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Tree-to-tree competition in mixed European beech-Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions

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Running headline: Competition drives growth and iWUE in beech-pine mixedwoods

Summary

1. Mixed conifer-hardwood forests can be more productive than pure forests and they are increasingly considered as ecosystems that could provide adaptation strategies in the face of global change. However, the combined effects of tree-to-tree competition, rising atmospheric CO₂ concentrations and climate on such mixtures remain poorly characterized and understood.
2. To fill this research gap, we reconstructed 34-year series (1980-2013) of growth (basal area increment, BAI) and intrinsic water-use efficiency (iWUE) of Scots pine (*Pinus sylvestris* L.) – European beech (*Fagus sylvatica* L.) mixed stands at two climatically contrasting sites located in the southwestern Pyrenees. We also gathered data on tree-to-tree competition and climate variables in order to test the hypotheses that (i) radial growth will be greater when inter-specific competition exceeds intra-specific competition, i.e. when species complementarity occurs, and (ii) enhanced iWUE could be linked to improved stem radial growth.
3. Growth of both species was reduced when intra-specific competition increased. Species complementarity was linked to improved growth of Scots pine at the continental site, whilst competition overrode any complementarity advantage at the drought-prone Mediterranean site. Beech growth did not show any significant response to pine admixture likely due to shade tolerance and the highly competitive nature of this species. Increasing inter-specific competition drove recent iWUE changes, which increased in Scots pine but decreased in European beech. The iWUE enhancement did not involve any growth improvement in Scots pine. However, the positive BAI-iWUE relationship found for beech suggests an enhanced beech growth in drought-prone sites due to improved water use.
4. *Synthesis.* Complementarity may enhance growth in mixed forests. However, water scarcity can constrict light-related complementarity for shade intolerant species (Scots pine) in drought-prone sites. BAI-iWUE relationships were negative for Scots pine and positive for European beech. These contrasting behaviours have got implications for coping with the expected increasing drought events in Scots pine-European beech mixtures located near the ecological limit of the two species. Complementarity effects between tree species should be considered to avoid overestimating the degree of future carbon uptake by mixed conifer-broadleaf forests.

Key words: basal area increment, drought, *Fagus sylvatica*, *Pinus sylvestris*, biotic interactions, stable carbon isotopes, atmospheric CO₂ concentration.

1. Introduction

Over the past two centuries, many anthropogenic influences on the global carbon (C) biogeochemical cycle have been reported (Francey *et al.* 1999). The major human influence on the C cycle is the rapid rise of atmospheric CO₂ concentration (C_a) due to fossil fuels burning and other anthropogenic activities, leading to substantial increases in air temperatures over many regions and to an altered distribution of rainfall in some of them (IPCC 2013). The occurrence of increased C_a coupled with more frequent and intense dry spells in some areas, as in drought-prone southern Europe, is affecting trees' gas-exchange metabolism, water use and radial growth (Peñuelas *et al.* 2008; Andreu-Hayles *et al.* 2011). In controlled experiments, increased C_a enhances trees' photosynthesis and reduces stomatal conductance (Mousseau & Saugier 1992; Norby *et al.* 1999). As a consequence, intrinsic water-use efficiency (iWUE; i.e. the ratio of assimilated C to transpired water) and growth are expected to increase (Farquhar, Ehleringer & Hubick. 1989; Huang *et al.* 2007). In contrast, decreases in soil water potential due to drought can reduce trees' photosynthetic C uptake as trees close stomata to prevent hydraulic dysfunction (Körner 2000).

Thus, on one hand, rising C_a can increase iWUE and improve trees' ability to withstand dry conditions. On the other hand, stomatal closure induced by drought could cancel out any potential growth benefit from C_a increase (Körner 2000; Huang *et al.* 2007). Moreover, a progressively diminishing tree response to increasing C_a and a decoupling of growth and iWUE have been reported (Waterhouse *et al.* 2004; Linares *et al.* 2009; Peñuelas, Canadell, & Ogaya 2011). Therefore, assessments of the growth-iWUE relationship in natural forests are necessary to predict future forest responses to combined rising C_a and warmer conditions in areas subjected to seasonal droughts (Körner 2000; Boisvenue & Running 2006). Several studies have revealed that trees vary in their response to increasing C_a , often showing improved iWUE but not enhanced growth, which points to species-specific responses (Lévesque *et al.* 2014), and influences of availability of other resources (Warren *et al.* 2001).

Tree-rings are a valuable tool to reconstruct long-term effects of environmental variables on growth, and their C isotope ratio ($^{13}\text{C}/^{12}\text{C}$) can provide an insight into trees' iWUE for the period when the ring was formed (Farquhar, Ehleringer & Hubick 1989; McCarroll & Loader 2004). Most research has focused on the relationship between tree-ring variables (e.g. tree-ring width, $\delta^{13}\text{C}$ or iWUE), climatic factors, and rising C_a . However, such studies have been focused on freely growing, dominant or isolated trees, whereas interactions among neighbouring trees have not been often analysed despite the well-known fact that trees compete for light, water, and other resources. In fact, the effects of such interactions may be more important than climate factors (Linares *et al.* 2009; Primicia *et al.* 2013; Fernández-de-Uña *et al.* 2016). Previous studies have shown a common trend that indicates an evident negative effect of increased competition on growth (e.g. McDowell *et al.* 2006; Martín-Benito *et al.* 2010; Primicia *et al.* 2013), whilst the effects on iWUE depend on whether C assimilation or stomatal

conductance is more strongly affected by trees' competition (Fernández-de-Uña *et al.* 2016, and references therein).

Nowadays, species mixtures are receiving increasing attention because they can be more productive than pure stands. Therefore, mixing tree species has been identified as an adaptation strategy in forest management to cope with climate change (e.g. Zhang, Cheng & Reich 2012; Forrester 2015; Pretzsch *et al.* 2015; González de Andrés *et al.* 2016). In mixed stands, growth and drought response of trees are altered by both intra- and inter-specific competition. Inter-specific differences in physiology, phenology or morphology can modify iWUE and growth of mixed stands as compared to pure stands (Forrester 2015; Forrester & Bauhus 2016). Hence, species interactions may promote net competition, facilitation (i.e. one species improves the resource availability, climatic or biotic conditions of another species) or competitive reduction (i.e. inter-specific competition in the mixture is lower than intra-specific competition in the pure stands) (Kelty & Cameron 1995). In this sense, the identity of the competing neighbours has a strong influence on the interaction effects among trees. Therefore, each species combination should be considered when studying competition and environmental impacts on mixed stands performance. The inter-dependence among ecological processes in mixtures makes extremely difficult to separate the effects of facilitation and competitive reduction, so both interaction types have been described collectively as complementarity (Loreau & Hector 2001). The assessment of such complementarity concept in terms of growth and iWUE changes can provide valuable insights towards understanding drought sensitivity of trees in mixed stands.

Here we focus on the interactions between a light-demanding conifer (Scots pine, *Pinus sylvestris* L.) and a shade-tolerant broadleaf (European beech, *Fagus sylvatica* L.). Although mixtures of beech and pine have been observed to provide an overall increase in yield of 12 % in comparison with pure stands (Pretzsch *et al.* 2015), there is a scarcity of knowledge on the physiological mechanisms that can favour species complementarity. They are the most widely distributed conifer and broadleaf tree species in Europe. Their distributions overlap over a large area of the continent and the Iberian Peninsula represents the south-western distribution limits of both species (Fig. S1 in Supporting Information). In addition, this region is likely to be highly sensitive to climate change, as it has been predicted an increase in the frequency and severity of drought events (IPCC 2013). Therefore, the Iberian Peninsula could be one of the first regions where growth-related features of both species would be altered by climate change.

Primicia *et al.* (2013) reported a higher sensitivity of Scots pine growth to temperature and precipitation in thinned than in unthinned plots in the south-western Spanish Pyrenees. The same authors also highlighted the influence of the identity of the competing neighbours in sensitivity responses to climate. The importance of competition on the response of beech to environmental factors has been also reported in “core” areas of the species distribution, such as central Europe (Metz *et al.* 2016). Hence, an analysis of the physiological mechanisms underlying species interactions on

rear-edge populations, located close to the species' southern limit of distribution, will contribute to understand current patterns in tree growth and iWUE in pine-beech mixtures and to predict their future response to climate change throughout the broader range of these species.

Since intra- and inter-specific competition dynamics can be managed to minimize the negative effects of droughts associated with climate change on tree physiology and growth, we aimed to assess the ecological relevance of competition as a potential constraint on iWUE and growth for Scots pine and European beech in mixed stands of the western Spanish Pyrenees. Our specific objectives were: 1) to evaluate the differential effects that competition, rising C_a trends and climate exert on iWUE and growth of pine and beech trees, 2) to relate iWUE to growth changes, and 3) to test whether possible increases in iWUE linked to rising C_a can compensate the negative effects of drought on growth of both species. We hypothesized that: 1) trees' radial growth is greater when exposed to inter- than to intra-specific competition when species interactions improve the availability of a limiting resource (following the 'complementarity – competition' framework *sensu* Forrester & Bauhus 2016), and 2) increases in iWUE would enhance radial growth due to improved photosynthesis with lower water loss which is advantageous to face water shortage. To test these hypotheses we employed a combination of dendrochronological tools and measurements of carbon isotope composition to evaluate iWUE and growth trends of pine and beech mixtures at two climatically contrasting sites.

2. Materials and methods

2.1. Study area and climatic data

The study area is located in the south-western Pyrenees, northern Spain (province of Navarre; Fig. S1). In this region, beech is limited to the northern slopes and valley bottoms with deep soils, while Scots pine usually appears in southern and dry slopes. Management plans together with abandonment of former pastures have favoured Scots pine, replacing the pre-existing oak and beech forests (Loidi & Bascónes 1995). However, over recent decades, mixed stands have been encouraged by allowing beech growth under pine canopy (MMA 2002). Two contrasting sites were sampled: a sub-xeric site located at low elevation with a cool and dry Mediterranean climate (Aspurz), and a mesic site situated at high elevation and characterized by cold-wet continental climate (Garde). Apart from Scots pine and beech, other overstory tree species identified in the pine-dominated plots were *Quercus humilis* L., *Q. ilex* L. and *Ilex aquifolium* L. at the Mediterranean site, whereas only the latter is present at the continental site. In the case of the beech-dominated plots, *I. aquifolium*, *Buxus sempervirens* L., *Populus nigra* L. and *Acer campestre* L. were the main non-target woody species at the Mediterranean site. No significant presence of any other tree species was found in the beech-dominated plots at the continental site. Data describing soil characteristics were obtained by digging soil pits from each site. Further information on sites' characteristics and stands' structure is provided in Table 1.

In order to evaluate the impact of climatic conditions on growth and isotope series, historical climate data for the period 1980-2013 were obtained from the nearest weather stations to each site. Due to the large elevation difference between the continental site and the closest weather station (over 600 m), the mountain microclimate simulation model MT-CLIM (Running, Nemani & Hungerford 1987) was applied to correct climate data (Lo *et al.* 2011). Maximum and minimum temperature lapse rates and precipitation isohyets needed for extrapolation were calculated from regional climate data. Missing data were calculated by interpolating values from nearby weather stations.

The 0.5°-gridded CRU TS 3.22 data set produced by the Climate Research Unit (University of East Anglia) was used to complete the climate data series from the date of birth of the oldest trees (1920) until 1980 (Harris *et al.* 2014). As CRU series are based on average elevation of their corresponding 0.5° grid, linear regressions between CRU and local weather station series (see above) were made for the common period 1980-2013 and the correction was applied to CRU data from 1920 to 1980 to obtain adjusted climate series for the study sites. Water balance was obtained from the sum of monthly differences between precipitation data and potential evapotranspiration (PET). PET was estimated following Thornthwaite & Mather (1957). Seasonal values of climate variables were calculated from monthly data: previous autumn (September to November prior to the year of tree-ring formation), winter (previous December to February), spring (March to May), and summer (June to August). Temporal trends in annual and seasonal temperatures and water balance were calculated by using linear simple regressions. Since 1920, annual temperatures have significantly risen ($P < 0.001$) at both study sites with a rate *ca.* $+0.020$ °C year⁻¹ (Fig. S2A). Water surplus showed a significant decreasing trend at both sites ($P < 0.001$), which was more pronounced in the Mediterranean site (Fig. S2B). These trends were also present at seasonal level for temperature (all seasons, both sites) and water balance (spring and winter, both sites) (results not shown).

2.2. Field sampling and dendrochronological procedures

At each location, three plots dominated by Scots pine (30 m x 40 m) and three plots dominated by European beech (20 m x 20 m) were set up and diameter at the breast height was measured (dbh, measured at 1.30 m height) for every tree inside the plots (Table 1). We randomly chose eight dominant and co-dominant trees per plot ($n = 98$, 50 pine trees from the pine-dominated plots and 48 beech trees from the beech-dominated plots) to obtain a representation of stand historical growth (Lo *et al.* 2010). Selected trees were sampled at breast height perpendicular to the maximum slope using a Pressler increment borer. Two complete radii were extracted from each tree. Cores were air dried, glued onto wooden mounts and sanded until tree rings were clearly visible (Fritts 2001). All samples were visually cross-dated using the identification of signature years. Tree-ring width was measured to a precision of 0.01 mm using a LINTAB measuring device (Frank Rinn, Heidelberg, Germany). Cross-dating was further validated using the COFECHA software, which calculates moving correlations among individual tree series (Holmes 1983). For each tree, measurements from the two

cores were averaged. In those cases when tree cores did not reach the pith, the distance to the theoretical centre of the stem was estimated by fitting a template of concentric circles to the curve of the innermost rings (Norton, Palmer & Ogden 1987). These geometric corrections were used to estimate the age at 1.30 m of all trees. For each tree, measurements from the two cores were averaged as they were considered as replicates. We transformed tree-ring width series into annual basal area increment (BAI) using the following formula and assuming concentric rings:

$$\text{BAI} = \pi (r_t^2 - r_{t-1}^2), \quad \text{eqn 1}$$

where r_t and r_{t-1} are the radii corresponding to years t and $t-1$, respectively. We used BAI because it is a more biologically meaningful expression of growth than tree-ring widths or indices, since BAI displays a young exponential phase and reaches an asymptotic phase when trees reach a mature stage (Biondi & Qaedan 2008).

2.3. Tree-ring isotopes analysis and water-use efficiency

Stable C isotopes in tree rings provide useful proxies of long-term changes in iWUE (McCarroll & Loader 2004). Isotopic discrimination in C3 plants is a result of the preferential use $^{12}\text{CO}_2$ over $^{13}\text{CO}_2$ during photosynthesis. The two stable C isotopes are incorporated in varying amounts depending on the ratio between the intercellular (C_i) and the atmospheric CO_2 concentrations (C_a). For example, if a drought event occurs, stomatal conductance will decrease relative to the rate of photosynthesis, and the diminished C_i will cause less discrimination against ^{13}C (Farquhar, Ehleringer & Hubick, 1989). We used $^{13}\text{C}/^{12}\text{C}$ isotope ratios in wood from cross-dated cores as proxies of the iWUE. We randomly chose five trees of each species at each study site ($n = 20$, 10 pine trees and 10 beech trees) among trees previously selected for growth analysis. We extracted two additional radii from these trees: 5-mm thick cores that were used as a support to cross-date 10-mm thick cores used for C isotope analyses. The 5-mm cores were prepared following dendrochronological methods as explained before. The 10-mm thick cores were cross-dated and tree rings (including earlywood and latewood) were separated manually from the cores using a scalpel under a stereomicroscope. The samples were milled to a fine powder using a ball mill (Retsch ZM1). We used intact wood tissue for C isotope analyses as both whole wood and cellulose isotope time-series show similar long-term trends related to atmospheric CO_2 and climate (Saurer, Siegwolf & Schweingruber 2004; Ferrio & Voltas 2005). The $^{13}\text{C}/^{12}\text{C}$ ratios of wood samples were determined by mass spectrometry using a Flash EA-1112 elemental analyser interfaced with a Finnigan MAT Delta C isotope ratio mass spectrometer at the Stable Isotope Facility (University of California, Davis, USA). The standard deviation for the repeated analysis of standard cellulose was better than 0.1‰ for C. The results were expressed as isotopic composition ($\delta^{13}\text{C}$) relative to the standard Vienna Pee Dee Belemnite (VPDB) (IAEA 1995) following Eq. 2.

$$\delta^{13}\text{C} (\text{‰}) = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000, \quad \text{eqn 2}$$

in which R_{sample} and R_{standard} represent the $^{13}\text{C}/^{12}\text{C}$ ratios of the sample and the VPDB international standard, respectively (Farquhar, O'Leary & Berry 1982).

Following Farquhar, O'Leary & Berry (1982) we estimated iWUE using Eq. 3.

$$iWUE = A / g = C_a [1 - (C_i / C_a)] 0.625, \quad \text{eqn 3}$$

where A is the rate of net photosynthesis, g is stomatal conductance to H_2O , and 0.625 is the relation among conductance of H_2O and CO_2 . To determine C_i , we used the following equation proposed by Francey & Farquhar (1982) (Eq. 4).

$$C_i = C_a [(\delta^{13}\text{C}_{\text{plant}} - \delta^{13}\text{C}_{\text{atm}} + 1) / (b - a)], \quad \text{eqn 4}$$

where $\delta^{13}\text{C}_{\text{plant}}$ and $\delta^{13}\text{C}_{\text{atm}}$ are the plant and atmospheric C isotope compositions, respectively, a is the diffusion fractionation across the boundary layer and the stomata (+4.4 ‰), and b is the Rubisco enzymatic biologic fractionation (+27.0 ‰). The long-term C_a and atmospheric $\delta^{13}\text{C}$ from 1923 (oldest tree-ring in all samples) to 2003 were obtained from McCarroll & Loader (2004). Additional data (from 2004 to 2013) for C_a and $\delta^{13}\text{C}$ were taken from the Earth Research Laboratory website (<http://www.esrl.noaa.gov/>).

2.4. Beech response to rising atmospheric CO_2 concentration

Due to the uneven age distribution of beech in the Mediterranean site, additional sampling of trees born before and after 1950 ($n = 10$) was performed at this site. That date was chosen as a turning point because C_a steeply rose after 1950 owing to the accumulated effects of the industrial revolution (which started *ca.* 1850). Two radii were extracted from each tree. The first core was prepared for assessing changes in growth and estimating BAI following dendrochronological methods as explained before. The 30 innermost tree-rings of the second core were separated at a 5-year resolution and then milled. The $^{13}\text{C}/^{12}\text{C}$ ratio of wood samples was determined and the iWUE values calculated. See section 2.3 for further details.

2.5. Competition index

The spatial position of every tree with a dbh larger than 2.5 cm within each experimental plot was measured. The degree of competition around each sampled tree was assessed using Hegyi's (1974) distance-dependent competition index (*DCI*). This index is derived from the hypothesis that the competitive effect of a neighbour tree increases with increasing size and proximity (Tomé & Burkhart 1989). The competition caused by tree j on focal tree i was calculated as the ratio $\text{dbh}_j/\text{dbh}_i$ divided by the distance between tree i and tree j (dist_{ij}), summed over all j neighbouring trees within a radius R of tree i (Eq. 5).

$$DCI = \sum [(dbh_j/\text{dbh}_i) \times (1/\text{dist}_{ij})] \quad \text{eqn 5}$$

In order to calculate *DCI* values prior to the sampling date, the diameters of all trees in the plots were reconstructed. Ring widths of cored trees were multiplied by two to obtain annual diameter increments. Diameter increments were fitted against measured diameter in 2013 (dbh_{2013}) and year using linear models for each site and each species. Based on the adjusted equation we estimated annual diameter increment of non-cored trees, which was sequentially subtracted to their dbh_{2013} to reconstruct dbh of all trees for the period 1980-2013. Although such approach leaves out those trees that died during stand development and were therefore not detected during the inventories and sampling, such trees are mostly sick and dominated individuals with small root systems, which had little effect on nutrient competition (Blanco *et al.* 2006, 2009). Not accounting for such small trees has been proven not significant for the performance of distance-diameter indexes as predictors of tree growth (Lorimer 1983). The competing neighbours were determined by the fixed-radius method. The *DCI* values were obtained using neighbourhood radii ranging 1 to 15 m (in 1 m increments) from the focal tree and these values were fit against mean *iWUE* of each sampled tree. Then, the distance with the highest coefficient of determination (R^2) was chosen, and the corresponding *DCI* was used in subsequent analyses. For each tree the *DCI* was divided into inter-specific and intra-specific competition *DCIs* when trees of different species from the focal tree species ($DCI_{inter-sp}$) and trees of the focal species ($DCI_{intra-sp}$) were considered, respectively.

2.6. Statistical analysis

Temporal trends in isotope data ($\delta^{13}C$ and *iWUE*) were assessed through linear mixed-effects models (LMMs). Tree nested in plot was included as a random effect, as well as a first-order autocorrelation structure to account for the repeated measures on the same tree (Zuur, Ieno & Elphick 2009). We included as fixed factors “Year” and the interaction “Year x site” to detect differences in the rates of change between populations in each location for the same species, and the interaction “Year x species” to test differences between species. The correlation between each $\delta^{13}C$ series and a master chronology built from all the other series was also calculated.

LMMs were used to assess the effect of environmental variables (competition status, C_a , climate), cambial age (the age of the tree when the ring was formed), site, and their interactions on *iWUE* and growth (BAI) trends for the period 1980-2013. A random intersection associated with tree nested in plot and a first-order autocorrelation structure was included in the models. We used an exponential variance structure in growth models since the residual spread enlarged at increasing cambial age (Zuur, Ieno & Elphick 2009). Variables were standardized to enable direct comparison of predictors' coefficients. We calculated variance inflation factors (VIF) of the models containing all explanatory variables to assess collinearity among explanatory variables. VIF values larger than 2.5 indicate high collinearity among variables (Dormann *et al.* 2013). Since saturated models presented high collinearity between C_a and cambial age, sequential regression was used to create a new variable: “ageRes”, which resulted from residuals obtained by fitting linear models of cambial age as a function

of C_a (Graham 2003). The C_a was used as the main explanatory variable as ontogenic processes are known to be minor when compared with long-term effects of changes in C_a and climate (McCarroll & Loader 2004). Additional LMMs were fitted to evaluate the impact of iWUE on growth, in which fixed factors were iWUE, site, C_a , ageRes and their interactions.

The response of beech trees born before and after 1950 at the Mediterranean site was also assessed with LMMs. Fixed effects were seasonal temperature and water balance, age group, iWUE (only in growth models), and C_a . A random intercept to account for correlation within tree, a first-order autocorrelation structure and an exponential variance structure associated with cambial age (only in growth models) were also included in the models.

Random, temporal autocorrelation and variance structures were determined by comparing nested models, with and without the aforementioned structures, with the likelihood ratio test using the restricted maximum likelihood estimation procedure (Zuur, Ieno & Elphick 2009). Fixed effects selection was based on the Akaike Information Criterion corrected for small sample size (AICc), and the models with the lowest AICc were selected, i.e. those most parsimonious (Burnham & Anderson 2002). We considered the models with substantial support to be those in which the difference in AICc was smaller than 2. The goodness-of-fit of selected models was evaluated with the pseudo- R^2 proposed by Nakagawa & Schielzeth (2013), which comprises marginal (R^2m) and conditional (R^2c) R^2 values. The R^2m accounts for the proportion of variance explained by the fixed effects, and the R^2c accounts for the proportion of variance explained by the whole model, i.e. fixed plus random effects. All statistical analyses were carried out with R version 3.1.3 (R Core Team 2014). Correlations between the mean $\delta^{13}\text{C}$ series were calculated using *dplR* package (Bunn *et al.* 2016) and LMMs and model selection were conducted using *nlme* (Pinheiro *et al.* 2015) and *MuMIn* (Barton 2015) packages, respectively.

3. Results

3.1. Growth patterns

Scots pine showed an increase in basal area increment (BAI) corresponding to the juvenile phase during the 1960s and early 1970s until the early 1980s when BAI stabilized at values of $\sim 10 \text{ cm}^2 \text{ year}^{-1}$ at both sites (Fig. 1). The beech population at the Mediterranean site reached an overall steady growth rate during the 1970s (BAI $\sim 7 \text{ cm}^2 \text{ year}^{-1}$). Note that a growth release was detected at this site during the late 2000s, which may be related to pine mortality due to strong wind events that enhanced beech BAI. At the continental site, beech individuals were younger and BAI stabilized in the early 1990s resulting in mean BAI values of *ca.* $15 \text{ cm}^2 \text{ year}^{-1}$ during the 2000s (Fig. 1).

3.2. Isotope data

$\delta^{13}\text{C}$ showed a significant decreasing trend for both Scots pine ($P < 0.001$) and beech ($P = 0.006$) populations and it was significantly higher ($P < 0.001$) in the case of pine (-25.6‰) than in beech (-27.2‰). Trends did not differ between sites for pine ($P = 0.245$) or for beech ($P = 0.569$) (Fig. 2A). The correlations between the mean $\delta^{13}\text{C}$ series were stronger between Mediterranean and continental Scots pine populations ($r = 0.465$, $P = 0.112$) than between beech populations ($r = 0.411$, $P = 0.077$).

Scots pine reached higher mean iWUE values ($92.93 \pm 0.44 \mu\text{mol mol}^{-1}$, mean \pm SE) than beech ($80.19 \pm 0.60 \mu\text{mol mol}^{-1}$). Both species significantly increased ($P < 0.001$) their iWUE since 1980, although beech experienced an increase (+21.9 %) significantly greater ($P < 0.001$) than Scots pine (+12.2 %). There were no significant differences between populations in the rate of change of iWUE for pine ($P = 0.236$) or for beech ($P = 0.585$). However, the increasing tendency was consistently higher at the Mediterranean site (+16.8 % pine and +28.2 % beech) than at the continental site (+7.6 % pine and +15.7 % beech) (Fig. 2B).

3.3. Climate-growth-isotope associations

We found significant effects of climatic variables on both growth and iWUE trends. Mild temperatures during the early growing season (spring) enhanced beech growth, while pine growth was negatively affected by warm temperatures during the autumn prior to tree-ring formation. Positive water balance during the growing season (spring and summer for Scots pine and only spring for beech) also improved growth. Water availability of the previous autumn also showed a positive effect on pine growth (Table 2). The drier summer conditions were, the greater the iWUE was. Warm summer temperatures also improved pine iWUE (Table 3).

3.4. Competition and environmental influences on growth and carbon isotopes

The highest R^2 of regressions of mean tree iWUE as a function of the spatial competition index (DCI) was reached for neighbourhoods at distances around the focal tree of 9 m for Scots pine and 5 m for European beech, respectively (Fig. S3).

LMMs highlighted significant relationships among DCI , atmospheric CO_2 concentration (C_a) and BAI of Scots pine and beech (Table 2). Growth was reduced at high levels of intra-specific competition compared to low DCI_{intra} values. However, the intra-specific competition influence on growth evolved differently as C_a changed in each tree species: differences between competition levels declined for pine but rose for beech as C_a increased (Figs. 3A and 3B). Significant differences between beech populations were found for the relationship BAI- C_a , so that trees from the continental site presented positive and more pronounced response to rising C_a than trees from the Mediterranean site (Fig. S4). The impact of inter-specific competition on pine growth differed between sites: it had a positive impact at the continental site and negative at the Mediterranean site (Fig. 4A). As expected, C_a affected significantly and positively iWUE of both pine and beech. Scots pine presented higher iWUE

under greater levels of both types of competition (Fig. 3C), although for inter-specific competition the trend was significant only at the Mediterranean site (Fig. 4B). Beech trees exposed to low inter-specific competition showed greater iWUE compared to those under high DCI_{inter} values, however the differences between inter-specific levels decreased as C_a rose (Table 3) (Fig. 3D).

3.5. Ontogenetic changes in growth and carbon isotopes

Despite the fact that the sampled trees were young to mature (34-97 years old in beech and 37-74 years old in Scots pine), the iWUE of both species was not significantly affected by tree-ring cambial age (Table 3). Thus, a juvenile effect of tree-ring cambial age on iWUE values can be regarded as negligible. However, growth presented significant positive effects of cambial age (Table 2), probably because the study period included juvenile growth phases of some trees. In the case of beech populations, the rising BAI effect as a result of increasing cambial age differed between sites: the population in the continental site, which is younger, presented higher rates of growth (see Table 1).

The iWUE showed significant associations with growth of both species but of different signs. Negative BAI-iWUE relationships were found in the case of Scots pine ($P < 0.001$; Fig. 5A) without differences between sites, while positive BAI-iWUE associations were observed in beech (Fig. 5B), although only the Mediterranean population showed a significant relationship ($P < 0.001$).

Finally, we analysed beech trees response in terms of BAI and iWUE at the Mediterranean site. Age group (two categories: born before and after 1950), C_a , as well as the interaction between them exerted an effect on both variables (Table S1). The higher C_a was, the greater the growth and iWUE were. However, trees born before 1950 had a more pronounced response to C_a increases than trees born during the second half of 20th century (Fig. S5). Beech iWUE was significantly associated to growth irrespective to the period of tree development (Table S1). Regarding climatic conditions, only summer water availability showed significant negative associations with iWUE.

4. Discussion

The beneficial effects of admixing have been shown to provide an overall 25 % increase in productivity across forest types (Zhang, Cheng & Reich 2012) and a 12 % increase at European scale in Scots pine – European beech mixtures (Pretzsch *et al.* 2015). However, there is a scarcity of knowledge on what are the mechanisms that promote such complementarity effects leading to increased productivity in pine – beech mixtures despite their frequent occurrence and economic importance (Pretzsch *et al.* 2015). In this study we combined the analysis of intrinsic water use-efficiency (iWUE) and basal area increment (BAI) trends to disentangle the species-specific responses to intra- and inter-specific competitive pressures and to long-term changes in atmospheric CO₂ concentration (C_a) and climatic conditions, focusing on the impacts of drought events on growth and iWUE. Our first hypothesis was supported only for Scots pine growth at the cold-wet continental site,

since competition for water prevented any beneficial effect of the admixture of beech at the warm-dry Mediterranean site. The positive relationship found between BAI and iWUE for beech populations supports our second hypothesis. However, any advantage conferred by an increased iWUE did not compensate for other growth constraints in pine populations.

4.1. Species and site-specific growth sensitivity to climate and competition

Tree water status has been proposed to be a major limiting factor of radial growth for both Scots pine (Martínez-Vilalta *et al.* 2008; Primicia *et al.* 2013) and beech (Gutierrez 1988; Dittmar, Zech & Elling 2003; Lebourgeois *et al.* 2005), in agreement with our results (Table 2). Drought constraint of growth is particularly important in the southernmost part of temperate species distributions (Linares & Camarero 2012). Soil water availability ought to be especially important in late spring and early summer, when the rate of wood production peaks (Rossi, Rathgeber & Deslauriers 2009; Primicia *et al.* 2013). Additionally, water supply at the end of the growing season has been proposed to indirectly affect pine growth through an enhanced synthesis of carbohydrates, which are then mostly allocated for earlywood formation during the following year (Michelot *et al.* 2012).

Growth of the two studied species responded differently to seasonal temperatures (Table 2). Negative effects of high autumn temperatures on pine growth may be caused by an increase in atmospheric water demand that produced greater drought stress, as has been observed for other Scots pine populations in northern Spain (Martínez-Vilalta *et al.* 2008). This stress promoted a strong reduction in stomatal conductance (g), together with an enhancement of respiration rates and a decrease in stored carbon pools (Wullschleger *et al.* 2002). For beech, warm temperatures and the absence of frosts during spring could favour early season photosynthesis and trigger cambial reactivation thus increasing growth rate (Michelot *et al.* 2012). Rising temperatures during the growing season generally had a negative effect on conifer growth but positive on broadleaved species (Way & Oren; 2010, Michelot *et al.* 2012; Coll *et al.* 2013). Several hypothesis have been proposed to explain this contrasting growth response, such as extended phenology (see Gómez-Aparicio *et al.* 2011), or differences in leaf traits (lifespan, mesophyll CO₂ conductance, photosynthetic capacity, stomatal density) resulting in significantly different physiological responses to environmental factors (Way & Oren 2010). Therefore, while a decrease in water availability will likely produce the same general reduction in growth of both species, a warmer climate would cause a performance disadvantage of pine compared to beech.

Nonetheless, tree growth is a multi-faceted biological process that can depend simultaneously on several interacting factors besides climate. In this study, site conditions and their interactions with biological variables, such as competition and tree age, outperformed climatic variables as tree growth drivers of both species (Table 2). Likewise, previous studies found tree growth and the effect of trees' interactions to be highly dependent on local environmental conditions across boreal, temperate and

Mediterranean forests (Gómez-Aparicio *et al.* 2011; Forrester *et al.* 2016; Madrigal-González *et al.* 2016). Resource availability and community structure are site-specific characteristics that may be critical for trees' function. The significant contribution of the random factors (tree and plot) in our LMMs, especially for pine growth, also pointed out that other site-specific drivers such as microclimatic or edaphic variations within sites and plots may affect the relationship tree growth – climate, competition and C_a .

Tree-to-tree competition has been shown to play a key role in tree sensitivity to environmental factors and in the resulting growth (Piutti & Cescatti 1997; Linares, Camarero & Carreira 2010; Martín-Benito *et al.* 2010; Fernández-de-Uña *et al.* 2016). The differential effects of intra- and inter-specific competition are receiving increasing attention due to the encouragement for managing mixed forests (Messier, Puettmann & Coates 2013). We found that intra-specific competition exerted negative influence on radial growth of both species (Fig. 3A and 3B), while inter-specific interactions enhanced growth in pine populations at the continental site and lessened it at the Mediterranean site (Fig. 4A).

Strong impact of intra-specific competition on pine growth (Fig. 4A) may be explained by the high susceptibility of this species to competition for light (e.g. Martín-Benito *et al.* 2010; Jucker *et al.* 2014). It agrees with the high mortality observed at the study area by Primicia *et al.* (2013, 2016). Besides, the fading of this effect as C_a rose might be explained by the reduction of the advantage conferred to less shaded trees as a consequence of the net rate of photosynthesis (A) enhancement resulting from increases in C_a . The admixture of beech likely benefited pine by opening gaps within pine stands, i.e. lessening self-shading. The different ecological traits and structural morphology of these two tree species can enhance stand structure heterogeneity resulting in canopy stratification and higher light interception and thus productivity (Pretzsch *et al.* 2016). Indeed, complementary traits regarding light use strategies have been proposed as mechanisms driving positive biodiversity-productivity relationships (e.g. Zhang, Cheng & Reich 2012; Forrester & Albrecht 2014; Forrester & Bauhus 2016).

However, tree species do not compete only for light but also for belowground resources. In this regard, our results suggest that light-related interactions can be overcome by competition for water in drought-prone environments if complementarity regarding water resources does not occur. Pretzsch *et al.* (2016) reported a positive relationship between water availability and vertical structuring in mixed stands of Scots pine and European beech at continental scale. Similarly, light absorption and light use-efficiency in mixtures have been shown to increase as climatic conditions improved (Forrester & Albrecht 2014). However, Grossiord *et al.* (2014a) stated that drought resistance is enhanced in mixtures as long as net water-use partitioning or water related facilitation processes take place. Consistently with our results, a strong dependence of drought stress reduction on species identity and site conditions in mixtures has been reported from different regions in Europe (Forrester *et al.* 2016).

This pattern is consistent with the ‘complementarity – competition’ framework proposed by Forrester & Bauhus (2016), since it predicts that species complementarity increases as water availability increases when interactions improve light absorption. In addition to water availability, nutrient cycling can also be affected by species mixtures (Blanco et al. 2017). European beech leaf litter has higher nutrient content, lower C/N ratio and less recalcitrant compounds compared to Scots pine litter (Rothe & Binkley 2001; Pretzsch et al. 2015). Hence, the input of beech litter may have improved nutrient availability and allowed pine trees to develop bigger crowns.

The Mediterranean site is characterized by summer water deficit that combined with faster depletion of soil water and higher canopy rainfall interception in mixtures compared to pure pine stands (Primicia 2012; Grossiord *et al.* 2014b), may have led to strong inter-specific competition for water resources. Larger pine stem sizes at this site could also increase their vulnerability to drought (Table 1; Hember, Kurz & Coops 2016). Supporting our results, Primicia *et al.* (2013, 2016) found a reduction in pine radial growth due to beech presence modulated by stand density at the same site. Therefore, such water-related competition would have cancelled the light-related complementarity effects. The trade-offs between shade and drought tolerance (due to contrasting structural and physiological adaptations required to face scarcity of each resource) has been supported by eco-physiological studies (reviewed in Holmgren *et al.* 2012).

On the other hand, we observed a significant effect of intra-specific competition on beech growth (Fig. 4B), agreeing with the low self-tolerance previously suggested for this species (e.g. Río, Condés & Pretzsch 2014). Contrary to the pine, differences between high and low competition levels grew bigger as C_a increased. Higher C_a would have boosted A , thus increasing the demand for limiting belowground resources, especially water. Thus negative effects of competition may have increased faster in denser stands (Sohn, Saha & Bauhus 2016). Regarding inter-specific competition, the lack of growth response to pine admixture is likely explained by the ability of beech to tolerate shade, as has been proposed for other *Fagaceae* species (i.e. oak) when mixed with pine species (Coll *et al.* 2013; Jucker *et al.* 2014). Besides, beech may have overcome pine when competing for above and belowground resources as a result of its highly efficient use of growing space (Dieler & Pretzsch 2013) and highly competitive root system (Curt & Prévosto 2003).

4.2. Contrasting responses of *iWUE* to competition

The observed increase of *iWUE* of both pine and beech during the last decades (Fig. 2B) has been also described for different tree species and across diverse biomes (e.g. Peñuelas, Canadell, & Ogaya 2011, and references therein). The observed *iWUE* changes laid in the same range previously reported for pine species (Andreu *et al.* 2008; Andreu-Hayles *et al.* 2011; Granda *et al.* 2014) and beech (Duquesnay *et al.* 1998; Peñuelas *et al.* 2008). This increase is mainly explained by the sharp rise in intercellular CO_2 concentration (C_i) because of the rise of C_a (+16.9 % since 1980) (see coefficients in

Table 3), which probably increased carbon assimilation or reduced water loss by transpiration (Waterhouse *et al.* 2004; Huang *et al.* 2007).

Even though increased C_a accounted for a high variation of the iWUE, there might be other environmental factors modulating the responses (Peñuelas, Canadell, & Ogaya 2011). We found an enhancement of iWUE when water shortage and high temperatures during summer occurred, and such enhancement was greater at the drought-prone Mediterranean site for both species (Table 3). iWUE has been shown to increase in response to the effect of a decrease in either air humidity or soil moisture (Wullschleger *et al.* 2002; Waterhouse *et al.* 2004; Linares & Camarero 2012). At the leaf level, trees under drought conditions have to manage the trade-off between optimum carbon gain for growth and loss of water through transpiration (Farquhar, O'Leary & Berry 1982), which results in a reduction in g and thus an increase in iWUE (see equation 3). Although iWUE was higher for Scots pine (likely due to a better stomatal control of water losses than beech, Madrigal-González & Zavala 2014), the magnitude of increase over time was lower (ca. +12 %) compared with that of beech (ca. +22 %). The stronger iWUE response of beech may be the result of the particularly drought-sensitive nature of this species (Waterhouse *et al.* 2004, Lebourgeois *et al.* 2005). Further, an age effect was not found in the iWUE response of any species, while growth was enhanced at increasing cambial age of tree-rings. Andreu *et al.* (2008) suggested that higher impacts of local and ontogenetic factors may be mirrored in radial growth and C stable isotopes might be more affected by climatic signals, which could explain the observed age effect pattern.

Stand structure exerted greater impact on iWUE patterns than climate, as observed with radial growth (Table 3). Previous studies have showed a variety of physiological responses to competition including increasing, decreasing or non-significant trends (McDowell *et al.* 2006; Linares *et al.* 2009; Martín-Benito *et al.* 2010; Metz *et al.* 2016). For our research sites, a contrasting response of iWUE of each species at increasing inter-specific competition was found: positive relationship for pine and negative for beech (Figs 3C and 3D). Differences in iWUE changes can result from variations in A , g or the ratio between them as a consequence of physical and biotic factors (Francey & Farquhar 1982).

In the case of Scots pine, both the reduction of self-shading mediated by beech and the enhancement of drought stress suffered by pine trees due to a strong competition for water resources (as supported by a significant impact of inter-specific competition only found at the Mediterranean site; Fig. 4B) could cause increases in A and reductions of g , respectively, and thus iWUE improvement at rising inter-specific competition levels. On the other hand, pine admixture could release beech's intra-specific competition for water and increase soil water availability through lower transpiration rates and canopy interception (González de Andrés *et al.* 2016). As a consequence, a reduction in water stress may have enhanced g and thus reduced iWUE. In addition, beech trees subjected to low inter-specific competition levels might have received higher radiation and then displayed greater A and iWUE (Linares *et al.* 2009). This explanation is supported by the small spatial scale (6 m) at which

competing neighbours influenced beech iWUE (Fig. S3), and the fading of the competition effect as beech trees reached the canopy (Fig. 4D). The contribution of each process cannot be resolved from our data since knowledge of the combined use of carbon and oxygen isotopes ratios would be required (Scheidegger *et al.* 2000). However, these results are consistent with those from Fernández-de-Uña *et al.* (2016), who suggested that competition may modulate iWUE response as long as water, nutrients or light availability are limiting.

4.3. Growth-iWUE relationship differ between tree species

Regardless of the iWUE improvement observed in Scots pine since 1980, stem radial growth enhancement was not observed (Fig. 5A). The uncoupling between iWUE and growth is evident for both populations of Scots pine. This phenomenon has been reported for other tree species, biomes and regions (e.g. Silva, Anand & Leithead 2010; Peñuelas, Canadell, & Ogaya 2011), including other pine species from Mediterranean, continental and high-elevation areas situated in the Iberian Peninsula (Andreu-Hayles *et al.* 2011; Granda *et al.* 2014). On the contrary, Martínez-Vilalta *et al.* (2008) found an overall increase in Scots pine radial growth in NE Spain during the 20th century, which they attributed to rising C_a and increase in nutrient availability. Therefore, a combination of climatic and non-climatic environmental stresses may explain our results. Drought stress could override the beneficial effects of rising C_a and enhanced iWUE in terms of radial growth if water availability is not enough to maintain the demand of higher priority organs (fine roots or foliage) rather than the xylem (Brueggemann *et al.* 2011; Lévesque *et al.* 2014). Further pine photosynthetic capacity was likely limited by nutrients at the study sites (Blanco, Imbert & Castillo 2008, 2009). Indeed, nutrient limitation has also been shown as an important factor preventing any CO₂ fertilization effect (Francey & Farquhar 1982; Silva, Anand & Leithead 2010).

As for European beech, our results suggest a positive growth trend at increasing iWUE, and a positive iWUE – growth association, particularly strong at the Mediterranean site (Fig. 5B). Similarly, Tegel *et al.* (2014) found growth increase in beech populations from the Balkan Peninsula (i.e. south-eastern edge of the species distribution) despite drier conditions. These findings contrast with climate-related growth declines previously reported in several studies focused on low-altitude populations at the southern range-edge of this species in Europe (Piovesan *et al.* 2005; Peñuelas *et al.* 2008). The enhancement of A due to a higher incident radiation as beech approached and reached the pine canopy may have enhanced not only iWUE but stem radial growth as well. However, such size-related effects do not explain this outcome because the relationship should be stronger at the continental site where water shortage is lower, an effect not noticed during our research.

A slower rate of soil water depletion as a result of the increase in iWUE, and thus reduced transpiration may increase the advantage of trees growing in drought-prone environments. In fact, changes in soil moisture induced by rising C_a have been proposed to be a major component of the CO₂

fertilization effect (Morgan *et al.* 2007). For instance, improved growth due to improved iWUE, especially in dry sites, was found in ponderosa pine forests (Soulé & Knapp 2006). However, growth decline was also reported for the same species (Lévesque *et al.* 2014). Warmer and longer growing seasons could also stimulate growth (Martínez-Vilalta *et al.* 2008). Additionally, the higher plastic nature of beech leaves (Forey *et al.* 2016) and vessel traits (Diaconu *et al.* 2016), among other characteristics, compared to pine (Pretzsch *et al.* 2016) could promote a better physiological adjustment of beech trees under long-term environmental changes.

Thus, beech trees experienced a potential CO₂-fertilization effect even though there was a decrease in water availability. Nonetheless, we observed a progressive uncoupling between beech's growth, iWUE and rising C_a (Table S1; Fig. S5). Similar declining responses have been reported in other studies for beech (Peñuelas *et al.* 2008), and for other tree species (Waterhouse *et al.* 2004; Linares *et al.* 2009; Linares & Camarero 2012). Several explanations have been proposed for decreasing sensitivity of iWUE to C_a , such as a threshold in low water availability that limits the iWUE improvement (Peñuelas *et al.* 2008; Linares *et al.* 2009), or long-term anatomical and physiological adaptations for adjusting C_i to increasing C_a such as changing stomatal density or A (Ward *et al.* 2005). The rise in C_a may not compensate the reduction in water availability, explaining the reduced growth response to rising C_a as has been suggested for several Iberian forests (e.g. Peñuelas *et al.* 2008; Camarero *et al.* 2015). Additionally, forest densification due to increased abandonment of both agricultural fields and forest management practices over the last decades could have led to competition intensification in extensive areas of mountainous Spanish forests (e.g. Coll *et al.* 2013). Such competition intensification may have played an important role reducing both iWUE and growth of beech trees born after 1950 (see sections 4.1 and 4.2).

In summary, Scots pine and European beech show contrasting responses to changes in climate and rising C_a , depending on their physiological strategies to face increasing water stress. Additionally, tree species responses to these global-change components may be also modulated by local factors, such as nutrient availability, and vary with ontogeny (Blanco *et al.* 2017). Species complementarity was only found in Scots pine populations at the moistest site, suggesting a trade-off between drought and shade tolerance. Regarding iWUE, both species responded differently to inter-specific competition, with the response being positive for Scots pine but negative for European beech. The combined effect of competition and resource limitation could cause changes in photosynthetic rates and stomatal conductance and modulate iWUE, although the contribution of both processes cannot be disentangled with certainty. Therefore, tree-to-tree competition should be taken into account when designing management plans that improve forests' adaptation to climate change, as it has been shown to exert a varying influence on species performance.

A review of the literature highlights the variety of radial growth responses to iWUE increases between and within species. Hence the influence of water use on growth processes depends on species features

and climatic and site conditions. In our study, BAI-iWUE relationships were negative for Scots pine and positive for European beech. These contrasting behaviours have got implications for coping with the predicted increasing drought events of Scots pine-European beech mixtures located near the ecological limit of the two species. Furthermore, if the long-term CO₂ fertilization effect on forests is absent or undetectable (Scots pine) or declining (European beech) at broad continental scales as it is for the local scale tested in this work, the capacity of mixed conifer-broadleaf forests for carbon uptake and storage in the future could have been overestimated.

Author's Contributions

E.G.A., J.J.C., J.A.B., Y.H.L. and G.S.B. carried out the field and lab analysis. E.G.A. analysed the data and wrote most of the initial manuscript. J.J.C., J.A.B., J.B.I. and F.J.C. collaborated discussing the results and writing the final manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

Data deposited in the Dryad repository: <http://dx.doi.org/doi:10.5061/dryad.kj3km> (González de Andrés et al. 2017).

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Supporting information

Additional Supporting Information:

Table S1. Linear mixed-effects models fitted to explain changes in radial growth and intrinsic water use-efficiency of *Fagus sylvatica* young trees in the Mediterranean site born before and after 1950.

Figure S1. Location of experimental plots and weather stations. Natural European distribution of Scots pine and European beech, and the common area between both species. Pictures from experimental pine and beech stands.

Figure S2. Variation of mean annual temperature and annual water balance for the period 1920-2013 in the study sites.

Figure S3. Coefficients of determination obtained by relating the intrinsic water use-efficiency and the distance-dependent competition index calculated by increasing the radii of the competition neighborhood around the focal tree at 1-m intervals.

Figure S4. Relationship between basal area increment and atmospheric CO₂ concentration at the two study sites for *Pinus sylvestris* and *Fagus sylvatica*.

Figure S5. Intrinsic water-use efficiency (iWUE) and radial growth of *Fagus sylvatica* young trees born before and after 1950 in the Mediterranean site. Relationships of growth and iWUE with atmospheric CO₂ concentration.

TABLES

Table 1. Sites and stands characteristics (mean \pm standard error) measured in 2014. Stands descriptors were taken from Puertas (2001) and Iriarte and Puertas (2003).

Site	Mediterranean warm-dry site (Aspurz)		Continental cold-wet site (Garde)	
Latitude	42°42'31'' N		42°48'50'' N	
Longitude	1°8'40'' W		52'30'' W	
Altitude (m a.s.l.)	625		1335	
Climate type (Papadakis, 1970)	Cold wet Mediterranean		Cold wet continental	
Mean annual temperature (°C) ^a	11.9 \pm 0.1		9.4 \pm 0.1	
Total annual precipitation (mm) ^a	922 \pm 25		1346 \pm 61	
Soil	Haplic Alisol		Dystric Cambisol	
Soil depth (cm) ^b	93.8		79.7	
CEC (cmol+ kg ⁻¹) ^c	14.6		12.6	
Maximum field capacity (%)	38.8		38.8	
	Scots pine stands	Beech stands	Scots pine stands	Beech stands
Slope (%)	7	37	40	45
Density (stems ha ⁻¹) ^d	2400 \pm 301	995 \pm 105	2019 \pm 212	982 \pm 185
Basal area (m ² ha ⁻¹)	57.5 \pm 2.25	47.2 \pm 6.1	56.0 \pm 6.3	30.6 \pm 8.1
Tree species richness	18	7	10	3
Density proportion of <i>P. sylvestris</i> (%)	69.34 \pm 0.02	24.63 \pm 0.10	85.22 \pm 0.06	12.78 \pm 0.06
Density proportion of <i>F. sylvatica</i> (%)	11.73 \pm 0.04	64.16 \pm 0.09	13.71 \pm 0.05	87.22 \pm 0.06
Site Index at stand age 80 years (m) ^e	29	21	23	18
Age (years) ^e	47	72	51	38
Dominant height (m) ^{e, f}	20.4 \pm 0.3	17.3 \pm 0.8	17.3 \pm 0.9	13.2 \pm 0.5
Mean dbh (cm) ^{e, g}	17.2 \pm 1.1	15.5 \pm 1.5	17.9 \pm 0.8	13.0 \pm 1.1
<i>DCI</i> _{intra-sp} ^h	6.59 \pm 0.49	2.02 \pm 0.49	6.16 \pm 0.59	1.94 \pm 0.42
<i>DCI</i> _{inter-sp} ^h	1.04 \pm 0.13	1.38 \pm 0.25	0.28 \pm 0.14	0.46 \pm 0.19

^a Referred to the period 1980-2013.^b Sum of horizons O, A and B.^c Average value between horizon A and horizon B.^d Trees with a diameter at breast height (1.30 m, dbh) > 7.5 cm.^e Referred to plots' dominant species (*P. sylvestris* in Scots pine stands and *F. sylvatica* in beech stands).^f Measured averaging (n = 100) the height of the thickest dominant trees per hectare.^g Measured by double cross measurement.^h Hegyi's (1974) distance-dependent competition index (*DCI*) was calculated following Eq. 5. Presented values correspond to all neighbouring trees within a fixed radius plot of *R* = 9 m from the focal tree in Scots pine stands, and *R* = 5 m in beech stands. Values are calculated as the average competition experienced by trees during the period 1980-2013.

Table 2. Parameter estimates for the selected linear mixed-effects models fitted to explain changes in basal area increment (BAI) during the period 1980-2013. Bold values indicate effects significant at $P < 0.05$. Only those factors of the best model obtained by minimizing the Akaike's information criterion (AIC) are shown.

Species	R^2_m	R^2_c	Fixed effects				
Scots pine (<i>Pinus sylvestris</i>)	0.190	0.681	T _{aut-1}	-0.059			
			P-PET _{aut-1}	0.032			
			P-PET _{spr}	0.031			
			P-PET _{sum}	0.056			
			site	-0.165			
			C_a	0.010			
			ageRes	0.358			
			DCI _{intra-sp}	-0.203			
			DCI _{inter-sp}	-0.020			
			$C_a \times$ DCI _{intra-sp}	0.067			
			site \times DCI _{inter-sp}	0.534			
			European beech (<i>Fagus sylvatica</i>)	0.415	0.524	T _{spr}	0.016
						P-PET _{spr}	0.022
site	1.830						
C_a	0.032						
ageRes	0.216						
DCI _{intra-sp}	-0.116						
$C_a \times$ site	0.574						
$C_a \times$ DCI _{intra-sp}	-0.075						
site \times ageRes	1.163						

Fixed effects were: seasonal temperature (T) and water balance (P-PET), site, atmospheric CO₂ concentration (C_a), derived variable from the cambial age of the tree-ring (ageRes), intra-specific degree of spatial-competition (DCI_{intra-specific}), and inter-specific degree of spatial-competition (DCI_{inter-specific}). In the case of climate variables, subscripts correspond to seasons and “-1” indicates the year prior to tree-ring formation.

R^2_m and R^2_c correspond to marginal (proportion of variance explained by the fixed factors) and conditional (proportion of variance explained by fixed plus random factors) R^2 values, respectively, calculated following Nakagawa and Schielzeth (2013). Random factors were the trees nested in plots sampled at each site, being the residual variance $\sigma^2 = 0.563$ and $\sigma^2 = 0.643$ for *P. sylvestris* and *F. sylvatica* models, respectively. A first-order autocorrelation structure and exponential variance structure associated with cambial age were also included in the models.

Table 3. Parameter estimates for the selected linear mixed-effects models fitted to explain changes in intrinsic water use-efficiency (iWUE) during the period 1980-2013. Bold values indicate effects significant at $P < 0.05$. Only those factors of the best model obtained by minimizing the Akaike's information criterion (AIC) are shown.

Species	R^2m	R^2c	Fixed effects	
Scots pine (<i>Pinus sylvestris</i>)	0.454	0.707	T _{sum}	0.064
			P-PET _{sum}	-0.190
			C_a	0.226
			site	0.161
			DCI _{intra-sp}	0.532
			DCI _{inter-sp}	0.998
			site x DCI _{inter-sp}	-0.816
European beech (<i>Fagus sylvatica</i>)	0.346	0.541	P-PET _{sum}	-0.208
			C_a	0.443
			DCI _{inter-sp}	-0.415
			C_a x DCI _{inter-sp}	0.145

Fixed effects were: seasonal temperature (T) and water balance (P-PET), site, atmospheric CO₂ concentration (C_a), derived variable from the cambial age of the tree-ring (ageRes), intra-specific degree of spatial-competition (DCI_{intra-specific}), and inter-specific degree of spatial-competition (DCI_{inter-specific}). In the case of climate variables, subscripts correspond to seasons and “-1” indicates the year prior to tree-ring formation.

R^2m and R^2c correspond to marginal (proportion of variance explained by the fixed factors) and conditional (proportion of variance explained by fixed plus random factors) R^2 values, respectively, calculated following Nakagawa and Schielzeth (2013). Random factors were the trees nested in plots sampled at each site, being the residual variance $\sigma^2 = 0.594$ and $\sigma^2 = 0.688$ for *P. sylvestris* and *F. sylvatica* models, respectively. A first-order autocorrelation structure was also included in the models.

FIGURES

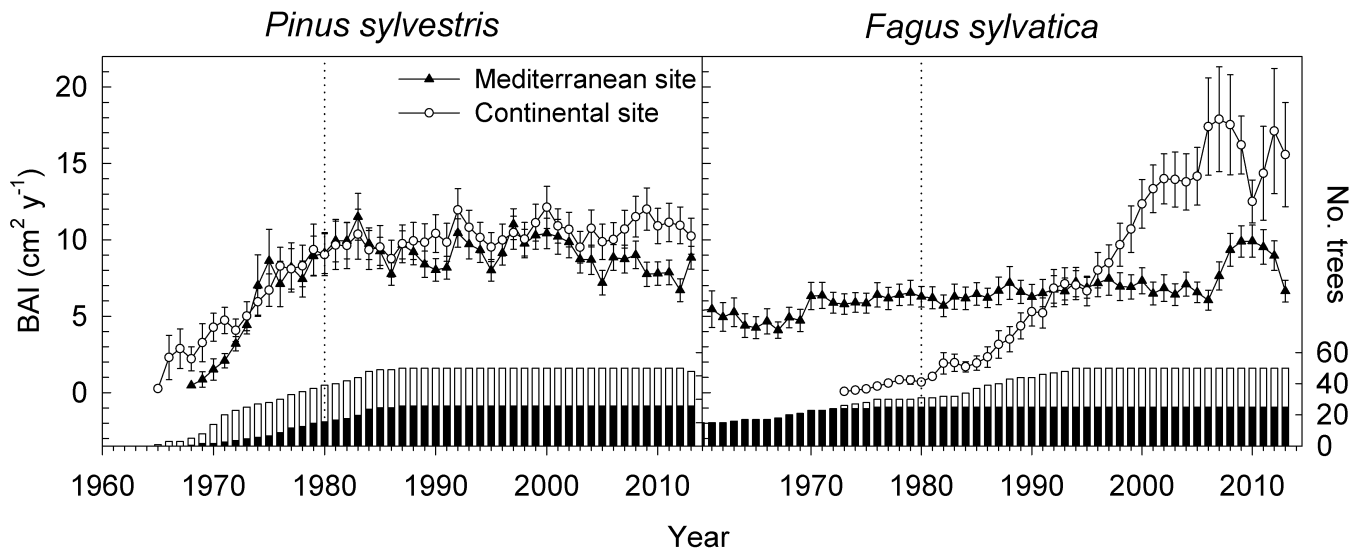


Fig. 1. Annual basal area increment (BAI) of the two study species: Scots pine (*Pinus sylvestris*, left plot) and beech (*Fagus sylvatica*, right) in the two study sites. The bottom bars represent the number of radii measured every year. Error bars correspond to SEs. The dashed vertical lines indicate the start of $\delta^{13}\text{C}$ wood and iWUE data.

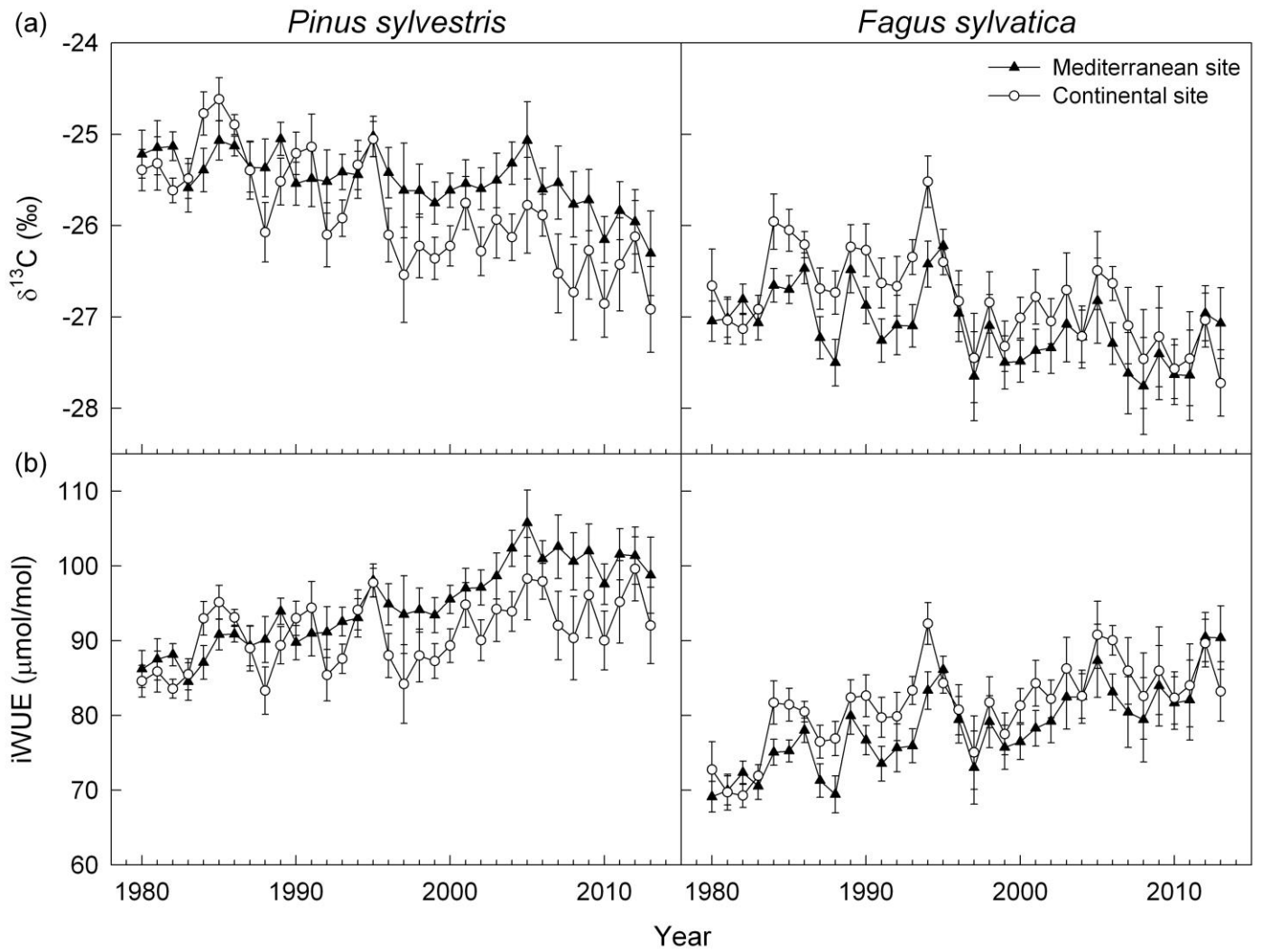


Fig. 2. Variations in carbon isotope ratio ($\delta^{13}\text{C}$) (A) and intrinsic water use efficiency (iWUE) annual values (B) of Scots pine (*Pinus sylvestris*, left) and European beech (*Fagus sylvatica*, right) in the two study sites. Error bars correspond to SEs.

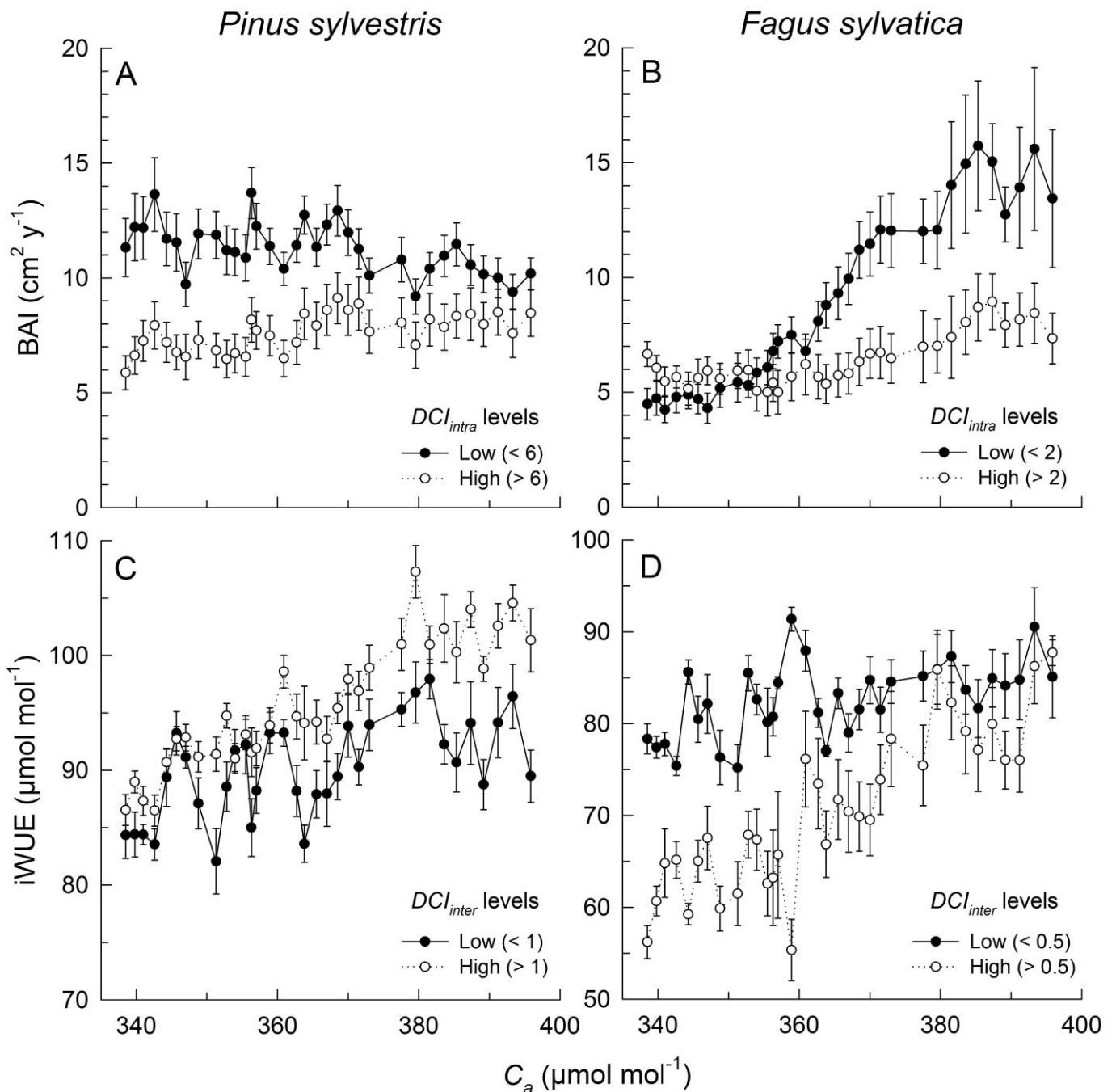


Fig. 3. Variations in basal area increment (BAI) as a function of changes in atmospheric CO₂ concentrations (C_a) for low and high intra-specific competition levels for Scots pine (*Pinus sylvestris*, **A**), and European beech (*Fagus sylvatica*, **B**). The lower plots show changes of intrinsic water use efficiency (iWUE) and C_a for low and high inter-specific competition levels of Scots pine (**C**), and beech (**D**). Each tree has been assigned to a competition level according to whether its competition status was below (low) or above (high) the average competition for the species.

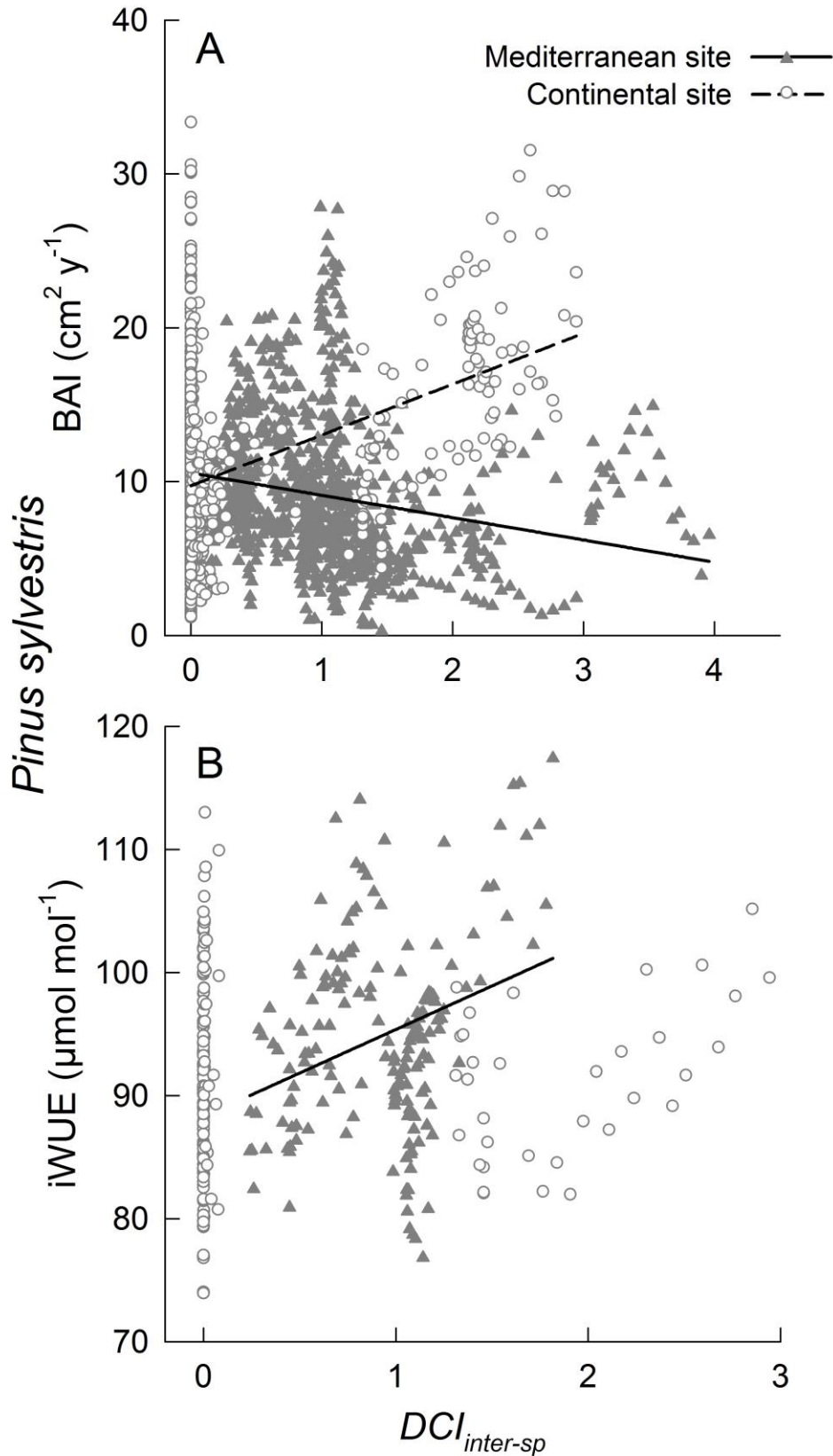


Fig. 4. Site differences in the relationships found between inter-specific competition degree and basal area increment (BAI) (A) and intrinsic water use-efficiency (iWUE) (B) of Scots pine (*Pinus sylvestris*). Solid lines represent significant trends for the Mediterranean site data and dash lines represent significant trends for the cold-wet continental site data.

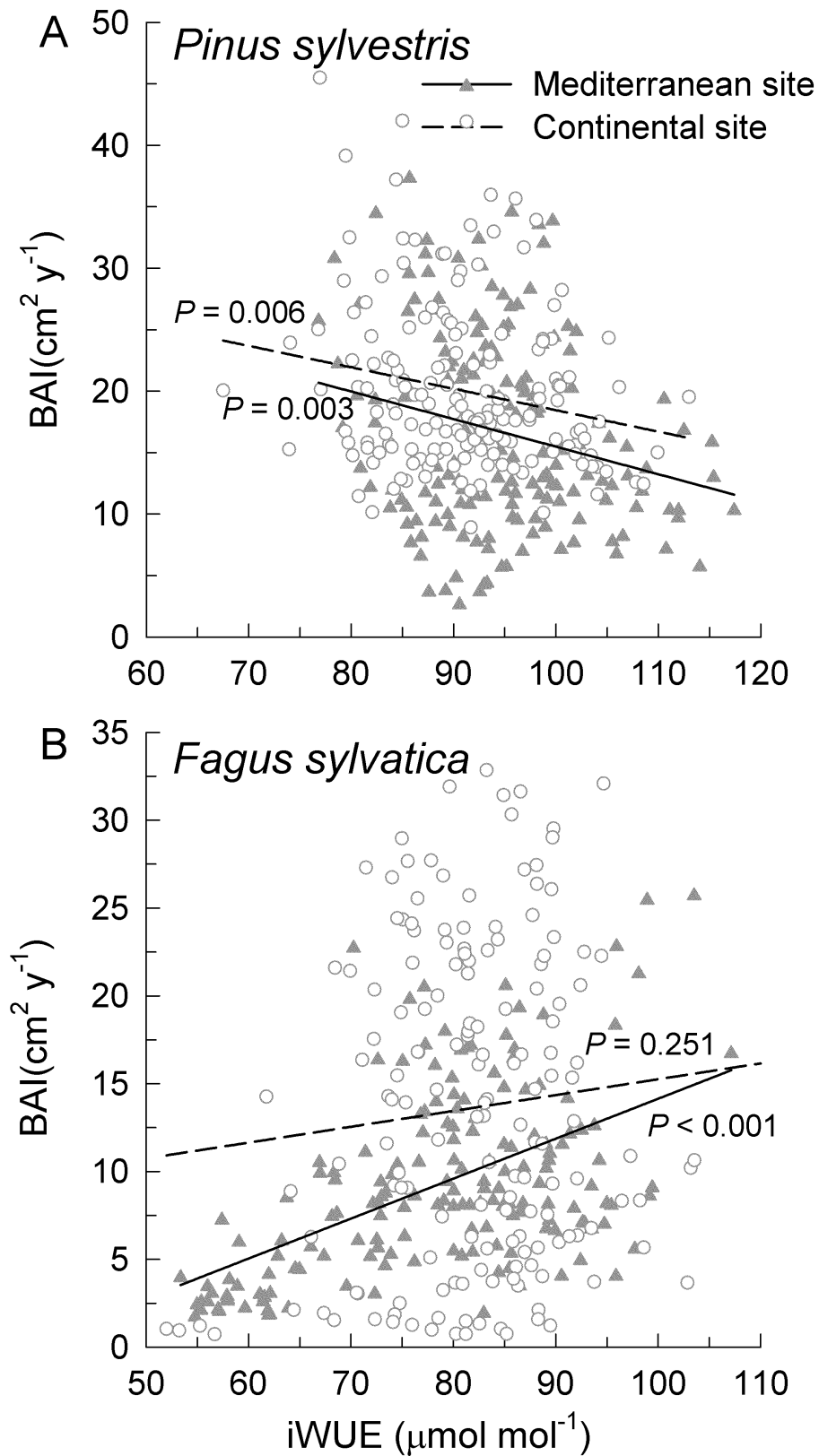


Fig. 5. Relationships observed between intrinsic water use-efficiency (iWUE) and growth (basal area increment, BAI) in the two study sites for Scots pine (*Pinus sylvestris*, **A**), and European beech (*Fagus sylvatica*, **B**).