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Attributing forest responses to global-change drivers: limited evidence of a CO_2-fertilization effect in Iberian pine growth

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ABSTRACT

Aim Forest responses to global-change drivers such as rising atmospheric CO_2 concentrations (C_a), warming temperatures and increased aridification will depend on tree species and site characteristics. We aim to determine if rising C_a enhances growth of coexisting pine species along broad ecological gradients in a drought-prone area.

Location Iberian Range, Spain.

Methods We sampled 557 trees of five pine species encompassing a wide climatic gradient and measured their radial growth. We used non-linear flexible statistics (generalize additive mixed models) to characterize growth trends and relate them to C_a, temperature and water balance.

Results The sites most responsive to the growing-season water balance were dominated by *Pinus pinaster* and *Pinus nigra* at low elevations whereas those most responsive to temperatures were high-elevation *Pinus sylvestris* and *Pinus uncinata* stands. From 1950 onwards, most sites and species showed decreasing radial- growth trends. Growth trends were coherent with a CO_2-related fertilization effect only in one *P. sylvestris* site.

Main conclusions We found little evidence of growth stimulation of Iberian pine forests due to rising C_a. The results indicated that any any positive effect of a C_a-induced growth increase was unlikely to reverse or cancel out the drought-driven trends of reduced growth in most Mediterranean pine forests. Further assessments of CO_2-fertilization effects on forest growth should be carried out in sites where climatic stressors such as drought do not override the effects of rising C_a on forest growth.

Keywords: basal area increment, CO_2-fertilization effect, dendroecology, drought, Generalized Additive Models, Mediterranean pines, *Pinus,* Spain, water balance.

Introduction

Forests dominate the carbon fluxes of terrestrial communities since wood accounts for 80% of land biomass (Bonan, 2008). Thus, forest responses to rising atmospheric CO_2 concentrations (C_a) will determine their role as carbon sinks (Le Quéré *et al*., 2009). In May summer 2014, C_a surpassed 400 ppm and this concentration may double in the 21^{st} century relative to that previous to 1850, with air temperatures projected to increase globally, possibly by as much as 4°C (IPCC, 2013). Forests could partially mitigate the effects of anthropogenic increasing C_a and the related planetary warming through net carbon uptake if growth rates increase. However, warmer temperatures can induce drought stress, leading to slowed radial growth rates in areas with water deficit despite rising C_a (Granier *et al*., 2007). The interplay between C_a and climate warming could explain why some forests show growth saturation signals, particularly in drought-prone areas (Nabuurs *et al*., 2013).

Rising C_a level may affect tree photosynthesis and growth by improving the intrinsic water-use efficiency (iWUE, i.e. the carbon fixed per unit of water transpired), which could reduce water loss through partial closure of stomata, particularly in areas with water deficit (Huang *et al*., 2007). However, improved iWUE and increasing forest growth are not usually related in temperate and boreal forests (Silva *et al*., 2010; Linares & Camarero, 2012; Lévesque *et al*., 2014). In addition, rising temperature associated with the current rise in C_a could also affect how trees react to climate by lengthening the growing season (Reyes-Fox *et al*., 2014), or by changing soil water availability (Zavaleta *et al*., 2003). Rising C_a could also selectively modify the growth of certain tree species (Streit *et al*., 2014) and specific stands such as those located in dry sites and undergoing greater iWUE increase (Silva & Anand, 2013).

Forest responses to rising C_a could depend on tree species and site conditions. Tree species show site specific patterns and trends in their growth responses to climate warming as has been observed in European silver fir forests (e.g. Gazol *et al*., 2015). These responses could influence how each species reacts to rising C_a at climatically contrasting sites. For example, conifer forests subjected to continental Mediterranean conditions would show enhanced growth and earlywood formation at high elevations in response to warmer winters, whereas warmer summers would reduce growth and latewood production at low elevation sites due to increased evapotranspiration rates (Sánchez-Salguero *et al*., 2015). Therefore, the dominant response to climate of each species in each site could alter the balance between earlywood and latewood formation and thus how growth responds to rising C_a.

To address these issues reliable and long-term growth data are needed. Tree-ring data allows testing if radial growth and carbon uptake are impacted by covarying C_a and climate (Babst *et al*., 2014). Nevertheless, radial growth could respond nonlinearly to rising C_a (Norby *et al*., 2010) but also to warmer temperatures (Way & Oren, 2010; De Grandpré *et al*., 2011). In addition, to detect potential influences of those drivers on growth we must remove long-term growth trends due to size or age (Brienen *et al*., 2012) and tree ontogeny (Voelker *et al*., 2006). Tree-ring data have shown contradictory results supporting either a positive fertilization effect of rising C_a on tree growth (Voelker *et al*., 2006; Soulé & Knapps, 2014) or negative to neutral responses (Gedalof & Berg, 2010; Girardin *et al*., 2011). Contrastingly, tree ring isotopic C composition and eddy covariance flux measurements indicate increasing iWUE in response to rising C_a (Peñuelas *et al*., 2011; Keenan *et al*., 2013). Such conflicting findings could be caused by distinct growth responses of co-occurring tree species to C_a and climate. For instance, the increase in the amount of carbon uptaken per unit of water lost could mitigate the carbon losses due to water shortage in some species or sites but not in others which are more sensitive to drought stress (Linares & Camarero, 2012; Brzostek *et al.*, 2014).

Iberian pine forests provide a template to answer those questions as they are dominated by several tree species coexisting along elevational gradients characterized by changing climatic conditions and vegetation types (Tapias *et al.*, 2004). Consequently, we aim to evaluate the long-term growth responses of coexisting Iberian pine species to C_a and climate at the site and tree levels. To reach this objective we sampled 557 trees pertaining to five pine species distributed in 33 populations in eastern Spain. To mitigate the effects of sampling biases on growth estimations we sampled trees of different sizes and ages and used nonlinear statistical models of growth. Our specific objectives were: (i) to characterize the growth trends and responses to climatic drivers in five pine species across a wide ecological gradient; and (ii) to test if those trends and responses were linked to rising C_a. We hypothesize that a CO_2-fertilization effect due to rising C_a should enhance growth in drought-prone sites because of iWUE improvement (cf. Fig. 1a). Alternatively, if growth is mainly constrained by water deficit we expect to detect growth enhancement only in mesic sites.

Materials and methods

Study area and pine species

The study area was located in the southern Iberian Range, eastern Spain (Teruel, Aragón) and includes 33 pine populations distributed among 29 sites located in the Gúdar (23 sites), Javalambre (4 sites) and Albarracín (2 sites) ranges (Fig. 2, Table 1). Most stands (*n* =12) were dominated by *Pinus nigra* Arn. subsp. *salzmannii* (Dunal) Franco, followed by *Pinus sylvestris* L. (n = 7), *Pinus pinaster* Ait. (n = 3), *P.*

halepensis Mill. (n = 2), and *Pinus uncinata* Ram. (n = 1). The most intensively sampled species was *P. nigra* (235 trees, 42% of total) followed by *P. sylvestris* (173 trees, 31%), *P. pinaster* (82 trees, 15%), *P. uncinata* (34 trees, 6%) and *P. halepensis* (33, 6%). We also sampled eight mixed stands dominated by *P. uncinata*-*P. sylvestris* (1 site), *P. nigra*-*P. sylvestris* (2 sites) and *P. nigra*-*P. pinaster* (1 site). The *P. uncinata* population constitutes the southernmost limit of distribution of the species in Europe. The study sites were distributed along an elevational gradient ranging from 1055 to 2020 m a.s.l. Two species dominated the cold high-elevation (1800-2020 m a.s.l.) sites (*P. uncinata*, *P. sylvestris*), whereas two species (*P. pinaster*, *P. pinaster*) dominated the low-elevation (1055-1350 m a.s.l.) warmt and dry sites most subjected to prolonged summer droughts (Table 1, Fig. 2). In sub-Mediterranean transitional areas *P. nigra* occurs along the widest range of elevations (1090-1700 m a.s.l.). Soils in the study area are basic and clayey or loamy with a mean C:N ratio of 18.2, except in Albarracín where acidic soils abound. Relatively undisturbed sites (no indications of recent logging, fire or grazing) were selected (Table 1). Human impacts in the the study area (logging, grazing) greatly diminished after the 1950s at a time when massive migration to cities triggered local depopulation. Nowadays, this region is among the less densely populated areas in Europe (http://appsso.eurostat.ec.europa.eu/nui/show.do?dataset=demo_r_d3dens&lang=en, accessed June 18, 2015). It is also recording low nitrogen deposition rates with for instance, mean NH_4 througfall deposition in a *P. nigra* forest (site VC1, Fig. 2) being 1.82 kg ha^{-1} yr^{-1} during the 1997-2010 period. This value corresponded to the lowest decile in European data (Waldner *et al.* 2014).

Field sampling and dendrochronological methods

Field sampling was conducted in late summer 2006. We randomly selected on average 17 dominant trees per site and species in 0.5-1 ha sampling areas. The basal area at each site was estimated from two representative prism points using the Bitterlich (1984) method. Specifically, we aimed to sample mature trees reaching the phase when their radial growth rates tend to stabilize. We also measured diameter at breast height (dbh; 1.3m) and total height of each tree. Sampled trees showed wide dbh (16.6-86.0 cm) and height (2.5-20.0 m) ranges. Two increment cores were taken at 1.3 m from each tree using a Pressler increment borer. Wood samples were air-dried, sanded and visually cross-dated. Tree-ring widths were measured under a binocular scope at a precision of 0.001 mm using a Velmex measuring system. Earlywood (EW) and latewood (LW) widths were separately measured in one site per species to detect seasonal influences of climate on growth. Visual cross-dating and tree-ring measurements were validated using the program COFECHA (Holmes, 1983). Tree age at 1.3 m varied from a minimum of 35 years (*P. halepensis*) to a maximum of 445 years (*P. nigra*).

To minimize the impact of defoliations by the pine processionary moth (*Thaumetopoea pityocampa* Dennis and Schiff.) on short-term growth trends we discarded recently defoliated *P. nigra* trees; this species being most susceptible to the insect defoliation (Sangüesa-Barreda *et al*., 2014). We avoided sampling in areas with recent outbreaks and we discarded those tree-ring series whose characteristics reflected past defoliation episodes (e.g., presence of several consecutive narrow and/or missing rings).

To quantify the growth-climate associations we developed both tree and site chronologies and tree-ring width (RW), EW and LW indices were calculated using the ARSTAN (ver. 4.4; Cook & Krusic, 2005), which uses specific methods to correct for the age/size trends. Tree-ring widths were transformed into growth indices with both stable mean and variance by dividing observed values by expected values estimated using a cubic-smoothing spline curve of 100 years with a fixed 50% cut off frequency of 75% of each series length. Autoregressive modelling was also performed to remove temporal autocorrelation and to generate residual indices at the individual tree level. Lastly, a biweight robust mean was used to compute mean residual site chronologies for each species. Among the developed chronologies, we considered only those covering the period 1950-2006 which corresponded to the period of most reliable climatic data in the study area. Finally, to assess the strength of the chronologies routine descriptive statistics used in dendrochronology were calculated for the common period 1950-2006 by using the ARSTAN program.

Climate and atmospheric CO_2 *data*

To obtain regional climatic series characterizing the entire study area, mean temperature and total precipitation data from ten meteorological stations located within the study area were combined into a regional mean of seasonal and monthly data (see more details in Sangüesa-Barreda *et al.*, 2014). To take into account the elevation difference among sampling sites, we corrected the regional mean temperature calculated from the 10 meteorological stations to generate site specific corrected temperature data using a Digital Terrain Model (Pasho *et al.*, 2011) and considering a mean lapse rate of -7.8 ºC km^{-1}. We also calculated the monthly water balance at each site as the difference between precipitation and potential evapotranspiration (PET) following the method of Hargreaves and Samani (1982). The regional climate data indicated no significant warming trend in seasonal temperature since 1950 (results not presented) but drought years were frequently observed (Fig. 1d).

As a quality control, the site-derived climate data were also compared with the gridded (0.5º grids) homogenised and high-quality spatial climate estimates for the period 1950-2006 obtained from the the CRU TS 3.1 database (Harris *et al.*, 2014). To estimate the drought intensity at each site we also used the gridded (0.5º grid) multi-scalar Standardised Precipitation-Evapotranspiration Index (SPEI). This drought index shows the cumulative water stress for several months on different time scales with negative and positive values corresponding respectively to dry and wet periods (Vicente-Serrano *et al.*, 2010). The SPEI values for the period 1950-2006 were obtained from the SPEI webpage http://sac.csic.es/spei/index.html, accessed April 20, 2015).

At last, annual C_a values were computed from monthly values taken from the Mauna Loa (Hawaii) with data available from 1959 onwards (these data are available at http://www.esrl.noaa.gov/gmd/ccgg/trends, accessed April 22, 2015). Both the mean and the annual increment of C_a were obtained because increments represent a global average of the CO_2 added to, and removed from, the atmosphere (see http://www.esrl.noaa.gov/gmd/ccgg/trends/#mlo_data, accessed April 22, 2015).

Growth-climate associations

To determine which were the main climatic drivers of year-to-year variability in tree growth monthly mean temperature and water balance (total monthly precipitation yielded similar results to that of water balance and will thus not be presented) were correlated to RW, EW and LW chronologies developed at the the tree/species and site/species levels. We also performed these analyses using both local or CRU climatic data and compared their performances based on the Pearson correlations obtained for the common period 1950-2006. The temporal window of growth-climate comparisons included from the previous up to the current September (13 months).

Modelling the effect of C_a on tree growth

To model the impact of rising C_a on tree growth, basal area increment (hereafter abbreviated as BAI) was calculated as:

$$\mathrm{BAI} = \pi \left(r_t^2 - r_{t-1}^2\right) \qquad (1)$$

where r_t and r_{t-1} are the squared stem radial increments at the end and the beginning of a given annual ring increment corresponding to rings formed in years t and t-1, respectively.

We considered that BAI may respond nonlinearly to C_a and climatic constraints and we assumed that these reponses depend on species-, site- and tree-related attributes. Therefore, we modeled separately the BAI series of each site and species as a function of tree attributes (dbh, height and age) and calendar year during the timespan of each tree series (see Table 2). We used Generalized Additive Mixed Models (GAMM; Wood, 2006) to model BAI for each study site and species as:

$$log\ (BAI_i+1) = s(dbh_i) + s(height_i) + s(age_i) + s\ (calendar\ year_i) + Z_iB_i + \upsilon_i \qquad (2)$$

where the BAI of a tree i is modelled as smooth functions (s) of tree variables (dbh, height, age) and calendar year, and trees (Z_iB_i) are regarded as random effects. The smooth terms were represented using thin plate splines (Wood, 2006). Since BAI of year t depends on the previous-year (t-1) BAI, we also included in the model an error term (υ_i) with an AR1 (p=1, q=0) correlation structure. We tested that analyzed variables fulfilled the statistical criteria required to apply GAMMs such as normality, heterogeneity and independence (results not presented).

According to our theoretical framework, the BAI values predicted by GAMMs represent long-term growth trends without the influence of year-to-year climatic variations, while BAI residuals characterize the year-to-year growth variation (Fig. 1).

Therefore, firstly BAI was modeled with the aforementioned GAMMs (Fig. 1b). We also quantified the BAI trends during the period 1950-2006 since positive growth trends could indicate a fertilization effect by rising C_a (Fig. 1c). Since the detection of growth trends may be influenced by the data at hand, we compared three approaches based on mean site series: BAI, RW indices obtained from the ARSTAN program (as described before), and RW indices obtained after regional curve standardization which uses an average curve describing age/size trends of tree growth (Peters *et al*., 2015).

Secondly, we related the standardized BAI residuals, representing the short-term growth variability, with the annual C_a increment and monthly climate variables most strongly related to RW chronologies (e.g. water balance) (Fig. 1d). To determine if the associations between climatic factors and BAI residuals were unstable during the period 1950-2006 we also calculated running correlations considering 20-year long intervals. The *mgcv* package was used to calculate the GAMMs (Wood, 2006). All statistical analyses were done using the R software (R Development Core Team, 2014).

Results

Structure and growth

The sampled sites form relatively open stands showing diverse values of basal area and tree diameter with a mean tree age of 125 years (Table 2). Basal area increased with site elevation ($r = 0.47$, $P < 0.01$), which suggests better growing conditions as temperatures decrease and the water balance improves with elevation. Regarding RW, both its year-to-year variability (MSx, $r = -0.76$, $P < 0.001$) and the coherence among trees (r_{bt}, $r = -0.83$; PC1, $r = -0.80$; $P < 0.001$) decreased with elevation with the opposite trend observed with the persistence in growth (AC1, $r = 0.78$, $P < 0.001$). For instance, *P. uncinata* and *P. sylvestris* sites had significantly higher AC1 values (mean = 0.80) than

P. pinaster and *P. halepensis* sites (mean = 0.66), while the reverse was observed for the RW coherence (mean r_{bt} = 0.62 *vs*. 0.81; Tukey HSD test, *P*<0.05).

Climatic drivers of growth

A positive water balance from May to July was the main positive driver of RW, particularly at low-elevation *P. nigra* and *P. pinaster* sites (Fig. 3). The relationships between RW and climate shifted along the elevation gradient indicating species-specific phenological differences. For instance, a positive July water balance and cool August conditions enhanced *P. uncinata* RW, whereas in other species wet May and cool June conditions dominated (Fig. 3). Warm but dry conditions in the previous October also enhanced RW of high-elevation *P. uncinata* and *P. sylvestris* sites. The EW presented similar responses to climate as RW whereas LW was favoured by cool and wet conditions from July to September, particularly in the case of *P. nigra* and *P. pinaster* sites. Similar results were observed when using gridded CRU climate data but the correlations were stronger using local site climate data (results not presented).

The species most responsive to drought were *P. nigra* and *P. pinaster* followed by *P. halepensis* with RW responding to May to August SPEI at 7-15 months long scales (Fig. 4). In the case of EW, *P. pinaster* was the most drought-sensitive species, showing a similar behaviour to RW, whilst its LW responded positively to short-term (2-8 months long scales) wet conditions in late summer (see Appendix S1 in Supporting Information). In general, the elevation gradient separated temperature- (e.g. *P. uncinata*) and drought-responding species (e.g. *P. pinaster*) and this division was detected at both the tree and site levels.

Regarding the climate-BAI residuals associations, all species and sites showed positive and significant BAI responses to the growing season water balance, with the exception of the *P. sylvestris* SJ site (Table 3). A negative and significant effect of a warmer growing season (May to July) on BAI was observed in low-elevation drought-prone sites (e.g., *P. pinaster* MI site) and also to a lesser extent in some high-elevation sites (e.g., *P. uncinata* sites) (Table 3). Nevertheless, BAI responded less to the summer water balance as elevation increased (r = -0.52, P <0.01).

Relationships between growth and C_a

We detected significant negative (10 sites) or positive (7 sites) associations between BAI and C_a (Table 3). The strongest positive BAI-C_a associations were found in the *P. sylvestris*-SJ and the *P. pinaster*-MI sites (see BAI patterns of all sites in the Appendix S2 of Supporting Information). These findings are consistent with site-specific BAI responses to climate and C_a, which were similar among coexisting species (results not presented).

At the site level, changes in growth along the elevation gradient were associated with how BAI and C_a were related (Fig. 5). Indeed, the association between BAI and C_a decreased as basal area (r = -0.50, P = 0.004) or mean tree height (r = -0.46, P = 0.01) increased considering all species (results not presented). Elevation and the BAI-C_a *t*-statistics were negatively related at the site level if the *P. sylvestris*-SJ site was excluded (r = -0.41, P = 0.023).

At the tree level no BAI enhancement was detected in the low-elevation driest sites (Fig. 6). Finally, some tree attributes modified the BAI-climate climate associations but not the BAI-C_a- associations. For instance, in *P. nigra* trees the response of BAI residuals to the growing season water balance increased as trees aged (results not presented).

Growth, climate and C_a *trends*

Summer water balance decreased slightly (r = -0.23, P = 0.12, n= 48) for the period 1959-2006, whereas the annual increment in CO_2 increased significantly (r = 0.47, P<0.001). Only 5 sites presented a higher percentage of trees showing significant positive BAI trends than trees presenting negatived trends (Table 3). The site with the highest percentage of trees (71%) showing significant and positive BAI trends was the *P. sylvestris*-SJ site. Furthermore, the positive trends detected in this site were similarly observed using conservative growth-detection methods based on spline- or regional curve standardization detrendings (results not presented). As expected, sites with older trees tend to present more significant and negative BAI trends (r = 0.44, P = 0.019). Sites whose trees showed larger diameters (r = -0.47, P = 0.010) and were older (r = -0.45, P = 0.009) presented significant positive trends in the running correlations calculated between BAI residuals and summer water balance (results not presented). Thus, the importance of summer water balance for the year-to-year BAI variability is increasing in sites with larger and usually older trees, particularly in the case of *P. nigra* which showed a significant association between tree age and the BAI residuals (r = 0.32, P < 0.05).

Discussion

CO_2 fertilization effect in Iberian pine forests

We found little evidence of a CO_2-fertilization effect on radial growth in five Iberian pine species distributed across wide climatic and ecological gradients. The results provided little indication that rising C_a has stimulated radial growth even in drought-prone sites where iWUE would have been most improved. In contrast, the water balance during the growing season, as well as previous-fall and current-spring temperatures in the case of high-elevation *P. uncinata* sites (see Tardif *et al.*, 2003), were the major drivers of growth; potentially overriding any effects of increasing C_a. The results further indicated that BAI trends were only consistent with C_a-related growth stimulation in mesic sites such as the *P. sylvestris*-SJ stand, where the negative effects of drought on growth were less apparent. However, we can not discard that increasing C_a could lessen the negative impact of drought on growth in the driest sites, i.e. the negative BAI trends could have been more pronounced if C_a remained stable. The comparison of observed and simulated growth data based on process-based models could help to answer this last question (Girardin *et al.*, 2011).

Water balance as major driver of growth across Iberian pine forests

The growth-climate associations corroborated that growth of Iberian pine species, and particularly EW formation, would be enhanced by warm conditions during the previous winter up to the summer. This implies that warmer winters will stimulate EW formation in Mediterranean populations of widely distributed conifers as *P. sylvestris*, whilst warmer and drier summers will constrain EW and also LW development in those stands and in Mediterranean tree species (e.g., *P. nigra*, *P. pinaster*). Some of these results echo those of previous authors (Andreu *et al.*, 2007). Growth of the southernmost *P. uncinata* stand also responded positively to wet summer conditions. This was rarely observed in *P. uncinata* stands located in the core of the species distribution area with the exception of rocky and steep sites where soil water retention is low (Tardif *et al.*, 2003; Galván *et al.*, 2014). This exceptional behaviour in a typically subalpine tree species adapted to cold conditions suggests local adaptation to cope with seasonal but episodic summer water shortage occurring at that southernmost stand. Such biogeographical differences suggest that warming trends should be jointly analysed with data on precipitation variability to fully characterize the major climatic drivers of Mediterranean forest growth (Andreu *et al*., 2007). Furthermore, those analyses should explicitly consider climate and growth seasonality coupled with carbon isotopes since EW formation mostly corresponds to carbohydrates synthesized before the growing season starts, whereas LW formation mainly depends on carbon fixed during the growing season and how it is allocated to growing tissues (Babst *et al*., 2014).

The forest responses to drought change as a function of tree species, site conditions (e.g. competition, disturbances) and tree attributes (size, age). For instance, in this study the most drought-responsive species were *P. pinaster* and *P. nigra*, i.e. the dominant species growing at dry low-elevation sites with *P. halepensis*. These responses also changed as a function of climate variables and species attributes since *P. pinaster* responded more strongly to changes in spring water availability, whereas *P. nigra* was more sensitive to changes in early-summer temperature (Candel-Pérez *et al*., 2012). The different responses to climate could modulate how each species responds to rising C_a since strong warming trends are forecasted for the Circum-Mediterranean area but future precipitation trends are more uncertain (IPCC, 2013). This research showed that mid- (*P. nigra*) and high-elevation (*P. sylvestris*, *P. uncinata*) species would be the most affected species by warmer growing-season temperatures, with negative and positive effects, respectively. On the other hand, growth of low-elevation *P. pinaster* stands may decline if drought stress steeply increases. These results contribute information on the potential growth responses of Mediterranean pine forests to climate warming and drying. However, these findings do not fully agree with conclusions based on forest inventory data predicting that high-elevation *P. sylvestris* will show negative responses to warmer conditions across Spain (Coll *et al*., 2013). Inventory data compared to tree-ring data cover most frequently a short time period and often assume space-for-time substitutions in evaluating future growth trends.

Iberian pine growth responses to CO_2 are overriden by drought influences

Soil water availability in Mediterranean forests decreases during the growing season when drought becomes the major constraint of radial growth, especially in mid- and low-elevation stands. During that period maximum growth rates usually occur and wood formation and productivity are coupled (Babst *et al.*, 2014). This indicates again the prominent role played by drought as driver of carbon sequestration in the study stands. Therefore, we would also expect to detect weaker running correlations of growth with the growing-season water balance as iWUE is improved by rising C_a, but this was not observed. In addition, the responsiveness of growth to water balance increases as *P. nigra* trees age and become more drought-stressed. Therefore, conservation of forests dominated by old trees, as some *P. nigra* sites, is a priority given that they act as long-term carbon sinks (Luyssaert *et al.*, 2008) and show different sensitivity to water deficit than young trees (Linares *et al.*, 2013).

At the site level, the strength of the association between BAI and C_a decreased as basal area or tree height increased. This suggests that an effect of competition on the BAI-C_a association cannot fully be discarded (see Madrigal-González & Zavala, 2014). In our study, relatively open stands were sampled with the assumption that competition for light played a minor role as a driver of growth compared with drought tolerance. Interestingly, trees showed growth patterns consistent with a CO_2-fertilization effect in the mesic *P. sylvestris*-SJ site, at an elevation where growth started to depend more on temperature than on water balance. Disturbances could also modify growth-C_a

relationships in this site (Etzold *et al*., 2014), which was affected by a *Lymantria monacha* outbreak in the 1950s.

In the case of high-elevation *P. uncinata* stands, elevated CO_2 concentrations have been shown at the Swiss alpine treeline to increase the photosynthetic rate but this enhanced carbon uptake did not translate in enhanced growth (Streit *et al*., 2014). Such findings again confirm the existence of species-specific growth responses to climate and C_a, or more precisely site-dependent responses given that coexisting pine species show similar BAI responses to climatic constraints and also to C_a.

Climate warming can improve forest carbon uptake through an enhanced allometric partitioning to wood (Way & Oren, 2010). However, warming-induced drought stress may reverse that positive effect if a higher evapotranspiration demand leads to water deficit below a critical threshold which triggers abrupt drops in growth and carbon fixation (Granier *et al*., 2007). Finally, severe nutrient limitation of growth seems not to be plausible in the study area, where nitrogen deposition rates and soil data do not support that idea. Additional coupled tree-ring / isotopic studies should test if severe drought leads to growth decline and mediates the lack of CO_2-stimulation by impairing the use or availability of nutrients as nitrogen.

In conclusion, no strong indication of a CO_2-fertilization effect was observed in Iberian pine forests except in a mesic *P. sylvestris* site. Results showed that growth of five pine species was mainly controlled by the growing season water balance. Elevated C_a could increase productivity in forests where all major climatic constraints of radial growth (drought, cold temperatures) do not operate. While we cannot discard the possibility that growth decline in the driest sites may be lessen with rising C_a this question should be addressed by comparing process-based models of growth with tree-ring data. The presented statistical models allowed quantifying how long-term growth data related to rising C_a and climate. This is a first and necessary step to explicitly incorporate these parameters into mechanistic models simulating how tree species distributions will change according to CO_2-climate-driven scenarios.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Correlations obtained by relating the SPEI drought index and the mean earlywood and latewood width chronologies of the five study pine species.

Appendix S2 Patterns in basal area increment during the 20th century for each study site and pine species.

Appendix S3 The mesic site SJ dominated by Scots pine shows an enhancement in basal area increment.

BIOSKETCHES

Our research team aims to understand, from a multidisciplinary and global perspective, the effects of global-change drivers (climate warming, shifting biogeochemical cycles, land-use changes) on the growth and distribution of woody plant species, with a particularly emphasis on trees.

Author contributions: J.J.C., A.G. and J.C.T. conceived the ideas; J.J.C., F.C. and J.C.T. collected and processed the data; A.G. and J.J.C. analysed the data; and J.J.C. led the writing. All the authors read and approved the final draft.

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Table 1. Geographical and topographical characteristics of the Iberian pine forests sampled in 33 sites. Sites are arranged from low to high elevation.

Range	Site	Code	Latitude (N)	Longitude (W)	Elevation (m)	Aspect	Substrate[1]	Main pine species	Woody species[2]
Gúdar	Valbona-halepensis	VH	40º 16’ 03’’	0º 48’ 02’’	1055	S-SE	S	*P. halepensis*	*Pp, Qi, Qc, Jo, Jp*
Gúdar	Valbona	VL	40º 16’ 00’’	0º 48’ 53’’	1070	SE	S	*P. pinaster*	*Qi, Av, Jo, Jp, Q*
Gúdar	Alto de Cabra	AC	40º 19’ 55’’	0º 48’ 26’’	1090	E	S	*P. nigra, P. pinaster*	*Qf, Qi, Jo, Jp*
Gúdar	Pino Halepensis	PH	40º 17’ 17’’	0º 48’ 03’’	1095	S-SW	L	*P. halepensis*	*Pp, Gs, Jp, Qi*
Javalambre	Fuente del Gavilán	FG	40º 02’ 00’’	0º 53’ 30’’	1140	N	L	*P. nigra*	*Po, Ps*
Gúdar	Valle de Cabra	VC1	40º 17’ 46’’	0º 47’ 17’’	1165	NE	S	*P. nigra*	*Pp, Qf, Jo*
Gúdar	Valle de Cabra	VC2	40º 17’ 46’’	0º 47’ 17’’	1165	N	S	*P. pinaster*	*Pn, Qf, Jo*
Gúdar	Mora-Los Campillos	ML	40º 18’ 34’’	0º 45’ 59’’	1200	W	S	*P. nigra*	*Jo, Jp, Gs, Qi, Ll*
Gúdar	Fuendenarices	FU	40º 18’ 24’’	0º 43’ 30’’	1230	W	L	*P. nigra*	*Jp, Qi, Jo, Gs, Ea*
Gúdar	Alto de Mora	AM	40º 17’ 43’’	0º 42’ 51’’	1330	SE-SW	L	*P. nigra*	*Jp, Jc, Gs, Qi, Ll*
Albarracín	Mina Amparo	MI	40º 13’ 23’’	1º 18’ 58’’	1345	NW-NE	S	*P. pinaster*	*Jo, Jp, Qi, E, Cl*
Gúdar	Alcalá (Cabra)	AL	40º 21’ 02’’	0º 45’ 58’’	1350	SE	L	*P. nigra, P. sylvestris*	*Jo, Jp, Sd, Gs, Ll*
Gúdar	Masía Peñarroya	MP	40º 18’ 40’’	0º 41’ 37’’	1435	S	L	*P. nigra*	*Jp, Jo, Gs, Ll*
Javalambre	Alto de la Fuensomera	AF	40º 00’ 32’’	0º 51’ 33’’	1445	W	L	*P. nigra*	*Qi, Jo, Ll*
Javalambre	Torrijas	PO	40º 00’ 29’’	0º 53’ 26’’	1455	NE	L	*P. nigra*	*Ps, Jt, Js, Jc*
Gúdar	Camino Olmedilla 1	CO1	40º 20’ 05’’	0º 43’ 56’’	1495	SW	L	*P. nigra*	*Ps, Jc, Bv, Gs, Ll*
Gúdar	Camino Olmedilla 2	CO2	40º 20’ 10’’	0º 43’ 51’’	1510	SE	L	*P. sylvestris*	*Pn, Jc, Qi, Gs*
Gúdar	Las Roquetas	RO	40º 18’ 36’’	0º 42’ 58’’	1550	W	L	*P. nigra*	*Jc, Jt, Ao, Ea, Ll*
Gúdar	Elevation gradient-middle	G2	40º 18’ 13’’	0º 40’ 40’’	1605	W	L	*P. nigra*	*Jc, Js, Ea, Qf, Ra*
Gúdar	Las Roquetas	LR	40º 19’ 19’’	0º 42’ 08’’	1615	SE	L	*P. nigra, P. sylvestris*	*Jc, Jt, Bv, Qi, Ao*
Gúdar	Elevation gradient-up	G1	40º 18’ 32’’	0º 40’ 22’’	1675	W	L	*P. nigra*	*Ps, Jc, Js, Ea, Ao*
Gúdar	Mora-El Chaparroso	MC	40º 19’ 05’’	0º 40’ 28’’	1770	SW	L	*P. sylvestris*	*Jc, Cm, Sa*
Gúdar	Peñarroya-low	PN3	40º 23’ 00’’	0º 39’ 36’’	1805	SE	L	*P. sylvestris*	*Jc, Bv*
Albarracín	Muela de San Juan	SJ	40º 25’ 20’’	1º 43’ 13’’	1860	NE	L	*P. sylvestris*	*Jc, Bv*
Javalambre	Javalambre	JA	40º 03’ 23’’	0º 59’ 35’’	1865	SW	L	*P. sylvestris*	*Jc, Js, Bv, Sa*
Gúdar	Valdelinares-middle	VA2	40º 22’ 50’’	0º 38’ 03’’	1950	SW	L	*P. sylvestris*	*Jc, Js, Bv*
Gúdar	Valdelinares-high	VA1	40º 22’ 51’’	0º 37’ 60’’	1955	SW	L	*P. uncinata*	*Ps, Jc, Js*
Gúdar	Peñarroya-middle	PN2	40º 23’ 22’’	0º 39’ 38’’	1990	SW	L	*P. sylvestris*	*Pu, Jc*
Gúdar	Peñarroya-high	PN1	40º 23’ 30’’	0º 39’ 50’’	2020	N-NE	L	*P. uncinata, P. sylvestris*	*Jc, Js, Ra*

[1] Geological substrates: L, limestones, S, sandstones.

[2] Species' codes: *Ao, Amelanchier ovalis*; *Av, Arctostaphylos uva-ursi*; *Bv, Berberis vulgaris*; *Cl, Cistus laurifolius*; *Cm, Crataegus monogyna*; *Ea, Erinacea anthyllis*; *E, Erica* spp.;*Gs, Genista scorpius*; *Jc, Juniperus communis*; *Jo, J. oxycedrus*; *Jp, J. phoenicea*; *Js, J. sabina*; *Jt, J. thurifera*; *Ll, Lavandula latifolia*; *Ph, Pinus halepensis*; *Pn, P. nigra*; *Pp, P. pinaster*; *Ps, P. sylvestris*; *Pu, P. uncinata*; *Po, populus nigra*; *Qc, Quercus coccifera*; *Qf, Q. faginea*; *Qi, Q. ilex*; *Ra, Rhamnus alpine*; *Sa, Sorbus aria*; *Sd, S. domestica*.

Table 2. Structural and dendrochronological characteristics of the Iberian pine trees sampled in 33 sites. See sites' codes in Table 1. The underlined sites are those where earlywood and latewood widths were also measured. Sites are arranged from low- to high-elevation.

Site	Basal area (m^2 ha^{-1})	Dbh (cm)	Height (m)	Species	No trees	No cores	Age^1 (years)	RW (mm)	AC1	MSx	r_{bt}	PC1 (%)	Timespan
VH	12.2	34.4 ± 1.4	10.6 ± 0.3	*P. halepensis*	17	34	58 ± 2	2.08 ± 0.20	0.70	0.34	0.80	73.80	1950-2006
VL	39.1	39.1 ± 0.9	12.0 ± 0.3	*P. pinaster*	25	50	105 ± 4	1.13 ± 0.10	0.64	0.46	0.85	75.80	1903-2006
AC	28.0	38.8 ± 2.7	10.1 ± 0.5	*P. pinaster*	16	32	91 ± 3	1.28 ± 0.15	0.74	0.42	0.81	73.20	1927-2006
AC	28.0	35.6 ± 1.4	10.0 ± 0.4	*P. nigra*	17	34	105 ± 8	1.11 ± 0.13	0.68	0.47	0.75	64.10	1890-2006
PH	8.2	40.0 ± 2.7	8.6 ± 0.8	*P. halepensis*	16	32	73 ± 4	1.75 ± 0.18	0.55	0.44	0.77	76.40	1934-2006
FG	39.0	56.8 ± 4.0	20.0 ± 1.1	*P. nigra*	3	6	–	–	–	–	–	–	–
VC1	24.0	32.3 ± 0.9	12.7 ± 0.6	*P. nigra*	15	30	105 ± 4	1.03 ± 0.15	0.66	0.55	0.84	76.50	1920-2006
VC2	26.3	32.2 ± 1.2	11.2 ± 0.4	*P. pinaster*	15	30	78 ± 3	1.28 ± 0.12	0.58	0.38	0.83	74.00	1937-2006
ML	4.2	33.8 ± 2.9	6.9 ± 0.3	*P. nigra*	21	42	85 ± 5	1.57 ± 0.17	0.65	0.53	0.72	67.90	1946-2006
FU	19.1	40.0 ± 1.6	9.9 ± 0.3	*P. nigra*	21	42	169 ± 7	0.84 ± 0.10	0.75	0.41	0.67	46.70	1867-2006
AM	14.1	33.3 ± 1.4	6.7 ± 0.3	*P. nigra*	15	30	125 ± 4	0.85 ± 0.12	0.67	0.58	0.76	68.60	1907-2006
MI	25.0	42.9 ± 2.1	9.2 ± 0.3	*P. pinaster*	26	52	126 ± 4	1.08 ± 0.09	0.74	0.36	0.77	61.50	1909-2006
AL	14.2	35.9 ± 1.4	11.6 ± 0.5	*P. nigra*	17	34	121 ± 4	1.07 ± 0.14	0.75	0.39	0.78	63.60	1901-2006
AL	14.2	33.9 ± 1.2	9.5 ± 0.4	*P. sylvestris*	22	44	108 ± 5	1.10 ± 0.12	0.77	0.39	0.71	55.80	1926-2006
MP	4.7	42.0 ± 0.9	7.6 ± 0.4	*P. nigra*	17	32	115 ± 2	1.30 ± 0.16	0.73	0.46	0.75	67.00	1915-2006
AF	28.0	50.1 ± 1.8	12.0 ± 0.6	*P. nigra*	15	28	176 ± 12	0.93 ± 0.15	0.71	0.56	0.68	68.30	1895-2006
PO	27.2	65.1 ± 0.2	10.0 ± 0.1	*P. nigra*	4	9	–	–	–	–	–	–	–
CO1	9.5	49.6 ± 1.5	12.1 ± 0.4	*P. nigra*	20	40	155 ± 4	1.11 ± 0.16	0.70	0.35	0.78	62.80	1879-2006
CO2	32.1	40.3 ± 1.6	12.8 ± 0.7	*P. sylvestris*	15	29	103 ± 6	1.37 ± 0.16	0.72	0.35	0.68	47.90	1938-2006
RO	14.8	36.6 ± 1.4	7.3 ± 0.5	*P. nigra*	26	52	238 ± 13	0.46 ± 0.04	0.71	0.39	0.71	56.30	1850-2006
G2	13.5	46.9 ± 2.9	11.8 ± 0.7	*P. nigra*	17	34	153 ± 3	1.09 ± 0.11	0.70	0.37	0.74	58.50	1875-2006
LR	38.0	46.6 ± 2.7	9.9 ± 0.5	*P. nigra*	10	20	137 ± 5	1.15 ± 0.16	0.73	0.36	0.71	58.60	1899-2006
LR	38.0	41.0 ± 2.0	10.5 ± 1.0	*P. sylvestris*	11	22	134 ± 13	1.13 ± 0.14	0.76	0.34	0.64	54.60	1828-2006
G1	29.0	37.9 ± 1.8	10.5 ± 0.7	*P. nigra*	17	34	187 ± 8	0.74 ± 0.09	0.72	0.41	0.78	62.90	1858-2006
MC	29.2	38.4 ± 0.7	13.2 ± 0.4	*P. sylvestris*	20	40	153 ± 5	0.92 ± 0.08	0.72	0.28	0.67	53.00	1878-2006
PN3	49.0	38.3 ± 1.6	14.0 ± 0.6	*P. sylvestris*	15	30	81 ± 3	1.64 ± 0.18	0.86	0.24	0.58	40.30	1939-2006
SJ	19.0	39.0 ± 1.4	7.8 ± 0.2	*P. sylvestris*	20	40	138 ± 6	0.92 ± 0.10	0.85	0.27	0.60	37.20	1901-2006
JA	31.0	55.9 ± 3.4	9.2 ± 0.5	*P. sylvestris*	16	32	126 ± 8	1.51 ± 0.16	0.76	0.34	0.66	62.20	1909-2006
VA2	29.7	51.8 ± 2.0	11.3 ± 0.4	*P. sylvestris*	14	28	80 ± 4	2.07 ± 0.18	0.78	0.22	0.58	42.60	1950-2006
VA1	34.6	59.4 ± 2.6	10.4 ± 0.4	*P. uncinata*	16	32	146 ± 12	1.45 ± 0.14	0.85	0.20	0.53	37.00	1900-2006
PN2	27.8	57.9 ± 3.7	9.2 ± 0.6	*P. sylvestris*	10	20	162 ± 10	1.28 ± 0.13	0.83	0.23	0.54	37.90	1875-2006
PN1	36.6	43.6 ± 2.0	9.3 ± 0.5	*P. sylvestris*	30	52	140 ± 11	1.18 ± 0.14	0.85	0.26	0.62	39.40	1910-2006

PN1	36.6	39.8 ± 1.7	10.4 ± 0.3	*P. uncinata*	18	33	102 ± 9	1.52 ± 0.15	0.83	0.22	0.64	55.50	1928-2006

[1] Age at 1.3 m, number of annual rings of oldest core sampled at 1.3 m; RW, tree-ring width; AC1, mean of first-order autocorrelation of raw residual tree-ring width series; *MSx*, the mean sensitivity of residual tree-ring width series, which provides an indication of the year-to-year variability in width of consecutive tree rings; r_{bt}, the mean between-trees correlation which quantifies the similarity in growth among trees; PC1, percentage of variance explained by the first principal component which estimates the common variability in growth among all trees at each site; time span, statistically reliable time span based on sample replication and the latter two statistics.

Table 3. Summary table of basal-area increment (BAI) trends of Iberian pine forests and the main statistics (R^2, *t value*, *P*) obtained by relating BAI residuals to the annual increment in CO_2 concentrations and to climatic variables (May to July mean temperature and water balance; see Fig. 1d). The BAI trends were obtained for the period 1950-2006 and are expressed as the percentage of trees showing either positive or negative significant trends ($P<0.05$). The explained variance of BAI (R^2) is based on Generalized Additive Mixed Models fitted as a function of calendar year and tree attributes (diameter at breast height, height and age). The *t*-statistics and their corresponding significance levels (*P*, asterisks) are indicated for each explanatory variable. The sites are arranged from low to high elevation.

Site	Species	BAI trends (%)		R^2	year §	Annual increment in CO_2	Temperature	Water balance§
		Positive	Negative					
VH	*P. halepensis*	8.3	41.7	0.40	-10.25	1.62	-5.62***	10.12
VL	*P. pinaster*	44.0	4.0	0.36	17.84	0.34	-10.34***	15.62
AC	*P. pinaster*	14.3	42.9	0.60	-57.73	0.24	-9.45***	14.50
AC	*P. nigra*	0.0	58.3	0.55	-637.99	-2.10*	-7.08***	10.32
PH	*P. halepensis*	50.0	8.3	0.33	10.88	2.25*	-6.85***	12.96
VC1	*P. nigra*	13.3	20.0	0.22	350.34	-1.09	-5.15**	8.11
VC2	*P. pinaster*	46.1	7.7	0.33	166.69	0.15	-5.25***	9.24
ML	*P. nigra*	16.7	50.0	0.34	-89.65	2.64*	-2.54	4.15
FU	*P. nigra*	0.0	88.9	0.28	-132.80	-2.41**	-7.85**	7.28
AM	*P. nigra*	0.0	80.0	0.30	-111.46	3.61**	-3.55**	4.07
MI	*P. pinaster*	0.0	52.0	0.55	-453.25	3.78**	-10.94***	11.48
AL	*P. nigra*	18.7	12.5	0.31	-4.41	-0.97	-5.20***	7.31
AL	*P. sylvestris*	35.0	40.0	0.17	-8.07	-2.06*	-3.86***	5.95
MP	*P. nigra*	0.0	88.2	0.20	-215.48	1.56	-0.81	2.37
AF	*P. nigra*	0.0	92.9	0.21	-325.53	2.05*	-5.92***	4.49
CO1	*P. nigra*	10.5	42.1	0.31	-249.41	2.66*	-6.15***	10.22
CO2	*P. sylvestris*	6.7	60.0	0.37	-169.24	-1.84	-6.55***	8.66
RO	*P. nigra*	4.2	83.3	0.36	-200.84	0.85	-8.33***	9.65
G2	*P. nigra*	6.2	75.0	0.50	-368.75	-2.02*	-7.68***	10.71
LR	*P. nigra*	0.0	90.0	0.39	-242.19	0.08	-5.97***	6.66
LR	*P. sylvestris*	0.0	90.9	0.69	-131.10	-2.91*	-6.97***	8.12
G1	*P. nigra*	0.0	73.3	0.36	-157.17	-1.67	-6.23***	10.41
MC	*P. sylvestris*	35.0	35.0	0.36	-6.07	1.46	-6.22***	7.18
PN3	*P. sylvestris*	8.3	83.3	0.56	-131.40	-3.25**	-3.88***	5.19
SJ$^{\#}$	*P. sylvestris*	70.6	11.8	0.32	-185.60	4.14***	2.84**	-4.99
JA	*P. sylvestris*	35.7	35.7	0.27	-14.78	1.23	-1.34	3.98
VA2	*P. sylvestris*	0.0	80.0	0.16	-453.18	-2.85*	-3.41**	4.28
VA1	*P. uncinata*	7.1	71.4	0.34	-989.12	-3.01**	-2.54*	5.01
PN2	*P. sylvestris*	11.1	66.7	0.59	-120.54	-1.99*	-1.93	2.42
PN1	*P. sylvestris*	0.0	78.3	0.69	-107.95	-0.11	-1.94	4.01
PN1	*P. uncinata*	37.5	37.5	0.54	-288.94	-2.45*	-3.35**	6.49

Significance levels: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

§In all cases $P < 0.01$.

$^{\#}$This pine stand was affected in the 1950s by a *Lymantria monacha* outbreak causing a BAI increase afterwards in some trees (see Appendix S3 in Supporting Information).

Figure legends

Figure 1. Theoretical background assuming a more noticeable growth enhancement due to rising atmospheric CO_2 concentrations (C_a) and higher water-use efficiency under more severe dry conditions (a) and statistical procedures implemented to test that idea in the current study (b, c, d). In a first step, growth (assessed as basal area increment, BAI) of each tree (small symbols) in each site (black lines with symbols show the mean BAI value for that site) was modeled with Generalized Additive Mixed Models (smoothed lines show predicted means ± SD) as a function of calendar year and tree attributes (diameter at breast height, height and age) (b). In a second step, the GAMM residuals representing the year-to-year BAI variability were regressed against either the annual increment in C_a (c, bars) or climate drivers (e.g., water balance or difference between precipitation and potential evapotranspiration, P-ETP; blue line and associated negative trend in Fig. 1d). We also quantified the long-term BAI trends (Fig. 1c).

Figure 2. Location and topography of the pine forests studied in eastern Spain. The different symbols in the map of Spain indicate the three study regions (Albarracín, Gúdar and Javalambre) and the elevation profiles (lower figures with insets showing some views of study forest) and the most detailed map correspond to the most intensively sampled region (Gúdar range). The upper right maps shows the Gúdar study sites (see codes in Table 1) and the profile shows a simplified view of pine forests across the elevation gradient. The elevation profile was built using GPS visualizer (http://www.gpsvisualizer.com/profile_input, accessed April 22, 2015).

Código de campo cambiado

Figure 3. Growth-climate correlations (Pearson coefficients) calculated at the site (lines with filled symbols) and tree (lines with empty symbols) levels based on tree-ring width (left graph) indices or considering separately earlywood (EW, circles) and latewood (LW, triangles) width indices (right graph). Climatic variables are monthly mean

temperature and water balance (P-PET, difference between precipitation and potential evapotranspiration). Coefficients located outside the grey boxes are significant at the 0.05 level. Correlations were calculated from September of the year prior to growth (months abbreviated by lowercase letters) up to September of the year of tree-ring formation (months abbreviated by uppercase letters).

Figure 4. Correlations calculated between the SPEI drought index and the indexed tree-ring width chronologies of the five study pine species. The SPEI is calculated at monthly scales ranging from 1 to 24 months (*x* axis). Values of the correlation coefficients higher and lower than 0.30 or -0.30, respectively, are significant ($P<0.05$).

Figure 5. Negative relationship observed at the site level between the *t*-statistics describing the associations between the annual increment in atmospheric CO_2 concentrations and basal area increment (BAI) and site elevation (see also Table 3). The continuous and dashed lines represent the fitted linear regression and its 95% prediction intervals, respectively. Note that the Scots pine SJ site was located outside the prediction intervals of the linear regression (black arrow).

Figure 6. Relationships at the tree level observed between basal area increment (BAI) residuals of five pine species vs. the annual increment in atmospheric CO_2 concentrations (upper panel) and growing-season (May to July) water balance (P-PET; lower panel; correlation coefficients are displayed). Colors and symbols refer to the different pine species as shown in the inset, while the diagonal line in the lower panel shows a significant linear regression in the lower panel calculated for all trees. The red and blue areas illustrate temperature and water balance trends along the elevational gradient, respectively. Symbol size is proportional to tree age.