BRILL

IAWA Journal 0 (0), 2023: 1-14

Latewood intra-annual density fluctuations indicate wet summer conditions and enhanced canopy activity in a Mediterranean ring-porous oak

J. Julio CAMARERO [1,*], Xavier SERRA-MALUQUER [2], Michele COLANGELO [1,3], Antonio GAZOL [1] and Manuel PIZARRO [1]

[1] *Instituto Pirenaico de Ecología (IPE-CSIC), Avenida Montañana 10005, Zaragoza 50009, Spain*
[2] *Universidad de Alcalá, Grupo de Ecología y Restauración Forestal, Departamento Ciencias de la Vida, Campus Universitario, Madrid, Spain*
[3] *Scuola di Scienze Agrarie, Forestali, Alimentari e Ambientali, Università della Basilicata, Viale dell'Ateneo Lucano 10, 85100 Potenza, Italy*
**Corresponding author; email: jjcamarero@ipe.csic.es*
ORCID iDs: Camarero: 0000-0003-2436-2922; Serra-Maluquer: 0000-0002-1880-0511;
Colangelo: 0000-0002-6687-3125; Gazol: 0000-0001-5902-9543; Pizarro: 0000-0002-6981-0154

Accepted for publication: 4 October 2023; published online: 1 November 2023

Summary – The climatic significance and ecosystem implications of latewood intra-annual density fluctuations (IADFs) are still not fully understood in Mediterranean ring-porous oak species. To solve this issue, we investigated: (i) the climate drivers of radial growth and latewood IADFs in the Mediterranean oak *Quercus faginea*, and (ii) whether they were correlated to increased canopy cover and greenness as recorded by the Normalized Difference Vegetation Index (NDVI). IADFs were formed in the mid to late latewood and they were characterized by rows of parenchyma cells. Such IADFs were uncommon and only present in 30–50% of sampled trees during 1999 and 2014, both years characterized by high precipitation in late July and early August. This relationship between IADFs formation and summer wet conditions differed from the conditions that enhance *Q. faginea* annual growth, wet winter-spring conditions, and low summer temperatures. Furthermore, IADFs formation showed a positive relationship with August NDVI values, indicating a correspondence of canopy greenness with secondary growth reactivation. We conclude that latewood IADFs in *Q. faginea* are a robust proxy of rare late-summer wet conditions and enhanced canopy activity as reflected by increased August NDVI values. Further monitoring of xylogenesis in other Mediterranean hardwoods along climatic gradients is suggested to mechanistically explain IADF production in seasonally dry biomes.

Keywords – drought, false rings, Mediterranean forests, NDVI, *Quercus faginea*.

Introduction

In regions with seasonal climate conditions tree radial growth results in annual rings and also leads to intra-annual wood-anatomical features reflecting xylem plasticity (Fritts 1976; Larson 1994; Wimmer 2002). Intra-annual, discrete wood features such as intra-annual density fluctuations (IADFs), also called false or double rings, reveal tree growth responses to short-term extreme events, giving a more detailed picture of how trees respond to stressors at finer temporal scales (De Micco *et al.* 2016a).

IADFs result from abrupt changes in cell lumen area and/or wall thickness during the growing season in response to sudden, and often transitory, changes in climate conditions (Battipaglia *et al.* 2016). In Mediterranean ecosystems,

DOI 10.1163/22941932-bja10141

where precipitation usually peaks in winter-spring and autumn, IADFs are often associated with bimodal growth patterns (Camarero *et al.* 2010; Campelo *et al.* 2018). Historically, IADFs have been seen as a problem due to their interference in the cross-dating process (Yamaguchi 1991). However, IADFs offer relevant ecological information about the capacity of tree populations and individuals to adapt to rapid changes in water availability (De Micco *et al.* 2012, 2016a). Therefore, in a climate warming context, where extreme droughts may become more frequent and intense (IPCC 2021), exploring which species are capable of reactivating growth after the summer drought, and under which conditions they do so, becomes of interest in Mediterranean forest ecosystems. Such post-drought reactivation could be a mechanism for improving the growth resilience after the summer drought.

Earlywood and latewood IADFs in the Mediterranean Basin and nearby seasonally dry areas have been widely described in conifers such as pines and junipers (Wimmer *et al.* 2000; Rigling *et al.* 2001; Campelo *et al.* 2007b, 2013, 2017; De Micco *et al.* 2007; Bogino & Bravo 2009; Vieira *et al.* 2009, 2010; De Luis *et al.* 2011; Rozas *et al.* 2011; Novak *et al.* 2013; Olano *et al.* 2015; Zalloni *et al.* 2016). Earlywood IADFs are often related to changes in earlywood density in response to dry spring conditions inducing smaller lumen areas, i.e. increasing density (Camarero *et al.* 2014). Latewood IADFs are characterized by the formation of tracheids with wide lumen areas in response to wet summer-autumn conditions (Rozas *et al.* 2011; Collado *et al.* 2018). In hardwood species, IADFs have been described in several tree and shrub species from the Mediterranean region such as *Quercus ilex*, *Phyllirea latifolia*, *Erica* sp., *Cistus* sp. and *Arbutus unedo* (Zhang & Romane 1991; Cherubini *et al.* 2003; Campelo *et al.* 2007a, 2021; De Micco & Aronne 2009; Battipaglia *et al.* 2010, 2014; De Micco *et al.* 2016b; Balzano *et al.* 2018, 2021) and associated to shifts in climatic conditions. For instance, IADFs were formed in response to anomalously dry-warm springs followed by wet-warm late summers in Patagonian *Nothofagus pumilio* forests (Masiokas & Villalba 2004).

In the Iberian Peninsula, mixed *Q. ilex*–*Quercus faginea* or *Q. humilis* forests are widespread and provide multiple economic and ecological services (Loidi & Herrera 1990). Such oak species present different wood anatomy, phenology, and growth response to drought (Corcuera *et al.* 2004a, b; Alla & Camarero 2022). *Q. ilex* forms latewood IADFs in response to late-summer and autumn rainfall enhancing growth reactivation after the dry summer (Campelo *et al.* 2007a, 2018). However, less is known on the capacity of *Q. faginea* to form latewood IADFs. A recent study in northeast Spain found that *Q. faginea* may show a bimodal growth pattern in Mediterranean sites with wet-warm summer-autumn conditions (Tumajer *et al.* 2022), and this is supported by dendrometer data (Vieira *et al.* 2022). However, it remains unclear if these sudden changes in growth favored by the presence of abnormally high precipitation values in summer are also correlated with changes in canopy activity. At the tree scale, evidence suggests that there exists a positive relationship between secondary and primary growth in oaks which is mediated by climate stress (Alla *et al.* 2011). It remains unclear if changes in growth translate into changes in canopy activity. During the last decades, several studies have linked inter-annual growth patterns and satellite-derived estimates of canopy activity (e.g., Vicente-Serrano *et al.* 2016). Both, canopy activity and growth respond to climate, but they tend to do at different temporal and spatial scales (Kannenberg *et al.* 2019). However, it can be expected that rare, favorable conditions may also favor both, growth (Serra-Maluquer *et al.* 2021) and canopy activity, during periods of climatic stress such as the Mediterranean dry summer (Li *et al.* 2023). So far, no studies have tested whether the occurrence of late IADFs at the tree population level correlates with increases in canopy activity at the landscape level.

In this study, we evaluate the capacity of *Q. faginea* to form latewood IADFs and under which climatic conditions it does so. We study individuals growing in Alcubierre, a continental Mediterranean site located in northeast Spain. We combine information from tree rings, wood anatomy, and remote sensing to test if IADFs can be used as proxies of wet summer-autumn conditions and elevated canopy cover and greenness in the late growing season.

Material and methods

Study site and tree species

The study site is located at Sierra de Alcubierre (41°49′06″N, 0°30′49″W, 425–620 m a.s.l.), a mountain range located northeast of Zaragoza city (Aragón, Spain). Monthly and weekly climate data (mean maximum and minimum temperatures, precipitation) were obtained from the Alcubierre meteorological station (41°48′24″N, 0°27′12″W, 466 m a.s.l.), located at ca. 5 km from the study site. Alcubierre has a continental Mediterranean climate with mean annual temperatures of 14.3°C and 395 mm of annual precipitation (Fig. A1 in the Appendix). Most of the precipitation is accumulated during the months of April and May in spring and October and November during autumn. It presents a strong water shortage during summer and relatively cold winters. The vegetation in Alcubierre is dominated by forests with presence of *Q. faginea*, *Q. ilex*, *Pinus halepensis* and *Juniperus thurifera*, as well as by Mediterranean shrubs (*Juniperus phoenicea*, *Quercus coccifera*, *Pistacia lentiscus*, *Rhamnus lycioides*, *Rhamnus alaternus*, *Salvia rosmarinus*, *Thymus* spp. and *Ephedra nebrodensis*). In the study area, grazing and agricultural activities were intense until the 1960s when massive migration of rural population to cities triggered forest and shrubland encroachment until the present. Soils in the study site are basic and formed on marls with some gypsum locations.

Quercus faginea is a Mediterranean, winter-deciduous, ring-porous oak widely distributed across the Iberian Peninsula and northwest Africa, particularly in sites with basic soils (Loidi & Herrera 1990). Secondary growth of *Q. faginea* peaks in early spring (Montserrat-Martí *et al.* 2009). Secondary growth and wood anatomy of *Q. faginea* is more plastic in xeric sites such as Alcubierre (Alla & Camarero 2012).

Field sampling and tree-ring width data

During October 2017, one to two cores were extracted from 31 adult *Q. faginea* individuals with an increment borer of 5 mm (Haglöf, Långsele, Sweden). Once in the laboratory, cores were air-dried and mounted on wooden supports. Cores were progressively sanded until tree rings were visually cross dated under the binocular microscope. Then, ring widths were measured to the nearest 0.01 mm using a stereomicroscope and the LINTAB measuring table device connected to a computer running TSAP-Win (Time Series Analysis Program) software (Rinntech, Heidelberg, Germany). Cross-dating quality was checked using the COFECHA program (Holmes 1983).

To perform climate–growth correlations age-related growth trends and competition effects in the ring-width series were removed. A one-step detrending was applied to each tree-ring width series, using the R package dplR (Bunn 2008; R Core Team 2022). Cubic smoothing splines with a 50% frequency-response cutoff of 30 years were applied to remove low- to medium-frequency signals and enhance the year-to-year signal (Bunn 2008). First-order autocorrelation was then removed by fitting autoregressive models. Finally, a site ring-width chronology was obtained by averaging the individual, residual series of ring-width indices using a bi-weight robust mean.

Dendrometer data

Ten of the oak trees sampled in 2017 were used for measuring radial increment rates and growth peaks. In those trees, manual band dendrometers (Agricultural Electronics, Tucson, AZ, USA) were installed in March 2008 at 1.3 m after carefully removing the dead bark. Dendrometers were read biweekly (growing season) or monthly with a 0.1 mm resolution from 2008 to 2011 (for further details, see Tumajer *et al.* 2022). These data allowed calculating mean radial growth rates by subtracting consecutive dendrometer readings and dividing the result by the number of days elapsed between sampling dates.

Remote sensing data

We used remote-sensing data to test if years, when most trees formed latewood IADFs, were associated with higher canopy greenness and activity. For the period 1980–2017, we calculated biweekly and monthly values of the Normalized Difference Vegetation Index (NDVI), which is based on how healthy green vegetation differently reflects red and near-infrared radiation (Tucker 1979). We calculated standardized NDVI values to compare them among years. In all cases we applied cloud masks using the CFMask algorithm and using a 40% cloud threshold in addition to radiometric and topographic corrections using the USGS GMTED2010 digital elevation model (Hantson & Chuvieco 2011). We also harmonized Landsat ETM+ surface reflectance records to Landsat 8 OLI surface reflectance series (Roy *et al.* 2016). We considered a 50-m buffer area around the study site to quantify the NDVI. These calculations were carried out using the Google Earth Engine platform (https://earthengine.google.com, accessed on 8 May 2023).

Statistical analyses

To evaluate the presence of IADF we visually explored all cores from each individual and counted the percentage of trees with IADF presence. The Mann–Whitney test was used to compare widths of rings with or without IADFs. After that we calculated climate-growth correlations between the site series of ring-width indices and monthly climatic variables (mean maximum and minimum temperatures, precipitation) from the previous year September to the current year September. Furthermore, mean season climatic variables (previous autumn, winter, spring and summer) were also correlated with ring-width indices. After that, non-parametric Spearman correlations were used to evaluate IADFs-climate relationship between the percentage of IADFs and monthly maximum and mean temperatures and precipitation. Finally, correlations between IADFs and monthly NDVI data were also performed using again Spearman correlations.

Results

The *Q. faginea* IADFs were formed in the mid to late latewood, in specific years such as 1999, and they were characterized by the presence of parenchyma cells, fibers and latewood-like vessels (Fig. 1). The mean (± SD) ring width of sampled oak trees ($n = 31$, best-replicated period 1989–2017) was 1.29 ± 1.00 mm (Fig. 2a), and their mean age at 1.3 m was 44 ± 8 years, i.e., they corresponded to a secondary forest. The mean first-order autocorrelation was 0.46, and the mean correlation among individual series was 0.66.

Latewood IADFs were mainly produced in 1999 and 2014, when 50% and 30%, of sampled trees formed them, respectively. A few trees (3–6%) also presented IADFs in 1997, 1998 and 2013 (Fig. 2b). The ring width in the years 1999 and 2014 was 1.36 ± 0.72 mm, and it was not significantly different (Mann–Whitney test, $p = 0.63$) from the mean width during the other years (1.14 ± 0.51 mm).

In the years 1999 and 2014, late July and early August had significantly higher precipitation values than their long-term means (Mann–Whitney tests, $p < 0.01$; Fig. A2 in the Appendix). In the case of NDVI, the late August (second half) values were significantly higher than the 1980–2017 mean ($p < 0.05$) (Fig. A3 in the Appendix). Based on dendrometer data for the study site, the main radial-growth peak occurs from May to July, and growth stops or is severely reduced in late summer, from August to September (Fig. A4 in the Appendix). In some years (e.g., 2008), a second but minor growth peak was observed from October to November.

Pearson correlations between the series of ring-width indices and monthly climate variables show that *Q. faginea* growth in Alcubierre is highly dependent on precipitation, particularly during winter (December–January) and spring–summer (April–June) (Fig. 3). Warm conditions (high maximum temperatures) in summer (June–July) are associated with lower growth indices.

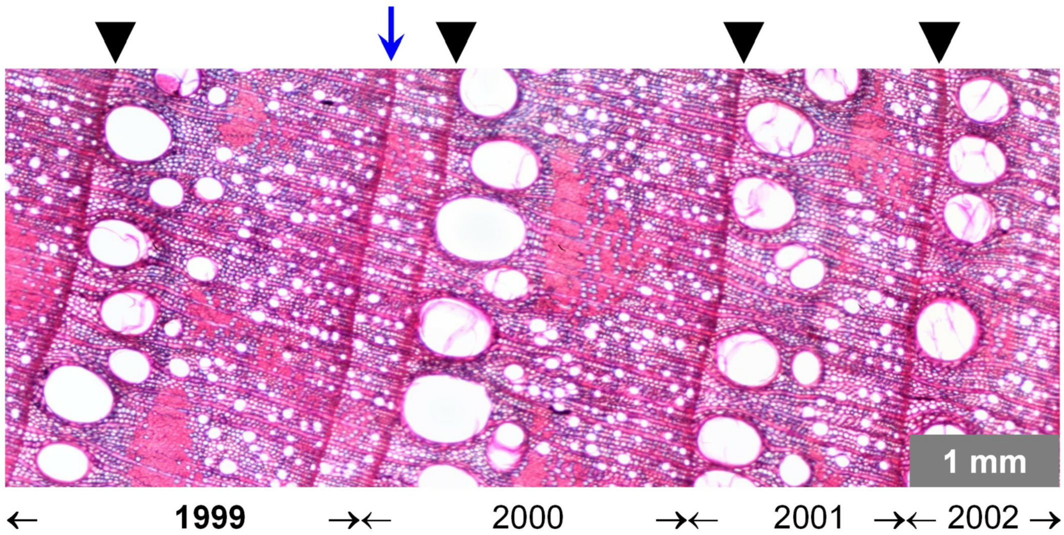

Fig. 1. Growth rings of *Quercus faginea* showing a latewood IADF in the ring formed in 1999 (blue arrow). The black triangles show tree-ring boundaries.

Spearman correlations between IADF frequency and climate variables showed that wet conditions in July and August were related to IADF formation (Fig. 4a). Negative associations between IADF frequency and July temperatures were also found. Furthermore, a significant and positive association between the frequency of IADFs and late-spring and summer NDVI, particularly strong in August, was also found (Fig. 4b). Pearson correlations between biweekly climate and NDVI data showed that NDVI was constrained by high maximum temperatures in early July ($r = -0.27$, $p = 0.026$).

Discussion

In general, years with abundant latewood IADFs are scarce (two in 37 years) in this xeric site and correspond to wet conditions during summer. Thus, it may be plausible that a water surplus in late July and early August causes the reactivation of growth after summer arrest imposed by the Mediterranean summer drought (Vieira *et al.* 2022), and consequently the formation of latewood IADFs, which is also coupled to increased canopy greenness at the landscape scale (NDVI). In this sense, the rare formation of these IADFs would be an expression of facultative bimodal behavior in the continental study site (Camarero *et al.* 2010; Campelo *et al.* 2018; Tumajer *et al.* 2022).

To the best of our knowledge, this is the first report of latewood IADF formation in *Q. faginea*. Previous studies already reported the relevance of winter-spring precipitation for growth and earlywood production in *Q. faginea* (Alla & Camarero 2012; Camarero 2018), whereas dry summer conditions were often related to a reduced or even null latewood production (Corcuera *et al.* 2004a). Here, we showed that latewood IADFs reflect rare events of wet summer conditions, which may correspond to convective storms and sporadic rainfall episodes leading to lower maximum temperatures, reduced evapotranspiration rates, higher relative humidity, increased soil moisture and punctual peaks in forest productivity (Camarero 2022). Quantitative wood anatomy data indicate that vessel lumen area slightly increased after the IADF, suggesting increased hydraulic conductivity (data not shown). However, further IADF rings and sensitive study sites would be required to test this idea, considering that wood anatomy and growth variations are very responsive to precipitation variability in xeric sites such as the one studied here (Alla & Camarero 2012). Anyway, the increase in wood density associated with the IADF band parenchyma cells confirms an improved capacity to grow and capture carbon as stem wood, in agreement with the positive association between IADF frequency and August

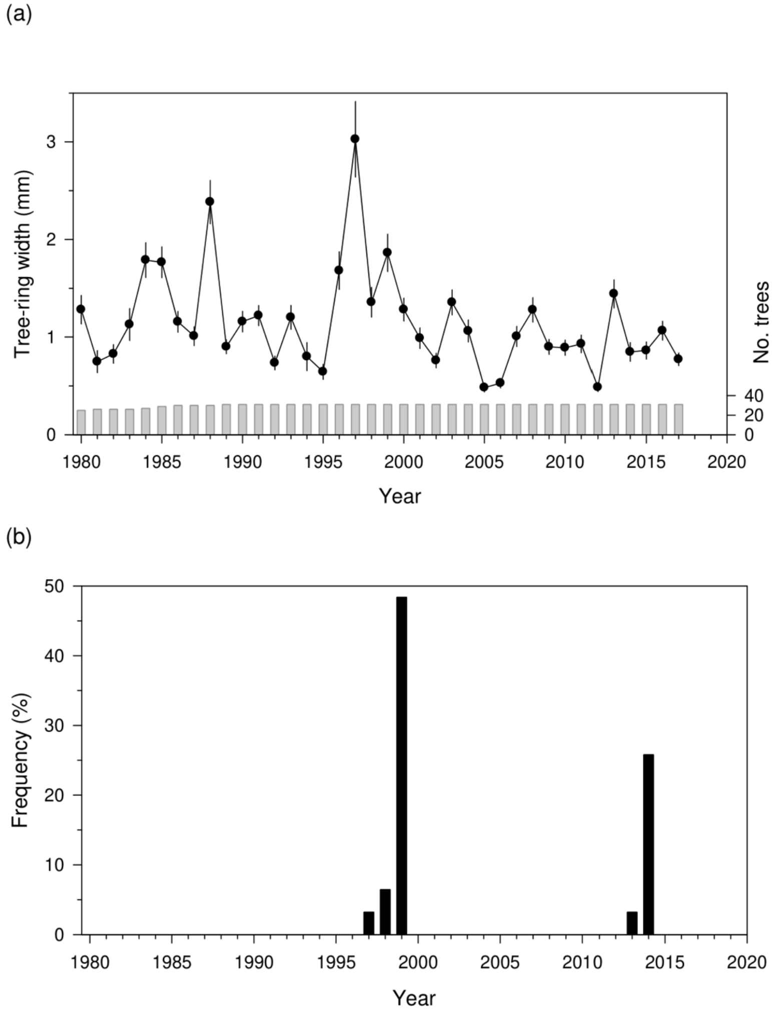

Fig. 2. (a) Year-to-year growth variability in the study *Q. faginea* population (b) Percentage of trees showing latewood intra-annual density fluctuations (IADF) each year.

NDVI. Such rare summer wet conditions would lead to increased canopy activity, thus potentially enhancing forest productivity. This is indicated by the positive association found between NDVI and cool summer conditions, which correspond to low evapotranspiration rates and higher soil moisture levels. Reductions in vapor pressure deficit could increase cambium activity and tracheid turgor pressure, thus enhancing radial growth, particularly during night and early morning as has been reported for conifers (Zweifel *et al.* 2021; Camarero 2022; Vieira *et al.* 2022).

Xylogenesis studies in sites with seasonally dry climate regimes have confirmed bimodal to multimodal growth patterns and how increased precipitation and soil moisture reactivated growth after the dry season in several conifer and hardwood species leading to IADF formation (De Luis *et al.* 2007; Camarero *et al.* 2010; De Micco *et al.* 2012, 2016b; Balzano *et al.* 2018, 2021; Ziaco *et al.* 2018; Morino *et al.* 2021). However, similar data are still lacking for hardwoods from continental seasonally dry regions, despite simulation outputs based on climate-growth models and dendrometer data showing the relevance of facultative bimodality in *Q. faginea* (Camarero *et al.* 2021; Tumajer *et al.* 2022; Campelo *et al.* 2023). This second period of growth could represent almost half of the annual growth in years with high precipitation after the summer and low precipitation in spring (Campelo *et al.* 2007a, 2023; Balzano *et al.* 2021). It

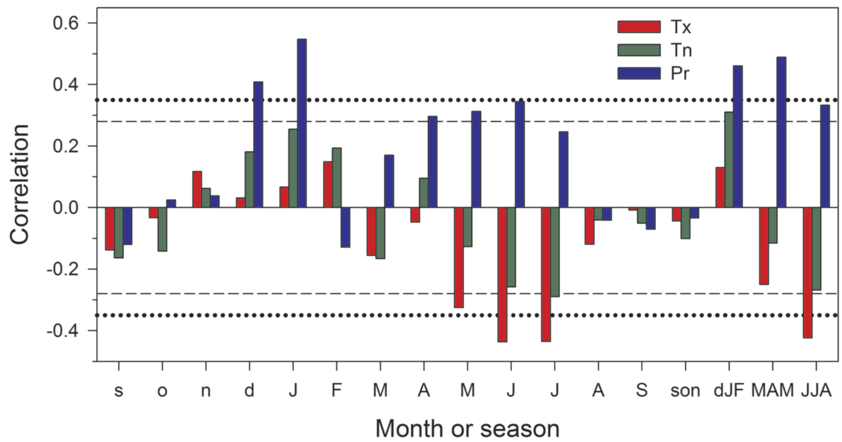

Fig. 3. Climate-growth relationships (Pearson correlations) in *Q. faginea* considering monthly or seasonal climate variables (Tx, mean maximum temperature; Tn, mean minimum temperature; Pr, precipitation). Months abbreviated by lowercase and uppercase letters correspond to the previous and current years, respectively. The dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively.

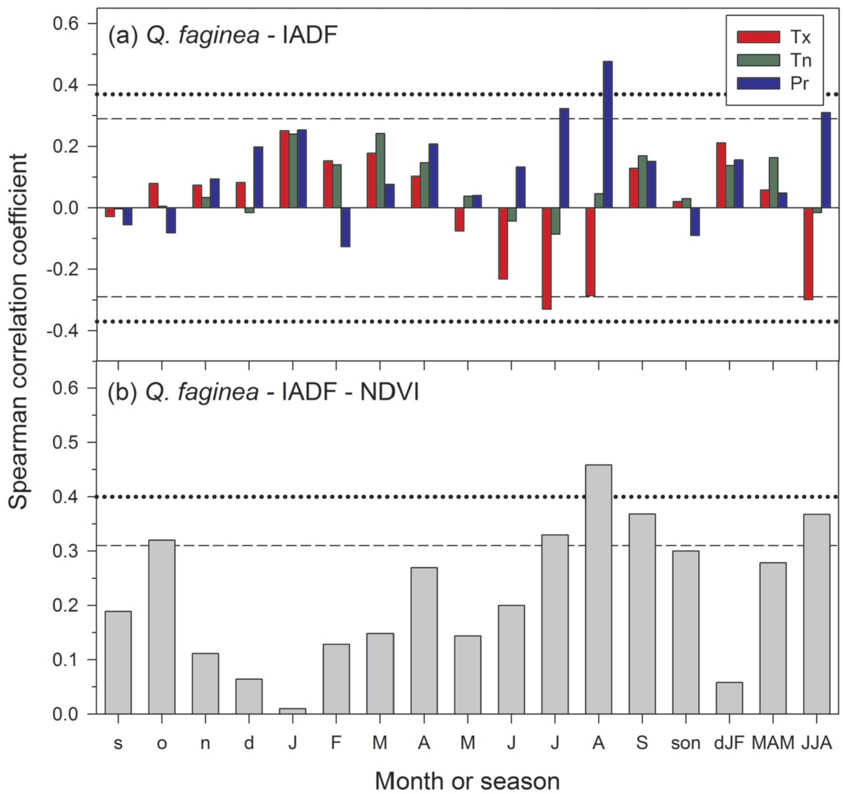

Fig. 4. (a) Climate-IADF and (b) NDVI-IADF relationships (Spearman correlations) in *Q. faginea*. Monthly or seasonal climate variables (Tx, mean maximum temperature; Tn, mean minimum temperature; Pr, precipitation). Months abbreviated by lowercase and uppercase letters correspond to the previous and current years, respectively. The dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively.

is plausible that latewood IADF formation is linked to growth bimodality in hardwood species. Similar associations as those presented here between summer-autumn wet conditions and IADF formation were already reported for the evergreen *Q. ilex* which is considered more bimodal than *Q. faginea* (Zhang & Romane 1991; Campelo *et al.* 2007a, 2018, 2021). *Q. faginea* tends to show an earlier and stronger growth peak in spring whilst *Q. ilex* can grow more in autumn if soil moisture is not too low (Montserrat-Martí *et al.* 2009; Gutiérrez *et al.* 2011; Balzano *et al.* 2021; Camarero *et al.* 2021). The formation of latewood IADFs in *Q. faginea* is triggered by high precipitation in late summer, which suggests a shorter potential growing season than in coexisting evergreen species such as *Q. ilex* which can grow and form IADFs in mid to late autumn (Balzano *et al.* 2021; Campelo *et al.* 2021, 2023; Tumajer *et al.* 2022). The shift from unimodal to bimodal growth patterns in *Q. faginea* and the consequent IADF production occurs in response to particular and rare climatic conditions (summer storms). Therefore, an increase in the frequency of IADFs could be related to more extreme climate events (Vieira *et al.* 2010). More sites and hardwood species showing potential bimodality could be screened searching for similar latewood IADFs and climatic proxies in seasonally dry regions.

To conclude, we found that latewood IADFs were formed by *Q. faginea* in response to wet late summer conditions which also enhanced NDVI. These climatic conditions are different from those enhancing *Q. faginea* growth which corresponded to wet winter-spring conditions and cool summer temperatures. Albeit rarely produced, latewood IADFs are a robust proxy of summer wet conditions and increased canopy activity in Mediterranean continental regions. To test the robustness of this proxy, we suggest further studies of this wood-anatomical feature in other ring-porous, winter-deciduous oak species along climatic gradients with different spring/summer precipitation ratios (Valeriano *et al.* 2023).

Acknowledgements

XSM is supported by "Juan de la Cierva" Formación fellowship (FJC2021-046451-I) from the Spanish Ministry of Science and Innovation. AG is supported by the "Ramón y Cajal" Program of the Spanish MICINN under Grant RyC2020-030647-I, and by CSIC under grant PIE-20223AT003. This research was funded by the Science and Innovation Ministry and the AEI with projects PID2021-123675OB-C43 and TED2021-129770B-C21. We thank the editors and reviewers for their very constructive comments on an earlier version of the manuscript.

References

Alla AQ, Camarero JJ. 2012. Contrasting responses of radial growth and wood anatomy to climate in a Mediterranean ring-porous oak: implications for its future persistence or why the variance matters more than the mean. *Eur. J. For. Res.* 131: 1537–1550. DOI: 10.1007/s10342-012-0621-x.

Alla AQ, Camarero JJ, Rivera P, Montserrat-Martí G. 2011. Variant allometric scaling relationships between bud size and secondary shoot growth in *Quercus faginea*: implications for the climatic modulation of canopy growth. *Ann. For. Sci.* 68: 1245–1254. DOI: 10.1007/s13595-011-0093-z.

Balzano A, Čufar K, Battipaglia G, Merela M, Prislan P, Aronne G, De Micco V. 2018. Xylogenesis reveals the genesis and ecological signal of IADFs in *Pinus pinea* L. and *Arbutus unedo* L. *Ann. Bot.* 121: 1231–1242. DOI: 10.1093/aob/mcy008.

Balzano A, Čufar K, De Micco V. 2021. Xylem and phloem formation dynamics in *Quercus ilex* L. at a dry site in southern Italy. *Forests* 12: 188.

Battipaglia G, De Micco V, Brand WA, Linke P, Aronne G, Saurer M, Cherubini P. 2010. Variations of vessel diameter and $\delta^{13}C$ in false rings of *Arbutus unedo* L. reflect different environmental conditions. *New Phytol.* 188: 1099–1112. DOI: 10.1111/j.1469-8137.2010.03443.x.

Battipaglia G, De Micco V, Brand WA, Saurer M, Aronne G, Linke P, *et al.* 2014. Drought impact on water use efficiency and intra-annual density fluctuations in *Erica arborea* on Elba (Italy). *Plant Cell Env.* 37: 382–391. DOI: 10.1111/pce.12160.

Battipaglia G, Campelo F, Vieira J, Grabner M, De Micco V, *et al.* 2016. Structure and function of intra–annual density fluctuations: mind the gaps. *Front. Plant Sci.* 7: 595. DOI: 10.3389/fpls.2016.00595.

Bogino S, Bravo F. 2009. Climate and intraannual density fluctuations in *Pinus pinaster* subsp. *mesogeensis* in Spanish woodlands. *Can. J. For. Res.* 39: 1557–1565.

Bunn AG. 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26: 115–124. DOI: 10.1016/j.dendro.2008.01.002.

Camarero JJ. 2018. Linking functional traits and climate-growth relationships in Mediterranean species through wood density. *IAWA J.* 40: 215–240. DOI: 10.1163/22941932-40190225.

Camarero JJ. 2022. Why intra-annual density fluctuations should be formed at night? Implications for climate-growth relationships in seasonally dry conifer forests. *Forests* 13: 1425.

Camarero JJ, Olano JM, Parras P. 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. *New Phytol.* 2: 471–480. DOI: 10.1111/j.1469-8137.2009.03073.x.

Camarero JJ, Rozas V, Olano JM. 2014. Minimum wood density of *Juniperus thurifera* is a robust proxy of spring water availability in a continental Mediterranean climate. *J. Biogeogr.* 41: 1105–1114. DOI: 10.1111/jbi.12271.

Camarero JJ, Rubio-Cuadrado A, Gazol A. 2021. Climate windows of intra-annual growth and post-drought recovery in Mediterranean trees. *Agric. For. Meteorol.*: 308–309: 108606. DOI: 10.1016/j.agrformet.2021.108606.

Campelo F, Gutiérrez E, Ribas M, Nabais C, Freitas H. 2007a. Relationships between climate and double rings in *Quercus ilex* from northeast Spain. *Can. J. For. Res.* 37: 1915–1923. DOI: 10.1139/x07-050.

Campelo F, Nabais C, Freitas H, Gutiérrez E. 2007b. Climatic significance of tree-ring width and intra-annual density fluctuations in *Pinus pinea* from a dry Mediterranean area in Portugal. *Ann. For. Sci.* 64: 229–238.

Campelo F, Vieira J, Nabais C. 2013. Tree-ring growth and intra-annual density fluctuations of *Pinus pinaster* responses to climate: does size matter? *Trees Struct. Funct.* 27: 763–772. DOI: 10.1007/s00468-012-0831-3.

Campelo F, Gutiérrez E, Ribas M, Sánchez-Salguero R, Nabais C, Camarero JJ. 2018. The facultative bimodal growth pattern in *Quercus ilex* — a simple model to predict sub-seasonal and inter-annual growth. *Dendrochronologia* 49: 77–88. DOI: 10.1016/j.dendro.2018.03.001.

Campelo F, Ribas M, Gutiérrez E. 2021. Plastic bimodal growth in a Mediterranean mixed-forest of *Quercus ilex* and *Pinus halepensis*. *Dendrochronologia* 67: 125836. DOI: 10.1016/j.dendro.2021.125836.

Campelo F, Rubio-Cuadrado Á, Montes F, Colangelo M, Valeriano C, Camarero JJ. 2023. Growth phenology adjusts to seasonal changes in water availability in coexisting evergreen and deciduous Mediterranean oaks. *For. Ecosyst.* 10: 100134. DOI: 10.1016/j.fecs.2023.100134.

Cherubini P, Gartner BL, Tognetti R, Bräker OU, Schoch W, Innes JL. 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. *Biol. Rev.* 78: 119–148.

Collado E, Camarero JJ, Martínez de Aragón J, Pemán J, Bonet JA, de-Miguel S. 2018. Linking fungal dynamics, tree growth and forest management in a Mediterranean pine ecosystem. *For. Ecol. Manage.* 422: 223–232. DOI: 10.1016/j.foreco.2018.04.025.

Corcuera L, Camarero JJ, Gil-Pelegrín E. 2004a. Effects of a severe drought on growth and wood-anatomical properties of *Quercus faginea*. *IAWA J.* 25: 185–204. DOI: 10.1163/22941932-90000360.

Corcuera L, Camarero JJ, Gil-Pelegrín E. 2004b. Effects of a severe drought on *Quercus ilex* radial growth and xylem anatomy. *Trees Struct. Funct.* 18: 83–92. DOI: 10.1007/s00468-003-0284-9.

De Luis M, Gričar J, Čufar K, Raventós J. 2007. Seasonal dynamics of wood formation in *Pinus halepensis* from dry and semi-arid ecosystems in Spain. *IAWA J.* 28: 389–404. DOI: 10.1163/22941932-90001651.

De Luis M, Novak K, Raventós J, Gričar J, Prislan P, Čufar K. 2011. Climate factors promoting intra-annual density fluctuations in Aleppo pine (*Pinus halepensis*) from semiarid sites. *Dendrochronologia* 29: 163–169. DOI: 10.1016/j.dendro.2011.01.005.

De Micco V, Aronne G. 2009. Seasonal dimorphism in wood anatomy of the Mediterranean *Cistus incanus* L. subsp. *incanus*. *Trees Struct. Funct.* 23: 981–989. DOI: 10.1007/s00468-009-0340-1.

De Micco V, Saurer M, Aronne G, Tognetti R, Cherubini P. 2007. Variations of wood anatomy and $\delta^{13}C$ within-tree rings of coastal *Pinus pinaster* showing intra-annual density fluctuations. *IAWA J.* 28: 61–74. DOI: 10.1163/22941932-90001619.

De Micco V, Battipaglia G, Brand WA, Linke P, Saurer M, Aronne G, Cherubini P. 2012. Discrete versus continuous analysis of anatomical and $\delta^{13}C$ variability in tree rings with intra-annual density fluctuations. *Trees Struct. Funct.* 26: 513–524. DOI: 10.1007/s00468-011-0612-4.

De Micco V, Campelo F, de Luis M, Bräuning A, Grabner M, Battipaglia G, *et al.* 2016a. Formation of intra-annual-density-fluctuations in tree rings: how, when, where and why? *IAWA J.* 37: 232–259. DOI: 10.1163/22941932-20160132.

De Micco V, Balzano A, Čufar K, Aronne G, Gričar J, Merela M, Battipaglia G. 2016b. Timing of false ring formation in *Pinus halepensis* and *Arbutus unedo* in Southern Italy: outlook from an analysis of xylogenesis and tree-ring chronologies. *Front. Plant Sci.* 7. DOI: 10.3389/fpls.2016.00705.

Fritts HC. 1976. *Tree rings and climate*. Academic Press, London.

Gutiérrez E, Campelo F, Camarero JJ, Ribas M, Muntán E, Nabais C, Freitas H. 2011. Climate controls act at different scales on the seasonal pattern of *Quercus ilex* L. stem radial increments in NE Spain. *Trees Struct. Funct.* 25: 637–646. DOI: 10.1007/s00468-011-0540-3.

Hantson S, Chuvieco E. 2011. Evaluation of different topographic correction methods for Landsat imagery. *Int. J. Appl. Earth Obs. Geoinf.* 13: 691–700.

Holmes RL. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43: 69–78.

IPCC. 2021. Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, *et al.* (eds.), *Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*: 3–32. Cambridge University Press, Cambridge, UK. DOI: 10.1017/9781009157896.001.

Kannenberg SA, Novick KA, Alexander MR, Maxwell JT, Moore DJP, Phillips RP, Anderegg WRL. 2019. Linking drought legacy effects across scales: from leaves to tree rings to ecosystems. *Glob. Chang Biol.* 25: 2978–2992.

Larson PR. 1994. *The vascular cambium: development and structure*. Springer, Berlin.

Li Y, Zhang W, Schwalm CR, Gentine P, Smith WK, *et al.* 2023. Widespread spring phenology effects on drought recovery of Northern Hemisphere ecosystems. *Nature Clim. Chang.* 13: 182–188. DOI: 10.1038/s41558-022-01584-2.

Loidi J, Herrera M. 1990. The *Quercus pubescens* and *Quercus faginea* forests in the Basque Country (Spain): distribution and typology in relation to climatic factors. *Vegetatio* 90: 81–92.

Masiokas M, Villalba R. 2004. Climatic significance of intra-annual bands in the wood of *Nothofagus pumilio* in southern Patagonia. *Trees Struct. Funct.* 18: 696–704. DOI: 10.1007/s00468-004-0355-6.

Montserrat-Martí G, Camarero JJ, Palacio S, Pérez-Rontomé C, Milla R, Albuixech J, Maestro M. 2009. Summer-drought constrains the phenology and growth of two co-existing Mediterranean oaks with contrasting leaf habit: implications for their persistence and reproduction. *Trees Struct. Funct.* 4: 787–799. DOI: 10.1007/s00468-009-0320-5.

Morino K, Minor RL, Barron-Gafford GA, Brown PM, Hughes MK. 2021. Bimodal cambial activity and false-ring formation in conifers under a monsoon climate. *Tree Physiol.* 41: 1893–1905. DOI: 10.1093/treephys/tpab045.

Novak K, Saz-Sánchez MA, Čufar K, Raventós J, De Luis M. 2013. Age, climate and intra-annual density fluctuations in *Pinus halepensis* in Spain. *IAWA J.* 34: 459–474. DOI: 10.1163/22941932-00000037.

Olano JM, García-Cervigón AI, Arzac A, Rozas V. 2015. Intra-annual wood density fluctuations and tree-ring width patterns are sex- and site-dependent in the dioecious conifer *Juniperus thurifera* L. *Trees Struct. Funct.* 29: 1341–1353. DOI: 10.1007/s00468-015-1212-5.

R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available online at https://www.R-project.org.

Rigling A, Waldner PO, Forster T, Bräker OU, Pouttu A. 2001. Ecological interpretation of tree-ring width and intraannual density fluctuations in *Pinus sylvestris* on dry sites in the central Alps and Siberia. *Can. J. For. Res.* 31: 18–31.

Roy DP, Kovalskyy V, Zhang HK, Vermote EF, Yan L, Kumar SS, Egorov A. 2016. Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity. *Rem. Sens. Environ.* 185: 57–70.

Rozas V, García-González I, Zas R. 2011. Climatic control of intra-annual wood density fluctuations of *Pinus pinaster* in NW Spain. *Trees Struct. Funct.* 25: 443–453. DOI: 10.1007/s00468-010-0519-5.

Serra-Maluquer X, Granda E, Camarero JJ, Vilà-Cabrera A, Jump AS, Sánchez-Salguero R, Sangüesa-Barreda G, Imbert B, Gazol A. 2021. Impacts of recurrent dry and wet years alter long-term tree growth trajectories. *J. Ecol.* 109: 1561–1574. DOI: 10.1111/1365-2745.13579.

Tucker C. 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Rem. Sens. Environ.* 8: 127–150.

Tumajer J, Serra-Maluquer X, Gazol A, González de Andrés E, Colangelo M, *et al.* 2022. Bimodal and unimodal radial growth of Mediterranean oaks along a coast-inland gradient. *Agric. For. Meteorol.* 327: 109234. DOI: 10.1016/j.agrformet.2022.109234.

Valeriano C, Gutiérrez E, Colangelo M, Gazol A, Sánchez-Salguero R, *et al.* 2023. Seasonal precipitation and continentality drive bimodal growth in Mediterranean forests. *Dendrochronologia* 78: 126057. DOI: 10.1016/j.dendro.2023.126057.

Vicente-Serrano SM, Camarero JJ, Olano JM, Martín-Hernández N, Peña-Gallardo M, *et al.* 2016. Diverse relationships between forest growth and the normalized difference vegetation index at a global scale. *Rem. Sens. Env.* 187: 14–29. DOI: 10.1016/j.rse.2016.10.001.

Vieira J, Campelo F, Nabais C. 2009. Age-dependent responses of tree-ring growth and intra-annual density fluctuations of *Pinus pinaster* to Mediterranean climate. *Trees Struct. Funct.* 23: 257–265. DOI: 10.1007/s00468-008-0273-0.

Vieira J, Campelo F, Nabais C. 2010. Intra-annual density fluctuations of *Pinus pinaster* are a record of climatic changes in the western Mediterranean region. *Can. J. For. Res.* 40: 1567–1575. DOI: 10.1139/X10-096.

Vieira J, Campelo F, Nabais C. 2022. Environment controls seasonal and daily cycles of stem diameter variations in Portuguese oak (*Quercus faginea* Lambert). *Forests* 13: 170. DOI: 10.3390/f13020170.

Wimmer R. 2002. Wood anatomical features in tree-rings as indicators of environmental change. *Dendrochronologia* 20: 21–36. DOI: 10.1078/1125-7865-00005.

Wimmer R, Strumia G, Holawe F. 2000. Use of false rings in Austrian pine to reconstruct early growing season precipitation. *Can. J. For. Res.* 30: 1691–1697. DOI: 10.1139/x00-095.

Yamaguchi DK. 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* 21: 414–416.

Zalloni E, de Luis M, Campelo F, Novak K, De Micco V, *et al.* 2016. Climatic signals from intra-annual density fluctuation frequency in Mediterranean pines at a regional scale. *Front. Plant Sci.* 7. DOI: 10.3389/fpls.2016.00579.

Zhang SH, Romane F. 1991. Variations de la croissance radiale de *Quercus ilex* L. en function du climat. *Ann. Sci. For.* 48: 225–234.

Ziaco E, Truettner C, Biondi F, Bullock S. 2018. Moisture-driven xylogenesis in *Pinus ponderosa* from a Mojave Desert Mountain reveals high phenological plasticity. *Plant Cell Environ.* 41: 823–836. DOI: 10.1111/pce.13152.

Zweifel R, Sterck F, Braun S, Buchmann N, Eugster W, *et al.* 2021. Why trees grow at night. *New Phytol.* 231: 2174–2185. DOI: 10.1111/nph.17552.

Edited by Veronica de Micco

Appendix

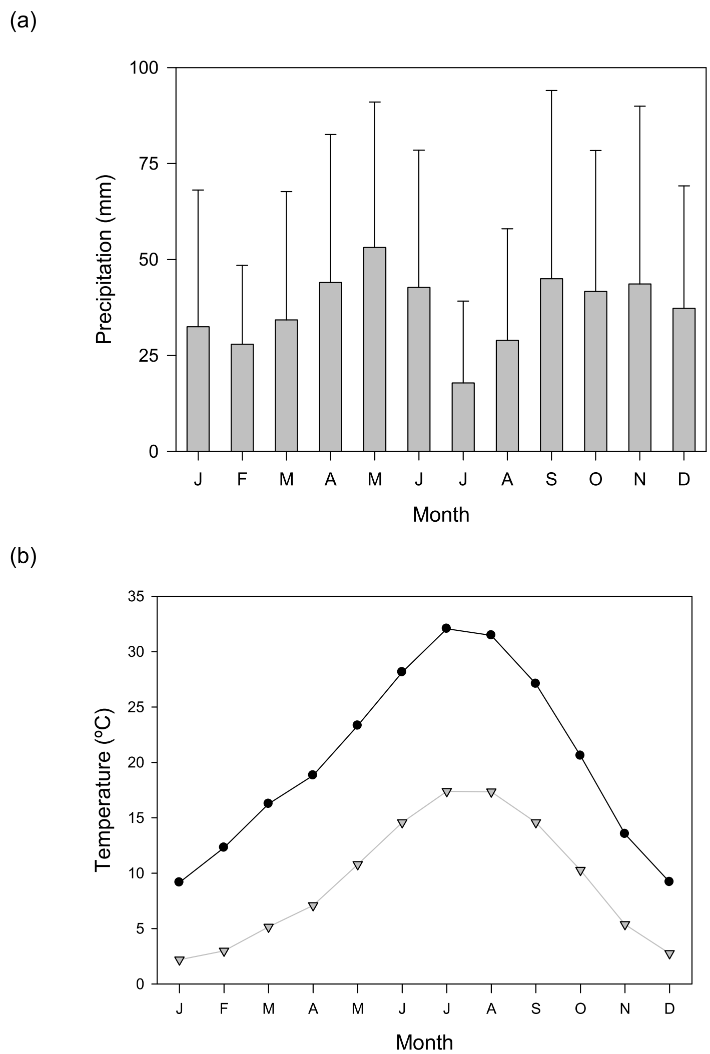

Fig. A1. (a) Monthly precipitation data (means ± SD) and (b) maximum and minimum temperatures from the Alcubierre station (41.82°N, 0.45°W, 466 m a.s.l.), located at ca. 5 km from the study site. Data correspond to the 1950–2020 period.

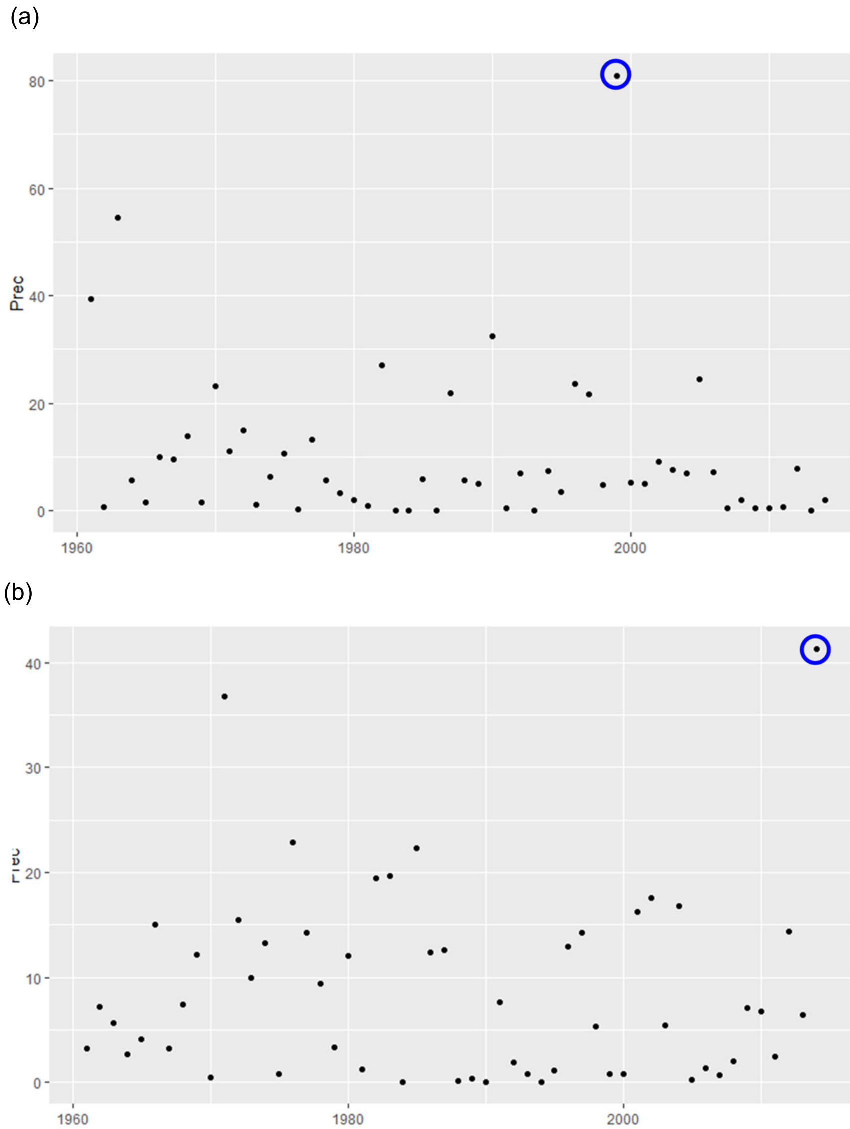

Fig. A2. Weekly precipitation (in mm) was recorded in the (a) last week of July and the (b) first week of August showing high values (blue circles) in 1999 (a) and 2014 (b), respectively. Note the different *y*-axis scales.

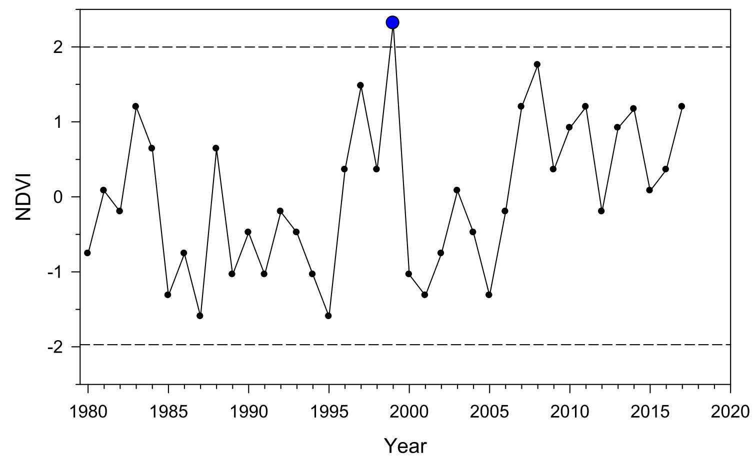

Fig. A3. Standardized NDVI values during the second half of August. The blue symbol shows the value in 1999, and the dashed lines show the 0.05 significance levels.

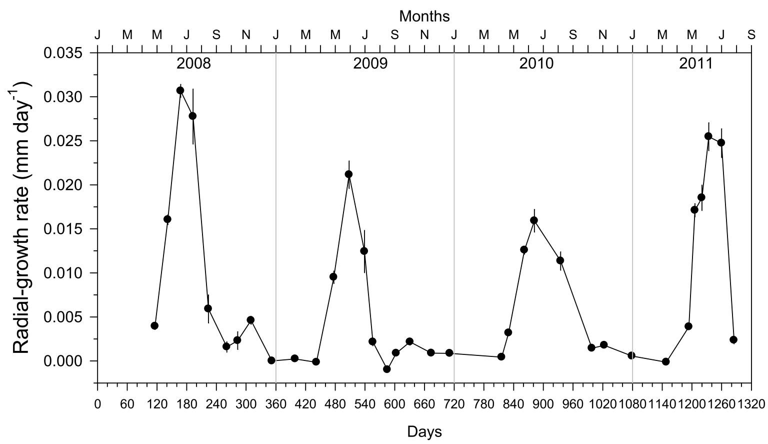

Fig. A4. Radial increment rates of *Q. faginea* according to band dendrometer data (period 2008–2011). Values are means ± SE (n = 10 trees).