

Effects of thinning and canopy type on growth dynamics of *Pinus sylvestris*: inter-annual variations and intra-annual interactions with microclimate

Irantzu Primicia · J. Julio Camarero ·
J. Bosco Imbert · Federico J. Castillo

Received: 21 December 2011 / Revised: 6 September 2012 / Accepted: 25 September 2012 / Published online: 4 November 2012
© Springer-Verlag Berlin Heidelberg 2012

Abstract We assessed the effects of thinning (0, 20 and 30 % extraction of basal area) and canopy type (pine–beech vs. pine plots, beech accounting for 12 % of total basal area) on radial growth of dominant and codominant Scots pine at inter-annual scale and on microclimatic conditions, radial growth and xylogenesis 9 years after thinning at intra-annual scale. Thinning weakly affected pine growth, which was enhanced 3 years after harvesting. Over time, a gradual reduction in pine growth in mixed canopy relative to pure canopy occurred only in unthinned plots apparently due to beech expansion. Indeed, 9 years after thinning, a higher seasonal radial increment and a greater number of tracheids were produced under pine canopy in the unthinned plots, whereas no differences between canopy types were observed in the thinned plots. Radial increment and tracheid production were mainly affected by tree water status (air and soil humidity, throughfall). The differences of tree water status caused by treatments, and plausibly disparities in tree size and tree-to-tree competition, were the main

drivers explaining the patterns observed for radial increment and xylogenesis. Our results suggest that the negative effects of beech competition on Scots pine growth in similar mixed forest may be controlled to some extent by thinning.

Keywords Competition · Forest management · Growth · Mixed forest · Xylogenesis

Introduction

Thinning is a widespread practice to manage forest stands (Oliver and Larson 1990). A great deal of knowledge has accumulated over decades about the effects of thinning on tree growth in monospecific stands, but much less is known about its effects on growth in mixed stands. Understanding growth dynamics of mixed forests is difficult, in part due to complex interactions among tree species and to the fact that species may differ greatly in functional traits such as growth rate and competitive ability.

Historically, pure conifer forests have been prioritized over mixed conifer–broadleaf ones in the European temperate zone to enhance wood production (Spiecker 2003; Pretzsch 2005). Nevertheless, mixtures could lead to a potential increase in stand productivity due to inter-specific processes (Kelty 1992). Indeed, the effects of mixture on productivity have been the target of numerous researches, the bulk of them with Scots pine as the dominant tree species. However, little is known about how tree-to-tree interactions in mixed Scots pine (*Pinus sylvestris* L.)–beech (*Fagus sylvatica* L.) stands and management affect growth and wood formation at different time scales.

Pine–beech forests constitute a frequent vegetation type in the south-western Pyrenees (e.g., Navarre), where they account for over 40 % of mixed woodlands (Government

Communicated by Christian Ammer.

I. Primicia · J. B. Imbert (✉) · F. J. Castillo
Dpto. Ciencias del Medio Natural, Universidad Pública de Navarra, Campus de Arrosadía s/n, Pamplona, 31006 Navarra, Spain
e-mail: bosco.imbert@unavarra.es

I. Primicia
e-mail: irantzu.primicia@unavarra.es

F. J. Castillo
e-mail: federico.castillo@unavarra.es

J. J. Camarero
ARAID—Instituto Pirenaico de Ecología, CSIC, Avda. Montañana, 1005, 50080 Zaragoza, Spain
e-mail: jjcamarero@ipe.csic.es

of Navarre 2010). The present study is part of a long-term project that focuses on one managed forest site where cover of beech is expanding relative to that of Scots pine. Our main objective in this investigation is elucidating how thinning can alter the functioning of pure Scots pine patches versus mixed beech–pine ones. In this work, we focus on inter-annual growth dynamics of Scots pine in the dominant stratum in relation to thinning and the presence or absence of beech. The effects of thinning and type of canopy on microclimatic conditions were also studied at intra-annual scale 9 years after thinning, providing a baseline for the assessment of the effects of a second thinning, applied in 2009, on the intra-annual growth patterns of Scots pine.

To characterize tree growth dynamics, most thinning studies involve either the measurement of changes in diameter at breast height (DBH) between regular intervals (>3 years) or the use of tree-ring analysis. The study of inter-annual tree growth responses to thinning is important as growth in thinned plots may interact with climate (e.g., dry vs. humid years), but patterns may not be observed if sampling intervals are too ample. Relating microclimatic variation to intra-annual patterns of growth may allow better understanding of the main drivers of tree growth (Bréda et al. 1995; Ma et al. 2010; Rambo and North 2009). Therefore, we employed an integrative approach to describe thinning effects on Scots pine growth in this mixed forest using the following: (1) tree-ring chronologies to characterize inter-annual growth patterns and (2) band dendrometers and microcores for describing the intra-annual dynamics of stem radial increment and xylogenesis, respectively (see Mäkinen et al. 2008).

The study of xylogenesis is paramount to understand mechanisms underlying growth patterns. Xylogenesis is controlled by several abiotic and biotic factors (Antonova and Stasova 1993; Vaganov et al. 2006). Most xylogenesis research has omitted to some extent how the interaction between microclimate and competition might affect wood development in closed forests (Deslauriers et al. 2008; Gruber et al. 2009). In this respect, changes in inter-annual tree growth sensitivity to climate as a function of different competition levels have been reported for *F. sylvatica* (Cescatti and Piutti 1998; Piutti and Cescatti 1997) and *Pinus nigra* (Martín-Benito et al. 2010). Additionally, different canopy types might modulate xylogenesis affecting microclimate (Horn 1971). Nevertheless, to our knowledge, there is no information about how competition may modify the response of xylogenesis to microclimatic variation. The lack of similar data is unjustifiable for areas experiencing water deficit such as Mediterranean mountain forests, where thinning may be an appropriate management tool to counteract the negative effects of a warming-induced reduction in water availability (Linares et al. 2009).

In this context, our specific objectives were (1) to evaluate the effects of thinning and presence of beech on the inter-annual growth dynamics of dominant Scots pines; (2) to assess whether thinning intensity and canopy type affected microclimatic variables 9 years after thinning; (3) to determine and compare the relationships between microclimatic variables and intra-annual radial-increment rates and xylogenesis of dominant Scots pines for the different treatments and (4) to evaluate the effects of thinning intensity and canopy type on intra-annual radial increment and xylogenesis of dominant Scots pines.

Materials and methods

Study site

The study site (Aspurz, 42°42′31″N, 1°08′40″W) is located in the western Spanish Pyrenees, Navarre. It is one of the most productive Scots pine forests in Spain (Puertas 2001), with a site index of 29 m at 80 years. The site is an even-aged mixed stand dominated by Scots pine, with mean age of 40 years and mean dominant tree height of 18.4 m. The second most abundant tree species is beech, with a mean crown cover of ca. 38 % and mean age of 35–40 years. Beech trees cover all strata, from suppressed to dominant ones. Plots are North oriented, located at a mean altitude of 642 m and a mean slope of 7 %. The forest is developed on a Haplic Alisol (Blanco 2004), with a mean annual precipitation of 913 mm and a mean annual temperature of 12.0 °C (data from nearby Navascués station located at 2.7 km from the study site, 42°43′06″N, 1°06′55″W, 615 m; period 1984–2008). The climate corresponds to a cold wet Mediterranean type with water deficit usually in July and August, and frequent frosts in winter and early spring. The meteorological conditions during the study year, 2008, did not significantly differ (paired T test, $P > 0.05$) from the historical mean (1984–2008).

Experimental design

Nine rectangular plots (30 m × 40 m) were installed by the Forest Service of the Government of Navarre, following a complete randomized block design (Andrew 1986). In 1999, different thinning intensities were carried out applying the same treatment in a buffer zone of 5–10 m around the plots. The experimental design consisted of three treatments with three replicates: unthinned plots (hereafter abbreviated as U plots); light-thinning plots (20 % of basal area removed—hereafter abbreviated as T20 plots); moderate-thinning plots (30 % of basal area removed—hereafter abbreviated as T30 plots). Only Scots pine trees were thinned following the silvicultural trends

applied currently in Navarre on mixed stands with beech as secondary species. Thinning was carried out with selection of crop trees, mainly removing suppressed or intermediate trees, and some dominant or codominant trees with malformed stems. Logs and branches from the felled trees were transported to the edges of the buffer zones. According to litterfall biomass data, canopy cover recovered from thinning in 2005–2006 (data not shown).

Each plot was divided into two discontinuous subplots based on the crown cover of beeches taller than 2 m: mixed beech–pine and pure pine subplots (hereafter abbreviated as MC and PC subplots). Six subplots are determined: UM (unmanaged mixed beech–pine), UP (unmanaged pure pine), T20 M (T20 mixed beech–pine), T20P (T20 pure pine), T30 M (T30 mixed beech–pine) and T30P (T30 pure pine). Thus, the experimental design can be specified as a split plot (von Ende 2001), which includes three replicates of six subplots (Table 1). Although data of beech trees are not available for 1999, comparison between data of beech cover in 2000 and 2008 suggests that mixed canopy area has remarkably spread over the plots within that period. There has not been pine regeneration between those years.

Dendrochronological methods

Two Scots pine trees were randomly selected in each subplot ($n = 36$) from those included in the xylogenesis study (see below). In March 2009, stem slices of the selected trees in the thinned plots and two cores per tree (with a Pressler increment borer) in the unthinned plots were extracted at 1.3 m. The cores were mounted on wood boards, and both, the stem slices and cores were air-dried and polished with sandpaper grits until tree rings were clearly visible. The wood samples were visually cross-dated, and the cross-dating was checked using the program COFECHA (Holmes 1983). Tree rings were measured to the nearest 0.001 mm using a binocular scope and a LINTAB measuring device (Rinntech, Heidelberg, Germany). Due to technical problems, rings data for 2008 were available only for 26 trees. Tree-ring width in 2008 of the 90 trees included for the xylogenesis study was measured on the microcores gathered at mid November as described below.

Microclimatic data

Two meteorological stations were placed in each plot (one per subplot; $n = 18$). From March to November 2008, continuous measurements of photosynthetically active radiation (PAR, QUANTUM-QSO sensor) at 2 m above the ground and soil humidity (ECHO-10 sensor) and temperature (TMCx-HD sensor) at 0.1 m depth were

Table 1 Characteristics of the six experimental subplots after the first thinning in 1999 and in 2008

Treatment (code)	After thinning 1999 ^a			Year of study: 2008						
	<i>Pinus sylvestris</i> L.			<i>Fagus sylvatica</i> L. ^b						
	Area (m ²)	Density (stems ha ⁻¹)	DBH (cm)	Area (m ²)	Density (stems ha ⁻¹)	DBH (cm)	BA (m ² ha ⁻¹)	Density (stems ha ⁻¹)	DBH (cm)	BA (m ² ha ⁻¹)
UM	385 ± 106	3156 ± 520	11.6 ± 0.9	456 ± 120	2145 ± 377	15.0 ± 1.0	38.8 ± 1.7	1448 ± 300	6.0 ± 0.6	4.1 ± 1.3
UP	815 ± 106	3792 ± 863	11.8 ± 1.1	744 ± 120	2228 ± 304	16.0 ± 0.8	47.2 ± 2.1	0		
T20M	338 ± 61	1579 ± 152	13.3 ± 0.8	423 ± 55	1687 ± 169	15.6 ± 0.7	34.7 ± 0.9	765 ± 158	7.5 ± 0.6	3.5 ± 0.4
T20P	862 ± 61	2416 ± 208	13.1 ± 0.4	777 ± 55	2215 ± 166	15.5 ± 0.6	45.7 ± 1.1	0		
T30M	404 ± 19	1864 ± 238	12.8 ± 1.1	490 ± 12	1800 ± 253	15.2 ± 1.1	34.6 ± 2.9	675 ± 113	9.3 ± 1.2	5.8 ± 1.3
T30P	796 ± 19	2382 ± 251	12.6 ± 0.7	710 ± 12	2408 ± 267	14.7 ± 0.8	43.5 ± 0.9	0		

UM unthinned mixed canopy, UP unthinned pure canopy, T20M light thinning mixed canopy, T20P light thinning pure canopy, T30M moderate thinning mixed canopy, T30P moderate thinning pure canopy, BA basal area, DBH diameter at breast height (1.3 m). Mean ± SE

^a Data of *Fagus sylvatica* trees in 1999 are not available. ^b Including all trees taller than 2 m

recorded every 30 min by Hobo U12 data loggers (Onset Co., USA). Relative humidity and air temperature at 1 m above ground were also recorded every 30 min using Hobo Pro.v2 data loggers. Rather than light intensity, we used understorey day length (i.e., number of hours per day when PAR radiation is higher than the minimum detectable level, 0.81 W m^{-2}) in further analyses. Daily minimum, maximum and mean air temperature and humidity were estimated. Monthly throughfall was determined with 54 containers placed in the plots (3 per subplot). These data were regressed against monthly precipitation data obtained from the nearby Navascués station. The resulting regression model was used to estimate daily throughfall by using daily precipitation as an independent variable.

Seasonal dynamics of radial increment

Two Scots pine trees per plot (one per subplot; $n = 18$) were selected from those included in the xylogenesis study (see below). At the beginning of March, the dendrometers (AEC, Tucson, USA) were placed at about 1.3 m height after removing carefully the rhytidome. From March to July, the dendrometers were read biweekly, while from August to November, they were read monthly. The measurements were done to the nearest 0.1 mm and corrected for temperature effects taking into account the dendrometer thermal expansion ($11.2 \times 10^{-6} \text{ mm}^{-1} \text{ }^\circ\text{C}^{-1}$). To avoid biases during recording, all measures were always taken before midday, and they were never taken after a rainy day. We used radial increment data for the study, as patterns of radial and basal area increment were similar in the different treatments.

Xylogenesis

Ten dominant or codominant Scots pine trees per plot ($n = 90$) were randomly selected (Table 2). One wood microcore per tree (2.0 mm thick and 15 mm long) was collected in early April, May, June, July, September and October. Only samples from May, June, July and September were fully processed, as this is the period when the main xylogenesis phases of Scots pine occur in the area (Camarero et al. 1998). Several randomly selected subsamples from the April and October samples were processed just to determine the beginning and ending of tracheid production. Wood microcores were collected following a spiral around the stem at a height of 1.3 m using a Trephor borer (Rossi et al. 2006a). The microcores were placed in Eppendorf tubes filled with a solution of formaldehyde, acetic acid and ethanol (5:5:90). Transversal wood sections 20–40 μm thick ($n = 360$) were obtained with a freezing microtome (Anglia Scientific AS 200). Wood sections were stained with cresyl fast violet (0.35 % in water) and fixed with

Table 2 Characteristics of the trees selected for the study of xylogenesis

Treatment (code)	Height (m)	DBH (cm)	Crown length (m)	Competition index (CI)*
UM	18.6 \pm 0.2	21.8 \pm 0.8	5.9 \pm 0.3	5.25 \pm 0.43
UP	19.2 \pm 0.3	24.0 \pm 0.8	6.6 \pm 0.3	4.41 \pm 0.42
T20M	18.6 \pm 0.3	21.6 \pm 0.8	6.3 \pm 0.3	4.62 \pm 0.42
T20P	18.5 \pm 0.4	22.7 \pm 0.5	6.4 \pm 0.2	4.14 \pm 0.37
T30M	18.0 \pm 0.4	21.0 \pm 1.2	6.1 \pm 0.2	5.16 \pm 0.57
T30P	16.8 \pm 0.9	21.0 \pm 0.8	5.7 \pm 0.5	4.67 \pm 0.40

* CI = $\Sigma ((D_j D_i^{-1}) / \text{DIST}_{ij}^{-1})$, where D_j is the DBH of neighbor tree, D_i is the DBH of subject tree and DIST_{ij} is the distance between neighbor and subject tree (see Daniels et al. 1986). The influence radius was 5 m. Abbreviations are as in Table 1. Mean \pm SE

Eukitt© for examination with a light microscope or under polarized light. The number of tracheids in different development phases of the last tree ring was counted along five radial rows, averaging the number for each date. Four cell development phases were considered according to cell shape and staining (Antonova et al. 1983; Antonova and Stasova 1993): cambium cells, radially enlarging tracheids, cell-wall thickening tracheids and mature tracheids. The first cells with evident radial diameter increments, but still containing a protoplast enclosed by a thin wall were regarded as radially enlarging tracheids. The end of radial expansion and the onset of secondary cell-wall thickening were defined by the appearance of cell corner rounding and because cell walls glistened when observed under polarized light. Tracheid lignification corresponded to a color change from violet to blue. The maturation zone ended when visible traces of cytoplasm were not observed within the tracheid lumen. Mature cells exhibited completely blue cell walls. Mature tracheids were classified as earlywood and latewood tracheids using Mork's method in relation to their radial lumen and cell-wall thickness (Denne 1989), where latewood tracheids are those with single cell-wall thickness $\times 4 \geq$ tracheid lumen. The total number of tracheids was the sum of the radially enlarging cell-wall thickening and mature tracheids.

Statistical analyses

The following statistical analyses were carried out using R 2.13.0 (R Development Core Team 2011).

The effects of thinning intensity and type of canopy on Scots pine growth variables and the microclimate were assessed using linear mixed-effects models (nlme package) following a split-plot design with a repeated measure (Pinheiro and Bates 2000). The proposed model included thinning intensity, canopy type and date as fixed effects and subplot or tree code as random effects. A correlation

structure was included to account for the repeated measures on the same subplot or tree. The significance of the fixed effects was analyzed with Wald tests and by comparing nested models with and without the effect using the likelihood ratio test and based on the maximum likelihood (ML) estimation procedure (Zuur et al. 2009). Similar results were obtained with both methods, and therefore, only Wald tests are shown. Linear contrasts were used for post hoc comparisons. Log transformations of the data were used to fulfill the requirements of the statistical analysis for normal distribution and homogeneity of variance.

Principal component analysis (PCA) (data not shown) was used to select the main microclimatic variables involved in the Scots pine growth dynamics: mean air temperature (meanT), minimum relative humidity (minRH), minimum soil humidity (minSH), understory day length (DL) and throughfall (Th). The values of these variables were averaged (mean or summed in the case of throughfall) 5, 10 and 15 days before the sampling date to take into account potentially lagged climate-growth responses (Camarero et al. 1998). Temporal autocorrelation of the microclimatic variables showed significant values for lags lower than five days. The selected period (10 days) was determined by fitting linear models between the different growing responses and the microclimatic data (5, 10 and 15 days mean), selecting the one with the lowest Akaike Information Criterion (Burnham and Anderson 2002). Relationships between the microclimatic variables and the radial-increment rates and tracheid number data were analyzed using Spearman's rank correlation coefficient. The growing season was split in three periods in relation to the radial increment and microclimatic data based on previous studies with Scots pine (Camarero et al. 1998): (1) spring, March–May; (2) summer, June–July; (3) late summer and fall, August–November. The Gompertz function was fitted to the cumulative radial increment of each tree (Camarero et al. 1998). Afterward, the residuals between the observed values and the Gompertz predictions were calculated in order to eliminate the annual intrinsic pattern of tree growth and elucidate relationships with microclimate that could have been otherwise disguised. Relationships between the microclimatic variables and the radial-increment rates and the residuals were analyzed for the three periods. On the other hand, the effects of the microclimatic variables on xylogenesis were analyzed directly on the number of cells in the different phases and on the total number of tracheids. As similar results were obtained for the three periods and the whole growing season, only data for the latter are shown. In this case, the fitting of a sigmoidal function such as the Gompertz one to the number of tracheids was considered to be meaningless due to the reduced number of sampling points along the growing season (4 sampling dates).

The relationships between the radial growth assessed through dendrometer measurement and xylogenesis data were analyzed using Pearson's correlations.

Results

Inter-annual basal area increment and tree-ring width

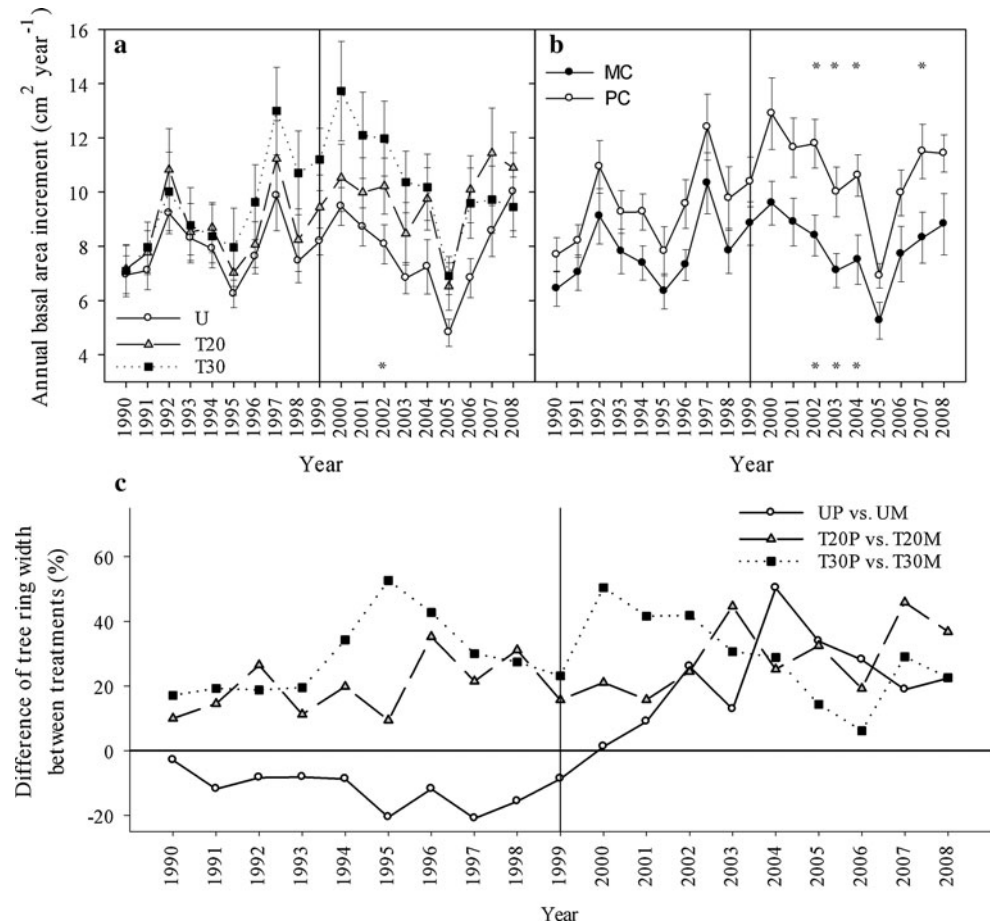
Neither TRW nor BAI of Scots pines showed significant differences among groups of plots before thinning (Fig. 1a), although plots were initially highly variable in Scots pine densities (from 2492 to 5667 trees ha⁻¹). TRW and BAI were significantly affected by the interaction between thinning intensity and year ($P < 0.01$ and $P < 0.05$, respectively). Thus, T30, followed by T20 and U plots (Fig. 1a) produced the highest BAI in 2002 ($P = 0.08$), and the highest TRW in 2000 ($P = 0.05$), 2002 ($P < 0.05$) and 2003 ($P = 0.07$). However, previously existing differences in BAI and TRW between U and T30 plots (i.e., 1999) generally increased little after thinning (i.e., <15 %), except for two relatively important increases that occurred for BAI in 2002 (30.4 %) and 2003 (40.2 %).

Scots pine showed higher growth rates in pure patches even before 1999, these differences becoming significant after thinning ($P < 0.05$, Fig. 1b). Between the types of canopy, differences were significant for BAI and TRW from 2002 to 2004, and in 2007, for BAI ($P < 0.05$). Almost significant differences ($0.05 < P < 0.07$) were also found for both variables in 2000 and 2005, as well as in 2007 for TRW. However, the divergence between types of canopy after thinning was mainly due to increasing differences between canopy types in the unthinned plots (Fig. 1c). In the unthinned plots, Scots pine grew less in pine than in mixed canopy before thinning (−13.4 %), but after thinning, it grew more in pine than in mixed patches (17 %). Contrastingly, in the thinned plots, Scots pine grew more under pine than under mixed canopy during the whole study period (1990–2008), being the differences between canopy types similar before and after thinning. Unexpectedly, unthinned and T20 plots appeared to recover faster from a severe drought in 2005 than T30.

Intra-annual microclimate

During the study year, most precipitation was recorded between May and June, whereas soil humidity decreased sharply in July, reaching minimum values in August, when the warmest air temperature was observed (Fig. 2). All the daily microclimatic variables showed a significant date effect (Table 3). The 1999 thinning still affected minimum soil humidity (minSH $P = 0.015$), being significantly

Fig. 1 Annual basal area increment (BAI, mean \pm SE) from 1990 to 2008 versus thinning intensity (a) and type of canopy (b) and relative difference of tree-ring width between UM versus UP, T20M versus T20P and T30M versus T30P (c). Calculations have been made as follows for each pair of comparisons, for instance, UP versus UM: $(TRW_{UP} - TRW_{UM}) \cdot 100 / TRW_{UM}$. U unthinned plots, T20 light thinned plots, T30 moderate thinned plots, MC mixed canopy, PC pine canopy, UM unthinned mixed canopy, UP unthinned pine canopy, T20M light thinning mixed canopy, T20P light thinning pine canopy, T30M moderate thinning mixed canopy, T30P moderate thinning pine canopy. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Significant differences for BAI are indicated above and for tree-ring width, below. The vertical line indicates the date of thinning



higher ($P < 0.05$) in unthinned (30.02 ± 0.26 %; mean \pm SE) than in thinned plots (27.34 ± 0.27 % and 27.30 ± 0.25 % in T20 and T30 treatments, respectively). Moreover, minimum relative humidity (minRH) and daily throughfall (Th) showed a significant ($P < 0.001$) thinning intensity \times date interaction. Hence, differences in Th between unthinned and thinned plots were detected (T20 = T30 > U) only at high daily precipitation values, whereas minRH was higher in U and T30 plots than in T20 plots for several dates.

The interaction between type of canopy and date had a significant effect ($P < 0.001$) on all the microclimatic variables, as differences became significant once beech had completely spread out its leaves. Thus, during the growing season, pure patches showed higher mean air temperature (meanT), minSH, understory day length (DL) and Th, but lower minRH.

Additionally, the triple interaction between thinning intensity, canopy type and date had a significant effect ($P < 0.001$) on daily throughfall, caused by frequent higher Th values under pine canopy in U and T30 plots, but no differences between canopy types in T20 plots.

Seasonal dynamics of radial increment

Cumulative radial increment and radial-increment rates of Scots pine were significantly affected by date and the interaction between thinning intensity, canopy type and date ($P < 0.05$, Fig. 3a). This interaction may be explained due to the finding of significant and consistent differences between treatments for some dates. Thus, growth values in the unthinned plots were always higher in pine canopy, whereas in the thinned ones, both, higher values in mixed patches or no significant differences between types of canopy were observed. Therefore, at the end of the growing season T20M and UP plots showed the highest cumulative radial increments (ca. 2.0 mm), followed by T20P and T30M (ca. 1.5 mm) and finally, by T30P and UM (ca. 1.0 mm).

Most radial increment (ca. 90 %) occurred from early April up to early September (Fig. 3a). Cumulative radial increment was higher for the first study period, from March to May (40 %), than for the other two periods (June to July, ca. 26 %; August to November, ca. 36 %). Cumulative radial increment achieved a maximum value around October

Fig. 2 Temporal patterns of selected microclimatic variables. *Unders.* understory, *DOY* day of the year, *MC* mixed canopy, *PC* pine canopy, *U* unthinned plots, *T20* light thinning, *T30* moderate thinning

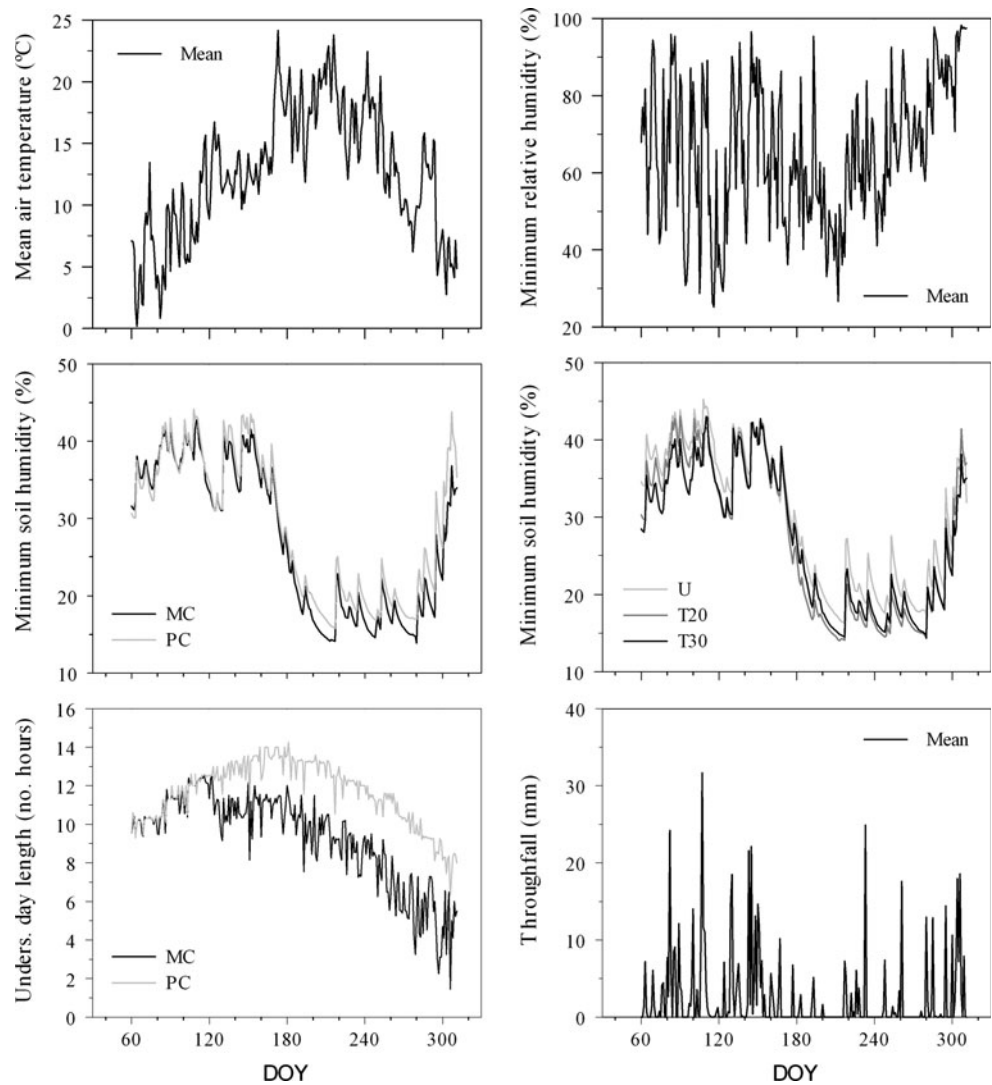


Table 3 Split plot with a repeated measure ANOVA (*F* values) for the selected microclimatic variables

	Thinning intensity (TI)	Type of canopy (C)	TI × C	Date (D)	TI × D	C × D	TI × C × D
meanT (°C)	0.88	7.85*	1.98	26628.61***	0.41	4.34***	0.46
minRH (%)	0.88	8.88*	0.86	665.74***	1.27***	1.39***	0.59
minSH (%)	14.23*	1.19	2.17	165.68***	0.88	1.32***	0.41
DL (no. hours)	0.01	64.65***	0.15	166.80***	0.77	28.87***	0.78
Th (mm)	1.93	18.26**	1.78	7620.45***	1.44***	13.00***	1.64***

Bold values indicate significant ($P < 0.05$) effects

TI thinning intensity, *C* type of canopy, *D* date, *meanT* mean air temperature, *minRH* minimum relative humidity, *minSH* minimum soil humidity, *DL* understory day length, *Th* throughfall

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

for all treatments excepting for T20P, whose maximum values were observed in mid November. The radial-increment rates showed two main peaks, one in late spring and the other in early autumn. The major peak occurred from April to the middle of June and was centred in mid May, whereas

the second and minor peak was observed from July to October, being centred in September (Fig. 3b).

The effects of the microclimatic variables on the radial-increment rates (RIr) and on the residuals of the cumulative radial increment versus Gompertz fitting (RI-G) were

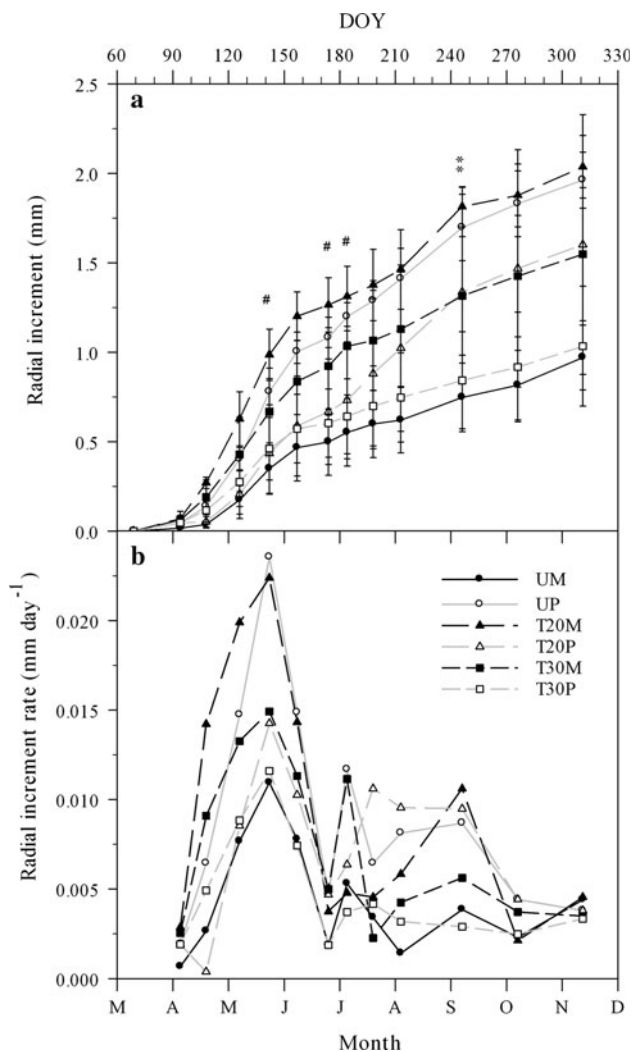


Fig. 3 Cumulative radial increment (a) and radial-increment rates (b) calculated from dendrometer data for the six treatments classified by type of canopy and thinning intensity (mean ± SE). *DOY* day of the year. Abbreviations of treatments are as in Fig. 1. Symbols above lines indicate dates when the interaction between thinning intensity and canopy type was significant or marginally significant. Significance levels: # $P < 0.1$, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

similar, although some differences were observed during the third period (Fig. 4). At the early growing season (March–May), both variables were positively influenced by meanT ($P < 0.01$ and $P < 0.001$ for RIr and RI-G, respectively) and DL ($P < 0.01$ and $P < 0.001$) and negatively by Th ($P < 0.001$). From June to July, RIr and RI-G were positively correlated with minRH ($P < 0.001$), minSH ($P < 0.001$) and Th ($P < 0.01$ and $P < 0.001$), and negatively with meanT ($P = 0.080$ and $P < 0.001$). Finally, at the late growing season from August to November, only RI-G showed significant relationships with the microclimatic variables. Thus, RI-G showed positive correlations ($P < 0.001$) with minRH, minSH and Th, and negative associations with meanT and DL.

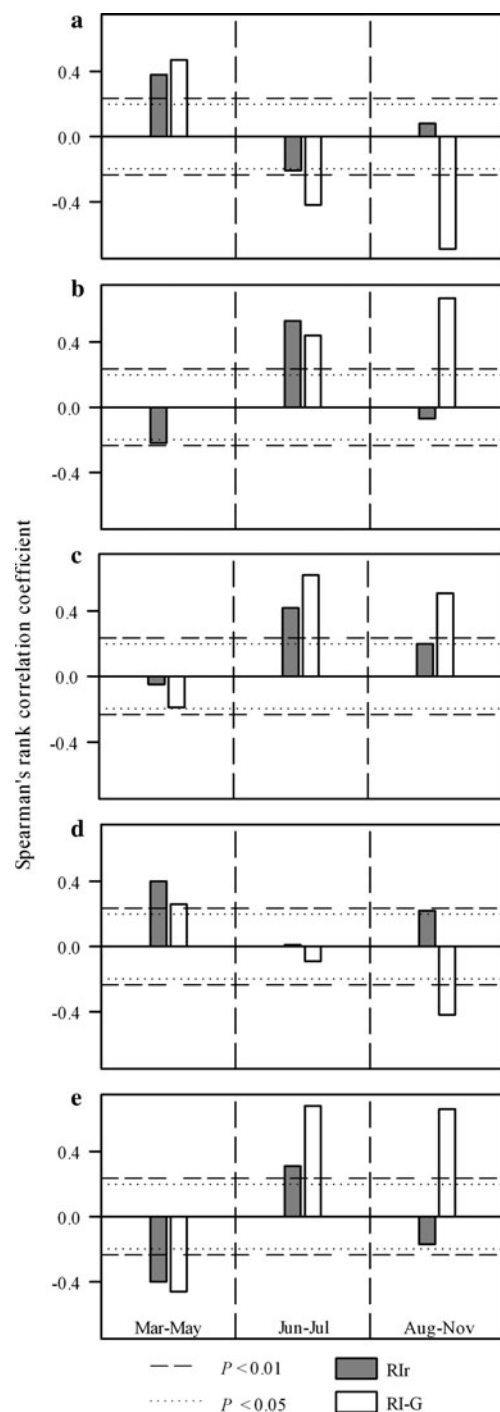


Fig. 4 Spearman's rank correlation coefficients calculated between selected microclimatic variables at 10-days lags and radial-increment rates (RIr) and the residuals of the fits of Gompertz functions to cumulative radial increment (RI-G) for three study periods: March–May, June–July and August–November. Microclimatic variables: mean air temperature (a), minimum relative humidity (b), minimum soil humidity (c), understorey day length (d) and throughfall (e). The statistical analysis was carried out on the whole data set. Significance levels: $P < 0.05$ (dotted line); $P < 0.01$ (dashed line)

Xylogenesis

The onset of tracheid formation in Scots pines occurred in March or April, and in May several rows of radially enlarging tracheids were detected. No additional latewood formation was observed in October when compared with September samples.

The number of mature latewood tracheids (LW) showed marginally significant differences ($P = 0.080$) among thinning intensities ($T20 > T30 = U$, Table 4). The interaction between thinning intensity and date had a significant effect on the number of mature tracheids ($P < 0.05$), as different effects of thinning intensity ($T20 > T30 = U$) were detected only for one date (DOY 246). Furthermore, the total number of tracheids was significantly affected by the

interaction between thinning intensity, canopy type and date ($P < 0.05$). A consistent temporal pattern was observed; Scots pines in pine canopy showed a higher number of total tracheids in unthinned plots, whereas in the thinned plots, no differences between canopy types were found. In summary, T20M and T20P plots showed the highest number of total tracheids, followed by T30P and UP and finally, by T30M and UM plots (Fig. 5). Significant differences were found for all types of tracheids according to their developmental phase as a function of date ($P < 0.001$). The number of cambial cells peaked between May and June, whereas radially enlarging tracheids reached maximum values in June. The cell-wall thickening phase of tracheids began in May and ended in October, reaching its maximum number in June–July. Mature tracheids were observed since early June.

Table 4 Split plot with a repeated measure ANOVA (F values) for the number and type of tracheids

Factor	No. cambial cells	No. radially enlarging tracheids	No. cell-wall thickening tracheids	No. mature earlywood tracheids	No. mature latewood tracheids	No. mature tracheids	No. total tracheids
Thinning intensity (TI)	1.518	2.176	0.032	0.560	5.009[#]	0.354	0.072
Type of Canopy (C)	0.842	0.675	0.830	0.346	0.356	0.271	0.021
TI × C	0.991	0.921	0.054	0.804	0.619	0.649	0.024
Date (D)	16.854***	87.494***	163.621***	453.733***		552.331***	311.401***
TI × D	0.297	0.538	0.338	1.931		2.865*	1.244
C × D	0.842	0.620	0.892	1.673		1.910	1.764
TI × C × D	0.278	0.696	1.364	1.512		1.372	2.703*

Bold values indicate significant ($P < 0.05$) effects

The factor *Date* was not included in the split-plot analyses for No. mature latewood tracheids as they were only detected on one sampling date
[#] $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

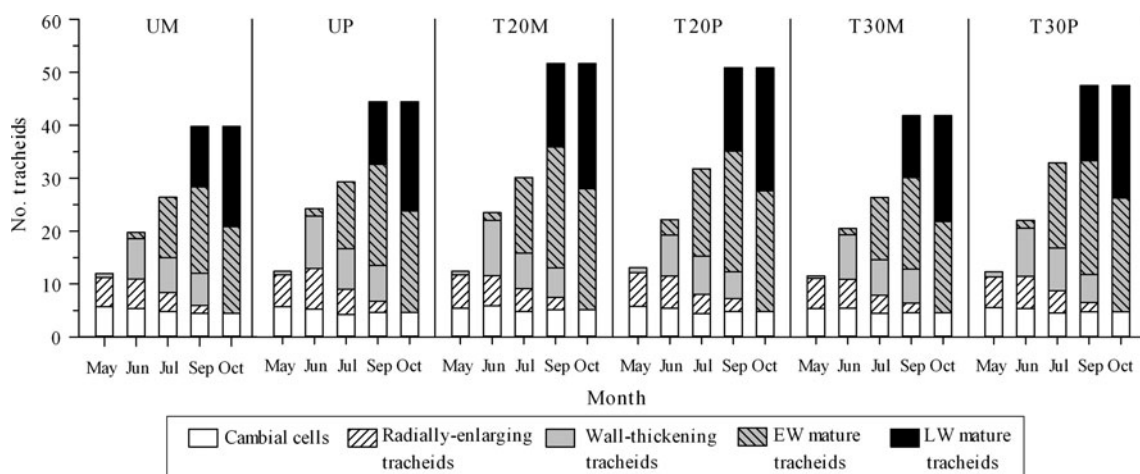


Fig. 5 Number of cambial cells, radially enlarging, cell-wall thickening and earlywood (EW) and latewood (LW) mature tracheids of Scots pine by treatment in the sampling months plus the final

number of EW and LW tracheids estimated for October. Abbreviations of treatments are as in Fig. 1

All types of cells except the production rate of mature tracheids (no. cells day⁻¹) showed positive correlations with minRH and Th, but their response to other variables was more diverse (Fig. 6). Thus, radially enlarging tracheids, which were the type of cells most influenced by the microclimatic variables, significantly decreased as meanT increased (in pine

and mixed canopies, PC and MC) and as minSH (PC and MC) and DL (MC) decreased. On the contrary, the production rate of mature tracheids increased as meanT increased (PC and MC), but minSH (PC and MC) and DL (MC) decreased. Finally, the production rate of tracheids was positively related with minRH for trees in U and T30 plots.

Fig. 6 Spearman's rank correlation coefficients calculated between microclimatic variables (10-days lag) and number of cambial cells (a), radially enlarging tracheids (b), cell-wall thickening tracheids (c) and production rate of mature tracheids (d) and total tracheids (e) of Scots pine ($n = 12$) for the different treatments. *meanT* mean air temperature, *minRH* minimum relative humidity, *minSH* minimum soil humidity, *DL* understorey day length, *Th* throughfall. Abbreviations of treatments are as in Fig. 2. Gray bars mixed beech–pine canopy, white bars pure pine canopy, empty bars unthinned plots, hatched bars thinned plots. Significance levels: $P < 0.05$ (dotted line); $P < 0.01$ (dashed line)

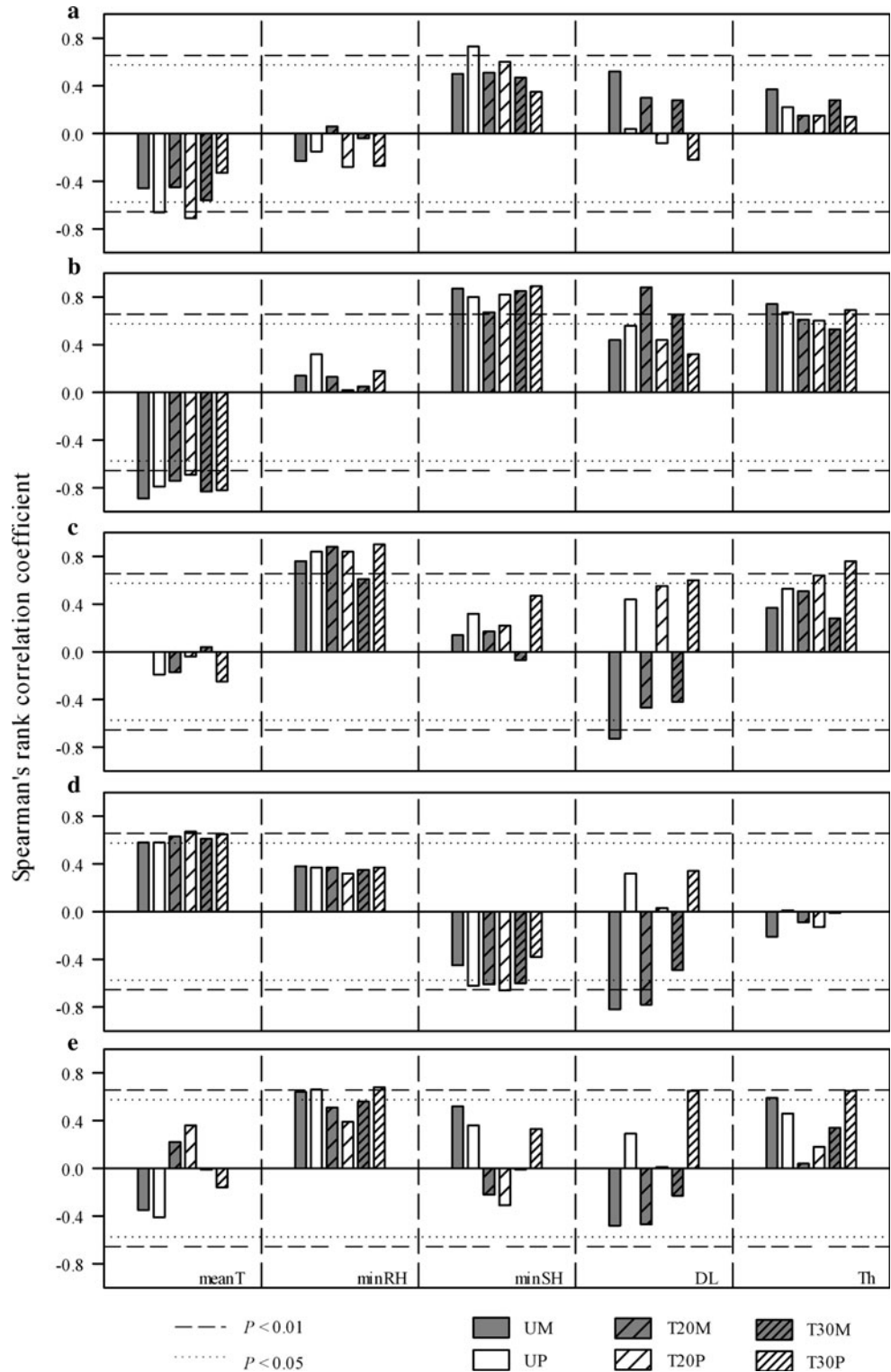
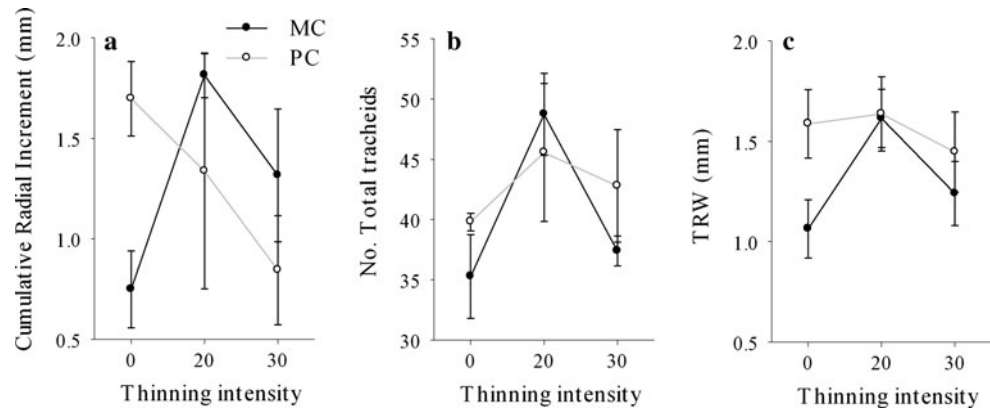


Fig. 7 Effects of the interaction between thinning intensity and canopy type on cumulative radial increment estimated from dendrometer data in DOY 246 (a), total number of tracheids in DOY 246 (b) and tree-ring width (TRW) measured on the microcores in DOY 311 (c). Mean \pm SE. MC mixed canopy, PC pine canopy. Lines don't imply continuous relationships



Thinning increased sensitivity of growth to climate (Fig. 6) in radially enlarging tracheids for understorey day length (MC), cell-wall thickening tracheids for throughfall (PC) and understorey day length (PC), and production rate of mature tracheids for mean air temperature (PC and MC). Conversely, thinning decreased sensitivity of growth to climate in cell-wall thickening tracheids for understorey day length (MC).

Relationships between radial-increment dynamics and xylogenesis

Dendrometers captured the main dynamics of radial increment since the radial-increment rates were significantly correlated with the number of radially enlarging tracheids ($r = 0.47$, $P = 0.058$; $r = 0.40$, $P = 0.021$ and $r = 0.70$, $P = 0.001$, for the first, second and third period, respectively). Moreover, the patterns of cumulative radial increment and number of total tracheids were generally similar for the common sampling dates of dendrometer and xylogenesis (DOY 184 and 246, Fig. 7).

Discussion

Effects of thinning and canopy type on inter-annual Scots pine growth

Pre-thinning Scots pine density was highly variable among plots, becoming similar between T20 and T30 plots after thinning. This may be one reason why only a weak and temporary (1 or 3 years based on BAI or TRW, respectively) effect of thinning on growth of dominant and codominant Scots pine trees was detected. Moreover, the thinning effect might have been disguised after the severe drought of 2005, when an abrupt decrease in BAI was observed. It apparently caused high tree mortality via auto-thinning of Scots pines in the unthinned plots, and to a lesser extent in T20 plots, resulting in more similar densities among thinning intensities (mean density reduction of 38 and 8 % and BA reduction of 13 and 2 % in U and T20 plots, respectively). This levelling off of

densities, particularly in pure patches, may be related to the fact that tree-growth recovery at the highest thinning intensity after the drought was not the fastest as expected, a pattern that is supported by several studies (Bréda et al. 1995; Gracia et al. 1999). Mäkinen and Isomäki (2004) attributed the lack of response or slight effect of thinning on growth of dominant trees found in several *P. sylvestris* studies to insufficient thinning intensity (i.e., light thinning). Therefore, our dominant trees might have had a stronger response than that for moderate thinning (i.e., 30 %) had the foresters carried out heavy thinning in our site. Moreover, thinning from below in other Scots pine stands in Spain appears to mainly favor the development of intermediate trees (Del Río et al. 2008).

Reduction in Scots pine growth in mixed patches as compared with pure ones appears to result from competition between Scots pine and beech. Indeed, lower increments of BAI and TRW under mixed than under pine canopy were observed for several years after thinning. The reduction in Scots pine radial growth may have been caused by an increase in competitive pressure by beech trees as they reached the upper canopy layers. Indeed, beech trees may have also benefited from thinning due to their efficiency in space occupation (Pretzsch 2005). Nevertheless, the reduction in tree growth in response to the type of canopy after thinning was more noticeable in the unthinned plots. Thus, thinning might have been able to counteract the increasing competitive effects of beech on Scots pine by reducing pine density. Accordingly, in 2008, although not significantly, tree-ring width was higher in pure than in mixed patches in unthinned plots, but no differences between canopy types were found in the thinned plots (Fig. 7). Indeed, similar responses were obtained after the second thinning carried out in 2009 in the study site in U and T20 plots (data not shown).

Long-term effects of thinning and canopy type on intra-annual microclimatic conditions

Higher soil humidity values were recorded in the unthinned than in the thinned plots, even though throughfall was higher in the thinned plots at high precipitation events.

These differences could be explained by a higher transpiration rate of the canopy in the thinned plots, as no significant differences in understorey day length or cover of the canopy and main understorey species (e.g., *Pteridium aquilinum* and *Rubus ulmifolius*, data not shown) were found as a function of thinning. The transpiration rate of individual trees increases after thinning as the wind speed within the stand raises, enhancing evaporation (Aussenac 2000). Nevertheless, transpiration may increase (Lagergren et al. 2008), decrease (Morikawa et al. 1986) or remain similar (Vesala et al. 2005) after thinning.

Soil humidity, throughfall and understorey day length were lower under mixed than under pine canopy in summer and fall, after the sprouting of beech leaves. Beech crown, contrarily to pine crown, involves multiple layers of leaves with higher leaf area than pine needles (Horn 1971). Transpiration rate has been directly related with leaf area index (LAI) until a threshold value (Granier et al. 2000). Thus, transpiration of mixed canopy may be higher than that of pine canopy, enhancing the differences of soil humidity between canopy types. This result is supported by the idea that the beech root system is highly plastic, allowing them to be highly competitive for water and nutrient resources (Curt and Prevosto 2003).

The differences in canopy cover structure plus the differences observed in stand characteristics (density, crown height) may be the reason why the triple interaction between thinning intensity, canopy type and date had a significant effect on daily throughfall. Thus, for several dates, throughfall was higher in pure patches in U and T30 plots, while no differences between canopy types occurred in T20 plots.

Effects of microclimate on the dynamics of radial increment and xylogenesis

Tracheid formation started between March and April, when mean daily air temperatures higher than 8 °C were achieved. However, the first positive radial-increment rates observed in mid-March, before the onset of tracheid formation, were probably due to stem water replenishment after winter dehydration (Zweifel et al. 2001). From March to May, radial-increment rates were positively influenced by mean air temperature. In agreement, earlier researches have suggested that in spring, radial growth and cambial activity are mainly controlled by temperature in temperate or boreal conifer forests since soil water availability is usually high (Brix and Mitchell 1980; Deslauriers and Morin 2005; Schmitt et al. 2004). Moreover, the radial increment was also enhanced by the understorey day length in this period, which also concurs with previous findings (Camarero et al. 2010; Rossi et al. 2006b). From June to July, the noticeable reduction in radial-increment rates coincided with a sharp

decrease in soil humidity. This reduction in radial increment may be a tree response to summer drought through stem shrinkage (Zweifel et al. 2001), but it might be also caused by a decline in the cambial activity, possibly constrained by water-deficit stress (Camarero et al. 1998; 2010). In fact, radial increment was positively influenced by soil humidity and throughfall, suggesting that tree water status may be the main constraining factor for radial increment during summer. The abrupt decline in soil moisture synchronized with high temperatures may be also linked to the beginning of latewood formation (Cregg et al. 1988; von Wilpert 1991), as our data suggest. In the study site, although water stress could have produced the cessation of tracheid production (Gruber et al. 2010; Oberhuber and Gruber 2010), we observed a noticeable second growing peak from July–August to October. Similar bimodal patterns are common for other conifers growing under continental Mediterranean conditions characterized by two mild and wet seasons in spring and autumn (Camarero et al. 2010). Nevertheless, unimodal xylogenesis of Scots pine has also been observed in more mesic sites in northern Spain (Camarero et al. 2010), suggesting that this may be a plastic feature of Scots pine.

The number of cambial cells and radially enlarging tracheids was enhanced by soil humidity and throughfall, which was in agreement with previous studies (Horacek et al. 1999; Rossi et al. 2006b). Moreover, the number of radially enlarging tracheids augmented when increasing the understorey day length, which reflects the annual pattern of above-crown day length. This enhanced cambial activity may be linked to the increasing production of carbohydrates and growth regulators in the crown (Larson 1994). The number of wall-thickening tracheids was mainly positively related to minimum relative humidity. This result was different from the one obtained by Antonova and Stasova (1993), who noted a positive relationship between the number of wall-thickening tracheids and temperature, and to the findings of Yasue et al. (2000) who found that cell-wall thickness is influenced positively by summer temperature. However, cell-wall thickening may also respond to water availability which would explain the relationship found with air humidity. For instance, in Norway spruces subjected to induced drought, cell-wall thickness of latewood tracheids increased in response to water deficit (Jyske et al. 2010). The production rate of matured tracheids was positively influenced by mean air temperature and negatively by minimum soil humidity. Such responses suggest the effect of a temperature threshold for tracheid maturation, probably related to colder conditions after summer. However, the temperature-constrained maturation phase in Scots pine supports the idea that air temperature positively influences lignin deposition in the cell walls (e.g., Antonova and Stasova 1993) and, therefore, tracheid maturation. Finally, the production rate of tracheids was mainly

enhanced by minimum relative humidity, highlighting that the main constraining factor for tracheid production in our study site was the tree water status.

Reducing tree competition by thinning has been shown to increase sensitivity of radial growth to temperature in *P. nigra* (Martín-Benito et al. 2010), while unthinned plots responded more to precipitation. In our study, the effects of thinning intensity on growth sensitivity to climate was observed for xylogenesis, but not for radial increment data, probably because the response of the latter was masked by changes in water status of the trees. Our results for the production rate of mature tracheids support the idea that the sensitivity of growth to temperature is higher at low competition levels. However, the responsiveness in the production of wall-thickening tracheids to precipitation was higher in thinned than in unthinned plots, which does not fully agree with the aforementioned studies. Indeed, enhanced soil humidity in our control plots may explain differences among studies. Furthermore, our study also shows that the type of canopy may modulate sensitivity responses to climate.

Effects of thinning and canopy type on intra-annual radial increment and xylogenesis

Thinning usually leads to higher rates of radial increment and/or tracheid number (Corcuera et al. 2006; Jaakkola et al. 2005; Linares et al. 2009; Mörling 2002) due to the modification of several factors, such as an increase in soil water and nutrients availability (Blanco et al. 2005), or the photosynthetic capacity of the canopy through the increment of the foliar mass of the crown (Aussenac 2000). However, the inexistence of significant increases in radial growth after thinning has also been recorded, particularly after light thinning from below or even after moderate thinning when light and water might be the limiting factors (Martín-Benito et al. 2010). Our results may have been disguised by several factors: (a) the stand structure was initially highly variable among plots; (b) the stronger thinning applied may have been insufficient; (c) the auto-thinning process occurred in the unthinned plots after a severe drought.

In our study, even 9 years after thinning, differences of radial increment were detected for the interaction between thinning intensity, canopy type and date. Thus, for those dates when significant differences for the interaction between thinning intensity and canopy type were found, a consistent higher radial increment in the pine canopy was observed in unthinned plots, while no differences between canopy types occurred in the thinned ones. This result coincides with the treatment effects on the total number of tracheids and the tree-ring width in 2008 (Fig. 7). Indeed, these effects remained from 2009 to 2011 in U and T20 plots (data not shown) after a second thinning

was carried out at the beginning of 2009. The disparities between the results obtained from dendrometer measurement and xylogenesis data could be explained by differences in tree water status or in tracheids diameter. Moreover, xylogenesis provides reliable estimates of radial growth and cambial dynamics, but only for localized points around the stem.

The aforementioned patterns were in accordance with those observed for tree water status, as this was the main constraining factor for Scots pine radial growth and xylogenesis. Furthermore, the observed trend for Scots pine growth among treatments coincided also with those for crown length and tree height of Scots pine (Table 2). Actually, tree growth has been associated with crown length (Assman 1970), crown area and tree height (Rathgeber et al. 2011). Furthermore, the response of Scots pine radial growth to the treatments seems to be also caused by small disparities in competition status of the trees (Table 2).

In Navarre, managed mixed Scots pine–beech forests with beech as secondary species have been lately described as forest sites with potential to produce higher quality of Scots pine wood than pure forests (G. Oyaregui, personal communication). If this is the case, the enhancement of a Scots pine–beech mixed forest would be desirable due to the benefits that mixed stands may provide, such as greater diversity, protection from disease, resistance to abiotic stress or stability to disturbances (Kelty 1992; Pretzsch 2005) among others.

Conclusions

Light and moderate thinning from below in our beech–Scots pine stand caused a weak and temporary effect on BAI and tree-ring width of dominant or codominant Scots pine trees. As beech developed and reached the upper canopy layers, a gradual reduction in Scots pine radial growth relative to pure patches was only observed in the unthinned plots. Nine years after thinning, growth rates and the number of tracheids produced by pines were higher under pure than under mixed canopy patches in the unthinned plots, but no differences between canopy types in the thinned plots were detected. Actually, in the study site, where Scots pine and beech are close to their south-western distributional limit in Europe, the tree water status was the main limiting factor for Scots pine radial growth and xylogenesis. Indeed, between-treatments differences in tree water status plus differences in competition status and tree size (height, crown length) explained the radial growth and xylogenesis patterns observed on Scots pine. Our results show how negative effects of beech on Scots pine growth may be mitigated by silviculture.

Acknowledgments We thank the GLOBIMED thematic network for making possible the collaboration between the ARAID-IPE and the “UPNA Ecology & Environment Research Group.” The “Departamento de Medio Ambiente” of the Government of Navarre for the experimental setting of silvicultural treatments and, in particular, Fernando Puertas, Carmen Traver and Ana Iriarte and the “Concejo” of Aspuz for permitting the access to the plots. The research has been carried out in the framework of the AGL2006-08288 project (“Ministerio de Economía y Competitividad” of the Spanish Government). I. Primicia was financially supported by the FPI program from the “Ministerio de Economía y Competitividad” of the Spanish Government and the European Social Fund (ESF). J. J. Camarero thanks the support of ARAID. We also thank the two anonymous reviewers for their comments.

References

- Andrew I (1986) Simple experimental design for forestry trials. FRI Bull, vol 71. Forest Research Institute, Roturua
- Antonova GF, Stasova VV (1993) Effects of environmental factors on wood formation in Scots pine stems. *Trees* 7(4):214–219
- Antonova GF, Shebeko VV, Maljutina ES (1983) Seasonal dynamics of cambial activity and tracheid differentiation in the stem of Scots pine. *Chem Wood* 1:16–22
- Assman E (1970) The principles of forest yield study. Pergamon Press, Oxford
- Aussenac G (2000) Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Ann For Sci* 57(3):287–301
- Blanco JA (2004) La práctica de las claras forestales y su influencia en el ciclo interno de nutrientes en dos bosques de pino silvestre de los Pirineos Navarros. Dissertation, Universidad Pública de Navarra, Pamplona
- Blanco JA, Zavala MA, Imbert JB, Castillo FJ (2005) Sustainability of forest management practices: evaluation through a simulation model of nutrient cycling. *For Ecol Manag* 213:209–228
- Bréda N, Granier A, Aussenac G (1995) Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus-petraea* (Matt) Liebl). *Tree Physiol* 15(5):295–306
- Brix H, Mitchell AK (1980) Effects of thinning and nitrogen fertilization on xylem development in Douglas-fir. *Can J For Res* 10(2):121–128
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Camarero JJ, Guerrero-Campo J, Gutiérrez E (1998) Tree-ring growth and structure of *Pinus uncinata* and *Pinus sylvestris* in the Central Spanish Pyrenees. *Arct Alp Res* 30(1):1–10
- Camarero JJ, Olano JM, Perras A (2010) Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. *New Phytol* 185(2):471–480
- Cescatti A, Piutti E (1998) Silvicultural alternatives, competition regime and sensitivity to climate in a European beech forest. *For Ecol Manag* 102:213–223
- Corcuera L, Camarero JJ, Sisó S, Gil-Pelegrín E (2006) Radial-growth and wood-anatomical changes in overaged *Quercus pyrenaica* coppice stands: functional responses in a new Mediterranean landscape. *Trees* 20(1):91–98
- Cregg BM, Dougherty PM, Hennessey TC (1988) Growth and wood quality of young loblolly-pine trees in relation to stand density and climatic factors. *Can J For Res* 18(7):851–858
- Curt T, Prevosto B (2003) Rooting strategy of naturally regenerated beech in Silver birch and Scots pine woodlands. *Plant Soil* 255(1): 265–279
- Daniels RF, Burkhart HE, Clason TR (1986) A comparison of competition measures for predicting growth of loblolly-pine trees. *Can J For Res* 16(6):1230–1237
- Del Río M, Calma R, Cañellas I, Roig D, Montero G (2008) Thinning intensity and growth response in SW-European Scots pine stands. *Ann For Sci* 3:308–318
- Denne MP (1989) Definition of latewood according to Mork (1928). *IAWA Bull* 10(1):59–62
- Deslauriers A, Morin H (2005) Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables. *Trees* 19(4):402–408
- Deslauriers A, Rossi S, Anfodillo T, Saracino A (2008) Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. *Tree Physiol* 28(6):863–871
- Government of Navarre (2010) Memoria del Mapa de Cultivos y Aprovechamientos de Navarra 1/200.000. Departamento de Agricultura, Ganadería y Alimentación del Gobierno de Navarra, Pamplona
- Gracia CA, Sabaté S, Martínez JM, Alveza E (1999) Functional responses to thinning. In: Rodà F, Retana J, Gracia CA, Bellot J (eds) Ecology of Mediterranean evergreen forests. Springer, Berlin, pp 328–329
- Granier A, Loustau D, Bréda N (2000) A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index. *Ann For Sci* 57(8):755–765
- Gruber A, Baumgartner D, Zimmermann J, Oberhuber W (2009) Temporal dynamic of wood formation in *Pinus cembra* along the alpine treeline ecotone and the effect of climate variables. *Trees* 23(3):623–635
- Gruber A, Stöbl S, Veit B, Oberhuber W (2010) Impact of drought on the temporal dynamics of wood formation in *Pinus sylvestris*. *Tree Physiol* 30(4):490–501
- Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree Ring Bull* 43:68–78
- Horacek P, Slezingerova J, Gandelova L (1999) Effects of environment on the xylogenesis of Norway Spruce (*Picea abies* (L.) Kartst.). In: Wimmer R, Vetter RE (eds) Tree-ring analysis: biological, methodological and environmental aspects. CAB International Publishing, New York, pp 33–54
- Horn HS (1971) The adaptive geometry of trees, Monographs in population biology, vol 3. Princeton University Press, Princeton
- Jaakkola T, Mäkinen H, Sarén MP, Saranpää P (2005) Does thinning intensity affect the tracheid dimensions of Norway spruce? *Can J For Res* 35(11):2685–2697
- Jyske T, Hölttä T, Mäkinen H, Nöjd P, Lumme I, Spiecker H (2010) The effect of artificially induced drought on radial increment and wood properties of Norway spruce. *Tree Physiol* 30(1):103–115
- Kelty MJ (1992) Comparative productivity of monocultures and mixed-species stands. In: Kelty MJ, Larson BC, Oliver CD (eds) The ecology and silviculture of mixed-species forests. Kluwer, Dordrecht, pp 125–141
- Lagergren F, Lankreijer H, Kucera J, Cienciala E, Molder M, Lindroth A (2008) Thinning effects on pine-spruce forest transpiration in central Sweden. *For Ecol Manag* 255(7) 2312–2323
- Larson PR (1994) The vascular cambium, development and structure. Springer, Berlin
- Linares JC, Camarero JJ, Carreira JA (2009) Plastic responses of *Abies pinsapo* xylogenesis to drought and competition. *Tree Physiol* 29(12):1525–1536
- Ma SY, Concilio A, Oakley B, North M, Chen JQ (2010) Spatial variability in microclimate in a mixed-conifer forest before and after thinning and burning treatments. *For Ecol Manag* 259(5):904–915

- Mäkinen H, Isomäki A (2004) Thinning intensity and growth of Scots pine stands in Finland. For Ecol Manag 201:311–325
- Mäkinen H, Seo JW, Nöjd P, Schmitt U, Jalkanen R (2008) Seasonal dynamics of wood formation: a comparison between pinning, microcoring and dendrometer measurements. Eur J For Res 127(3): 235–245
- Martín-Benito D, Del Río M, Heinrich I, Helle G, Cañellas I (2010) Response of climate-growth relationships and water use efficiency to thinning in a *Pinus nigra* afforestation. For Ecol Manag 259(5):967–975
- Morikawa Y, Hattori S, Kiyono Y (1986) Transpiration of a 31-year-old *Chamaecyparis obtusa* Endl. stand before and after thinning. Tree Physiol 2(1–3):105–114
- Mörling T (2002) Evaluation of annual ring width and ring density development following fertilisation and thinning of Scots pine. Ann For Sci 59(1):29–40
- Oberhuber W, Gruber A (2010) Climatic influences on intra-annual stem radial increment of *Pinus sylvestris* (L.) exposed to drought. Trees 24(5):887–898
- Oliker CD, Larson BC (1990) Forest stand dynamics. McGraw-Hill, Inc., New York
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Statistics and Computing Series. Springer, New York
- Piutti E, Cescatti A (1997) A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Can J Bot 75:277–284
- Pretzsch H (2005) Diversity and productivity in forests: evidence from long-term experimental plots. In: Scherer-Lorenzen M, Körner C, Schulze ED (eds) Forest diversity and function: temperate and boreal systems, ecological studies-analysis and synthesis, vol 176. Springer, Berlin, pp 41–64
- Puertas F (2001) Sitios de ensayo de claras de masas de pino silvestre en Navarra, Garde y Aspuz., Pamplona, Navarra, Spain
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, 2.13.0 edn. R Development Core Team, Vienna
- Rambo TR, North MP (2009) Canopy microclimate response to pattern and density of thinning in a Sierra Nevada forest. For Ecol Manag 257:435–442
- Rathgeber CBK, Rossi S, Bontemps J-D (2011) Cambial activity related to tree size in a mature silver-fir plantation. Ann Bot 108(3):429–438
- Rossi S, Anfodillo T, Menardi R (2006a) Trephor: a new tool for sampling microcores from tree stems. IAWA J 27(1):89–97
- Rossi S, Deslauriers A, Anfodillo T, Morin H, Saracino A, Motta R, Borghetti M (2006b) Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytol 170(2):301–310
- Schmitt U, Jalkanen R, Eckstein D (2004) Cambium dynamics of *Pinus sylvestris* and *Betula* spp. in the northern boreal forest in Finland. Silva Fennica 38(2):167–178
- Spiecker H (2003) Silvicultural management in maintaining biodiversity and resistance of forests in Europe-temperate zone. J Environ Manage 67(1):55–65
- Vaganov EA, Hughes MK, Shaskin AV (2006) Growth dynamics of conifer tree rings: images of past and future environments. Springer, Berlin
- Vesala T, Suni T, Rannik U, Keronen P, Markkanen T, Sevanto S, Gronholm T, Smolander S, Kulmala M, Ilvesniemi H, Ojansuu R, Uotila A, Levula J, Makela A, Pumpanen J, Kolari P, Kulmala L, Altimir N, Berninger F, Nikinmaa E, Hari P (2005) Effect of thinning on surface fluxes in a boreal forest. Glob Biogeochem Cycles 19, GB2001(2)
- von Ende CN (2001) Repeated-measures analysis: growth and other time dependent measures. In: Scheiner S, Gurevitch I (eds) The design and analysis of ecological experiments. Oxford University Press, New York, pp 134–157
- von Wilpert K (1991) Intraannual variation of radial tracheid diameters as monitor of site specific water stress. Dendrochronol 9:95–113
- Yasue K, Funada R, Kobayashi O, Ohtani J (2000) The effects of tracheid dimensions on variations in maximum density of *Picea glehnii* and relationships to climatic factors. Trees 14(4):223–229
- Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York
- Zweifel R, Item H, Hasler R (2001) Link between diurnal stem radius changes and tree water relations. Tree Physiol 21(12–13):869–877