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Inter- and intra-annual ring width and $\delta^{13}C$ responses to drought in tree species of a laurel cloud forest (Tenerife, Canary Islands)

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ABSTRACT

Subtropical cloud forests grow under particular climate conditions characterized by narrow thermal ranges, high relative humidity and low radiation levels. These diverse ecosystems include many endemisms and are threatened by climate and anthropogenic land-use pressures, particularly in islands. This is the case of some laurel cloud forests found in Macaronesian archipelagos such as the Canary Islands. To assess growth response to climate variability, we studied tree-ring series in three evergreen species (the Macaronesain endemisms *Laurus novocanariensis* and *Morella faya,* and the Mediterranean *Prunus lusitanica*) co-occurring in a laurel cloud forest (Anaga) located in Tenerife, Canary Islands, Spain. The intra-annual wood $\delta^{13}C$ was also measured in the rings formed from 2011 to 2013 in two of these species (*L. novocanariensis*, *P. lusitanica*) to determine how they responded to the severe 2012 drought. Sampled trees were young (age ranged from 33 to 54 years). *L. novocanariensis* and *P. lusitanica* presented the highest (2.44 mm) and lowest (1.84 mm) mean growth rates, respectively. Wet, cool and foggy conditions in the prior winter enhanced the growth of *L. novocanariensis* and *M. faya*, whereas *P. lusitanica* was less responsive to climate variability. The tree-ring $\delta^{13}C$ values were higher in *P. lusitanica* (mean ± SE = −26.10 ± 0.07 ‰) than in *L. novocanariensis* (-26.56 ± 0.08 ‰), and the difference intensified during the dry year of 2012. In *P. lusitanica*, $\delta^{13}C$ values decreased as the number of foggy days increased. These findings demonstrate species-specific differences in growth and $\delta^{13}C$ responsiveness to climate. The study of these proxies at different temporal resolutions highlights how reduced fog input and drought, affecting atmospheric water demand and soil moisture availability, respectively, constrain tree growth in laurel cloud forests.

1. Introduction

Extreme climate events such as hotter droughts are negatively impacting forest productivity, tree growth and vigour worldwide (Babst et al., 2019; Gazol and Camarero, 2022; Hammond et al., 2022). For instance, water-shortage conditions accompanied by elevated temperatures are triggering growth decline, die-off episodes and high mortality rates of major tree species (e.g., *Pinus sylvestris*, *Abies alba*) in the Mediterranean basin (Camarero et al., 2015). A particular case is the Canary Islands, a Macaronesian archipelago where Mediterranean climate conditions with cool winters and warm and dry summers are dominant (del Arco Aguilar et al., 2010). However, we still lack information on the impacts of drought on tree growth and water use at inter- to intra-annual scales in Macaronesian cloud forests.

Macaronesia is a biogeographical region including the main volcanic islands across the North East Atlantic Ocean which harbor a high number of tree species, many of them endemics (Fernández-Palacios et al., 2024). The climatic and topographic complexity of these islands leads to very different forest communities, but some Macaronesian archipelagos are characterized by preserving laurel cloud forests

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("laurisilva" in Spanish). In some Canary Islands such as Tenerife, laurel cloud forests appear in the montane and sub-montane belts (400 −1500 m a.s.l.) on the windward slopes of the islands, where the humid trade winds are intercepted by mountains (del Arco Aguilar et al., 2010; Aboal et al., 2015).

Laurel forests are biogeographical remnants of the thermophilous Tertiary forests which occupied Europe and northern Africa during the Tertiary period (Fernández-Palacios et al., 2011; Nogué et al., 2013). These are unique and diverse communities dominated by thermophilous, evergreen broadleaf trees and characterized by abundant epiphytes and lianas (Betzin et al., 2016; Fernández-Palacios et al., 2017). These forests are also considered topographical refugia (Keith et al., 2020), where the moisture taken by oceanic fronts condenses by canopy interception and falls as horizontal rain leading to a narrow thermal range, foggy conditions, high relative humidity and reduced transpiration (Ritter et al., 2009, 2015, 2019, Regalado and Ritter, 2021). Laurel forests depend on the formation of a cloud belt along the elevation gradient providing high humidity levels (Fernández-Palacios and de Nicolás, 1995). However, these communities are threatened by climate and land-use changes because: (i) heat waves and droughts (e.g., 2005, 2012, 2018) are exacerbating in the Macaronesia, and (ii) laurel forests are located in highly populated and touristic islands (Sperling et al., 2004; Arozena and Panareda, 2013; Cropper and Hanna, 2014). Moreover, climate observations and projections indicate a reduction in soil moisture and warmer night conditions in some Canary Islands for the late 21st century due to elevational shifts of the stratocumulus cloud layer (Martín et al., 2012; Expósito et al., 2015).

Recent studies have shown the importance of assessing how climate variability and drought impact the growth of laurel forests in the Azores (Matos et al., 2019; Pavão et al., 2023a, 2023b) and Canary Islands (García-López et al., 2022, 2025; Rozas et al., 2023). Nevertheless, we need more functional knowledge of how an increase in drought severity impacts tree growth and water-use efficiency in Macaronesian laurel forests. Severe droughts occurring during the last decades, which have negatively impacted the growth of laurel forest tree species (e.g., 1995, 1999, 2008 and 2012) in Tenerife (Canary Islands), provide a unique setting for this purpose (García-López et al., 2022). Moreover, drought severity in the Canary Islands must be assessed considering large-scale circulation patterns such as the North Atlantic Oscillation (NAO), which is negatively correlated with rainfall of this subtropical region (Herrera et al., 2001). Positive (negative) NAO phases, which reflect a strengthening (weakening) of the Azores High, lead to dry-warm (wet-cool) winter conditions over Macaronesia, reducing (increasing) the growth of some tree species in the Canary Islands laurel forests (García-López et al., 2025).

In addition to tree growth, a widely used measure of drought stress is the intrinsic water-use efficiency (iWUE), i.e. the ratio between the photosynthesis and stomatal conductance rates (Farquhar et al., 1982), which is often estimated by analysing the stable carbon isotope composition (δ^{13}C) of annual tree rings (McCarroll and Loader, 2004). Recent advances have allowed measuring high-resolution iWUE through laser-ablation δ^{13}C analyses of tree rings at intra-annual resolution (Rinne-Garmston et al., 2022; Tang et al., 2023). We expand on these developments and apply them to assess the intra-annual responses of trees to drought in terms of iWUE in a laurel forest.

We aimed to (i) quantify growth variability and drought-response in three tree species in the Anaga laurel forest (Tenerife), two Macaronesian endemics (*Laurus novocanariensis* and *Morella faya*) and one Mediterranean species (*Prunus lusitanica*), and (ii) examine intra-annual wood δ^{1} ^{3}C (as a proxy for intrinsic water-use efficiency) in *L. novocanariensis* and *P. lusitanica* over 2011–2013, which includes the severe 2012 drought. Although laurel cloud forests are subjected to low radiation levels and foggy conditions, which reduce the evaporative demand (lower vapour pressure deficit, VPD) during the growing season (Ritter et al., 2009), we hypothesised that hot atmospheric droughts—often linked to elevated radiation levels and sunny conditions—would reduce growth and increase wood δ^{13}C.

2. Material and methods

2.1. Study site and tree species

This study was carried out in a protected laurel forest situated in the Anaga Rural Park (16.2465º W, 28.5368º N, elevation 803−960 m a.s.l.), northeastern Tenerife, Canary Islands, Spain (Fig. 1). Anaga is located on a massif formed by basalt materials from the Miocene reaching a maximum elevation of 1024 m a.s.l. The climate in Anaga has an annual precipitation of about 440 mm and mainly occurs during the humid period from October to April, while a dry period spans from May to September (Fig. S1). The orographic lifting of moist air masses driven by trade winds from the ocean creates frequent fogs which lead to horizontal precipitation of up to 1800–2100 mm within the laurel forest belt (Ritter et al., 2009). In the laurel forests of the Canary Islands, such foggy conditions reduce transpiration and lead to narrow thermal ranges (10.5–20.5 ºC; cf. Regalado and Ritter, 2021). Nevertheless, intercepted fog water, net radiation and evapotranspiration rates in summer greatly vary near the low-elevation limit (700–900 m) of laurel forests (Marzol, 2008).

According to data on the monthly number of foggy days from the Tenerife-Los Rodeos meteorological station (16.332º W, 28.447° N, N, 632 m a.s.l.; period 1966 −2019), which is located at ca. 8 km SW from Anaga study site, July is the month with the highest average number of

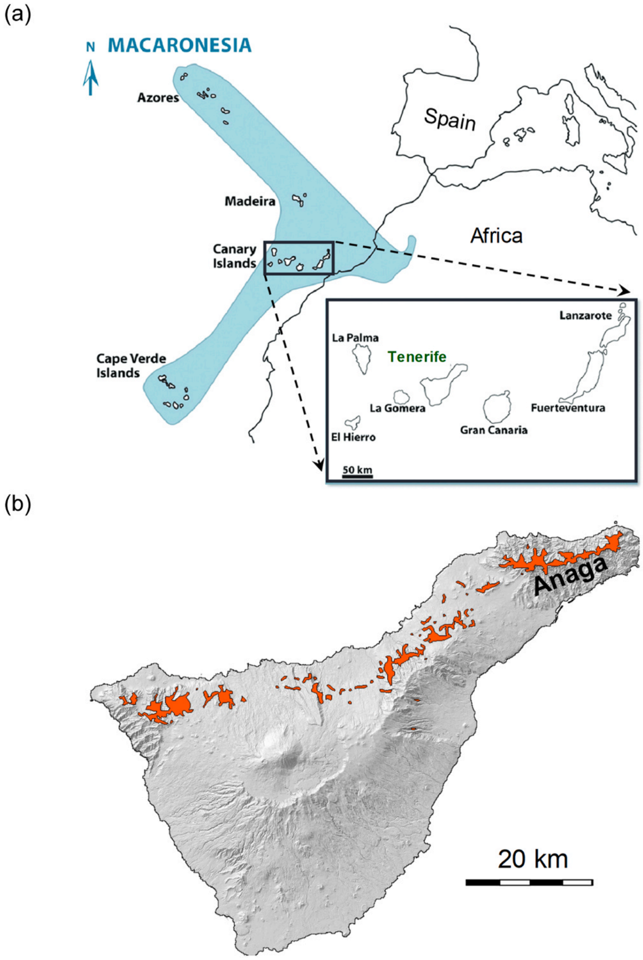

Fig. 1. Maps of the four Macaronesian volcanic archipelagos showing the Canary Islands (a) and the location of Anaga in the Tenerife island, Spain (b). The orange patches show the distribution of *L. novocanariensis* in Tenerife, which corresponds to the distribution of laurel cloud forests.

foggy days (11 days), whereas November is the least foggy month (5 days; Fig. S2). Soils are fertile and of volcanic origin.

The laurel forests of the Canary Islands are subtropical cloud forests with Mediterranean plants (del Arco Aguilar et al., 2010; del Arco Aguilar and Rodríguez Delgado, 2018). They are dominated by *Laurus novocanariensis* Rivas Mart., Lousa, Fern. Prieto, E. Días, J. C. Costa & C. Aguiar (previously *L. azorica* (Seub.) Franco), "laurel" in Spanish, and other tree species of the Lauraceae family (del Arco Aguilar and Rodríguez Delgado, 2018). The study species are evergreen and were selected because they form distinct, datable tree rings (cf. García-López et al., 2022; Rozas et al., 2023). Two of the study species are Macaronesian endemic species, *L. novocanariensis* (Lauraceae) and *Morella faya* (Aiton) Wilbur (Myricaceae), whereas the third species is the Mediterranean *Prunus lusitanica L.*, albeit the study subspecies is Macaronesian (*P. lusitanica* subsp. *hixa* (Willd.) Franco (Rosaceae); hereafter *P. lusitanica*). Other tree and shrub species abundant in Anaga include *Ilex canariensis* Poir and *Ilex perado* Aiton subsp. *platyphylla* (Webb & Berthel.) Tutin (Aquifoliaceae), and *Erica platycodon* (Webb & Berthel.) Rivas-Mart. et al. (Ericaceae).

L. novocanariensis and *P. lusitanica* form large to mid-size leaves, have light to medium wood density (0.54 g cm^{-3}) and show high tolerance to shade, whereas *M. faya* forms medium-size leaves, has dense wood (0.64 g cm^{-3}) and shows low tolerance to shade (Peraza Oramas and López De Roma, 1967; Arévalo and Fernández-Palacios, 2007; Fernández-Palacios et al., 2017; Ganivet et al., 2019). The study species reproduce through suckers and seedlings.

2.2. Climate data and drought indices

Due to the lack of long and homogeneous climate records near the study area, we used 0.1°-gridded daily and monthly climate data (mean maximum and minimum temperatures, total precipitation) corresponding to the E-OBS climate dataset version 28.0e (Cornes et al., 2018). We also obtained daily and monthly data of the number of foggy days as a proxy of cloudiness from the Tenerife-Los Rodeos meteorological station located in the northern Tenerife airport (period 1966−2019). To assess the quality of the gridded climate dataset, we calculated annual precipitation for the E-OBS and Tenerife-Los Rodeos data and found they were positively correlated ($r = 0.5630, p = 0.0097$, period 1998−2017). In addition, the daily and monthly data of cloud fractional cover (%) was also retrieved at a 0.05° resolution (period 1983−2020) from the EUMETSAT database (Stöckli et al., 2024). Finally, the VPD was obtained from the 4-km-gridded Terraclimate dataset (Abatzoglou et al., 2018).

To assess changes in drought severity and duration at regional and local scales we used Standardized Precipitation Evapotranspiration Index (SPEI) monthly and weekly data gridded at 0.1° and 1.1 km^2 resolutions, respectively. The 0.1° SPEI data were calculated from monthly temperature and precipitation obtained from the 0.1° grid, whereas the 1.1 km^2 SPEI data were downloaded at a weekly resolution from the Spanish Drought Monitor website (https://monitordesequia.csic.es/). The 0.1°- and 1.1-km^2 gridded monthly and weekly SPEI data were used to assess inter- and intra-annual growth responses to drought severity, respectively. The SPEI is a multi-scalar drought index calculated on cumulative climate water balances which depend on temperature and precipitation (Vicente-Serrano et al., 2010). Negative and positive SPEI values correspond to dry and wet conditions, respectively. In both cases, we considered SPEI values calculated at several time scales, specifically considering 1-, 3-, 6-, 9- and 12-month long scales. The 12-month SPEI showed a significant negative trend since 1980 indicating ongoing aridification in the study area with severe droughts observed from the 1990s onwards including the 2012 drought (Fig. S3). This drought was characterized by low precipitation in winter 2011–2012 and spring 2012 followed by warm summer conditions and ending with abundant rainfall in early autumn 2012 (Fig. S4). Finally, we obtained monthly NAO indices from the CRU webpage (https://crudata.uea.ac.uk/cru/data/nao/).

2.3. Field sampling

First, we selected mature, apparently healthy trees of big diameters for sampling and located in topographically homogeneous areas usually covered by clouds (Table 1). Second, the location, topographical conditions (elevation, slope), diameter at 1.3 m (diameter at breast height −dbh) and height of all sampled trees were measured using a GPS (resolution ± 5 m), tapes and a rangefinder (Nikon Forestry Pro II). All sampled *L. novocanariensis* and *M. faya* individuals were dominant, whereas 72 % of sampled individuals were dominant in the case of *P. lusitanica*.

We sampled from 24 to 25 individuals per species. We took two cores from each tree at 1.3 m from opposite sides of the main stem and perpendicular to the maximum slope. This was done using a 5-mm wide, 40-cm long Pressler increment borer.

2.4. Tree-ring width measurements

Wood samples were processed using dendrochronological techniques (Fritts, 1976). Wood cores were air-dried, glued onto wooden supports and transversally cut using a sledge microtome to detect and distinguish tree-ring boundaries (Gärtner et al., 2015). Then, cores were visually cross-dated under the binocular scope and scanned at 1200 dpi (Epson Expression 10000XL). The width of the annual rings (TRW) was measured along the two radii of each tree with a 0.01 mm resolution using the CDendro-CooRecorder software (Maxwell and Larsson, 2021). The visual cross-dating was checked using the COFECHA software, which was used to calculate 20-year moving correlations between individual series and the mean series of each species (Holmes, 1983). Despite a previous study could not cross-date *M. faya* wood samples because of few distinct ring boundaries (García-López et al., 2022), we were able to detect tree-ring boundaries after careful inspection of cores and to develop a robust chronology in this challenging species. The COFECHA output was used to calculate the mean correlation of each series with the mean species series or master chronology (r_{xy}). We also obtained other statistics to characterize the tree-ring width mean series including the first-order autocorrelation (AR1), the mean sensitivity or relative difference between consecutive ring-width indices (MSx), and the Expressed Population Signal (EPS) which measures how well replicated is a chronology (Wigley et al., 1984; Briffa and Jones, 1990). Lastly, tree age at 1.3 m was estimated by counting the number of rings along the oldest core of each tree whenever it reached the pith or presented curved, innermost rings.

The individual TRW series were converted into indexed TRW series through standardization and detrending (Fritts, 1976). This was done to remove size- and age-related trends in ring-width data and to keep high-frequency variability. We fitted negative exponential functions to individual ring-width series and obtained ring-width indices by dividing observed values by fitted values. Then, first-order autoregressive models were fitted to remove the autocorrelation of the indices. The resulting pre-whitened index series were averaged using a bi-weight robust mean to obtain residual series or chronologies for each species (Fritts, 1976). These procedures were done using the *dplR* package (Bunn, 2008, 2010; Bunn et al., 2024) in the R statistical software (R Development Core Team.,2024).

2.5. Intra-annual wood $\delta^{13}C$ analyses

Intra-seasonal δ^{13}C was analysed for each tree-ring sample using LA-IRMS at the Stable Isotope Laboratory of Luke (SILL) at Natural Resources Institute Finland (Luke, Helsinki, Finland). Shortly, ablated dust particles were carried by helium flow through a combustion device, the resulting CO_2 was collected with liquid nitrogen, and subsequently, the CO_2 was released upon heating to room temperature and purified in a

Table 1
Topographical and size statistics of sampled tree species. Dbh is the diameter at breast height. Values are means ± SE. Different letters indicate significant ($p < 0.05$) differences between species according to Mann-Whitney tests.

Species	No. sampled trees	Elevation (m a.s.l.)	Slope (°)	dbh (cm)	Height (m)
Laurus novocanariensis	24	929 ± 9b	29.6 ± 2.7b	26.30 ± 1.24b	9.5 ± 0.5c
Prunus lusitanica	25	893 ± 11a	27.8 ± 2.2b	19.49 ± 1.12a	8.4 ± 0.4b
Morella faya	25	916 ± 9b	22.2 ± 3.3a	27.52 ± 1.37b	7.5 ± 0.3a

GC-column before its introduction to IRMS. A series of tangential laser tracks were sampled along the same radial direction on tree rings at an interval of 40–60 μm. Each sample was run against an in-house CO_2 reference gas. The raw $\delta^{13}C$ values were calibrated against USGS-55 (Mexican ziricote tree powder, −27.13 ‰) and two in-house references (yucca plant powder, −15.46 ‰ and VWR cellulose pads, −26.5 ‰), which were measured concurrently with the tree-ring samples. In addition, IAEA-C3 cellulose paper was measured multiple times during each run for quality control of the measured $\delta^{13}C$ values. The LA-IRMS measured $\delta^{13}C$ value for IAEA-C3 was −24.82 ± 0.09 ‰ (n = 49) in line with the reported value of −24.91 ± 0.49 ‰. More details on these procedures can be found in Tang et al. (2023).

In the study species, ten laser tracks per tree ring were ablated for $\delta^{13}C$ analysis considering the rings formed in years 2011 (pre-drought year), 2012 (drought year) and 2013 (post-drought year).

2.6. Statistical analyses

We used Mann-Whitney tests to compare the means of several variables (topography, tree size, tree-ring width series) between species. We selected this non-parametric test because some of them (e.g., TRW) did not follow normal distribution according to Shapiro-Wilk tests.

Given that we do not know the exact timing when the tree-ring sections used for measuring intra-annual wood $\delta^{13}C$ in *L. novocanariensis* and *P. lusitanica* were formed, we calculated Pearson correlations between those $\delta^{13}C$ values and climate variables averaged over 10-day periods from March to October, i.e. the assumed growing season based on previous data and climate-growth analyses (Jiménez et al., 1996, 1999, 2000; García-López et al., 2022). This included 10-day averages (maximum and minimum temperatures, VPD, cloudiness, 6-month SPEI) and 10-day sums (precipitation, number of foggy days). Because these time series may contain temporal autocorrelation, we calculated corrected significance levels (p_{corr}) following Mudelsee (2003). In addition, to reduce the influence of strong seasonal trends in some variables (e.g., temperature), we also calculated correlations using differenced values, obtained by subtracting the current 10-day value from the previous 10-day period. These differences corresponded to climate rates calculated between consecutive 10-day periods.

To quantify climate-growth correlations in the three studied species we calculated Pearson correlations between the residual series of TRW indices and monthly series of climate variables (temperature, precipitation, VPD and number of foggy days). This was done from previous October to current September and also considering the hydrological year following previous studies (García-López et al., 2022). Climate variables were either averaged (temperature, VPD) or summed (precipitation, number of foggy days) for the hydrological year, i.e. from prior October to current September.

In the case of the SPEI, correlations were calculated for 1- (SPEI 1), 3- (SPEI 3), 6- (SPEI 6), and 12-month (SPEI 12) monthly values considering the same climate window in the three studied species. In the case of weekly SPEI values, correlations were obtained for SPEI for 1-, 3-, 6-, and 9-month long SPEIs along the year. Correlations with climate variables or the SPEI were calculated for the best-replicated period (1977 −2020) using the *dcc* function of the *treeclim* R package (Zang and Biondi, 2015).

3. Results

3.1. Tree characteristics, growth data, and chronology statistics

On average, *P. lusitanica* trees were found at lower elevations and showed smaller diameters at 1.3 m than the other two species (Table 1). *L. novocanariesis* trees were located at the steepest sites and showed the tallest stems, whereas *M. faya* trees were the shortest ones.

Regarding tree-ring width data, sampled trees were young (age ranged 33 −54 years) corresponding to secondary forests (Table 2, Fig. 2). The highest and lowest growth rates corresponded to *L. novocanariesis* (2.44 mm) and *P. lusitanica* (1.84 mm), respectively.

Regarding chronology statistics, the first-order autocorrelation did not vary among species showing a global average of 0.39, but the mean sensitivity was the highest in the case of *P. lusitanica* (0.53). Finally, the highest correlations with the master series and EPS values corresponded to *L. novocanariesis* and *M. faya*, confirming we achieved a well-replicated series in these two species for the period 1977−2020. In contrast, *P. lusitanica* showed the lowest correlation and EPS values.

Years when the three species presented abrupt growth reductions corresponded to severe droughts such as 1995 and 2012 (Figs. 2 and S3). However, in other dry years, (e.g. 1999, 2005, 2009 and 2018), some species showed growth loss (e.g., *P. lusitanica* in 1999, 2009, and 2018; *L. novocanariensis* in 2005), whereas others did not (e.g., *L. novocanariensis* in 1999, and 2018; *M. faya* in 2005). Consequently, correlations among the species' ring-width data and indexed series were not significant (Table S1), suggesting species-specific growth responses to climate variability.

3.2. Intra-annual tree-ring $\delta^{13}C$: links with climate and drought

The wood $\delta^{13}C$ values measured in the period 2011 −2013 were significantly higher (less negative) in *P. lusitanica* (mean ± SE = −26.10 ± 0.07 ‰) than in *L. novocanariensis* (-26.56 ± 0.08 ‰; t = -4.19, p = 0.0004; Fig. 3). Considering different years, *P. lusitanica* showed higher values than *L. novocanariensis*, but the differences between species were amplified in the driest year, 2012 (2011, t = -2.29, p = 0.034; 2012, t = -3.31, p = 0.004; 2013, t = -2.19, p = 0.045). The tree-ring $\delta^{13}C$ values peaked in the earlywood to latewood transition (3rd to 6th laser tracks). The intra-annual $\delta^{13}C$ series of the two tree species were highly correlated (r = 0.632, p < 0.001).

Tree-ring $\delta^{13}C$ increased in both species with increasing temperature and VPD (Table 3). In contrast, cloudy and foggy conditions were associated with lower $\delta^{13}C$ values. Neither precipitation nor SPEI showed significant correlations with $\delta^{13}C$. However, climate−$\delta^{13}C$ correlations changed when considering climate rates calculated between consecutive periods. In this case, cloud cover in the case of *L. novocanariensis* and the number of foggy days and minimum temperatures in the case of *P. lusitanica* were negatively associated with tree-ring $\delta^{13}C$. In addition, minimum temperatures and $\delta^{13}C$ of *P. lusitanica* showed a positive correlation.

3.3. Growth responses to climate variability, drought and teleconnection indices

The TRW indices were positively correlated with prior autumn-winter precipitation in *L. novocanariensis* and *M. faya* (Fig. 4). A

Table 2

Tree-ring width statistics of sampled tree species calculated for the best-replicated period 1977–2020. Abbreviations: AR1, first-order autocorrelation; MSx, mean sensitivity; r_{xy}, mean correlation with master series; EPS, Expressed Population Signal. Values are means ± SD. Different letters indicate significant ($p < 0.05$) differences between species according to Mann-Whitney tests.

Species	No. trees	Timespan	Age (years)	Ring width (mm)	AR1	MSx	r_{xy}	EPS
L. novocanariensis	22	1959 –2020	46 ± 9a	2.44 ± 0.22b	0.40 ± 0.23a	0.39 ± 0.05a	0.47 ± 0.08b	0.90
P. lusitanica	18	1964 –2020	42 ± 9a	1.84 ± 0.08a	0.38 ± 0.20a	0.53 ± 0.07b	0.43 ± 0.08a	0.80
M. faya	16	1963 –2020	44 ± 9a	2.04 ± 0.15ab	0.41 ± 0.20a	0.36 ± 0.05a	0.46 ± 0.09b	0.86

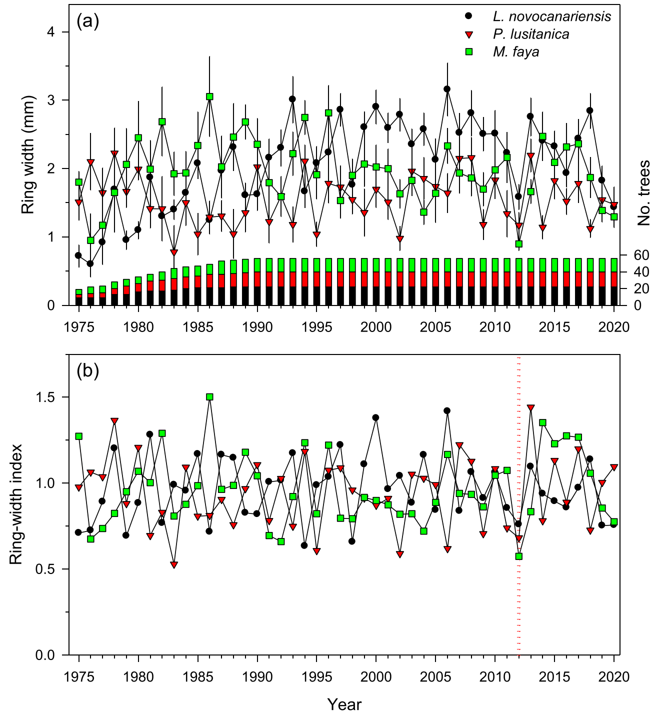

Fig. 2. Mean series of (a) ring-width data and (b) ring-width indices of the three study species. In plot (a) values are means ± SE. In plot (b) the 2012 drought is highlighted with a dotted vertical line. The bars in plot (a) show the annual number of sampled trees (right y-axis).

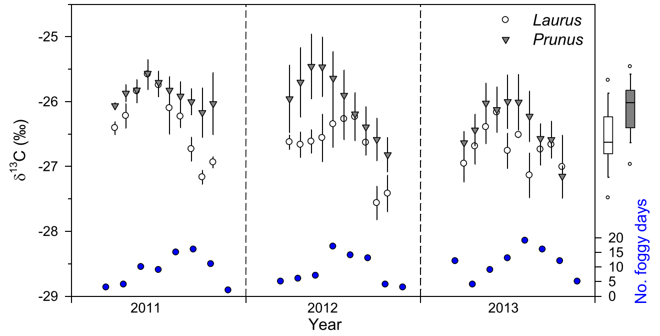

Fig. 3. Intra-annual wood δ^{13}C values for the period 2011 –2013 for *Laurus novocanariensis* (white circles and boxplot) and *Prunus lusitanica* (grey triangles and boxplot). Values are means ± SE and 2012 was the drought year. The blue circles show the 10-day number of foggy days from March to October. Boxplots show the distribution of δ^{13}C values for the two species.

similar association was observed with the number of foggy days in the three species, being particularly strong in *M. faya*. High temperatures and VPD in summer were negatively correlated with *L. novocanariensis* growth indices. Wet conditions during the hydrological year enhanced growth of *L. novocanariensis* and *M. faya*, whereas *P. lusitanica* showed a low responsiveness to climate variability.

The correlations between TRW indices and weekly SPEI values highlighted the highest responsiveness of *M. faya* to dry conditions from February to May for 3- to 6-month-long droughts (Fig. 5). In contrast, *L. novocanariensis* growth was constrained by 6-month-long summer droughts. Lastly, *P. lusitanica* only responded to 3- to 9-month-long droughts of the prior winter.

The correlations between TRW indices and monthly SPEI values showed again the highest and lowest responsiveness to drought in *M. faya* and *P. lusitanica*, respectively (Fig. S5). The highest correlations with SPEI were found for 6- and 3-month-long SPEI values of May and March in *L. novocanariensis* ($r = 0.434$, $p = 0.003$) and *M. faya* ($r = 0.608$, $p = 0.00001$), in that order.

Regarding the NAO, we only found a significant and positive relationship between *L. novocanariensis* growth and April NAO indices ($r = 0.457$, $p = 0.002$), and between *M. faya* growth and May NAO indices ($r = 0.317$, $p = 0.036$).

4. Discussion

Elevated evaporative water demand, i.e. high VPD, and high radiation levels characterized some of the droughts in our study region during the period 1977–2020 (e.g., 2012). These dry-warm and sunny conditions reduced growth in the species sampled in the Anaga laurel cloud forest. This finding aligns with previous research in subtropical and tropical forests with other Lauraceae tree species showing how tree growth was reduced by drought stress (Morales et al., 2004; Mendivelso et al., 2014; López et al., 2019; Zuidema et al., 2022). This negative impact of water shortage on wood production was also reported for other Macaronesian laurel forests (García-López et al., 2022, 2025).

Dry and sunny winter conditions reduced growth of *M. faya* and *L. novocanariensis* (Fig. 4), whereas *P. lusitanica* showed a reduced responsiveness to climate variability (Fig. 4) and a low coherence between individuals (Table 2). Such high growth variability among individuals of the same population is common in tropical forests where microtopography, soil conditions, disturbances and competition for light also impact wood production (Brienen and Zuidema, 2005; Espinosa et al., 2018). In addition, the sampled trees were young and established after massive rural migration of Canary people to cities, when traditional land uses shifted to modern touristic activities (Rozas et al., 2023). Young trees may be less responsive to climate than older conspecifics (Szeicz and MacDonald, 1994).

The growth of *M. faya*, the most sensitive species, positively responded to foggy conditions in winter (Fig. 4), a response also observed in the other species. *M. faya* shows a weak control of the transpiration rate and a profligate water use (Sánchez-Díaz et al., 2008; Regalado and Ritter, 2021). Furthermore, the stomatal response to VPD exhibited greater sensitivity in *M. faya* compared to *L. novocanariensis* (González-Rodríguez et al., 2002). We used *M. faya* to illustrate how growth of laurel forest tree species can be differently impacted by soil drought (low precipitation and SPEI) and atmospheric drought (high VPD and radiation levels, few foggy days). For instance, years of poor growth such as 2012 or 1995 corresponded to dry soil and atmospheric conditions, respectively (Fig. 6). Accordingly, low precipitation and warm-sunny conditions could synergistic and negatively impact tree growth of these species leading to compound climate events

Table 3

Pearson correlations (*r*) and corrected significance levels (p_{corr}) calculated between intra-annual wood $\delta^{13}C$ data of *L. novocanariensis* and *P. lusitanica* and climate variables (TMx, mean maximum temperature; TMn, mean minimum temperature; VPD, Vapour pressure deficit; Prec, summed precipitation; Cloud, cloudiness; SPEI, 6-month drought index). Correlations were calculated for raw data or considering differences between consecutive periods. Climate variables correspond to 10-day averages (TMx, TMn, VPD, cloudiness, SPEI) or sums (precipitation, No. foggy days) computed from March to October. Significant ($p < 0.05$) correlations are indicated with bold characters.

Variable	Raw data				Rates between periods			
	L. novocanariensis		*P. lusitanica*		*L. novocanariensis*		*P. lusitanica*	
	r	p_{corr}	*r*	p_{corr}	*r*	p_{corr}	*r*	p_{corr}
TMx	**0.443**	0.014	**0.442**	0.015	0.142	0.481	0.246	0.217
TMn	**0.421**	0.021	**0.469**	0.010	0.009	0.965	**0.382**	0.049
VPD	**0.443**	0.014	**0.445**	0.014	0.107	0.594	0.291	0.142
Cloud	**−0.560**	0.001	**−0.497**	0.001	**−0.383**	0.049	−0.019	0.925
No. foggy days	−0.285	0.211	**−0.474**	0.030	0.367	0.085	**−0.724**	0.002
Prec	−0.248	0.187	−0.141	0.459	−0.304	0.123	−0.271	0.172
SPEI	−0.240	0.201	−0.056	0.768	−0.250	0.209	−0.345	0.078

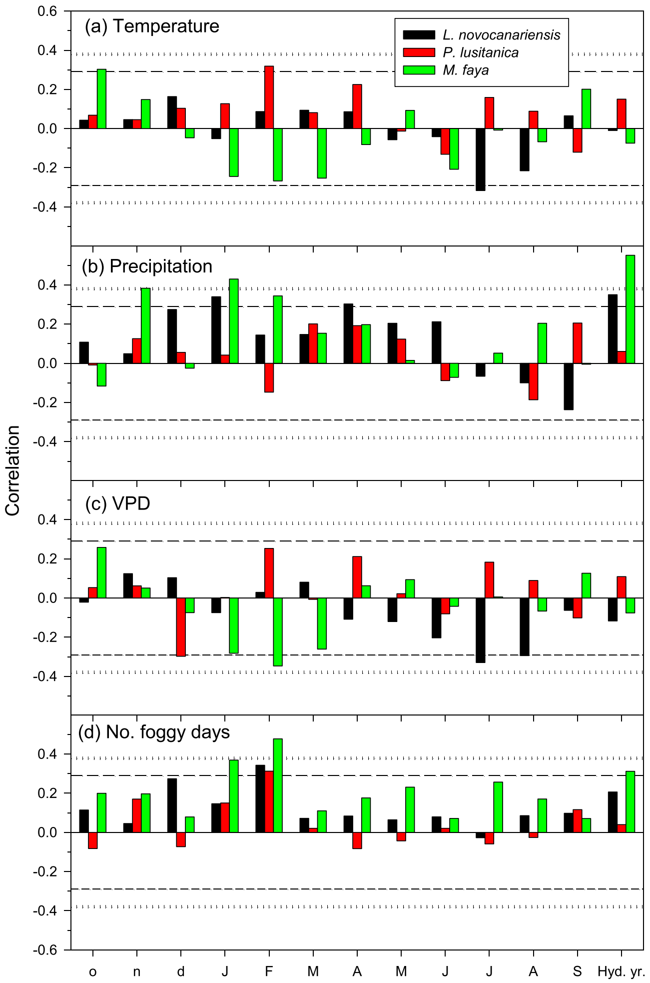

Fig. 4. Pearson correlations calculated between the species series of ring-width indices and monthly climate variables (a, mean temperature; b, total precipitation; c, VPD, vapour pressure deficit; d, number of foggy days). Correlations were calculated from the prior (months abbreviated by lowercase letters) to the current (months abbreviated by uppercase letters) years. The last bars show the correlations for the hydrological year (Hyd. yr.). The horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively.

characterized by dry soil conditions and elevated atmospheric demand (Gazol and Camarero, 2022). Interestingly, the number of foggy days during the hydrological year was not related to precipitation of the same period ($r = 0.21$, $p = 0.19$), but it was related to the 6-month-long SPEI

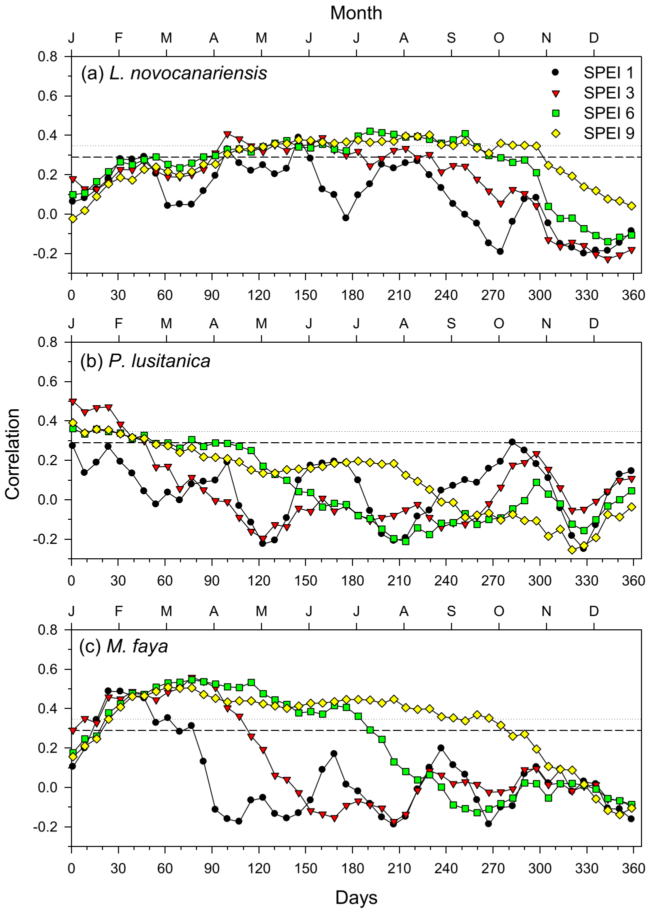

Fig. 5. Pearson correlations calculated between species' series of ring-width indices and weekly values of the SPEI for 1- (SPEI 1), 3- (SPEI 3), 6- (SPEI 6), and 9-month (SPEI 9) long droughts. The horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively.

of February ($r = 0.32$, $p = 0.04$) suggesting certain co-variability. This indicates that drought severity should be combined with other variables (radiation, VPD) to properly study the effects of compound extreme climate events on laurel forests.

The positive relationship between growth and foggy conditions found in *M. faya* (Fig. 4) can be interpreted as an alleviation of atmospheric drought stress. In this species, the sap flow rate peaks in summer as evaporative demand and radiation do (Jiménez et al., 1996, 1999, 2000). Thus, cloudy conditions leading to high relative humidity may be critical to alleviate summer drought stress in water-spending laurel

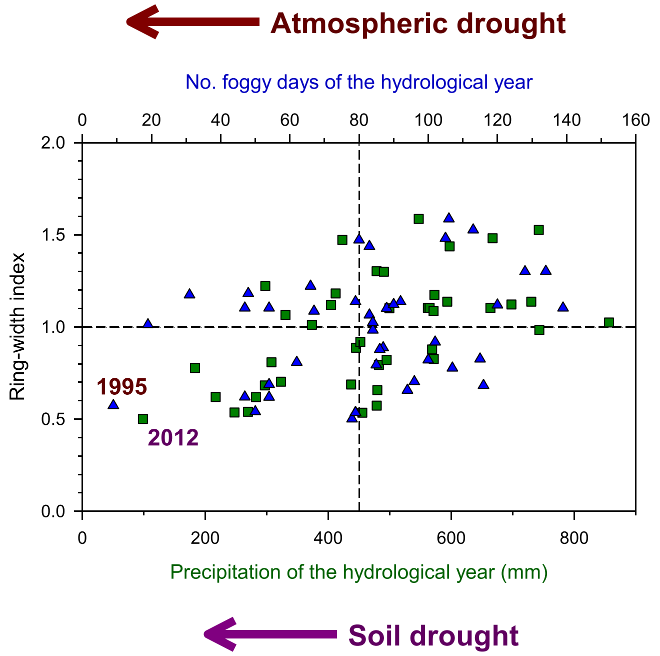

Fig. 6. Positive relationships observed between *M. faya* tree-ring width (TRW) indices and precipitation of the hydrological year (green squares, lower x-axis) or number of foggy days during the hydrological year (blue triangles, upper x-axis). The arrows indicate increasing atmospheric (less foggy days) or soil drought (less precipitation). Precipitation and the number of foggy days are used as proxies of soil and atmospheric drought, respectively. The low TRW indices observed in 2012 and 1995 correspond to low precipitation and few foggy days, respectively.

forest tree species (Morales et al., 1996). *L. novocanariensis* also shows high transpiration rates and poor stomatal control (Jiménez et al., 1996, 1999). Thus, severe droughts can trigger xylem embolism and explain the negative relationships between VPD and *L. novocanariensis* TRW indices (Fig. 4).

The positive correlations of spring NAO and *L. novocanariensis* and *M. faya* TRW indices may indicate a shift from wet-cool winter conditions towards warmer and drier conditions. Remarkably, the NAO January index was negatively correlated with the number of foggy days in January ($r = -0.32$, $p = 0.038$) indicating that positive NAO phases and sunny winter conditions characterize periods of low growth rates. In general, NAO impacts on climate and tree growth are stronger in north western Macaronesian archipelagos (e.g. Madeira) subjected to wetter conditions than in the central Canary Islands (García-López et al., 2025).

Warm and foggy winter conditions enhanced the growth of *P. lusitanica* (Fig. 4). Under wet conditions, broad-leaved species with diffuse porous wood, which are dominant in laurel forests, showed low responsiveness to precipitation and their growth was enhanced by warmer spring conditions (Pavão et al., 2023b). This suggests that *P. lusitanica* better tolerated dry conditions than *L. novocanariensis* in accordance with the lower elevation of sampled individuals of the first species located near the lowermost limit of the "sea cloud". In light-limited rainforests, cloud cover reduces photosynthesis rates (Graham et al., 2003), thus decoupling canopy photosynthetic capacity and wood productivity (Wagner et al., 2016). It is plausible that warm winter conditions enhanced the synthesis of non-structural carbohydrates used to grow in spring (Mendivelso et al., 2014).

The negative impact of summer temperature on *L. novocanariensis* growth (Fig. 4) can be explained by amplified drought stress leading to lower cambial activity or enhanced respiration rates reducing the pool of available photosynthates (Clark et al., 2010). Physiologically, this species is considered to follow a "non-conservative use of water" making it very sensitive to drought stress (González-Rodríguez et al., 2001). According to García-López et al. (2022), (2025), after the severe 2012 drought in Tenerife, *L. novocanariensis* showed better recovery, whereas *P. lusitanica*, exhibited higher resistance to drought. This resistance could be explained by the low responsiveness of *P. lusitanica* to climate and its higher tree-ring δ^{13}C values during that extreme drought (Fig. 3). *P. lusitanica* showed greater water-use efficiency, perhaps through a rapid stomatal closure and a "water-saving" strategy. In contrast, *L. novocanariensis*, with lower water-use efficiency and correspondingly lower δ^{13}C values, likely reduced both photosynthesis and stomatal conductance rates in response to water shortage showing a "water-spending" strategy (González-Rodríguez et al., 2001). The intra-annual tree-ring δ^{13}C analyses are clearly limited by our lack of knowledge on the cambium phenology and growing season of the study tree species, which leads us to tentatively align climate and tree-ring δ^{13}C data.

The lack of coherent year-to-year growth variability among the three study species indicates they respond individualistically to regional climate (Enquist and Leffler, 2001). Such different responses may depend on leaf and cambium phenology, which could explain the lower δ^{13}C values at the end of the growing season for *L. novocanariensis*, shade and drought tolerance or other traits driving the temporal scales of climate-growth relationships (Mendivelso et al., 2014). Further research using dendrometers or xylogenesis could better pinpoint the growth timing of the main tree species of laurel cloud forests and determine the drivers of water-use efficiency changes during dry periods using tree-ring H (δ^{2}H) and O (δ^{18}O) isotopes.

5. Conclusions

We measured the inter-annual growth responses to climate variability and the intra-annual tree-ring δ^{13}C responses to drought in tree species of a subtropical laurel cloud forest. Wet, cool and foggy conditions in the prior winter enhanced radial growth of *L. novocanariensis* and *M. faya* and cool summer conditions also increased growth of *L. novocanariensis*. However, *P. lusitanica* showed a low responsiveness to climate variability with only a positive influence on growth of warmer winter conditions. In contrast, *P. lusitanica* presented higher wood δ^{13}C during the 2012 drought and in response to warm-sunny conditions indicating higher resistance in terms of water-use efficiency than *L. novocanariensis*. Therefore, a species showing low growth sensitivity to inter-annual climate variability may show a high sensitivity in terms of intra-annual wood δ^{13}C. Our findings show the relevance of both soil and atmospheric droughts as key stressors of tree growth in laurel cloud forests, where different physiological strategies of water use may exist according to isotopic analysis. The conservation of these unique and singular forests should consider ongoing aridification trends driven by the rise in temperatures and develop measures to alleviate atmospheric and soil drought stress. Lastly, it should be emphasized that the laurel forest can adapt to climate change through elevation shifts on the islands of the Macaronesia. These displacements probably facilitated the persistence of Macaronesian cloud forests since the Tertiary period.

CRediT authorship contribution statement

J. Julio Camarero: Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Águeda M. González-Rodríguez:** Writing – review & editing, Validation, Supervision, Resources, Investigation, Data curation, Conceptualization. **Beatriz Fernández-Marín:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Cristina Valeriano:** Writing – review & editing, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **José Carlos Miranda:** Writing – review & editing, Supervision, Software, Resources, Methodology, Investigation, Data curation, Conceptualization. **Katja T. Rinne-Garmston:** Writing – review & editing, Validation, Software, Methodology, Investigation, Funding

acquisition, Formal analysis, Data curation, Conceptualization. **Elisa Tamudo:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation.

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.dendro.2025.126414.

Data Availability

Data will be made available on request.

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