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RESEARCH ARTICLE

Water use efficiency and climate legacies dominate beech growth at its rear edge

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Abstract

1. Rear-edge tree populations are experiencing a combination of higher temperatures and more intense droughts that might push individuals beyond their tolerance limits. This trend towards rising atmospheric [CO_2] is concurrent with an increase in intrinsic water use efficiency (iWUE), which theoretically enhances photosynthesis and decrease evapotranspiration rates, consequently improving tree resistance to drought. However, it remains unclear whether iWUE is favouring tree growth under current climate conditions, particularly when climate and iWUE legacy effects are simultaneously considered.
2. We evaluated this question with an extensive sampling along Iberian rear-edge (dry) populations comprising four mountain ranges and two distinct altitudes. We simultaneously examined the effects of climate and iWUE on secondary growth using annually resolved basal area increments (BAIs) for the period 1901–2017. We used linear mixed models including second-order autocorrelation and 1-year legacy effects of iWUE and summer drought.
3. BAI and iWUE increased across the studied period. iWUE increase was driven by changes in atmospheric CO_2 concentration and water availability during the growing season. Climate and iWUE exerted direct and lagged effects on beech growth. Water availability during growing season was the main driver of tree growth, combining direct and indirect effects through its impact on iWUE. Legacy effects of water availability and iWUE were more important than growing season conditions. The net effect of iWUE shifted when lagged effects were considered, resulting in a net negative impact on tree growth.
4. *Synthesis*: Our results reveal that climate and iWUE legacy effects must be considered to assess the net iWUE effect on secondary growth. Considering lagged effects, the current increase in iWUE is constraining tree growth. Modelling efforts of tree growth response to climate warming should include climate and iWUE legacy effects to adequately assess terrestrial ecosystem carbon balance.

KEYWORDS
drought, *Fagus sylvatica*, gamm models, iWUE, legacy effect, rear-edge

1 | INTRODUCTION

This century, atmospheric CO_2 concentration has increased above the 400 ppm mark. Under increased CO_2 levels, trees experience the duality of the stress caused by warmer temperatures and drought, and the advantage of increased intrinsic water use efficiency. The relative interplay between both factors could push species towards the limits of their climate niches (Antão et al., 2022). A progressive rise in temperature might lead to taxonomic replacement through changes in the relative fitness of the species (Loarie et al., 2009). Even if the entire species should cope equally with these pressures, populations close to the distribution edge may experience nonlinear responses to climate constraints as they are already growing under conditions approaching their tolerance limits (Illés & Móricz, 2022). Understanding the combined impacts of climate change and higher intrinsic water use efficiency (iWUE) in rear-edge populations is paramount, since these forests can play the role of the proverbial canary in a coal mine in foreseeing how a warmer climate will affect future forest distribution and productivity.

Higher atmospheric CO_2 concentrations increase photosynthetic rates (A) by alleviating C uptake limitation (Sun et al., 2014). In parallel, higher CO_2 concentrations have been shown to decrease stomatal conductance (g_s) during drought (Medlyn et al., 2001), thereby enabling plants to mitigate the impact of water scarcity (Soulé & Knapp, 2006). Higher primary production (A) and lower water loss (g_s) result in higher iWUE. However, the effects of CO_2 increase on plant drought response are complex and involve physiological adjustments at different scales in time and space (De Kauwe et al., 2021; Jiang et al., 2021). This research avenue is of great interest because it could lead to a negative feedback mechanism on climate system (Wang et al., 2020). In fact, despite the presence of other limiting factors (Terrer et al., 2019), these positive effects may overtake climatic constraints as photosynthetic activity has increased globally (Huntingford & Oliver, 2021). However, it is not yet known whether the balance between CO_2 fertilization and drought stress will be positive in drought-prone areas such as Mediterranean forests (Keenan et al., 2011).

Despite the wealth of studies relating iWUE and tree growth, no conclusive support for a positive relationship has emerged (Peñuelas et al., 2011). The lack of evidence has been attributed to climate change constraints overcoming the beneficial effects of iWUE on tree growth (Norby et al., 2010). To account for this climate effect, the correct formulation should be that the influences of climate and iWUE on growth are simultaneous. As a result, the question shifts from whether iWUE drives higher tree growth over time to whether iWUE favours tree growth under current climate conditions (Heilman et al., 2021). Moreover, an adequate consideration of such a question must incorporate some degree of climate legacy (Marqués et al., 2022; Ogle et al., 2015), including lagged effects of iWUE, since resilience to drought and future tree growth have already been related to previous iWUE (Wen et al., 2022; Wu et al., 2020).

Mediterranean rear-edge beech *Fagus sylvatica* L. populations are already experiencing a warmer and drier climate. Warmer springs have a positive effect, promoting longer growing seasons (Jeong et al., 2011), albeit at the expense of a higher risk of late frost defoliation (Olano et al., 2021; Sangüesa-Barreda et al., 2021). Beech is a drought sensitive species (Ruehr et al., 2009), albeit is hydraulic vulnerability, measures as a 50% loss of conductivity (P50), shows a significant variation between −2.8 and −3.8 MPa (Stojnić et al., 2018; Walthert et al., 2021). Summer droughts affect beech trees by causing a moderate to severe reduction in gas exchange, driving premature leaf wilting and shedding (Bigler & Vitasse, 2021). Thus, the reduction in summer precipitation is particularly worrisome, especially in combination with warmer temperatures, which amplify the evapotranspirative demand. In fact, growth declines in rear-edge populations have already been reported (Jump et al., 2006), and studies have predicted a rapid decline (Martínez del Castillo et al., 2022). Strikingly, despite their vulnerability to drought, beech forests in Spanish rear-edge populations growing under dry summer conditions show a lower response to growing season precipitation than in core (wet) populations (Muffler et al., 2020), while experiencing a strong legacy effect from the previous summer's precipitation (Hacket-Pain et al., 2016; Marqués et al., 2022; Olano et al., 2022). iWUE has been reported to favour beech growth (Gonzalez de Andres et al., 2018; Rezaie et al., 2018), so its recent increase associated with higher atmospheric CO_2 concentration may serve to mitigate the adverse effects of warmer and drier conditions. Moreover, beech populations occupy a large altitudinal gradient at their rear edge (Costa et al., 1997), with constraints shifting from greater water limitations at lower (dry) elevations to lower temperatures at higher altitudes. Thus, we expect that the impact of climate warming and rising iWUE may vary across altitudes.

To understand the simultaneous effect of changes in iWUE and climate on tree growth for the period 1901–2017, we collected wood samples from beech forests in four mountainous regions along the southwestern Iberian coast. In each region, we accounted for the altitudinal effect by sampling at both the upper and lower boundaries of the forests. Our first step was to elucidate the relative contributions of atmospheric CO_2 and climate variability on beech iWUE. Subsequently, we tested the combined effect of iWUE and climate on growth. We hypothesized that beech growth is positively influenced by climatic factors that promote xylogenesis, such as spring temperatures (Rossi et al., 2008), and those that favour cambial cell division, such as wet and cool summers that favour water availability during the growing season (Peters et al., 2021), with iWUE exerting a positive effect by reducing water loss (Heilman et al., 2021). We also hypothesized that the previous year's conditions will exert a similar lagged (legacy) effects on tree growth through changes in hydraulic structure and/or resource levels among other factors (Galiano et al., 2011; Huang et al., 2021; Olano et al., 2022; Peltier et al., 2016; Zweifel & Sterck, 2018). Moreover, we expected diverging tree growth responses, dependent on altitude; low-altitude populations will respond more strongly to precipitation and iWUE, whereas high-altitude populations will be more responsive to higher spring temperatures.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling design

We sampled beech forests in four mountain ranges in the Iberian Peninsula across the species southwestern distribution range (Figure 1). In each mountain range we selected four plots of mature forest at different altitudes (Table S1): two plots at the upper boundary of the local forest and two at the lower boundary (Figure 1). The plots sampled ranged from 1045 to 1619 m a.s.l. In each plot, we selected eight dominant or codominant trees that were georeferenced with submeter-level accuracy using a GPS (Trimble Geo 7X), and from these we extracted three wood cores per tree at 1.3 m height using Pressler increment borers. Sampling took place between 2017 and 2018, with some trees being revisited in 2019 for additional core collection.

2.2 | Basal area increment

Two of three cores for each tree sampled were air-dried and mounted on wooden supports. The cores were gradually sanded down with increasingly finer sandpaper until the cellular structure could be assessed. Tree-ring series of the cores were visually cross-dated and measured with a minimum resolution of 0.01 mm using a VELMEX (Inc.) measuring system, and the cross-dating quality checked using COFECHA (Holmes, 1983). We converted ring-width measurements into basal area increments (BAIs), which were used as a measure of secondary growth rates, since BAI provides a more robust estimate of growth than ring width (Biondi & Qeadan, 2008). BAI was calculated as the annulus between consecutive annual rings, assuming a circular shape of the stem using the bai.out() function in the DPLR package (Bunn, 2008) in R (R Core Team, 2022).

2.3 | Estimation of intrinsic water use efficiency

To assess changes in annual intrinsic water use efficiency, we evaluated $^{13}C/^{12}C$ isotope ratios ($\delta^{13}C$) in tree rings correctly dated within the studied period (1901–2017). For each mountain and altitude, we selected the 10 oldest individuals that showed high Pearson correlations with the local master chronology and had no missing rings. The third core from each of these individuals was used to obtain its $^{13}C/^{12}C$ signature. The first step was to create a cross-sectional planar surface on the cores using a sledge microtome (H. Gärtner/F. H. Schweingruber, WSL, Birmensdorf, Switzerland). High resolution images of the core's surface were obtained using the CaptuRING device (García-Hidalgo et al., 2022).

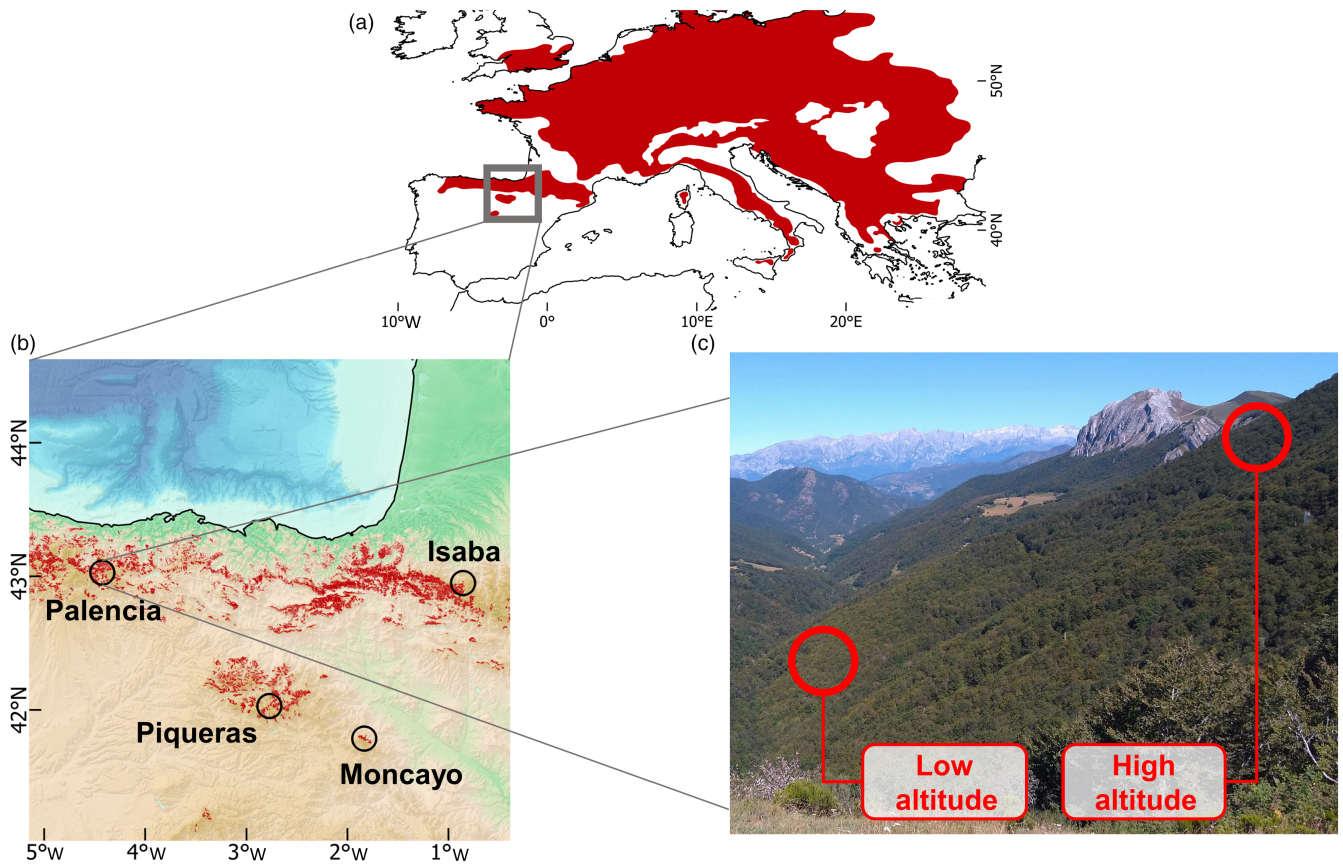

FIGURE 1 Beech *Fagus sylvatica* distribution (in red) across Central and Southern Europe (a), detail of four sampling locations (b) and sampling schema across Piedras Luengas (Palencia) sampling location, showing 300 m altitudinal gradient (c).

The images were used to properly cross-date the tree-ring series from these cores with the previously created master chronologies using CooRecorder 9.6 (Cybis Elektronik & Data AB). The second step was to separate the annual rings from each core with a scalpel under a binocular lens (Nikon SMZ8000, Nikon), merging the rings corresponding to the same year for each mountain range and altitude. The samples for each year of formation, and for each site and altitude, were homogenized and powdered using a mixer mill (Retsch MM400, Retsch GmbH). Cellulose was not extracted as several studies show good correlations between $\delta^{13}C$ in cellulose and wood, and therefore both show similar relationships with atmospheric CO_2 and climate (Roden & Farquhar, 2012; Taylor et al., 2008). The wood powder was weighed into tin cups and combusted at 1000°C in an elemental analyser (NA1500 series 2, Carlo Erba Instruments), CO_2 was separated by gas chromatography and carried by a current of helium towards an interface attached to an isotope ratio mass spectrometer (Deltaplus XP, Thermo Electron) where the ratio $^{13}C/^{12}C$ was analysed. The measurements obtained were expressed as the relative difference between the sample $^{13}C/^{12}C$ ratio (parts per thousand, ‰) and the standard V-PDB, resulting in $\delta^{13}C_{plant}$. This parameter was used to calculate isotopic discrimination (Δ; Farquhar & Richards, 1984; McCarroll & Loader, 2004). We then calculated the iWUE (expressed in μmol of CO_2 per mol of H_2O), using available data of $\delta^{13}C$ in atmospheric CO_2 (Graven et al., 2017) and atmospheric CO_2 concentrations (see Supplementary Materials for a detailed description of iWUE calculation).

2.4 | Statistical analyses

In the first stage, we assessed the temporal trend of iWUE and BAI along the studied period (1901–2017) at different altitudes. We performed linear mixed-effects models considering iWUE and BAI as dependent variables and including the following as fixed factors: time in years as a continuous term, altitude as a two-level nominal factor, and the interaction between both terms. Mountain range was conceived as a random intercept. Predictors were tested in a backward model selection using ΔAICc (Burnham & Anderson, 2002).

Next, we performed two different modelling approaches: (i) to elucidate the relative importance of atmospheric CO_2 concentration and climate variability on beech iWUE; and (ii) to test the effect of the combination of iWUE and climate on BAI. Prior to modelling, all continuous independent variables were standardized to *z*-scores to make all estimated coefficients comparable. Then, we built a full generalized additive mixed model (for iWUE) and a full linear mixed-effects model (for BAI) using, in both cases, mountain range as a random intercept. In addition, since iWUE and BAI showed strong temporal autocorrelation, both the first- and second-order temporal autocorrelations were considered. In both modelling approaches, we performed model selection to test the validity of variables and interaction terms as predictors of iWUE and BAI. The model selection was computed using maximum likelihood (ML). The model with the lowest ΔAICc was the best model and computed again using restricted maximum likelihood (REML; Zuur et al., 2009). The best models were finally compared using ΔAICc with the equivalent null models, in which all covariates were set as constant but retained a random structure. Normalized residuals were extracted and checked for normality and homoscedasticity in all the best models to verify models' assumptions.

To test the combined effects of CO_2, current and past summer climate conditions, and altitudinal position on iWUE, we performed a general additive mixed model (gamm). We fitted CO_2 with a smooth function to enable potential nonlinear responses of iWUE due to the sharp change in atmospheric CO_2 concentration over the study periods. The remaining terms were fitted as linear functions. The full gamm included altitudinal position (low vs. high), summer and past summer accumulated precipitation and summer mean temperature, as well as the interactions between summer temperature and precipitation, and altitude and summer precipitation for past and current growth years. Summer conditions were selected because it is when the greatest carbon fixation occurs.

Since BAI is determined by a set of concurring factors, including conditions from the immediate past few years, we designed a more sophisticated model that considers the effects of iWUE (current and previous year), summer climatic conditions (current and previous), May temperature and altitude on BAI. The climate parameters were selected according to previous information on the main climate drivers of growth in these forests (Olano et al., 2022). We performed a linear mixed model for the studied period (1901–2017). Full model included the following terms: altitude (low vs. high), previous and current year iWUE, summer temperature and precipitation, and the interactions of summer temperature and precipitation for previous and current growing year, as well as the interactions of altitude with May temperature and current and previous summer precipitation and iWUE.

All analyses were performed in R (R Core Team, 2022). Statistical models were performed using *lme* function from nlme (Pinheiro et al., 2017) and *gamm* function from MGCV package (Wood, 2017). Model selection was performed using the *dredge* function of MuMIn (Barton & Barton, 2015).

3 | RESULTS

BAI and iWUE increased during the study period, albeit showing strong interannual variability (Figure 2, Table 1). BAI was affected by the interaction between altitude and year, with BAI increasing more rapidly at high-altitude sites (Figure 2). In contrast, the best model for iWUE only included the effect of year.

The best generalized additive mixed model included the effect of CO_2 as well as summer precipitation and temperature on iWUE, with the nonrandom part of the model explaining a large fraction of total variance ($R^2_m = 0.34$). iWUE increased in response to enhanced CO_2 levels, but not in a linear fashion as reflected by the estimated degrees of freedom of 2.283 in the smooth term reflect (Table 2). The rate of iWUE increase slowed at higher CO_2 concentrations, with a

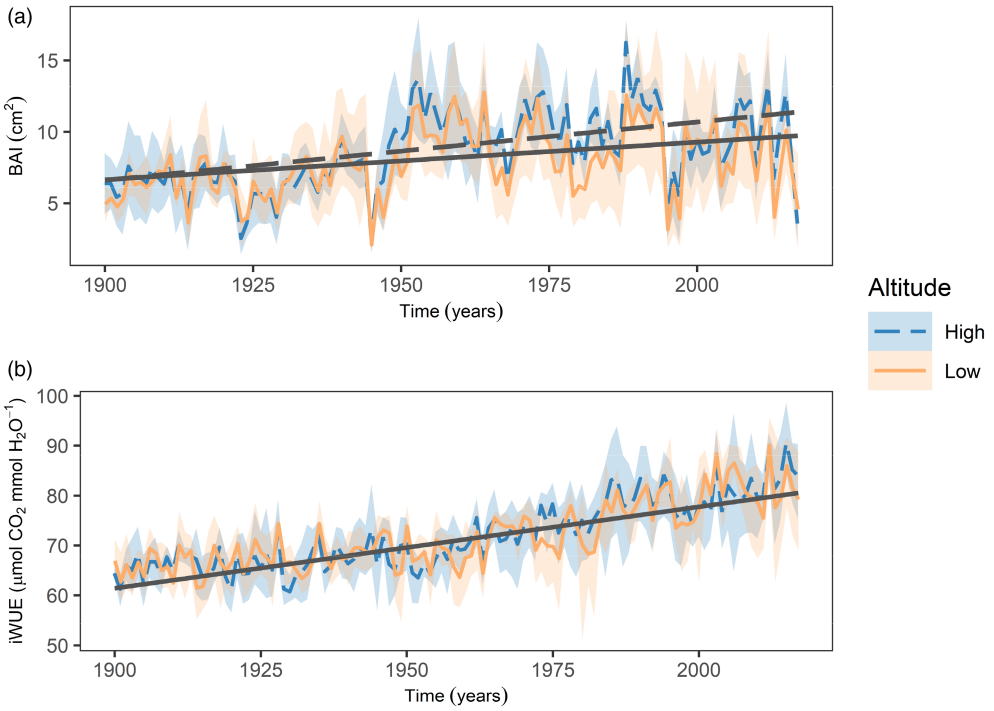

FIGURE 2 Temporal trends of (a) basal area increment (BAI) and (b) intrinsic water use efficiency (iWUE) for 1901–2017 models. Solid (blue and orange) lines report averaged time series for each altitude and shaded areas depict their mean confidence limits. Straight lines show the predicted values obtained in linear mixed-effects models (Table 1). In the case of iWUE, since no significant differences between altitudes were found, only one regression line is shown.

TABLE 1 Results of basal area increment (BAI) and intrinsic water use efficiency (iWUE) best models (Table S2) fitted to assess altitudinal and temporal effects.

	BAI			iWUE		
Predictors	**Estimates**	**SE**	***p***	**Estimates**	**SE**	***p***
(Intercept)	−71.43	8.88	**<0.001**	−247.83	11.95	**<0.001**
Year	0.04	0.00	**<0.001**	0.16	0.01	**<0.001**
Altitude [Low]	27.62	12.54	**0.028**			
Year × Altitude [Low]	−0.01	0.01	**0.024**			
Observations			944			944
Marginal R^2			0.112			0.365
Conditional R^2			0.184			0.531

$p < 0.05$ in bold.

TABLE 2 Summary of the best generalized additive mixed model for intrinsic water use efficiency (iWUE). T Sum stands for summer mean T, P Sum for summer accumulated precipitation and edf for estimated degrees of freedom of the smooth term.

iWUE	Predictors	Estimates	SE	*p*
Linear terms	Intercept	71.84	3.23	**<0.001**
	T Sum	2.10	0.42	**<0.001**
	P Sum	−1.16	0.21	**<0.001**
	T Sum × P Sum	−0.61	0.20	**0.002**
Smooth term	CO_2 (edf = 2.283)	4.23	1.54	**0.006**
	Observations			928
	Marginal R^2			0.340
	Conditional R^2			0.687

$p < 0.05$ in bold.

slope shift at about 338 ppm (Figure 3). Precipitation had a negative effect and temperature a positive effect, the interaction of the two resulting in an enhanced iWUE in dry and warm summers (Figure S1).

BAI was controlled by a complex set of factors including iWUE and climate factors at different timepoints, as well as their interaction with altitude (Table 3). BAI benefitted from warm conditions during the early growing season (May temperature) and, to a lesser extent, by the wet conditions during summer. Previous summer conditions had a stronger impact on BAI with cool and wet summers having a positive effect (Table 3, Figure S2). The effect of previous summer precipitation was modulated by altitude, with precipitation making more of an impact at low altitudes (Figure 4a). The effect of iWUE on BAI was complex: growth year iWUE had a positive effect on BAI, while previous year iWUE exerted a negative effect on BAI, given secondary growth was reduced following years with high iWUE. However, this effect again varied with altitude, with a stronger effect being observed at higher altitudes (Figure 4b). The estimated coefficient for the previous year's iWUE was four times higher than that for the current year's iWUE resulting in an overall strong negative effect of iWUE on secondary growth rate.

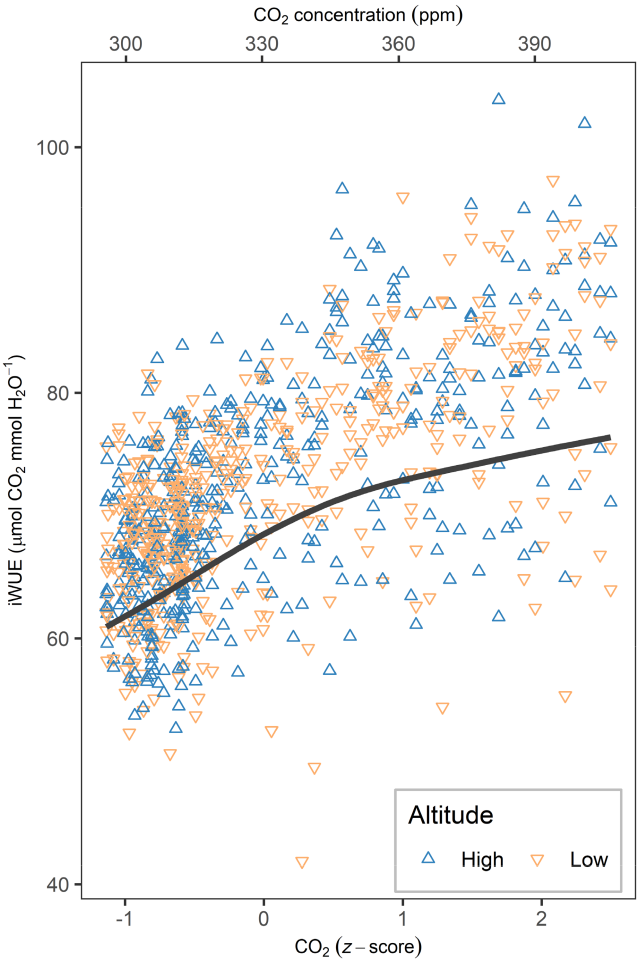

FIGURE 3 Effect of CO_2 on intrinsic water use efficiency (iWUE). Triangles depict observations by altitude (blue upper looking upward, high altitude, orange looking downward, low altitude) and the solid line is the iWUE prediction from the generalized additive mixed model where CO_2 is expressed as a smoothing function of with 2.283 estimated degrees of freedom. Altitude did not show significant effect in this relationship.

4 | DISCUSSION

Climate and iWUE exerted a combination of direct and lagged effects on beech growth in rear-edge populations in the Iberian Peninsula. Water availability, dependent on both precipitation and temperature in the summer, was the main driver of tree growth, affecting it both directly and through the control of iWUE at different timescales. The effect of iWUE shifted dramatically from positive to negative when 1-year lagged responses were considered. These results reveal the complexity with which climate and iWUE drive beech growth in dry regions. Furthermore, this highlights the need to consider legacy effects to determine the influence of iWUE on tree growth.

iWUE has increased in response to the rise in atmospheric CO_2 concentration, which has steadily increased, culminating in current levels being 25% greater than those at the beginning of 20th century. This phenomenon occurred across the board, regardless of the location. However, the impact of CO_2 on iWUE was not temporally uniform, with the intensity of the effect decreasing in the latter part of the study period, as observed for other terrestrial ecosystems (Adams et al., 2020). The causes behind this pattern are not clear; this reduction has been attributed either to a CO_2 saturation effect (Waterhouse et al., 2004), or to the occurrence of nutrient or climate limitations on photosynthetic activity (Norby et al., 2010; Wang et al., 2020). However, in our case climate limitation could be discarded as a cause, since iWUE increased in response to dry and warm (limiting) climate conditions. This response seems to be the norm in water-limited areas in the Mediterranean climate (Andreu-Hayles et al., 2011; Olano et al., 2014, 2017; Peñuelas et al., 2011), suggesting that carbon gain reduction is more intense than stomatal conductance reduction. Therefore, warmer, and drier conditions, such as those found in Mediterranean areas, would be expected to exacerbate rather than decrease iWUE values.

iWUE increase was concurrent with an overall higher secondary growth rate, as indicated by the positive relationship between BAI and iWUE (Table 3). A parallel increase in iWUE and BAI follows the global trend of CO_2 fertilization effect, driving higher global terrestrial carbon uptake with a relative reduction in water use (Cheng et al., 2017). Nevertheless, this fertilization effect is not ubiquitous, with a frequent disconnection between iWUE and growth being observed (Andreu-Hayles et al., 2011; Peñuelas et al., 2011). This could be interpreted as a decoupling of iWUE and BAI in the case of severe drought. Tree age and forest management are additional factors explaining the decoupling of secondary growth and iWUE since the level of intertree competition is usually the main factor explaining tree growth (Gómez-Aparicio et al., 2011; Luo et al., 2020). Therefore, age structure and forest management history should be considered to accurately explain the relationship between iWUE and secondary growth (del Río et al., 2017; Linares et al., 2010).

TABLE 3 Summary of the best linear mixed model for basal area increment (BAI). T Sum stays for summer mean T, and P Sum for summer accumulated precipitation.

Predictors	Estimates	SE	*p*
(Intercept)	8.60	0.58	**<0.001**
iWUE	0.20	0.12	0.103
$iWUE_{t-1}$	−0.88	0.20	**<0.001**
Altitude [Low]	−0.76	0.72	0.294
T May	0.53	0.11	**<0.001**
P Sum	0.22	0.09	**0.014**
$T\ Sum_{t-1}$	−0.78	0.17	**<0.001**
$P\ Sum_{t-1}$	0.55	0.13	**<0.001**
$WUE_{t-1} \times$ Altitude [Low]	0.65	0.25	**0.010**
$T\ Sum_{t-1} \times P\ Sum_{t-1}$	0.33	0.08	**<0.001**
Altitude [Low] $\times P\ Sum_{t-1}$	0.29	0.17	0.081
BAI	Observations		928
	Marginal R^2		0.120
	Conditional R^2		0.138

$p < 0.05$ in bold.

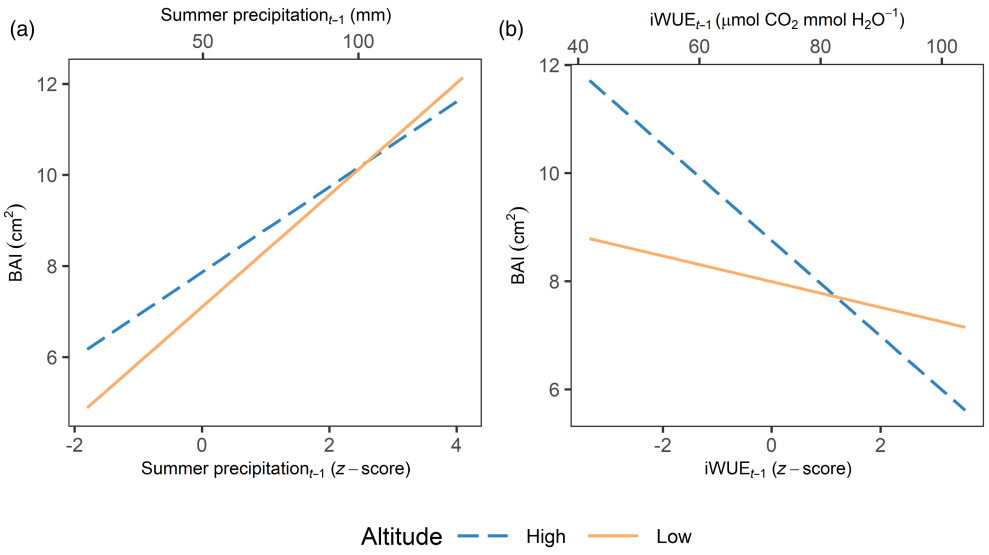

FIGURE 4 Graphical representation of predicted basal area increment (BAI) computed by the marginal effects of (a) summer precipitation of the previous year and (b) previous year intrinsic water use efficiency (iWUE).

A more thorough analysis of secondary growth drivers improved our insight into the combined impact of iWUE and climate on BAI. Secondary growth was promoted by climatic factors, with a direct effect on xylogenetic activity; the conditions that promoted secondary growth were warmer conditions at the beginning of the growing season (May) and higher water availability during the summer. Furthermore, cambial cell division requires a temperature threshold to be met to initiate (Rossi et al., 2008), and warmer conditions promote longer growing seasons (Jeong et al., 2011), which could result in larger secondary growth rates (Chen et al., 2022), particularly in Mediterranean mountain forests (Gao et al., 2022; Martínez del Castillo et al., 2016). Moreover, higher temperature increases cambial cell division rate, particularly in the initial stages of the growing season (Rossi et al., 2014). However, in forests where growth is drought constrained, the major limitation on xylogenesis shifts from being temperature to water availability later in the growing season (Cabon et al., 2020; Camarero et al., 2010; Olano et al., 2014), with cambial division rate as well as vessel lumen size being determined by cell turgor (Olano et al., 2022; Peters et al., 2021). Interestingly, iWUE had a positive effect on BAI suggesting that a higher efficiency in water use during the growing season might limit water loss and maintain cell turgidity, as well as increased rates of cell division. This agrees with the observed overall positive relationship between iWUE and secondary growth during dry periods (Heilman et al., 2021).

Interestingly, the conditions during the previous year's growing season were the most relevant in the model, revealing the importance of delayed effects of climate and iWUE on beech secondary growth (Ogle et al., 2015). The impact of wet and cool conditions in the previous summer was higher than growing season summer

precipitation. The strong response of secondary growth to previous summer conditions within beech rear-edge populations is well documented (Hacket-Pain et al., 2016; Martinez del Castillo et al., 2019, 2022; Olano et al., 2022; Rozas et al., 2015) and it has been hypothesized that dry and warm conditions promote beech masting in the next year, draining tree resources for secondary growth (Hacket-Pain et al., 2015; Nussbaumer et al., 2021). In the case of iWUE, our model also shows that this lagged effect is related to a stronger response of iWUE to the previous year's conditions, which is four times higher than in the current year (Table 3). Furthermore, contrary to our expectations, an opposite effect was observed for previous and current years iWUE, resulting in an overall negative effect of iWUE on beech growth.

Beech trees respond to drought by minimizing cavitation risks and diminishing water loss through stomata down-regulation (Leuschner, 2020). Evapotranspiration reduction occurs at the expense of lowering overall gas exchange, with a resulting reduction in carbon uptake (Bréda et al., 2006), in turn causing an overall increase in iWUE. The effect of this stomata closure, and the resulting decrease in carbon uptake, has an effect on phloem transport from leaves to consumer and storage organs (Dannoura et al., 2019; Ruehr et al., 2009). Temporal changes in nonstructural carbohydrates (NSCs) have been proposed as a secondary growth legacy mechanism (Kannenberg et al., 2019). Therefore, the combination of low precipitation during the previous summer and high iWUE could have an adverse effect on carbon assimilation, affecting NSC storage and its availability for canopy formation and the onset of secondary growth during the subsequent growing season (Wong et al., 2003), as well as a potentially higher inversion to reproduction (Hacket-Pain et al., 2015). In response to drought stress, carbon storage is prioritized over growth (Galiano et al., 2017) to prevent the higher mortality risk associated with low NSC levels (Fierravanti et al., 2019; Galiano et al., 2011). Xylogenesis demands large NSC loads (Deslauriers et al., 2009; Oberhuber et al., 2011), with interindividual variability in NSC levels correlated with individual performance: individual trees with higher stem NSC loads exhibit higher secondary growth rates (DeSoto et al., 2016; Pérez-de-Lis et al., 2016; von Arx et al., 2017). Moreover, the effect of NSC storage in the previous year might be concurrent with changes in xylem configuration associated with water availability since vessel size and its conductive capacity are directly controlled by water availability during vessel formation (Olano et al., 2022). Under dry conditions, beech produces xylem with higher resistance to embolism and lower conductivity at the expense of a reduction in lagged secondary growth (Herbette et al., 2021) due to higher xylem production costs (Hacke et al., 2001). Thus, the combination of xylem structure, cavitation history and cavitation repair costs (McDowell & Sevanto, 2010; Trifilò et al., 2014) might negatively impact on growth (Anderegg et al., 2013). The lagged effect of the previous year's conditions might therefore be a consequence of concurrent changes in NSC levels and the tree's hydraulic pathway (Galiano et al., 2011; Pérez-de-Lis et al., 2017).

In contrast to previous evidence of drought decline at beech lowest populations in Eastern Spain (Jump et al., 2006; Peñuelas & Boada, 2003), secondary growth increased along the study period, probably due to the increasingly earlier onset of the growing season. Although observed at both elevations, there was a larger secondary growth increase at higher altitudes, since greater limitations in water availability at lower altitudes might reduce the gains associated with longer growing seasons, as suggested by the stronger response to precipitation. Interestingly, larger growth rates at high altitudes have been sustained despite the recent increase in the frequency of late frost events (Olano et al., 2021; Sangüesa-Barreda et al., 2021). This suggests that the benefits of a warmer growing season may outweigh the reductions in growth due to sporadic late frost defoliations. In contrast to previous results in beech rear edge, we found no differences in iWUE trend across altitudes (Peñuelas et al., 2008). However, the effect of previous year iWUE differed across altitude, with higher altitude showed a higher negative responsiveness to the previous year's iWUE, suggesting greater limitations caused by the previous year's reserves.

Our results remark that climate effects and temporal legacies must be combined to adequately assess the effect of iWUE on secondary growth. In fact, the initial positive impact of iWUE on tree growth was reversed by the following year's delayed effect. Moreover, considering this delayed effect on tree growth revealed a strong environmental control over beech growth. Thus, the lower responsiveness of Iberian rear-edge beech populations to summer drought (Muffler et al., 2020) is only an effect of the considered timescale, hence the inclusion of temporal legacy effects is critical to understand beech's response to future climatic contexts.

AUTHOR CONTRIBUTIONS

J. M. Olano and G. Sangüesa-Barreda conceived the study. J. M. Olano and H. Hernández-Alonso performed statistical analyses. J. M. Olano, G. Sangüesa-Barreda, M. García-Hidalgo, A. I. García-Cervigón and V. Rozas performed field sampling. M. García-Hidalgo and G. Sangüesa-Barreda prepared chronologies, and M. A. García-López and H. Hernández-Alonso prepared samples for isotopic analysis. A. Delgado-Huertas did isotopic analyses. J. M. Olano did the first draft. All authors contributed to improve that version and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at Zenodo: https://doi.org/10.5281/zenodo.8108737 (Olano et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Graphical representation of summer precipitation × temperature based on the best gamm model. Lines and colours depict predicted intrinsic water use efficiency (iWUE) values and points represent observations.

Figure S2. Graphical representation of summer $\text{precipitation}_{t-1}$ × temperature_{t-1} based on the best lme model. Lines and colours depict predicted basal area increment (BAI) values and points represent observations.

Table S1. Altitude and meteorological traits of the sampling sites and mean tree age (± standard error). Annual and summer (June–August) precipitation and mean temperature obtained from gridded data from CHELSA v2.1 for the 1980–2018 period (Karger et al., 2018a, 2018b). This climatic repository provides higher spatial resolution (1 km) but does not fully cover the study period (1901–2017).

Table S2. Backward AICc model selection among models accounting for linear trends in basal area increment (BAI) and intrinsic water use efficiency (iWUE). Candidate models are ordered from the more complex model to the simplest and show the Akaike Information Criterion corrected for small samples (AICc), the difference between the AICc of the best model and the candidate model (ΔAICc) and the number of parameters in the model (df).

Supplementary Materials. Intrinsic water use efficiency (IWUE) calculation.

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