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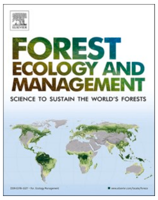

Tree size and site environment affects sessile oak growth and intrinsic water-use efficiency response to wet-dry years

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ABSTRACT

Drought is a significant global environmental stressor that impacts tree growth and survival, often causing substantial die-offs in temperate forests. Hence, contemporary forest management strategies increasingly aim to transition from spruce-dominated to mixed forest with more climate-resilient species such as oaks. Sessile oak (*Quercus petraea* (Matt.) Liebl.), a key forest tree species, is widespread across central Europe, but its response to climate extremes, especially individual intraspecific variability, remains poorly understood. In this study, we analysed tree-ring cores from 404 sessile oak trees in Thayatal National park, Austria. We assessed radial growth through tree-ring width and evaluated intrinsic water-use efficiency (iWUE) by analyzing $\delta^{13}C$ in latewood from wet (1987) and dry (1994) years. Further, we investigated the effects of site conditions, specifically light and water status inferred from potential daylight duration and the topographic wetness index (TWI), on key tree characteristics such as diameter at breast height (DBH), height, and the height-to-diameter ratio (HDR). We then examined how these factors affected iWUE and radial growth under wet and dry years, assessing radial growth's resistance, resilience, and recovery. As expected, iWUE was increased and radial growth was decreased during the dry year compared to the wet year, but there was high intraspecific variability. Tree age and size influenced these responses; age positively affected growth during the dry year, followed by decreased drought recovery. Increased daylight duration improved iWUE and reduced growth during the dry year but supported drought recovery. During the dry year, iWUE positively affected growth and resistance to drought. The TWI correlated with increased tree height and DBH but did not affect iWUE and growth responses under extreme years. Our findings suggest promoting mixed-age stands could enhance forest resilience against drought. Moreover, forest management strategies should integrate specific environmental conditions, including light availability and water status, to effectively mitigate impact of climate extremes.

1. Introduction

Climate extremes such as high precipitation and drought are a significant global environment stressor with increasing frequency and intensity due to climate change (IPCC, 2022; Allen et al., 2010). These extreme events are known to impact tree growth and survival, and even leading to a substantial die-off of temperate forests (Camarero et al., 2021; Klos et al., 2009). Contemporary forest management strategies aim to foster tree species with enhanced resistance and resilience to climate extremes (Bolte et al., 2009), for example, a potential future transition from spruce-dominated to mixed forests with more species adapted to predicted climatic conditions such as oaks, driven by both ecological and economic considerations (Perkins et al., 2018; Löf et al., 2023). Sessile oak (*Quercus petraea* (Matt.) Liebl.) has broad distribution across central Europe capturing a wide spectrum of habitats (Rabarijaona et al., 2022). Despite its ecological significance and importance, the response of this species to climate extremes remains poorly understood. Specifically, there is limited knowledge on the vulnerability of individual trees within the species, or intraspecific variability (Rabarijaona et al., 2022; Jansen et al., 2013), which is crucial to understand why some trees survive while others succumb to drought.

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Dendrochronology, a widely used method in tree growth and forest research, examines the relationship between climate and the yearly radial growth of trees, or annual xylem production using tree ring width measurements (Lamb, 1980; Cook and Kairiukstis, 1990). The relationship between climate and tree rings is particularly stronger under climate extremes such as drought (Bräuning et al., 2016). Additionally, the carbon isotope composition in tree rings, specifically δ^{13}C, provide useful insights on tree water use strategy. Analysis of tree-ring δ^{13}C allows for the calculation of plant isotope fractionation, which gives an estimation of the changes in the ratio of carbon assimilation (A) and stomatal conductance for water vapor (g) (Farquhar et al., 1982; Francey and Farquhar, 1982; Vogel, 1980). This ratio, known as intrinsic plant water use efficiency (iWUE), provides valuable retrospective information about changes in photosynthetic capacity or stomatal conductance and indicates how trees have responded to past climate conditions. During drought, trees can regulate their water intake by partially closing their stomata to conserve water and maintain leaf water potential (Ripullone et al., 2009; Adams and Kolb, 2004), which results in improved water use efficiency (Ponton et al., 2002; Cregg et al., 2000). However, this reduced carbon uptake from photosynthesis may have negative consequences for tree growth and result in carbon starvation if the tree is unable to produce enough carbon to meet its metabolic needs (McDowell, 2011). On the other hand, if a tree prioritizes carbon uptake, it may lead to less stringent control of stomata during drought and thus water loss and increase the risk of hydraulic failure, a disruption in water transport caused by xylem embolism (McDowell et al., 2008). The analysis of tree ring radial growth and carbon isotope patterns can provide insight into a tree's susceptibility to these drought-related impacts (Gessler et al., 2018). This susceptibility is assumed to be influenced by tree intrinsic properties such as tree age, height and diameter (McDowell et al., 2011; Donovan and Ehleringer, 1991; Meinzer et al., 2011), as well as environmental factors such as water and light availability, however, remains poorly understood.

In temperate forests, the heterogeneity of plant-relevant environmental factors, such as light and water availability, even at small scales, can greatly impact a tree's growth response to climate extremes. This is especially evident in mountainous areas where solar radiation, soil moisture, and water flow conditions vary greatly (Allen et al., 2010; Tromp-van Meerveld and McDonnell, 2006). Topography is often used as a proxy of light and site water status due to its correlation with site environment characteristics (Wang et al., 2021; Salinas et al., 2011). For instance, in northern hemisphere, the north-facing slopes typically experience lower temperatures and higher moisture due to decreased exposure to solar radiation compared to south-facing slopes (Campelo et al., 2018; Eilmann et al., 2013). Forest declines due to drought is commonly observed at low elevations and southern aspects (Tai et al., 2017). Site water status, highly correlated to topography, plays a crucial role in a tree responses to drought (Trouvé et al., 2017). For example, trees growing in valleys close to water sources are often more susceptible to poor water conductivity and embolism than those on plateaus (Garcia et al., 2022). Moreover, the difference in site specific water status has also been shown to affect drought recovery, especially for sessile oaks (Bose et al., 2024). However, the extent to which topography influences these site-specific differences in the climate-growth and climate-iWUE relationship of sessile oaks, and whether it can mitigate or exacerbate drought effects through altered light and water availability, remains largely unknown (Trouvé et al., 2017; Garcia et al., 2022).

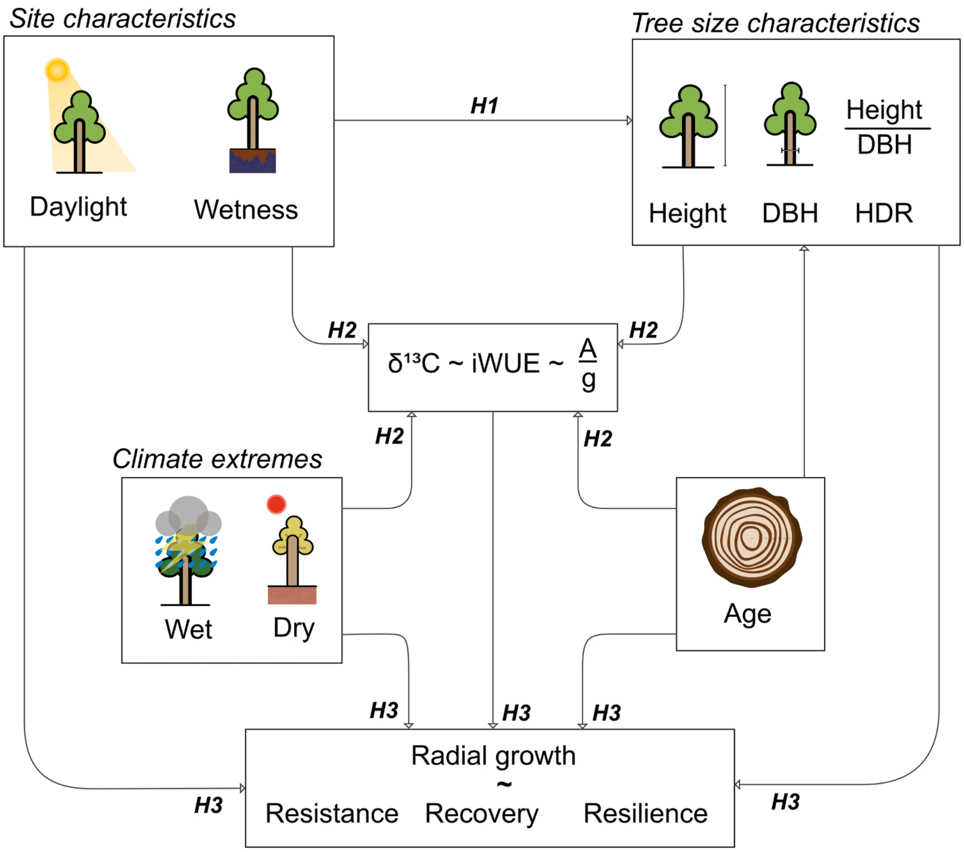

Fig. 1. The conceptual framework and hypothesized relationship of intraspecific variability in tree growth response under climate extremes to tree age and size, intrinsic water use efficiency (iWUE) and site environment characteristics. Tree height, diameter at breast height (DBH), and height-diameter ratio (HDR) serve as the tree size characteristics. Site characteristics are represented by the variables of potential daylight hours and topographic wetness index, respectively. The δ^{13}C is proportional to the iWUE, which is defined as the ratio of assimilation (A) to stomatal conductance (g). Ring width index (RWI), along with assessments of resistance, recovery, and resilience, are used to assess shifts in tree growth in response to drought. H1, H2, and H3 denote hypotheses one, two, and three, respectively.

Here, we investigate the influence of site environmental conditions, specifically light and site water status, on tree size by analyzing key tree characteristics such as diameter at breast height (DBH), height, and height-diameter ratio (HDR, Fig. 1). Then, we investigate how site water status, potential daylight duration, and tree age and size affected the response of tree iWUE and radial growth under both wet and dry years, providing insight into how trees adapt and optimize growth under climate extremes. Lastly, our study explores the impact of site environment, tree age and size, and water use efficiency on tree radial growth during wet and dry years, including resistance, resilience and recovery of radial growth to the extremes (Fig. 1). We hypothesized that light and site water status would play a primary role in determining intraspecific variability in tree size (H1), which in turn would affect tree growth and iWUE response to drought. Specifically, we anticipated that trees growing in areas with higher water availability and longer daylight duration to be larger (H1). Trees under high site water status were expected to show lower iWUE during both wet and dry years (H2). Additionally, trees exposed to longer daylight were expected to exhibit increased iWUE, particularly in dry years (H2). We also hypothesized that larger and older trees would have higher iWUE due to enhanced photosynthetic potential (H2). Finally, we hypothesized that trees with longer daylight duration, higher water status, and higher iWUE would show greater resistance, and recovery to drought (H3).

2. Methods

2.1. Study site and sampling

Our research was conducted in the National park Thayatal, designated in the year 2000. Situated in the eastern region of Austria, the park spans an area of approximately 77 km^2. Its protected status ensures the preservation and non-disturbance of the area, establishing it as a significant international transboundary protected site along the north-eastern state border of Austria and the Czech Republic (Fig. 2a). The park is primarily characterized by forests, constituting 90 % of the landscape, and is dominated by oak and beech trees, with a lesser presence of coniferous trees (van Loo et al., 2023). The mean annual precipitation of the park from 1950 to 2020 is 482 mm, and the mean annual temperature is 9.1°C.

Field sampling for the study took place in spring 2020, where a total of 404 sessile oak trees were carefully selected ensuring spatial distribution throughout the forest (Fig. 2a) (van Loo et al., 2023). Two cores per tree were extracted using a hole borer at breast height. The GPS coordinates were recorded, and the diameter at breast height (DBH) was measured for each selected tree. The height was determined using an ultrasound hypsometer (Vertex IV, Haglöf, Sweden) with an accuracy of 1 %. We employed a comprehensive sampling strategy to avoid bias by including trees of varying sizes, ages, which prevents false growth rate calculations (Nehrbass-Ahles et al., 2014; Bowman et al., 2013).

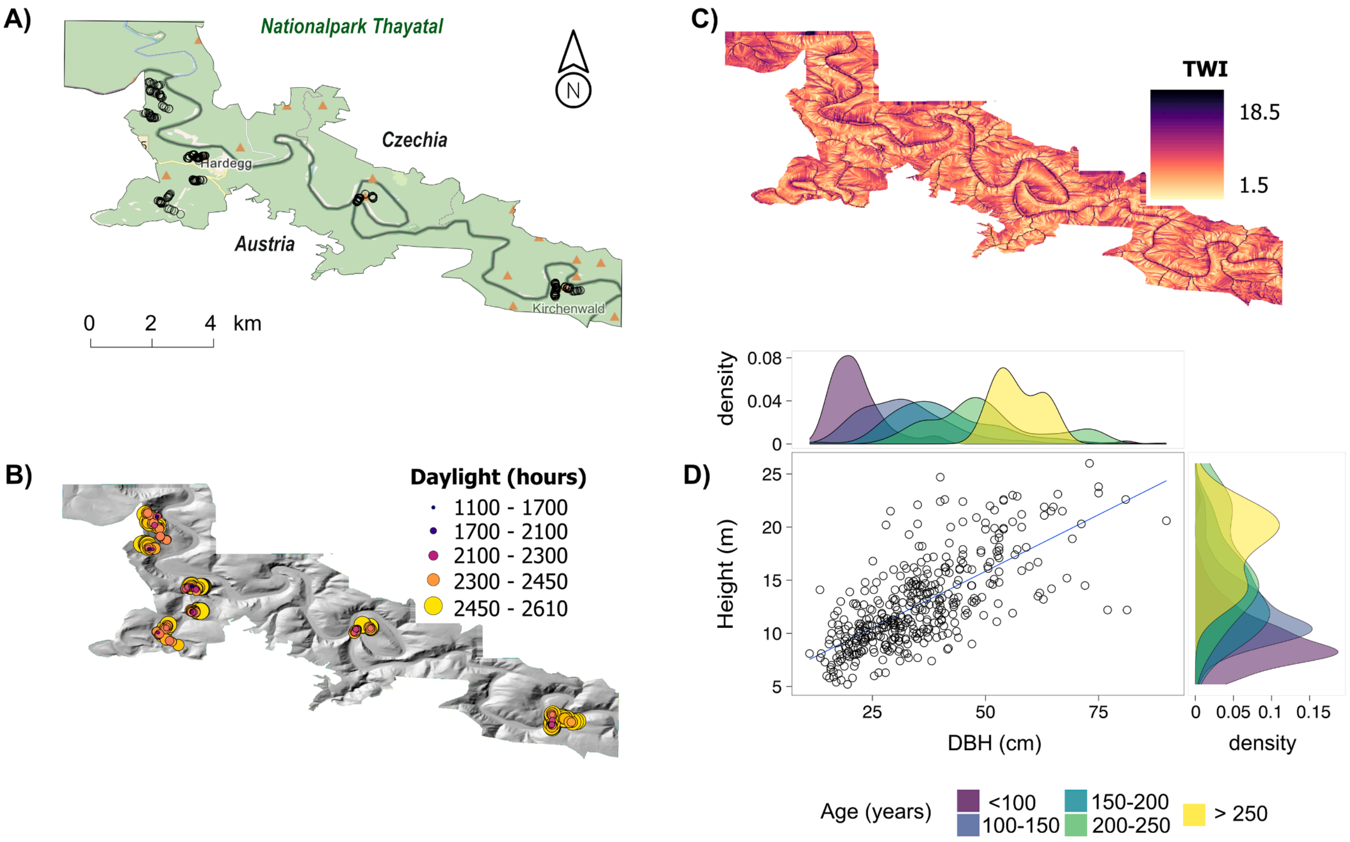

Fig. 2. An overview of the tree size characteristics and site environment characteristics of the *Quercus petraea* (sessile oak) trees under study. Panel A features base map of the study site (National Park, Thayatal) from OpenStreetMap, displaying the location of the trees. Panel B shows shaded relief map created using a 10 m resolution digital elevation model (DEM), with the color and size of the points indicating the potential daylight hours during the growing season between April and September during the year 1994 (year 1987: Fig. S4). Panel C displays the topographic wetness index (TWI) of the study site. Panel D shows the tree size characteristics, including height, diameter at breast height (DBH), and age, grouped and presented as density on the sides. The map lines delineate study area and do not necessarily depict accepted national boundaries.

2.2. Climate data and SPEI calculations

In this study, we used daily minimum and maximum temperature and precipitation data (Figure S1) from the R package '*easyclimate*' (Cruz-Alonso et al., 2023) which covers the period from 1950 to 2019 at a spatial resolution of 1 km. To assess the drought conditions in the study area, we used the standardized precipitation evapotranspiration index (SPEI), which is a drought index that considers both precipitation and potential evapotranspiration (PET) in determining drought intensity (Vicente-Serrano et al., 2010). We used the R package SPEI (Beguería et al., 2014) to calculate the SPEI on 3-, 6-, and 12-month timescales, which represent short-, medium-, and long-term droughts, respectively (Figure S2).

2.3. Dendrochronology and Isotope Analysis

The tree cores were analyzed for dendrochronology using standard methods. Briefly, the cross-section of the fresh (wet) cores were cut using ultra-sharp knife blades. The samples where digitalized with an Epson scanner at 1200 dpi resolution. Then the tree ring width was measured with an accuracy of 0.001 mm using the software Windendro 2013 (Regent Instruments Inc, 2022b). By cross-dating the individual samples, temporal synchronization of the tree rings were ensured. Tree age was estimated by adding the pith-offset, calculated as the distance from the circle template to the pith radius divided by the mean width of the innermost four tree rings, to the measured tree rings of the sample.

We considered 1987 as the extreme wet year and 1994 as the extreme dry year as it was one of the most severe and prolonged (George et al., 2015) at our study site in the past recent decades (Figures S1, S2). In addition to climate, these years were chosen based on factors including tree age, the non-overlapping occurrence of wet and dry years, and the timing of droughts during critical growth periods (spring and summer). Each tree chronology was detrended with a 20-year spline using the R-package 'dplR' (Bunn, 2010). The resulting ring width index (RWI) were then used to infer the radial growth of each tree in respective years. The RWI between the selected dry and wet year was compared using the relative growth ratio, calculated as the ratio of radial growth during the dry year to that during the wet year. For the years 1987 and 1994, we analyzed three aspects of tree radial growth response—resistance, resilience, and recovery (Lloret et al., 2011)—separately for both wet and dry years for each tree (van der Maaten-Theunissen et al., 2021; Figure S3). Resistance, representing an individual tree's capacity to sustain growth, is calculated by comparing the growth of the extreme event year to the mean growth of the previous four years. Recovery is defined as the ratio of the mean growth in the four years following an event to the growth during the event (Figure S3). Resilience, signifying the ability to restore pre-disturbance performance levels, is estimated as the ratio between mean growth after and before the climate extreme event. Although the use of recovery indices for favorable conditions is uncommon, including this comparison provides a balanced perspective between wet and dry years, indicating both the resistance to favorable conditions and any decline in recovery benefits over time following the wet year.

Measurements of carbon stable isotope ratio in latewood samples of the wet and the dry years were conducted by continuous flow isotope ratio mass spectrometer coupled to an elemental analyser (Flash EA – Delta V advantage, Thermo Fisher Scientific, Bremen, Germany). Latewood, known for conveying a strong climate signal (Wimmer and Grabner, 2000), serves as an indicator of the current year's climate conditions for oak trees. The latewood from the core of each specified year was carefully dissected, and a 1 mg sample was cut for isotope analysis. The decision to use a 1 mg sample was driven by restricted availability of sample material as in many cases the total latewood from a tree ring was not more than 1 mg, and by the need to maintain consistent peak heights across all samples during isotope analysis, allowing us to use a fixed dilution for the entire batch. Thus, we also sought to avoid grinding and then weighing an aliquot of the material, because it could have resulted in further material loss. Since we did not sample the entire ring, we tested the homogeneity within the ring and found the standard deviation to be 0.11 ‰ (n=5), which is close to the analytical scatter (0.07 ‰, n=107). The samples packed in tin cups were measured along with laboratory calibration standards (IVA wheat, IVA sorghum, IVA protein) from IVA, Meerbusch, Germany, which had been referenced against certified stable isotope standards (IAEA-CH6, IAEA-600, NBS 22) from IAEA, Seibersdorf, Austria. The resulting isotope ratio was expressed as δ^{13}C value in ‰ normalized against VPDB. The combined uncertainty of measurements (1σ) was 0.15 ‰, calculated following the methodology of (Watzinger et al., 2021). Each tree was sampled twice, and the standard deviation of δ^{13}C values between the two cores was calculated for each tree. The mean of these standard deviations were 1σ = 0.50 ‰ (1994, n=85) and 0.58 ‰ (1987, n=78).

2.4. Intrinsic water use efficiency calculations

The ^{13}C discrimination of the plant tissues (Δ^{13}C), the intercellular CO_2 concentration (c_i) and the iWUE were calculated by the equations established by (Francey and Farquhar, 1982; Farquhar et al., 1982; Vogel, 1980):

$$\Delta^{13}\mathrm{C} = \frac{\delta^{13}C_{atmosphere} \quad - \quad \delta^{13}C_{latewood}}{\left(1 + \quad \frac{\delta^{13}C_{latewood}}{1000}\right)} \tag{1}$$

$$C_i \quad = \quad C_a\left[\frac{\Delta^{13}\mathrm{C} - \mathrm{a}}{b - a}\right] \tag{2}$$

$$iWUE = C_a\left[1 - \quad \frac{C_i}{C_a}\right] \quad \times 0.625 \tag{3}$$

with c_a represents atmospheric CO_2 concentration, '*a*' signifies fractionation during stomatal diffusion, and '*b*' represents fractionation during carboxylation (Farquhar et al., 1982). The CO_2 concentrations and δ^{13}C values were 348.0 ppmv and −7.70 ‰ for the year 1987, and 357.7 ppmv and −7.83 ‰ for the year 1994, respectively (Keeling et al., 2005), calculated as the average of annual records of atmospheric samples collected at Mauna Loa, Hawaii and the South Pole Observatory (Saurer and Voelker, 2022; Keeling et al., 2005). The fractionation factors used for stomatal diffusion and carboxylation were 4.4 and 25.5 ‰, respectively, following the methodology of (Cernusak and Ubierna, 2022).

2.5. Topographic wetness index and daylight duration

The Topographic Wetness Index (TWI) is a measure of the relative wetness of a landscape. In our study, we used TWI as a proxy to infer the site water status for the location of the trees under study (Grabs et al., 2009). To calculate the TWI, we first obtained a digital elevation model (DEM) of the study area from Datasets Applications Organizations of Austria (data.gv.at; Digitales Geländemodell Österreich). This DEM was then used to calculate the slope and aspect of each grid cell in the study area. The slope and aspect were then used to calculate the local upslope contributing area for each grid cell (10 ×10 m), which represents the area of the landscape that contributes water to that cell. Next, we calculated the specific catchment area (SCA) for each grid cell, which is the ratio of the upslope contributing area to the cell's slope. The SCA is a dimensionless index that represents the relative wetness of a cell compared to the surrounding landscape. Finally, we calculated the TWI for each grid cell as the ratio of natural logarithm of the SCA to the tangent of terrain slope as shown below.

$$TWI = \frac{\ln SCA}{\tan slope} \tag{4}$$

The calculation of daylight hours for the study site was conducted utilizing the Python library 'TPPSS' (Vellut, 2021). This process involved determining the duration between sunrise and sunset at the precise location of each tree within the study site, spanning from April to September for the years 1987 and 1994, respectively (Figure S4). To enhance accuracy, calculations considered factors such as the angle of the sun and the topographical features of the hilly terrain, leveraging the DEM. This approach ensured calculation of the hours of potential daylight experienced by each tree during the growing season, considering the seasonal variations in solar exposure within the growing period.

2.6. Data analysis and statistics

All hypothesized relationships (Fig. 1) were examined using multiple linear regression, with variables standardized before statistical analysis. To ensure the assumptions of normality, the residuals of the regression underwent a Shapiro-Wilk normality test (R-package "stats"). In instances where the residuals deviated from normal distribution, variables were either transformed or filtered using Cook's distance, investigating any point exceeding three times the mean of all distances. Specifically, tree height, diameter at breast height (DBH), and height-diameter ratio (HDR) exhibited skewness and were subjected to square root transformations. The variable HDR was utilized instead of height to mitigate multicollinearity when employed as a regressor. The multicollinearity of all the variables in the regression was assessed using the VIF function (Variance Inflation Factor, R-package "car") and found to be less than three for all performed regressions. We also tested for heteroscedasticity using the Breusch-Pagan test (Breusch and Pagan, 1979) with the 'ncvTest' function (R-package "car"). In addition, we performed visual inspections of residuals versus fitted values to ensure the assumptions of homoscedasticity were met. Pearson correlation was performed between height and diameter for the correlation coefficient. ANOVA tests were conducted using 'aov' function (R-package "stats") to examine the effects of wet and dry events on iWUE and ring width. A structural equation modeling (SEM) approach was employed to assess the hierarchical relationship between tree age, site environment and tree size, as well as the influence of these factors on iWUE and RWI (Figure S5). The analysis was conducted using the 'piecewiseSEM' package in R (Lefcheck, 2016). Separate SEMs were developed for the wet and the dry years. Each SEM pathway was initially modeled using linear regression, and any pathways found to be statistically insignificant ($p > 0.05$) or that raised the Akaike information criterion (AIC) score were removed to refine the model. The final, optimized model was selected based on the lowest AIC value, and its goodness-of-fit was assessed using a chi-square test (Shipley, 2009). A non-significant chi-square result ($p > 0.05$) indicated an acceptable fit. The final optimized SEM for the wet year showed a Fisher's C statistic of 14.8 ($p = 0.54$, $df = 6$), while the dry year model had a Fisher's C statistic of 3.7 ($p = 0.95$, $df = 10$), confirming the adequacy of both models. The results from the SEM analysis were consistent with the results from linear regression analyses. All statistical analyses were performed in R version 4.2.2.

3. Results

3.1. Tree characteristics

Our study of 404 trees involved a diverse mix of trees with varying characteristics (Fig. 2). The diameter at breast height (DBH) of the sampled trees ranged from 20 to 90 cm, while their heights varied from 5 to 25 m (Fig. 2d). There is a positive correlation ($r = 0.71$, $t = 20.3$, $df = 402$, p-value < 0.001) between a tree's DBH and its height (Fig. 2d). The age of the trees in our sample spanned from 34 to 268 years (as in 1994), providing a broad representation of the maturity levels within the study population.

Our results on the daylight duration for the trees show that the photoperiod varied between 1178 and 2610 hours in total from April until end of September (Fig. 2b). The trees located in the narrow valley and region received less light compared to the trees located on the ridges. The topographic wetness index (TWI), an indicator of site water status, showed that the ridge and high slope regions have less wetness index than valley regions (Fig. 2c). The daylight duration shows marginal correlation with the TWI ($p = 0.04$; Figure S6), but this correlation did not lead to multicollinearity in hypothesis testing (VIF ≤ 1.2; Tables S1–S6).

3.2. Effects of site characteristics and age on tree size

Indeed, tree size, as indicated by both DBH and height, increased with age (Fig. 3a, g), with DBH showing a greater increase compared to height (Fig. 3d). TWI and the daylight duration influenced the tree size (Table S1). The TWI affected the size of the trees (Fig. 3b, h), by significantly increasing the height ($t = 2.29$; $df = 171$; $p < 0.05$) and the DBH ($t = 2.07$; $df = 157$; $p < 0.05$). The TWI marginally affected the HDR ($t = 1.83$; $df = 149$; $p = 0.06$) and increased height more than DBH (Fig. 3e). The daylight duration did not affect the DBH and HDR but had a significant positive effect on tree height (Fig. 3c; $t = 2.05$; $df = 171$; $p < 0.05$).

3.3. Response of iWUE and tree growth under wet and dry year

The iWUE of sessile oaks ranged from 34.4 to 94.7 µmol mol^{-1} during the wet year and from 50.5 to 111.7 µmol mol^{-1} during the dry year (Fig. 4b). Our results show that iWUE was generally higher in the dry year compared to the wet year, with a mean difference of 10.3 ± 9.4 µmol mol^{-1} (Fig. 4a). The iWUE exhibited a decreasing trend with the tree age (wet year: $t = -3.0$; $df = 350$; $p < 0.01$; dry year: $t = -4.8$; $df = 348$; $p < 0.001$), irrespective of the precipitation levels (Fig. 5; Table S2). We find that DBH had a positive effect on iWUE during both wet ($t = 3.3$; $df = 350$; $p < 0.001$) and dry ($t = 6.0$; $df = 348$; $p < 0.01$) years. In the case of HDR, our results indicated a positive effect on iWUE during the dry year ($t = 3.2$; $df = 348$; $p < 0.01$) but not in the wet year. TWI showed no significant impact on iWUE in either dry or wet years. During the dry year, daylight duration increased iWUE ($t = 2.0$; $df = 348$; $p < 0.05$), while no such effect was observed during the wet year (Fig. 5a).

In terms of tree ring width index (RWI), indicative of radial growth, we observed that RWI was generally lower during the dry year compared to the wet year, with a mean difference of -0.29 ± 0.26 mm (Fig. 4a, c). During the dry year, tree age significantly increased RWI (Fig. 5b, Table S3; $t = 3.3$; $df = 324$; $p < 0.01$). During the wet year, a trend of decreasing ring width with age was observed, although not statistically significant (Fig. 5b; $t = 1.8$). Similar trends were noted for DBH, indicating a positive trend during dry years ($t = 1.2$) and a significant negative effect on ring width during the wet year ($t = -2.7$; $df = 348$; $p < 0.01$). HDR exhibited a negative effect on ring width under the dry year ($t = -2.5$; $df = 324$; $p < 0.05$) but showed no effect in the wet year (Fig. 5). The iWUE had a positive effect on ring width, particularly significant during the dry year ($t = 2.9$; $df = 324$; $p < 0.01$; Fig. 5b). TWI did not affect ring width in either dry or wet years (Fig. 5). Daylight duration had the strongest effect and decreased ring width during the dry year ($t = -3.7$; $df = 324$; $p < 0.001$), with no observable effect during the wet year (Fig. 5b).

3.4. Effects on resistance, resilience, and recovery

The resistance, recovery and resilience of the trees were found to be influenced by tree diameter, iWUE and site environment conditions (Fig. 6b, c). The tree age did not affect the resistance in either wet year or

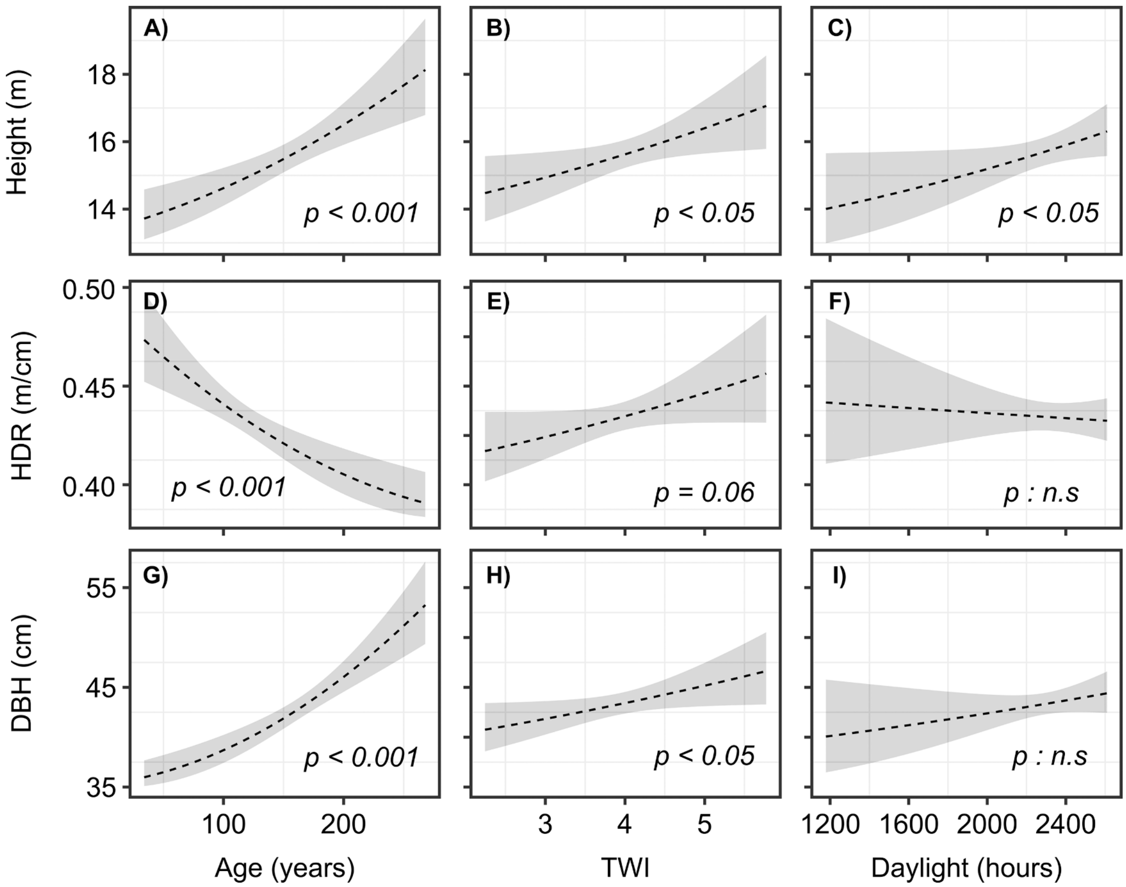

Fig. 3. Effects of tree age and site characteristics on tree size. Panels A, B, and C depict the impact of age, topographic wetness index (TWI), and daylight on height, respectively. Panel D, E, and F present the effects on height-to-diameter ratio (HDR), while panels G, H, and I showcase the impact on diameter at breast height (DBH). The effect sizes, confidence intervals, and p-values were derived from multiple linear regression models (Table S1).

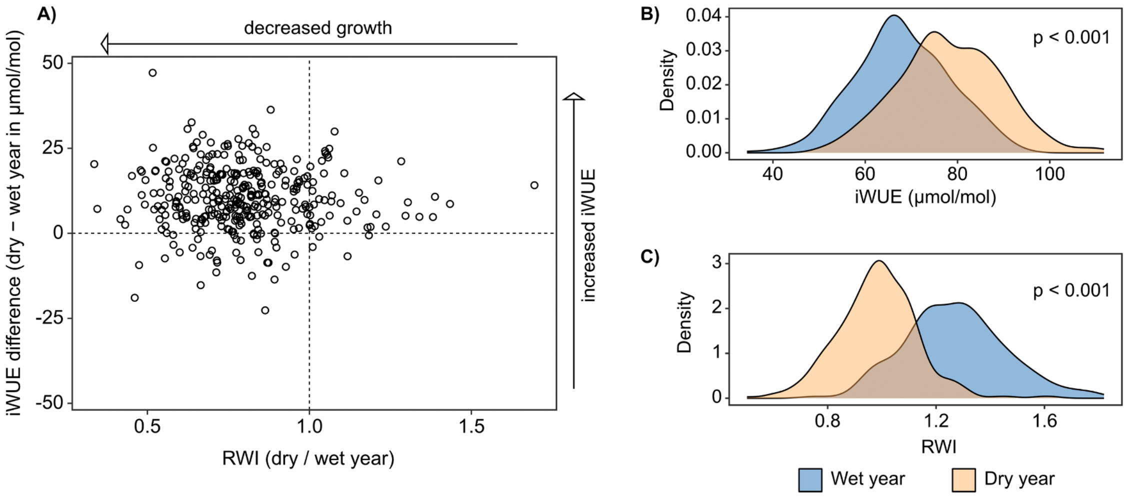

Fig. 4. Variability in relative growth (RWI for dry/wet year) and the difference in intrinsic water use efficiency (iWUE) between wet and dry years (A). Density plot depicting iWUE (B) and ring width index (C) during the wet (blue) and dry (yellow) years. P-values were derived from ANOVA.

dry year (Fig. 6; Table S4). However, it significantly increased both recovery ($t = 4.8$; $df = 330$; $p < 0.001$) and resilience ($t = 7.9$; $df = 321$; $p < 0.001$) during the wet year, while conversely decreasing recovery ($t = -4.5$; $df = 321$; $p < 0.001$) and resilience ($t = -4.6$; $df = 326$; $p < 0.001$) during the dry year (Fig. 6; Tables S5, S6). During the wet year, DBH negatively affected resistance ($t = -3.4$; $df = 348$; $p < 0.001$), and positively affected recovery ($t = 2.2$; $df = 330$; $p < 0.05$), with no marked effect on resilience. In contrast, during the dry year, DBH showed no significant effect on resistance but notably decreased recovery ($t = -3.2$; $df = 321$; $p < 0.01$), and resilience ($t = -5.1$; $df = 326$; $p < 0.001$; Fig. 6).

The tree iWUE measured for the wet year positively affected resistance ($t= 2.1$; $df =348$; $p < 0.05$) and resilience ($t = 2.3$; $df = 321$; $p < 0.05$; Fig. 6a, b; Tables S4, S6). During dry year, iWUE significantly

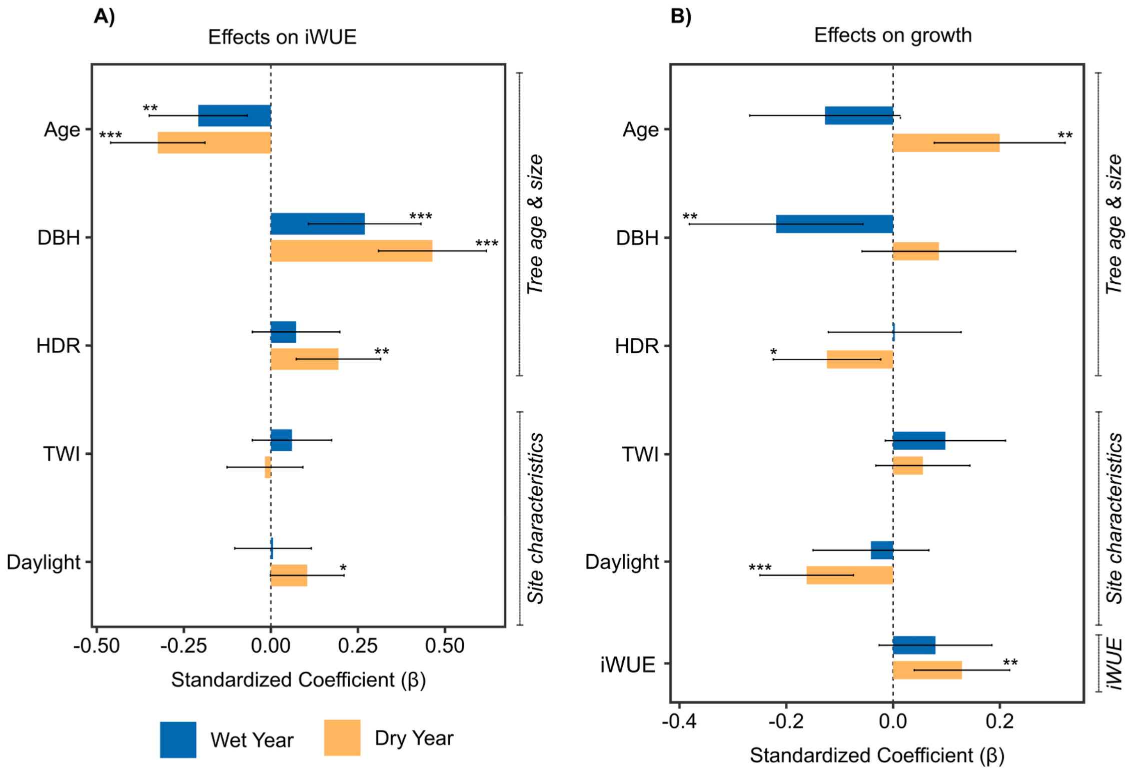

Fig. 5. The effects of tree age, size characteristics, and site characteristics on iWUE (panel A) and ring width index (RWI, panel B) during wet year and dry year. Panel B includes the effect of iWUE on RWI. The effect size denotes standardized regression coefficients (β) derived from multiple linear regression (Table S2, S3). Asterisks indicate significant effects (p-value: 0.05 > *,0.01 > **,0.001 > ***).

increased resistance ($t = 3.3$; $df = 325$; $p < 0.01$) but did not affect resilience (Fig. 6b). Notably, iWUE measurements from both wet and dry years showed no significant impact on recovery (Fig. 6c). TWI increased resistance under wet year ($t = 2.0$; $df = 348$; $p < 0.01$) but exhibited no such effect under dry year (Fig. 6a). Additionally, TWI didn't affect resilience or recovery in either wet or dry years. During the wet year, daylight duration negatively affected both resistance ($t = -2.5$; $df = 348$; $p < 0.05$) and resilience ($t = -4.3$; $df = 321$; $p < 0.001$; Fig. 6b, c). Conversely, in dry years, daylight duration decreased resistance ($t = -3.2$; $df = 325$; $p < 0.01$) and increased recovery ($t = 3.4$; $df = 321$; $p < 0.001$) and resilience ($t = 3.2$; $df = 326$; $p < 0.01$) following the dry year (Fig. 6).

4. Discussion

Climate extreme such as drought is expected to have severe impacts on European forest (Carnicer et al., 2011). However, the role of tree age, size, and site environmental conditions, along with associated water use strategies, on the drought response of individual trees within a species is less understood. Here, we studied 404 sessile oak (*Quercus petraea*) trees in a hilly forested area for their radial growth rate and iWUE inferred from tree ring latewood $\delta\ ^{13}C$ of the wet and the dry year (Fig. 1). Our study finds that iWUE was increased and RWI was decreased during the dry year compared to the wet year (Fig. 4). Trees could undergo a reduction in growth, crown dieback, and mortality as a result of two main physiological processes: hydraulic failure or carbon starvation. While sessile oak is known for its drought tolerance and ability to prevent drought-induced embolism (Härdtle et al., 2013; Kunz et al., 2018), various structural strategies are employed by oaks under drought conditions (Peguero-Pina et al., 2015; Klein et al., 2014; Bréda et al., 2006). Moreover, our study highlights intraspecific variability in the response of RWI and iWUE (Fig. 4a), underscoring the importance of intrinsic tree characteristics like age and size, as well as the impact of small-scale variations in topographic factors such as water and light availability (Fig. 7).

4.1. Effects of tree age and size

Tree age and size are the primary drivers of intraspecific variability in tree responses to climate extremes, as they may reflect different physiological and morphological characteristics of trees (Saurer and Voelker, 2022; Merlin et al., 2015). In our study, tree age and size affected RWI and iWUE (Fig. 5a,b), as found in other studies on oaks (Fernández-de-Uña et al., 2016). During dry years, tree age had a positive effect on RWI (Fig. 5b), but negatively affected post-drought recovery (Fig. 6c). In contrast, age decreased growth during the wet year (Fig. 5b), and increased growth in the post-wet year (Fig. 6c). This suggests that as trees age, their responsiveness to climate fluctuations diminishes. Mature trees, particularly species like sessile oaks and other deciduous trees, often benefit from deeper root systems, enhanced water storage (Donovan and Ehleringer, 1991; Wilson and Hanson, 2003), and accumulated carbohydrates (Bazot et al., 2013; Barbaroux et al., 2003), which support their resistance. The observed decline in RWI with age could partly be attributed to a size effect, as similar trends were observed for both growth (Fig. 5b) and recovery (Fig. 6c) when comparing the effects of age and diameter.

The tree iWUE tends to decrease with tree age under both wet and the dry year. The decrease in iWUE with age is often attributed to the juvenile effect (McCarroll and Loader, 2004). However, the juvenile effect in sessile oak is found to be typically short-lived, lasting only a few decades (Duffy et al., 2017). Our results suggest that the observed decrease in iWUE with age is unlikely to be caused by the juvenile effect. Instead, it may be linked to factors such as reduced nutrient availability or age-related genetic changes in the meristem (Ryan et al., 1997; Köhl et al., 2017). Tree DBH did not affect iWUE under wet year, but positively affected iWUE in dry year. This is possibly due to improved

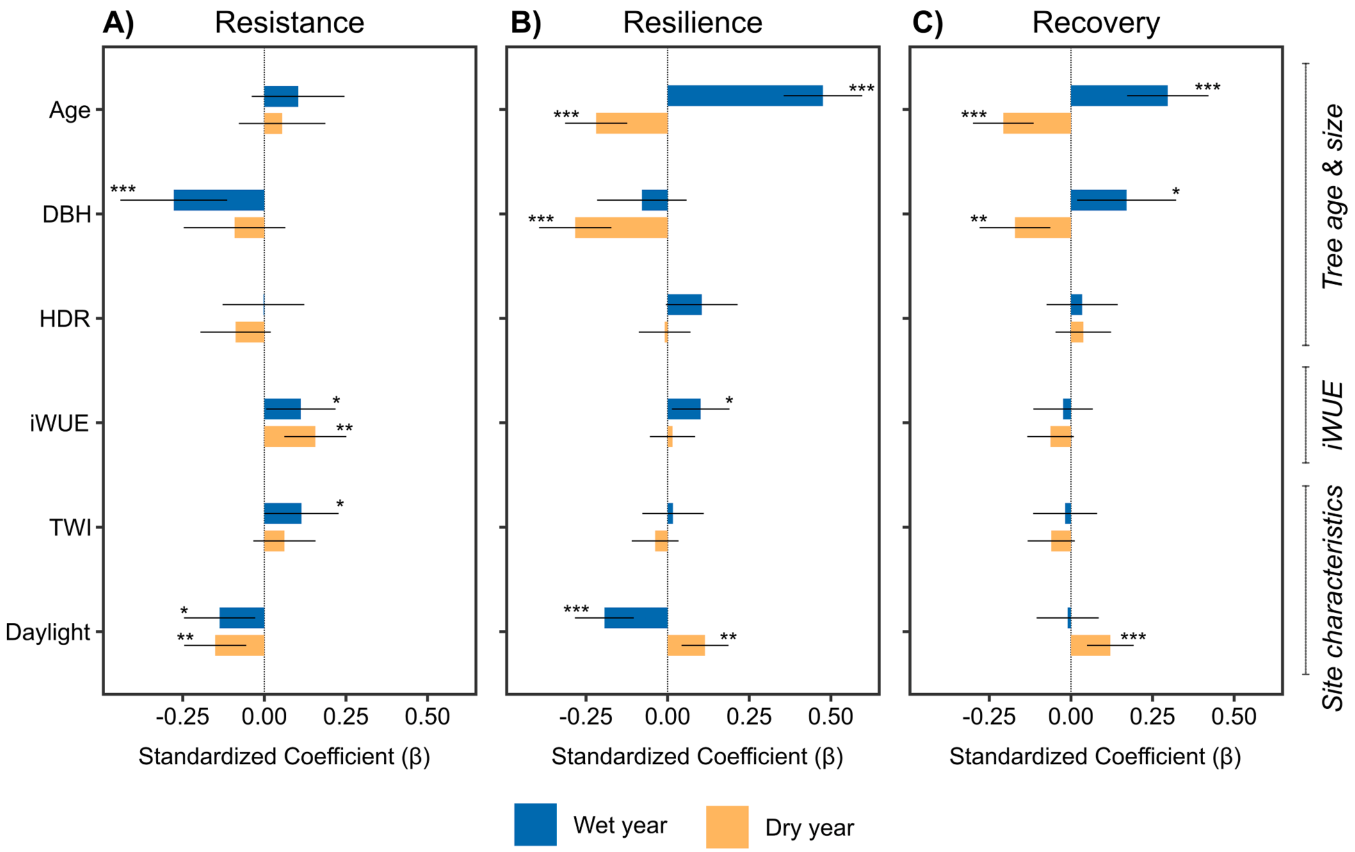

Fig. 6. The effects of tree age, size, intrinsic water use efficiency (iWUE), and site characteristics on the resistance (A), resilience (B), and recovery (C) of tree ring width index (RWI) under dry and wet years. Effect sizes for resistance, resilience, and recovery are regression coefficients determined through individual multiple linear regression analyses for both wet and dry years. Asterisks indicate significant effects (linear regression, p-value: 0.05 > *; 0.01 > **; 0.001 > ***).

hydraulic efficiency and higher photosynthetic rates (Kotowska et al., 2021), which might result from reduced stomatal limitations in larger trees, especially under drought. During dry years, a higher HDR was associated with increased iWUE (Fig. 5a). Taller trees face greater hydraulic resistance from leaf to soil (Zaehle, 2005), leading to earlier stomatal closure (Ryan et al., 1997; Fernández-de-Uña et al., 2023) and reduced photosynthesis and stomatal conductance, particularly under drought conditions (Ryan and Yoder, 1997). This is further supported by the observed decrease in RWI during dry years influenced by HDR (Fig. 5b). Our results suggest that variations in age and size provide complementary strategies for coping with water stress, implying that promoting age diversity in forests could enhance overall resilience of the forest to drought.

4.2. *Effects of topographic wetness and daylight duration*

The environment of a site, including light and water availability, can have a significant impact on tree morphology and metabolic processes. Our study examined the role of these factors in shaping tree growth under drought using the topographic wetness index (TWI) as a proxy for site water status (Grabs et al., 2009) and the calculated potential daylight at each tree location as a proxy for light availability (Fig. 2b, c). We found that TWI positively affected tree height and DBH (Fig. 3b, h), indicating that increased site water conditions promotes tree size (Fig. 7). However, we did not find a significant effect of TWI on iWUE and RWI under the wet and the dry years (Fig. 5), contrasting with studies in semi-arid forests that are highly sensitive to changes in water availability (Adams et al., 2014; Liu et al., 2013). Our results suggest that site water status does not mitigate drought impact on sessile oaks in temperate forests (Fig. 7). It's important to note that this could also be due to our focus on extreme years, where variability in water availability within the site might be strongly reduced (Tromp-van Meerveld and McDonnell, 2006), masking any subtle changes in tree response associated with TWI variation.

Our study revealed that daylight duration positively impacts tree height (Fig. 2c). This finding highlights the importance of light as a limiting resource for sessile oaks (Toïgo et al., 2018). During the dry year, daylight duration positively affected iWUE (Fig. 5a), likely due to higher CO_2 assimilation with more light availability (Stokes et al., 2010). Trees exposed to more daylight had lower RWI during the dry year (Fig. 5b), but not during the wet year (Fig. 5a), potentially reflecting an enhanced temperature response under drought conditions (Grossiord et al., 2020). The reduction in RWI under longer daylight during drought could be attributed to faster soil drying and higher vapor pressure deficit (VPD) (Kašpar et al., 2024), triggering greater stomatal regulation and increases iWUE (Fig. 5a, Fig. 7). The reduction in growth, despite the increased iWUE under prolonged daylight, could also be attributed to trees prioritizing carbon allocation towards essential metabolic processes, belowground structures, or storage to meet water requirements, rather than aboveground growth, to meet water requirements. Such carbon dynamics have been associated with enhanced recovery from drought (Vries et al., 2019; Karlowsky et al., 2018). Indeed, our study shows that trees receiving more daylight had faster recovery of growth after the dry year (Fig. 6c; Fig. 7b). These findings suggest that light availability plays a critical role in shaping water use strategies and growth responses during and after drought conditions.

4.3. *Role of iWUE*

The ratio of photosynthetic capacity to stomatal conductance (iWUE) is a key physiological trait that influences how plant respond to environmental changes, reflecting their ability to assimilate carbon while

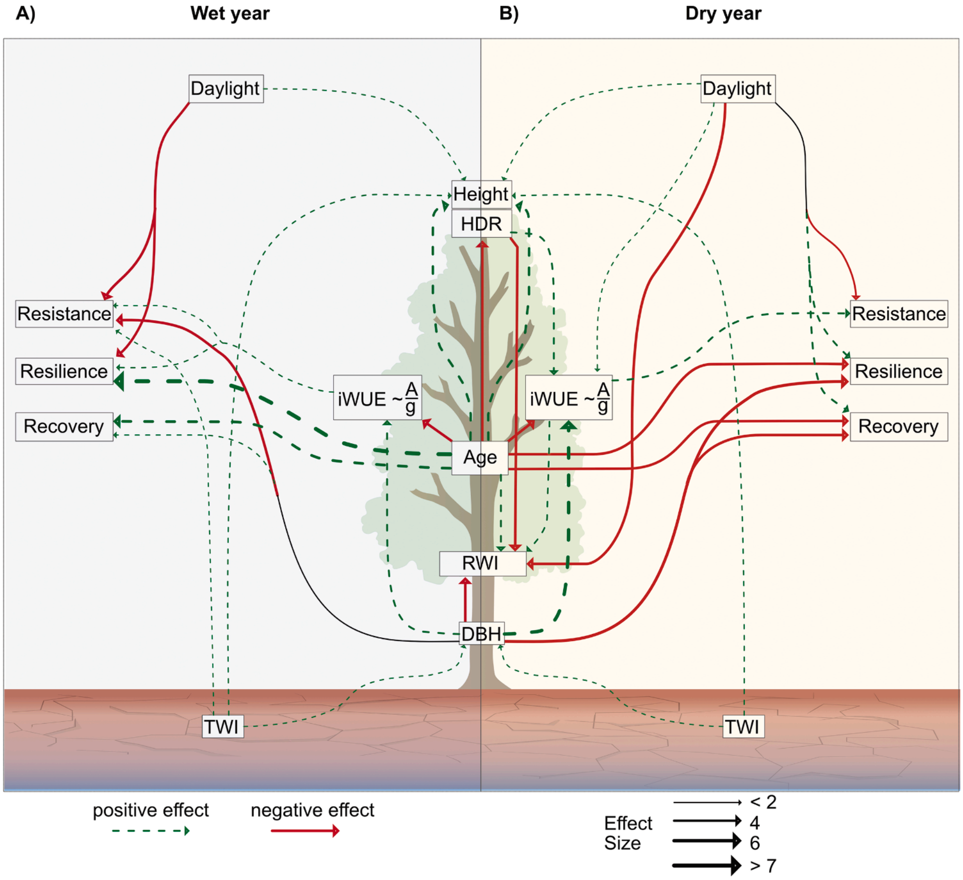

Fig. 7. Graphical summary on the effects of tree age, size, topographic wetness index (TWI) and daylight duration on the intrinsic water use efficiency (iWUE), ring width index (RWI) as well as resistance, recovery and resilience during wet (a) and dry (b) years. The effects sizes are standardized regression coefficients obtained from linear regression. The effects of TWI, daylight, and age on tree size are tested in general, whereas the effects on iWUE, RWI, resistance, recovery, and resilience were tested separately for the wet and the dry year. The green dotted lines and red solid lines represent positive and negative effects, respectively.

minimizing water loss. During drought, trees often exhibit increased iWUE, a strategy to conserve water and maintain carbon assimilation. Our results show that, during the dry year, iWUE had significant positive effect on RWI (Fig. 5b; Fig. 7b). This suggests that the trade-off between water conservation and carbon assimilation can be advantageous for sessile oaks under drought conditions (Heilman et al., 2021). Although drought generally reduces tree growth (Trouvé et al., 2017; Brzostek et al., 2014), sessile oaks can enhance their iWUE to sustain carbon gain and minimize water loss, as indicated by our findings on resistance (Fig. 6a; Fig. 7b). For Mediterranean oaks like *Quercus frainetto*, growth often decouples from iWUE due to susceptibility to embolism cola (Colangelo et al., 2017). However, our study found that growth increased with iWUE during the dry year, suggesting that sessile oaks maintain a coupled response, contributing to their survival during drought. This finding along with higher iWUE reflects a more conservative water use strategy, and indicate a reduced mortality risk (Scheidegger et al., 2000), highlighting a mechanism behind increased resilience of sessile oaks.

5. Conclusion

In conclusion, our study found that sessile oak trees had reduced growth and increased iWUE during dry years compared to wet years, showing significant intraspecific variability. This variability was influenced by factors such as tree age, diameter, height, and site environmental conditions. Specifically, we observed that iWUE played a role in enhancing growth and drought resistance, with older and larger trees buffering their growth response to climate extremes and adjusting their iWUE based on their age and size. Although site water status positively impacted tree size, it did not significantly affect growth during climate extremes. Conversely, light availability increased tree size, and increased iWUE during the dry year, and supported drought recovery.

These findings can have important implications for forest management. Promoting mixed-age stands could enhance forest resilience, as trees of different ages and sizes employ varied strategies to cope with drought stress. Additionally, models of forest development and management strategies aimed at mitigating the effects of climate extremes should take into account specific environmental conditions, such as light and water availability. Our study underscores the importance of understanding the roles of tree age, size, and site environment in shaping the response of sessile oak to climate extremes.

CRediT authorship contribution statement

Michael Grabner: Writing – review & editing, Supervision, Project administration, Investigation, Conceptualization. **Katharina Schott:** Writing – review & editing, Investigation, Data curation. **Kathiravan Meeran:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Andrea Watzinger:** Writing – review & editing, Supervision, Project administration, Investigation, Formal analysis, Conceptualization. **Elisabeth Wächter:** Writing – review & editing, Investigation, Data curation. **Marcela van Loo:** Writing – review & editing, Supervision, Project administration, Investigation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122413.

Data availability

Data will be made available on request.

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