

Temporal interactions among throughfall, type of canopy and thinning drive radial growth in an Iberian mixed pine-beech forest

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ABSTRACT

Many factors can influence tree growth over time such as different forest management practices, climate or tree-to-tree interactions, especially in mixed forests. We show in this work how the temporal growth patterns for Scots pine and European beech depend on thinning intensity (0%, 20% and 40% extraction of basal area), canopy type (pine-beech vs. pine patches), throughfall and their interactions. To fulfill this objective we monitored radial growth of both species using band dendrometers during a 6-year long period including two very dry years. Temporal growth patterns differed between both species. Whereas Scots pine showed two main peaks of growth in May–June and October, European beech mainly grew from May to early September even when throughfall was very limited. Effects of thinning on growth generally increased for both species during dry periods both at the seasonal and annual scales. The treatment with 20% of thinning intensity was the most effective at the annual scale for enhancing growth of both species. However, increases in growth due to thinning were much higher in beech than in pine and lasted longer. Thinning effects on pine were higher in mixed canopy than in pure canopy and appeared to be modulated by throughfall. Global differences in pine growth between canopy types as a function of throughfall increased during the main growing season as beech canopy developed. Growth of Scots pine, but not that of European beech, generally increased with throughfall which suggests that pine might be more dependent for its growth on water from the soil surface layer while beech would depend more on water from deeper soil layers. Our findings have implications to select the most convenient thinning treatments and canopy type under a potential climate change scenario characterized by warmer conditions, more severe droughts and less throughfall.

1. Introduction

Forest researchers and managers consider that a conversion of pure coniferous forests into a mixed conifer-hardwood forest, is greatly meaningful from an ecological and economic point of view (Knoke et al., 2005; Spiecker, 2003). Mixed conifer-hardwood woodlands may provide multiple benefits such as higher biodiversity, protection from disease or stability (resilience) to disturbances including climate extremes as droughts (Knoke et al., 2005; Pretzsch et al., 2015a). Additionally, mixed forests may increase stand productivity when inter-specific processes are not dominated by competition (Kelty, 1992). Nevertheless, empirical data on these topics is often nonexistent in mixed conifer-hardwood forests (Forrester and Tang, 2016), particularly long-term data are needed to elucidate mechanisms underlying observed patterns.

The growth dynamics in mixed conifer-hardwood forests are often difficult to predict due to a high number of interactions among

coexisting tree species as well as to the fact that resource availability and climatic conditions change temporally and from site to site (Forrester and Tang, 2016). Although many studies have been carried out on the growth of Scots pine (*Pinus sylvestris* L.) or European beech (*Fagus sylvatica* L.) forests (Camarero et al., 1998; Jeřík et al., 2011), relatively few scientific literature is available about inter-specific processes in mixed Scots pine and European beech forests (but see Pretzsch et al., 2015a, Pretzsch et al., 2016 and references therein). This is one of the most widespread and economically relevant mixed forest type in Europe (Pretzsch et al., 2015b), with a high ecological amplitude spanning from mesic conditions in central Europe up to drought-prone conditions in sub-Mediterranean sites (del Río et al., 2014; Primicia et al., 2016, Primicia et al., 2013). A more severe drought stress due to warmer conditions, higher evapotranspiration rates and more frequent heat waves (Cardil et al., 2014) are one of the major climatic concerns negatively impacting forest productivity and vitality, particularly in the Mediterranean Basin (Camarero et al., 2015). Indeed, temperature and

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water availability during the summer are the main climatic drivers of Scots pine (Martínez-Vilalta et al., 2008; Sánchez-Salguero et al., 2015) and European beech (Rozas et al., 2015) long-term growth in Mediterranean populations. In this respect, ongoing long-term increases in drought frequency and intensity in the Iberian Peninsula (Andreu et al., 2007; Candel-Pérez et al., 2012) are reducing the productivity and increasing the incidence of canopy dieback and mortality in Scots pine (Camarero et al., 2015; Gea-Izquierdo et al., 2014; Martínez-Vilalta and Piñol, 2002). In NE Spain increased summer drought stress is impacting negatively on Scots pine growth, although so far the magnitude of such punctual growth declines is not enough to counteract the overall increase of growth during the 20th century (Martínez-Vilalta et al., 2008). In this region, summer drought increase has even caused an upward shift (Peñuelas and Boada, 2003) and a dramatic growth decline of beech over the last half-century (Jump et al., 2006). However, the beech populations are expanding across the mostly humid and temperate areas of NW Spain, particularly in lowlands, and stand growth is expected to show similar positive trends (Sánchez de Dios et al., 2016).

Drought-stress release of beech may be enhanced in mixed forests or stands relative to pure ones (Mölder and Leuschner, 2014). However, mixing may not fully compensate for lower field capacities or frequent lack of precipitation as shown by Metz et al. (2016) when beech was admixed with Scots pine. Furthermore, mixing of Scots pine and European beech may result in a reduction of throughfall (Primicia et al., 2013) affecting tree growth negatively. Another strategy for minimizing forest drought vulnerability in temperate forests (D'Amato et al., 2013; Elkin et al., 2015; Sohn et al., 2016a) and also in drought-prone Mediterranean forests (Martín-Benito et al., 2010) is thinning. Thinning has been recommended as a short-term solution to reduce drought vulnerability by increasing resilience in mixed forests, albeit the initial enhancement of resilience may be reversed as stands mature and bigger trees increase water demand (D'Amato et al., 2013). Heavy thinning has been shown to improve resistance and particularly resilience of Scots pine to drought events in Germany, but these benefits diminish with time since the last intervention (Sohn et al., 2016a). In this case, progressive decreases in growth recovery apparently resulted from decreased throughfall and increased transpiration rather than from tree ageing. With regard to beech, thinning can increase its growth during wet and also in dry years (Diaconu et al., 2015; van der Maaten, 2013) but also affect growth negatively during dry periods by reducing soil water availability layer (Geßler et al., 2004). Sohn et al., (2016a) suggested that long-lasting effects on growth recovery are related to relatively larger leaf area and fine-root biomass in thinned mixed stands. Consequently, they predicted that European beech would recover faster from drought than Scots pine given its faster expansion of crown and root systems. However, to our knowledge no single study has dealt with the relationship between thinning intensity and growth response to drought in mixed pine-beech forests. This is important because synergies between pine and beech may result in different growth responses to thinning and drought relative to monospecific stands. Furthermore, growth responses to thinning are typically studied at an annual scale, but studying seasonal scales (Aldea et al., 2017; Primicia et al., 2013) may be important to elucidate the mechanisms implied and the long-term effects on growth. For instance, temporal patterns of rainfall and leaf phenology may interact and modulate the effects of thinning on tree growth.

In this work we analyse whether temporal interactions among throughfall, canopy type and thinning affected radial growth of Scots pine and European beech during a 6-year long period (2009–2014) which included two very dry years. The research site, Aspuz, is a thinned pine-beech forest located in the western Spanish Pyrenees, close to the southern European limit of Scots pine and European beech. Previous research has shown that throughfall is the most important growth limiting factor for Scots pines at this site (Primicia et al., 2013). Aspuz can be considered as a transitional site between the Eurosiberian and Mediterranean regions, respectively characterized by cool-wet and

warm-dry climate conditions, in which since 1920 mean annual temperatures have risen $+0.020\text{ }^{\circ}\text{C year}^{-1}$ and water surplus has significantly decreased (González de Andrés et al., 2017).

Linear mixed models are a valuable statistical tool for describing and predicting the radial-growth patterns in relation to different factors such as thinning and canopy type in mixed forests (Pretzsch et al., 2015a). Therefore, these models were used in this study in order to fulfill the following objectives: (1) To compare intra-annual and inter-annual basal-area growth patterns of Scots pine and European beech in a mixed forest; (2) To evaluate the effects of canopy type and thinning on Scots pine basal-area growth dynamics, and of thinning on basal area growth dynamics of European beech; and (3) To assess the effects of throughfall and its interactions with other factors (i.e., month, year, type of canopy and thinning) or combinations of these factors on basal-area growth dynamics of Scots pine and European beech.

2. Methods

2.1. Study area

The study area is located in Aspuz ($42^{\circ}42'31''\text{N}$, $1^{\circ}08'40''\text{W}$), a forest situated in the western Spanish Pyrenees, Navarre. Plots are North-oriented, located at a mean altitude of 642 m, a mean slope of 7% and on a soil classified as Haplic Alisol (Blanco, 2004). The climate is considered as a cold wet Mediterranean type with water deficit usually in July and August with frequent frosts from winter to early spring. In the 1984–2014 period, mean annual precipitation was 921 mm and mean annual temperature $12.0\text{ }^{\circ}\text{C}$ (data from Navascués weather station located at 2.7 km from the plots, $42^{\circ}43'06''\text{N}$, $1^{\circ}06'55''\text{W}$, 615 m). The forest is an even-aged mixed stand dominated by *Pinus sylvestris* L. (Scots pine), naturally regenerated in the mid-1960s after strip-like clear-cutting, with a mean dominant tree height of 20.4 m in 2014, being one of the most productive Scots pine forests in Spain (Primicia et al., 2016). *Fagus sylvatica* L. (European beech) is the second most abundant tree species, with a mean crown cover of ca. 38% and mean age of 35–40 years. Most beech trees were codominant or dominant, although they covered all strata from suppressed to dominant ones.

2.2. Experimental design

A complete randomized block design (Andrew, 1986) was used in this study, including nine plots ($30\text{ m} \times 40\text{ m}$) installed by the Servicio Forestal del Gobierno de Navarra. The experimental design can be thus specified as a split-plot (von Ende, 2001). Three different thinning intensities (3 thinning intensities with 3 replicates) were applied in November 1999 (0%, 20% and 30% basal area removed) and March 2009 (0%, 20% and 40%) in the plots and in a buffer zone of 5–10 m around them. The first thinning was carried out removing mainly suppressed or intermediate trees, and some dominant or codominant trees with malformed stems. However, during the second thinning, mainly subdominant or dominant trees were removed. The highest thinning intensity was increased up to the 40% of the basal area during the second thinning in accordance to the silvicultural trends applied on similar surrounding stands at that moment. Similarly, following the silvicultural guidelines applied in Navarre on mixed stands with beech as secondary species, only Scots pine trees were thinned.

Within each plot, two discontinuous subplots can be distinguished: mixed beech-pine and pure pine subplots (hereafter abbreviated as MC and PC sub-plots). To establish the subplots, first we divided each plot into $300\text{ }2\text{ m} \times 2\text{ m}$ quadrats by using banderoles. Then, we delimited the projection on the ground of beech canopy taller than 2 m by using plastic bands. Lastly we used plot maps with georeferenced trees and a grid of $2\text{ m} \times 2\text{ m}$ quadrats to draw the contours of each type of subplot. In each plot, we randomly selected three Scots pines in PC sub-plots, three Scots Pines and three beeches in MC subplots. Only dominant or codominant trees were selected. Six treatments are thus determined for

pinus (P) and three for beeches (B): BMT0 (beeches in unmanaged mixed beech-pine), PMT0 (pinus in unmanaged mixed beech-pine), PPT0 (pinus in unmanaged pure pine), BMT20 (beeches in mixed beech-pine in moderate thinning), PMT20 (pinus in mixed beech-pine in moderate thinning), PPT20 (pinus in pure pine in moderate thinning), BMT40 (beeches in mixed beech-pine in severe thinning), PMT40 (pinus in mixed beech-pine in severe thinning) and PPT40 (pinus in pure pine in severe thinning).

2.2.1. Seasonal dynamics of radial increment

In total, 54 Scots pine trees (6 per plot) and 27 beeches (3 per plot) were selected to assess seasonal patterns of radial increments considering thinning intensities, canopy type, throughfall, month, year and their interactions. Band manual dendrometers (DB20 Environmental Measuring Systems, Brno, Czech Republic) were placed at about 1.3 m height around the stem after removing carefully the rhytidome (dead bark) to quantify cumulative radial growth. We read them from March 2009 to November 2014 with a biweekly frequency from March to June, when most growth occurs in the study species (Camarero et al., 2010) and monthly from July to November. To avoid biases during recording, all measures were always taken before midday, and they were never taken after a rainy day. Finally, the cumulative radial growth data was converted to basal area increment assuming a circular shape of the stems. These data were subtracted from the previous data measured and the result divided by the days elapsed between measurements to calculate growth rates as daily basal-area increment (hereafter BAIR, in $\text{cm}^2 \text{day}^{-1}$).

2.3. Throughfall

We measured throughfall monthly using 54 collectors placed in the plots (3 per subplot) in mixed and pure areas. Each collector consisted of a plastic funnel (diameter 23.5 cm) mounted onto a 25 L opaque polyethylene collection container. A filter of fiber-glass coated with polyethylene (1.5 mm mesh size) was placed into the neck of the funnel to avoid the entrance of coarse debris. Throughfall data were regressed with monthly precipitation data obtained from the nearby Navascués station in the nine plots considering mixed and pure patches within each plot (18 regressions) to estimate daily throughfall in each container ($r^2 = 0.88\text{--}0.99$, $p < 0.001$).

2.4. Xylogenesis

The cambium generates tracheids passing through different developmental stages. The xylem differentiation process is called xylogenesis and can be studied by repeatedly taking and observing wood samples (Fukuda, 1996). Two dominant or codominant Scots pines ($n = 18$) and one European beech per plot ($n = 9$) were randomly selected for this purpose. Xylogenesis was monthly monitored from April to December 2011 by sampling wood microcores (2 mm in diameter, 1–2 cm in length) at a height of 1.3 m following a spiral around the stem using a Trephor borer (Rossi et al., 2006). Microcores were always collected in areas apart from dendrometers to avoid distorting dendrometer records. The methods of processing, sectioning and staining micro-core wood sections are described with more detail elsewhere (Antonova et al., 1983; Primicia et al., 2013). For both species, we measured the intra-annual radial growth in wood microcores. Microcore data were used to validate the dendrometer recordings and to justify its use for representing radial growth and not swelling-shrinking dynamics of the trunk (Sheil, 2003). Lastly, correlations between radial-increment measurements taken by dendrometers and those obtained from microcores were calculated to justify the accuracy and reliability of the growth measurements recorded by dendrometers.

2.5. Statistical analyses

All models and the statistical analyses were carried out using R 3.2.4 (R core development team, 2017). Linear mixed-effects models were used to assess the effects of type of canopy (pure pine, mixed beech-pine), thinning intensity (0%, 20%, 40%), throughfall (continuous variable), month (April–October), year (2009–2014) and their interactions on Scots pine and beech growth (BAIR) using the “nlme” package (Pinheiro and Bates, 2000), following a split-plot design with repeated measures. Thinning intensity, canopy type, throughfall, month and year were included in the model as fixed effects, and tree nested in plot, as random effect. Additionally, we included an autoregressive correlation structure of first order to account for the repeated measures on the same tree, and a variance structure, if the residual spread differed per month (Pinheiro and Bates, 2000). Thus, the proposed model was stated as follows:

$$\text{BAIR} = I + \text{thinning} * \text{canopy} * \text{throughfall} + \text{month} + \text{year} + \text{tree:} \\ \text{plot} + \text{corAR}(\text{tree:plot}) + \text{varIdent}(\text{month}) \quad (1)$$

where: BAIR represents the daily basal area increment measured with dendrometers; I is the intercept; thinning, canopy and throughfall represent the study treatments; month and year are the sampled month and year for which BAIR has been estimated; tree:plot, a random term specifying the effect of individual trees nested within each plot; corAR (tree:plot), the autoregressive correlation structure to account for the repeated measures on each tree within each plot; varIdent (month), variance structure to account for the different spread of residuals per month. Throughfall was included in the model as a continuous variable considering the sum of 10 days before each dendrometer sampling date to take into account potentially lagged climate-growth responses (Camarero et al., 1998; Primicia et al., 2013).

We compared nested models with and without the random and the correlation and variance structures to analyse their appropriateness calculating the likelihood ratio test using the restricted maximum likelihood estimation procedure. Similarly, the significance of the fixed effects was determined by comparing nested models with and without the fixed terms, but using the maximum likelihood estimation procedure (Zuur et al., 2009). When interpretable, significant three- and two-way interactions were described. If there was no evidence for dependence between factors, main factors were analyzed (Underwood, 1997).

Throughfall intervals were delimited in the graphs in order to highlight the growth patterns, to show significant differences in growth between different levels of thinning, canopy type or month for each throughfall interval by using Helmert contrasts (Chambers and Hastie, 1992), and to describe the results more clearly. Five throughfall intervals ([0–10], [10–20], [20–40], [40–80], > 80 mm) were selected by using histograms to provide the most uniform distribution of measurements.

3. Results

3.1. Relationships between radial-increment dynamics and xylogenesis

Similar values of radial increment for Scots pine and European beech were recorded using dendrometers and xylogenesis during 2011 as shown in Fig. 1. Measurements between the two methods were highly correlated ($r = 0.905$ for Scots pines and $r = 0.951$ for European beeches). Therefore, measurements of radial growth based on dendrometers allow interpreting and discussing adequately the results of this work.

3.2. Annual and seasonal trends of tree growth

Month and year significantly influenced BAIR in both Scots pine and European beech (Table 1, $p < 0.001$). Intra-annual growth patterns

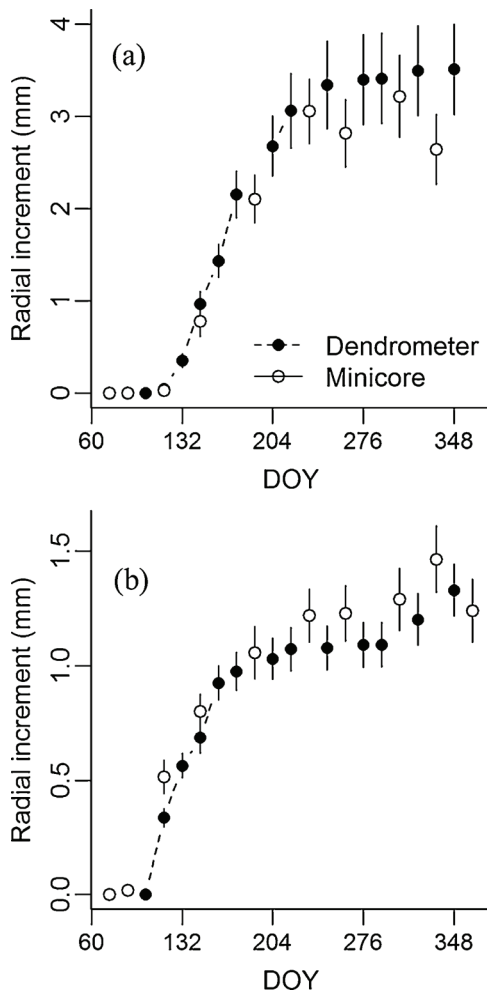


Fig. 1. Cumulative radial increment for European beech (a) and Scots pine (b) from April to December in 2011 using micro-cores and band dendrometers. DOY stands for day of the year.

Table 1
Likelihood ratio test (LRT) and significance of treatments (thinning intensity, canopy type, throughfall, month and year) on daily basal area increments of Scots pine and European beech considering the 2009–2014 period. Bold LRT values indicate significant effects ($P < 0.05$).

Variable	Scots pine		European beech	
	LRT	P value	LRT	P value
Thinning (TH)	1.837	0.39	5.599	0.061
Canopy type (C)	4.056	0.044	Not applicable	Not applicable
Throughfall (T)	860.829	< 0.001	69.709	< 0.001
Month (M)	1406.414	< 0.001	983.442	< 0.001
Year (Y)	139.301	< 0.001	99.588	< 0.001
TH*C	1.651	0.43	Not applicable	Not applicable
TH*T	6.707	0.034	1.989	0.370
TH*M	33.283	0.006	134.203	< 0.001
TH*Y	25.383	0.005	10.16	0.426
C*T	2.552	0.11	Not applicable	Not applicable
C*M	19.864	0.011	Not applicable	Not applicable
C*Y	8.561	0.13	Not applicable	Not applicable
T*M	188.626	< 0.001	7.135	0.309
T*Y	120.568	< 0.001	32.464	< 0.001
TH*C*T	6.059	0.041	Not applicable	Not applicable
TH*C*M	10.851	0.82	Not applicable	Not applicable
TH*C*Y	10.160	0.43	Not applicable	Not applicable
TH*T*M	6.152	0.046	8.179	0.771
TH*T*Y	73.419	< 0.001	2.697	0.987
C*T*M	18.659	0.017	Not applicable	Not applicable
C*T*Y	9.715	0.084	Not applicable	Not applicable

differed between both species (Fig. 2). BAIR in Scots pine showed two main peaks in the year, a major peak in late spring from the beginning of May (Day of the Year, DOY 105) to the middle of July (DOY 192), centered in mid May and June, and the other in early autumn (October, specifically from DOY 285 to 303). However, the temporal growth pattern was different for European beeches with a peak from late spring (DOY 130) to late summer (DOY 255) from May to early September, centered in June and July (Fig. 2), being throughfall very limited in the latter. The highest growth rates were observed in late May and late June in the case of Scots pine ($2.4 \text{ cm}^2 \text{ day}^{-1}$) and European beech ($7.0 \text{ cm}^2 \text{ day}^{-1}$), respectively. The growing period during the six study years took around 105 days considering the two main peaks for Scots pines and 125 days for European beech. In 2011, the onset of xylogenesis was 60–90 and 122–152 DOY, and the cessation occurred in 270 and 276 DOY for Scots pine and European beech, respectively.

3.3. Type of canopy and thinning

A significant interaction ($p = 0.011$) between type of canopy and month was found for Scots pine (Table 1). Thus, except for August, BAIR in Scots pines was significantly higher in pure patches during the months when most growth occurred (May to July and October) but no significant differences between pure and mixed patches were found at low BAIR values (i.e., April and September) (Fig. 3a). On an annual basis, BAIR in pure pine patches was on the average 22.1% (range 17.3–28.2%) higher than in mixed pine-beech patches, being these differences significant ($P < 0.05$) for all years excepting 2012 (Fig. 3b).

Thinning interacted significantly with month and year in Scots pine and with month in European beech (Table 1, Fig. 4). Thinning effects on Scots pine were only significant ($P < 0.01$) in May (Fig. 4a) but for European beech significant differences ($P < 0.01$) were observed from May to September (Fig. 4c). In Scots pine, growth differences in moderately (20% of removed basal area) and severely (40% of removed basal area) thinned plots relative to unthinned plots diminished from almost 50% in April to about 10% in June. Then, in July and August differences remained at 10% for moderate thinning but increased to 25–30% in severe thinning (Fig. 4a). In contrast, beech differences relative to unthinned plots were almost constant from May to September (around 40%) in severe thinning, being the effects of moderate thinning much higher especially from June (80%) to August (120%) (Fig. 4c). On an annual basis, significant differences for pine occurred only in 2011 ($P < 0.001$) and for beech from 2009 to 2012 ($P < 0.001$), and in 2013 ($p < 0.01$) and 2014 ($P < 0.05$) (Fig. 4b,d). Growth of pine in thinned plots relative to that of unthinned plots showed a unique positive peak in 2011 for both moderate (58%) and severe thinning (40%); by 2014, five years after thinning, the effect diminished until 20% and –5% under severe and moderate thinning, respectively (Fig. 4b). In contrast, beech exhibited a progressive growth increase under moderate thinning from 2009 (83%) until 2012 (123%), to decrease afterwards to a minimum in 2014 (60%); under severe thinning relative growth increased from 20% in 2009 to a plateau from 2010 to 2012 (around 48%) decreasing subsequently to 24% in 2014 (Fig. 4d).

3.4. Throughfall influences tree growth dynamics

Throughfall significantly influenced BAIR in both Scots pine and European beech and it was included in most of the significant interactions with other variables (Table 1).

3.4.1. Scots pine

The interaction between throughfall and type of canopy changed monthly as no significant effects of canopy on BAIR at different throughfall levels were found in April and November, but significant effects were found for the other months, particularly during the months

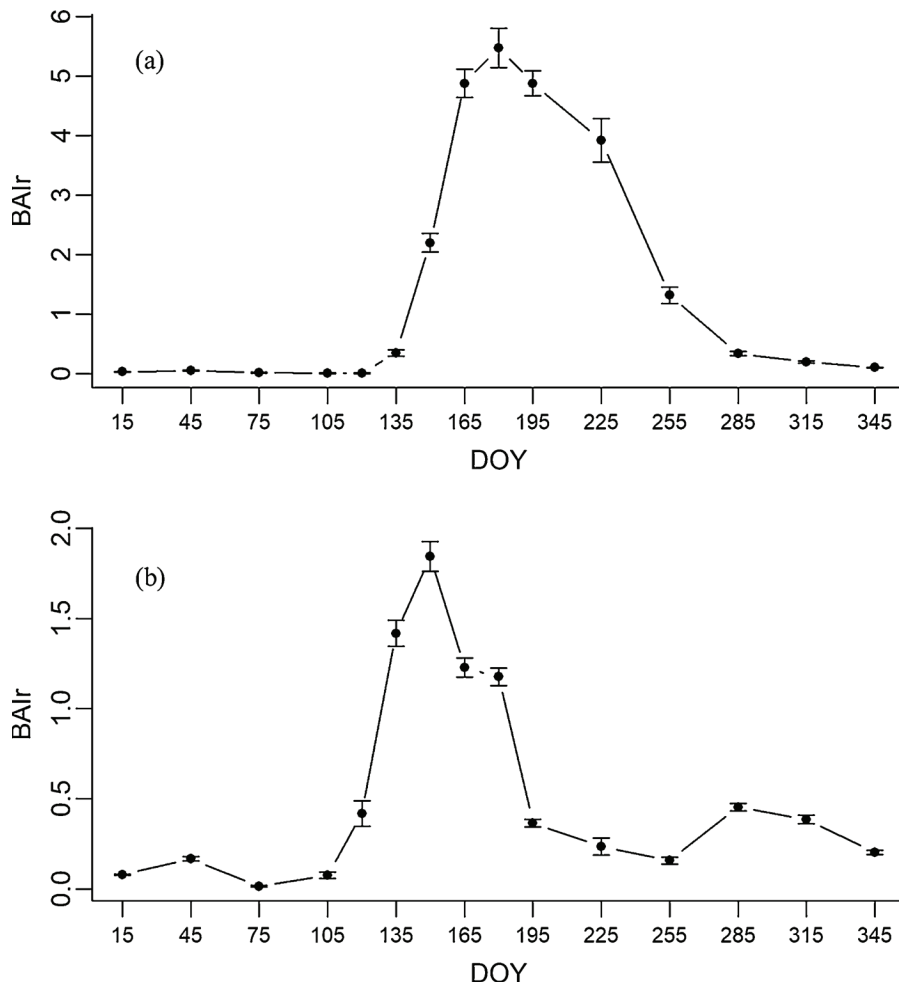


Fig. 2. Daily basal area increment (BAIr, cm² day⁻¹; values are means ± SE) for European beech (a) and Scots pine (b) and from 2009 to 2014. DOY stands for day of the year.

with highest tree growth ($P = 0.017$; Table 1; Fig. 5). Thus, global canopy effects (pure > mixed) on pine growth increased from May to July. Significant effects between canopy types were found in May, June (0–10 mm and 10–20 mm) and July (0–10 mm and 20–40 mm). It is also interesting to point out that no canopy effects on BAIr were detected above 20–40 mm.

The interaction between throughfall and thinning changed depending on the type of canopy (Fig. 6). Thus, in pure patches, thinning significantly affected BAIr at 0–10 mm in pure (0% > 20% = 40%,

$P = 0.01$) and mixed patches (20% > 0%, 20% = 40%, 0% = 40%, $P = 0.05$), but the effects were relatively small. However, thinning did significantly ($P = 0.001$) affect BAIr in mixed patches at throughfall intervals 20–40 mm (20% > (40% = 0%)) and 40–80 mm ((20% = 40%) > 0%) being the effects bigger than at 0–10 mm.

The interaction between thinning and throughfall also changed monthly ($P < 0.046$; Table 1) and annually ($P < 0.001$; Table 1). The monthly change is not shown as the pattern is difficult to interpret. Significant relationships between throughfall and thinning were

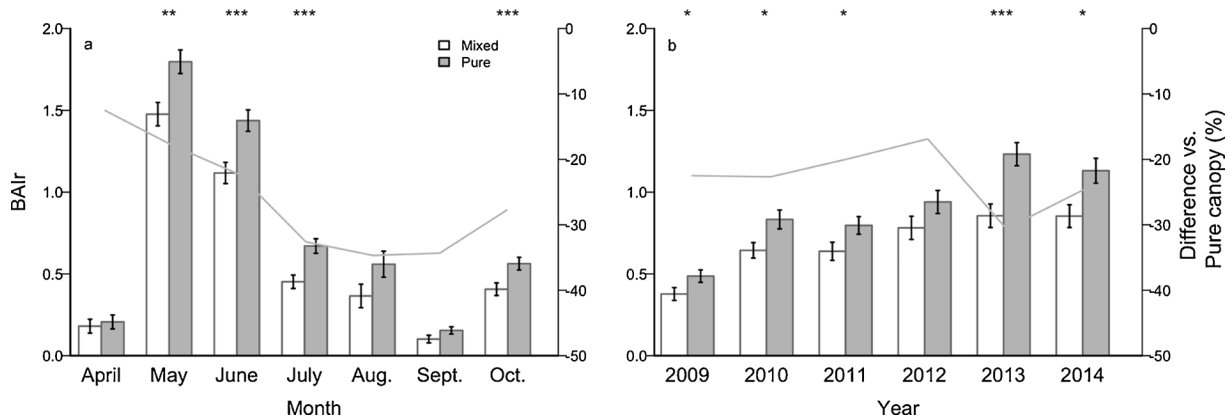


Fig. 3. Monthly (a) and yearly (b) basal area increment rates (BAIr, cm² day⁻¹) of Scots pine as a function of type of canopy (pure pine patches, mixed pine-beech patches) for the growing-season months during the 2009–2014 period. Significant differences in BAIr between types of canopy are indicated as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Percentage pine growth reductions of mixed patches relative to pure patches (light lines) are shown on the right y axis.

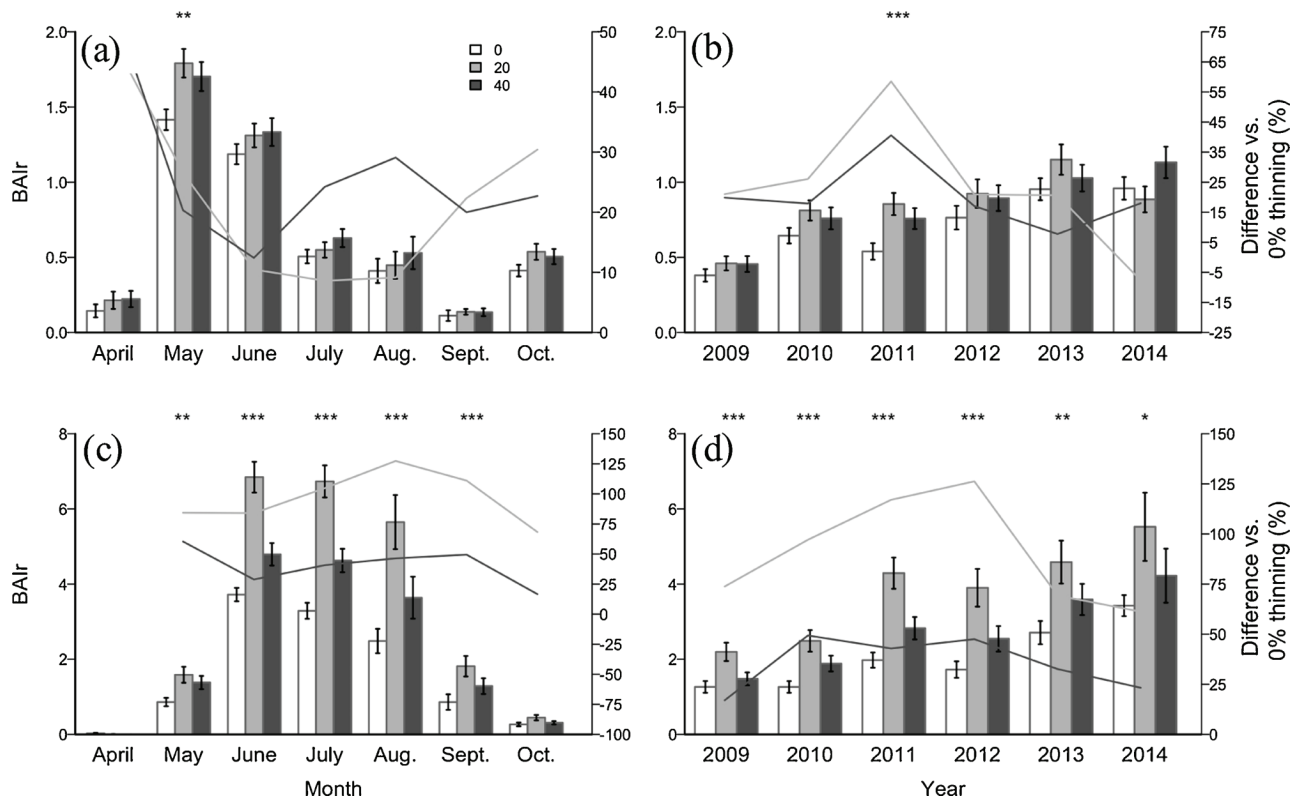


Fig. 4. Monthly and yearly basal area increment rates (BAIR, $\text{cm}^2 \text{day}^{-1}$; means \pm SE) of Scots pine (a and b, respectively) and European beech (c and d, respectively) as a function of thinning intensity (0%, 20% and 40% of basal reduction) for the growing-season months during the 2009–2014 period. Significant differences in BAIR among thinning treatments are indicated as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Percentage growth differences of moderate (20%, light line) and severe (40%, dark line) thinning relative to unthinned plots are shown on the right y axes.

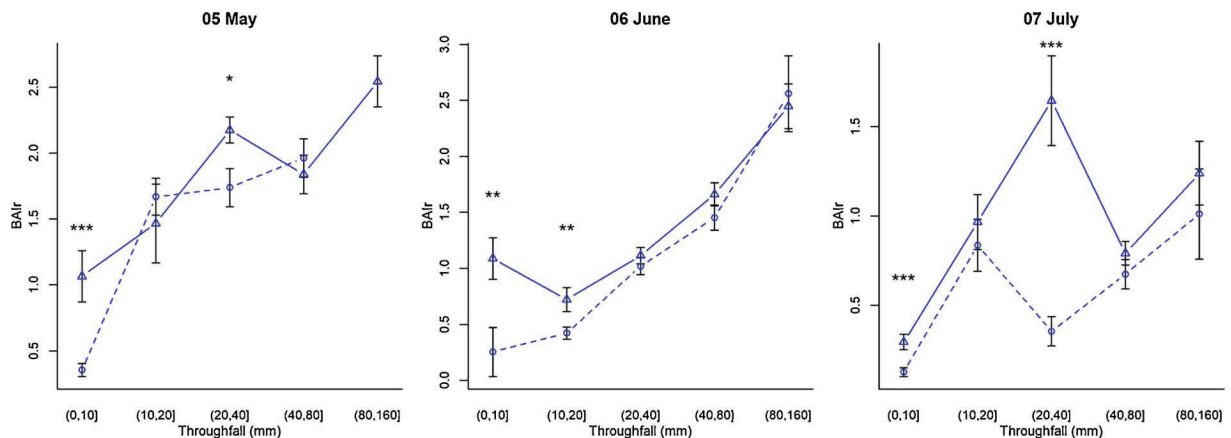


Fig. 5. Growth rates (daily basal area increment, BAIR in $\text{cm}^2 \text{day}^{-1}$; means \pm SE) for Scots pine in relation to throughfall, canopy type (triangles, pure forest; circles, mixed forest) during the months with highest tree growth in the 2009–2014 period. Significant differences in BAIR between canopy treatments are indicated as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Note the different scales in the “y” axes.

detected in 2010 and 2013 (40–80 mm throughfall) and especially in 2011, the driest year of the study period (10–20 mm, 20–40 mm and 80–160 mm) (Appendix, Fig. A1a). Normally, higher values of throughfall were linked to greater growth for Scots pine, in most years and except for 2011 (Table 1, throughfall * year, $P < 0.001$, Fig. A1a), and especially during the growing season (i.e., May–July) (Table 1, throughfall * month, $P < 0.01$; Fig. 7). Particularly, BAIR increased concomitantly with throughfall in May, June, August and October, whereas generally no matching was found in relation to throughfall in

April, July, September and November.

3.4.2. European beech

Unlike for pine, the interaction between throughfall, thinning and year was not significant for beech ($P = 0.987$; Table 1). However, significant thinning effects were observed in 2011 (0–10, 10–20 mm) and 2012 (0–10, 10–20, 20–40 mm), the two driest years, and in 2010 (40–80 mm) and 2013 (20–40 mm) (Fig. A1b). Also differently to pine, monthly BAIR generally did not increase concomitantly with

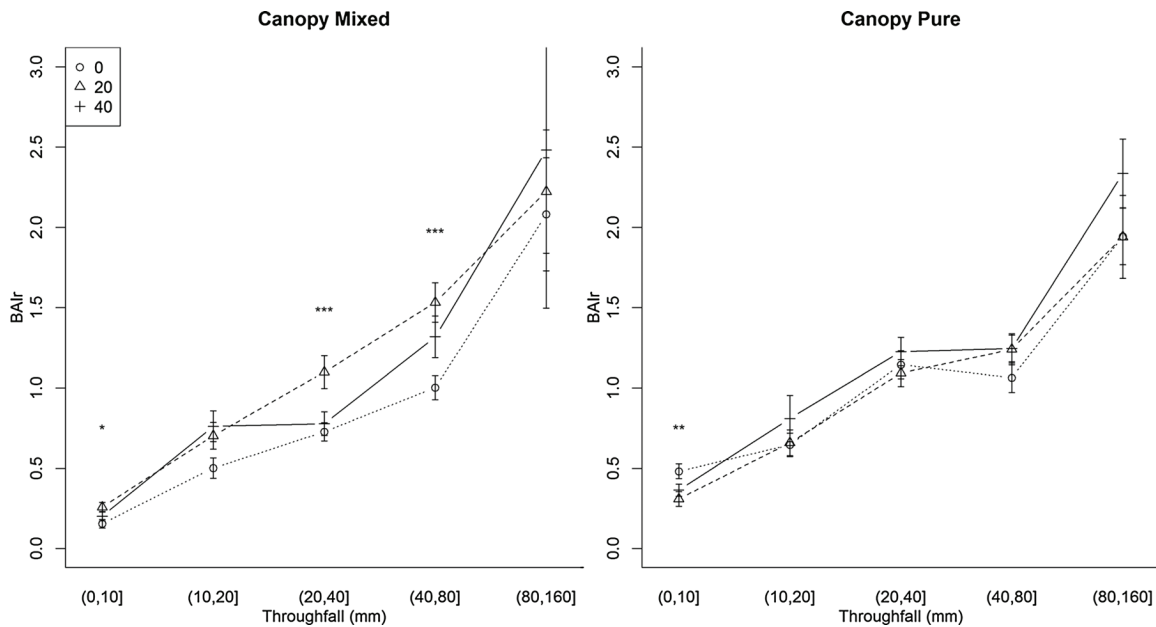


Fig. 6. Growth rates (daily basal area increment, BAIr, in $\text{cm}^2 \text{day}^{-1}$; means \pm SE) for Scots pine in relation to throughfall, thinning (0%, 20% and 40% basal area removed) and canopy type from April to November and for the 2009–2014 period. Significant differences among thinning treatments in year month for BAIr are indicated above: * $P < 0.05$; ** $P < 0.01$; ***.

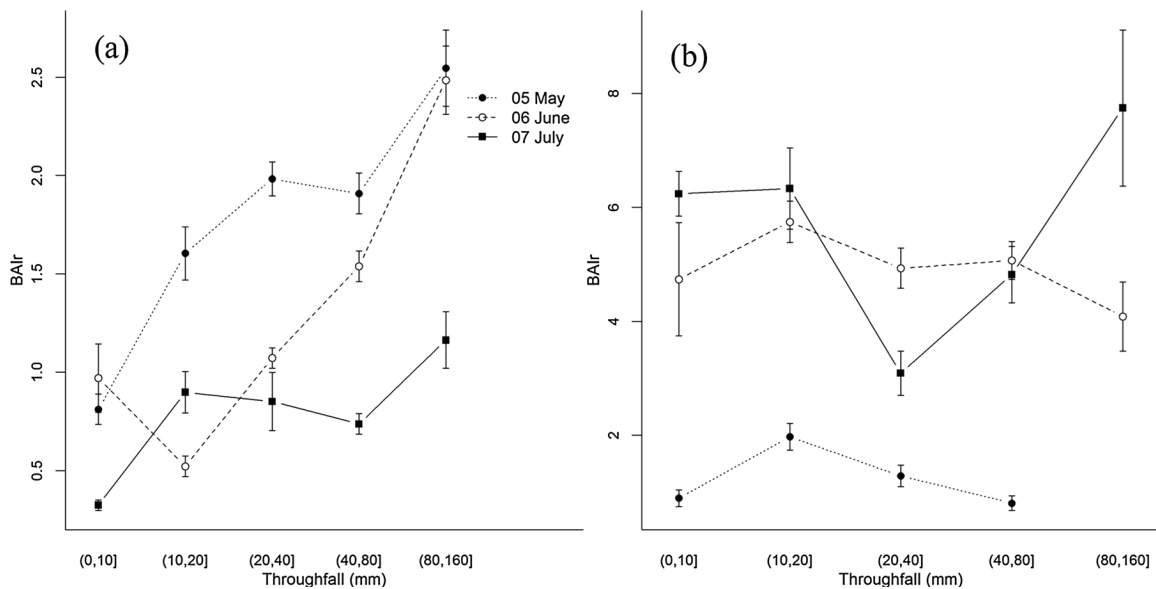


Fig. 7. Growth rates (daily basal area increment, BAIr, in $\text{cm}^2 \text{day}^{-1}$; means \pm SE) as a function of throughfall for Scots pine (a) and European beech (b) during the months with highest tree growth in the 2009–2014 period.

throughfall, being the interaction between throughfall and month not significant ($P = 0.309$; Table 1; Fig. 7B).

3.4.3. Canopy and thinning influence throughfall

Moderate and severe thinning presented the highest values of throughfall at annual scale (Appendix, Fig. A2). Significant differences were found in the mean annual amounts of throughfall as a function of canopy type ($P < 0.01$). Containers placed in mixed patches received less amount of throughfall than those in pure patches, especially in unmanaged mixed beech-pine plots. Thinning increased average throughfall only in mixed patches, 29.2% and 21.5% in moderate and severe thinning, respectively.

4. Discussion

4.1. Temporal and seasonal trends of tree growth

Tree growth and cambial resumption in both Scots pine and European beech started from April to May coinciding with a raise in air temperatures and with enough soil humidity as occur in other boreal, temperate and Mediterranean forests (Camarero et al., 2010; Čufar et al., 2008; Deslauriers et al., 2008; Schmitt et al., 2004). However, differences in daily basal area increments patterns were found between both species which presented the main growth peaks in May (pine) and June (beech) (Fig. 2). These different growth peaks agree with

xylogenesis studies carried out in nearby sites (Martinez del Castillo et al., 2016). Scots pine exhibited a sharp reduction in growth in mid-July, similarly to a previous study at this site (Primicia et al., 2013), whereas European beech showed high growth until early September. This growth of beech during summer might be related in part to the creation of parenchyma as the temperature was raised (Morris et al., 2016). The reduction in BAIR in Scots pine matched with the summer drought (i.e., low amounts of throughfall and high evapotranspiration rates) and was probably caused by a decline in the cambial activity (Camarero et al., 2010; Gruber et al., 2010), and possibly stem shrinkage (Zweifel et al., 2001). Relatively high growth of beech during the summer dry period, as compared with pine, appears to be caused by tapping of water by beech roots from deep soil horizons despite fine roots of pine and beech reach highest densities at the upper soil layers (Curt and Prévosto, 2003). However, as stands mature beech roots become predominant throughout the soil profile. This seems to be the case at our experimental plots as sampled beech trees are dominant or codominant. Furthermore, beech fine roots may shift deeper within the soil profile in response to drought (Meier and Leuschner, 2008), and even show highest surface area in deeper soil horizons in mixed stands (Bolte and Villanueva, 2006). Taken altogether these patterns would explain the high growth rates of beech during the dry period linked to its greater capacity to uptake soil water, but more research needs to be carried out to link root functioning with wood formation. In contrast, Martinez del Castillo et al. (2016) and Michelot et al. (2012), found a severe reduction of beech cambial activity in mid-August. A second growing peak was found for Scots pine from September to October; and this bimodal pattern has been previously observed by analysing wood microcores in the study site (Primicia et al., 2013) and elsewhere (Linares et al., 2009). However, under colder conditions, Scots pine, that has a Euro-Siberian distribution, may show a unimodal pattern (Camarero et al., 1998) suggesting an interaction of climate with other factors to drive xylogenesis plasticity. In this context, unimodal patterns have been reported for European beech, which has mainly an Euro-Siberian distribution.

4.2. Effects of canopy type and thinning on tree growth dynamics

Beech presence in Aspuz has caused an increase in average yearly reduction of BAIR for Scots pine in mixed relative to pure patches from 17% in 2007–2008 (Primicia et al., 2013) to 27% in 2014. This reduction is expected to increase as more beeches reach the upper part of the canopy. Scots pine growth reduction resulting from competition with beech has also been documented in other Pyrenean mixed forests (del Río et al., 2014). The fact that this growth reduction pattern occurred from May to October suggests that Scots pine and beech may be competing for different types of resources (i.e., light, water and nutrients) or a combination of resources along the year. Competition may be particularly intense in May when Scots pine shows its highest growth and sprouting and accelerated expansion of beech leaves occurs, and in June when pines reach its second highest growth value and beech its maximum growth (Fig. 2). During this period competition for water and nutrients needed for shoot, leaf and flower production may be important. Indeed, significantly lower soil N-NH_4^+ content in mixed than in pure patches was detected in the same plots in 2007 and 2008 which suggests higher ammonium uptake in mixed patches due to beech presence (Primicia, 2012). Beech may have also outcompete pine by decreasing throughfall in mixed patches by 11.4% during the leafless season and 20.5% during the leafed season (Primicia, 2012). This effect on growth was apparently higher in July and August, the driest months, when throughfall reduction was higher (see Fig. 2 and A1). On a longer timescale, light was probably the most limiting factor for suppressed

pine trees growing nearby dominant or codominant beech trees, whose leaves sprouted in April-May and were fully expanded in September (Arretxe, 2010).

Thinning usually leads to improved growth in the short term (Elkin et al., 2015; Linares et al., 2009; Primicia et al., 2016), an effect which can be explained by an increase in soil water and nutrients availability to competing trees (Blanco et al., 2005), and by an improved growth and photosynthetic capacity due to the increment of the foliar mass of the crown (Aussenac, 2000). Absolute and relative increases in growth due to thinning were much higher in beech than in Scots pine and lasted longer (Fig. 4). This is not surprising given the fact that cover of beech at this site is increasingly expanding relative to that of pine (Primicia et al., 2013) by taking advantage of its high efficiency in space occupation (Pretzsch and Schütze, 2005). Additionally, based on mean temperature and annual precipitation for Aspuz, conditions appear to be more favorable for European beech than for Scots pine (Pretzsch et al., 2016).

Scots pine and beech showed different monthly and annual responses to thinning (Fig. 4, Table 1). Positive growth differences between thinned and unthinned plots for both species increased in July and August, the two driest months, indicating the efficacy of thinning to mitigate drought stress. However, while severe thinning allowed Scots pine to maintain relatively higher growth rates during the drought period, in the case of beech the highest growth rates were achieved with moderate thinning. Wind speed within the stand and evaporation may have increased following tree reduction, more so at severe thinning, enhancing transpiration rates (Aussenac, 2000). Additionally, larger crown surface area (Sohn et al., 2016b) and increases in understory vegetation cover (unpublished results) under severe thinning may have also contributed to increase transpirational demand. This would explain the more positive effect of moderate thinning on beech growth, as less transpiration in this treatment than under severe thinning could have resulted in a water balance more favorable. In this context, thinning intensity probably did not affect so much between different thinning intensities in transpiration of Scots pine, a drought-avoider species (Zweifel et al., 2001). Pine probably reduced its stomata conductance at critical periods during the daytime as indicated by low relative growth rates because of low surface soil water potential (unpublished results). Consequently, severe thinning might have been more effective than moderate thinning to mitigate growth reduction especially if root system development of pines increased (Kneeshaw et al., 2002) and/or average fine-root depth decreased (Giuggiola et al., 2016) with thinning intensity. The latter would be a response to increased soil water availability in shallower soil depths resulting from an increase in throughfall with thinning intensity.

On an annual basis growth in thinned plots relative to that of unthinned plots showed a positive peak in 2011 under moderate and to a less extent under severe thinning for Scots pine, and a positive maximum in 2011 and 2012 under moderate thinning for beech. These were the driest years during the study period, especially 2011 (663 mm of rainfall; 1042 mm of mean in 2009–2014 period; data from Navascués weather station; Appendix Fig. A3). Therefore, thinning also mitigated growth reduction during drought of Scots pine and European beech at an annual scale as it has been shown for Scots pine in Switzerland (Giuggiola et al., 2013) and Central Europe (Sohn et al., 2016a) and for beech in southwestern Germany (van der Maaten, 2013). Thus, if mean annual temperature continues increasing and water surplus continues decreasing over the long term at this region (González de Andrés et al., 2017), a 20% thinning intensity treatment could be the more efficient management option in terms of maximizing growth.

4.3. Throughfall influences growth dynamics

Monitoring both intra-annual and inter-annual growth dynamics is a necessary approach for characterizing the tree growth responses to different forest management treatments such as thinning intensity and canopy type (Michelot et al., 2012). However, to elucidate some mechanisms underlying the observed patterns it can be very relevant looking at throughfall changes in relation to these treatments.

Global differences in pine BAIr between canopy types (pure > mixed, see Fig. 5) as a function of throughfall increased from May to July, when most pine growth occurred. Shoot elongation and leaf expansion of beech during this period apparently resulted in less light (Pretzsch et al., 2016) and water (Primicia, 2012; Primicia et al., 2013) reaching pine needles and roots, respectively, which could have led to reduced growth in mixed patches. Significant differences between canopy types were mainly observed at low throughfall (0–10 mm) due in part to lower growth variability, and to a less extent at medium flow (20–40 mm). No significant differences between canopy types were found at high throughfall (40–80 mm, 80–160 mm) suggesting a throughfall threshold to trigger these differences. These patterns may imply an increase in growth differences between canopy types if the frequency of high throughfall events decreases, and that of low-medium throughfall events increases. Furthermore, unlike in pure-canopy patches, rainfall interception in mixed-canopy patches caused the reduction of maximum throughfall input (i.e., the disappearance of throughfall interval 80–160 mm) into the soil in May and October, and consequently a direct reduction of pine growth occurred given the positive relationships between growth and throughfall amounts (see Fig. 7). This pattern may strengthen as more beeches reach the upper canopy level, contributing further to growth differences between canopy types. However, growth reduction over time in mixed patches in response to decreasing throughfall probably will increase faster in pine than in beech. This is because, at this site, water use efficiency (iWUE, i.e. the ratio of assimilated carbon to water lost through stomata) of beech has increased more (ca + 22%) than that of pine (ca + 12%) from 1980 to 2013 apparently as an adaptation to increasing dryness (González de Andrés et al., 2017).

Although the double interaction thinning* canopy and the triple interactions thinning*canopy* month or year were not significant for pine growth, the interaction thinning* canopy changed significantly as a function of throughfall. This effect was especially noticeable in mixed patches with throughfall of 20–40 mm and 40–80 mm in which average growth was higher under moderate thinning than in severely thinned or unthinned plots. In other words, the throughfall changed the thinning effects in mixed patches but not in pure patches. This effect may have been caused by nutrients, especially nitrates (Primicia, 2012), washed away by throughfall from the beech canopy and the forest floor which is thicker in mixed patches. The higher effect of thinning on pine growth in mixed patches under moderate thinning might be related to the lower basal area of beech at these plots (Primicia et al., 2016) which would have resulted in less competition on pines. A similar pattern was observed for the interaction between thinning and type of canopy for throughfall (Fig. A2) indicating that the above response of pine growth to thinning in mixed patches can also be generated by differences in throughfall amounts among thinning intensities. Furthermore, in

normal or wet years significant thinning effects on pine and beech as a function of throughfall were scarce. However, their frequency considerably increased in 2011 and 2012 in beech for low-medium throughfall, and in 2011 in pine for low, medium and high throughfall. The 2011 and 2012 years were especially dry, therefore these patterns confirm that thinning treatments were effective to reduce some of the negative effects of drought on growth, and that the main limiting resource during these years was water.

Growth of Scots pine generally increased with throughfall, especially in those months when BAIr was higher. This confirms the role played by precipitation to enhance radial growth in similar forests subjected to Mediterranean seasonal droughts (Bogino et al., 2009; Camarero et al., 2010; Gutiérrez, 1989; Primicia et al., 2013). However, monthly beech growth was not generally related to throughfall. These two distinct patterns suggest that pine might be more depending for its growth on water recently incorporated into the soil (i., soil surface layer) while beech might depend relatively more on water from previous rainfall events (i.e., deeper soil layers). These difference strategies could be further investigated analyzing the isotope discrimination of oxygen and hydrogen in xylem and soil water to identify the isotopic signature of water sources.

5. Conclusions

Scots pine and beech showed bimodal and unimodal temporal growth patterns, respectively, but the spring growth peak was the most important in both species. The relatively high growth of beech during the summer dry period, as compared with pine, could be explained by tapping of water by beech roots from deep soil horizons. Competition between Scots pine and beech appeared to be high in May and June coinciding with their respective peaks of growth. As beech competition for light intensifies, pine growth is progressively diminishing in mixed patches relative to pure patches. Absolute and relative increase in growth due to thinning were much higher in beech than in Scots pine, providing to beech a high efficiency in space occupation in sites with favorable growing conditions (e.g., drought stress). Differences in growth between thinned and control plots for both species increased during the driest months and years indicating the efficacy of thinning to mitigate drought stress. On an annual basis moderate thinning appeared to be the most efficient treatment to maximize growth. Finally, interactions between throughfall and the analyzed factors explain mechanisms underlying pine growth reduction in mixed patches relative to pure patches, differences in thinning effects on pine growth in pure and mixed patches, higher efficiency of thinning during drought periods, and why beech trees were capable of growing during the dry months.

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Appendix A

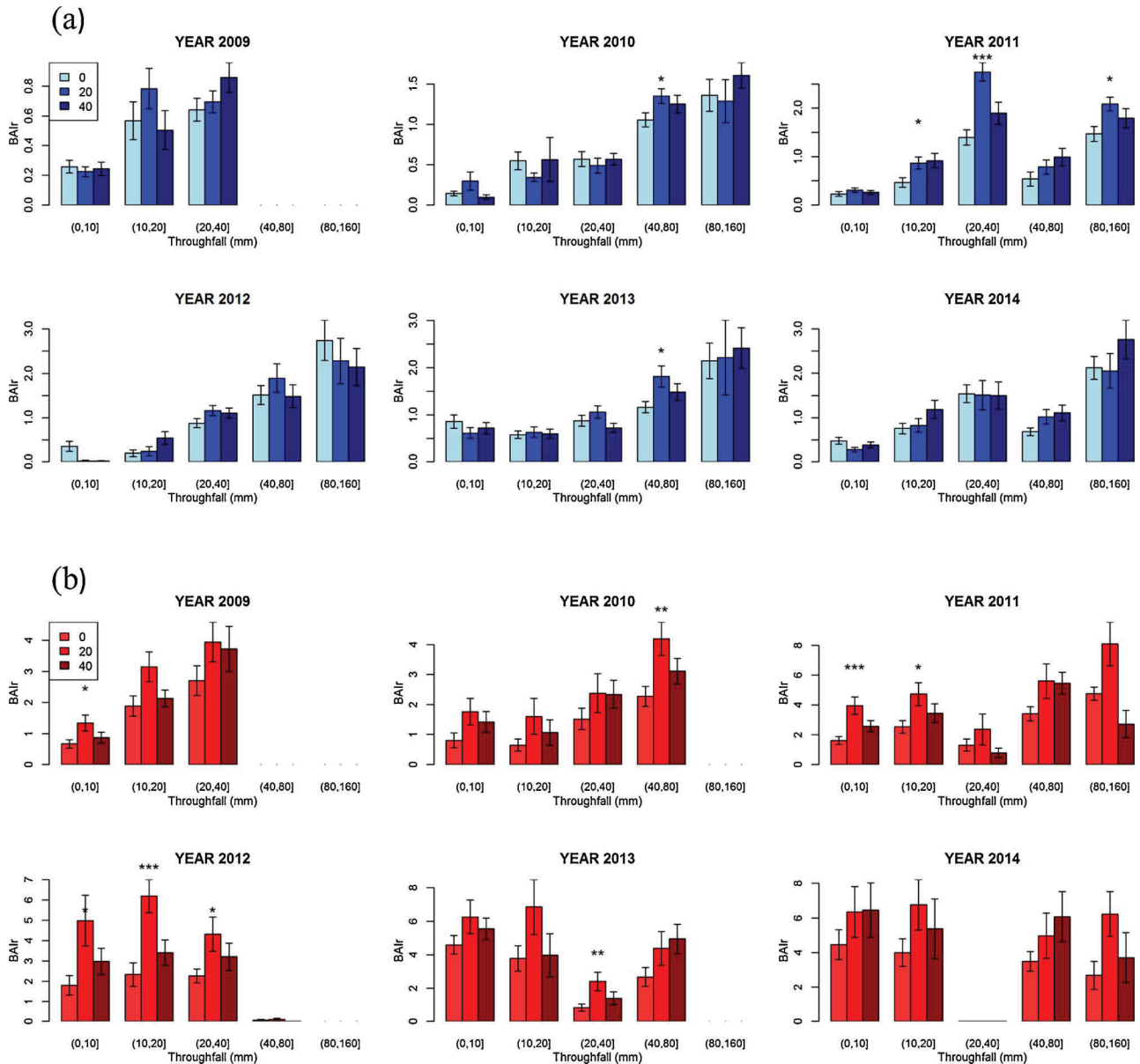


Fig. A1. Growth rates (daily basal area increment, BAIR, in $\text{cm}^2 \text{day}^{-1}$; means \pm SE) as a function of throughfall and thinning severity (0%, 20% and 40% of basal area removed) during different years for Scots pine (a; blue bars) and European beech (b; red bars) considering the 2009–2014 period. Significant differences between thinning treatments in each year for BAIR are indicated above: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

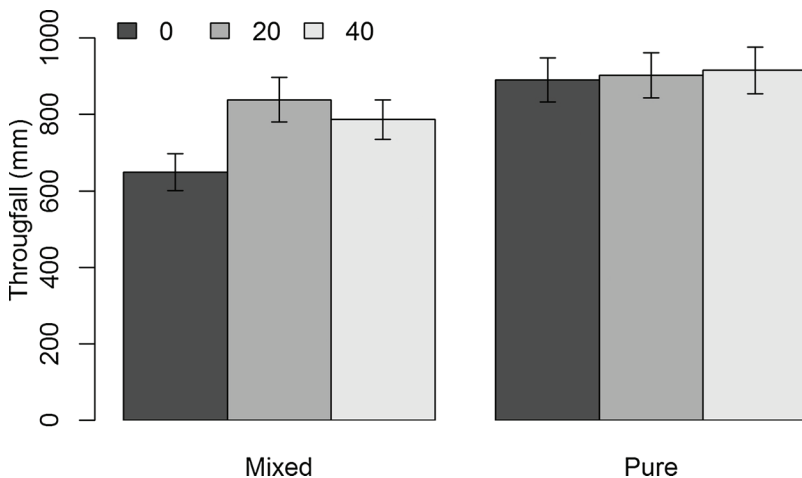


Fig. A2. Mean annual amount of throughfall (means \pm SE) considering thinning intensity (0%, 20 and 40% of basal area removed) and type of canopy from 2009 to 2014.

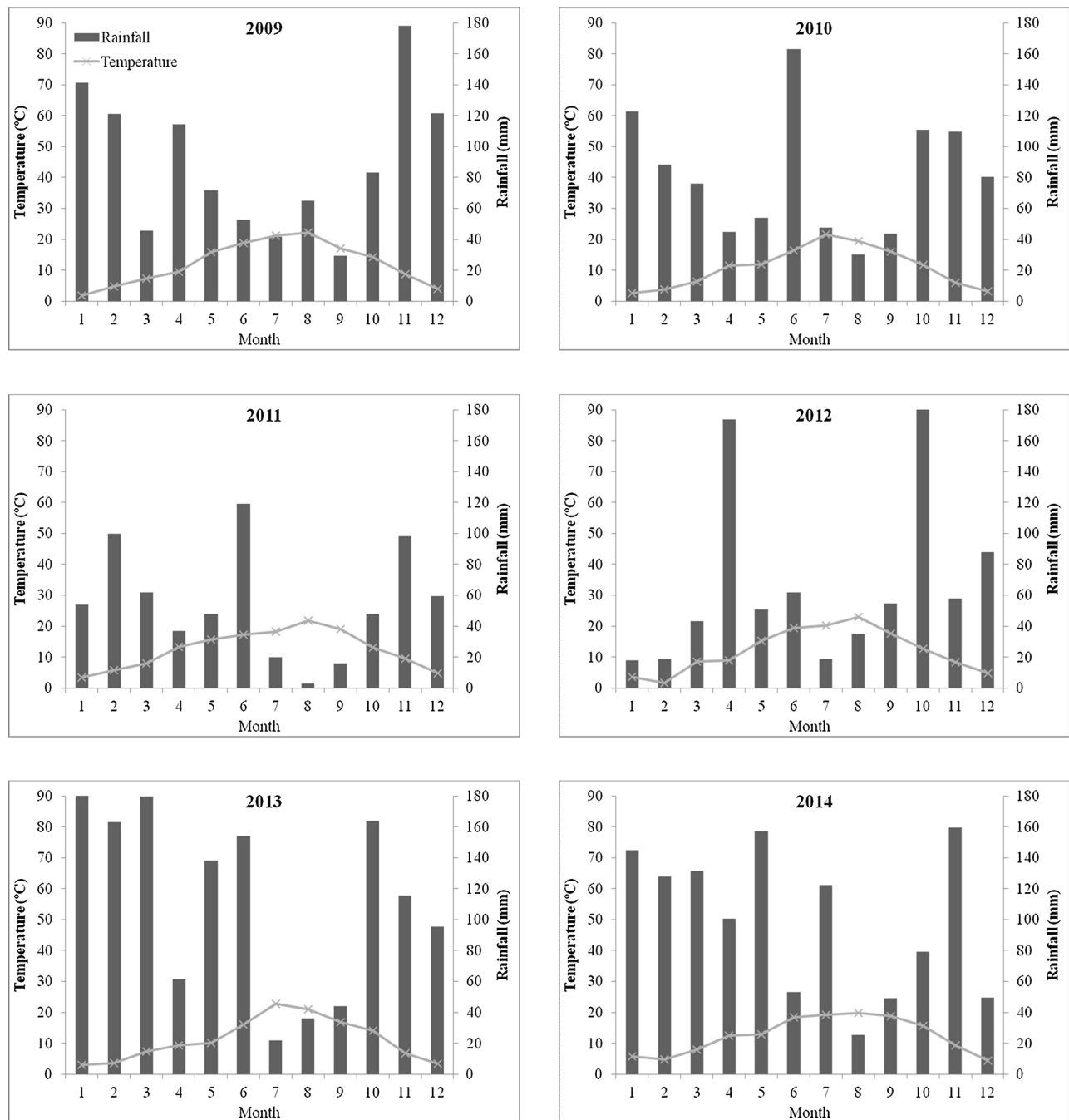


Fig. A3. Climographs for the Aspuz study site (Navascués weather station) from 2009 to 2014.

References

- Aldea, J., Bravo, F., Bravo-Oviedo, A., Ruiz-Peinado, R., Rodríguez, F., del Río, M., 2017. Thinning enhances the species-specific radial increment response to drought in Mediterranean pine-oak stands. *Agric. For. Meteorol.* 237, 371–383. <http://dx.doi.org/10.1016/j.agrformet.2017.02.009>.
- Andreu, L., Gutiérrez, E., Macías, M., Ribas, M., Bosch, O., Camarero, J.J., 2007. Climate increases regional tree-growth variability in Iberian pine forests. *Glob. Chang. Biol.* 13, 804–815. <http://dx.doi.org/10.1111/j.1365-2486.2007.01322.x>.
- Andrew, I., 1986. Simple experimental design for forestry trials. *FRI Bull.* 71. Forest Research Institute, Rotorua, New Zealand.
- Antonova, G., Shebeko, V., Malyutina, E., 1983. Seasonal dynamics of cambial activity and tracheid differentiation in the stem of Scots pine. *Chem. Wood* 1, 16–22.
- Arretxe, A., 2010. Influencia de las claras y el tipo de dosel en la morfología y la composición química foliar de pino silvestre (*Pinus sylvestris*) y haya (*Fagus sylvatica*) en un bosque mixto del Pirineo navarro (marzo 2008-enero 2009). Public university of Navarre.
- Aussenac, G., 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Ann. For. Sci.* 57, 287–301. <http://dx.doi.org/10.1051/forest:2000119>.
- Blanco, J., 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. Universidad Pública de Navarra, Spain.
- Blanco, J., Zavala, M., Imbert, J., Castillo, F., 2005. Sustainability of forest management practices: evaluation through a simulation model of nutrient cycling. *For. Ecol. Manage.* 213, 209–228.
- Bogino, S., Fernández Nieto, M.J., Bravo, F., 2009. Climate effect on radial growth of *Pinus sylvestris* at its southern and western distribution limits. *Silva Fenn.* 43, 609–623.
- Bolte, A., Villanueva, I., 2006. Interspecific competition impacts on the morphology and distribution of fine roots in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.). *Eur. J. For. Res.* 125, 15–26. <http://dx.doi.org/10.1007/s10342-005-0075-5>.
- Camarero, J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., Vicente-Serrano, S., 2015. To die or not to die: early warnings of tree dieback in response to a severe drought. *J.*

- Ecol. 103, 44–57.
- Camarero, J.J., Guerrero-Campo, J., Gutierrez, E., 1998. Tree-ring growth and structure of *Pinus uncinata* and *Pinus sylvestris* in the Central Spanish Pyrenees. *Arct. Alp. Res.* 30, 1–10.
- Camarero, J.J., Olano, J.M., Parras, A., 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. *New Phytol.* 185, 471–480. <http://dx.doi.org/10.1111/j.1469-8137.2009.03073.x>.
- Candel-Pérez, D., Linares, J.C., Viñeola, B., Lucas-Borja, M.E., 2012. Assessing climate–growth relationships under contrasting stands of co-occurring Iberian pines along an altitudinal gradient. *For. Ecol. Manage.* 274, 48–57. <http://dx.doi.org/10.1016/j.foreco.2012.02.010>.
- Cardil, A., Molina, D.M., Kobziar, L.N., 2014. Extreme temperature days and their potential impacts on southern Europe. *Nat. Hazards Earth Syst. Sci.* 14, 3005–3014. <http://dx.doi.org/10.5194/nhess-14-3005-2014>.
- Chambers, J.M., Hastie, T.J., 1992. In: Chambers, J.M., Hastie, T.J. (Eds.), *Statistical Models in S*. Hall/CRC, C. p. 624.
- Čufar, K., Prislán, P., De Luis, M., Gričar, J., 2008. Tree-ring variation, wood formation and phenology of beech (*Fagus sylvatica*) from a representative site in Slovenia, SE Central Europe. *Trees-Struct. Funct.* 22, 749–758. <http://dx.doi.org/10.1007/s00468-008-0235-6>.
- Curt, T., Prévosto, B., 2003. Rooting strategy of naturally regenerated beech in Silver birch and Scots pine woodlands. *Plant Soil* 255, 265–279. <http://dx.doi.org/10.1023/A:1026132021506>.
- D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecol. Appl.* 23, 1735–1742. <http://dx.doi.org/10.1890/13-0677.1>.
- del Río, M., Condés, S., Pretzsch, H., 2014. Analyzing size-symmetric vs. size-asymmetric and intra- vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. *For. Ecol. Manage.* 325, 90–98. <http://dx.doi.org/10.1016/j.foreco.2014.03.047>.
- 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, 863–871. <http://dx.doi.org/10.1093/treephys/28.6.863>.
- Diaconu, D., Kahle, H.P., Spiecker, H., 2015. Tree- and stand-level thinning effects on growth of European Beech (*Fagus sylvatica* L.) on a Northeast- and a Southwest-facing slope in Southwest Germany. *Forests* 6, 3256–3277. <http://dx.doi.org/10.3390/f6093256>.
- Elkin, C., Giuggiola, A., Rigling, A., Bugmann, H., 2015. Short- and long-term efficacy of forest thinning to mitigate drought impacts in mountain forests in the European Alps. *Ecol. Appl.* 25, 1083–1098. <http://dx.doi.org/10.1890/14-0690.1>.
- Forrester, D.I., Tang, X., 2016. Analysing the spatial and temporal dynamics of species interactions in mixed-species forests and the effects of stand density using the 3-PG model. *Ecol. Modell.* 319, 233–254. <http://dx.doi.org/10.1016/j.ecolmodel.2015.07.010>.
- Fukuda, H., 1996. Xylogenesis: initiation, progression, and cell death. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 47, 299–325.
- Gea-Izquierdo, G., Viguera, B., Cabrera, M., Cañellas, I., 2014. Drought induced decline could portend widespread pine mortality at the xeric ecotone in managed mediterranean pine-oak woodlands. *For. Ecol. Manage.* 320, 70–82. <http://dx.doi.org/10.1016/j.foreco.2014.02.025>.
- Geßler, A., Keitel, C., Nahr, M., Rennenberg, H., 2004. Water shortage affects the water and nitrogen balance in Central European beech forests. *Plant Biol.* 6, 289–298. <http://dx.doi.org/10.1055/s-2004-820878>.
- Giuggiola, A., Bugmann, H., Zingg, A., Dobbertin, M., Rigling, A., 2013. Reduction of stand density increases drought resistance in xeric Scots pine forests. *For. Ecol. Manage.* 310, 827–835. <http://dx.doi.org/10.1016/j.foreco.2013.09.030>.
- Giuggiola, A., Ogée, J., Rigling, A., Gessler, A., Bugmann, H., Treydte, K., 2016. Improvement of water and light availability after thinning at a xeric site: which matters more? A dual isotope approach. *New Phytol.* 210, 108–121. <http://dx.doi.org/10.1111/nph.13748>.
- González de Andrés, E., Camarero, J.J., Blanco, J.A., Imbert, J.B., Lo, Y.-H., Sangüesa-Barreda, G., Castillo, F.J., 2017. Tree-to-tree competition in mixed European beech–Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions. *J. Ecol.* <http://dx.doi.org/10.1111/1365-2745.12813>.
- Gruber, A., Strobl, S., Veit, B., Oberhuber, W., 2010. Impact of drought on the temporal dynamics of wood formation in *Pinus sylvestris*. *Tree Physiol.* 30, 490–501.
- Gutiérrez, E., 1989. Dendroclimatological study of *Pinus sylvestris* L. in southern Catalonia (Spain). *Tree-Ring Bull.* 49, 1–9.
- Ježík, M., Blaženeč, M., Střelcová, K., Ditmarová, L., 2011. The impact of the 2003–2008 weather variability on intra-annual stem diameter changes of beech trees at a submontane site in central Slovakia. *Dendrochronologia* 29, 227–235. <http://dx.doi.org/10.1016/j.dendro.2011.01.009>.
- Jump, A.S., Hunt, J.M., Peñuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob. Chang. Biol.* 12, 2163–2174. <http://dx.doi.org/10.1111/j.1365-2486.2006.01250.x>.
- Kelty, M.J., 1992. Comparative productivity of monocultures and mixed-species stands. In: Kelty, M.J., Larson, B.C., Oliver, C.D. (Eds.), *The Ecology and Silviculture of Mixed-Species Forests: A Festschrift for David M. Smith*. Springer, Netherlands, Dordrecht, pp. 125–141. http://dx.doi.org/10.1007/978-94-015-8052-6_8.
- Kneeshaw, D.D., Williams, H., Nikinmaa, E., Messier, C., 2002. Patterns of above- and below-ground response of understorey conifer release 6 years after partial cutting. *Can. J. For. Res.* 32, 255–265. <http://dx.doi.org/10.1139/x01-190>.
- Knoke, T., Stimm, B., Ammer, C., Moog, M., 2005. Mixed forests reconsidered: A forest economics contribution on an ecological concept. *For. Ecol. Manage.* 213, 102–116. <http://dx.doi.org/10.1016/j.foreco.2005.03.043>.
- Linares, J.C., Camarero, J.J., Carreira, J.A., 2009. Plastic responses of *Abies pinsapo* xylogenesis to drought and competition. *Tree Physiol.* 29, 1525–1536. <http://dx.doi.org/10.1093/treephys/tp084>.
- 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. Manage.* 259, 967–975. <http://dx.doi.org/10.1016/j.foreco.2009.12.001>.
- Martínez-Vilalta, J., López, B.C., Adell, N., Badiella, L., Ninyerola, M., 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Glob. Chang. Biol.* 14, 2868–2881. <http://dx.doi.org/10.1111/j.1365-2486.2008.01685.x>.
- Martínez del Castillo, E., Longares, L.A., Gričar, J., Prislán, P., Gil-Pelegrín, E., Čufar, K., de Luis, M., 2016. Living on the edge: contrasted wood-formation dynamics in *Fagus sylvatica* and *Pinus sylvestris* under Mediterranean conditions. *Front. Plant Sci.* 7, 370. <http://dx.doi.org/10.3389/fpls.2016.00370>.
- Martínez-Vilalta, J., Piñol, J., 2002. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *For. Ecol. Manage.* 161, 247–256. [http://dx.doi.org/10.1016/S0378-1127\(01\)00495-9](http://dx.doi.org/10.1016/S0378-1127(01)00495-9).
- Meier, I.C., Leuschner, C., 2008. Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Glob. Chang. Biol.* 14, 2081–2095. <http://dx.doi.org/10.1111/j.1365-2486.2008.01634.x>.
- Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E.-D., Ammer, C., 2016. Site-adapted tree species reduce drought susceptibility of mature European beech. *Glob. Chang. Biol.* 22, 903–920. <http://dx.doi.org/10.1111/gcb.13113>.
- Michelot, A., Simard, S., Rathgeber, C., Dufrene, E., Damesin, C., 2012. Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree Physiol.* 1033–1043. <http://dx.doi.org/10.1093/treephys/tps052>.
- Mölder, I., Leuschner, C., 2014. European beech grows better and is less drought sensitive in mixed than in pure stands: tree neighbourhood effects on radial increment. *Trees* 28, 777–792. <http://dx.doi.org/10.1007/s00468-014-0991-4>.
- Morris, H., Plavcová, L., Cvecko, P., Fichtler, E., Gillingham, M.A.F., Martínez-Cabrera, H.I., McGlenn, D.J., Wheeler, E., Zheng, J., Ziemińska, K., Jansen, S., 2016. A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. *New Phytol.* 209, 1553–1565. <http://dx.doi.org/10.1111/nph.13737>.
- Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). *Glob. Chang. Biol.* 9, 131–140. <http://dx.doi.org/10.1046/j.1365-2486.2003.00566.x>.
- Pinheiro, J., Bates, D., 2000. *Mixed-effects models in S and S-PLUS*. Springer, New York.
- Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dimberger, G., Drössler, L., Fabrika, M., Forrester, D.I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellemont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A., 2015a. Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* 134, 927–947. <http://dx.doi.org/10.1007/s10342-015-0900-4>.
- Pretzsch, H., Forrester, D.I., Rötzer, T., 2015b. Representation of species mixing in forest growth models: a review and perspective. *Ecol. Modell.* 313, 276–292. <http://dx.doi.org/10.1016/j.ecolmodel.2015.06.044>.
- Pretzsch, H., del Río, M., Schütze, G., Ammer, C., Annighöfer, P., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Drössler, L., Fabrika, M., Forrester, D.I., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Skrzyszewski, J., Sramek, V., Sterba, H., Svoboda, M., Verheyen, K., Zlatanov, T., Bravo-Oviedo, A., 2016. Mixing of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect increases with water availability. *For. Ecol. Manage.* 373, 149–166. <http://dx.doi.org/10.1016/j.foreco.2016.04.043>.
- Pretzsch, H., Schütze, G., 2005. Crown allometry and growing space efficiency of Norway Spruce (*Picea abies* [L.] Karst.) and European Beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant Biol.* 7, 628–639. <http://dx.doi.org/10.1055/s-2005-865965>.
- Primicia, I., 2012. Influence of thinning and canopy type on the internal nutrient cycling and the secondary growth of *Pinus sylvestris* L. in a mixed forest in the Pyrenees. Public University of Navarre, Spain.
- Primicia, I., Camarero, J.J., Imbert, J.B., Castillo, F.J., 2013. Effects of thinning and canopy type on growth dynamics of *Pinus sylvestris*: inter-annual variations and intra-annual interactions with microclimate. *Eur. J. For. Res.* 132, 121–135. <http://dx.doi.org/10.1007/s10342-012-0662-1>.
- Primicia, I., Imbert, J., Puertas, F., Traver, Mdel C., Castillo, F.J., 2016. Influence of thinning intensity and canopy type on Scots pine stand and growth dynamics in a mixed managed forest. *For. Syst.* 25, e057.
- R core development team, 2017. R 3.2.4.
- Rossi, S., Anfodillo, T., Menardi, R., 2006. Trephor: A new tool for sampling microcores from tree stems. *IAWA J.* 27, 89–97. <http://dx.doi.org/10.1163/22941932-90000139>.
- Rozas, V., Camarero, J., Sangüesa-Barreda, G., Souto, M., García-González, I., 2015. Summer drought and ENSO-related cloudiness distinctly drive *Fagus sylvatica* growth near the species rear-edge in northern Spain. *Agric. For. Meteorol.* 201, 153–164.
- Sánchez-Salguero, R., Camarero, J.J., Hevia, A., Madrigal-González, J., Linares, J.C., Ballesteros-Canovas, J.A., Sánchez-Miranda, A., Alfaro-Sánchez, R., Sangüesa-Barreda, G., Galván, J.D., Gutiérrez, E., Génova, M., Rigling, A., 2015. What drives growth of Scots pine in continental Mediterranean climates: drought, low temperatures or both? *Agric. For. Meteorol.* 206, 151–162. <http://dx.doi.org/10.1016/j.agrfor.2015.03.004>.

- agrformet.2015.03.004.
- Sánchez de Dios, R., Hernández, L., Montes, F., Sainz-Ollero, H., Cañellas, I., 2016. Tracking the leading edge of *Fagus sylvatica* in North-Western Iberia: Holocene migration inertia, forest succession and recent global change. *Perspect. Plant Ecol. Evol. Syst.* 20, 11–21. <http://dx.doi.org/10.1016/j.ppees.2016.03.001>.
- Schmitt, U., Jalkanen, R., Eckstein, D., 2004. Cambium dynamics of *Pinus sylvestris* and *Betula* spp. in the northern boreal forest in Finland. *Silva Fenn.* 38, 167–178.
- Sheil, D., 2003. Growth assessment in tropical trees: large daily diameter fluctuations and their concealment by Dendrometer bands. *Can. J. For. Res.* 33, 2027–2035.
- Sohn, J.A., Hartig, F., Kohler, M., Huss, J., Bauhus, J., 2016a. Heavy and frequent thinning promotes drought adaptation in *Pinus sylvestris* forests. *Ecol. Appl.* 26, 2190–2205. <http://dx.doi.org/10.1002/eap.1373>.
- Sohn, J.A., Saha, S., Bauhus, J., 2016b. Potential of forest thinning to mitigate drought stress: A meta-analysis. *For. Ecol. Manage.* 380, 261–273. <http://dx.doi.org/10.1016/j.foreco.2016.07.046>.
- Spiecker, H., 2003. Silvicultural management in maintaining biodiversity and resistance of forests in Europe-boreal zone: case Finland. *J. Environ. Manage.* 67, 47–54. [http://dx.doi.org/10.1016/S0301-4797\(02\)00187-1](http://dx.doi.org/10.1016/S0301-4797(02)00187-1).
- Underwood, A.J., 1997. *Experiments in ecology. Their logical design and interpretation using analysis of variance.* Cambridge University Press, Cambridge (UK).
- van der Maaten, E., 2013. Thinning prolongs growth duration of European beech (*Fagus sylvatica* L.) across a valley in southwestern Germany. *For. Ecol. Manage.* 306, 135–141. <http://dx.doi.org/10.1016/j.foreco.2013.06.030>.
- von Ende, C., 2001. *Repeated-measures analysis: growth and other time dependent measures. The Design and Analysis of Ecological Experiments.* Oxford University Press, New York, pp. 134–157.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A., Smith, G., 2009. *Mixed effects models and extensions in ecology with R.* Springer, New York.
- Zweifel, R., Item, H., Häslner, R., 2001. Link between diurnal stem radius changes and tree water relations. *Tree Physiol.* 21, 869–877. <http://dx.doi.org/10.1093/treephys/21.12-13.869>.