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RESEARCH

Phenology, growth, and drought: how species interactions shape intra-annual tree dynamics in mediterranean forests

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Abstract

In Mediterranean forests, where seasonal drought imposes severe physiological constraints, the dynamics of tree growth are shaped not only by climate but also by interspecific interactions. However, how these factors influence intra-annual growth phenology remains poorly understood. Here, we used biweekly band dendrometer data collected since May 2022 to June 2024, from 154 trees across seven pure and mixed sample plots in the Spanish Northern Plateau. Our aim was to investigate how stand composition and interspecific competition affect phenological events, seasonal growth rates, and tree water deficit (TWD) in four tree species: *Pinus pinea* L., *Pinus pinaster* Ait., *Quercus ilex* L. and *Juniperus thurifera* L. We found that the identity of surrounding species significantly altered the xylogenesis phenology as the daily growth rate, particularly in spring and early summer, but not in autumn. Species mixing tended to advance spring onset in *J. thurifera* (by 9±3 days), but caused a delay in *Q. ilex* (by 9±2 days) and *P. pinaster* (by 9±3 days). Under stronger interspecific competition *Juniperus thurifera*, *Pinus pinea* and to lesser extent, *Pinus pinaster* showed increased daily basal area growth rates during dry springs (up to 0.024–0.067 cm^2/day, depending on the species), consistent with the stress gradient hypothesis. In contrast, *Q. ilex* exhibited the opposite pattern, suffering increased TWD and reduced daily growth rates in mixtures. These divergent responses were likely driven by species-specific water use strategies and seasonal asynchrony in root activity. Our findings demonstrate that interspecific interactions can either buffer or amplify climatic stress, depending on species identity and season. By linking cambial phenology, growth dynamics, and water deficit under varying competition contexts, this study provides new insights into the possible effects of species mixing towards more resilience under climate change in Mediterranean forests.

Keywords Intra-annual growth · Interspecific competition · Mediterranean forests · Tree water deficit · Mixed stands · Band dendrometers · Stress-gradient hypothesis

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Introduction

Forests in the Mediterranean Basin are crucial to the environmental and economic stability of the region. They regulate ecosystem functions, buffer extreme weather events, and support vital services like water purification and aquifer recharge (David et al. 2016; Vicente et al. 2018; Appiagyei et al. 2022). However, the region is increasingly threatened by aridification, water scarcity, and land degradation (Kutiel 2019; Noto et al. 2023b), largely driven by declining spring precipitation (Bevacqua et al. 2022; Gonzalez-Hidalgo et al. 2024). These trends undermine forest productivity and carbon sequestration (Díaz-Martínez et al. 2023) and increase mortality risks (Noto et al. 2023a). Understanding the factors that sustain forest stability in Mediterranean forests

under climate change is therefore essential. While forest management can reinforce resilience (MedECC 2020), the health of individual trees – reflected in their secondary growth – plays a crucial role. This growth results from complex physiological processes that unfold at an intra-annual scale and respond to climatic fluctuations (De Swaef et al. 2015; Lambers and Oliveira 2019).

Band dendrometers enable high-resolution monitoring of forest growth dynamics, providing insights into plant water status (De Swaef et al. 2015), the relationship between growth and short-term climatic conditions (Miller et al. 2022) and the amount of carbon uptake (McMahon and Parker 2015). Cambium activity in trees is broadly influenced by temperature and soil water availability, which regulates growth dynamics across seasons (Balducci et al. 2016; Vieira et al. 2019; Larysch et al. 2022). On drier sites intra-annual tree growth follows a bimodal pattern (Garcia-Forner et al. 2019; Tumajer et al. 2021), and that is the case of Mediterranean forests (Camarero et al. 2010; Campelo et al. 2018, 2021), with active growth occurring during favourable water conditions in spring and autumn, while pausing during the dry summer. Nevertheless, Mediterranean tree species differ in their sensitivity to climate, often resulting in species-specific growth rates – even within the same site, although differences are not always apparent (Tumajer et al. 2021). Such variability can alter the general bimodal pattern of intra-annual growth, demonstrating the plasticity of Mediterranean trees in adapting to diverse conditions (Gutiérrez et al. 2011; Camarero et al. 2021). Nevertheless, multiple factors modulate the timing and intensity of xylogenesis throughout the year. A deeper understanding of these processes is crucial for developing strategies to support tree vitality and forest stability under changing environmental conditions.

Under wetter conditions, when water availability is not the primary limiting factor, the bimodal growth pattern may decrease or even disappear (Martínez-Sancho et al. 2017; Campelo et al. 2018; Askarieh et al. 2024). In general, Mediterranean tree species show a convergent response to favourable spring weather, during which most of the annual growth is concentrated (Gutiérrez et al. 2011; Lempereur et al. 2015; Vieira et al. 2020).

In summer, however, growth becomes highly variable, being closely linked to both current precipitation regime and residual soil moisture from spring (Vieira et al. 2014; Martín et al. 2014; Moreno-Fernández et al. 2021), which together shape plant water potential (Lempereur et al. 2015). Interestingly, drought tolerance varies considerably among species: less drought-tolerant, isohydric species (e.g., *Pinus pinea*) tend to strictly follow a bimodal growth pattern, while more drought-tolerant, anisohydric, species (e.g., *Quercus ilex*) can maintain summer growth (Mayoral et al. 2015; Sperlich et al. 2019; Campelo et al. 2021), thereby avoiding carbon starvation (Calama et al. 2023). Resuming cambial activity in autumn is a consequence of summer drought and allows trees to recover from the stem shrinkage caused by it (Martín et al. 2014; Vieira et al. 2019; Garcia-Forner et al. 2019). Autumn growth depends on late summer and autumn precipitation, and only occurs if water availability is sufficient (Aldea et al. 2017; Vieira et al. 2020; Campelo et al. 2021). In winter, low temperatures and short photoperiods (Huang et al. 2020) inhibit cambial activity (Gutiérrez et al. 2011; de-Dios-García et al. 2018). However, in Mediterranean regions, winter temperatures may not be low enough to fully supress cambial activity, allowing for limited cambial activity even in colder month (Martín et al. 2014).

As Mediterranean tree species respond to seasonal fluctuations in water availability and temperature, they adjust their growth patterns through distinct phenological events. These adaptations are reflected in the phenology of both primary meristems (budburst, flowering, leafing) and secondary meristems (cambial activity), which together define annual growth cycles. However, as long-lived organisms, trees have limited capacity to track rapid environmental changes through phenological adjustments (Kramer et al. 2000; Huang et al. 2020). Photoperiod remains the dominant cue for growth initiation and cessation in many species (Huang et al. 2020). While warmer temperatures can advance growth onset and potentially prolong the wood formation period (Gordo and Sanz 2010; Rossi et al. 2016; Gao et al. 2022),these responses are not strictly linear (Morin et al. 2010). In fact, drought can override temperature-induced phenological shifts, constraining growth (Díaz-Martínez et al. 2023) and ultimately increasing mortality risk (Morin et al. 2010; Valeriano et al. 2021).

The duration of cambial activity, determined by the onset and cessation of xylogenesis, may greatly influence annual growth accumulation, as shown for *Quercus ilex* (Lempereur et al. 2015, 2017). However, this relationship is not universal. In certain conifer species, such as *Pinus pinaster*, *Pinus ponderosa*, and *Juniperus przewalskii*, it is the rate of growth, rather than the duration of the growth period, that primarily determines final wood production (Vieira et al. 2014, 2015; Ren et al. 2019). While temperature-driven responses tend to be consistent across species, responses to soil water balance are often species-specific. As a result, phenological patterns remain relatively stable in areas with moderate temperatures, whereas in drier environments, year-to-year variability in growth phenology can be substantial (Tumajer et al. 2021).

Interspecific interactions, such as competition or facilitation (Grossiord 2020), can significantly modify tree responses to environmental conditions and also shape intra-annual growth dynamics (Metz et al. 2020; Pretzsch 2022).

For example, *Pinus pinaster* trees in mixed-species stands have shown enhanced intra-annual growth (Askarieh et al. 2024). Reducing stand density – and thereby relieving competition pressure – can promote the growth of remaining individuals, as demonstrated in thinning experiments involving *Quercus spp.* (Moreno-Fernández et al. 2021) and in mixed *Pinus spp.* and *Quercus spp.* forests in Catalonia (Collado et al. 2023). Daily growth of *Pinus pinea* and *Juniperus thurifera* appears to be constrained more by conspecific neighbours than by heterospecifics, indicating a competition reduction effect in mixed stands (de-Dios-García et al. 2018). Similarly, suppressed *Quercus ilex* individuals responded only weakly to increased light and water availability when surrounded by conspecifics, even after thinning (Aldea et al. 2017). However, other studies suggest that intra-specific competition may not significantly affect *Quercus ilex* growth (de-Dios-García et al. 2018). Both *Pinus spp.* and *Quercus spp.* exhibited synchronous daily growth responses to temperature and precipitation, particularly in spring (Sánchez-Costa et al. 2015a; Campelo et al. 2021), indicating that they may compete within similar spatio-temporal niche (Aldea et al. 2018). However, such niche overlap appears limited to periods when water availability is not a major limiting factor, and competition remains low. As the dry season progresses, species may access different soil water pools, as shown for *Pinus halepensis* (shallow water use) and *Quercus ilex* (deep water uptake) (del Castillo et al. 2016). These examples are reminiscent of the *stress gradient hypothesis*, which predicts that under harsh conditions niche complementarity may outweigh competition (Forrester 2014; Grossiord 2020). However, its application in forestry requires caution: complementarity occurs only up to a threshold of resource scarcity (Haberstroh and Werner 2022), and the hypothesis was originally formulated to describe facilitation rather than competition reduction (see more in: Forrester and Bauhus 2016).

A growing body of evidence indicates that in Mediterranean ecosystems, species with contrasting hydraulic traits can benefit from growing in mixed stands through *complementary mechanisms*, which may enhance growth and mitigate stress under climate change conditions (de-Dios-García et al. 2015; Calama et al. 2019; del Río et al. 2021; Pardos et al. 2021a; Vergarechea et al. 2021; Jankowski et al. 2024). Yet, few studies have investigated how interspecific interactions impact xylogenesis phenology and subsequent growth patterns. If facilitation or more acute competition occurs in mixed stands, it may lead to altered responses to climatic conditions compared to pure stands, potentially resulting in distinct growth patterns. Unfortunately, the role of interspecific interactions in shaping the timing and dynamics of intra-annual wood formation remains insufficiently understood – particularly in water-limited environments, where seasonal climate constraints and species-specific physiology interact in complex ways.

In this study, we investigate the intra-annual growth dynamics of *Pinus pinea* L. (*P. pinea*), *Pinus pinaster* Ait. (*P. pinaster*), *Juniperus thurifera* L. (*J. thurifera*), and *Quercus ilex* L. (*Q. ilex*), which are the primary tree species of pure and mixed stands of the Spanish Northern Plateau. We address the following questions: (1) Does stand composition (mixed vs. pure) alter the growth phases across species? (2) Do interspecific interactions modulate tree growth differently among species and across the growing season? (3) Is summer growth depression intensified or mitigated by interspecific interactions? These questions form the basis for three hypotheses, guided by the expectation that mixed stands generally promote higher growth performance and buffer environmental stresses.

Hypothesis I *Stand composition influences the phenology of the studied species, with trees in mixed stands showing shifts in growth onset and cessation compared to those in pure stands.*

Hypothesis II *Interspecific interactions have seasonally distinct effects on tree stem growth. Specifically, we hypothesize that mixed stands enhance growth rates during favourable periods (spring and autumn) and buffer environmental stress during summer.*

Hypothesis III *Summer growth depression is less pronounced in mixed stands due to interspecific interactions.*

Materials and methods

Area of the study

The study was conducted on the Public Forest "El Carrascal" (41°35'17.9" N 4°21'28.0" W), located in the Spanish Northern Plateau, at 885 m a.s.l. The forest covers a uniform area of ~1100 ha and is composed mainly of *P. pinea*, *P. pinaster*, *J. thurifera* and

Q. ilex tree species, which constitute pure and mixed stands within the unit. The main soil types are calcareous cambisols and arkosic sands with water holding capacity of 176 mm × m^{-1} (de-Dios-García et al. 2018). Since 1985, the forest is owned and managed by the Forest Service of Junta de Castilla y León.

The climate is continental Mediterranean. Between 1996 and 2021, the climate was characterized by (a) very hot summers (average maximum daily temperatures of 30 ± 2.5 °C during June - September); (b) cold winters (daily temperatures during December-February of 0.2 ± 1.8 °C on average);

(c) lack of water supply during summer months (June - September), when the water deficit reached − 89 ± 31 mm. The mean temperature was 12.2 ± 6.5 °C and the yearly precipitation sum reached 444 ± 105 mm (Fig. 1: 1996–2021, Table S1). During the study period (2022–2024), climatic conditions varied across years, especially in autumn and winter. Autumn and winter were wetter in 2023 and 2024 compared to 2022. In contrast, spring and summer conditions were more stable, with modest interannual variation in temperature and consistently low summer rainfall. Spring precipitation ranged from 45 mm in 2023 to 136 mm in 2024, while summer rainfall remained below 80 mm each year. Temperatures showed only slight differences across seasons and years (Fig. 1, Table S2).

Experimental design

We collected the data on seven rectangular sample plots, ranging between 0.15 and 0.48 ha, which were installed on November 2021. The plots cover a total area of 2.05 ha. Four of the plots represent pure stands of the analysed species (*J. thurifera* (Jt), *P. pinea* (Pp), *P. pinaster* (Pt), *Q. ilex* (Qi)) and three of them are mixed stands.

The characteristics of the plots and species-level dendrometric attributes are detailed in Table S3 All trees with diameter at breast height (DBH) over 7 cm (in *P. pinea*, *P. pinaster*) or 5 cm (in *J. thurifera*, *Q. ilex*) were inventoried. Basic dendrometric measurements of the trees were taken, including DBH (cm, tape), height (m; Vertex®) and position (X, Y coordinates, using distance from the plot centre [m] and azimuth [°]; Suunto®). On April 2022, we installed 15 stainless-steel band dendrometers (precision up to 0.01 mm) per plot and species, making up to a total of 154 dendrometers. Trees selected for dendrometer installation spanned the full DBH range of each species (Fig. S4); their detailed characteristics are presented in Table S4. Initial DBH after dendrometers installation was recorded. Since installation, changes in circumference were recorded 44 times, at intervals of 16 ± 1 days (every 30 ± 7 days during winter), using an electronic calliper (Fig. S2). The measurements spanned over a total of 26 months. The first three measurements (six weeks of observations) were excluded, due to the need of dendrometer adjustment over the trunk. Hence, the dataset we used in the analyses started since mid-May 2022.

Single tree competition

Using the position of trees within each plot, we calculated the competition experienced by each tree where dendrometers were installed (subject tree) (Figs. S3, S4), using the same settings as in Jankowski et al. (2024), most importantly, setting the search radius for neighbouring trees to 30 times DBH. We accounted for the edge effect assuming that the unknown competition within the influence area outside the sample plot is proportional to that inside the plot (Martin et al. 1977). We used the distance-dependent *Hegyi competition index* (HGCI), which describes competition as the ratio of DBH of every k^{th} competitor tree (DBH_k), and the product between the DBH of i^{th} subject tree's (DBH_i) and the distance between the

i^{th} subject tree and the k^{th} neighbour tree ($dist_{ik}$). The ratios are then summed up over all n competitors separately for every subject tree (Hegyi 1974):

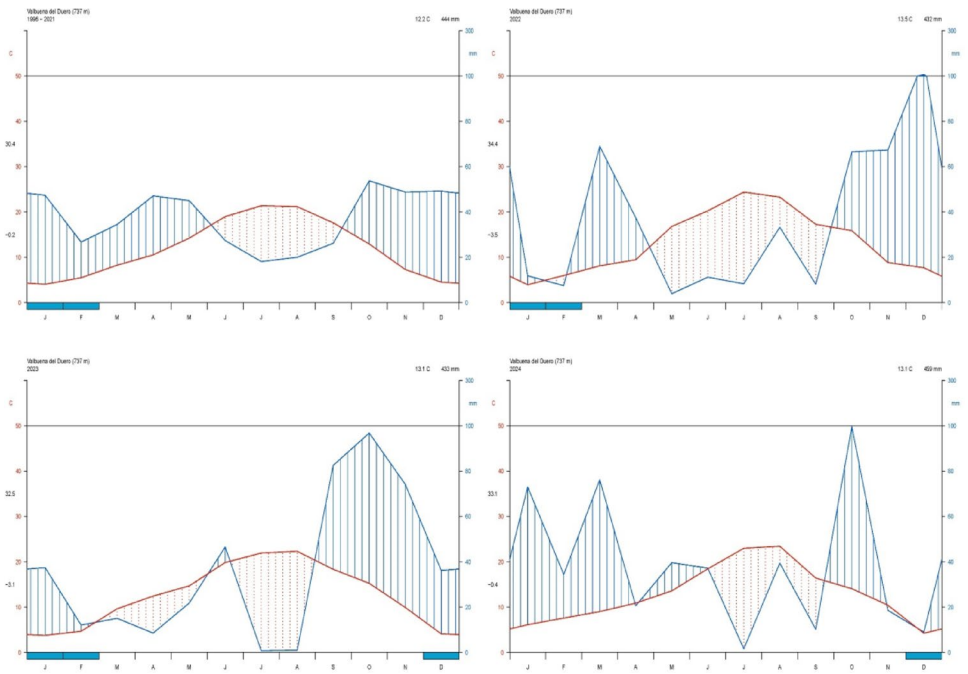


Fig. 1 Walther – Lieth climatograms representing the climate of the study site during the period 1996–2021, and separately for each year of the study (2022–2024)

$$HGCI_i = \sum_{k=1}^{n} DBH_k \Big/ (DBH_i \times dist_{ik})$$

We also quantified how much of this overall competition is due to heterogeneous species influence on each i^{th} dendrometer tree, as $CI.inter_i$:

$$CI.inter_i = HGCI_{inter|i} \Big/ HGCI_i \times 100\,[\%]$$

where: $HGCI_{inter|i}$: sum of competition exerted by heterogenous tree's species neighbours on dendrometer tree *i*.

Data preparation

Cumulative basal area increment (CBA; cm^2) was derived from raw girth increment measurements recorded on dendrometers. First, each tree DBH was converted to an initial girth. Subsequent changes in girth (as recorder by the dendrometers) were then summed up to estimate girth at each measurement date. From these girth values, we derived the corresponding basal area for each measurement. Next, we computed the daily basal area increment

(DBA; cm^2 / day) by dividing the difference between consecutive basal area measurements by the number of days separating those measurements. The CBA for each tree was then obtained by summing up these daily basal area increments from the first measurement date until the last. Finally, we reset CBA curves at the start of each year. A detailed step-by-step explanation of the calculations is available in Supplementary Information (SI), paragraph 1.

Phenological events identification

In order to analyse the CBA curves trajectory, we identified the *phenological events* (PEs), as days of year (DOY) when a significant change in the tree's growth dynamics occurred. Taking into account the bimodal pattern of annual growth typical of Mediterranean species (Camarero et al. 2010), four main PEs were proposed:

- *Growth onset (PE_1);* representing the moment when a tree restarts girth growth after winter stop.
- *Summer cessation (PE_2)*: representing the moment when a tree reduces or even stops growth as a response to summer limiting conditions.
- *Autumn onset (PE_3)*: representing the moment when, at the end of summer and in coincidence with the beginning of rainfall season, tree experiences a second period of significant growth.
- *Year cessation (PE_4);* representing the moment when tree reduces or even stops growth as a response to winter limiting conditions.

The PEs were identified separately for every *i*th tree of the *j*th plot within each year *y*. To prevent bias due to subjectivity on visual identification of the PEs, we used an automatized algorithm, the Two Stage Threshold Approach (2STA) described in Jankowski et al. (2025). The proposed approach relies on the premise that the physiological activity of the cambium depends primarily on temperature and water availability (Balducci et al. 2013; Lambers and Oliveira 2019), in effect shaping the growth curve trajectory recorded by the band dendrometers. The algorithm uses mean biweekly temperatures and precipitation sums to make a preliminary identification of growth periods. PEs are then recognised by searching an inflection point within the period, defined as the moment when a certain CBA threshold is surpassed. The different steps of the algorithm can be summarised as:

- *Step 1. Determination of thermal seasons.* Assigning each two-week period of y^{th} year to a thermal season (winter, spring, summer and fall) and based on average temperature (< 8 °C, 8–20 °C, > 20 °C, 8–20 °C).
- *Step (2) Standardization of daily basal area increment.* To make DBA increment values comparable across years and trees within a species, we standardized them for all trees of a species, year by year, creating the standardized daily basal area variation measure.
- *Step (3) Identification of spring and autumn thresholds*: growth and autumn onset are identified based on the DOY within a thermal season when each tree surpasses an established threshold of standardized daily basal area increment.
- *Step (4) Identification of summer threshold.* Identified as the first maximum in the growth curve once seasonal summer has started.

Duration of the seasons

Because Mediterranean trees exhibit a bimodal growth pattern, each year contains more than one growing phase (Camarero et al. 2010; Vieira et al. 2013). From the four PEs described above, we additionally calculated the duration of the intra-annual growth periods, separately for each tree and year. It is common to establish intra-annual growth periods common to all the trees within a study (Vieira et al. 2013; Aldea et al. 2018). As we intended to explain the variability of period duration, we calculated them separately for each tree, as follows:

Spring growth duration ($SG_{|ijy}$) = $PE_{2|ijy} - PE_{1|ijy}$.
Summer cessation duration (SC_{ijy}) = $PE_{3|ijy} - PE_{2|ijy}$.

Autumn growth duration ($AG_{|ijy}$) = $PE_{4|ijy} - PE_{3|ijy}$.

Periodical growth variables

In order to analyse intra-annual growth dynamics of the species, we calculated the rates of yearly cumulative basal area increment (ΔCBA_{Year} ; $mm^2 \times day^{-1}$) and periodical cumulative basal area increment (ΔCBA_p ; $mm^2 \times day^{-1}$), for two growth periods (p = *Spring*, *Autumn*). The periodical growth rate was defined as the sum of DBA, separately for *i*th tree from *j*th plot, within *y*th year of analysis, using the respective PEs for each tree, and then divided by the duration of the respective period (Fig. 2).

$$\Delta CBA_{Spring|ijy} = \frac{\left(\sum_{PE_{1|ijy}}^{PE_{2|ijy}} DBA_{ijy}\right)}{SG_{|ijy}} = \frac{CBA_{Spring}}{SG_{ijy}}$$

$$\Delta CBA_{Autumn|ijy} = \frac{\left(\sum_{PE_{3|ijy}}^{PE_{4|ijy}} DBA_{ijy}\right)}{AG_{ijy}} = \frac{CBA_{Autumn}}{AG_{ijy}}$$

$$\Delta CBA_{Year|ijy} = \frac{\left(\sum_{PE_{1|ijy}}^{PE_{4|ijy}} DBA_{ijy}\right)}{(PE_{4|ijy} - PE_{1|ijy})} = \frac{CBA_{Year}}{(PE_{4|ijy} - PE_{1|ijy})}$$

Tree water deficit approximation

An additional characteristic to the bimodal growth pattern of Mediterranean tree species is the fact their stem shrinks during summer months, due to water loss from elastic tissues (De Swaef et al. 2015; Lambers and Oliveira 2019). A significant related metric is the *Tree Water Deficit* (TWD), which is observed when the stem size does not exceed the previously attained maximum size, water loss solely being a causative factor (Zweifel et al. 2016). High-resolution studies often examine TWD on a daily basis, using automated dendrometers (Schäfer et al. 2019). Our study adopts the TWD concept, but scales it to a lower temporal resolution (biweekly), allowing us to evaluate the severity of summer drought stress using data from band dendrometers. Such approach is an approximation not capable of pinpointing the exact moment of the cessation or reassumption of cambium cell division. The lag between water deficit and changes in cambium activity can last from two to four weeks (Balducci et al. 2013). Hence, it intends to capture the variations in secondary growth recorded by band dendrometers, which are the reflection of cambial activity. Our method defines TWD as the area between the CBA curve and a horizontal line at $y = CBA_{MaxSpring}$, which represents the maximum CBA reached at the start of summer's growth cessation (Fig. 3). The x-axis interval extends from the day of maximum spring CBA ($DOY_{MaxSpring}$) to the day CBA recovers during autumn ($DOY_{FullRehydr}$).

The absolute TWD (TWD_{Abs}.; cm^2) calculation is mathematically represented as follows:

$$TWD_{Abs} = \int_{DOY_{MaxSpring}}^{DOY_{FullRehydr}} (CBV_{MaxSpring} - f(CBV))\, d(DOY)$$

This integral quantifies the TWD as the area between the CBA curve and the horizontal line established by $CBA_{MaxSpring}$, across the specified DOY interval.

In order to account for the fact that the absolute growth depression during summer may be dependent on the individual tree's size, we calculated *relative TWD* (TWD). This metric is defined as the ratio between TWD_{Abs} and the area under the CBA curve limited from DOY 150 until DOY 365, assuming no growth depression occurs during summer ($CBA_{Optimal}$):

$$TWD = {}^{TWD_{Abs}} \Big/ \int_{DOY=150}^{DOY=365} f(CBV_{Optimal})\, d(DOY) \times 100 \quad (1)$$

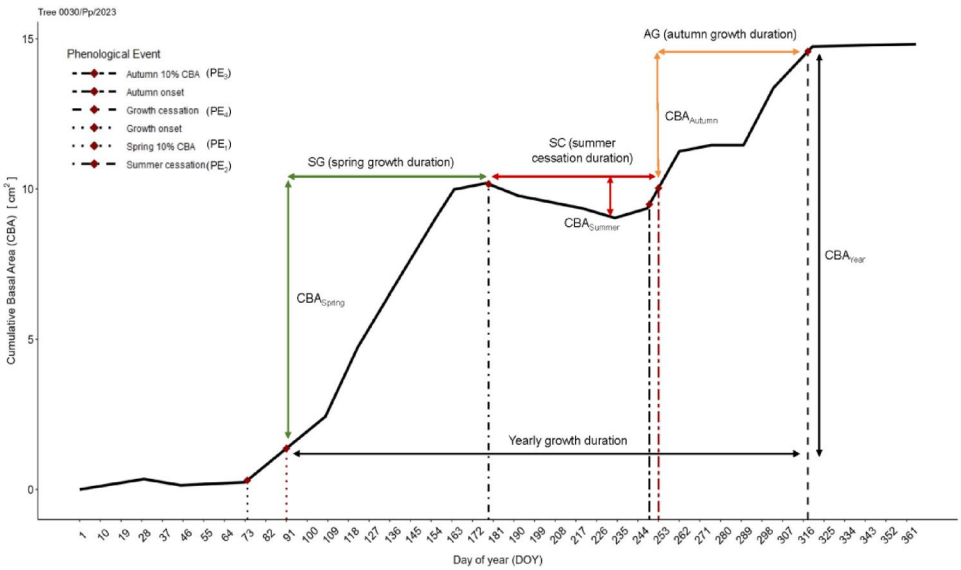


Fig. 2 Illustration of phenological events determination using cumulative basal area variation (CBA) for tree no 0030 (*P. pinea*). The black solid line represents observed CBA values, with annotations showing phenological events (PEs), seasonal growth durations and cumulative growth phases

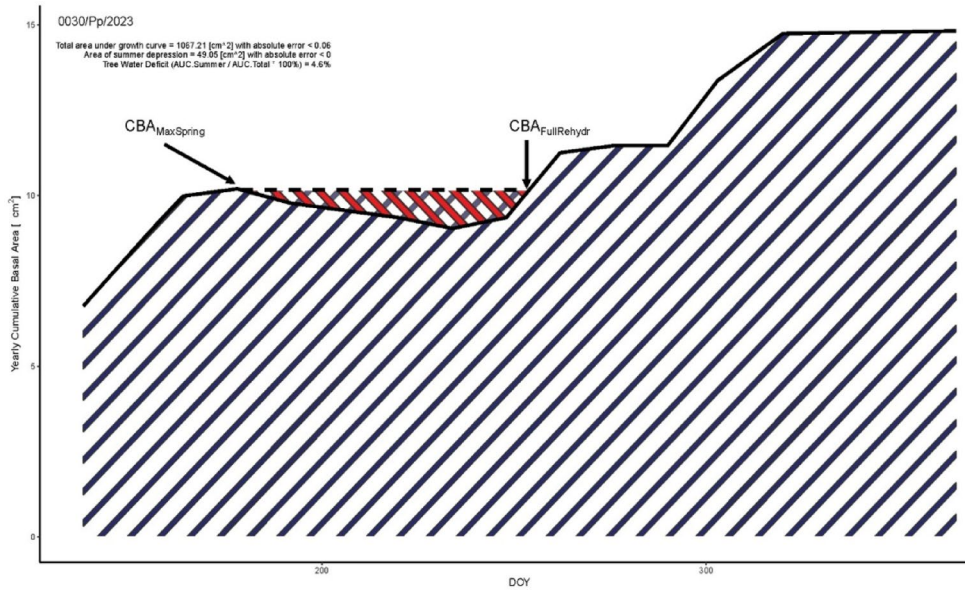


Fig. 3 Representation of the concept of absolute Tree Water Deficit (the area between red lines) calculated for low temporal (biweekly) scale. TWD is the proportion between red lined area and blue lined area

We used the period from DOY 150 until DOY 365, as this was the time common to both 2022 and 2023 years, for which complete summer data was available.

Data analysis

In order to contrast Hypotheses I-III we proposed a generalised linear mixed model (GLMM) approach. For each hypothesis we fitted different GLMMs, and compared

(i) Gaussian, Tweedie or Beta conditional distribution (Burnham et al. 2002, pp. 318–321),
(ii) inclusion of a random intercept acting at sampling plot (ω_j) or not (Zuur et al. 2009; Bates et al. 2015),
(iii) possible heteroscedasticity on the residuals and dependency of the dispersion parameter on several explanatory variables,
(iv) identification of significant two-way interactions to enter the model. At the end of every step, the final model was established by AIC minimisation (Fieberg 2022).

Once the final model for each hypothesis was selected, post-hoc comparisons between the different levels of the main explaining factors were carried out. All the statistical analyses were performed in the R Environment for Statistical Computing (R Core Team 2022). We fitted all the models using glmmTMB package (Brooks et al. 2017). The selection of optimal dispersion parameter dependency structure as of two-way interactions within fixed effects model's part was done using MuMIn package (Bartoń 2024). The post-hoc analyses were performed using the emmeans (Lenth 2023) and marginaleffects (Arel - Bundock 2023) packages. Residuals analysis – conditional distribution appropriateness, dependency, homoscedasticity and within group homogeneity was carried out using DHARMa package (Hartig 2022). Finally, we assessed multicollinearity of predictors and models' posterior predictions using performance package (Lüdecke et al. 2021). An overview of data availability by response variable and year is provided in Table S5.

Hypothesis I. Stand composition (mixed-pure) influences the phenology of the studied species

Hypothesis I tried to unravel if the phenology of the trees, represented by the phenological events (PE_1-PE_4) and the growth period duration (SG, SC, AG), can vary significantly depending on the type of stand. To this aim we fitted seven different GLMM (one for each phenological trait), including as predictors the species, stand type, year of measurements, diameter at breast height and the competition experimented by the tree from all its neighbours regardless their species. The full (saturated) models were formulated as:

$$Y_{n||ijy} = \beta_1 Species_{ij} + \beta_2 StandType_j + \beta_3 Year + \beta_4 DBH_{ij} + \beta_5 HGCI_{ij} + f\,(Two - WayInteractions) + \omega_j + \varepsilon_{ijy} \quad (3)$$

where:

$Y_{n|ijy}$: each of the seven phenological traits *(PE_1-PE_4, SG, SC, AG)* computed for the tree *i* from plot *j* within year *y*.

$Species_{ij}$: factor with four levels determining the tree's species (*Jt*, *Pp*, *Pt*, *Qi*).

$StandType_j$: factor with two levels determining the stand type (*Mixed*, *Pure*).

DBH_{ij} : diameter at breast height of tree *i*, standardized (DBH-μ/σ).

$HGCI_{ij}$: overall competition exerted on tree *i*.

Year : factor with three levels (*2022*, *2023*, *2024*).

f(Two – Way Interactions) : all possible two-way interactions between categorical × categorical and categorical × continuous predictors.

ω_j random plot intercept.

ε_{ijy} : random error term.

The post hoc analysis consisted in pairwise comparisons performed between marginal means estimated for each *Species* and *StandType* across *Years* (if respective interaction was included). All other covariates were maintained at their mean values, computed separately for every *Species.*

Hypothesis II Inter-specific competition as modifier of periodical intra-annual growth

To answer the question stated in Hypothesis II, we tried to explain the periodical cumulative basal area increment rate (ΔCBA_p) attained by each i^{th} tree from j^{th} plot within every *Year* by the inter-specific competition share in total competition (*CI.inter*). Additionally, we accounted for tree size and overall competition influences, by adding DBH and HGCI as their proxies to the model, respectively. The full-model formulation was therefore, as follows:

$$\begin{aligned}\Delta \mathrm{CBA}_{p|ijy} =& \beta_1 Species_{ij} + \beta_2 Year + \beta_3 DBH_{ij} + \beta_4 HGCI_{ij} \\ &+ \beta_5 CI.inter_{ij} + f(Two - WayInteractions) + \omega_j + \varepsilon_{ijy}\end{aligned} \quad (4)$$

where:

$\Delta CBA_{p|ij}$: cumulative basal area increment rate during period *p = (Spring*, *Autumn*, *Total)* [$cm^2 \times day^{-1}$].

$CI.inter_{ij}$: inter-specific competition share within overall (HGCI) competition [%].

The rest of symbols as stated before.

Post hoc analyses consisted in testing the trend (slope β_5) of CI.inter over ΔCBA_p, calculated at each level of *Species* (and *Year*) against 0, therefore checking if true influence of competition on growth exists. Additionally, we made pairwise comparisons between the beforementioned slopes across *Species* within the same years.

Hypothesis III. Species-specific competition influence on summer's tree water deficit

The main aim of Hypothesis III was to analyze how the inter-specific competition (CI.inter) impacts the summer growth depression experimented by trees, measured by TWD (Eq. 1). Specifically, we wanted to check if the competition exerted by a given species might have differing impact on summer water deficit, depending which species was exposed to that competition. We added DBH to the model – larger (higher) trees tend to be more susceptible to cavitation, and therefore to water stress impact (Bennett et al. 2015). Therefore, the model structure became:

$$\begin{aligned}TWD_{ijy} =& \beta_1 Species_{ij} + \beta_2 Year + \beta_3 DBH_{ij} + \beta_4 HGCI_{ij} \\ &+ \beta_5 CI.inter_{ij} + f(Two - WayInteractions) + \omega_j + \varepsilon_{ijy}\end{aligned} \quad (5)$$

where:

TWD_{ijy} : tree water deficit, experienced by tree *i*, from plot *j* within year *y* (Eq. 1).

The rest of symbols as stated before.

Post hoc analyses were performed by testing the trend of TWD over CI.inter against 0. Also, pairwise comparisons of TWD trend over CI.inter across all species within different years were done in order to check, if the inter-specific competition may affect TWD differently, depending on the species.

Results

It was not possible to reliably identify PEs in trees exhibiting irregular growth – such as decaying trees with a negative annual trend in the CBA curve due to water loss, or in trees that have died. In some instances, the algorithm also failed to pinpoint PEs. Consequently, depending on the specific model, 7–25% of observations had to be excluded (Table S5, showing the counts per variable and year). Although PEs were derived from biweekly measurements, the modelling approach allowed for estimation of mean differences smaller than the raw sampling interval. These estimates should be interpreted as population-level tendencies rather than exact event dates for individual trees.

To provide context for the following analyses, Fig. 4 shows the relative contribution of neighbouring species to the competitive pressure experienced by dendrometer trees in pure and mixed stands. In mixed stands, *P. pinea* exerted the strongest interspecific pressure, accounting for 68% of the competition experienced by *J. thurifera* and 39% by *Q. ilex*, while also being the main source of intraspecific competition for itself (60%). *P. pinaster*, even in mixed stands, was affected predominantly by conspecifics (57%), with *P. pinea* and *Q. ilex* contributing similarly (21–22%). For *Q. ilex*, competition from conspecifics (38%) was comparable to that imposed by *P. pinea*.

Phenology of trees is influenced by the surrounding stand composition

The timing of phenological events that mark the first phase of annual growth – namely spring onset and summer cessation of growth – varied among species and according to the surrounding stand composition. This was evidenced by the

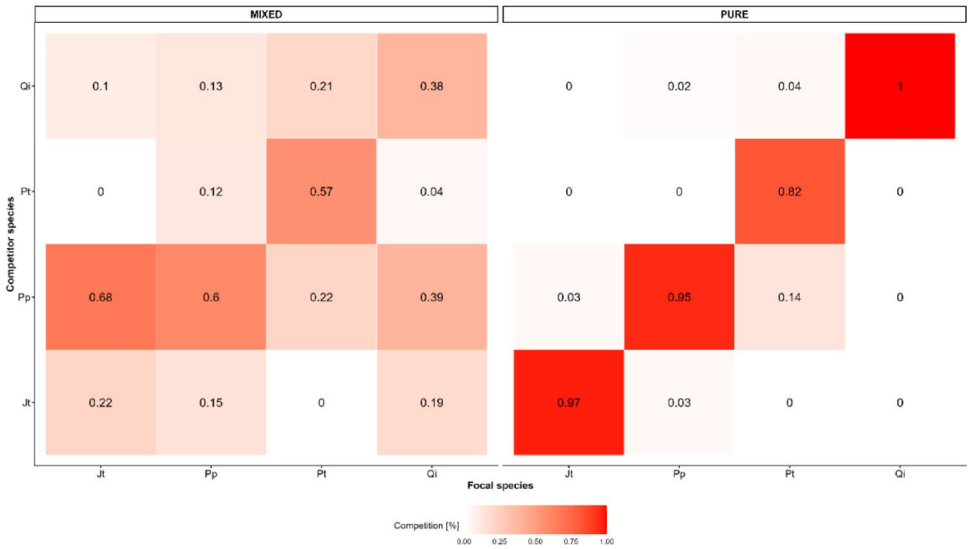


Fig. 4 Species-specific competition matrices for dendrometer trees in pure and mixed stands. Each tile represents the proportion (%) of total competition (HGCI) exerted by neighbouring species on focal trees, with darker colours indicating stronger relative influence. Values within tiles denote the percentage contribution of each competitor species. Pp – *P. pinea*; Pt – *P. pinaster*; Jt – *J. thurifera*; Qi – *Q. ilex*

inclusion of the *Species* × *StandType* interaction in the final models (Table S6). These differences also extended to the duration of spring and summer growth periods. In contrast, stand composition did not influence the timing of phenological events during the second phase of annual cycle – autumn onset and year cessation. For these variables, neither *StandType* nor *Species* × *StandType* terms were significant (Table S6). Notably, *Type* × *Year* interaction was absent in all PEs final models, indicating that when stand composition influenced phenology, the effect was consistent across years. The size of trees did not alter the estimates of PEs – *DBH* term was only relevant for the autumn onset and summer cessation duration. Tree size also modified the year cessation moment, differently for each stand type (*DBH* × *StandType* term) (Table S6).

A synthesis of differences across species in phenology, growth phases duration and seasonal growth rates is shown in Table 1.

The growth phenology of *J. thurifera* showed little variation between pure and mixed stands. The only significant difference was an earlier spring onset occurring 9±3 days earlier compared to pure stands (*p*-val. = 0.003; Table 2; Fig. 5). The duration of growth periods did not differ significantly between stand types. Although the trees in mixed stands showed a trend toward a longer spring growth phase, this difference was not statistically significant (Table 3; Fig. 5). The overall model structure for phenological variables confirmed this limited stand type effect in *J. thurifera* (Table S6).

The growth dynamics of *Q. ilex* also differed notably between pure and mixed stands. Spring growth onset occurred significantly later in mixed stands (by 9±2 days, *p*-val. < 0.001), as did summer cessation (by 14±4 days. *p*-val. < 0.001). In contrast, no significant differences were found for autumn onset or year cessation. Regarding growth period duration, *Q. ilex* showed a markedly shorter summer cessation phase in mixed stands (by 20±5 days, *p*-val. < 0.001; Table 3; Fig. 5), while spring and autumn growth durations remained similar across stand types. Model significance patterns supported these findings (Table S6).

For *P. pinea*, intra-annual growth patterns did not differ significantly between pure and mixed stands, except for summer cessation phase, which was shorter by 6±3 days in mixed stands. (p-val. = 0.015; Table 2; Fig. 5). Accordingly, *P. pinea* trees in mixed stands tended to extend growth slightly longer into summer and resume it earlier in autumn, although these differences were not statistically significant (Table 2; Fig. 5.). In contrast, *P. pinaster* showed more pronounced phenological differences. In mixed stands, spring onset was delayed (by 9±3 days, p-val. < 0.001), while summer cessation occurred earlier (by 7±4 days, *p*-val. = 0.07; Table 2; Fig. 5). Autumn onset and year cessation remained unaffected by stand composition. Consistent with these shifts, *P. pinaster* experienced considerably shorter spring growth in mixed stands (by 26±12 days, *p*-val. ≈ 0.03), while summer cessation duration increased (by 6±2 days, *p*-val. = 0.01; Table 3; Fig. 5). These results align with the phenological model outputs (Table S6).

Inter-specific competition influence on periodical growth rate

Modelled effects of interspecific competition on periodical growth rates revealed that the main term (*CI.inter*) was consistently significant across species, showing a positive effect on cumulative basal area increment rate (ΔCBA) at both seasonal (spring, autumn) and annual scales (Table S7). Notably, the magnitude of this effect varied between species, as indicated by the significant *CI.inter* × *Species* interaction in all three models. In the case of spring growth rate

Table 1 Summary of stand composition effects across all phenological events and intra-annual growth traits, analysed for each species

Species	Spring onset	Summer cessation	Autumn onset	Year cessation	Spring growth duration	Summer cessation duration	Autumn growth duration	Spring growth rate[1]	Autumn growth rate[2]	Yearly growth rate	TWD
Juniperus thurifera	←	–	–	–	–	–	–	↑	↑/–	↑	↓
Quercus ilex	→	→	–	–	–	↓	–	↑/↓	–	↑	↑
Pinus pinea	–	–	–	–	–	↓	–	↑	↑/–	↑	↓
Pinus pinaster	→	→	–	–	↓	↑	–	↑/–	–	–	↓

Green arrows indicate a positive effect of mixed stands compared to pure stands; red arrows indicate a negative effect; hyphens denote no effect; bars indicate variable effects across study years. Horizontal arrows refer to moments in time (left arrow – sooner, right arrow – later). Vertical arrows describe quantities (upper – increase, lower – decrease). The interpretation follows the structure: "Trait of species X was higher (sooner) / lower (later) in mixed stands compared to pure stands." Years analysed for each metric are specified in the footnotes. The years under study were [1] 2023 and 2024 or [2] 2022 and 2023

Table 2 Timing of intra-annual phenological events (PE_1–PE_4) for analysed species in pure and mixed stands

Phenological event	Species	Year	PE mixed	PE pure	Mixed - pure	*p*-value
Spring onset (PE_1)	Jt	**Global effects**	99±2	108±3	−9±3	**0.0025**
	Pp		101±2	99±3	2±3	0.5561
	Pt		115±2	106±2	9±3	**0.0008**
	Qi		138±2	129±2	9±2	**0.0002**
Summer cessation (PE_2)	Jt	Global effects	181±3	178±3	3±4	0.4551
	Pp		186±2	182±3	4±3	0.3019
	Pt		184±4	191±3	−7±4	**0.0709**
	Qi		186±3	172±4	14±4	**0.0004**
Autumn onset (PE_3)	Jt	2022	270±5	274±5	−4±3	0.115
	Pp		285±2	290±2	−4±3	0.115
	Pt		264±5	269±4	−4±3	0.115
	Qi		285±4	289±2	−4±3	0.115
	Jt	2023	239±3	239±3	0±0	0.617
	Pp		251±1	251±1	0±0	0.617
	Pt		246±2	246±2	0±0	0.617
	Qi		237±1	237±1	0±0	0.617
Year cessation (PE_4)	Jt	2022	334±3	336±3	−2±2	0.4162
	Pp		351±1	352±1	−1±1	0.4143
	Pt		347±2	348±1	−1±1	0.4203
	Qi		318±12	321±11	−2±3	0.4293
	Jt	2023	340±3	341±3	−1±2	0.4188
	Pp		346±2	347±2	−1±1	0.4192
	Pt		331±4	333±4	−2±2	0.4235
	Qi		328±6	330±5	−2±2	0.4228

Estimated marginal means for each phenological event [days of year±SE] are presented for both stand types (*PE Mixed/Pure*), along with their differences (*Mixed - Pure*) and significance levels (*p-value*). Significant differences (*p*-val. < 0.10) between pure and mixed stands are highlighted in bold. Negative values of differences (*Mixed-Pure*) depict sooner occurrence of a given PE in mixed stand, than in pure stand. Residual degrees of freedom: PE_1 = 269; PE_2 = 247; PE_3 = 211; PE_4 = 216

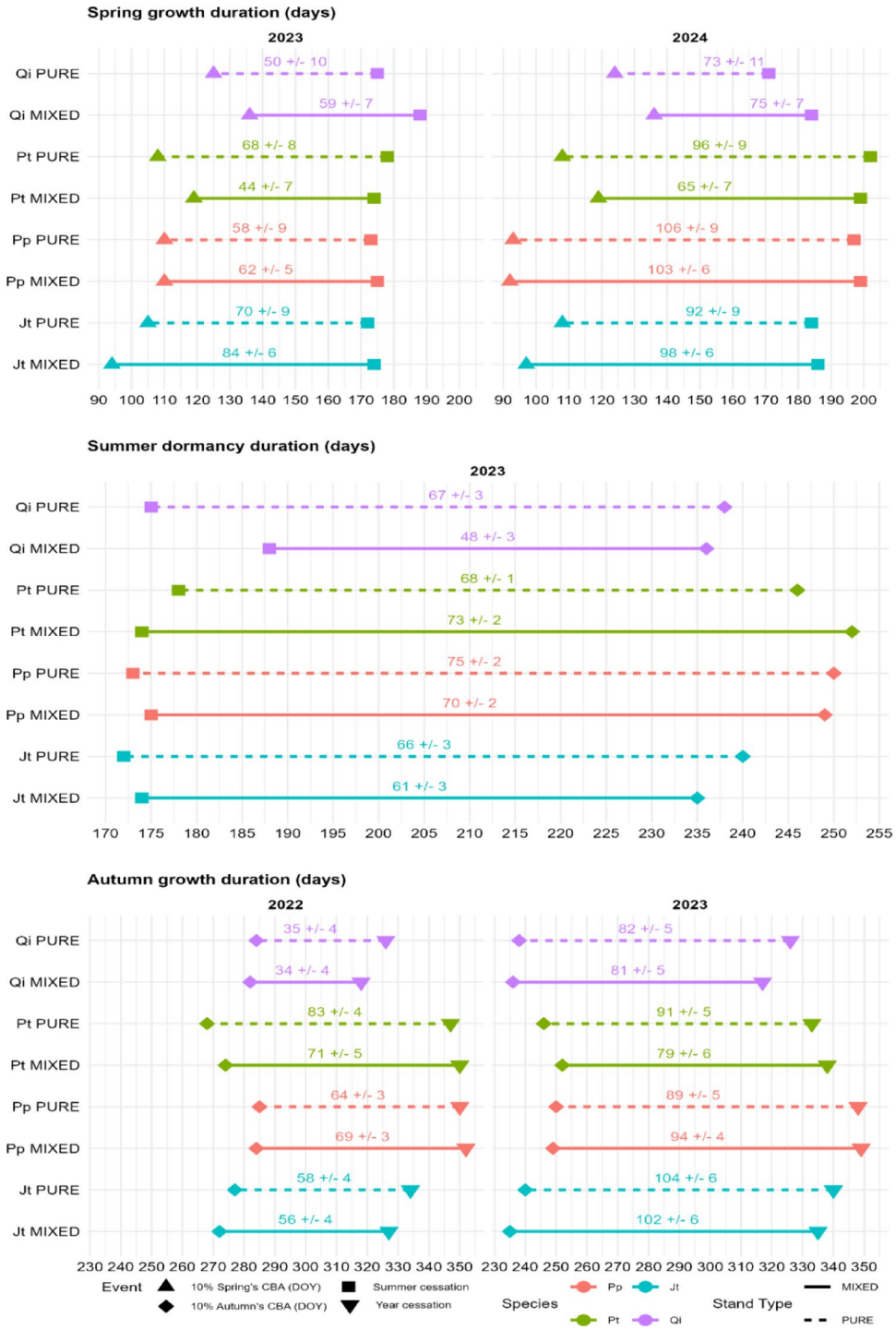


Fig. 5 Phenological events and duration of intra-annual growth periods (estimated marginal means) of analysed species across pure (dashed line) and mixed stands (solid line) presented over years of study. Pp – P. pinea; Pt – P. pinaster; Jt – J. thurifera; Qi – Q. ilex

(ΔCBA_{Spring}) the influence of CI.inter also varied between years, supported by a significant *Year* × *CI.inter* interaction (Table S7). *Species* × *HGCI* model term resulted to be significant in models of spring and autumn growth rates (Table S7).

An increasing share of inter-specific competition had a consistent positive effect on spring growth rates, for *P. pinea* and *J. thurifera*, with the strongest effects in 2023. (P. pinea: + 0.062 ± 0.011 to 0.173 ± 0.019 cm^2/day; J. thurifera: + 0.016 ± 0.001 to 0.024 ± 0.001 cm^2/day; Fig. 6; Table 4). For *P. pinaster*, the effect was also positive in spring 2023. (+ 0.067 ± 0.008 cm^2/day), but it disappeared in 2024. Similarly, *Q. ilex* showed a weak positive trend in 2023 (+ 0.002 ± 0.00 cm^2/day), which shifted to a negative one in 2024 (− 0.007 ± 0.001 cm^2/day) (Table 4; Fig. 6).

Table 3 Duration of intra-annual growth phases for analysed species in pure and mixed stands

Phenological event	Species	Year	EMM mixed	EMM pure	Mixed - pure	*p*-value
Spring growth duration (SG) (natural days)	Jt	Global effects	90 ± 7	78 ± 11	12 ± 12	0.325
	Pp		85 ± 6	82 ± 10	3 ± 12	0.7945
	Pt		60 ± 7	86 ± 10	−26 ± 12	**0.0292**
	Qi		65 ± 7	60 ± 11	5 ± 13	0.6735
Summer cessation duration (SC) (natural days)	Jt	Global effects	62 ± 2	62 ± 3	0 ± 3	0.9986
	Pp		76 ± 2	82 ± 3	−6 ± 3	**0.0148**
	Pt		73 ± 2	67 ± 2	6 ± 2	**0.001**
	Qi		45 ± 4	65 ± 4	−20 ± 5	**< 0.001**
Autumn growth Duration (AG) (natural days)	Jt	Global effects	87 ± 3	85 ± 4	2 ± 2	0.5219
	Pp		83 ± 2	81 ± 2	2 ± 2	0.5219
	Pt		85 ± 3	83 ± 3	2 ± 2	0.5219
	Qi		63 ± 20	61 ± 20	2 ± 2	0.5219

Estimated marginal means are presented for each species and stand type (*EMM Mixed/Pure*) alongside their differences (*Mixed - Pure*) with corresponding significance levels (*p-value*). Significant differences (p-val. < 0.10) between pure and mixed stands are highlighted in bold. Residual degrees of freedom: SG = 270; SC = 130; AG = 215

The strength of CI.inter effects on ΔCBA_{Spring} clearly differed across species and years, as shown by pairwise comparison (Table 4). In absolute terms, *P. pinea* showed the strongest growth enhancement from interspecific competition, followed by *P. pinaster* and *J. thurifera*. *Q. ilex* exhibited only a minor positive trend in 2023 and a weakening effect in 2024. By that year, the response of *P. pinaster* had also diminished, aligning more closely with the patterns observed for *J. thurifera* and *Q. ilex* (Fig. 6 "Spring").

During autumn, a positive effect of CI.inter on growth (ΔCBA_{Autumn}) was observed only in.

J. thurifera during 2022 (+0.013 ± 0.006 cm^2/day). In all other species, and in 2023, this effect disappeared entirely (Table 4; Fig. 6 "Autumn").

In line with the seasonal trends, interspecific competition also enhanced annual growth (ΔCBA_{Year}) in *P. pinea* (+0.048 ± 0.026 cm^2/day) and *J. thurifera* (+0.015 ± 0 cm^2 / day).

Q. ilex showed a marginally positive effect (+0.003 ± 0 cm^2/day), whereas *P. pinaster* displayed no response to increasing CI.inter (Table 5; Fig. 6 "Year").

Summer growth depression and species- specific competition effects

A higher share of heterospecific neighbours in overall competition was associated with reduced summer growth depression, as indicated by decreasing TWD with increasing CI.inter (Fig. 7). This pattern held true across all species and years, with one notable exception: in.

Q. ilex, TWD actually increased with higher CI.inter, only in 2022 (+0.033 ± 0.02) any effect disappearing in 2023 (0.003 ± 0.006). Among the remaining species, *P. pinea* benefited the most from interspecific interactions with TWD reductions ranging from −0.29 ± 0.06 to –0.123 ± 0.039, especially in 2022. *P. pinaster* and *J. thurifera* showed similar, but no so marked responses, the differences between the two species being not statistically significant (Table 6). Pairwise comparisons confirmed that *Q. ilex* differed significantly from the other species in its response to interspecific competition, exhibiting an opposite TWD trend under increased CI.inter (Table 6).

Discussion

We aimed to discern for the analysed tree species, if: (i) the intraannual growth trajectory approximated by the PEs differs between stand types (H I); (ii) the seasonal growth rate is increased by interspecific interactions (H II); the summer growth depression approximated by TWD is alleviated by heterospecifics presence (H III). Our findings show that interspecific interactions significantly shape intraannual growth dynamics in the studied Mediterranean tree species, though with strong species-specific differences. Stand composition altered the timing of spring onset and summer cessation in most species (*J. thurifera*, *P. pinaster*, *Q. ilex*), but had no consistent effect on autumn onset or year cessation (Tables 2 and 3; Fig. 5), partially supporting Hypothesis I. It is important to note that the 2STA method does not pinpoint the exact onset or cessation of cambial cell activity, which can only be determined from microcore analyses. Instead, the method approximates PEs from growth curve trajectories, and was shown to provide robust and precise estimates for PE_1–PE_3 using the same dataset analysed here (Jankowski et al. 2025). Nevertheless, because raw dendrometer measurements were collected at a biweekly resolution, modelled PEs should be interpreted as estimates rather than exact calendar days. This source of uncertainty, however, is consistent across species, and stand types,

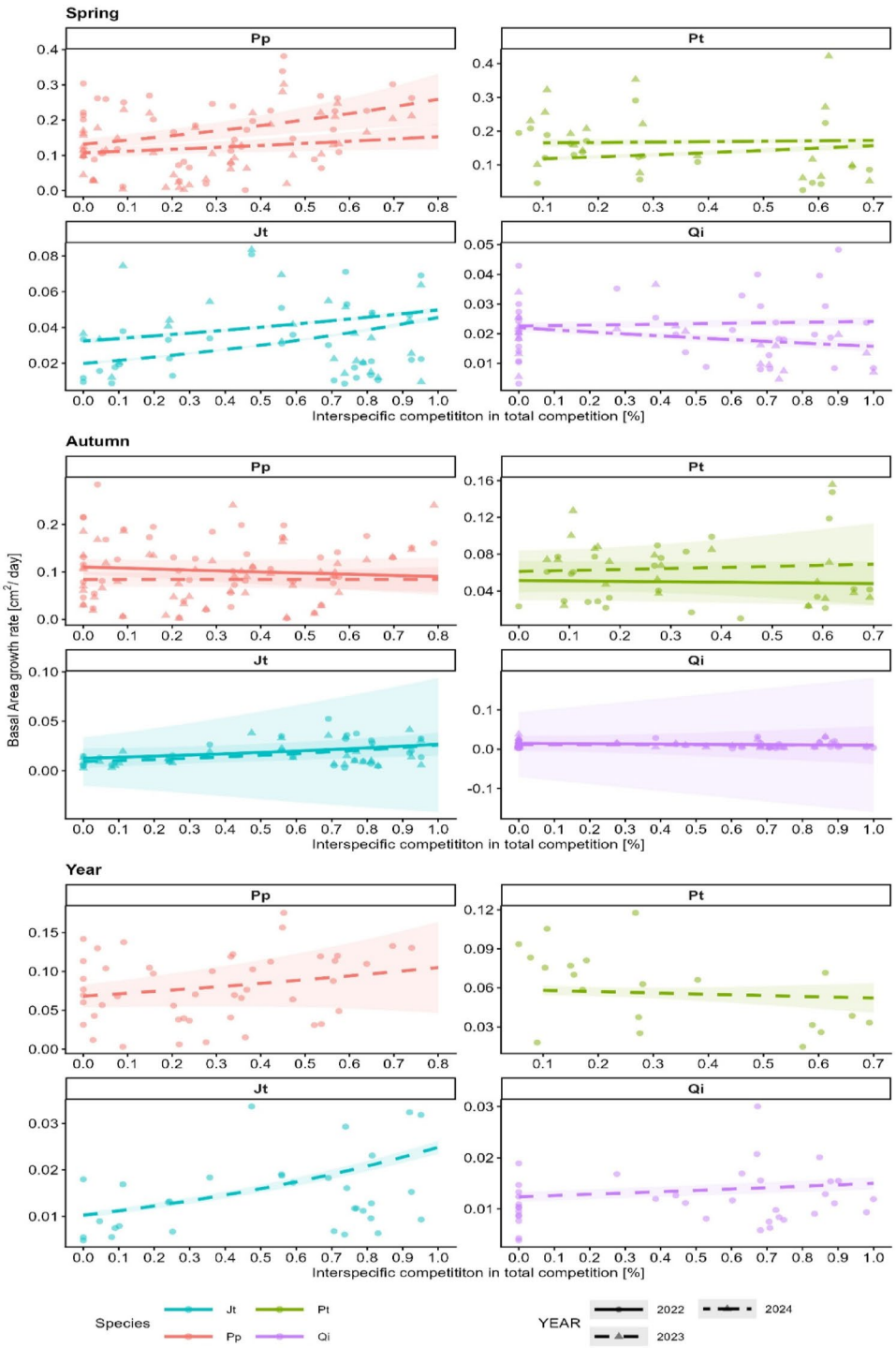


Fig. 6 Relationship between cumulative basal area increment rate (ΔCBA_p) [$cm^2 \times day^{-1}$] and inter-specific competition share in overall competition (CI.inter) across species and the study years, for different intra-annual growth periods. Remaining model variables (diameter at breast height, overall competition) were held at their species-specific mean values

ensuring that relative comparisons remain valid. Moreover, the uncertainty is explicitly reflected in the standard errors of the model outputs. In line with Hypothesis II, competition effects were most evident in spring, where species experiencing intensified interspecific competition (*J. thurifera*, *P. pinea*, *Q. ilex*) showed higher spring and annual growth (Tables 4 and 5; Fig. 6), reinforcing the critical role of spring growth in determining yearly increments (Lempereur et al. 2017; Camarero et al. 2021). We used Hegyi competition index which was proven to be adequate for describing single-tree competition in arid areas (Contreras et al. 2011), and it was shown to correlate the strongest with basal area increment on the same stand (see Table S4 in: Jankowski et al. 2024). That being said, we did not decompose CI.inter into species-specific competition effects, which would be a great improvement, as that would allow to isolate the exact

Table 4 Pairwise comparisons of interspecific competition share effects (trends) ($\beta_A - \beta_B \pm SE$) on periodical ($p = Spring, Autumn$) basal area growth rates ($\beta\Delta CBA|_{CI.inter} \pm SE$) between species and across years of study

Year	Contrast (A – B)	$\beta\Delta CBA\|_{CI.inter}$ (A)	$\beta\Delta CBA\|_{CI.inter}$ (B)	$\beta_A - \beta_B$	t-stat	*p*-value
p = Spring						
2023	Pt - Pp	0.067 ± 0.008	0.173 ± 0.019	− 0.106 ± 0.021	− 5.056	**< 0.001**
	Jt - Pp	0.024 ± 0.001	0.173 ± 0.019	− 0.149 ± 0.019	− 8.014	**< 0.001**
	Qi - Pp	0.002 ± 0	0.173 ± 0.019	− 0.171 ± 0.019	− 9.187	**< 0.001**
	Jt - Pt	0.024 ± 0.001	0.067 ± 0.008	− 0.043 ± 0.008	− 5.459	**< 0.001**
	Qi - Pt	0.002 ± 0	0.067 ± 0.008	− 0.065 ± 0.008	− 7.834	**< 0.001**
	Qi - Jt	0.002 ± 0	0.024 ± 0.001	− 0.022 ± 0.001	− 28.41	**< 0.001**
2024	Pt - Pp	0.013 ± 0.012	0.062 ± 0.011	− 0.049 ± 0.017	− 2.94	**0.003**
	Jt - Pp	0.016 ± 0.001	0.062 ± 0.011	− 0.046 ± 0.011	− 4.181	**< 0.001**
	Qi - Pp	− 0.007 ± 0.001	0.062 ± 0.011	− 0.069 ± 0.011	− 6.312	**< 0.001**
	Jt - Pt	0.016 ± 0.001	0.013 ± 0.012	0.003 ± 0.012	0.294	0.769
	Qi - Pt	−0.007 ± 0.001	0.013 ± 0.012	− 0.019 ± 0.012	− 1.644	0.1
	Qi - Jt	−0.007 ± 0.001	0.016 ± 0.001	− 0.023 ± 0	− 63.103	**< 0.001**
p = *Autumn*						
2022	Pt - Pp	−0.005 ± 0.009	− 0.022 ± 0.018	0.017 ± 0.019	0.91	0.363
	Jt - Pp	0.013 ± 0.006	− 0.022 ± 0.018	0.035 ± 0.014	2.48	**0.013**
	Qi - Pp	−0.005 ± 0.021	− 0.022 ± 0.018	0.017 ± 0.035	0.477	0.634
	Jt - Pt	0.013 ± 0.006	− 0.005 ± 0.009	0.018 ± 0.008	2.185	**0.029**
	Qi - Pt	−0.005 ± 0.021	− 0.005 ± 0.009	0 ± 0.02	− 0.024	0.981
	Qi - Jt	−0.005 ± 0.021	0.013 ± 0.006	− 0.018 ± 0.024	− 0.75	0.453
2023	Pt - Pp	0.011 ± 0.031	0 ± 0.016	0.011 ± 0.019	0.606	0.544
	Jt - Pp	0.015 ± 0.025	0 ± 0.016	0.015 ± 0.014	1.034	0.301
	Qi - Pp	−0.001 ± 0.046	0 ± 0.016	− 0.001 ± 0.034	− 0.035	0.972
	Jt - Pt	0.015 ± 0.025	0.011 ± 0.031	0.004 ± 0.008	0.474	0.635
	Qi - Pt	−0.001 ± 0.046	0.011 ± 0.031	− 0.012 ± 0.019	− 0.642	0.521
	Qi - Jt	−0.001 ± 0.046	0.015 ± 0.025	− 0.016 ± 0.023	− 0.711	0.477

Significant differences between trends (p-value < 0.10, in bold) highlight where interspecific competition substantially differed in its impact into ΔCBA_p between two species. The results include t-ratio and p-value for each comparison between species

Residual degrees of freedom: Spring = 243; Autumn = 272

Table 5 Inter-specific competition effects on yearly basal area growth rate of a given species ($\beta\Delta CBA|_{CI.inter} \pm SE$) and pairwise comparisons between them ($\beta_A - \beta_B \pm SE$)

Year	Contrast (A – B)	$\beta\Delta CBA\|_{CI.inter}$ (A)	$\beta\Delta CBA\|_{CI.inter}$ (B)	$\beta_A - \beta_B$	t-stat	*p*-value
2023	Pt - Pp	− 0.01 ± 0.011	0.048 ± 0.026	− 0.058 ± 0.02	− 2.923	**0.003**
	Jt - Pp	0.015 ± 0	0.048 ± 0.026	− 0.033 ± 0.026	− 1.254	0.21
	Qi - Pp	0.003 ± 0	0.048 ± 0.026	− 0.045 ± 0.027	− 1.687	**0.092**
	Jt - Pt	0.015 ± 0	-0.01 ± 0.011	0.025 ± 0.011	2.299	**0.022**
	Qi - Pt	0.003 ± 0	-0.01 ± 0.011	0.013 ± 0.011	1.124	0.261
	Qi - Jt	0.003 ± 0	0.015 ± 0	− 0.012 ± 0.001	− 22.844	**< 0.001**

The results include t-statistic (*t-stat*) and *p-value* for each comparison between species. Significant differences between trends (p-val. < 0.10, in bold) highlight where inter–specific competition substantially differed in its impact into ΔCBA_{Year} between two species

Residual degrees of freedom = 130

species-specific interactions. Hypothesis III received strong support: in nearly all species and years, increased interspecific competition mitigated summer water stress, as reflected by reduced TWD (Table 6; Fig. 7).

Surrounding stand composition shifts phenological events

Stand composition altered phenology mainly during spring and early summer, while autumn onset and winter cessation remained unaffected. In mixed stands, *J. thurifera* advanced spring growth, likely due to facilitation. At our study site, *J. thurifera* is the only species growing directly under *P. pinea* canopies, while *Q. ilex* forms single-species

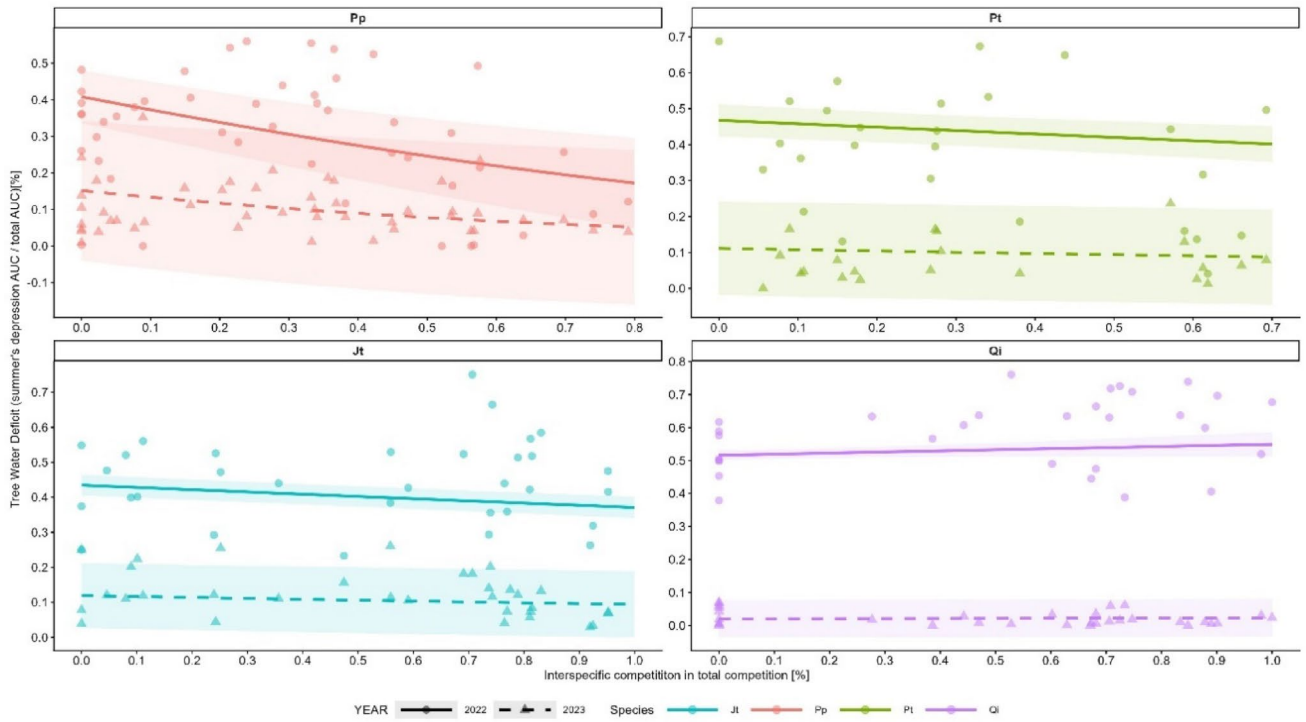


Fig. 7 Influence of inter-specific competition (CI.inter) on Tree Water Deficit (TWD) suffered by each species (*Pinus pinea* [Pp], *Pinus pinaster* [Pt], *Quercus ilex* [Qi] and *Juniperus thurifera* [Jt]). TWD (y-axis) is shown as a function of the share of competition experienced from other species (x-axis). Remaining model variables (diameter at breast height, overall competition) were held at their species-specific mean values

Table 6 Trends in tree water deficit caused by varying inter-specific competition share ($\beta TWD|_{CI.inter} \pm$ SE), across studied species and years and differences between species trends ($\beta_A - \beta_B \pm SE$)

Year	Contrast (A-B)	$\beta TWD\|_{CI.inter}$	$\beta TWD\|_{CI.inter}$	$\beta_A - \beta_B$	t-stat	*p*-value
2022	Pt - Pp	− 0.094 ± 0.026	− 0.29 ± 0.06	0.196 ± 0.075	2.605	**0.009**
	Jt - Pp	− 0.063 ± 0.009	− 0.29 ± 0.06	0.227 ± 0.066	3.441	**0.001**
	Qi - Pp	0.033 ± 0.02	− 0.29 ± 0.06	0.323 ± 0.045	7.176	**< 0.001**
	Jt - Pt	− 0.063 ± 0.009	− 0.094 ± 0.026	0.031 ± 0.022	1.376	0.169
	Qi - Pt	0.033 ± 0.02	− 0.094 ± 0.026	0.127 ± 0.04	3.201	**0.001**
	Qi - Jt	0.033 ± 0.02	− 0.063 ± 0.009	0.097 ± 0.024	4.039	**< 0.001**
2023	Pt - Pp	− 0.034 ± 0.022	− 0.123 ± 0.039	0.089 ± 0.05	1.766	**0.077**
	Jt - Pp	− 0.025 ± 0.004	− 0.123 ± 0.039	0.098 ± 0.041	2.4	**0.016**
	Qi - Pp	0.003 ± 0.006	− 0.123 ± 0.039	0.125 ± 0.035	3.546	**< 0.001**
	Jt - Pt	− 0.025 ± 0.004	− 0.034 ± 0.022	0.009 ± 0.023	0.407	0.684
	Qi - Pt	0.003 ± 0.006	− 0.034 ± 0.022	0.037 ± 0.026	1.407	0.159
	Qi - Jt	0.003 ± 0.006	− 0.025 ± 0.004	0.028 ± 0.008	3.517	**< 0.001**

The results include t-statistic (*t-stat*), and *p-value* for each comparison between species. Significant differences (*p*-val. < 0.10, in bold) highlight where inter-specific competition substantially differed in its impact into TWD between two species

Residual degrees of freedom = 255

patches. *P. pinaster* occupies the same strata as *P. pinea*. As a shallow-rooted understory species, *J. thurifera* may exploit topsoil moisture retained under *P. pinea* canopies, where shading reduces evaporation (Camarero et al. 2021; Pardos et al. 2021b). Additionally, the earlier growth onset of *J. thurifera* may be linked to higher temperature under *P. pinea* canopies, which triggers cambium activity earlier. Interestingly, cambial reactivation of *Juniperus przewalskii* was driven mainly by temperature, water availability in spring being a secondary factor (Zeng et al. 2020; Zhang et al. 2021). Accordingly, *Q. ilex* winter's photoinhibition state was abolished earlier in the understory, due to higher air temperature there (Valladares et al. 2008; Marañón et al. 2009).

In *P. pinaster*, both delayed spring onset and earlier summer cessation in mixtures likely result from intensified

water competition with *P. pinea*. Both are overstory, light-demanding, isohydric species with similar physiological thresholds. Importantly, *P. pinea* is less strictly isohydric (Férriz et al. 2021; Aranda et al. 2024), which allows it to maintain gas exchange longer under drought, potentially depleting shared soil reserves. Therefore, mixed stands may delay rehydration of *P. pinaster* cambium and limit its ability to sustain growth into summer (Vieira et al. 2014, 2015; Lempereur et al. 2015). However, this pattern should not be attributed solely to competition, as it has been observed that *P. pinaster* reaches its peak radial increment near the vernal equinox, independent of soil moisture conditions (Vieira et al. 2020).

Q. ilex typically resumes growth after winter even one month later than *Pinus spp.* (Campelo et al. 2021), and this reactivation was further delayed in mixtures (Table 2), probably by water pre-emption from the already competing pines. In wet conditions, *Q. ilex* uses the same water pool as *Pinus spp.*, and shifts to deeper water sources during drought (del Castillo et al. 2016). This may explain its shortened summer cessation period in mixtures, effectively extending *Q. ilex'* growth season (Aldea et al. 2017) (Tables 2 and 3). Moreover, *Q. ilex* can capitalize on early-summer moisture, by maintained photosynthesis under water potentials lower than other species (Mayoral et al. 2015). Yet, this activity could intensify competition in autumn, particularly with isohydric species that remain inactive during dry spells (Sperlich et al. 2019; Campelo et al. 2021). *Q. ilex* may as well facilitate *P. pinea* during summer, which also exhibited a reduced summer cessation period in 2023 in mixtures (Tables 1 and 3; Fig. 5). This facilitation may involve *Q. ilex* extracting deeper soil moisture that *P. pinea* could later exploit, though only when drought conditions are not too prolonged or severe (del Castillo et al. 2016; Zalloni et al. 2019; Muñoz-Gálvez et al. 2021). Additionally, when *P. pinea* grows in mixture with *P. pinaster*, it may benefit from greater water availability during drought periods, as *P. pinaster* tends to reduce transpiration earlier.

Species-specific growth rate differences and their facultative bimodality

Species differed markedly in their daily growth rates (Tables 4 and 5; Fig. 6). *P. pinea* showed the highest rates, followed by *P. pinaster*, while *J. thurifera* and *Q. ilex* remained consistently lower. These differences reflect contrasting ecological strategies: pines are fast-growing, light-demanding pioneers (de-Dios-García et al. 2018; Aldea et al. 2018) whereas *Q. ilex* and *J. thurifera* follow more conservative trajectories. *Pinus spp.* can photosynthesize during mild winters, accumulating carbohydrates outside the main growth period (Eggemeyer et al. 2008; Lebourgeois et al. 2009), which enables rapid early-season increments. Interestingly, that is in contrast to the conservative growth strategy followed by *Pinus sylvestris* from temperate climate, where its growth rates were lower than i.e. in firs (Cuny et al. 2012) or beech (Larysch et al. 2021).

Autumn reactivation occurred consistently across stand types, likely due to spring-like temperatures and post summer rainfall sufficient to restore stem water potentials and hence, cambial activity (Baquedano and Castillo 2007) (Fig. 1, Table S2). Hence, a clear bimodal growth pattern was produced – also reported in other Mediterranean sites (Aldea et al. 2018). Nevertheless, autumnal growth rate was not consistent across years. In *P. pinaster* autumn growth was minimal in the drier 2022 but resumed in 2023, confirming its reliance on sufficient autumn moisture for cambial reactivation (Vieira et al. 2019, 2020). In contrast, *Q. ilex* displayed minimal autumn growth in both years, suggesting limited recovery from summer photoinhibition (Campelo et al. 2018, 2021) and aligning with its characterization as weakly bimodal (Tumajer et al. 2022). Notably, even a wet autumn did not enhance *Q. ilex* minimal growth if spring had been too dry (2023 case; Table S2), contradicting earlier suggestions of this species seasonal compensation (Martín et al. 2014). Our results highlight that both adequate moisture and temperature are needed to trigger second growth phase (Tumajer et al. 2021).

Interspecific interactions enhance the growth dynamics

Our analysis integrated two complementary measures of competition that capture both the intensity and the composition of neighbourhood interactions. The Hegyi competition index (HGCI; Hegyi 1974) quantifies the total competitive pressure acting on an individual tree by combining the size and distance of all neighbouring stems. In contrast, the interspecific competition share (CI.inter) expresses the proportion of this total pressure exerted by heterospecific neighbours. Hence, HGCI describes the overall strength of competition, whereas CI.inter reveals its species identity component. Similar approaches have proven effective in semi-arid forests for disentangling crowding from compositional effects (Contreras et al. 2011; Forrester and Bauhus 2016; Pretzsch 2022). Interpreting both variables jointly allows us to distinguish whether growth reductions result mainly from high neighbourhood density or from interactions among species with contrasting resource-use strategies (Grossiord 2020).

Across species, the two indices frequently showed opposite effects on growth. For example, *J. thurifera* displayed a decline in spring basal-area increment (ΔCBA) with increasing HGCI (Fig. S5) but an enhancement under higher

CI.inter (Table 4; Fig. 6 and S5). This pattern implies that while overall crowding constrained growth, the presence of heterospecifics mitigated these negative effects through facilitation or niche complementarity (Forrester 2014; Grossiord 2020). In our stands, *J. thurifera* typically grows beneath *Pinus pinea* canopies; the pine overstory likely reduces evaporative demand and temperature extremes (Camarero et al. 2021; Pardos et al. 2021b) while leaving shallow soil moisture available to the juniper because of contrasting rooting depth (del Castillo et al. 2016), which the latter can use more intensively (Breshears et al. 1997). Moreover, the early growth onset detected only in mixed stands.

Figure 5 allows the species to start to photosynthesize earlier, and to use for longer water reserves stored during winter. Finally, the anisohydric strategy permits *J. thurifera* to photosynthesize under higher water stress than *P. pinea* (Mayoral et al. 2016; Aranda et al. 2024). Such spatio-temporal segregation of water uptake has been documented as a key mechanism enabling coexistence and growth enhancement in mixed Mediterranean forests (de-Dios-García et al. 2018; Zalloni et al. 2019).

For *P. pinea* and *P. pinaster*, both isohydric and light-demanding species (Mayoral et al. 2016; Aranda et al. 2024), spring growth increased not only with CI.inter (Table 4; Fig. 6) but even under higher HGCI (Fig. S5), particularly in the dry year 2023. This apparently counter-intuitive response suggests competition reduction under climatic stress, consistent with the stress-gradient hypothesis (Forrester 2014; Forrester and Bauhus 2016). As discussed above (Sect. 4.1), functional trait differences – such as earlier growth onset in *Pinus spp.* compared to *Q. ilex* and shallow rooting in *J. thurifera* – enable partitioning of water use in mixed stands. Hence, we hypothesize that during the drier 2023 spring both *Pinus* profited from *Q. ilex* early season inactivity, and *P. pinea* additionally from differing root stratification with *J. thurifera*. Still, lack of vertical niche differentiation between *P. pinea* and *P. pinaster* shifts the competition primarily to water resources (Férriz et al. 2021; Askarieh et al. 2024), which *P. pinaster* loses with more flexible *P. pinea*, ultimately risking carbon starvation (Ledo et al. 2014; Perdiguero et al. 2015; Calama et al. 2023). Accordingly,

P. pinaster respiration (hence, growth) becomes much lower at air temperature above 15 °C, comparing to *P. pinea* (Arriga et al. 2025). Once active, *Q. ilex* can respond synchronously with *Pinus spp.* (*P. pinea* and *P. pinaster*) to temperature and precipitation, restoring competition for the same spatio-temporal niche (Sánchez-Costa et al. 2015b; Aldea et al. 2018; Campelo et al. 2021). In the wetter 2024 season, these effects vanished, reinforcing that facilitative interactions are context-dependent and most pronounced under harsh conditions (Grossiord 2020; Haberstroh and Werner 2022).

Q. ilex shifted from benefitting slightly from facilitation in dry year of 2023 to experiencing growth suppression by CI.inter in the wetter 2024 season (Table 4; Fig. 6). Stem water potential of *Pinus halepensis* and *Q. ilex* has shown to vary with previous month precipitation, pointing to deeper soil as a source of water for both species (Baquedano and Castillo 2007). Probably, during the dry year *Pinus spp.* reduced its competitive effect on *Q. ilex* by diminished water uptake triggered by their isohydric strategy (Zalloni et al. 2019). Moreover, even if active, *Pinus spp.* might shift from deeper to shallow water uptake in dry periods, while *Q. ilex* could increase its reliance on deeper layers (Barbeta et al. 2015; Comas et al. 2015; del Castillo et al. 2016), the effect being stronger at higher *Pinus spp.* presence (del Castillo et al. 2016). These seasonal shifts suggest that competitive and facilitative interactions may evolve throughout the growing season, depending on species physiology and climatic conditions. Very interestingly, *Q. ilex* benefitted consistently across years from HGCI in spring, the effect vanishing in autumn (Fig. S5-S6). This points out to positive influence of conspecifics on *Q. ilex* growth. A plausible, yet hypothetical explanation is that as *Q. ilex* trees in our stand are resprouters, they form dense single-species patches, within which many trees may use the same well-developed rooting system, allowing them to capture water more efficiently. Heterospecifics presence equals to "broken" patches, with less hydraulic efficiency, moreover – adds competition for water, especially from both *Pinus spp.* within the same spatial niche (Baquedano and Castillo 2007). Additionally, *Q. ilex* was found to photosynthesize with maximal efficiency at direct sunlight in spring (Valladares et al. 2008), hence shading by taller *Pinus spp.* might be decreasing its carbon uptake.

Overall, the joint interpretation of HGCI and CI.inter indicates that species identity and functional complementarity (Pardos et al. 2021a), rather than competition intensity alone, govern intra-annual growth responses. High total competition (HGCI) generally suppresses growth, yet when a substantial part of that pressure arises from heterospecifics (high CI.inter), growth can recover or even increase – demonstrating that mixed stands convert structural crowding into physiological complementarity (de-Dios-García et al. 2015; Calama et al. 2019; del Río et al. 2021). This synthesis supports the view that facilitation and competition reduction coexist within Mediterranean mixtures, with their balance shifting across seasons according to water limitation, canopy structure, and species-specific hydraulic strategies (Vieira et al. 2020; Camarero et al. 2021; Pretzsch 2022).

Summer growth depression is alleviated by interspecific interactions

Tree water deficit (TWD) was substantially higher in 2022 across all species – a year marked by low winter and early spring precipitation (Figs. 1 and 6; Table 6 and S2). This underscores the importance of winter – spring water balance not only for supporting spring growth (Aldea et al. 2017; Camarero et al. 2021), but also for sustaining stem hydration well into the summer. In 2023, higher winter rainfall replenished groundwater, reducing TWD across all species, regardless of stand composition (Table 6; Fig. 7), in line with the stress-gradient hypothesis (Forrester 2014). Interestingly, overall competition (HGCI) model term was not significant while explaining TWD suffered by trees, in contrast to interspecific competition term (CI.inter; Table S7). That would indicate the functional traits of neighbours are more important in shaping water availability of a tree rather than the number of its neighbours solely (Rog et al. 2021; Demir et al. 2024). Additionally, mixed stands composed by *Juniperus* – *Pinus* – *Quercus* were shown to have higher soil water holding capacity, as they contributed to lower soil water repellence and higher content of organic matter (Zema et al. 2021).

Q. ilex exhibited the highest TWD, especially in 2022 – despite spring rainfall nearly doubling that of 2023 (Fig. 1; Table S2) – suggesting that total rainfall alone is not sufficient to buffer drought. Its anisohydric behaviour and relatively large leaf area enables gas exchange under high temperatures, but also increase transpirational demand and diurnal stem shrinkage (Aldea et al. 2018; Aranda et al. 2024). *Q. ilex* TWD increased with higher CI.inter (Table 6; Fig. 7), likely because *P. pinea*, with its large sapwood and less dense wood, efficiently stores and uses spring water, reducing availability for *Q. ilex* during its summer-active phase (Zalloni et al. 2018; Lambers and Oliveira 2019; Camarero et al. 2021). Although *Q. ilex* may improve water use efficiency in mixtures with *P. pinea* (Zalloni et al. 2019), its carbon gain might be allocated to roots or reserves rather than stem growth (Montagnoli et al. 2019).

In contrast, *J. thurifera* experienced lower TWD in more heterospecific neighbourhood (Table 6; Fig. 7). Following examples from Mediterranean climate, it has been observed that *Juniperus phoenicea* stem water potential was negatively correlated with summer ambient temperature (Baquedano and Castillo 2007). Accordingly, *Quercus calliprinos* showed higher biomass production caused by shading from taller species (*Pinus* between others) present in the mixed stand (Rog et al. 2021). Therefore, it is likely that *J. thurifera* is facilitated by the same mechanism observed for growth: canopy shading by *P. pinea* reduces evaporative demand and improves surface moisture conditions (Marañón et al. 2009; Lozano-Parra et al. 2018). Our results are also consistent with enhanced regeneration and drought tolerance of *J. thurifera* under pine canopies (Pardos et al. 2021b; Pardos and Calama 2022). Although *J. thurifera* is drought-tolerant – due to anisohydry and xylem resistant to cavitation (Camarero et al. 2014; Camarero 2019; Aranda et al. 2024) – it still exhibited higher TWD than *P. pinea*, partly confirming earlier findings (de-Dios-García et al. 2018).

P. pinea and *P. pinaster* both showed reduced TWD under CI.inter, but only in 2022. As early starters (Fig. 5), they may have filled stem reservoirs during wet spring conditions (Lebourgeois et al. 2009) (Table S2). In 2023, low spring rainfall delayed water availability until June (Fig. 1), by which time the anisohydric species – *Q. ilex* and *J. thurifera* – had resumed transpiration, increasing water demand. This may have neutralized any facilitative effects. For isohydric *Pinus spp.*, the identity of neighbours in summer appears to play a limited role. Their drought responses – early stomatal closure and reliance on stored stem water – are largely determined during spring. Thus, facilitation or competition likely takes place before summer, during the critical window of spring water accumulation. Finally, deeper TWD suffered by *P. pinaster* at higher CI.inter confirms that in dry conditions it loses competition for water with its main competitor in mixed stands, more drought-tolerant *P. pinea* (Arriga et al. 2025).

Final considerations

Understanding the interaction between xylem phenology and interspecific competition is crucial, as the timing of cambial activity controls both annual growth and carbon sequestration – two key processes under climate change (Lempereur et al. 2015, 2017). While warming may extend the growing season by advancing spring onset, it also intensifies drought, potentially offsetting these gains – a phenomenon known as the climate hiatus effect (Tumajer et al. 2021). Our results show that species mixing can enhance spring growth and reduce summer water deficits, especially in water-limited sites. This suggests that combining species with contrasting hydraulic traits may help reduce mortality risks in Mediterranean forests facing increasing aridity (Rog et al. 2021; Peñuelas and Sardans 2021; Aranda et al. 2024). While not assessed in this study, site-specific conditions – like soil water holding capacity or local climate – may influence when facilitation turns into competition (Sánchez-Costa et al. 2015a; Zalloni et al. 2019; Moreno-Fernández et al. 2021).

To our knowledge, this is among the first studies to link phenological shifts in cambial activity to interspecific competition across multiple growth phases. However, band dendrometers may blur the distinction between stem hydration

and true growth – particularly in autumn (Zweifel et al. 2016; Vieira et al. 2020). Our mechanistic interpretations are based on literature, not direct physiological measurements. Finally, the temporal scope of our dataset is limited to one full growing year, so results should be interpreted cautiously. Still, this study provides new insight into how interspecific interactions shape intra-annual tree growth under climatic stress.

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Data availability The data used for this study is available under the following ZENODO link: 10.5281/zenodo.15808868.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval Not applicable.

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Consent for publication Not applicable.

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