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Growth dynamics, climate sensitivity and water-use efficiency in pure vs. mixed pine and beech stands in Trentino (Italy)

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Key words: mountain forests, climate adaptation, Mediterranean environments, climate change, stable isotopes

Abstract

Understanding to what extent the species mixture modifies the growth of trees and their responses to climate, in comparison with monospecific stands, is important to support forest adaptation and mitigation strategies. Trees are able to record and store information useful to identify, assess and reconstruct the environmental factors influencing their growth and adaptation capacity. This paper aimed at (i) defining the tree growth trends, then analysing possible correlations with the climatic trends (*Standardised Precipitation-Evapotranspiration Index*; SPEI), and (ii) evaluating the intrinsic Water Use Efficiency (WUE_i) of two important tree species, occurring in pure and mixed forest stands through the support of isotopic analysis. Three sites with similar pedo-climatic conditions were identified in the Italian Alps. The first two are characterized by monospecific stands, respectively dominated by European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.). The third site refers to a mixed stand of both the previous species. In particular, in order to assess the annual changes in WUE_i, we analysed $\delta^{13}\text{C}$ in tree rings. The influence of the stomatal conductance was also investigated through $\delta^{18}\text{O}$. Our results indicated that: (i) Basal Area Increments (BAI) consistently increased in all stands (except for pure stand of Scots pine), in the 1994-2003 period; (ii) SPEI highlighted a drought period between 1991 and 2007; and (iii) the WUE_i values were generally higher in pure than in mixed stands. The divergence between BAI and SPEI values in the 90s and early 00s may be explained as consequence of moderate thinning.

Indeed, our findings showed how past forest management (namely thinning) might be more influential on tree growth than current climatic oscillations (temperature and precipitation).

Introduction

European mountain forests play a very important role as providers of ecosystem services, functions and goods (Stenger et al., 2009). However, climate change and increased demands on forests and forest products pose threats on the quantity or quality of these services (Schröter et al., 2005). Climate change has large impacts on short-term forest functioning (Anderegg et al., 2016) and long-term ecosystem dynamics (Millar and Stephenson, 2015), yet our physiological understanding of the mechanisms leading to improvements in adaptation of tree species is still limited. In particular, global change exerts a growing pressure on the sensitive mountain regions and, therefore, the resilience of existing forests to climate change and natural disturbances is an important issue to identify locally appropriate climate-adaptive strategies.

Mixed-species forests are considered more resistant to disturbances and extreme events than mono-specific stands (Pretzsch et al., 2013) and may provide higher levels of multiple ecosystem services (Gamfeldt et al., 2013; Loreau and Hector, 2001). These results could be attributed to the niche complementarity, which reduces the competition for resources in mixed stands (Morin et al., 2011), and in favourable interaction between the two populations of plants within a mixed stand (Yachi and Loreau, 2007). Differences between species in shade tolerance, crown phenology, canopy structure and root depths have been associated to increased productivity in mixed stands (Brassard et al., 2013; Forrester and Albrecht, 2014; Toïgo et al., 2015). However, mixed-species forests are not always more productive and stable than mono-specific stands (Epron et al., 2013; Grossiord et al., 2014; Merlin et al., 2015), which suggests the need for carefully considering the reciprocity of species assemblages and the specificity of site conditions (del Río et al., 2016). Understanding dynamics (growth, resistance, productivity, etc.) of mixed forests is very important to define proactive management measures towards sustainable adaptation to and mitigation of climate change (Condés and del Río, 2015). In particular, a better understanding of the exceeding/decreasing productivity of mixed stands in comparison with pure stands is essential for both ecology and management of forest ecosystems.

Although climatic signals are often confounded with management effects, warming temperatures are likely to induce changes in species distribution and community composition in mountain regions by altering physiological thresholds and disturbance regimes (Gonzalez

et al., 2010). In this context, extreme climatic events are very useful pointers to highlight the reactions of forest ecosystems to disturbance patterns and to allow in-depth study of growth-climate relationships (Pretzsch et al., 2013). Drought, in particular, is one of the most relevant indicators for response analyses of forest ecosystems in terms of tree growth (Pretzsch and Dieler, 2011), allometric modification (Pretzsch et al., 2012), water-use efficiency (Tognetti et al., 2014) and plant mortality (McDowell et al., 2008). Tree responses to drought depend on species, age, and size, as well as within-stand competition for resources and other issues associated with stand structure (Cavin et al., 2013; Lloret et al., 2011; Pretzsch and Dieler, 2011; Zang et al., 2012). The sensitivity of plants to drought varies according to the severity and duration of stress, and the combination with other stress factors (Niinemets, 2010). Increasing drought exposure could alter the competitive hierarchy between tree species with distinct drought tolerance, resulting in shifts in tree species composition in mixed forest stands (Cavin et al., 2013).

Stable carbon and oxygen isotopes from tree rings ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) provide a continuous, annually resolved record of environmental conditions and show stronger correlations between tree individuals and environmental variables than annual growth rings that are laid down during each growing season (McCarroll and Loader, 2004). Tree-ring $\delta^{13}\text{C}$ is controlled by the balance between stomatal conductance (i.e., supply of CO_2) and photosynthetic rate (i.e., demand for CO_2), and is often used to calculate intrinsic water-use efficiency (WUE_i) and differences in water use between trees (McCarroll and Loader, 2004). Restrictions in water availability generally reduce stomatal conductance and intercellular CO_2 concentration (c_i), leading to an increase in $\delta^{13}\text{C}$, though light limitation of photosynthesis increases c_i . Conversely, tissue $\delta^{18}\text{O}$ is not strongly influenced by photosynthetic rate, being controlled by the source water $\delta^{18}\text{O}$, and land-plant water exchange, so that combined measurements of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ allow stomatal and photosynthetic effects on $\delta^{13}\text{C}$ to be teased apart (Sheidegger et al 2000; Barnard et al., 2012; Tognetti et al., 2014).

Below-ground and above-ground mixing effect can change over time, productivity and stability advantages of mixed vs. pure stands becoming weaker, due to changes in resource acquisition and species interactions with stand development (Cavard et al., 2011, Battipaglia et al 2017). In this study, we considered two important tree species, Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.), which are widely distributed throughout Europe (Pretzsch et al., 2015). Scots pine and European beech growing in mono-specific and mixed-species stands allow for inferring the effects of admixture on functional

traits and tree growth, comparing an early and light-demanding conifer and a late-successional and shade-tolerant broad-leaves (del Río et al., 2016). This mixture was found to show significant mixing effects in terms of productivity and structural heterogeneity (Pretzsch et al., 2016, 2015).

Our main objectives were: (i) to investigate whether there exist differences in WUE_i of Scots pine and European beech growing in mixed-species and mono-specific stands, and their response to drought periods; (ii) to elucidate if mixing tree species of contrasting physiological traits increases stand productivity; (iii) to detect the seasonal climatic signals that control tree-ring $\delta^{13}C$ and $\delta^{18}O$ in the studied species. Aiming at better understanding the inter-specific dynamics of European beech and Scots pine under a global warming scenario, we hypothesized that: (i) differences in productivity between mixed-species and mono-specific stands decrease over time, due to the temporal dynamics of resource partitioning and the species differences in functional traits; (ii) WUE_i is higher in mixed-species than in mono-specific stands, because of complementarity effects; (iii) European beech is more sensitive to climate than Scots pine.

Materials and Methods

Study area

The study area is located near the village of Ranzo (Trento, Northern Italy), at an altitude of about 1000 m a.s.l.. The site morphology is flat or gently sloping, with moderately deep soil, high organic matter content in the surface and bedrock mainly dominated by limestone. Three plots were identified, as hereinafter described. The first two plots are characterized by monospecific stands, dominated respectively by European beech (PF) and Scots pine (PP). The third plot refers to a mixed beech-pine stand (MFP). The plots have similar site conditions in terms of geographical location, topography, aspect, climate, soil substrate, and soil type. The pure stands are used as the reference for the mixed stands and for the quantification of mixing effects. The pure stands were selected when the corresponding species represented ~90% of the stand basal area. The mixed stand was defined as the stand in which the two species of interest together represented at least ~80% of the total stand basal area, and the sum of the basal area of other species was lower than that of each of the two species studied.

Meteorological data and drought index

The climatic data available for the study area cover only a short period and they are also spatially fragmented. For this reason, interpolated climatic data were here used, deriving them from a spatial downscaling of European climate data. In particular, a downscaled version of E-OBS in combination with WorldClim climate surfaces to obtain a 0.0083° (about 1 × 1 km grid) resolution climate data set (Moreno and Hasenauer, 2015) was used. Monthly minimum, mean and maximum temperatures, as well as total monthly precipitation from 1951 to 2012, were considered.

In order to assess climatic anomalies through time and their effects on water availability for tree growth, a multi-scalar drought index (Standardized Precipitation Evapotranspiration Index; SPEI) based on climatic data was calculated (<https://climatedataguide.ucar.edu/climate-data/standardized-precipitation-evapotranspiration-index-spei>). The SPEI uses the monthly difference between precipitation and potential evapotranspiration (PET) at different time scales ($D_i = P_i - PET_i$) and have been proved useful to detect and monitor drought episodes across timescales in a global warming scenario (Vicente-Serrano et al., 2010). It merges the sensitivity of Palmer Drought Severity Index (PDSI) (Palmer, 1965) to changes in evaporation demand with the advantages of the Standardized Precipitation Index (SPI; Mckee et al., 1993). The multi-scalar features of SPEI allow identifying different drought types, their duration and intensity, as well as the time lag of drought episodes (<http://sac.csic.es/spei/home.html>).

Tree sampling and ring-width chronologies

The three study sites were fully inventoried in order to derive the dendrometric state variables at the stand level. Furthermore, in each plot 20 dominant trees were sampled, and two increment cores at breast height were collected from each tree. In order to avoid the effect of wood alteration and exogenous disturbances on ring growth, only trees without abrasion scars or other visible evidence of injury were selected. The summary of structural data is reported in Table 1.

Ring widths were measured with a resolution of 0.01 mm using the LINTAB measurement equipment (Frank Rinn, Heidelberg, Germany) fitted with a Leica MS5 stereoscope (Leica Microsystems, Germany); tree ring widths were visually cross-dated and statistically verified with the software TSAP software package and COFECHA (Holmes, 1983). Once all measurement series had been validated, tree-ring chronologies were developed for the three stands. The ARSTAN program was used to process the tree ring data into final chronologies

(Cook et al., 1990) and the standard deviation (SD), the expressed population signal (EPS) and the mean RBAR were calculated for the three chronologies (Table 2). Ring width was converted into tree basal area increment (BAI) according to the following standard formula:

$$\text{BAI} \sim \pi \cdot (r_n^2 - r_{(n-1)}^2) \quad (1)$$

where r is the radius of the stem at breast height and n is the year of tree-ring formation. In order to examine the mean growth trend for the dominant trees, BAI for each year was averaged over all the individuals, to remove variation in radial growth attributable to increasing circumference. We worked with mean not-standardized BAI values to preserve the long-term cumulative effects of climatic events on tree growth.

Stable isotope analysis

The five best cross-dated trees per site and species (i.e., those showing the highest correlation with the residual ring-width chronology) were selected for carbon and oxygen isotope measurements. Then, tree cores from these selected trees were extracted only for the stable isotope analyses.

Rings corresponding to the same year were pooled into a single sample before analysis. Every ten years, however, tree rings were individually handled and analysed (1951, 1961, etc.) to have an estimate of between-tree variability in the isotopic signal. The resulting samples were homogenized to a fine powder with a ball mixer mill (Retsch MM301, Haan, Germany).

The stable isotope compositions (C and O) were measured at the IRMS Lab (SUN, Caserta, Italy) by continuous-flow isotope ratio mass spectrometry (Delta V plus Thermo electron corporation, Bremen Germany), using 0.06 mg of dry matter for ^{13}C measurements, 0.3-0.6 mg for ^{18}O determinations.

The $\delta^{13}\text{C}$ series were corrected for the Suess Effect (decrease in $\delta^{13}\text{C}$ of atmospheric CO_2 since the beginning of industrialization), resulting from the emission of fossil carbon dioxide, which is depleted in ^{13}C (Francey et al., 1999; McCarroll and Loader, 2004).

The isotopic compositions are expressed in delta notation (‰) relative to accepted reference standards: Vienna Pee Dee belemnite (VPDB) for carbon isotope values and Vienna Standard Mean Ocean Water (VSMOW) for oxygen isotope values. The standard deviation for the repeated analysis of an internal standard (commercial cellulose) was better than 0.2‰ for carbon and better than 0.4 ‰ for oxygen.

Intrinsic water use efficiency (WUE_i)

We used the $\delta^{13}\text{C}$ measured in tree rings to calculate the WUE_i ; since:

$$\delta^{13}\text{C}_{\text{plant}} = \delta^{13}\text{C}_{\text{atm}} - a - (b-a) \cdot (c_i/c_a) \quad (2)$$

where c_i is the internal leaf CO_2 concentration, c_a is the atmospheric CO_2 concentration, a is the fractionation factor due to CO_2 diffusion through stomata (4.4‰) and b is the fractionation factor due to Rubisco enzyme during photosynthesis (27‰).

Deriving c_i from equation 2, the formula reported by Ehleringer and Cerling (1995) was used to calculate WUE_i :

$$\text{WUE}_i = A/g_s = (c_a - c_i)/1.6 \quad (3)$$

where 1.6 is the ratio of diffusivities of water and CO_2 in the atmosphere.

The carbon isotope discrimination Δ represents the difference between the carbon isotopic ratio of atmospheric CO_2 ($\delta^{13}\text{C}_{\text{air}}$) and of plant organic matter ($\delta^{13}\text{C}_{\text{plant}}$), calculated as:

$$\Delta = (\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}})/(1 + \delta^{13}\text{C}_{\text{plant}}) \quad (4)$$

We used $\delta^{13}\text{C}_{\text{air}}$ estimated values for the period 1960–2003 from McCarroll and Loader (2004), and measured values for the period 2004–2012 available online (<http://www.esrl.noaa.gov/gmd/>), while $\delta^{13}\text{C}_{\text{plant}}$ were the values measured in the rings of our samples.

Combining equation 2 and equation 4, we derived c_i as:

$$c_i = c_a \cdot [(\Delta - a)/(b - a)] \quad (5)$$

Inserting c_i from equation 5 into equation 3, we obtain:

$$\text{WUE}_i = (c_a - c_i)/1.6 = [c_a - c_a (\Delta - a/b - a)] \cdot 1/1.6 = c_a \cdot [(1 - (\Delta - a/b - a)) \cdot 1/1.6] \quad (6)$$

Again, a and b are known values and c_a is the concentration of CO_2 in the atmosphere, estimated for each year and obtained by NOAA (<http://www.esrl.noaa.gov/>, Mauna Loa station).

Data treatment and statistical analysis

In order to extract the climatic data within each sampling plot, a multi-step method was developed starting from the European climate data grid proposed by Moreno and Hasenauer (2015).

At first, a R-script was settled to automatically identify, for each inventory plot (X, Y coordinates), the corresponding 1 km² cell from the climatic data grid. The climatic information at local scale were extracted from the grid and then organized using a specifically built C# program. Finally, a R-script was developed using the R-Package ‘SPEI’ for calculating the SPEI from the climatic data sets within each plot.

The BAI and stable isotope values were, therefore, correlated with the monthly precipitation and temperature. In order to simplify and explore the large amount of data, a PCA approach was applied. Multiple correlation analyses were then used and the relations between the considered variables were highlighted using the Pearson's correlation coefficients.

The SPEI was used as composite index of climate data (temperature and precipitation) in order to further clarify the relations between growth-climate variables. The SPEI was calculated for the period ranging from October of the previous year to September of the current year (SPEI12sep). This methodological approach avoids correlating the tree growth-trend to climate parameters in the months following the cessation of the seasonal growth. The correlations were realized within the same species (beech and pine), occurring both in the pure and mixed stands.

A generalized linear mixed model (GLMM) was used taking into consideration the differences in terms of stand and species, incorporating BAI and SPEI, as fixed effects (constant across individuals). Sites were regarded as random effects (varying across individuals). The GLMM makes it possible, incorporating the random effects in the model and allowing the non-independence of the observations (Zuur et al., 2013). Moreover, the intercept and slope of the model were analysed considering the site's random effects. Again, we used the GLMM to assess the impact of forest management on the tree growth trends, taking into account the fixed climate effect and the random site effect. The information on past management options (1992-2009) applied on the three stands was provided by the Corpo Forestale della Provincia Autonoma di Trento. Values of the model output were considered significant at a probability level of 5% and R-squared values were used to assess the impact of random effects (Nakagawa et al., 2013). Afterwards, correlation and time series analyses were carried out using XLSTAT 2013 (Microsoft Corp., Seattle, WA, USA), while the GLMM was carried out using the R software.

Results

BAI, WUE_i, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

Tree chronologies refer to the period 1886-2014; however, since the climatic data were available for a shorter time period, only the time-span 1951-2012 was used for further analyses.

Tree ages varied significantly among the investigated stands: as average (years \pm standard deviation), 124 \pm 5 in PP and 55 \pm 8 in PF; in MFP, tree ages were of 86 \pm 31 and 63 \pm 9 for Scots

pine and European beech, respectively (Table 1).

Trees, in general, showed higher BAI values ($\text{cm}^2 \pm$ standard error) in FP and PP than in MFP. However, BAI of European beech in MFP was lower than that of the same species when growing in PF. Until mid-80s, Scots pine revealed higher BAI when growing in PP than in MFP; later, an opposite trend was observed. Furthermore, a consistent increase of BAI in all stands (except for PP) in the period 1994-2003 was observed (Fig. 1a,b).

Tree-ring $\delta^{13}\text{C}$ -derived WUE_i values ($\mu\text{mol mol}^{-1} \pm$ standard error) in PF ($89 \pm 8 \mu\text{mol mol}^{-1}$) and PP ($84 \pm 7 \mu\text{mol mol}^{-1}$) (Fig. 2a,b, respectively), were higher than those obtained for the corresponding species in MFP (European beech = $67 \pm 10 \mu\text{mol mol}^{-1}$; Scots pine = $71 \pm 11 \mu\text{mol mol}^{-1}$). Moreover, WUE_i showed a slight uptrend over the investigated time-span for all the studied species-stand combination.

European beech showed mean $\delta^{13}\text{C}$ values ($\text{‰} \pm$ standard deviation) higher in PP (-25.02 ± 1) than in MFP (-27.06 ± 1), $p < 0.001$ (Fig. 3a). Again, mean $\delta^{13}\text{C}$ values for Scots pine were higher in PP (-25.33 ± 1) than in MFP (-26.60 ± 1), $p < 0.001$ (Fig. 3b).

European beech showed mean $\delta^{18}\text{O}$ values ($\text{‰} \pm$ standard deviation) similar in PF and MFP (Fig. 4a). On the contrary, mean $\delta^{18}\text{O}$ values for Scots pine were higher in PP ($26.70 \pm 2 \text{‰}$) than in MFP ($25.20 \pm 1 \text{‰}$), $p < 0.001$ (Fig. 4b).

Drought index, growth-climate correlations, and GLMM

Exploratory climate data analysis for the three stands revealed a period of low precipitation between 1991 and 2007 (467 mm per year, on average), while the overall time-span of 1951-2012 was characterized by mean precipitation of 750 mm per year. Details are reported in Figure 5. Temperatures showed a significant increase from 80's onwards, both for maximum and minimum values.

The values of SPEI highlighted a drought period between 1991 and 2007, according to the lower amount of precipitation recorded in the same period (Fig. 1a,b and Fig. 5).

Furthermore, multiple correlation analyses were applied to highlight the relationships between WUE_i , BAI, SPEI and $\delta^{18}\text{O}$. In MFP, a significant and positive correlation between WUE_i and $\delta^{18}\text{O}$ was found, with p-value < 0.001 for European beech ($r=0.363$) and < 0.005 for Scots pine ($r=0.351$). In FP and PP, no significant correlations between WUE_i and $\delta^{18}\text{O}$ were found. A significant and negative correlation between WUE_i and BAI was found in PP ($r=0.365$; $p < 0.005$), while correlations were not significant in FP. A significant and positive

correlation between WUE_i and BAI was found in MFP, but only for European beech ($r=0.449$; $p<0.001$).

We didn't find any significant correlation between SPAI and BAI in all the plots. However, we reported for European beech a negative relation between SPEI and BAI, both in PP and MFP, while Scots pine showed a negative relation between SPEI and BAI, in MFP only. On the contrary, Scots pine showed a positive relation between SPEI and BAI ($r=0.348$), in PP only.

Finally, the GLMM model was used to consider the management as variable, taking into account its effect on tree growth, together with the natural variability of the site and climatic conditions (SPEI12sep). Results highlighted a significant role of forest management (i.e. thinning) in influencing the tree growth across the investigated years. In detail, forest management was significantly related with tree growth ($p<0.05$), while the effect SPEI was not significant. The marginal R squared (R^2_m) values took into account the fixed effects, while the conditional ones (R^2_c) considered the fixed effects plus the random effects. In our case, the random effects increased the R squared (from 0.12 to 0.39), as reported in Table 3.

Discussion

The results obtained on the growth dynamics showed that European beech did not get benefit from growing mixed with Scots pine in MFP, European beech showing consistently higher growth across the examined period in FP than in MFP. Conversely, Pretzsch et al. (2015) highlighted a general overyielding in mixed stands of European beech and Scots pine. However, these authors showed also a large variability in relative productivity from case to case. The mixture of species appeared favourable in terms of tree productivity and radial growth also in other studies (Morin et al., 2011; Hans Pretzsch et al., 2013; Vallet and Pérot, 2011). The reasons for the lack of complementarity effects of ecological traits in the case of European beech are complex (Condés et al., 2013; Kelty, 1992). The late-successional European beech, in our study site, dominated by the close proximity of the Garda Lake and the influence of the Mediterranean Sea, might suffer from the competition with the pioneer Scots pine, when growing in mixed forests, in comparison with central European regions, rarely experiencing prolonged and severe drought (Metz et al., 2016). Nevertheless, MFP with a larger proportion of European beech stand basal area might negatively affect the growth of Scots pine, closing the canopy and excluding the species that is less shade-tolerant. In order to investigate this hypothesis, we explored the climatic conditions across the examined years, portrayed by SPEI that integrate precipitation and evapotranspiration signals.

Target trees, whose competitive ground consisted of neighbouring stands, were characterized by similar climate conditions. Forrester (2014) demonstrated that increasing resilience and resistance to climatic stress were inferred by the interactions between European beech and Scots pine. However, optimal growth induced by mixtures is also a matter of stand structure other than of species proportion only (Manso et al., 2015). Indeed, visible differences in European beech growth between PF and MFP in the present study might be related to management legacy and sampling bias (we sampled dominant trees). It is worth noting that dominant Scots pine, starting from mid-80s, limited their growth to a larger extent in PP than in MFP. Complementarity processes might have a role in this behavior, Scots pine probably benefiting from improved water availability and the contiguity with the drought sensitive European beech. The stress-gradient hypothesis theorizes that complementarity in belowground resources uptake should become manifest in water limited sites (Bertness and Callaway, 1994), namely under conditions of scarce water supply (Pretzsch et al., 2013).

Nevertheless, starting from the 90s, the growth of Scots pine declined in PP in comparison with MFP. The pattern of SPEI (1991-2007 time-span) revealed relatively adverse climatic conditions. According to the drought classification system of Mckee et al. (1993), SPEI (i.e., SPEI12sep) highlighted only two years as severely dry (i.e., 2000 and 2003); while most of the remaining years of the period 1991-2007 were identified as moderately dry or mild dry. These levels of water stress alone hardly decreased the growth performance of Scots pine, which rather experienced the negative decrease of radiation intensity once the canopy closed, as opposed to the very shade-tolerant European beech.

Although the sensitivity of European beech, in terms of growth trends, under climatic oscillations and water deficits is well known (Nielsen and Jørgensen, 2003; Rose et al., 2009; Metz et al., 2013; Cavin and Jump, 2016), also in this species we did not observe a collapse of tree growth in severe dry years. Several studies highlighted high resistance of European beech to drought episodes, both in pure and mixed stands (e.g., Tegel et al., 2014). Moreover, the extreme drought of 2003 in Central Europe did not result in a substantial radial growth reduction for European beech (Leuzinger et al., 2005).

The only positive relation between BAI and SPEI (despite not significant) was observed for the Scots pine in PP. Indeed, the analysis of BAI highlighted growth trends above average during the period 1994-2003, though this was not the case for Scots pine in PP. These results induced to consider the human-induced disturbances (e.g., forest management) as focal determinant of differences in growth patterns between tree species and amid forest types. The GLMM used to assess the impact of forest management on tree growth, considering the years

interested by customary thinning (thinning from below of moderate intensity), showed a significant and positive correlation between management interventions and growth trends, for the time-span 1991-2007. Indeed, the shift in the relationship between BAI and SPEI, in the 90s and early 00s, could be explained with more resources becoming available to the remaining trees. The legacy of forest management was more influent in determining shift in tree growth than climatic variation, across the considered time period and in the local environmental condition.

Differences between pure and mixed stands were more clearly defined by WUE_i . An increase in WUE_i , due to variation in $\delta^{13}C$ might potentially lead to higher tree growth and productivity (e.g., Duquesnay et al., 1998; Peñuelas et al., 2008; Battipaglia et al., 2013; Tognetti et al., 2014; Giammarchi et al., 2016). Higher $\delta^{13}C$ -derived WUE_i values were observed for European beech in FP than in MFP, while a positive correlation between WUE_i and BAI was found in MFP only, which questions the effect of increased photosynthetic capacity on stem radial increment (Silva et al., 2009). However, changes in $\delta^{13}C$ might be also induced by additional factors, such as drought, high temperature and nutrient limitation (Peñuelas et al., 2011; Silva et al., 2010; Switsur and Waterhouse, 1998). Accordingly, Scots pine showed a decrease of BAI in PP, since the 90s, while the corresponding WUE_i values increased. As the correlations between BAI and SPEI were not significant, the reason of this contrasting trend could be attributed to factors other than strictly climatic, such as nutrient limitation (Cavard et al., 2011). Furthermore, forest management did not affect Scots pine in PP, as opposed to the same species in MFP. The increase in WUE_i , without univocal effect on tree growth, poses issues on whether WUE_i reflected actual physiological responses to changing climate conditions; indeed, nitrogen deposition and other drivers potentially affecting gas exchange might also have an impact on WUE_i .

In general, WUE_i (as well as $\delta^{13}C$) remained higher in FP and PP than in MFP throughout the investigated period. Conversely, other studies showed opposite WUE_i patterns, with greater values in mixed than in monospecific stands (Forrester, 2015; Pretzsch et al., 2012). This divergence could depend on the site-specific conditions (Forrester, 2014). In particular, climate at our site was moderately moist, without prolonged episodes of extreme drought. The lack of coupling amongst climatic, physiologic and growth indices is consistent with oscillating climate patterns (Tognetti et al., 2014). Therefore, the investigated species, generally, did not need to enable all the complementary resource use mechanisms (Kelty, 2006; Richards and Schmidt, 2010), resulting in increased water use efficiency, as shown in

other climatic contexts (González de Andrés et al., 2016).

Fluctuations of $\delta^{13}\text{C}$ in tree rings are associated with both variations in stomatal conductance and photosynthetic capacity, making it difficult to discern whether differences between stands in WUE_i were due more to changes in the photosynthetic capacity or stomatal conductance. Indeed, $\delta^{13}\text{C}$ in tree rings reflect c_i/c_a , which depends on photosynthetic capacity and the response of stomatal conductance to water availability (Farquhar et al., 1989). Variation in c_i (and stomatal conductance), this reduction inducing enrichment in ^{13}C , would impact $\delta^{13}\text{C}$ variability across tree rings, although certain variance in $\delta^{13}\text{C}$ might eclipse long-term trends of c_i regulation (Cullen et al., 2008). However, in contrast to $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ is insensitive to photosynthetic capacity, reflecting the isotopic signature of source water taken up during its formation and the effects of evaporation and diffusion during transpiration (Gessler et al., 2014; Roden and Farquhar, 2012; Scheidegger et al., 2000). No significant changes in $\delta^{18}\text{O}$ were observed for European beech (FP vs. MFP), while $\delta^{18}\text{O}$ of Scots pine was higher in PP than in MFP.

Overall, the relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was weak (not shown), across tree species and forest types, suggesting that variation in photosynthetic capacity exerted a major influence on c_i and $\delta^{13}\text{C}$ (Tognetti et al., 2014). Therefore, according to the conceptual model developed by Scheidegger et al. (2000), the variation of WUE_i was mainly attributable to an increase in the photosynthetic rate, and stomata operated over a limited range (e.g., Chang et al. 2016). Conversely, a positive relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ would occur if stomatal conductance is more limiting to photosynthesis than photosynthetic capacity, all else being equal. Given that photosynthetic capacity controlled tree-ring $\delta^{13}\text{C}$ signatures, photosynthetic capacity could be a dominant driver of carbon source-sink dynamics in these forest ecosystems.

Water use of Scots pine appeared to be more conservative in PP than in MFP. However, Scots pine in PP was affected by the drought period, recorded as SPEI. This confirmed that the mixing of the two species had positive effects on Scots pine water relations. However, attention must be paid when interpreting WUE_i and $\delta^{18}\text{O}$ results, since the role of forest management was also an important driver of tree growth and physiological behaviour. In addition, uncertainties in the interpretation of the dual-isotope conceptual model might derive from partial decoupling between the leaf signals (recording instantaneous gas exchange and the response to climate) and the wood or cellulose signals (storing historic ecophysiological records) (Gessler et al., 2014).

Conclusion

Many studies showed that mixed forests are more productive and resistant to disturbances than corresponding mono-specific stands. Other studies explained that this is not always true. In general, our results showed that pure stands had higher growth performance than the mixed one, at least in the current site conditions, without decreasing over time. Contradicting our initial hypothesis, WUE_i was found to be higher in pure stands of both species. Complementarity effect provided a positive contribution only to Scots pine and only in the drought period, as identified by SPEI. European beech was not affected by this level of drought, and showed higher BAI in the pure stand. Furthermore, we found that during the drought period, BAI showed higher values (except for Scots pine in the pure stand). This could be associated to moderate thinning, affecting tree growth more than environmental variables.

The complexity of the relationships between the two species, but also the contrasting results here obtained when compared with other studies, suggest caution in addressing questions on the adaptive capacity of mixed forest stands to climate change. The availability of detailed information on site-specific environmental conditions, but also on legacies associated with silvicultural treatments, is fundamental to assess the interactions between the investigated species and possible impacts of climate change.

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References

- Anderegg WR, Martinez-Vilalta J, Cailleret M et al. (2016b) When a tree dies in the forest: scaling climate driven tree mortality to ecosystem water and carbon fluxes. *Ecosystems*, 19, 1133-1147.
- Barnard, H.R., Brooks, J.R., Bond, B.J., 2012. Applying the dual-isotope conceptual model to interpret physiological trends under uncontrolled conditions. *Tree Physiol.* 32, 1183–1198.
- Brassard, B.W., Chen, H.Y.H., Cavard, X., Laganière, J., Reich, P.B., Bergeron, Y., Paré, D., Yuan, Z., 2013. Tree species diversity increases fine root productivity through increased soil volume filling. *J. Ecol.* 101, 210–219.
- Bertness, M.D. and Callaway, R. 1994 Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193.
- Cavard, X., Bergeron, Y., Chen, H.Y.H., Paré, D., Laganière, J., Brassard, B., 2011. Competition and facilitation between tree species change with stand development. *Oikos* 120, 1683–1695.
- Cavin, L., Jump, A.S., 2016. Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. *Glob. Chang. Biol.* 23, 362–379.
- Cavin, L., Mountford, E.P., Peterken, G.F., Jump, A.S., 2013. Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Funct. Ecol.* 27, 1424–1435.
- Chang, C.Y.-Y., Fréchet, E., Unda, F., Mansfield, S.D., Ensminger, I., 2016. Elevated temperature and CO₂ stimulate late season photosynthesis but impair cold hardening in pine. *Plant Physiology*, 172, 802-818.
- Condés, S., del Río, M., 2015. Climate modifies tree interactions in terms of basal area growth and mortality in monospecific and mixed *Fagus sylvatica* and *Pinus sylvestris* forests. *Eur. J. For. Res.* 134, 1095–1108.
- Condés, S., Del Rio, M., Sterba, H., 2013. Mixing effect on volume growth of *Fagus sylvatica* and *Pinus sylvestris* is modulated by stand density. *For. Ecol. Manage.* 292, 86–95.
- Cook, E.R., Briffa, K., Shiyatov, S., Mazepa, V., 1990. Tree-ring standardization and growth-trend estimation, *Methods of dendrochronology: applications in the environmental sciences.* 104-123.
- Cullen LE, Adams MA, Anderson MJ, Grierson PF 2008. Analyses of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in tree rings of *Callitris columellaris* provide evidence of a change in stomatal control of photosynthesis in response to regional changes in climate. *Tree Physiology* 28, 1525–1533.
- del Río, M., Pretzsch, H., Ruíz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Drössler, L., Fabrika, M., Forrester, D.I., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Madrickiene, E., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Zlatanov, T.M., Bravo-Oviedo, A., 2016. Species interactions increase the temporal stability of community productivity in *Pinus sylvestris*-*Fagus sylvatica* mixtures across Europe. *Journal of Ecology*. doi:10.1111/1365-2745.12727.
- Epron, D., Nouvellon, Y., Mareschal, L., Moreira, R.M. e, Koutika, L.S., Geneste, B., Delgado-Rojas, J.S., Laclau, J.P., Sola, G., Gonçalves, J.L. de M., Bouillet, J.P., 2013. Partitioning of net primary production in Eucalyptus and Acacia stands and in mixed-species plantations: Two case-studies in contrasting tropical environments. *For. Ecol.*

Manage. 301, 102–111.

- Duquesnay A, Bréda N, Stievenard M, Dupouey JL (1998) Changes of tree-ring $\delta^{13}\text{C}$ and water-use efficiency of beech (*Fagus sylvatica* L.) in north-eastern France during the past century. *Plant, Cell and Environment* 21: 565–572.
- Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon Isotope Discrimination and Photosynthesis. *Annu. Rev. Plant Physiol. and Plant Mol. Biol.* 40, 503–537.
- Forrester, D.I., 2015. Transpiration and water-use efficiency in mixed-species forests versus monocultures: Effects of tree size, stand density and season. *Tree Physiol.* 35, 289–304.
- Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. *For. Ecol. Manage.* 312, 282–292.
- Forrester, D.I., Albrecht, A.T., 2014. Light absorption and light-use efficiency in mixtures of *Abies alba* and *Picea abies* along a productivity gradient. *For. Ecol. Manage.* 328, 94–102.
- Francey, R.J., Allison, C.E., Etheridge, D.M., Trudinger, C.M., Enting, I.G., Leuenberger, M., Langenfelds, R.L., Michel, E., Steele, L.P., 1999. A 1000-year high precision record of $\delta^{13}\text{C}$ in atmospheric CO_2 . *Tellus, Ser. B Chem. Phys. Meteorol.* 51, 170–193.
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Froberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andren, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun.* 4, 1340.
- Gessler, A., Ferrio, J.P., Hommel, R., Treydte, K., Werner, R.A., Monson, R.K., 2014. Stable isotopes in tree rings: Towards a mechanistic understanding of isotope fractionation and mixing processes from the leaves to the wood. *Tree Physiol*, 34, 796–818.
- Giammarchi, F., Cherubini, P., Pretzsch, H., Tonon, G., 2016. The increase of atmospheric CO_2 affects growth potential and intrinsic water-use efficiency of Norway spruce forests: insights from a multi-stable isotope analysis in tree rings of two Alpine chronosequences. *Trees - Struct. Funct.* 1–13.
- Gonzalez, P., Neilson, R.P., Lenihan, J.M., Drapek, R.J., 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Glob. Ecol. Biogeogr.* 19, 755–768.
- González de Andrés, E., Seely, B., Blanco, J.A., Bosco Imbert, J., Lo, Y.-H., Castillo, F.J., 2016. Increased complementarity in water-limited environments in Scots pine and European beech mixtures under climate change. *Ecohydrology*. e1810.
- Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruehlheide, H., Čečko, E., Forrester, D.I., Dawud, S.M., Finér, L., Pollastrini, M., Scherer-Lorenzen, M., Valladares, F., Bonal, D., Gessler, A., 2014. Tree diversity does not always improve resistance of forest ecosystems to drought. *Proc. Natl. Acad. Sci.* 111, 14812–14815.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bull.* 43(1), 69–78.
- Kelty, M.J., 2006. The role of species mixtures in plantation forestry. *For. Ecol. Manage.* 233, 195–204.
- Kelty, M.J., 1992. Comparative productivity of monocultures and mixed-species stands, in: *The Ecology and Silviculture of Mixed-Species Forests*. Springer Netherlands, pp. 125–141.
- Leuzinger, S., Zotz, G., Asshoff, R., Körner, C., 2005. Responses of deciduous forest trees to severe drought in Central Europe. *Tree Physiol.* 25, 641–650.
- Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120, 1909–1920.
- Loreau, M.; Naeem, S.; Inchausti, P.; Bengtsson, J.; Hector, A.; Hooper, D.U.; Huston, M.A.;

- Raffaelli, D.; Tilman, D.; Wardle, D.A.; Grime, J.P.; Schmid, B., 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science*. 294, 804–808.
- Manso R., Morneau F., Ningre F., Fortin M., 2015. Effect of climate and intra- and inter-specific competition on diameter increment in beech and oak stands. *Forestry* 88: 540 (2015).
- McCarroll, D., Loader, N.J., 2004. Stable isotopes in tree rings. *Quat. Sci. Rev.* 23, 771–801.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytol.* 178, 719–739.
- Mckee, T.B., Doesken, N.J., Kleist, J., 1993. The relationship of drought frequency and duration to time scales. *AMS 8th Conf. Appl. Climatol.* 179–184.
- Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. *For. Ecol. Manage.* 339, 22–33.
- Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E.-D. and Ammer, C. (2016), Site-adapted admixed tree species reduce drought susceptibility of mature European beech. *Glob Change Biol*, 22: 903–920.
- Metz, J.Ô., Seidel, D., Schall, P., Scheffer, D., Schulze, E.D., Ammer, C., 2013. Crown modeling by terrestrial laser scanning as an approach to assess the effect of aboveground intra- and interspecific competition on tree growth. *For. Ecol. Manage.* 310, 275–288.
- Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. *Science*, 349, 823–826.
- Moreno, A., Hasenauer, H., 2015. Spatial downscaling of European climate data. *Int. J. Climatol.* 36, 1444–1458.
- Morin, X., Fahse, L., Scherer-Lorenzen, M., Bugmann, H., 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecol. Lett.* 14, 1211–1219.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142.
- Nielsen, C.N., Jorgensen, F. V, 2003. Phenology and diameter increment in seedlings of European beech (*Fagus sylvatica* L.) as affected by different soil water contents: variation between and within provenances. *For. Ecol. Manage.* 174, 233–249.
- Niinemets, Ü., 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *For. Ecol. Manage.* 260, 1623–1639.
- Peñuelas J, Hunt JM, Ogaya R, Jump AS (2008) Twentieth century changes of tree-ring $\delta^{13}C$ at the southern range-edge of *Fagus sylvatica*: increasing water use efficiency does not avoid the growth decline induced by warming at low altitudes. *Global Change Biology* 14: 1076–1088.
- Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Glob. Ecol. Biogeogr.* 20, 597–608.
- Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.P., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M., Zingg, A., 2013. Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *Eur. J. For. Res.* 132, 263–280.
- Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G.,

- Coll, L., Dirnberger, 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., Vanhellefont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A., 2015. 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.
- 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.
- Pretzsch, H., Dieler, J., 2011. The dependency of the size-growth relationship of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in forest stands on long-term site conditions, drought events, and ozone stress. *Trees - Struct. Funct.* 25, 355–369.
- Pretzsch, H., Dieler, J., Seifert, T., Rötzer, T., 2012. Climate effects on productivity and resource-use efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in stands with different spatial mixing patterns. *Trees - Struct. Funct.* 26, 1343–1360.
- Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. *Plant Biol.* 15, 483–495.
- Pretzsch, H., Uhl, E., Biber, P., Schütze, G., Coates, K.D., 2012. Change of allometry between coarse root and shoot of Lodgepole pine (*Pinus contorta* DOUGL. ex. LOUD) along a stress gradient in the sub-boreal forest zone of British Columbia. *Scand. J. For. Res.* 27, 532–544.
- Richards, A.E., Schmidt, S., 2010. Complementary resource use by tree species in a rain forest tree plantation. *Ecol. Appl.* 20, 1237–1254.
- Roden, J.S., Farquhar, G.D., 2012. A controlled test of the dual-isotope approach for the interpretation of stable carbon and oxygen isotope ratio variation in tree rings. *Tree Physiol.* 32, 490–503.
- Rose, L., Leuschner, C., Köckemann, B., Buschmann, H., 2009. Are marginal beech (*Fagus sylvatica* L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research*, 128(4), 335-343.
- Scheidegger, Y., Saurer, M., Bahn, M., Siegwolf, R., 2000. Linking Stable Oxygen and Carbon Isotopes with Stomatal Conductance and Photosynthetic Capacity: A Conceptual Model. *Oecologia* 125, 350–357.
- Schröter D, Cramer W, Leemans R, Prentice IC, Araújo MB, Arnell NW, Bondeau A, Bugmann H, Carter TR, Gracia CA, De La Vega-Leinert AC, Erhard M, Ewert F, Glendining M, House JI, Kankaanpää S, Klein RJT, Lavorel S, Lindner M, Metzger MJ, Meyer J, Mitchell TD, Reginster I, Rounsevell M, Sabaté S, Sitch S, Smith B, Smith J, Smith P, Sykes MT, Thonicke K, Thuiller W, Tuck G, Zaehle S, Zierl B (2005) Ecology: Ecosystem service supply and vulnerability to global change in Europe. *Science* 310: 1333–1337.
- Silva, L.C.R., Anand, M., Leithead, M.D., 2010. Recent widespread tree growth decline despite increasing atmospheric CO₂. *PLoS One* 5, e11543.

- Silva, L.C.R., Anand, M., Oliveira, J.M., Pillar, V.D., 2009. Past century changes in *Araucaria angustifolia* (Bertol.) Kuntze water use efficiency and growth in forest and grassland ecosystems of southern Brazil: implications for forest expansion. *Glob. Chang. Biol.* 15, 2387–2396.
- Stenger, A., Harou, P., Navrud, S., 2009. Valuing environmental goods and services derived from the forests. *J. For. Econ.* 15, 1–14.
- Switsur, R., Waterhouse, J., 1998. Stable isotopes in tree ring cellulose. In: Griffiths H (ed) *Stable isotopes: integration of biological, ecological and geochemical processes*. BIOS, Oxford, pp 303–321.
- Tegel, W., Seim, A., Hakelberg, D., Hoffmann, S., Panev, M., Westphal, T., Büntgen, U., 2014. A recent growth increase of European beech (*Fagus sylvatica* L.) at its Mediterranean distribution limit contradicts drought stress. *Eur. J. For. Res.* 133, 61–71.
- Tognetti, R., Lombardi, F., Lasserre, B., Cherubini, P., Marchetti, M., 2014. Tree-ring stable isotopes reveal twentieth-century increases in water-use efficiency of *Fagus sylvatica* and *Nothofagus* spp. in Italian and Chilean Mountains. *PLoS One* 9(11), e113136.
- Toïgo, M., Vallet, P., Perot, T., Bontemps, J.D., Piedallu, C., Courbaud, B., 2015. Overyielding in mixed forests decreases with site productivity. *J. Ecol.* 103, 502–512.
- Vallet, P., Pérot, T., 2011. Silver fir stand productivity is enhanced when mixed with Norway spruce: Evidence based on large-scale inventory data and a generic modelling approach. *J. Veg. Sci.* 22, 932–942.
- van der Maaten, E., 2012. Climate sensitivity of radial growth in European beech (*Fagus sylvatica* L.) at different aspects in southwestern Germany. *Trees - Struct. Funct.* 26, 777–788.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *J. Clim.* 23, 1696–1718.
- Yachi, S., Loreau, M., 2007. Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. *Ecol. Lett.* 10, 54–62.
- Zang, C., Pretzsch, H., Rothe, A., 2012. Size-dependent responses to summer drought in Scots pine, Norway spruce and common oak. *Trees - Struct. Funct.* 26, 557–569.
- Zuur A.F., Hilbe J.M., Ieno E.N., 2013. *A beginner's Guide to GLM and GLMM with R: a frequentist and Bayesian perspective to ecologists*. Highland Statistics Ltd., Newburgh.

Tables

Table 1. Stand characteristics of the triplet of pure and mixed-species stands. Tree number, N (trees ha⁻¹); stand basal area, BA (m² ha⁻¹); standing volume, V (m³ ha⁻¹); mean tree diameter, DBH (cm); mean tree height, H (m); mean tree age, Ma (years +/- std. dev.); tree age range, AR (years).

	Pure stand (PP)	Pure stand (PF)	Mixed stand (MFP)	
	Scots pine	European beech	Scots pine	European beech
N (trees ha ⁻¹)	410.0	370.0	139.0	322.0
BA (m ² ha ⁻¹)	52.0	23.0	12.0	10.0
V (m ³ ha ⁻¹)	456.0	240.0	84.0	66.0
DBH (cm)	40.2	28.2	33.0	20.0
H (m)	18.1	19.2	13.8	13.6
Ma (years+/-std.dev.)	124±5	55±8	86±31	63±9
AR (years)	106-135	44-74	47-128	41-77

Table 2. Descriptive statistics for the raw tree-ring chronologies. Standard deviation (SD); the expressed population signal, EPS; the average correlation between all series, RBAR.

	Pure stand (PP)	Pure stand (PF)	Mixed stand (MFP)	
	Scots pine	European beech	Scots pine	European beech
Time span	1886-2014	1942-2014	1887-2014	1938-2014
SD	1.04	0.81	0.7	0.66
EPS	0.91	0.94	0.85	0.92
RBAR	0.35	0.53	0.33	0.41

Table 3. Summary of the GLMM (*Generalized linear mixed model*), after programming with. SPEI12sep relates to the time scale (12 months from October of the previous year to September of the current year); Management is related to the Boolean variable of management; R²m: marginal R squared; R²c: conditional R squared.

	Intercept	SPEI12sep	Management
Estimate	6.9691	-1.1638	1.9603
Standard Error	0.6348	0.8662	0.7783
t value	10.978	-1.344	2.519
Pr(> t)	0.00125**	0.26863	0.01245*

R² GLMM

R ² m	R ² c
0.1218021	0.319571

Figures

Figure 1a. SPEI (SPEI12sep - grey line) and BAI in cm^2 with standard error for European beech in PF (dotted black line) and MFP (dashed grey line). The dark grey line indicates the SPEI threshold of -1.5 (indicative of severe drought).

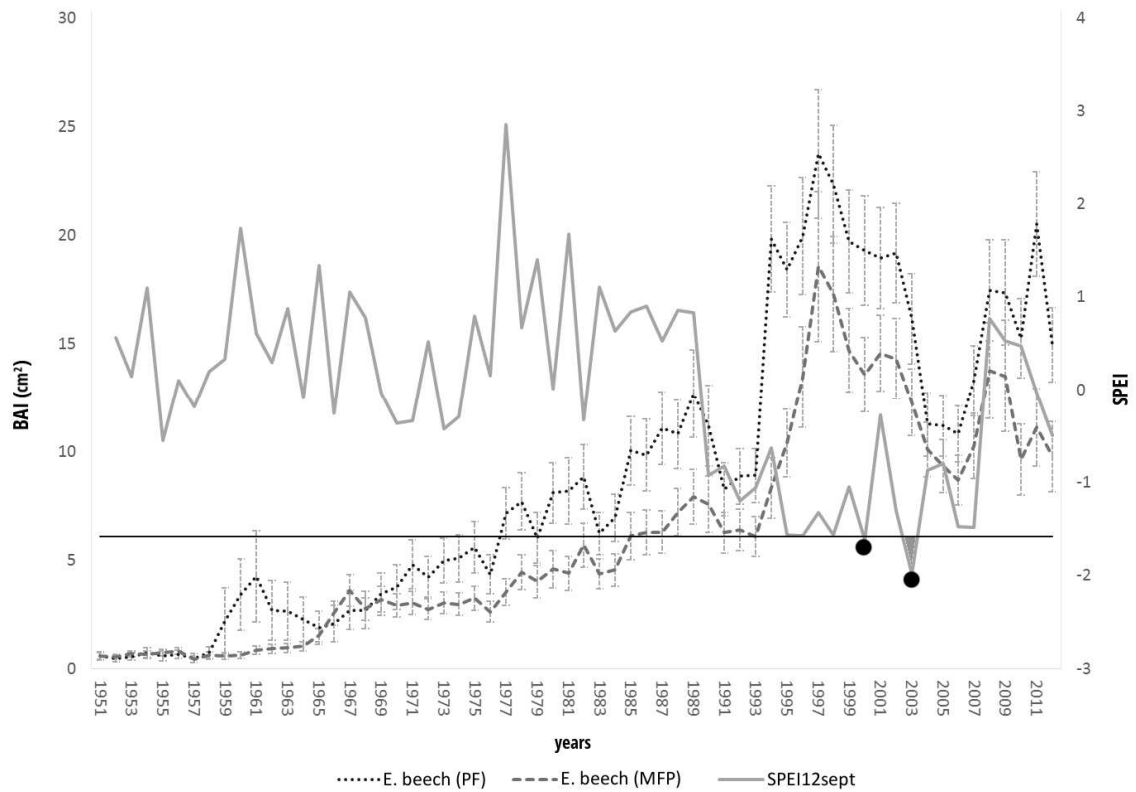


Figure 1b. SPEI (SPEI12sep - grey line) and BAI in cm² with standard error for Scots pine in PF (dotted black line) and MFP (dashed grey line). The dark grey line indicates the SPEI threshold of -1.5 (indicative of severe drought).

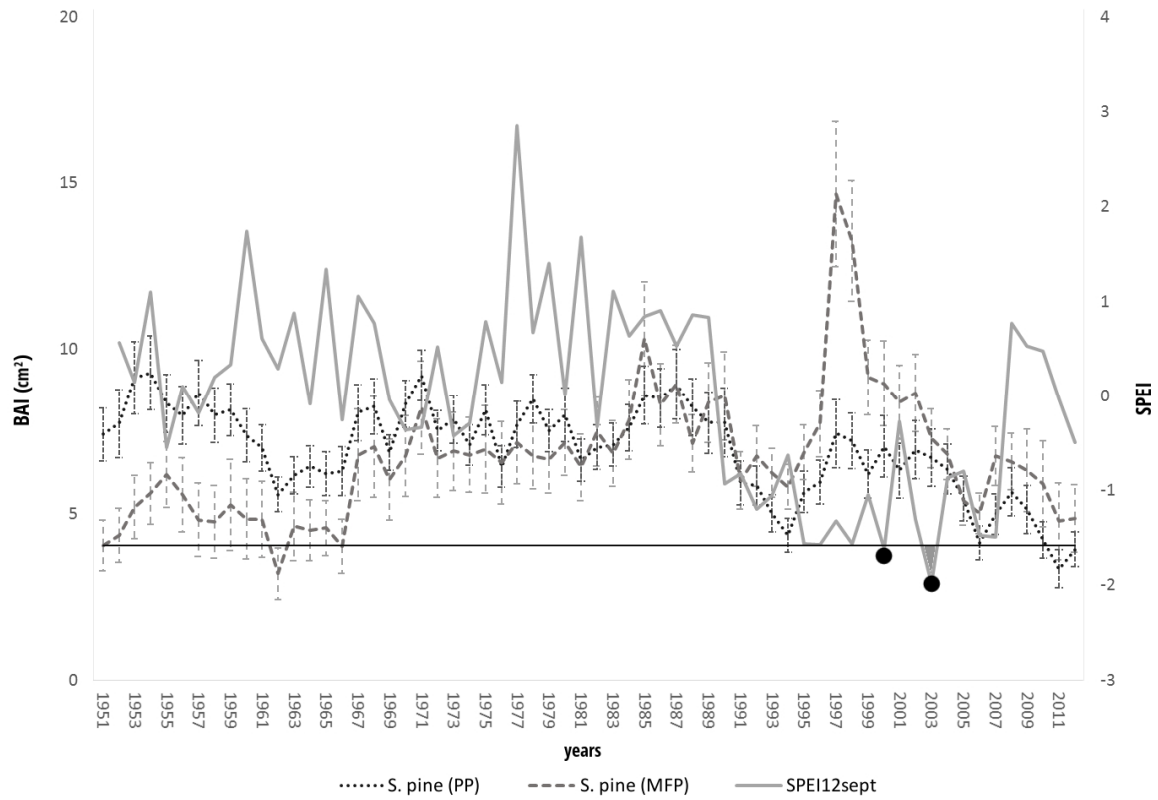


Figure 2a. Mean WUE_i values in $\mu\text{mol mol}^{-1}$ with standard deviation for European beech in PF (black line) and MFP (grey line).

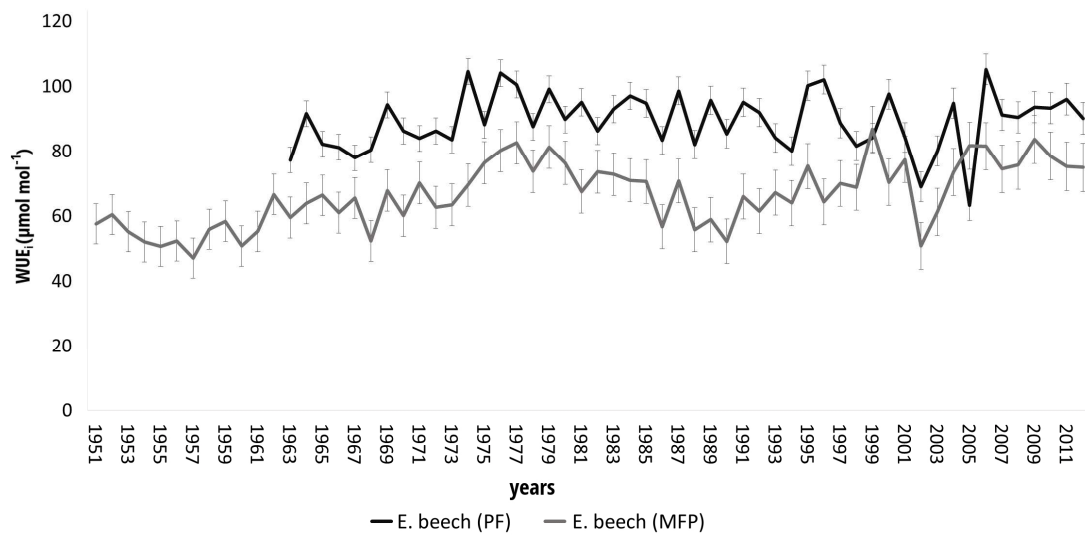


Figure 2b. Mean WUE_i values in $\mu\text{mol mol}^{-1}$ with standard deviation for Scots pine in PF (black line) and MFP (grey line).

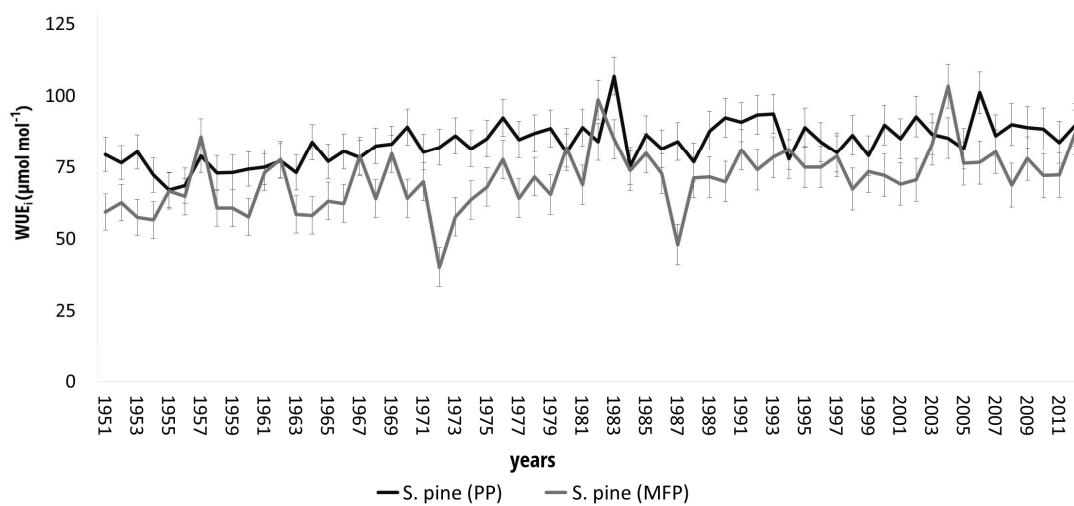


Figure 3a. Mean $\delta^{13}\text{C}$ values in ‰ with standard deviation for European beech in PF (black line) and MFP (grey line).

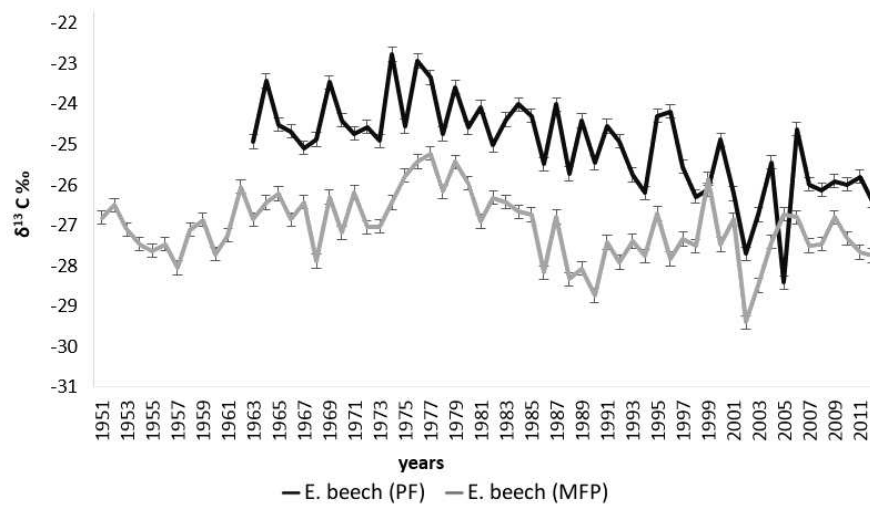


Figure 3b. Mean $\delta^{13}\text{C}$ values in ‰ with standard deviation for Scots pine in PF (black line) and MFP (grey line).

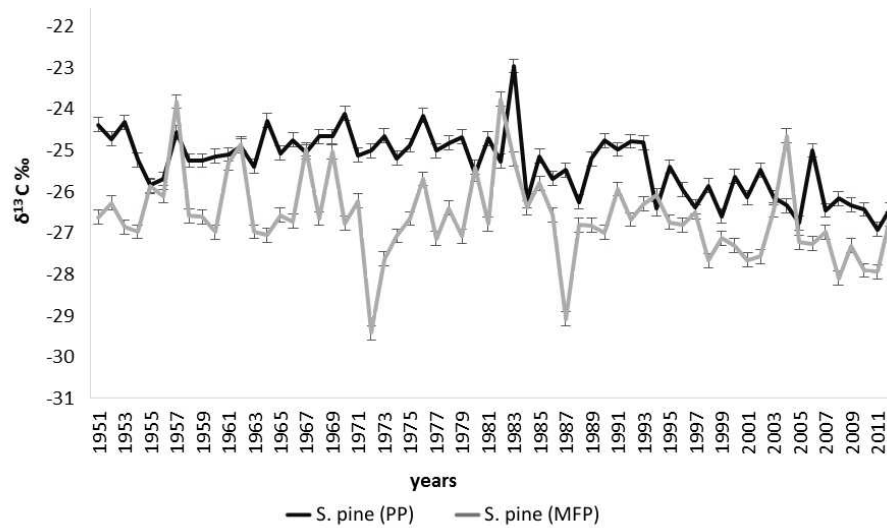


Figure 4a. Mean $\delta^{18}\text{O}$ values in ‰ with standard deviation for European beech in PF (black line) and MFP (grey line).

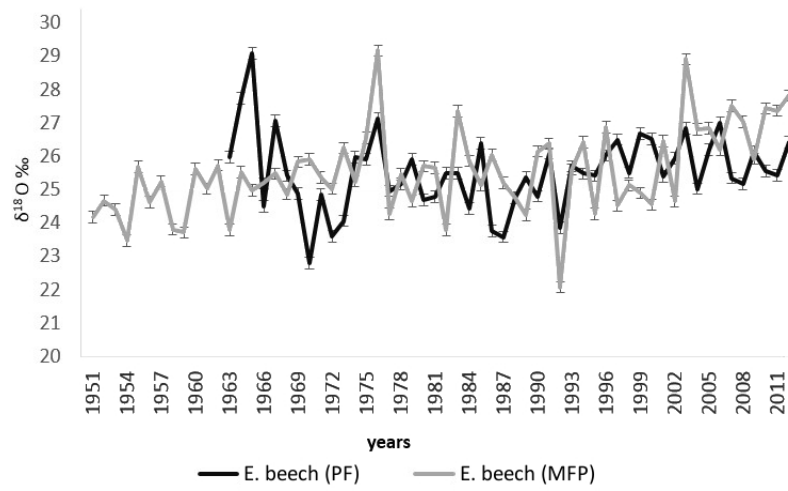


Figure 4b. Mean $\delta^{18}\text{O}$ values in ‰ with standard deviation for Scots pine in PF (black line) and MFP (grey line).

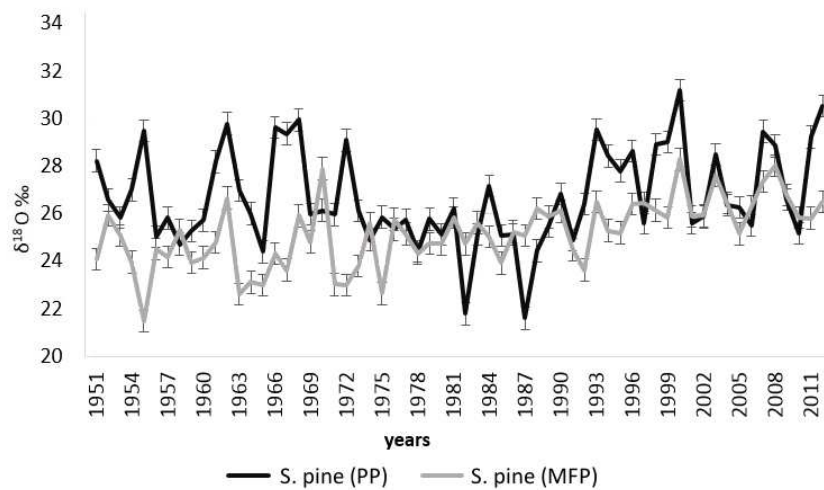


Figure 5. Mean annual precipitation in mm for the period 1951-2012. Original data set available at <ftp://palantir.boku.ac.at/Public/ClimateData> (Moreno and Hasenauer, 2015).

