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

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## ABSTRACT

Understanding to what extent species mixtures modify the growth of trees and their responses to climate, in comparison with pure stands, is important to support forest adaptation and mitigation strategies. In this sense, information stored in tree rings can be useful to evaluate whether the positive relationship between species diversity and tree productivity holds true under disturbance (e.g., drought). This paper aimed at assessing (i) how radial growth of trees responded to local variation in climate patterns (*Standardised Precipitation-Evapotranspiration Index*; SPEI), and (ii) whether there was a relationship with intrinsic water use efficiency (WUE$_i$) and tree-ring $\delta^{18}$O in two important tree species, occurring in pure and mixed forest stands. Three sites with similar topographic and pedo-climatic conditions were identified in a single location in the Italian Alps. The first two are characterized by pure 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 previous species. In particular, in order to assess the annual changes in WUE$_i$, we analysed $\delta^{13}$C in tree rings. The influence of the stomatal conductance was also investigated through $\delta^{18}$O. Our results indicated that: (i) Basal Area Increments (BAI) consistently increased in all stands except for the pure Scots pine stand, in the 1994–2003 period; (ii) SPEI highlighted a drought period between 1991 and 2007 (62.2% of the average precipitation); and (iii) the WUE$_i$ values were generally higher in pure than in mixed stands, especially for European beech. The divergence between BAI and SPEI values in the 1990s and early 2000s could be a consequence of moderate thinning. We conclude that past forest management (namely thinning) can be more influential on tree growth than current climatic oscillations.

## 1. 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 for 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 pure stands (Pretzsch et al., 2013b) and may provide higher levels of multiple ecosystem services (Gamfeldt et al., 2013; Loreau et al., 2001). Enhanced forest productivity in mixed stands can be attributed to the niche complementarity, which reduces the competition for resources (Morin et al., 2011), and in facilitation between the two populations of trees (Yachi and Loreau, 2007). Differences between species in shade tolerance, crown phenology, canopy structure, root depth and rhizosphere microbiome were associated with

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increased productivity in mixed stands (Berendsen et al., 2012; Brassard et al., 2013; Forrester and Albrecht, 2014; Toïgo et al., 2015). Observations that higher plant diversity may lead to greater ecosystem productivity aroused considerable interest and controversy over the recent decades (Naeem et al., 1994; Tilman and Downing, 1994). Major advances were made in understanding the factors that influence the assembly of plant communities and in revealing complementarity mechanisms that affect ecosystem functioning, especially in grassland ecosystems (Grime, 1997; Tilman et al., 2014).

The theoretical model on niche complementarity and efficiency of resource utilization predicts that individual plant productivity diminishes under biodiversity loss with an increasing rate, while all other factors stay constant (including the number of individuals) (Liang et al., 2015). Based on ground-sourced data, Liang et al. (2016) revealed a globally consistent positive biodiversity-productivity relationship, suggesting that continued biodiversity loss would result in an accelerating decline in forest productivity worldwide. However, mixed-species forests are not always more productive and stable than pure 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., 2017). Understanding the dynamics (growth, resistance, productivity, etc.) of mixed forests is 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 mountain 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; Palombo et al., 2014). 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., 2013b). 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., 2012b), 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 ($\delta^{13}C$, $\delta^{18}O$) 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 $\delta^{13}C$ 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 $\delta^{13}C$, though light limitation of photosynthesis increases $c_i$. Conversely, tissue $\delta^{18}O$ is not strongly influenced by photosynthetic rate, being controlled by the source water $\delta^{18}O$, and land-plant water exchange, so that combined measurements of $\delta^{13}C$ and $\delta^{18}O$ allow stomatal and photosynthetic effects on $\delta^{13}C$ to be teased apart (Barnard et al., 2012; Scheidegger et al., 2000; Tognetti et al., 2014).

Below-ground and above-ground mixing effects may 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 (Battipaglia et al., 2017; Cavard et al., 2011). 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 pure and mixed-species stands allow for inferring the effects of admixture on functional traits and tree growth, comparing an early-successional and light-demanding conifer and a late-successional and shade-tolerant broad-leaved deciduous tree species (del Río et al., 2017). 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 determine if mixing tree species of contrasting physiological traits increases stand productivity; (ii) to investigate whether there are differences in $WUE_i$ of Scots pine and European beech growing in mixed-species and pure stands, and their response to drought periods; (iii) to detect the seasonal climatic signals that control tree-ring $\delta^{13}C$ and $\delta^{18}O$ in the studied species. Aiming To better understand the interspecific dynamics of European beech and Scots pine under a global warming scenario in Mediterranean mountain conditions, we hypothesized that: (i) differences in productivity between mixed-species and pure 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 pure stands because of complementarity effects; (iii) European beech is more sensitive to variation in climate than Scots pine.

## 2. Materials and methods

### 2.1. Study area

The study area is located near the village of Ranzo (Trento, Northern Italy, centroid: 46°4′2″N, 10°56′3″E), 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 sites were at about 300–400 m from each other and were identified, as hereinafter described. The first two sites are characterized by pure stands, dominated respectively by European beech (PF) and Scots pine (PP). The third site is to a mixed beech-pine stand (MFP). These sites have similar site conditions in terms of geographical location, topography, aspect, climate, bedrock, and soil type. The pure stands are used as the reference for the mixed forest 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 forest was defined as the stand in which the two species of interest together represented at least ∼90% of the total stand basal area.

### 2.2. 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 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-