Plastic responses of *Abies pinsapo* xylogenesis to drought and competition

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Summary Radial growth and xylogenesis were studied to investigate the influence of climate variability and intraspecific competition on secondary growth in *Abies pinsapo* Boiss., a relic Mediterranean fir. We monitored the responses to three thinning treatments (unthinned control –C–, 30% –T30– and 60% –T60– of basal area removed) to test the hypothesis that they may improve the adaptation capacity of tree growth to climatic stress. We also assessed whether xylogenesis was differentially affected by tree-to-tree competition. Secondary growth was assessed using manual band dendrometers from 2005 to 2007. In 2006, xylogenesis (phases of tracheid formation) was also investigated by taking microcores and performing histological analyses. Seasonal dynamics of radial increment were modeled using Gompertz functions and correlations with microclimate and radiation were performed. Histological analyses revealed it as fundamental to calibrate the dendrometer estimates of radial increment and to establish the actual onset and end dates of tracheid production. The lower radial-increment rates and number of produced tracheids were observed in the trees subjected to high competition in the unthinned plots. The growing season differed among the plots, and its duration ranged from an average of 78 days in unthinned plots to 115 days in thinned ones (T60). Variations in the beginning of the growing season (13 April to 22 May) and earlywood–latewood transition (early August) were mainly determined by the temperature pattern, while the onset and the end of the growing season were related to both annual precipitation and tree-to-tree competition. The tracheid-formation phases of radial enlargement and cell-wall thickening showed similar patterns in the trees from thinned and unthinned plots subjected to low and high competition, respectively, but the mean number of tracheids in each phase was always higher in the trees from the thinned plots. The reduction of competition through thinning induced a longer growing season and enhanced the radial growth in *A. pinsapo*.

Introduction

Climate change is expected to modify the growth and distribution of tree species. Different researchers have found either enhancement or decline responses in radial growth to global warming (Boisvenue and Running 2006, Andreu et al. 2007). Phenological adjustments to climatic variability may lead to a greater biological activity in forest ecosystems due to a combination of increased plant growth and respiration (Keeling et al. 1996). For instance, warming has been linked to the extent of phenological growth during the 20th century in temperate European forests (Peñuelas and Filella 2001). Similar responses are not expected if water availability is the main constraint for tree growth, such as in the Mediterranean forests, because warming effects on evapotranspiration can result in a soil water deficit (Sabaté et al. 2002).

Temperature rise may also have important consequences on the intra-annual patterns of wood production. Phenological studies of wood structure and function should provide a mechanistic basis to clarify the long-term relationships between radial growth and climate described by dendroclimatologists (Gartner et al. 2002). However, despite studies on the radial-growth responses to severe drought events having been documented (Corcuera et al. 2004, Eilmann et al. 2006, Martinez-Meier et al. 2008), detailed information on intra-annual xylem dynamics in water-limited forests is scarce. On the other hand, trees of different sizes and crown classes compete for light, water and other resources within a stand (Orwig and Abrams 1997). Results on how water stress interacts with tree-to-tree competition to affect the growth are not conclusive and have been poorly explored (He et al. 2005, Martín-Benito et al. 2007, Pichler and Oberhuber 2007).

Therefore, an evaluation of these interacting effects on wood formation is required.

The study of the intra-annual patterns of secondary or radial growth, including xylem development (xylogenesis), is essential to understand the phenology of wood formation in response to climate (Camarero et al. 1998, Deslauriers and Morin 2005). The assessment of the intra-annual variability of radial growth under contrasting climatic conditions and competition intensities (CI) may serve to assess how plastic are radial growth and xylogenesis in the face of increasing climatic variability. Intra-annual secondary growth has been mainly investigated in boreal and high-altitude conifer species (Antonova et al. 1995, Camarero et al. 1998, Deslauriers et al. 2003, Rossi et al. 2006b, Ko Heinrichs et al. 2007). In contrast, little is known about secondary growth in the Mediterranean mountain conifers that are subjected to very unpredictable climatic and water stress constraints in addition to low temperature (Cherubini et al. 2003, Andreu et al. 2007, De Luis et al. 2007). Furthermore, regional climate simulations predict an increase in temperature and a decrease in spring precipitation in the mountainous areas of the Mediterranean Basin (IPCC 2007). For instance, climate models predict a decrease in the mean annual precipitation between 6% and 14% in SE Spain (Sumner et al. 2003). Thus, the frequency of extreme droughts may increase in these areas in the future, which could lead to a reduction in the forest productivity and changes in the species composition (Cowling et al. 1996). A precise quantification of the phenological responses of radial growth to climatic constraints will allow one to evaluate how important is xylogenesis for the growth and persistence of Mediterranean mountain conifers.

We assessed the intra-annual radial-growth patterns of *Abies pinsapo* Boiss., a relict Mediterranean fir species, using band dendrometers and wood microcores. We evaluated the phenology of radial growth during three consecutive years with contrasting climatic conditions and under different thinning intensities. In addition, we computed a distance-dependent competition index to account for the effect of tree-to-tree competition. Our aims were (i) to describe the intra-annual radial-growth and xylogenesis patterns in *A. pinsapo* and (ii) to quantify the plasticity of these patterns in response to contrasting climatic conditions and degrees of competition. We hypothesize that secondary growth will differ between years with contrasting climate (e.g., lower growth rates on drier years). We also expect that *A. pinsapo* would show different radial-growth rates and phenological patterns depending on the intra-specific CI. Therefore, we propose that density-dependent factors may greatly modulate the phenological patterns of radial growth.

Materials and methods

Study species

Abies pinsapo is a circum-Mediterranean fir that is found only in the mountain ranges of S Iberia and N Morocco, i.e., in the Baetic-Rifan biodiversity hotspot (Quézel et al. 1999). The study was carried out for over three seasons (2005–2007) in the natural stands of *A. pinsapo* that were located near the lower elevation limits of the species distribution. In each plot (ca. 0.1 ha), all trees with more than 3 cm dbh (diameter at 1.3 m) were tagged, mapped, measured for dbh and identified.

The CI was estimated using a distance-dependent competition index (Hegyi 1974, Daniels 1976). The degree of competition of the *i* tree was calculated as the sum of the quotients, for all *j* neighboring trees surrounding it within a radius of 7.62 m, between the ratio dbh$_j$/dbh$_i$ and the distance between the *i* and the corresponding *j* trees. The value of 7.62 m for the threshold radius above which neighbors were regarded as not competing was estimated in the preliminary tests comparing the CI figures obtained with several distances (from 1 to 10 m radiuses) and the long-term (1945–2004) radial growth expressed as basal-area increment (BAI) (Linares 2008).

Thinning treatments

Thinning treatments were conducted in October 2004 in stands with similar basal area and stand structure (Table 1). Three treatment levels, each one replicated in

Table 1. Study plots and their characteristics (mean values ± SE) before applying the thinning treatments (October 2004). Annual radial growth (tree-ring width) is based on dendrochronological estimates for the period 1945–2004 (Linares 2008).

Treatment (code)	Characteristics of sampling plots							
	Latitude (N)	Longitude (W)	Elevation (m)	dbh (cm)	Soil water holding capacity (l m^{-2})	Radial growth (mm)	Basal area (m^2 ha^{-1})	Density (ind ha^{-1})
Control (C)	36°43′28″	4°57′59″	1173	12.4 ± 0.6	103.4 ± 13.6	1.49 ± 0.03	30.8	2098
	36°43′29″	4°58′10″	1232	11.8 ± 0.7	116.5 ± 14.1	1.54 ± 0.04	37.7	1710
30% Basal area thinned (T30)	36°43′26″	4°58′03″	1199	17.3 ± 1.0	115.5 ± 15.6	1.43 ± 0.06	48.2	1323
	36°43′30″	4°58′06″	1200	12.3 ± 0.6	116.4 ± 15.3	1.21 ± 0.04	43.4	2199
60% Basal area thinned (T60)	36°43′27″	4°58′01″	1181	17.2 ± 0.8	115.8 ± 18.6	1.80 ± 0.07	38.0	1314
	36°43′26″	4°58′01″	1188	14.8 ± 0.8	103.2 ± 17.7	1.43 ± 0.07	41.3	1456

two 1000 m^2 plots, were considered: reduction of 60% of the total basal area in the plot (T60), reduction of 30% total basal area (T30) and an unthinned control (C). Selection of the trees that were to be removed was done considering two additional criteria: (i) to achieve an almost equifrequent diameter class distribution after thinning (this means that the most abundant size classes were preferentially felled) and (ii) to avoid that, conversely to common thinning practice, the spatial distribution of the remaining trees tended to be regular, i.e., the trees to be felled in each size class were selected by a spatial random procedure.

Microclimate was measured using two dataloggers per plot (Onset Co., Massachusetts) that registered air temperature and relative humidity every 6 h. Vapor pressure deficit was estimated using air temperature and relative humidity data. Soil water-holding capacity was estimated in each plot for a soil depth up to 50 cm. Monthly precipitation and climatic data were obtained from a nearby meteorological station (Cueva del Agua, Yunquera: 36°44′04″ N and 4°58′01″ W, 1083 m; 1.2 km apart from the study sites; see also Linares et al. 2009a). The nearest meteorological station providing daily solar radiation was located 24.2 km apart from the study site (Pizarra, 36°46′04″ N and 04°42′50″ W, 84 m). The mean annual temperature in the study area is 11.0 °C and the annual precipitation is ca. 1200 mm, with ca. 80% of all the precipitation falling between October and May.

Dendrometer measurements

To estimate the changes in radial increment, band dendrometers (D1 Permanent Tree Girth, UMS, Germany) were mounted in winter 2004 around the stem at ca. 1.3 m in 40 trees per treatment, i.e., 20 trees per plot, randomly selected. For the selected trees in the thinned plots, we registered their competition index before thinning, to check for differential responses to competition release. The mean dbh of trees equipped with dendrometers was 18.9 ± 0.9 cm. The bark was carefully smoothed with a rasp before attaching the dendrometer. Removing the bark allowed us to exclude one of the main components of radial-increment dynamics in trees that show thermal variations in wood and bark, stem swelling and irreversible growth (Zweifel et al. 2006). Dendrometer readings were done monthly between October and March, and biweekly between April and September. Dendrometer measurements were corrected using the linear thermal expansion coefficient that was provided by the manufacturer ($\alpha = 75 \cdot 10^{-6} \, \text{K}^{-1}$). To avoid diurnal biases, all measurements were done early in the morning. Individuals without growth during at least 1 year were discarded in the subsequent sampling periods. This phenomenon occurred on three trees, two trees and none of the trees that were subjected to C, T30 and T60 treatments, respectively.

Xylogenesis

Xylogenesis was studied in 2006 among trees with a contrasting CI. To study the effect of xylogenesis on the trees, we randomly selected five trees from a control plot and five from an intensively thinned plot (T60). Radial wood microcores were collected (one from each tree) in a spiral up the stems at a height of around 1.3 m using Trephor, a specially designed increment puncher with a thin piercing tube to extract the small cores of wood (Rossi et al. 2006a). Wood samples were taken on the same dates of dendrometer measurements. Successive samples along the stem were always taken at least 10 cm apart to avoid the effects of ringing and damaging the cambium for subsequent growth. The samples contained the wood of the preceding 3 or 4 years, the growing annual layer with a cambial zone and the adjacent layer of phloem. Any dead outer bark was removed before cutting the samples. The cores were stored in a formalin–ethanol–acetic acid (5:90:5 solution). Before cutting the sections, the microcores were always vertically oriented by marking the axial direction with a pencil. Transverse sections 20–50 μm thick (3–5 on each sample) were cut using a rotary microtome (Anglia Scientific AS 200, UK), dehydrated progressively with alcohol (50%, 75% and 90%) and xylene, and permanently fixed with Eukitt®. The sections were stained with a 0.05% water solution of cresyl violet acetate and observed with visible and polarized light at 100–1000× magnification to differentiate the types of xylem cells according to their developing stage (Antonova and Shebeko 1981). For each sample, the number of cambial cells and xylem tracheids in a radial enlargement (*ec*), cell wall thickening (*wt*) and mature (*ew*, earlywood and *lw*, latewood) phases were counted along three radial rows (Deslauriers et al. 2003, 2008). Earlywood and latewood tracheids were distinguished based on the Mork definition (Denne 1988).

The cambial zone and the cells undergoing a radial enlargement showed only primary walls that did not shine under the polarized light. In cross-section, the cambial cells were characterized by their fusiform shape, thin cell walls and small radial diameters. During cell enlargement, the tracheids were composed of a protoplast that was still enclosed in the thin primary wall, but with a radial diameter at least twice that of a cambial cell. In the wall-thickening phase, the color of the cells changed from light violet in the beginning of the process to deep violet close to the mature cell stage. Lignification was characterized by the appearance of a blue coloration, beginning in the cell corners and middle lamella and then spreading into the secondary walls of the differentiating tracheids. Xylem cells were considered lignified and mature when they were completely blue.

The total number of cells was regarded as the sum of cells in the enlargement and wall-thickening phases and mature cells. The onset of xylem reactivation in spring was defined as the date when at least one horizontal row of enlarging
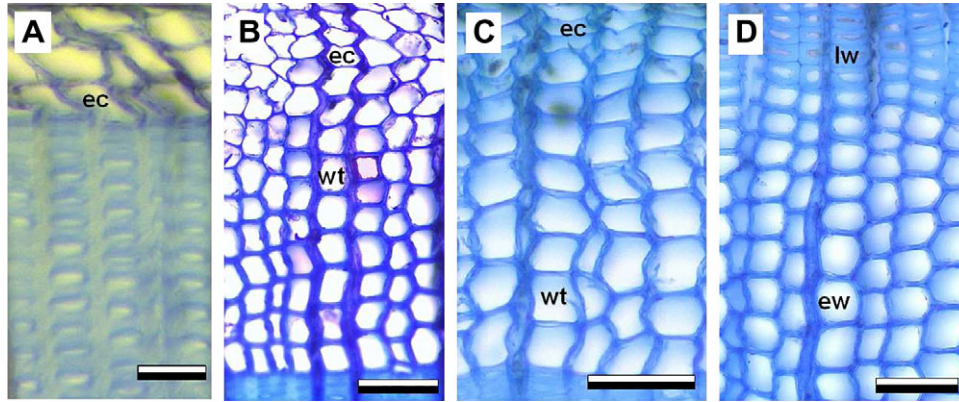
Figure 1. Xylogenesis phases in *A. pinsapo* during the year 2006. The growth onset (A, 8 May) corresponded to the formation of the first radially enlarging cells (*ec*). The development of wall-thickening cells (*wt*) started later (B, 21 May) and reached its highest rate between mid-June and early July (C, 19 June). Mature earlywood (*ew*) and latewood (*lw*) tracheids were evident since July (D, 30 August). Scale bars in A, C and D correspond to 200 μm and to 100 μm in B. This figure appears in color in the online version of *Tree Physiology*.

cells was observed, whereas the end of xylem formation in autumn was defined as the date when no further cells undergoing wall thickening and lignification were observed (Figure 1).

The earlywood, latewood and the total number of tracheids were also counted along three radial rows of the two rings preceding the thinning (2003 and 2004) to obtain a standardized number of 2005 tracheids (based on the mean number of tracheids for the period 2003–2006) for each tree because the cell number varied around the stem circumference, and hence among the different samples (Rossi et al. 2003). Radial growth was also measured in the microcores with a 1-μm resolution using a light microscope (Olympus BH2) that was attached to a LINTAB measuring device (Rinntech, Germany). Finally, the radial growth based on microcores was compared with the radial-increment estimates derived from the dendrometer recordings.

The Gompertz equation was used to model the mean cumulative values of stem increment or the number of formed tracheids in each plot and year (Camarero et al. 1998, Rossi et al. 2003):

$$y = a \exp\left(-e^{\beta - \kappa t}\right), \tag{1}$$

where y is the weekly cumulative sum of radial increment or the number of tracheids, t is time computed in days since the first sampling date ($t = 0$ in 1 April), a is the upper asymptote of the maximum growth attained or the number of formed cells, β is the x-axis placement parameter and κ is the rate of change parameter. Five biologically useful variables were calculated from the fitted statistics following Deslauriers et al. (2003) that include r, the weighted mean absolute increment or growth rate (Eq. (2)); tp, the time required for the maximum increment or growth to occur (Eq. (3)); td, the time required for the major portion of increment or growth to occur (Eq. (4)); the dates

of increment/growth onset and end, which were calculated by substituting the variable y in Eq. (5) by the values $0.1a$ and $0.9a$, respectively. Parameter ν was fixed to 0.0001 (Deslauriers et al. 2003):

$$r = \frac{a\kappa}{2(\nu + 2)}, \tag{2}$$

$$tp = \frac{\beta}{\kappa}, \tag{3}$$

$$td = \frac{2(\nu + 2)}{\kappa}, \tag{4}$$

$$t = \frac{\beta - \ln\left[\ln\left(\frac{a+1}{y}\right)\right]}{\kappa}. \tag{5}$$

Statistical analyses

The radial increment and the number of tracheid datasets were tested for the homogeneity of variance and for the assumption of compound symmetry of the variance–covariance matrix using the Bartlett–Box F test and the Mauchly criterion, respectively. The data were log-transformed to follow homoscedasticity. A repeated-measures MANOVA was used to compare the tree-ring width and tracheid number in the trees that were subjected to different thinning treatments (von Ende 2001). Because our main interest was to test the effects of thinning and its interaction with CI, the between-subject factor was thinning intensity (C, T30 and T60), whereas the competition index and tree size (dbh) were considered as covariates. Sampling date was regarded as the within-subject factor. We used the Greenhouse–Geisser statistic to adjust F tests. Paired comparisons were corrected using the Bonferroni adjustment. The MANOVA was calculated using SPSS Version 17.0 (Norussis 1993).

Table 2. Mean microclimatic conditions registered during three growing seasons (2005–2007) in the six study plots. Monthly precipitation and radiation were obtained from nearby meteorological stations.

Year	Month	Air temperature (°C)	Radiation (MJ m^{-2} d^{-1})	Relative humidity (%)	Precipitation (mm)
2005	April	13.04	23.18	49.90	3
	May	14.77	25.20	46.98	4
	June	18.60	27.06	44.44	0
	July	21.50	27.19	40.76	4
	August	21.06	23.83	44.61	3
	September	16.40	20.22	53.21	5
	October	12.32	13.57	71.76	77
2006	April	10.70	20.54	68.27	42
	May	14.50	22.41	61.69	16
	June	16.71	25.90	56.70	60
	July	21.67	26.61	38.80	1
	August	20.46	24.90	47.39	13
	September	17.20	20.17	55.78	22
	October	13.51	12.62	72.99	149
2007	April	7.31	17.37	77.08	90
	May	12.46	25.19	59.42	65
	June	16.25	28.87	54.39	0
	July	21.22	29.29	41.51	0
	August	20.60	24.08	49.67	8
	September	15.66	18.06	71.38	66
	October	11.54	15.20	79.55	119

Results

Microclimatic conditions

The climatic conditions in 2005 were among the driest in the late 20th century in S Spain. Total annual rainfall was 47% lower than the average of the last 30 years. Despite the winter being relatively cold in 2005 (minimal temperatures up to −15 °C in February), all months following March showed a mean temperature well above the average of the last 10 years. The period April–October was especially dry in 2005 (Table 2). In 2006, total precipitation was also low, but some fell in June, thus reducing the water deficit during the early growing season. In 2007, the spring was milder and more humid compared with those in the preceding 2 years, and temperatures in summer and autumn were near the mean values of the three study years.

Seasonal dynamics of radial increment and competition

Neither dbh as a covariate nor its interaction with sampling date showed a significant effect in any of the studied years. In contrast, both the CI and its interaction with date always showed significant effects. Radial increment was higher in trees from thinned plots (Figure 2). The period of radial increment varied significantly among plots all years, suggesting that secondary growth depended on the inter-annual climatic variability and CI (Table 2; Figure 2). Based on the Gompertz models, the onset date of radial increment ranged among 13 April–8 May over the study period (3 years). The date of cambial reactivation was unrelated to CI in the stand. In contrast, the time required for the maximum radial-increment rate to occur (tp), the date of increment end and the growing period (td) showed remarkable differences among the plots, which were coherent with the changes in thinning intensity (Table 3).

The radial-increment onset seems to be determined by temperature, because it started, in all populations and during the 3 years, when the mean air temperature was above ca. 13 °C during at least ten consecutive days. The temporal patterns of radial-increment rates followed day length (radiation) variations until maximum rates were reached between late May and early June (Tables 2 and 3). The maximum increment rates decreased as the CI increased (from the T60 thinning to the unthinned treatments; Table 3; Figure 2). Based on the Gompertz model, the trees for which intraspecific competition was reduced by thinning showed the longest period of radial increment: 114 days on average versus 78 days in trees from the unthinned plots. Radiation (day length) during the three study years and precipitation over the growing period (April–October) in 2007 were the only variables correlated with radial increment in all plots (see Supplementary Data, Figure A1).

Low BAI were clearly associated with high tree-to-tree competition (CI) in the six studied plots (Figure 3). All plots showed significant negative relationships between CI and BAI, accounting for 39–51% of the growth variance. Trees that were subjected to a higher competition showed lower BAI values, regardless of the year, but variations in the mean annual precipitation among them determined the
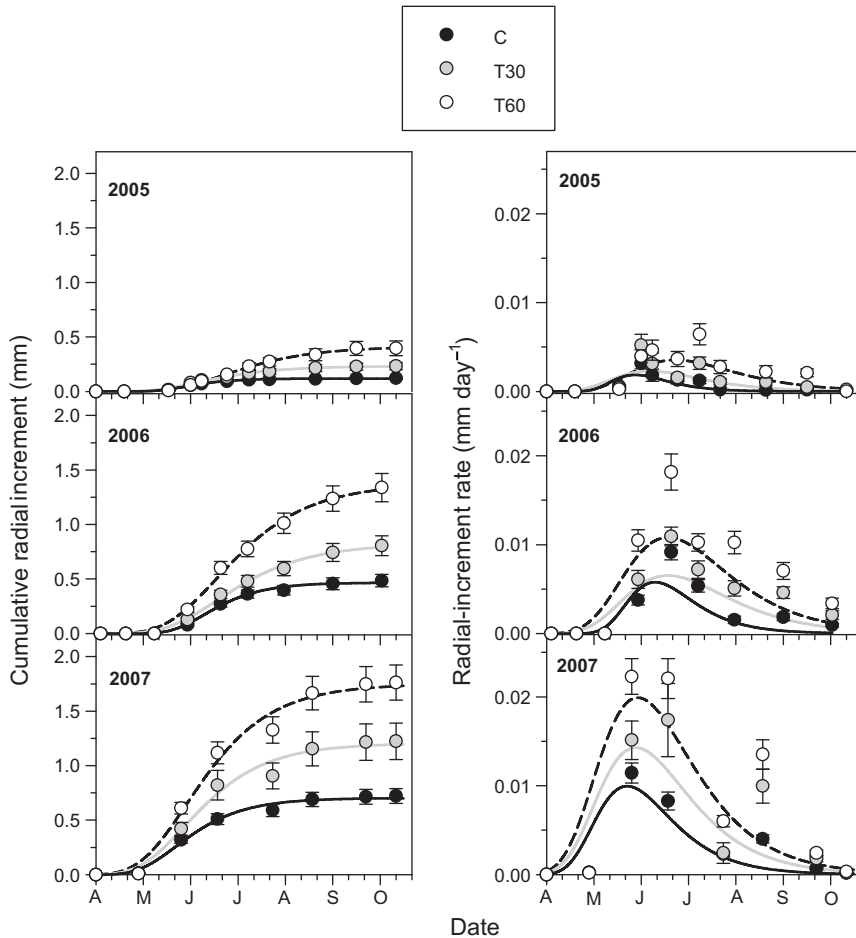
Figure 2. Cumulative radial increment (symbols) and fitted Gompertz models (lines) that were used to obtain radial-increment rates during the three consecutive growing seasons (2005–2007) following the application of thinning treatments in late 2004. Circles with different color fills represent thinning treatments: black circles, control plots (C); gray circles, 30% of basal-area reduction (T30); and white circles, 60% of basal-area reduction (T60). Note the different scales of radial growth used in the studied years. Error bars represent standard errors ($n = 40$ trees per treatment).

Table 3. Parameters of the Gompertz functions fitted to the datasets of cumulative radial increment and number of tracheids. Plot codes are as in Table 1. In all cases, the fits were highly significant ($R^2 = 0.995–0.999$, $P < 0.001$).

Plot	Variable	Year	a	β	κ	r	Growth onset	tp	Growth end	td, growing period (days)
C	Growth	2005	0.12	3.23	57.73	6.83	30 April	27 May	5 July	65
T30	Growth	2005	0.23	2.37	36.26	8.39	24 April	5 June	6 August	104
T60	Growth	2005	0.41	2.56	31.48	12.96	3 May	21 June	1 September	120
C	Growth	2006	0.47	3.31	48.35	22.57	8 May	9 June	25 July	78
T30	Growth	2006	0.82	2.37	30.99	25.51	28 April	17 June	28 August	122
T60	Growth	2006	1.37	2.36	30.76	42.26	28 April	17 June	29 August	123
C	Growth	2007	0.70	2.12	41.75	29.32	15 April	22 May	15 July	90
T30	Growth	2007	1.20	1.96	34.96	42.09	13 April	27 May	31 July	108
T60	Growth	2007	1.75	1.92	33.56	58.68	13 April	28 May	3 August	113
C	No. of tracheids	2006	30.24	1.94	0.042	1.27	11 April	17 May	10 July	90
T60	No. of tracheids	2006	59.77	1.82	0.036	2.17	9 April	21 May	22 July	104

Parameters of the Gompertz function: a, upper asymptote or maximum radial increment or growth (in millimeters or number of tracheids); β, time-axis placement parameter; κ and r, raw and weighted mean absolute radial-increment/growth rates (in μm day^{-1} or tracheids day^{-1} in the case of radial increment or tracheid number); tp, date when the maximum increment/growth rate occurs; growth onset and growth end correspond to the dates when 10% and 90% of maximum growth were attained, respectively. The growing period (td) is defined as the time required for the major portion of increment or growth to occur.

range of BAI values (lower in the 2005 dry period, see Figure 3A) and the strength of the BAI–CI relationship (weaker in the dry period). Thinning treatments diminished the CI that was experienced by each tree by ca. 40% on average in sites T30 and T60, which caused, 3 years later, enhancement of growth differences (Figure 3).
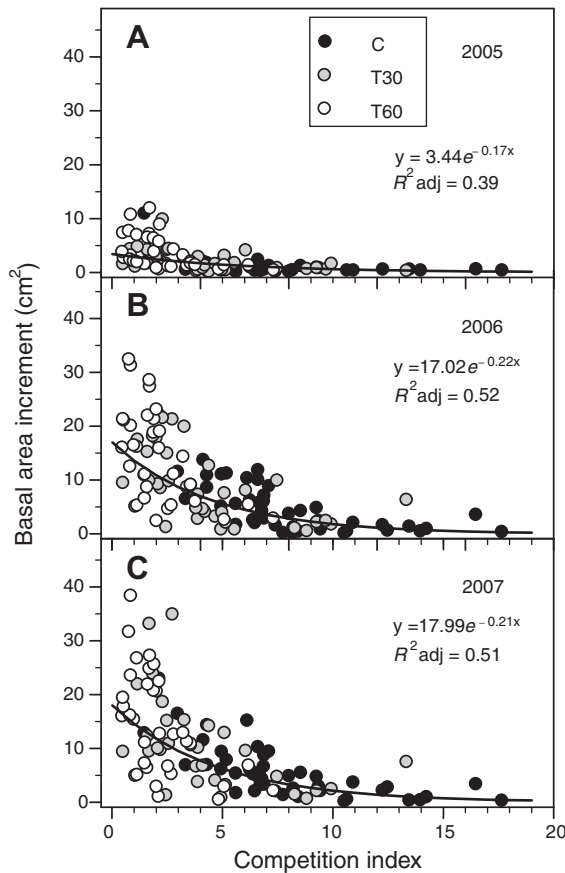
Figure 3. Relationships between the competition index and the BAI over 3 years studied. The negative-exponential functions corresponding to each year were fitted on the whole sample. Symbols are as in Figure 2. Note the different scales of radial growth used in the studied years ($n = 40$ trees per treatment).
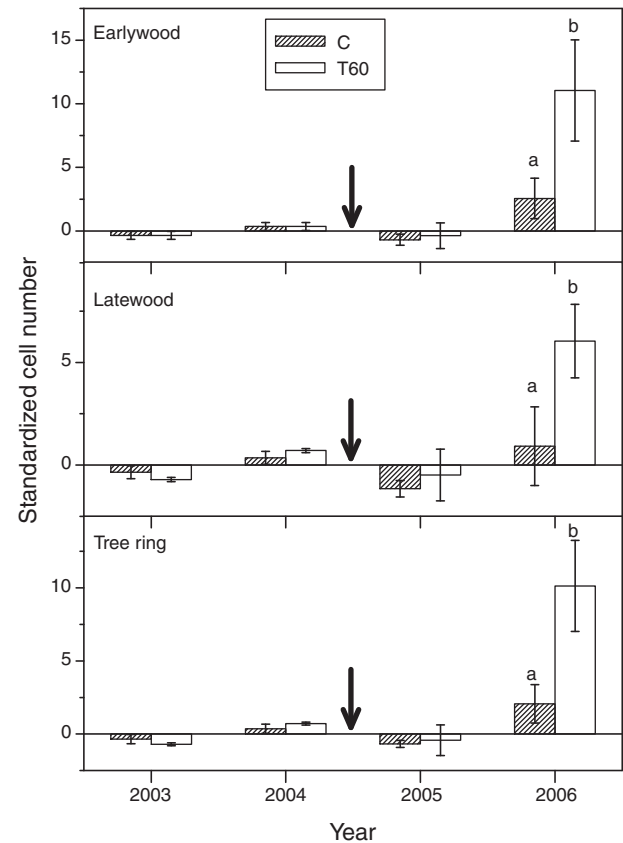

Figure 4. Standardized tracheid number in the earlywood, latewood and total tree ring for trees from the control unthinned (C, hatched bars) and the 60% of basal-area reduction (T60, white bars) treatments. Note that the numbers of tracheids in the tree ring were below the 2003–2006 average in 2003 and 2005 (negative standardized number). Different letters represent significant differences for one-way ANOVA, $P < 0.05$. The arrows indicate the thinning treatment. Error bars represent standard deviations ($n = 5$ trees per plot).

Thinning and drought effects on xylogenesis

Tree-ring width in the 2 years before thinning (2003–2004) confirmed that no significant differences existed between the trees from control and thinned plots, in terms of secondary growth before the application of density reduction (Figure 4). This is also valid for the mean number of earlywood and latewood cells. The number of latewood tracheids in the control was the variable that was most negatively influenced by the drought in 2005 (which, as we noted before, was among the driest years in the last decades), but differences with thinned plots were not significant. The thinning caused a significant increment in the standardized tracheid number in the earlywood, latewood and the tree ring in 2006 (Figure 4). Trees from the thinned plot (60% basal-area reduction) produced nearly two times more tracheids than trees from the unthinned plots in 2006 (57 ± 6 versus 30 ± 5). Finally, dbh did not show any significant effect as a covariate on the total number of tracheids.

The temporal patterns of the cell-enlargement and wall-thickening phases were similar in trees from the unthinned

(C) and thinned (T60) plots, but the mean number of tracheids in each phase was always higher in trees from the thinned plot (Figure 5). The greatest differences between treatments were observed for variables related to the cell-wall formation such as the number of wall-thickening and mature latewood tracheids. The total number of latewood cells was almost three times higher in T60 than in C trees (32 ± 2 versus 11 ± 3, see Figure 5), with significant differences between treatments in all dates and reaching maximum values in early October ($F = 29.21$, $P = 0.002$). The total number of tracheids was also significantly higher in T60 than in C plots for all dates, and the greatest difference among treatments was observed in late August (58 ± 5 versus 30 ± 5, $F = 16.0$, $P = 0.007$). Finally, the dates of earlywood–latewood transition (early August) and cessation of tracheid formation (late September) were not related to the thinning treatment.

Radial-increment estimates obtained from dendrometers and radial growth estimates based on microcores showed a highly significant linear relationship (see Supplementary
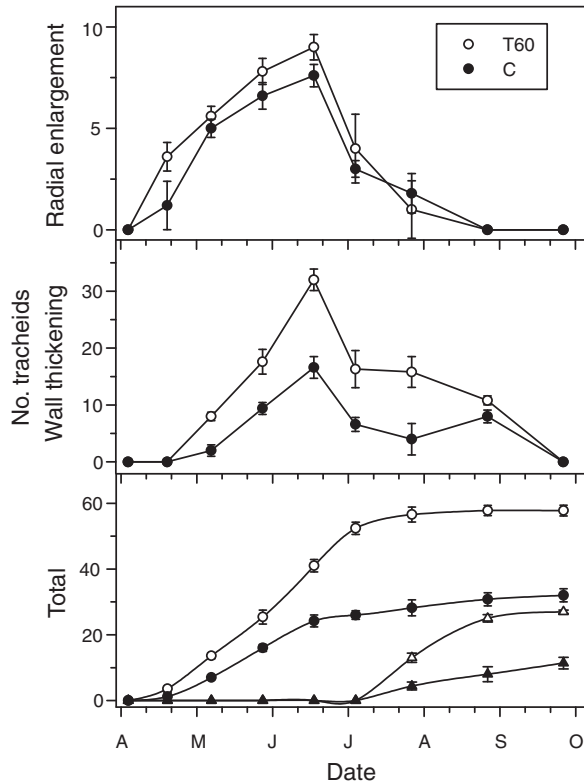
Figure 5. Xylogenesis patterns during 2006 in the control (C, black symbols) and intensively thinned (T60, 60% of basal-area reduction; white symbols) plots at the low-elevation site. The Gompertz functions fitted to the total number of cells are presented in the lowermost graph (triangles represent latewood cells). Error bars represent standard errors ($n = 5$ trees per treatment).

Data, Figure A2a). Microcore radial-growth estimates were on average slightly higher than the dendrometer-based radial-increment estimates. However, October values were not significantly different and therefore radial-growth assessments yielded comparable results with both methods (see Supplementary Data, Figure A2a). Major discrepancies occurred when defining the growth onset and arrest because according to the dendrometer data, *A. pinsapo* stems began to swell in late April to early May (28 April– 8 May), i.e., 17 days later than the true onset of wood formation (first observed radially enlarging tracheids) as measured by microcoring (9–11 April). However, the maximum increment or growth rates occurred in early to mid-June both according to dendrometers and microcore data (Figures 2 and 5; Table 3).

Discussion

Radial increment in trees consists of several components including irreversible growth, stem swelling due to water accumulation and thermal variations of wood and bark (Zweifel et al. 2006). Dendrometers measure changes

in the stem circumference and therefore water and thermal-related fluctuations such as swelling–shrinkage cycles are difficult to distinguish from irreversible growth and wood formation (Deslauriers et al. 2003, Mäkinen et al. 2008). In this study, radial-increment data based on dendrometer results differed slightly from the radial-growth data based on microcores (Figure A2; Table 3). Dendrometers showed a stem radius increase in early May, whereby the microcores indicated wood formation that started in late April (Figures 2 and 5). Dendrometer data suggested that trees reached most of their annual radial increment (90%) later than what microcore data indicated (Table 3). However, the period with a maximum rate of radial increment matched the moment when the most intense phase of wood formation was observed. Over the growing period, we obtained slightly higher radial-growth data based on microcores than those based on dendrometers, though the annual tree-ring widths derived from both methods did not significantly differ (Figure A2b). We conclude that the most precise method for defining the phenology of radial growth is the analysis of xylogenesis phases. Thus, inconsistencies between the dendrometer and microcore findings on the onset of the growing season and the timing of maximum growth rate should be accounted for as uncertainty estimates of dendrometer data. However, some discrepancies between both approaches such as slightly higher growth estimates based on microcore measurements than those based on dendrometer recordings could also be related to the fact that dendrometers integrate stem changes in volume over the whole perimeter of the trunk. In contrast, microcores are localized radial samples whose radial measure greatly depends on the sampling location around the stem (Mäkinen et al. 2008). In addition, dendrometers provide estimates of radial growth without causing potential disturbing effects due to direct wood sampling or similar techniques such as pinning.

In 2007, in spite of the relatively cold temperatures (Table 2), the growth onset occurred earlier than in 2005 and 2006. This could be related to a higher water availability in April, which could have influenced the dendrometers through a stem swelling due to rehydration processes before intense tracheid formation. On the other hand, swelling– shrinkage effects may be important during the spring– summer transition in tree species under water-stressed conditions such as those experienced in the Mediterranean areas (Zweifel et al. 2001). Therefore, the Gompertz and similar sigmoidal functions may not be suitable to model mean cumulative values of stem increment or number of formed tracheids in Mediterranean conditions, where tree growth is not necessarily monotonous as in temperate climates. According to Figure 2, radial-increment dynamics of *A. pinsapo* are characterized by low rates at the end of July and a slight reactivation in late summer. Summer cambial arrestment has been detected in Mediterranean tree species in semi-areas, i.e., subjected to drier conditions than in our study sites (De Luis et al. 2007). Thus, the Gompertz

function may be in its limit of applicability in the case of *A. pinsapo* because, although this species is subjected to summer drought, the mean annual precipitation in the distribution area of this species is higher (above 1000 mm) than in more water-stressed areas and the water deficit in these forests is among the lowest of the Mediterranean conifer woodlands (Quézel et al. 1999). On the other hand, predetermined growth and drought avoidance strategies of this fir (Linares 2008) could lead to only a limited late-summer growth reactivation.

The presented findings support the previous conclusions of several authors (Camarero et al. 1998, Deslauriers et al. 2003, Vaganov et al. 2006), suggesting that a comparison with cellular analyses is necessary to calibrate radial-increment dynamics and to obtain reliable radial-growth data. Despite the aforementioned shortcomings, our results show that dendrometers provide useful estimates of the radial-growth patterns in *A. pinsapo*. However, to provide new insights into the roles of climatic parameters on the intra-annual wood dynamics, dendrometers must be used in combination with phenological investigations on the number and types of formed tracheids (e.g., Camarero et al. 1998, Deslauriers et al. 2003).

Thinning treatments mainly affected the maximum radial-increment rates and the final tree-ring width, while the date of growth resumption derived from microcores was mainly related to temperature and day length as found in other conifers (Antonova and Stasova 1993, Rossi et al. 2006b). The greatest difference between the unthinned and intensively thinned treatments corresponded to the number of latewood tracheids. Differentiation of latewood tracheids in summer and autumn lasted longer in trees from thinned than in trees from unthinned stands. This protracted latewood formation suggests that the effects of thinning on secondary growth of *A. pinsapo* are mainly exerted on the wall-thickening and lignification phases of tracheids (Figure 5). Our findings are consistent with those of Gričar et al. (2005), who found that the cambium activity of less productive trees with narrower rings stopped earlier than in trees with broader rings in *Abies alba* Mill.

Xylogenetic differences in the number of cell-wall-thickening tracheids between thinned and unthinned stands may also affect the anatomy of latewood tracheids since the duration of tracheid maturation determines the final cell-wall thickness (Wodzicki 1971, Horacek et al. 1999). The wall thickness of the latewood cells affects the tree-ring maximum density (Yasue et al. 2000), which may be an indirect measure of wood lignification and durability. However, Bouriaud et al. (2005) found a strong positive correlation between soil water deficit and wood density, which they attributed to temperature-mediated reductions in the radial-growth rates due to an increasing soil-water deficit. The reduction in tracheid radial enlargement might also be associated with thicker cell walls. We found that thinning enhanced the formation of wall-thickening and latewood tracheids in 2006, which are able to keep a minimal

hydraulic conductivity even under a very low water potential (Mayr and Cochard 2003). The formation of more latewood tracheids with thicker walls might also be an additional advantage to trees in thinned sites because such tracheids are less prone to cavitation than wider tracheids with thinner walls. Further studies should test if the tracheid wall thickness is lower in the latewood of trees from unthinned and more water-stressed stands in comparison with thinned stands, and if these changes affected the hydraulic safety of tracheids.

Our results show how competition (as a long-term stressor) and drought (as a short-term stressor) interact to affect the seasonal dynamics of *A. pinsapo* radial growth. We proposed that thinning has the potential to modify the physiological thresholds imposed by both constraints thus mitigating the growth decline in response to severe or even moderate droughts that were observed in these forests (Linares et al. 2009a). Despite our finding of differential effects of competition strength on tree growth (Figure 3), the pattern of growth decline during the 2005 drought was very similar in unthinned and thinned stands. These findings are supported by short- and long-term studies on temperate mountain conifers. First, significant radial-growth reductions in dominant and suppressed trees in response to severe droughts had been previously observed by Eilmann et al. (2006) in *Pinus sylvestris* L. Second, climate warming and increasing water stress seem to be the main causes of growth decline in *A. alba* forests near the southern limit of the species distribution (Macias et al. 2006), and should also lead to a severe growth reduction in *A. pinsapo* according to dendrochronological studies (Génova 2007, Linares et al. 2009a). However, trees in the thinned stands showed a higher post-drought growth in comparison to pre-drought values (Figures 2, 5 and A1). On the other hand, apart from drought, predetermined growth could also play an important role to explain the lower growth differences obtained 1 year after the thinning.

The development of wood is the result of cambium activity, which mainly depends on the whole plant water–carbon balance and the external climatic conditions. Severe water stress affects processes related to xylem dynamics in conifers including carbon sink–source trade-offs within the tree (Vaganov et al. 2006). Water stress may alter the partitioning of newly fixed carbon in such a way that less carbon is diverted for secondary growth (Pichler and Oberhuber 2007) or more fixed carbon is lost through photorespiration (Laureano et al. 2008).

As a result of such effects, water-stressed conifers usually have a smaller tracheid transversal lumen area as compared with non-stressed individuals (von Wilpert 1991, Abe et al. 2003, Abe and Nakai 2008).

On the other hand, tree-to-tree competition, brought about by the capture of resources by neighbors, is a long-term stress that affects the carbon balance of individual trees (Linares et al. 2009b). Stress causes distinctive changes in the photosynthate allocation patterns and growth decline (Waring 1987). *A. pinsapo* trees became increasingly

vulnerable to competition, as reflected by the low growth values during the drier periods (Figures 3 and A1). Long-term competition could imply further challenges overcoming drought events, such as a requirement for superior carbon balance when faced with the need to recover from a drought-induced crown loss (Franklin et al. 1987).

Martín-Benito et al. (2007) found that radial growth of *Pinus nigra* Arn. in suppressed trees showed a less plastic response to severe droughts than in dominant individuals, which they interpreted as a sign of better adaptation to drought in trees subjected to a higher competition. However, the direct interpretation of response plasticity in terms of vulnerability may be misleading, as vulnerability to water stress is determined both by sensitivity and adaptation capacity (Linares et al. 2009b). Tree-ring width in suppressed trees is usually near the minimum survival threshold (Bigler and Bugmann 2004). Therefore, a less plastic response to climate in suppressed trees may just arise from a loss of adaptation capacity, which would indicate a higher vulnerability rather than a better adaptation (Linares et al. 2009a). On the contrary, in climatically favorable years, dominant trees may show a higher growth recovery as the detected positive growth response to the wet 2007 spring in dominant *A. pinsapo* trees (see Figure A1). Intraspecific competition remains fairly through time, and thus radial growth of suppressed trees is constrained in the long term (McDowell et al. 2003).

A functional basis for the different radial-growth patterns found in trees subjected to contrasting CIs may be due to a shallower root system development in suppressed than in dominant trees (López et al. 1998). Suppressed trees may have a poorer access to deep soil moisture than dominant trees, so that the former will experience severe water stress earlier in summer, when latewood is forming. Tree rings in suppressed trees would then be mainly composed of earlywood cells that were formed in spring, before severe water limitation. In addition, trees under high competitive stress have a lower autotrophic-to-heterotrophic-tissue ratio than dominant trees (Naidu et al. 1998), and therefore respiration might almost exceed photosynthesis during periods with high temperature (Pereira and Chaves 2001).

In summary, our results illustrate how competition affects both the radial-increment rate and the duration of the growing season, even in years with severe droughts, mainly by reducing the number of produced tracheids and shortening the growing period. Our results suggest that drought and competition modify both the rate and the duration of the cell differentiation processes, independently of the date the growing season begins that is primarily controlled by temperature and day length. The plastic responses in xylogenesis, reported here for the relict fir *A. pinsapo*, may be the evolutionary output from selective pressures under its current Mediterranean-type climate, representing an advantageous trait to adapt to extreme inter-annual changes in water availability.

Conclusions

Wood formation in *A. pinsapo* is greatly reduced during severe droughts. Trees in the thinned sites showed a higher and more plastic response regarding secondary growth than trees from the unthinned sites. Trees in the thinned sites reduced growth in response to drought up to values similar to those of trees from the unthinned sites, but showed a faster post-drought recovery through both a higher growth rate and an extended latewood formation period. Radial growth in suppressed trees was permanently constrained in the long term. Then, the reported lower plasticity in response to drought of suppressed trees may imply a lower adaptation capacity to climate stress and then enhanced vulnerability. Our results illustrate how competition modulates the effect of drought on the secondary growth in a relict Mediterranean fir, and underlines the essential role of both stand structure and environmental constraints for tree growth and wood formation. Thinning treatments in water-stressed sites may be a valuable management tool to foster drought resistance of *A. pinsapo*, a species regarded as very vulnerable to rising temperatures and decreasing soil water availability.

Supplementary Data

Supplementary data for this article are available at *Tree Physiology* Online.

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