s.		n.s.
k'		n.s.		n.s.		n.s.

Table 3 Tukey's multiple range tests for the traits with significant differences among clones (*SPG* growth due to spring cycles, *SMG* growth due to summer cycles, *%SPG* contribution of spring cycles to AG, *%SMG* contribution of summer cycles to AG, *NSMC* number of summer cycles)

| Clone	SPG	SMG	%SPG	%SMG	NSMC
1	214.4 cb	239.2 ba	45.5 b	55.2 a	2.4 a
2	282.9 a	167.9 c	62.2 a	40.6 b	1.4 b
3	257.8 ba	192.0 cb	57.1 a	42.7 b	2.0 ba
4	241.2 cba	212.7 cba	53.7 ba	47.5 ba	2.1 ba
5	191.0 c	261.0 a	45.2 b	54.4 a	2.0 ba

Fig. 6 Shoot elongation rate of each cycle for the shoot described in Fig. 7b. Maximum growth rate is reached in cycle 2, between May and June. Julian day 0= 1 January

Fig. 5 Diagrammatic representation of annual growth in three sampled shoots with: (**a**) 3 cycles. *Cycle 1* corresponds to spring growth; *cycle 2* corresponds to summer growth; *cycle 3* is the long shoot terminal bud (*LSTB*). (**b**) 5 cycles. *Cycles 1 and 2* correspond to spring growth; *cycle 3* corresponds to summer growth; *cycles 4 and 5* form the long shoot terminal bud (*LSTB*). In this shoot female flowers appeared in *cycles 2* (spring flowering) and *4* (autumn flowering). (**c**) 7 cycles. *Cycles 1 and 2* correspond to spring growth; *cycles 3–5* correspond to summer growth; *cycles 6 and 7* form the long shoot terminal bud (LSTB). In this shoot female flowers appeared in *cycle 2*, in spring. Representation of lateral branches only indicate their position, but number and length of the cycles are only approximate

growth was inverse to that obtained for summer-autumn growth. The contribution of preformed cycles to AG ranged from 62.2% in clone 2 to 45.2% in clone 5. The small value of SMG in clone 2 was related to the low number of summer cycles compared to the other clones.

The total number of cycles in the upper branches ranged from three to seven, with a mode of five cycles. A significant correlation (*r*=0.5) existed between this trait and total elongation (AG). The total number of cycles was not affected by clone, or by ramet within clone (*P*>0.05). Three representative shoots with three, five and seven cycles will be commented on in detail later. For the shoot with five cycles (Fig. 5b), the first two corresponded to SPG and originated from a multiple bud (LSTB) formed the previous autumn, which resumed growth between January and February. These cycles elongated steadily from day 12 and more evidently from day 40 (mid-February). SPG accounted for approximately 46% of the current year's shoot length with 67% of this percentage corresponding to the second cycle. Cycles 3–5 corresponded to summer flushing (SMG) developing from buds formed that year, but only cycle 3 developed completely that same season. Successive cycles started growing on day 150 (cycle 3, late-May), day 215 (cycle 4, early July) and day 266 (cycle 5, mid-September). The last two cycles formed the multiple bud (LSTB) for the next vegetative period, but cycle 4 experienced some degree of elongation during the autumn in most of the shoots studied. This cycle frequently reached a length of up to 150 mm without the presence of secondary needles (Fig. 8a). Seasonal elongation patterns for ramets with three (Fig. 5a), four and seven (Fig. 5c) cycles were similar to the pattern described above.

In general, the elongation of subsequent cycles commenced when the previous cycle had nearly attained its maximum growth rate and peaked after the previous cycle had almost ceased growth (Fig. 6). The maximum elongation rate in the first three cycles was reached at

Fig. 7a–c Multiple female flowering in *Pinus halepensis* grafts. (**a**) Multiple spring flowering, s_1: first ovulate strobili appearing in late February, s_2: second ovulate strobili appearing in mid April. (**b**) One year conelets derived from two flowering cycles of the previous year. (**c**) Autumn flowering, s_3: ovulate strobili appearing in October of year n, s_4: ovulate strobili appearing in spring of year $n+1$
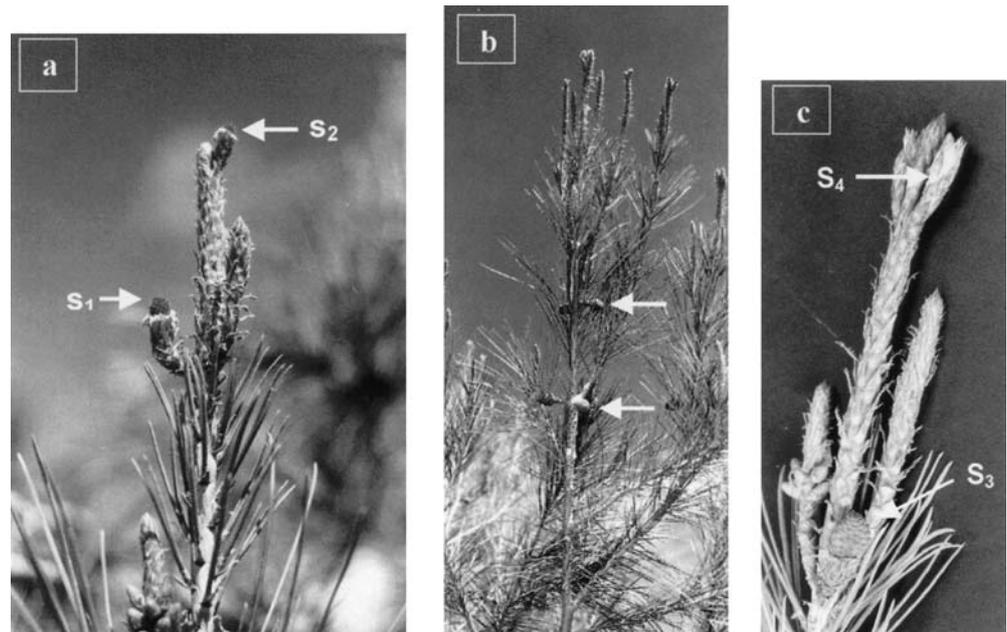
about 3–3.5 months following their initiation. Consecutive cycles (1–5) completed most of their seasonal elongation in about 5, 7, 6, 4 and 2 months, respectively.

Female flowering

Female strobili were observed in upper branches on four measuring dates: 22 February (day 53, 282 degrees×day), 8 March (day 67, 344.3 degrees×day), 5 April (day 95, 615.1 degrees×day) and 25 October (day 298, 4,064.0 degrees×day). Strobili were located at the end of the first or second cycles. Three ramets belonging to different clones displayed female strobili on the first measuring date. These cones appeared during the previous autumn, as occurred in October in one ramet from clone 3 (Fig. 7c). The number of female reproductive cycles in the same shoot ranged from 0 to 2, and the total number of strobili from 1 to 5 without a significant clonal effect ($P>0.05$). Only strobili that appeared on April 5 were present at the end of the measuring period.

Lower shoots

Lower shoots experienced only two cycles during the measuring period. The first cycle developed from the bud (LSTB) formed during the previous autumn and winter. Unlike the upper branches, low shoots terminated elongation once the bud was formed during early summer (day 179). Again, shoot growth had no clonal effect ($P>0.05$). Growth of pollinate strobili primordia (already visible at the first measurement) became more evident from March and continued until pollination. Pollen release was rather homogeneous among clones and ramets, commencing on day 95 and finishing on day 108.

Discussion

Total shoot growth

As expected, the behaviour of lower shoots was totally different to that of upper shoots in the *Pinus halepensis* grafts. Firstly, seed cones were located exclusively in upper shoots while, as in most species of the genus, pollen cones appeared only in lower shoots (Farjon and Styles 1997). Secondly, as reported in other conifers such as *P. taeda* (Boyer 1970) or *Larix occidentalis* (Joyce 1987), total elongation and polycyclism was far higher in upper shoots in accordance with their higher vegetative vigour.

The overlapping of individual cycles resulted in elongation occurring continuously until autumn, following a logistic function against Julian day and a Gompertz function against heat sum. Growth in the studied *P. halepensis* grafts was unimodal, probably because of the good water supply in an irrigated orchard. Under natural conditions, a bimodal growth curve was caused by a distinct decrease in growth rate before elongation of lammas shoots in other polycyclic species such as *P. brutia* (Calamassi et al. 1988) and *P. pinaster* (Kremer 1981). The shape of the elongation curves of upper shoots showed a high level of phenotypic variation but a weak clonal effect in the studied grafts. Noticeably, neither a standard behaviour nor clonal differences existed at the onset of elongation; while some ramets needed a slight or a clear release of night frosts to start growing, others started when night frosts where still intense ($<-7°C$). These results contrast with observations in *P. halepensis* saplings from Israel, where bud elongation did not take place until minimum temperatures reached 10°C (Weinstein 1989b).

Fig. 8 (**a**) Elongated cycle without the development of axillary shoots (secondary needles), as observed in many upper shoots in *Pinus halepensis*. (**b**) The cataphylls of a summer cycle are already formed when the former cycle is at an early developmental stage
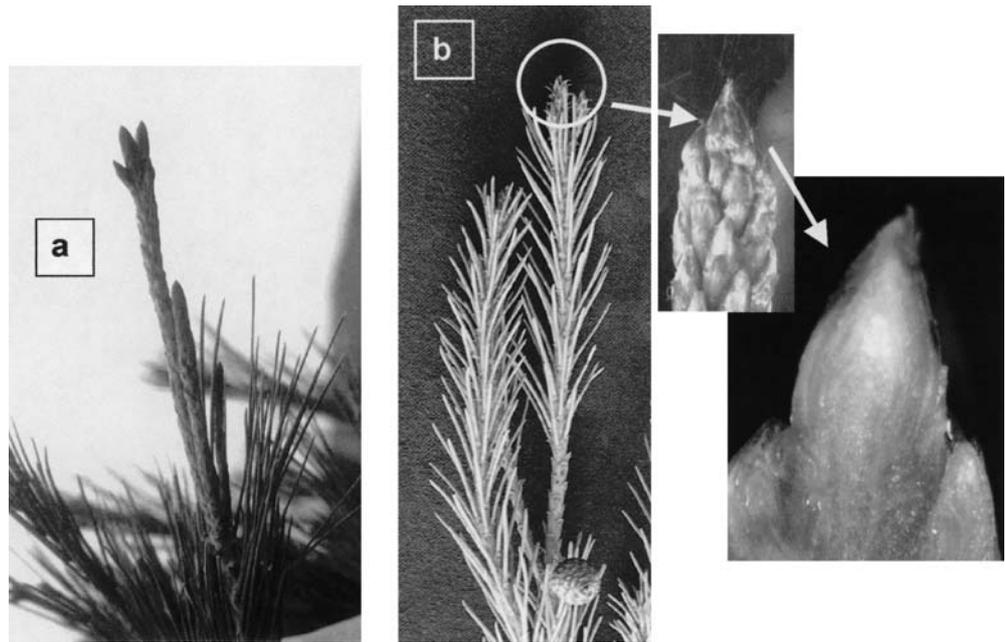
Components of shoot growth

Polycyclism in vigorous, upper shoots of the studied *P. halepensis* grafts was remarkable. Two initial cycles were usually distinguishable in the LSTB and a variable number of neo-formed cycles (usually two) occurred throughout summer and autumn. Typically, the penultimate cycle undergoes appreciable elongation before the cessation of growth in winter, without the development of secondary needles (Fig. 8a). This is also characteristic of *P. clausa* and *P. attenuata* (Lanner 1976). Shoot growth patterns in *P. halepensis* could be likened to the *Echinata* pattern, following Lanner (1976). Very similar behaviour has been described in the related *P. brutia* but in this pine the winter bud is always monocyclic (Calamassi et al. 1988, Isik et al. 2002), and closely follows Lanner's *Elliottii* pattern (1976). Further anatomical analysis would help attain a more precise idea of the preformed or neo-formed condition for a given cycle in *P. halepensis*. A macroscopic observation of some dissected buds in the studied shoots showed that the cataphylls of summer cycles were already distinguishable when the dwarf shoots of the previous cycles were still at the bud stage (Fig. 8b).

The mean number of total cycles in the studied grafts was lower than the number found in another clonal seed orchard of the same species located in a milder, coastal site (Roldán et al. 1992). In contrast, *P. halepensis* becomes monocyclic or bicyclic in drier natural conditions (Prada 1999). All evidence indicates that mild conditions favour multiple flushing in conifers; thus fixed growth replaces "free" growth (in fact, neo-formed growth) in proportion to the severity of the environment to which a species is exposed (Lanner 1976). Thus, the development of non-dormant temporal buds while the subtending stem units are still elongating occurs in tropical pines such as *P. kesiya* (Sirikul 1990) and in temperate or sub-tropical species grown as exotics in mild humid conditions, such as *P. caribaea* in northeastern Australia (Harrison and Slee 1992) and *P. radiata* in New Zealand (Bannister 1962; Burdon 1994).

The number of summer cycles and the contribution of spring and summer cycles to the annual shoot elongation were the variables studied with higher clonal effect in grafted *P. halepensis*. This is in agreement with results on Turkish *P. brutia* where summer growth was significantly different both among populations and among families within populations (Isik et al. 2002). On average, in grafted *P. halepensis,* spring and summer cycles contributed in a similar proportion (50%) to the annual shoot elongation and most resembled the ratios obtained in *P. brutia* seedlings and saplings (Calamassi et al. 1988; Isik et al. 2002). In contrast, the contribution of summer cycles to annual growth has been shown to be consistently lower than spring cycles in *P. pinaster* (Kremer 1981).

Female flowering

The timing of female flowering was noticeably variable in the sampled shoots, occurring from February to April and in October. The observed autumn flowering in *P. halepensis* seems exceptional among temperate pines considering the absence of references on this trait. However, this phenomenon is not rare in other Mediterranean spring-flowering tree species such as *Quercus suber* (Boavida et al. 1999; Díaz-Fernández 2000). The formation of several consecutive female reproductive cycles in the same shoot (Fig. 7a, b) is a neglected but remarkable trait in *P. halepensis*. This phenomenon was not frequent in the year of study but its frequency reached 20–23% in other years and it has also been observed in

saplings, adults (data not shown) and in the above-mentioned coastal seed orchard (Roldán et al. 1992). Since pollen release in the orchard occurs exclusively in April, there is no possibility of fecundation of autumn strobili taking place. This was also noted in multiple-flowering *P. radiata* (Bannister 1962). The fecundation of these precocious strobili is probably feasible under natural conditions, especially in bigger stands because of pheno-logical differences caused by environmental variability. Other pines seem to show exceptional multiple flowering in Spain, e.g. grafts and saplings of *P. pinea* (Mutke et al. 2003) and grafts of *P. pinaster* (Tadesse, personal communication) while it is reported as frequent in *P. caribaea* grafts in north Australia (Harrison and Slee 1992) and *P. radiata* saplings in New Zealand (Bannister 1962).

Ovulate strobili appear in cycles initiated between July and August when high temperatures may induce the formation of female reproductive primordia (Enescu 1987). Thus, summer flushes initiated earlier (during May and June) did not produce ovulate strobili. Mild climatic conditions in the study site favoured the preco-cious development of some female strobili in autumn. From their position in the shoot, it was concluded that ovulate strobili observed in February corresponded to the same cycles as the autumn strobili. It can be hypothesised that slight phenological differences lead to the advanced flowering of a given cycle either in autumn or late winter.

Results of this research indicate that shoot growth and female flowering are highly plastic in grafted *P. halepen-sis*. Although the number of ramets studied was small, genetic control of shoot and flowering phenology seems low in this species compared to other pines. This is totally consistent with the high individual variation and non-significant differences observed among families in prog-eny trials of this species (Prada 1999). It is significant that free growth or polycyclism has been related to low genetic control of shoot elongation in various conifers, such as *P. pinaster* (Kremer 1981) and *Calocedrus* (Harry 1987); however the observation of four shoots per ramet in two clones (two ramets per clone, data not shown) proved that within-tree variation surpassed both ramet and clone effect for all the traits considered in the grafts studied. This fact points towards the high developmental plasticity of individual shoots in adult crowns of *P. halepensis*. This seems to fit well with the postulation by Trewabas (1983), quoted by Greenwood (1995), that a plant can be considered a colony of semi-autonomous meristems simultaneously competing with one another but subtly altering their behaviour to serve the whole plant. Nevertheless, comparison between grafted individ-uals in a seed orchard and adult non-grafted material in natural conditions must be done with caution. Grafting of adult scions on young rootstocks can result in a significant reinvigoration, or a partial rejuvenation (Greenwood 1995; von Aderkas and Bonga 2000). On the other hand, rootstock-scion interactions may become an uncontrolled factor of variation unless clonal rootstocks are used (Melchior 1987; Climent et al. 1997).

P. halepensis is a successful coloniser in many Mediterranean ecosystems where severe droughts may alternate with heavy rainfall events. In such conditions, the ability to respond to favourable conditions producing many successive flushes is essential for the dominance of *P. halepensis* over the thick understorey (garriga, makis, etc.) since most other species resprout vigorously after a fire. In addition, this species is able to resume growth in late winter when temperatures are too low for other thermophyllous species. The *Echinata* pattern followed by *P. halepensis* combines the opportunism of summer free-growth with the security of the fixed-growth spring habit, facilitating the attainment of cone-bearing size (Lanner 1976). Fast juvenile height growth is closely related to precocious flowering and cone bearing in this species, starting as early as 4 years in progeny trials (Prada 1999). In addition, multiple flowering as reported in this paper together with high serotiny ensures the establishment of abundant aerial seed banks (Tapias et al. 2001) necessary to attain successful recruitment in the highly fire-prone Mediterranean ecosystems.

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