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Abstract

Macaronesian laurel forests are the only remnants of a subtropical palaeoecosystem dominant during the Tertiary in Europe and northern Africa. These biodiverse ecosystems are restricted to cloudy and temperate insular environments in the North Atlantic Ocean. Due to their reduced distribution area, these forests are particularly vulnerable to anthropogenic disturbances and changes in climatic conditions. The assessment of laurel forest trees' response to climate variation by dendrochronological methods is limited because it was assumed that the lack of marked seasonality would prevent the formation of distinct annual tree rings. The aims of this study were to identify the presence of annual growth rings and to assess the dendrochronological potential of the most representative tree species from laurel forests in Tenerife, Canary Islands. We sampled increment cores from 498 trees of 12 species in two well-preserved forests in Tenerife Island. We evaluated tree-ring boundary distinctness, dating potential, and sensitivity of tree-ring growth to climate and, particularly, to drought occurrence. Eight species showed clear tree-ring boundaries, but synchronic annual tree rings and robust tree-ring chronologies were only obtained for *Laurus novocanariensis, Ilex perado* subsp. *platyphylla*, *Persea indica* and *Picconia excelsa*, a third of the studied species. Tree-ring width depended on water balance and drought occurrence, showing sharp reductions in growth in the face of decreased water availability, a response that was consistent among species and sites. Inter-annual tree-ring width variation was directly dependent on rainfall input in the humid period, from previous October to current April. The four negative pointer years 1995, 1999, 2008 and 2012 corresponded to severe drought events in the study area. This study gives the first assessment of dendrochronological potential and tree-ring climate sensitivity of tree species from the Tenerife laurel forest, which opens new research avenues for dendroecological studies in Macaronesian laurel forests.

Keywords:

climate extremes, cloud forest, drought, Macaronesia, pointer years

1. Introduction

Laurel forests, also called *laurisilvas*, are subtropical forests that occur in extratropical areas with high relative humidity and mild average temperatures (Walter, 1970). They are usually located in the eastern sides of the continents, between 25º and 40º of latitude, and often occupy topographic refugia where the moisture from oceanic cloud fronts condenses by canopy interception and falls as horizontal rain (Fernández-Palacios et al., 2017; Keith et al., 2020). Laurel forests share with tropical forests the dominance of evergreen broadleaf trees, the presence of abundant epiphytes and lianas, and the existence of high floristic richness, including a relatively high diversity of tree species (Betzin et al., 2016; Fernández-Palacios et al., 2017).

Macaronesia harbors some of the most singular laurel forests in the world. This small biogeographic region is composed by five volcanic archipelagos in the North Atlantic Ocean, namely Azores, Madeira, Canary Islands, Selvagen and Cape Verde. Laurel forests are only present in the three first archipelagos. These forests represent relict stands from a thermophilous forest type that dominated Europe and northern Africa for more than 50 million years during the Tertiary period and sought refugia in the Macaronesia before the Quaternary glaciations (Mai, 1991; Fernández-Palacios et al., 2011; Nogué et al., 2013). The persistence of these forests is determined by the interception of trade winds by mountains and the subsequent formation of a cloud belt that controls the elevational range where laurel forests grow, usually between 400 and 1,500 m a.s.l., depending on the island and on the season (Fernández-Palacios and de Nicolás, 1995; Aboal et al., 2015; Regalado and Ritter, 2021). The dependency of the Macaronesian laurel forest on the distribution of the cloud belt and their reduced extension in highly populated oceanic islands makes this ecosystem particularly vulnerable to the combination of climate and land-use changes (Sperling et al., 2004; del Arco Aguilar et al., 2010; Arozena and Panareda, 2013).

The impact of extreme droughts associated to climate change is causing productivity loss, forest decline and tree mortality in Mediterranean and temperate areas (Camarero et al., 2015; Neumann et al., 2017). The occurrence of heat waves and droughts is currently exacerbating in the Macaronesia (Cropper and Hanna, 2014), but their effects on laurel forests are still unknown. Persistent cloudiness reduces thermal range and produces orographic horizontal precipitation when intercepted by vegetation. Low incident radiation derived from the cloud belt effect reduces vapor-pressure deficits during the growing season and translates into a general positive hydric balance that eventually mitigates summer drought (Prada et al., 2009; Ritter et al., 2009). Even if the incidence of droughts on tree growth is expected to be moderate due to the mitigating effect of wet trade winds and persistent fog (Izquierdo et al., 2011; Regalado and Ritter, 2021), the impact of climate variability and drought on the growth of trees in Macaronesian laurel forests needs to be addressed in order to estimate their potential responses to climate change.

For a long time, it was assumed that the lack of strong seasonality would prevent the formation of annual tree rings in laurel forests, as thought for tropical forests. Fortunately, this view has completely changed. Tropical dendrochronology has boosted in the last decades (Worbes, 2002; Rozendal and Zuidema, 2011; Brienen et al., 2016) and in Macaronesian laurel forests, annual tree rings have been registered in several native tree species from Azores (Matos et al., 2019; Pavão et al., 2022), Madeira (Pupo-Correia, 2016), and the Canary Islands, including the species used in this study (Peraza Oramas and López De Roma, 1967; Morales et al., 2002). However, the potential for studying the inter-annual variation of xylem secondary growth and the radial growth responses to climate fluctuations and drought still remains systematically unexplored.

In this work, we aim at identifying the presence of annual tree rings and assessing the dendrochronological potential of the most representative tree species from laurel forests in Tenerife Island, evaluating the influence of temperature and water availability on their inter-annual growth variation. Our specific goals are: (1) to characterize anatomically the formation of annual tree rings assessing the dating statistical quality of laurel forest tree species, (2) to quantify the sensitivity of tree-ring growth to inter-annual climate variations, and (3) to evaluate the association between sharp growth reductions and drought events.

2. Material and methods

2.1. Study area

This study was carried out in two well-preserved laurel forest stands included in the protected areas of Anaga Rural Park and Teno Rural Park, located 60 km apart at the eastern and western tips of Tenerife Island, respectively (Fig. 1a, Table 1). These massifs are formed by basalt materials from the Miocene that constitute the oldest parts of Tenerife, reaching maximum elevations of 1,342 m a.s.l. in Teno and 1,024 m in Anaga.

The climate in Anaga and Teno has similar characteristics. Annual vertical rainfall in both study areas is around 400 mm and mainly occurs during the humid period from October to April, while a dry period spans from May to September (Fig. 1b, 1c). Water deficit is usual in summer, especially under events of dry winds arrival from the close Sahara Desert (del Arco Aguilar et al., 2010). Horizontal precipitation plays a key role in the hydric balance, since the orographic lifting of moist air masses driven by trade winds produces frequent fogs that are intercepted by vegetation and allow reaching annual amounts of up to 1800–2100 mm within the laurel forest belt (Ritter et al., 2008). Canarian laurel forests grow under reduced variation ranges of absolute temperature (10.5–20.5 ºC) and daily mean temperature (12.2–17.3 ºC) (Regalado and Ritter, 2021).

2.2. Study species

This study includes a total of 12 tree species belonging to 8 families and 11 genera (Table 2). The species studied are *Laurus novocanariensis* Rivas-Mart., Lousa, Fern.Prieto, E.Dias, J.C.Costa & C.Aguiar, *Persea indica* (L.) C.K. Spreng, *Ocotea foetens* (Aiton) Baill. and *Apollonias barbujana* (Cav) Bornm. (Lauraceae), *Picconia excelsa* (Aiton) DC. (Oleaceae), *Ilex perado* Aiton subsp. *platyphylla* (Webb & Berthel.) Tutin and *I. canariensis* Poir. (Aquifoliaceae), *Prunus lusitanica* L. subsp. *hixa* (Willd.) Franco (Rosaceae), *Heberdenia excelsa* (Aiton) Banks ex DC. (Primulaceae), *Erica arborea* L. (Ericaceae), *Rhamnus glandulosa* Aiton (Rhamnaceae), and *Morella faya* (Aiton) Wilbur (Myricaceae).

The species are Canarian or Macaronesian endemics, except *Prunus lusitanica* and *Erica arborea*, which have a wider (Macaronesian-Mediterranean-African) range of distribution (Fernández-Palacios et al., 2017).

2.3. Sampling and dendrochronological procedures

To perform a systematic sampling, in September 2019 and January 2020 we established three circular study plots at Anaga and three at Teno laurel forests, each of 20–25 m radius (Table 1). We sampled all trees present in the plot with diameter at 1.30 m above ground (DBH) greater than 10 cm. Trees were identified to species level, and their DBH and total height were measured with a diameter tape and a hypsometer (Vertex III, Haglöf, Sweden), respectively. Two increment cores of 5.2 mm diameter were extracted per tree using increment borers (Haglöf, Sweden). Mean age of the sampled trees was 63 years in both areas, with maximum tree ages of 139 and 84 years in Anaga and Teno, respectively. Mean basal area increment (BAI) was 12.3 cm^2 yr^{-1} for Anaga and 12.1 cm^2 yr^{-1} for Teno (Table 1).

Wood cores were air-dried, glued on wooden mounts, and polished with sandpaper of successively finer grain until the xylem cellular structure was clearly visible in transverse section. Afterwards, complete cores were digitized using the CaptuRING device, which automatically captures multiple images at a resolution of 5,931 dpi (García-Hidalgo et al., 2022). Images were merged using PTGUI v8.3.10 Pro (New House Internet Services B.V., Rotterdam, The Netherlands). Tree-ring boundaries detection and preliminary visual cross-dating were performed on these merged images following standard procedures (Speer, 2010). Species were classified into three different categories, according to the pattern of tree-ring boundaries distinctness. A “distinct” pattern was characterized by tree-ring boundaries with clear anatomical marks, and an “indistinct” pattern was found in species in which tree-rings boundaries were not visible (Wheeler et al., 1989; Silva et al., 2019). A third category included those species that formed "inconsistent" tree rings, i.e. those that showed both distinct and indistinct tree rings in different trees or on different samples obtained from the same tree or even along a single sample.

The CooRecorder software was used to date tree-ring series of those species with distinct tree-ring boundaries by assigning calendar years to the tree rings and measuring tree-ring widths on the images (Maxwell and Larsson, 2021). Cross-dating and measuring errors were checked with the COFECHA software (Holmes, 1983), and those series with potential dating errors were corrected when possible or discarded otherwise. Species with a "distinct" pattern of ring boundaries were considered as "datable", those with an "indistinct" pattern were considered as "non-datable", and those forming "inconsistent" tree rings were considered as "problematic", since the high frequency of indistinct ring boundaries hampered tree-ring dating.

2.3. Development of tree-ring chronologies and quality quantification

In those particular species with datable tree rings and well-replicated sample sizes, with at least ten sampled trees per study site (López and Villalba, 2016), ring-width time series were standardized to obtain dimensionless ring-width indices (RWI). Trends in the raw radial growth time series associated with ageing and long-term growth dynamics were removed from each individual series using a linear or negative exponential function. A cubic smoothing spline with a 50% frequency response cut-off of 32 years was then applied to the obtained residuals. Chronologies of RWI for each site were calculated as a biweight robust mean of the individual series of the previously obtained growth indices.

Three chronology statistics were calculated for the optimum common period 1980–2019 to check the dating potential and common signal quality. The first one is the mean sensitivity (MS), which quantifies the year-to-year variability in tree-ring width ranging from 0 to 1. Complacent tree-ring series with low variability would have MS values close to 0, whereas MS values around 0.2 and larger are generally accepted for series that are sensitive enough for climate reconstruction (Speer, 2010). The second one is the series intercorrelation (r_{xy}) or mean value of all possible correlations between individual series and is computed as the average of correlations between each series (x) and the master dating chronology (y), which in our case represents the common signal recorded per species and site. The third one is the expressed population signal (EPS), a measure of the common variability in a chronology and is dependent upon sample depth (Speer, 2010). When EPS is higher than 0.85, the chronology is considered to have high replication level and dating quality, whereas for EPS values lower than 0.85 the chronology is considered to be possibly well dated but may produce large confidence limits in a climate reconstruction (Wigley et al., 1984; Buras, 2017). Chronologies and their quality statistics were obtained using the package *detrendeR* (Campelo et al., 2012) in R environment (R Core Team, 2020).

2.4. Assessment of tree-ring growth to climate relationships

We used high-resolution gridded time series for monthly mean temperature (T), total precipitation (P) and standardized precipitation-evapotranspiration index (SPEI; Vicente-Serrano et al., 2010) obtained from the CRU TS 4.01 data set (Harris et al., 2014). We downloaded monthly CRU time series for the period 1901–2019 from the Climate Explorer of the Royal Netherlands Meteorological Institute (http://climexp.knmi.nl/; Trouet and van Oldenborgh, 2013), for the two 0.5° longitude × 0.5° latitude sectors in which the study forests were located. We then performed Pearson’s correlations between RWI chronologies per species and site and the monthly climate time series.

Pointer years were used to evaluate the correspondence between strong decreases in radial growth and the occurrence of droughts events. A pointer year occurs when a majority of trees in a stand shows extraordinary growth responses, like very narrow or wide ring widths (Jetschke et al., 2019). To identify them, we used the normalization in a moving window method with the *Weiser* software (García-González, 2001). This method produces time series of so-called Cropper values (Cropper, 1979) by normalizing individual tree-ring width series in a moving window, with each year placed as the central point of that moving window. Cropper values are calculated for each year and reflect the variations in terms of standard deviations (SD) from the local mean of a moving window of 13 years width, as recommended by Jetschke et al. (2019). To identify negative pointer years, we considered three intensities of growth decrease: (1) weak with a reduction of al least 50% SD, (2) strong with a reduction of at least 100% SD, and (3) extreme with a reduction of at least 150% SD (García-González, 2001). We considered only those negative pointer years in which more than 50% of the tree-ring series of each species and site showed a growth reduction of at least 50% of standard deviation from the local mean. We tested the correspondence between negative pointer years and drought events by examining the yearly variation of SPEI in the humid period, i.e., since October of the year prior to growth to April of the current growth year.

3. Results

3.1. Tree-ring boundaries distinctness

The studied species showed diffuse-porous or semi-ring porous wood with different degrees of tree-ring distinctness. Six species (*Laurus novocanariensis*, *Persea indica*, *Ocotea foetens*, *Picconia excelsa*, *Ilex perado* and *Prunus lusitanica*) showed distinct tree-ring boundaries and in other six species (*I. canariensis*, *Apollonias barbujana*, *Heberdenia* *excelsa*, *Erica arborea*, *Rhamnus glandulosa* and *Morella faya*) tree-rings were not distinct for most part (Fig. 2). Tree-rings of *L. novocanariensis* (Fig. 2a), *P. indica* (Fig. 2b) and *O. foetens* (Fig. 2c) were characterized by solitary vessels and vessels in rows aligned parallel to the rays, showing a sudden change in wood coloration, due to the difference in wall thickness and flattening of the fibers between earlywood (thin-walled fibers and less flattened fibers) and latewood (thick-walled fibers and flattened fibers), that allowed to separate latewood from earlywood of the subsequent ring. *L. novocanariensis* and *O. foetens* also showed a marginal parenchyma band in the tree-rings boundaries. Tree-rings of *P. excelsa* (Fig. 2d) showed a slight change in the wood coloration to the latewood, with a marginal parenchyma band that marked the boundary between consecutive tree rings. Additional bands of axial parenchyma were frequent in the latewood of *P. excelsa*, which corresponded to false tree rings at the end of the growing period. Tree-ring boundaries of *I. perado* (Fig. 2e) and *I. canariensis* (Fig. 2f) were characterized by a marginal band of axial parenchyma delimiting the tree-ring boundary, with this feature being common in *I. perado* ring boundaries, but only occasional in *I. canariensis*. In addition, a change in wood coloration, as a result of an increase in the fiber wall thickness, and a decrease in vessels' number and size in the latewood in comparison to the earlywood, were found in both *Ilex* species. In *P. lusitanica* (Fig. 2g), tree-ring boundaries were marked by a marginal band of axial parenchyma, with lighter earlywood, due to the high incidence of apotracheal axial parenchyma, and lower density of vessels in the latewood.

Among the species with no clearly distinct tree-ring boundaries, *I. canariensis* (Fig. 2f), *A. barbujana* (Fig. 2h), *H. excelsa* (Fig. 2i), *R. glandulosa* (Fig. 2k) and *M. faya* (Fig. 2l) showed bands of darker wood with low vessel density alternating with bands of lighter wood with more abundant vessels, which corresponded to changes in fiber wall thickness and fiber flattening, but without a clear anatomical differentiation between consecutive tree rings. Finally, *Erica arborea* wood did not show distinct tree-ring boundaries (Fig. 2j).

3.2. Crossdating quality and dendrochronological potential

We could not date tree-rings of *E. arborea*, *H. excelsa*, *M. faya* and *R. glandulosa* due to the absence of clear growth ring boundaries, thus they were considered “non-datable” species without dendrochronological potential (Table 2). *Ilex canariensis* and *A. barbujana* were considered as “problematic” species due to the very frequently undefined tree-ring boundaries that hampered successful crossdating. Species belonging to the “non-datable” and “problematic” categories were discarded for further analyses.

The “datable” category included *L. novocanariensis*, *P. indica*, *O. foetens*, *P. excelsa*, *I. perado* and *P. lusitanica* (Table 2). These six species showed distinct annual tree rings, and it was even possible to identify wedging and false tree rings, which were particularly abundant in the latewood of *P. excelsa* (Fig. 2d). With the exceptions of *O. foetens* and *P. lusitanica*, from which a very low number of trees were sampled, enough tree-ring series were obtained from the *L. novocanariensis*, *P. indica*, *P. excelsa* and *I. perado* to calculate reliable tree-ring chronologies (Fig. 3).

The most abundant species at both study sites was *L. novocanariensis*, with more than 50 dated tree-ring series per site (Table 3). *Picconia excelsa* trees were also found at both study sites, with 23 and 17 dated tree-ring series obtained in Anaga and Teno, respectively. More than 20 dated tree-ring series were obtained for *I. perado* in Anaga and *P. indica* in Teno (Table 3). All tree-ring chronologies were significantly correlated among them in the common period 1980–2019. Pearson’s r between chronologies ranged from 0.293 (P = 0.035), which corresponded to the correlation between the chronologies of *I. perado* in Anaga and *P. excelsa* in Teno, to 0.746 ($P = 2.55\ 10^{-8}$), which corresponded to the correlation between the chronologies of *P. excelsa* and *P. indica* in Teno. All six chronologies showed characteristically narrow tree rings, several of which were consistent among species and between sites (Fig. 3). *Picconia excelsa* chronologies showed the highest MS values (0.577), followed by *I. perado* (0.550), *L. novocanariensis* (0.425) and *P. indica* (0.396). *P. excelsa* and *P. indica* in Teno showed the highest series intercorrelations (r_{xy} of 0.547 for *P. excelsa* and 0.627 for *P. indica*), followed by *L. novocanariensis* and *I. perado* in Anaga (r_{xy} of 0.444 and 0.438 respectively). *Laurus novocanariensis* in Anaga (0.887) and Teno (0.921), and *P. indica* in Teno (0.952), were the species that showed the highest EPS values (Table 3).

3.3. Climate influence on tree-ring width variation

Temperature records showed few significant negative correlations with tree-ring width chronologies, only in the cases of *I. perado* with mean July-September temperature in Anaga, and *P. indica* with mean summer temperature in Teno (Fig. 4a). Precipitation and SPEI showed positive correlations with tree-ring width chronologies in previous autumn, winter, current spring, and during the complete hydrological year from previous October to current September (Fig. 4b, 4c). All tree-ring chronologies of *L. novocanariensis*, *P. excelsa*, *I. perado* and *P. indica* showed significant positive correlations with total precipitation (Fig. 4b) and SPEI (Fig. 4c) during the humid period, from previous October to current April.

Negative pointer years were found in the tree-ring chronologies of “datable” tree species (Fig. 5). Pointer years were common among study species and sites, matching SPEI minima during the humid period (October to April). The negative pointer years in 1995, 1999, 2008 and 2012 were found for *L. novocanariesis* and *P. excelsa*, and in 1995, 2008 and 2012 for *I. perado* in Anaga (Fig. 5a). The same four pointer years were found for *L. novocanariensis*, *P. excelsa* and *P. indica* in Teno, except 2008 for *L. novocanariesis* (Fig.

5b). Other species-specific negative pointer years were found in 1992 and 2001 for *P. excelsa* in Anaga (Fig. 5a), and 2001 for *P. indica* in Teno (Fig. 5b).

4. Discussion

4.1. Wood traits and tree-ring distinctness

Half of the studied tree species in the laurel forests of Tenerife Island showed distinct tree-ring boundaries that supported datable tree-ring series. Changes in colors that allowed differentiating ring boundaries in the wood of *Laurus novocanariensis*, *Ocotea foetens* and *Persea indica* was due to the alternance of thin-walled fibres in the earlywood versus thick-walled and flattened fibres in the latewood, which is common in the Lauraceae family (Reis-Avila and Oliveira, 2017). Tree-ring boundary distinctness has been previously established for Mediterranean and Macaronesian *Laurus* species (Schweingruber, 1990; Morales et al., 2002; Pupo-Correia, 2016; Matos et al., 2019), and for diverse species of Lauraceae from tropical and subtropical areas as well (Reis-Avila and Oliveira, 2017; Fontana et al., 2019; Godoy-Veiga et al., 2019). The wood of *Apollonias barbujana*, the fourth species of the Lauraceae family, showed clearly distinct tree rings in Madeira Island (Pupo-Correia, 2016). However, our findings agree with a previous assessment in the Canary Islands in which distinct tree-rings were only occasionally found in this species (Peraza Oramas and López De Roma, 1967). Probably *A. barbujana* does not form tree-ring boundaries under the climate characteristics of the Canary Islands, but may form clear ring boundaries under the more seasonal climate of Madeira. Notwithstanding, this hypothesis needs to be empirically confirmed.

In the case of *P. excelsa*, marginal parenchyma bands that mark the boundaries between tree rings, or between false tree rings, are wood traits typical of the Oleaceae family (Baas et al., 1988). The abundant false tree rings found in the latewood of *P. excelsa* may occur as a consequence of sudden changes of cambial activity along the growing season, mainly related to the alternation of favorable-unfavorable periods, as is commonly found in tree species from Mediterranean areas (Olano et al., 2015; Zalloni et al., 2019; Rozas et al., 2021), tropical mountain forests (Krepkowski et al., 2011; Wils et al., 2011), and even lowland tropical forests with a dry season (Groenendijk et al., 2014). *Picconia excelsa* is a typical species of the lower-elevation drier laurel forest (Fernández-Palacios et al., 2017), and indeed all the sampled trees of this species were located at elevations ranging between 760 and 820 m, near the lower elevation edge of the study forests. Precipitation and orographic cloudiness are consistently variable near the cloud base and, as a result, the low-elevation Canarian laurel forests are periodically exposed to clear-sky radiation from June to August (Vial et al., 2019). This means that rainfall, intercepted fog water, net radiation and evapotranspiration can be very variable in summer at an elevation range of 700–900 m (Marzol, 2008; Ritter et al., 2008, 2015). Even if this interpretation should be validated by further xylogenetic and phenological analyses, the frequent false tree-rings in the latewood of *P. excelsa* may be a response to the alternation of periods with wet (foggy) and dry (fog-free) conditions in summer, as often occurs in Mediterranean tree species (Battipaglia et al., 2016; De Micco et al., 2016a).

Abundant well-defined tree-ring boundaries were found in most of the tree rings of *P. lusitanica* and *I. perado*, whereas this pattern was only occasional in *I. canariensis*. The lack of well-defined ring boundaries is common in the genus *Ilex*, with frequent unclear ring limits when climate seasonality is not clearly marked (Baas, 1973). Species-specific wood anatomical traits related to tree-ring boundaries detection, such as porosity and changes in fibre wall thickness and/or fibre radial diameter (Wheeler et al., 1989; Schweingruber, 1990), may be a feasible explanation for tree-ring distinctness in these species. The wood of *I. perado* has been considered as semi-ring porous with distinct tree rings, while those of *I.*

canariensis is diffuse porous with rather vague tree rings (Baas, 1973), and our results agree with this. As expected for species of the *Laurocerasus* subgenus (Zhang, 1992), tree-ring markers in *P. lusitanica* consisted of a marginal band of axial parenchyma, together with the different anatomical appearance of earlywood and latewood, due to radially flattened latewood fibres and smaller and less frequent vessels in the latewood.

Indistinct tree-ring boundaries were found in the wood of *E. arborea*, *H. excelsa*, *M. faya* and *R. glandulosa*, which prevented any further dendrochronological assessment of these species. Distinct but often fuzzy tree-ring boundaries have been previously described for *E. arborea* and *M. faya* in Madeira Island (Pupo-Correia, 2016), and tree-rings were considered distinct in 18 *E. arborea* trees among 50 sampled individuals in northern Ethiopia (Jacob et al., 2020). In addition, tree-ring boundaries are sometimes distinct in *E. arborea* wood under Mediterranean and temperate climates (Schweingruber, 1990; De Micco et al, 2016b). On the other hand, a previous histological assessment in the Canary Islands demonstrated that the wood of *H. excelsa* and *R. glandulosa* showed distinct tree-ring boundaries (Peraza Oramas and López De Roma, 1967). In the diffuse-porous and very homogeneous wood of *Heberdenia*, a fibrous zone is commonly found at the end of a tree ring (Lens et al., 2005). *Rhamnus glandulosa* shows diffuse-porous to semi-ring porous wood and ring boundaries are distinct thanks to a dark fibrous tissue in the latewood, in contrast to a pale earlywood in the subsequent ring (Gupta and Saxena, 2011). Further assessment of these species with a larger number of individuals growing in different habitats is required to assess the influence of local environmental conditions on tree-ring distinctness. Our findings confirm the difficulty of dendrochronological studies carried out in subtropical areas where a combination of genetic components, such as the wood anatomical markers characteristic of every taxonomic group, together with environmental components, such as the diversity of habitats and the local variation of climate seasonality, greatly complicate ring boundary distinctness and tree-ring analysis (Ferrero et al., 2014; Marcelo-Peña et al., 2019; Silva et al., 2019).

4.2. Dendrochronological potential and climate sensitivity

Crossdating performed on tree-ring series of those species with clear ring boundary distinctness and adequate sample size demonstrated that datable ring width series and site chronologies of enough quality can be obtained from tree species of the Tenerife laurel forests. The statistics of the tree-ring chronologies for the four studied species were within the common range of variation of MS (0.25–0.74), and even surpassed the common variation range of r_{xy} (0.15–0.60) and EPS (0.27–0.94) found in tropical and subtropical tree-ring chronologies (Locoselli et al., 2013; Mendivelso et al., 2014; López and Villalba, 2016; Pagotto et al., 2017; Islam et al., 2018; Blagitz et al., 2019; Fontana et al., 2019; Marcelo-Peña et al., 2019). Statistics of the studied tree-ring chronologies were also similar than those from the conifers *Juniperus brevifolia* and *Pinus canariensis* in Azores and the Canaries, respectively (Rozas et al., 2013; Weigel et al., 2018; Pavão et al., 2022). These evidences indicate that ring width series from laurel forests tree species have analogous dendrochronological potential than Macaronesian conifers and tree species from tropical and subtropical forests worldwide. The high EPS values of *L. novocanariensis* and *P. indica* tree-ring chronologies supported that tree species of the Lauraceae family show a strong common signal and are appropriate for dendrochronological studies (Reis-Avila and Oliveira, 2017; Fontana et al., 2019). It is necessary to increase the sampling effort in other species of the Lauraceae family, such as *Ocotea foetens*, which had well-defined ring boundaries but robust dating could not be performed due to the low number of sampled individuals.

Water availability modulated inter-annual ring-width variation, with a minor role of temperature, and climate sensitivity was remarkably homogeneous across species and sites. The combined effect of wet trade winds and the Azores high-pressure system keeps temperature in the Canary Islands relatively stable and moderate during the whole year (Cropper, 2013; Regalado and Ritter, 2021). The negative correlation between summer temperatures for *P. indica* and *I. perado* radial growth may be attributed to hydraulic stress associated to high temperatures in fog-free periods. A similar result has been found in a windward population of *Pinus canariensis* growing at 1120 m elevation within the domain of laurel forest in Tenerife (Rozas et al., 2013), but also in tropical and subtropical forests worldwide (Brienen et al., 2016; Locoselli et al., 2016; López and Villalba, 2016; Reis-Avila and Oliveira, 2017; Islam et al., 2018).

We found a species-specific variation in the timing of tree-ring response to water balance. Radial growth of *P. excelsa* particularly benefited from positive water balance in previous autumn, whereas radial growth of *L. novocanariensis* and *P. indica* was mainly dependent on water input in the previous winter and *I. perado* depended on spring rainfall. This suggests that the high water availability before the start of xylogenesis will result in higher growth (Bienen and Zuidema, 2005). Interestingly, all tree species, except *P. indica*, were sensitive to annual precipitation, a result shared with other tropical tree species (Schöngart et al., 2006; Brienen et al., 2016). These findings indicate that the amount of vertical rainfall incorporated to the laurel forest all year round, and particularly during the humid period, is a key factor controlling tree growth and forest productivity, as has been previously found in a variety of tropical and subtropical forests (Krepkowski et al., 2011; Wils et al., 2011; Wagner et al., 2012; Islam et al., 2018).

The correspondence between minimum October-April SPEI values and negative pointer years' occurrence in the radial growth series of the studied species suggests a high impact of drought events on growth of laurel forest trees. Strong detrimental effects of low water availability on tree growth have been also observed in tropical forests (Mendivelso et al., 2014; López et al., 2019). This is not surprising considering that water availability and drought are the main drivers of tree growth and forest productivity in the tropics (Bonal et al., 2016; Brienen et al., 2016; Wagner et al., 2012, 2014). In the particular case of the Canary Islands, local environmental conditions and cloud immersion are very variable throughout the sloppy and irregular topography where laurel forests occur, and thus fog water input can be irregularly distributed (Ritter et al., 2009; Aboal et al., 2015; Ritter et al., 2015). However, the positive link between growth rates and water availability occurred in all the studied species and in both study areas, irrespective of local environmental variation. To date, no effects of climate variability and extreme climate events on tree health and survival have been found, and evidences indicate that laurel forests have survived to harsh climate and human-driven changes in the past (Arozena and Panareda, 2013; Nogué et al., 2013). Forecasted climate scenarios include winter precipitation reduction, annual temperature rise and downward/upward shift of the stratocumulus cloud layer (Sperling et al., 2004; Martín et al., 2012; Cropper, 2013; Ritter et al., 2019), which can modify tree stress levels, forest productivity and even the altitudinal distribution range of laurel forests in the Canary Islands. In this sense, our results could be helpful for future studies regarding forest dynamics from a retrospective view assessing the past impact of land-use changes and forecasting the potential response of these species to climate warming (Sperling et al., 2004; Cropper and Hanna, 2014; Expósito et al., 2015).

5. Conclusions

Our study demonstrates the presence of distinct tree-ring boundaries in a large part of the tree species that dominate laurel forests in Tenerife Island. These results contribute to improve the knowledge on the dating potential of tree species in cloudy forest ecosystems with mild climatic seasonality and add to previous studies with particular species in Madeira and Azores archipelagos. In addition, our results confirm the dependency of tree secondary growth on water input in the humid period and the marked general response of laurel forest trees to drought, confirming the vulnerability of these ecosystems to climate warming. These results set the basis for future studies projecting the potential climatic response of laurel forests under global change scenarios, which would be critical for the preservation of these singular and biodiverse ecosystems.

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Table 1. Geographical coordinates, mean elevation, mean DBH, mean tree height, mean and maximum tree age, mean basal area increment (BAI) in the period 1980–2019, and total number of sampled trees with DBH ≥ 10 cm in three study plots in the laurel forests of Anaga and Teno, Tenerife Island.

	Anaga	Teno
North latitude (º)	28.53	28.33
West longitude (º)	16.29	16.82
Mean elevation ± SD (m asl)	844 ± 58	902 ± 79
Mean DBH ± SD (cm)	27.6 ± 12.6	25.7 ± 9.6
Mean tree height ± SD (m)	15.9 ± 4.1	18.1 ± 3.8
Mean tree age ± SD (yr)	63.8 ± 16.9	63.9 ± 10.9
Maximum tree age (yr)	139	84
Mean BAI ± SD (cm^2 yr^{-1})	12.3 ± 9.6	12.1 ± 9.8
Total no. of sampled trees	246	252

Table 2. Tree species, botanical family and total number of sampled trees per species in the laurel forests of Anaga and Teno, Tenerife Island. Shade tolerance (classification obtained from Arévalo & Fernández-Palacios, 2007, Fernández-Palacios et al., 2017 and Ganivet et al., 2019), dry wood density (Fernández-Palacios et al., 2017 and Peraza Oramas and López De Roma, 1967), tree-ring boundary distinctness and dating potential (obtained from this study) of each species are shown.

Species	Family	Anaga	Teno	Shade tolerance	Wood density (g/cm^3)	Tree-ring boundary	Dating potential
Apollonias barbujana	Lauraceae	5	0	Tolerant	0.725	Inconsistent	Problematic
Erica arborea	Ericaceae	19	11	Intolerant	0.619	Indistinct	Non-datable
Heberdenia excelsa	Primulaceae	31	0	Mid-tolerant	0.624	Indistinct	Non-datable
Ilex canariensis	Aquifoliaceae	34	24	Mid-tolerant	0.644	Inconsistent	Problematic
Ilex perado	Aquifoliaceae	15	0	Mid-tolerant	0.550	Distinct	Datable
Laurus novocanariensis	Lauraceae	70	171	Tolerant	0.535	Distinct	Datable
Morella faya	Myricaceae	45	13	Intolerant	0.635	Indistinct	Non-datable
Ocotea foetens	Lauraceae	3	0	Tolerant	0.511	Distinct	Datable
Persea indica	Lauraceae	2	22	Tolerant	0.473	Distinct	Datable
Picconia excelsa	Oleaceae	16	11	Mid-tolerant	0.711	Distinct	Datable
Prunus lusitanica	Rosaceae	5	0	Tolerant	0.548	Distinct	Datable
Rhamnus glandulosa	Rhamnaceae	1	0	Mid-tolerant	0.608	Indistinct	Non-datable

Table 3. Number of dated tree-ring width series included in the chronology and statistics of the obtained chronologies for the common period 1980–2019 in Anaga and Teno, Tenerife Island. Only species with datable tree-ring series from at least 10 trees per site are shown. MS: mean sensitivity. r_{xy}: series intercorrelation. EPS: expressed population signal.

Study sites and species	Series / trees in chronology	MS	r_{xy}	EPS
Anaga				
Laurus novocanariensis	55 / 35	0.425	0.444	0.887
Picconia excelsa	23 / 15	0.577	0.424	0.689
Ilex perado	22 / 14	0.550	0.438	0.696
Teno				
Laurus novocanariensis	54 / 45	0.424	0.438	0.921
Picconia excelsa	17 / 10	0.531	0.547	0.735
Persea indica	21 / 14	0.396	0.627	0.952

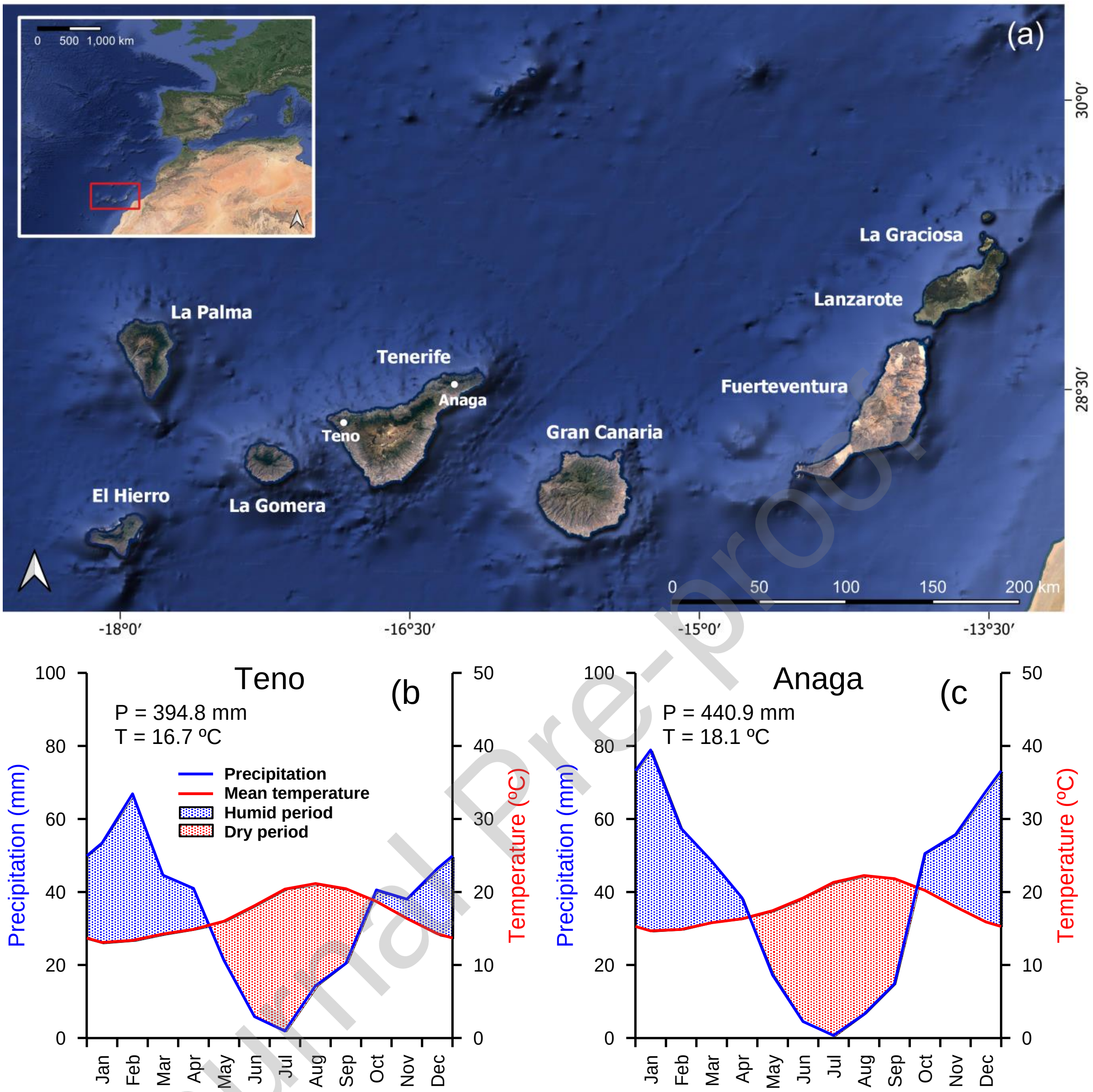

Fig. 1. Location (a) and climatic diagrams of Teno (b) and Anaga (c) in Tenerife Island. P: total monthly vertical precipitation. T: mean monthly temperature. Data for climatic diagrams were obtained from http://climexp.knmi.nl/ for the period 1970–2019.

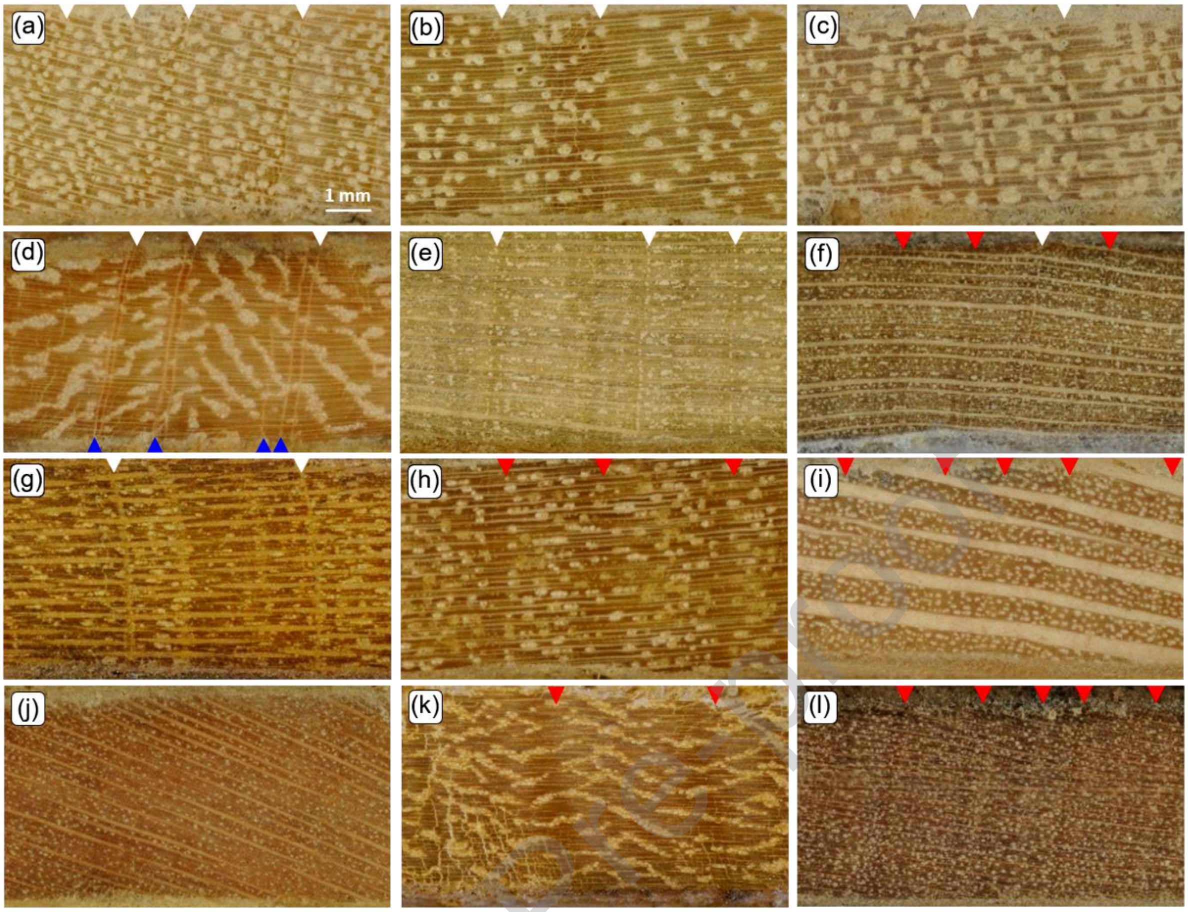

Fig. 2. View of the secondary xylem of the studied species in the laurel forests of Tenerife Island in transverse section. (a) *Laurus novocanariensis*, (b) *Persea indica*, (c) *Ocotea foetens*, (d) *Picconia excelsa*, (e) *Ilex perado*, (f) *Ilex canariensis*, (g) *Prunus lusitanica*, (h) *Apollonias barbujana*, (i) *Heberdenia excelsa*, (j) *Erica arborea*, (k) *Rhamnus glandulosa* and (l) *Morella faya*. Tree-ring growth progresses from left to right, finding the most recent tree rings on the right and the oldest on the left of the image. The scale bar in (a) is valid and similar for all the images. White triangles indicate distinct tree-ring boundaries; red triangles indicate inconsistent tree-ring boundaries. Note the false tree rings in the latewood of *Picconia excelsa* (blue triangles in d).

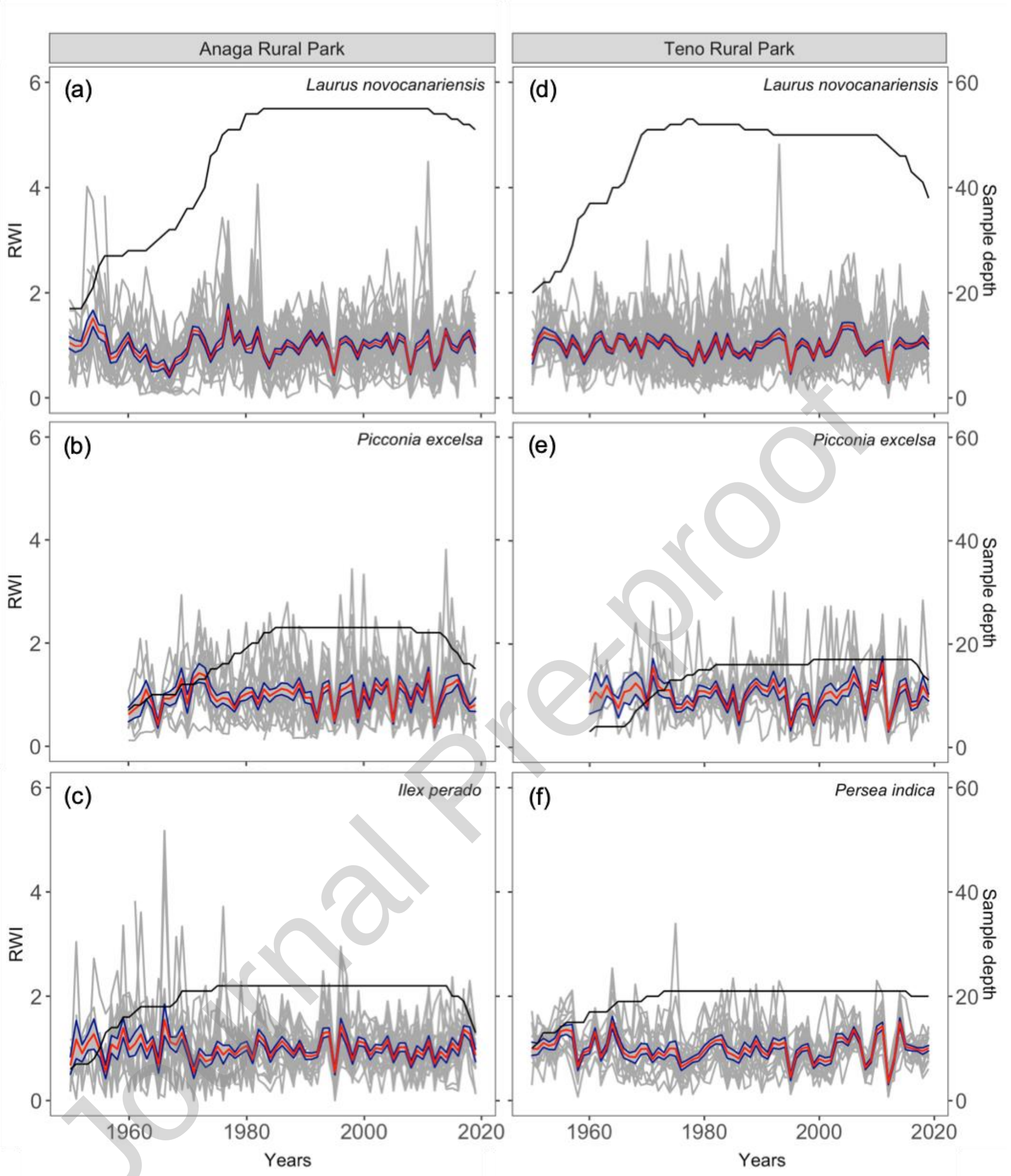

Fig. 3. Tree-ring index series (grey lines), standardized tree-ring chronologies (red lines) with their corresponding ±1 SE intervals (blue lines), and temporal variation of tree-ring series sample depth (black lines) for the main “datable” tree species in the laurel forests of Anaga and Teno Rural Parks (Tenerife Island).

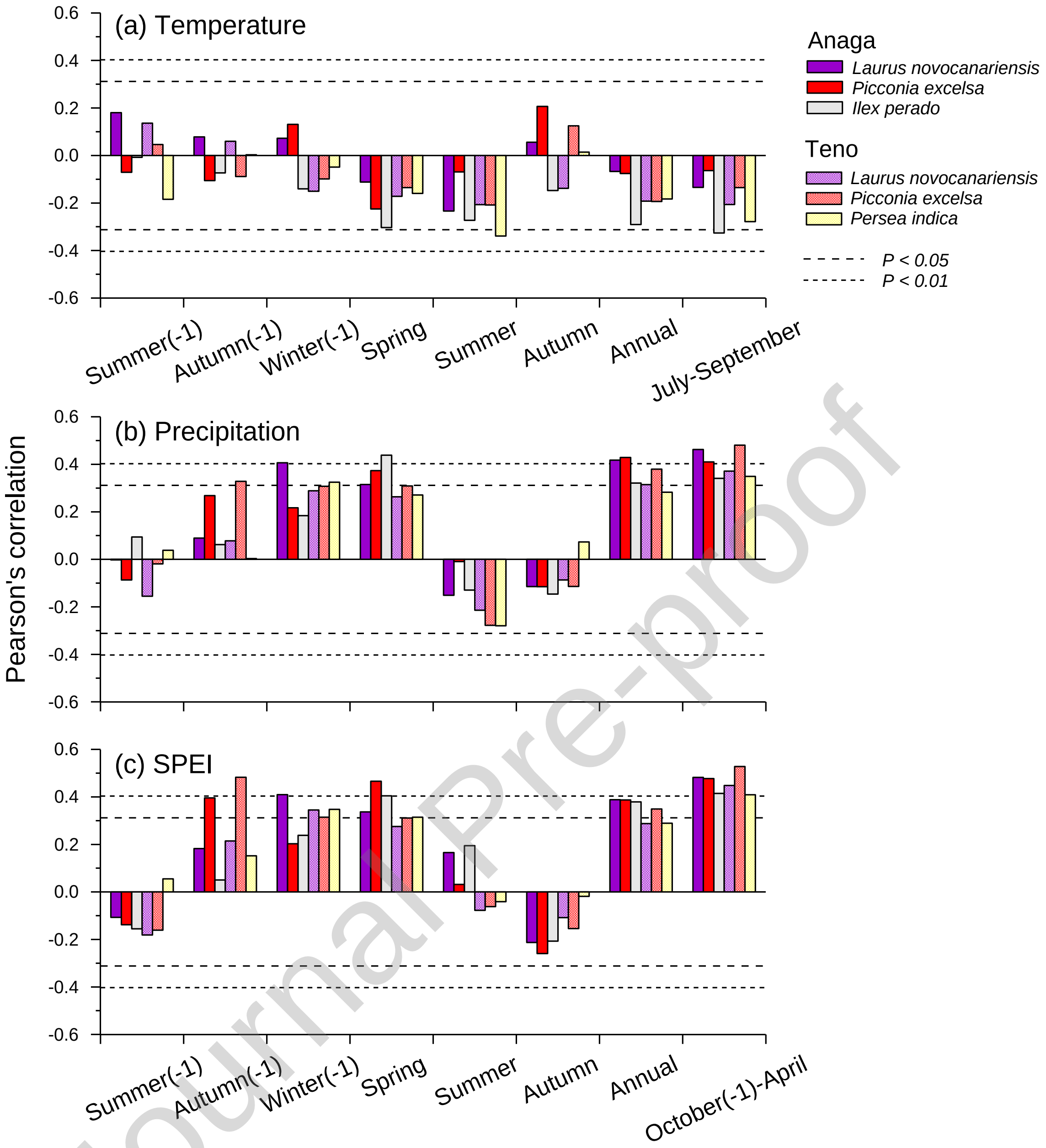

Fig. 4. Pearson's correlation coefficients of RWI chronologies with (a) temperature per season, year and in the warm period (July-September), and (b) precipitation and (c) standardized precipitation-evapotranspiration index (SPEI) per season, year and in the humid period (October-April) for the main "datable" tree species in the laurel forests of Anaga and Teno (Tenerife Island), calculated in the period 1980–2019. "(-1)" refers to the year previous to growth year. Horizontal long and short dashed lines indicate $P < 0.05$ and $P < 0.01$ confidence intervals, respectively.

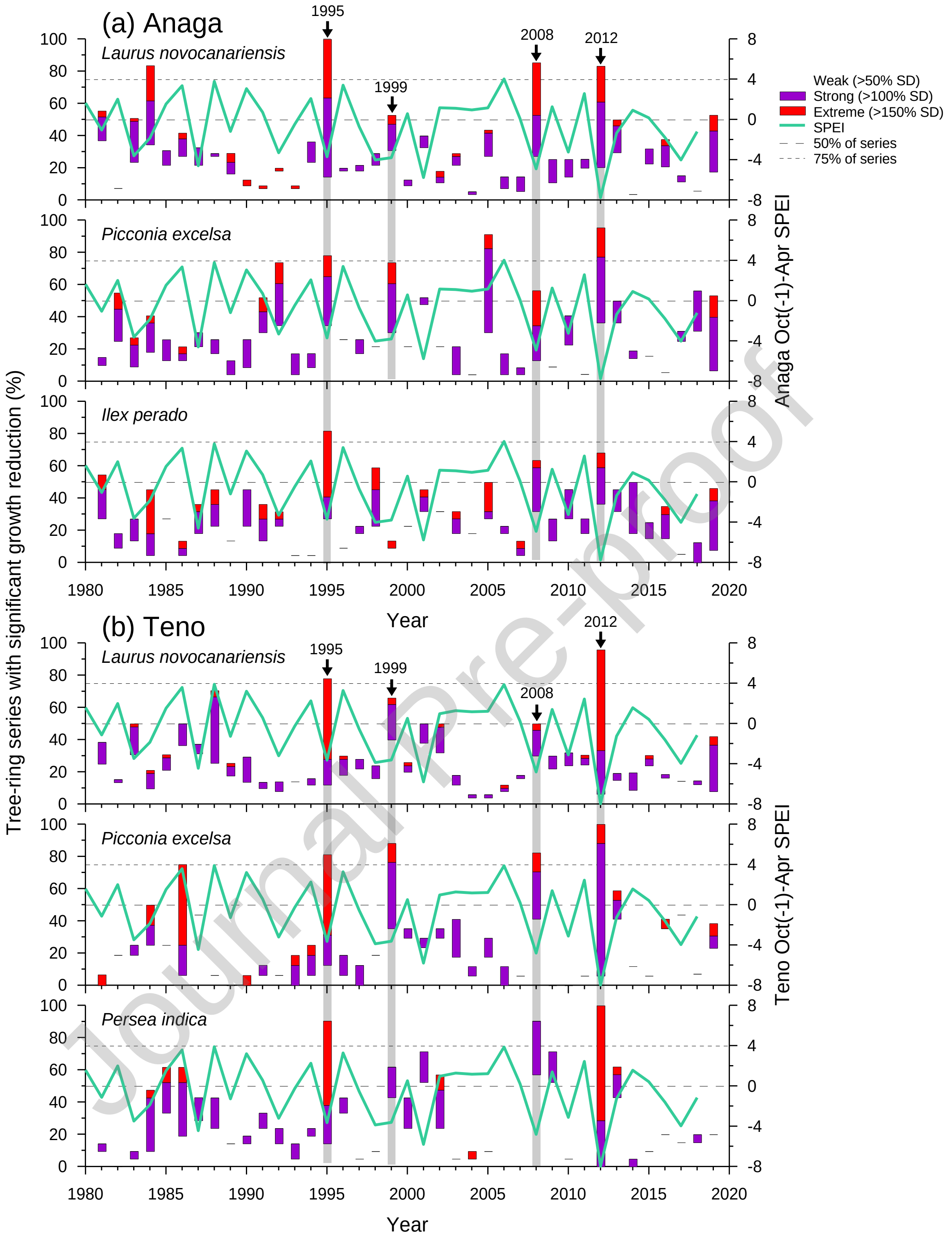

Fig. 5. Yearly variation of the percentage of tree-ring series showing significant growth reductions for the main "datable" tree species per site, and October-April SPEI in (a) Anaga and (b) Teno Rural Parks of Tenerife Island, in the period 1980–2019. The percentages of series with a weak (>50% SD), strong (>100% SD) and extreme (>150% SD) growth

reduction from the local mean within a 13 year moving window are shown. We identified negative pointer years as those in which more than 50% of the tree-ring series of each species and site showed a growth reduction of at least 50% of standard deviation from the local mean. Dashed horizontal lines indicate the 50% and the 75% of the series. The negative pointer years 1995, 1999, 2008 and 2012, common to several species at both sites, are highlighted (arrows and grey background).

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.

Highlights

- We characterized the tree-ring anatomy of twelve species from Tenerife Island.
- We obtained robust chronologies for four tree species.
- Radial growth variation directly depended on rainfall input during the humid period.
- Negative pointer years matched drought events.
- Climate sensitivity of growth was consistent across species and sites.