



Reproductive phenology determines the linkages between radial growth, fruit production and climate in four Mediterranean tree species

Sergi Garcia-Barreda^a, Gabriel Sangüesa-Barreda^b, Jaime Madrigal-González^c,
Francisco Seijo^d, Ester González de Andrés^e, J. Julio Camarero^{e,*}

^a Centro de Investigación y Tecnología Agroalimentaria de Aragón (CITA), Instituto Agroalimentario de Aragón – IA2 (CITA-Universidad de Zaragoza), Avda. Montañana 930, 50059 Zaragoza, Spain

^b EiFAB-iuFOR, University of Valladolid, Campus Duques de Soria, 42004 Soria, Spain

^c Climate Change Impacts and Risks in the Anthropocene, Institute for Environmental Sciences (IES), University of Geneva, 66 Boulevard Carl Vogt, 1025-CH Geneva, Switzerland

^d IE School of Global and Public Affairs, 28006 Madrid, Spain

^e Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, 50080 Zaragoza, Spain

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ABSTRACT

The influence of climate on seed or fruit production and tree growth is a central question in forest ecology, with a key role on forest dynamics. However, the mechanisms linking inter- and intra-annual climate variability, fruiting and growth remain poorly understood, although they seem to be largely species-specific. The resource-matching hypothesis posits that fruit production responds to annual environmental variability, predicting a positive relationship between reproduction and growth, whereas other hypotheses such as resource switching or resource budget imply allocation trade-offs between reproduction and growth. Climate control over fruiting is thought to be more likely in variable, limiting environments such as those existing in seasonally dry Mediterranean forests. However, the studies about these forests are much scarcer than on temperate ecosystems, probably due to the sparseness and shortness of fruit production records. Here we analysed the relationships between monthly climate variables, tree-ring widths and fruit production at stand level in four tree species under different climatic conditions in Spain (12–27 trees and 24–54 radii were sampled in each site). For the species from xeric sites such as *Pinus pinea*, *Castanea sativa* and *Quercus ilex*, tree-ring width positively correlated with fruit production, as envisaged by the resource-matching hypothesis. This association was driven by prior wet winter climate conditions, which enhanced growth. Some of the significant correlations between climate variables and fruit yield corresponded to key reproductive phenophases. On the other hand, for the species from mesic sites (*Abies alba*) no positive growth–fruit production correlation was found, likely due to the mismatch in the effect of climatic factors on growth and fruiting. These results support the hypothesis that climatic conditions, particularly a positive water balance, play a major role as a proximate cause of fruit production in seasonally dry Mediterranean forests and underscore the importance of species-specific reproductive phenology traits.

1. Introduction

The spatio-temporal dynamics of seed and fruit production in trees are a central question in forest ecology, playing a key role in forest regeneration and dynamics, shifts in forest composition and wildlife population dynamics (Pearse et al., 2016; Bogdziewicz et al. 2020). Moreover, some forest fruits (e.g., pine cones, chestnuts) have a relevant socio-economic importance that determines the management and planning of productive forests (Lovrić et al., 2020). Some forest tree

species show a high inter-annual variability in seed production while many others present a fairly regular pattern (Fernández-Martínez et al., 2019; Nussbaumer et al., 2018). Understanding and forecasting the climate-tree interactions in fruit production can help to improve the management of both the ecological and economic functioning of forests. It could also assist the conservation efforts for some endangered species or rear-edge tree populations, for which seed production could be a useful indicator of species fitness (González de Andrés et al., 2014; Lindner et al., 2010).

* Corresponding author.

E-mail address: jjcamarero@ipe.csic.es (J.J. Camarero).

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Seed and fruit production in trees is contingent upon different factors, including local climate, resources availability and acquisition, reserve storage endogenous dynamics or the availability of pollinators (Kelly and Sork 2002). Whereas adaptive benefits are the ultimate driver of synchronised, variable reproduction (i. e., large reproductive effort at irregular intervals), resources availability and climate forcing frequently act as proximate factors (Nussbaumer et al., 2018; Pearse et al., 2016; Piovesan and Adams, 2001; Selås et al., 2002; Vergotti et al., 2019). Despite this, the mechanisms linking climate and stored reserves to fruit production remain poorly understood and several hypothesis have been proposed (Koenig et al., 2016; Pearse et al., 2016; Piovesan and Adams, 2001). The resource-matching hypothesis posits that high seed production occurs in years when more resources are available, thus predicting a positive relationship between reproduction and growth (Kelly and Sork, 2002; Vergotti et al., 2019). The resource-budget hypothesis posits that “full” seed crops cannot occur every year because reproduction is costly, and the tree must accumulate resources beyond a certain threshold, with large reproductive efforts depleting reserves (Sala et al., 2012). The resource-switching hypothesis posits that a tree invests a relatively constant amount of the current-year resources to either growth or reproduction, thus predicting allocation trade-offs between reproduction and growth (Żywiec and Zielonka, 2013). In these hypotheses, climatic factors play a role either by constraining the acquisition of resources or as mere synchronising cues (Fernández-Martínez et al., 2017; Kelly et al., 2013; Vergotti et al., 2019).

The relationships among annual crop production, climatic factors and the stored reserves of trees seem to be largely species-specific and contingent on local conditions (Nussbaumer et al., 2018). In wind-pollinated trees, the role of climate is sometimes linked to flower production (or pollination success) and other times to fruit development, with both mechanisms being detected in genera such as *Quercus*, *Fagus*, *Nothofagus*, *Carpinus* or *Ostrya* (Bogdziewicz et al., 2017; Monks and Kelly, 2006; Pearse et al., 2016; Pesendorfer et al., 2016). Kelly and Sork (2002) suggested that evidences of climate control over fruiting are more likely in variable, limiting environments, which is consistent with the observations in seasonally dry Mediterranean climates (Pérez-Ramos et al., 2010; Shestakova et al., 2021; Vergotti et al., 2019). While seed production patterns have received great attention in temperate forests (Nussbaumer et al., 2018; Pesendorfer et al., 2016), the opposite is true in Mediterranean forests where information is limited to a few species such as *Pinus pinea* or *Quercus ilex* (Calama et al., 2011; Espelta et al., 2008; García-Mozo et al., 2012; Pérez-Ramos et al., 2010).

In this study, we explored the relationships at stand level between climate conditions, growth and fruit production in four tree species studied in Spain: two broadleaf (*Castanea sativa* and *Quercus ilex*) and two conifer species (*Pinus pinea* and *Abies alba*). We evaluated: (i) the influence of temperature variability and water deficit on fruit production, and (ii) the relationship between radial growth and fruit production in the four species. For the *Q. ilex* stand, we also evaluated the growth-fruiting relationships at tree level. For the xeric *Q. ilex* and *P. pinea* forests, located in the driest sites, previous studies have found a relationship between climatic factors and the main phases of the reproductive phenology during flower production or fruit development (Mutke et al., 2005; Pérez-Ramos et al., 2010), whereas for the mesic *A. alba* forests previous studies suggest a key role of allocation trade-offs (Davi et al., 2016). We hypothesised that in drier sites growth and reproduction would be more positively related and that this fact would be linked to the water availability on key periods for tree performance. We expected that this would not be the case in mesic sites (*A. alba*) or in Mediterranean sites with a marked summer drought but abundant precipitation in spring and autumn (*C. sativa*). Finally, we discuss how the differences in the reproductive phenology of the species determine the relationships between climate, growth and fruiting.

2. Materials and methods

2.1. Study area and target tree species

We analysed four sites located in Spain: a *P. pinea* site in Viloria (Tierra de Pinares, Valladolid province), a *C. sativa* site in Casillas (Sierra de Gredos, Ávila province), a *Q. ilex* site in Arascués (Sierra de Guara, Huesca province), and an *A. alba* site in Gamueta (Pyrenees, Huesca province). These sites are spread over a wide geographical area and contrasting altitudes (Table 1, Fig. S1), although in all cases the sites are situated within the core area of each species in Spain. The climate of the sites is continental Mediterranean in the three former and humid continental in the latter (*A. alba*), with the *P. pinea* and the *Q. ilex* sites being much drier than the *C. sativa* and *A. alba* sites (Table 1, Fig. S2). The *P. pinea* site is an open forest (about 50 trees ha⁻¹ with mean diameter at breast height of the dominant trees –DBH– of 54 cm), as usual for forests aimed at pine nut production (Calama et al., 2011). The *C. sativa* site is a closed-canopy forest with mean DBH of 42 cm, where chestnuts are traditionally harvested every year (Seijo et al., 2017). The *Q. ilex* site is a coppice forest with closed canopy cover and mean DBH of 8.4 cm (Camarero et al., 2010). The *A. alba* site is a mixed, old-growth forest in which *A. alba* (mean DBH of 58.4 cm) coexists with *Fagus sylvatica* (González de Andrés et al., 2014).

The four studied tree species are wind pollinated, although insect pollination also plays a relevant role in *C. sativa* (Table 2). The four species are monoecious with unisexual flowers. The fruits of the two broadleaf species, the deciduous *C. sativa* and the evergreen *Q. ilex*, mature the same year that the flowers are borne: *C. sativa* flowers in May-June and fruits are fully ripe in late October, whereas *Q. ilex* flowers in April-May and fruits are fully ripe in October-November (Table 2). By contrast, *P. pinea* takes about three years from floral bud differentiation to seed maturity, with seed dispersal taking place during the following year. Thus, floral bud induction and bud differentiation begins four years before seed dispersal (June of year $i - 4$), pollination takes place three years before seed dispersal (May-June of year $i - 3$), the main cone growth period takes place during the year before seed dispersal (April-June of year $i - 1$), and fruits are fully ripe in October-November of that year (Table 2; Calama et al., 2011). Finally, *A. alba* takes two growing seasons from bud differentiation to seed ripening, with bud differentiation beginning in July of the year before seed dispersal (year $i - 1$), pollination taking place in May of the following year (year i), and seeds being fully ripe in late September of that year (Table 2).

2.2. Climate data

Monthly values of mean minimum temperature, mean maximum

Table 1
Geographical characteristics and dendrochronological statistics of the studied forests. RW: tree-ring width (mean and standard deviation between parentheses). r_{bt} : mean between-trees correlation calculated for the common interval 1965–2013.

Species	<i>Pinus pinea</i>	<i>Castanea sativa</i>	<i>Quercus ilex</i>	<i>Abies alba</i>
Latitude (N)	41.5°	40.3°	42.2°	42.9°
Longitude (W)	4.4°	4.6°	0.4°	0.8°
Elevation (m a.s.l.)	900	1000	650	1400
Mean annual temperature (°C)	11.9	12.3	13.1	7.9
Mean annual rainfall (mm)	387	907	505	1366
Best replicated interval	1965–2016	1941–2013	1960–2017	1862–2018
No trees (No. radii)	20 (40)	12 (24)	27 (54)	22 (44)
RW (mm)	3.2 (1.2)	2.8 (1.1)	0.7 (0.2)	1.1 (0.3)
r_{bt}	0.59	0.35	0.43	0.30

Table 2

Timing of the reproductive phenology phases for the studied species, according to Feijó et al. (1999), Mutke et al. (2005), Gómez-Casero et al. (2007) and Pemán et al. (2012). Year *i*: year of seed dispersal.

	<i>Pinus pinea</i>	<i>Castanea sativa</i>	<i>Quercus ilex</i>	<i>Abies alba</i>
Initiation of buds containing flower primordia	June of year (<i>i</i> – 4)	April-May (year <i>i</i>)	February-April (year <i>i</i>)	April-May of year (<i>i</i> – 1)
Flower primordia differentiation and development	Spring of year (<i>i</i> – 3)	May-June (year <i>i</i>)	April-May (year <i>i</i>)	July-October of year (<i>i</i> – 1), early spring of year <i>i</i>
Pollination	June of year (<i>i</i> – 3)	May-June (year <i>i</i>)	April-May (year <i>i</i>)	Late May of year <i>i</i>
Fertilisation	June of year (<i>i</i> – 1)	Within 10-20 days from pollination	June-July (year <i>i</i>)	Mid July of year <i>i</i>
Period of fruit main growth (seed in the case of <i>A. alba</i>)	April-June of year (<i>i</i> – 1)	August-September (year <i>i</i>)	August-September (year <i>i</i>)	August-September of year <i>i</i>
Ending of fruit ripening (harvesting begins)	November of year (<i>i</i> – 1)	Late October (year <i>i</i>)	October-November (year <i>i</i>)	Late September of year <i>i</i>
Seed dispersal	April-September of year <i>i</i>	October-December (year <i>i</i>)	November of year <i>i</i> to January of year (<i>i</i> + 1)	Mid September to November of year <i>i</i>

temperature and precipitation for each study site were retrieved at 0.25° (ca. 27.5 km) spatial resolution from the gridded E-OBS dataset for the 1950-2019 period (Haylock et al., 2008). The monthly climatic water balance was calculated as precipitation minus potential evapotranspiration (P-PET). The data of potential evapotranspiration was directly retrieved from Laboratorio de Climatología y Servicios Climáticos – IPE-CSIC webpage (<https://lcsc.csic.es/>), which were calculated with Monteith-Penman method (Vicente-Serrano et al., 2017). To examine large-scale circulation atmospheric patterns affecting regional climate variability we also explored associations with the North Atlantic Oscillation (NAO), which influences winter-spring climate conditions and tree growth in the Iberian Peninsula (Camarero, 2011; López-Moreno et al., 2011), and El Niño Southern Oscillation in the 3.4 region (5°N-5°S, 120-170°W) (ENSO), which influences spring and autumn climate conditions and forest nutrient cycling in the Iberian Peninsula (González de Andrés et al., 2019; Shaman and Tziperman, 2011). NAO and ENSO data were retrieved from NOAA webpage (<https://www.cpc.ncep.noaa.gov/>).

2.3. Dendrochronological methods

One chronology or mean series of tree-ring width data was obtained for each of the selected sites and species, by sampling dominant trees of the site (Table 1). Generally two cores were extracted at 1.3 m from each tree using Pressler increment borers. Wood samples were sanded until tree rings were clearly visible and then visually cross-dated (Fritts, 2001). Once dated, tree-ring widths were measured to the nearest 0.01 mm along two radii per tree using a binocular scope and a LINTAB measuring device (Rinntech, Heidelberg, Germany). In *P. pinea*, early-wood –EW– and late-wood –LW– widths were also separately measured since it has been shown that they reflect different seasonal climatic influences (Natalini et al., 2016). The accuracy of visual cross-dating was checked with the program COFECHA (Holmes, 1983). To remove long-term changes due to tree aging and increase in size, tree-ring, EW and LW widths were standardised and detrended by applying a 32-year long cubic-smoothing spline curve. Then, the first-order autocorrelation

from the individual, detrended tree-ring width series was removed by applying autoregressive modelling. This resulted in pre-whitened or residual ring-, EW- and LW-width indices that were averaged for each species using biweight robust means. Chronology building procedure was carried out using the software ARSTAN v 4.4 (Cook, 1985; Cook and Krusic, 2005). For each of the selected stands, chronologies of ring, EW and LW widths were obtained by averaging the values of all the trees sampled in the site.

In the case of *P. pinea*, the total ring width and EW showed the same patterns (for this ring-width series, EW accounts as a mean for 80% of the total ring width; and both indices are highly correlated: $r = 0.99$, $P < 0.001$, $n = 62$, Fig. S3). We analyse separately EW and LW, which have been previously shown to correlate with different climatic variables (Natalini et al., 2016). In order to remove the dependence of LW on antecedent EW growth, the adjusted late-wood-width index (LW_a) was calculated as the residuals of the linear regression between EW and LW indices (Meko and Baisan, 2001).

2.4. Fruit yield data

We capitalized on the fact that the fruits of two study species (*P. pinea*, *C. sativa*) are economically valuable (Lovrić et al., 2020), and we found relatively long, local series for them. For *P. pinea*, the selected fruit yield data was the yield of cones (kg ha⁻¹) harvested each year in the public forests of Valladolid province (central Spain) for the 1960-2000 period (mean: 193 kg ha⁻¹, standard deviation SD: 175 kg ha⁻¹), according to the archives of the province Forest Service (Mutke et al., 2005). The great majority of *P. pinea* pine nut production in Valladolid province comes from “Tierra de Pinares” county, a 80 km east-west × 40 km north-south flat sedimentary plateau with homogeneous climate and soil conditions (Calama et al., 2011). The series used at the province scale were consistent with those used at stand scale by Shestakova et al. (2021), confirming they were reliable, comparable in time and did not depend on harvesting efforts.

For *C. sativa*, the selected fruit yield data was the annual chestnut harvest in the Casillas chestnut forest from 1986 to 2012 (mean: 123 t, SD: 67 t for ca. 400 ha forest). The data was provided by the co-op “Cooperativa de Castañas” from Casillas municipality, which sustainably exploits chestnuts in that locality. In this case, harvesting efforts are not variable through time since chestnut recollection is a traditional activity in this village.

For *Q. ilex*, the selected fruit yield data was an annual estimation of the acorn harvest in the Arascués forest for the 2003-2019 period. Every year, the acorn harvest was assessed in 150 trees using a semi-quantitative scale with five levels based on the percentage of the canopy occupied by shoots bearing acorns: 0 (no acorns), 1 (1-25%), 2 (25-50%), 3 (50-90%), and 4 (> 90% of the canopy shoots bearing acorns) (Camarero et al., 2010). For the 2003–2019 period the mean production index was 0.80 (SD: 0.81), with mean between-trees correlation being 0.60.

For *A. alba*, the selected yield data was the amount of seeds collected in traps located in the Gamueta site during the 2001-2018 period (mean: 61.5 seeds m⁻², SD: 36.7 seeds m⁻²). Thirty-six seed traps were placed in a 900 m² plot following a regular 5-m grid at the beginning of the study period. Traps had a 140 cm² circular section and were placed 0.5 m above the ground. Seeds were collected during the dispersal season, from September to May (González de Andrés et al., 2014).

The fruit yield series (seed yield for *A. alba*) of the four species were analysed for temporal trends with generalised additive models and for autocorrelation with autocorrelation function (ACF) tests, but no significant trends or autocorrelations were found in any case (Figs. S4-S5). Thus, the raw data were used for the statistical analysis. Pine cone yield was log transformed to meet the assumptions of constant variance and normal distribution of residuals.

2.5. Statistical analyses

The mean series of tree-ring width indices obtained for each site (EW and LWa for *P. pinea*) were correlated against monthly mean minimum temperature, mean maximum temperature and climatic water balance using Pearson correlation coefficients on a 14-month window from September of the year before tree growth until October of the year of tree-ring formation. An extended 17-month window was used for *A. alba* to account for the influence of the previous summer on tree growth (Gazol et al., 2015). The statistical significance of correlations were tested at $\alpha = 0.05$ level.

Similarly, Pearson correlations were used to analyse the relationships between fruit yield and climatic variables on a 14-month window from September of the year before fruit maturity until October of the year of fruit maturity. For *P. pinea* and *A. alba*, taking into account its reproductive phenology (Table 2), all the years from flower bud induction to fruit maturity were analysed (four years for *P. pinea* and two for *A. alba*). Pearson correlations between fruit yield and monthly values of NAO and ENSO indices were also explored.

Finally, Pearson correlations were also used to assess the relationship between fruit yield and tree-ring width indices (EW and LWa in the case of *P. pinea*) at stand level. The tree rings for the year of seed dispersal (year i), for the five previous years (years $i - 5$ to $i - 1$), and for the year after seed dispersal (year $i + 1$) were assessed. Then, for the significant correlations between ring width and fruit yield, we performed partial Pearson correlations controlling for climatic variables. The selected climatic variables were those showing significant correlations with both tree-ring width and fruit yield. In the case of *Q. ilex*, we tested winter climatic conditions despite not showing a significant correlation with fruit yield, because the NAO index indicated that fruit yield was responsive to prior winter climate conditions (García-Mozo et al., 2012).

For the *Q. ilex* stand, the only one with fruiting records for individual trees, the relationship between fruiting yield and tree-ring width was also assessed at tree level. This relationship was modelled with a generalised linear mixed model, using a Poisson error distribution, including the tree as a random variable and assessing the fit of the chosen distribution to the data through overdispersion.

All the statistical analyses were performed with the statistical software R (R Core Team, 2020). The mixed model analysis was conducted with the R package lme4 (Bates et al., 2015).

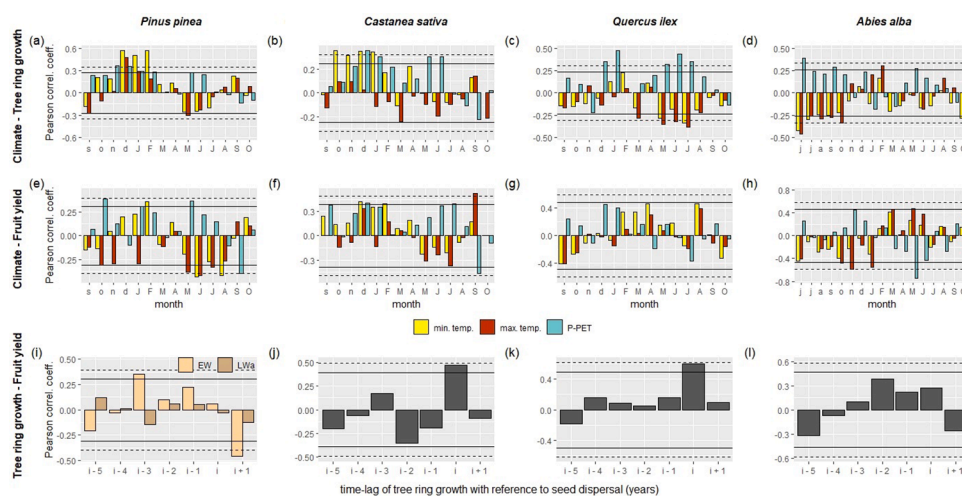


Fig. 1. Pearson correlation coefficients between climate, tree-ring width and fruit yield series for *P. pinea* (a, e, i), *C. sativa* (b, f, j), *Q. ilex* (c, g, k), and *A. alba* (d, h, l). (a-d) Correlations between monthly climatic variables (min. temp., mean minimum temperature; max. temp., mean maximum temperature; and P-PET, climatic water balance) and tree-ring width series (earlywood in the case of *P. pinea*) ($n = 52$, $n = 63$, $n = 68$ and $n = 58$ respectively). Months from the year before ring growth are shown in lowercase, and months from the year of ring growth are shown in capitals. (e-h) Correlations between fruit yield (seed yield in the case of *A. alba*) and monthly climatic variables of the same year (three years before in the case of *P. pinea*) ($n = 41$, $n = 26$, $n = 17$ and $n = 18$ respectively). (i-l) Correlations between fruit yield and tree-ring width of the same year, the five previous years and the year following seed dispersal ($n = 41$, $n = 26$, $n = 15$ and $n = 18$ respectively). Horizontal solid lines represent $P = 0.05$ significance level, and dashed lines represent $P = 0.01$.

dashed lines represent $P = 0.01$.

3. Results

3.1. Climate-growth associations

The EW growth of *P. pinea* showed positive correlations with the climatic water balance from the prior November to the current February, and that of the current May. *Pinus pinea* EW also showed positive correlations with the mean minimum temperatures from December to February, and with the mean maximum temperatures from December to January, as well as negative correlations with the maximum temperatures of the prior September and the current May (Fig. 1a). The LWa index of *P. pinea* showed positive correlations with the current March and September water balance (Fig. S6).

The ring width of *C. sativa* showed positive correlations with the water balance from the prior December to the current January, and from May to June. *Castanea sativa* growth also showed positive correlations with mean minimum temperatures from the prior October to the current January (Fig. 1b).

The ring width of *Q. ilex* showed positive correlations with the water balance from the prior December to the current January, and from May to July. *Quercus ilex* ring width also showed negative correlations with mean maximum temperatures of March and from May to July, and with mean minimum temperatures of May and July (Fig. 1c).

The ring width of *A. alba* showed positive correlations with the water balance of prior June, prior September and current May; negative correlations with the mean maximum temperatures from prior June to prior October; and negative correlations with the mean minimum temperatures from prior June, prior July and current October. *Abies alba* tree-ring width also showed a positive correlation with February mean maximum temperature (Fig. 1d).

3.2. Relationships between fruit yield and climate

The cone yield of *P. pinea* showed several significant correlations with climatic variables of three years before seed dispersal (year $i - 3$) and a few with four years before ($i - 4$), but none with the two years immediately before seed dispersal (years $i - 1$ and $i - 2$) (Fig. S7). Regarding year ($i - 4$), *P. pinea* cone yield showed a positive correlation with the water balance from January to February, negative correlations with August minimum and maximum temperatures, a positive correlation with October water balance and a negative correlation with October maximum temperature (Fig. S7). Regarding year ($i - 3$), *P. pinea* cone

yield showed a positive correlation with February mean minimum temperature, a positive correlation with May water balance, negative correlations with mean maximum temperatures from May to July, negative correlations with mean minimum temperatures of June and August and a negative correlation with September water balance (Fig. 1e). Finally, *P. pinea* showed a negative correlation with the February NAO index of year ($i - 3$) (Fig. S8a), a positive correlation with the October ENSO index of year ($i - 4$) and a negative correlation with the October ENSO index of year ($i - 3$) (Fig. S9).

The fruit yield of *C. sativa* showed positive correlations with water balance of prior December and current July, and with the mean minimum temperatures of prior December and current February. *Castanea sativa* fruit yield also showed a negative relationship with current September water balance and a positive relationship with current September mean maximum temperature (Fig. 1f).

The fruit yield of *Q. ilex* did not show any significant correlation with the climatic variables of the year (Fig. 1g). However, *Q. ilex* fruit yield showed a negative correlation with the NAO index for the November-January period previous to acorn formation ($r = -0.62$, $P = 0.008$, $n = 17$, see Fig. S8c).

The seed yield of *A. alba* showed a negative correlation with mean maximum temperatures of several months of the autumn-winter between years ($i - 1$) and i : October, November and January. *Abies alba* seed yield also showed a negative correlation with the water balance of May of year i , and a positive correlation with the mean maximum temperature of May of year i (Fig. 1h). Besides, *A. alba* seed yield showed significant correlations with some climatic variables of the autumn-winter between years ($i - 2$) and ($i - 1$): negative correlations with the mean maximum temperature of September, the mean minimum temperature of November and the mean maximum temperature of March (Fig. S10). Finally, *A. alba* seed yield showed a negative correlation with the NAO index for the November-January period between years ($i - 1$) and i ($r = -0.61$, $P = 0.007$, $n = 18$, see Fig. S8d).

3.3. Links between fruit yield and tree growth

The cone yield of the *P. pinea* stand showed a significant positive correlation with the EW of three years before (year $i - 3$), and a

significant negative correlation with the EW of the year after pine nut dispersal (year $i + 1$) (Fig. 1i, Fig. 2a). When controlling for winter climate variables affecting both tree growth and cone yield, the partial correlation between cone yield and EW of year ($i - 3$) was not significant (Table 3). No significant correlation between *P. pinea* cone yield and LWa was found (Fig. 1i, Fig. 2b).

The fruit yield of *C. sativa* and *Q. ilex* stands showed a significant positive correlation with the tree-ring width of the year of fruit ripening and dispersal (Figs. 1j-k and 2c). When controlling for winter water balance, the partial correlations between fruit yield and ring width were not significant (Table 3). When analysed at tree level, the fruit

Table 3

Partial Pearson correlations calculated between tree-ring width (earlywood width three years before pine nut dispersal in the case of *P. pinea*) and tree fruit yield after controlling for climatic effects. The climatic variables were selected on the grounds of their correlations with both growth (tree-ring width) and fruit or seed production. In order to allow comparisons, Pearson correlations between tree-ring width and fruit or seed production are also provided. P-PET: climatic water balance

Tree species	Controlling climatic variable	No of years of data	Partial correlation (P-value)
<i>P. pinea</i>	–	41	0.35 (0.023)
	Minimum temperature (December-February) ^a	41	0.18 (0.273)
	P-PET (December-February) ^a	36	0.29 (0.088)
	Minimum temperature (May-June)	41	0.30 (0.058)
	Maximum temperature (May-June)	41	0.29 (0.069)
<i>C. sativa</i>	P-PET (May-June) ^a	36	0.33 (0.052)
	–	26	0.47 (0.015)
	Minimum temperature (December-February) ^a	26	0.42 (0.035)
	P-PET (December-February) ^a	26	0.35 (0.090)
<i>Q. ilex</i>	P-PET (May-June)	26	0.39 (0.055)
	–	15	0.60 (0.019)
	P-PET (Dec.-Jan.) ^a	15	0.31 (0.278)

^a December corresponds to the year prior to tree-ring formation.

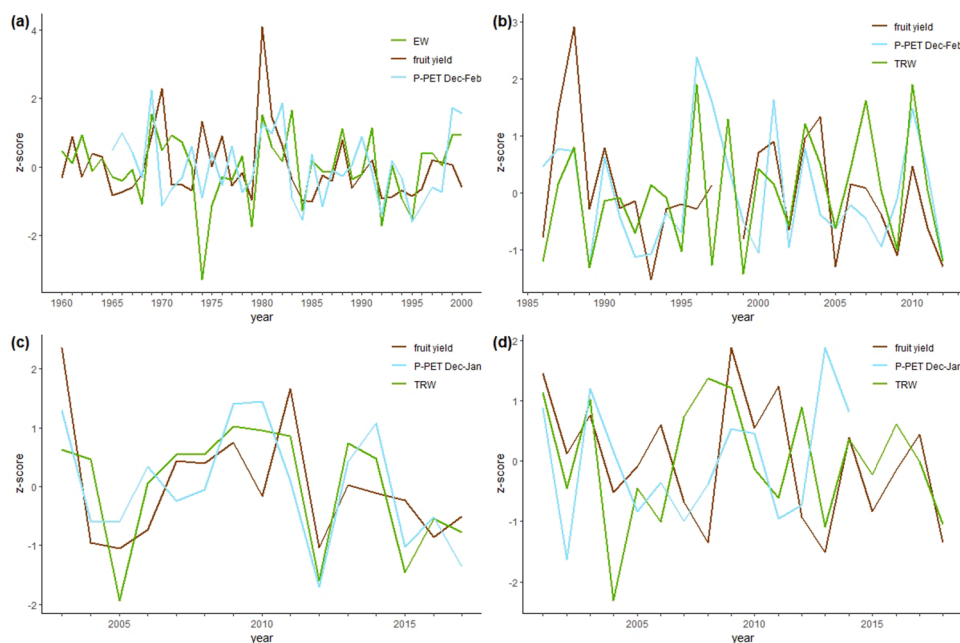


Fig. 2. Temporal patterns of standardised fruit yield, earlywood width (EW) and winter climatic water balance (P-PET) for *P. pinea* (a). Temporal patterns of standardised fruit yield, tree-ring width index (TRW) and winter climatic water balance (P-PET) in *C. sativa* (b), *Q. ilex* (c) and *A. alba* (d). In the case of *P. pinea*, the EW index and winter climatic balance of three years before are represented to enable the visual interpretation of patterns.

production index of *Q. ilex* was positively correlated with the tree-ring width of the same year ($P < 0.001$), whereas it was not affected by ring width of prior years (i-5) to (i-1) ($P > 0.05$ in all cases, Fig. 3).

The seed yield of the *A. alba* stand did not show any significant correlation with the tree-ring width of the same, the following or prior years (Figs. 1l and 2d).

4. Discussion

Our results indicate that winter climatic conditions enhancing tree growth also played a relevant role in explaining inter-annual variability of the fruit production of *P. pinea*, *C. sativa* and *Q. ilex* stands. For *P. pinea* and *C. sativa* stands, both ring width and fruit yield showed positive correlations with the prior winter minimum temperature and water balance. For the *Q. ilex* stand, ring width showed a positive correlation with the previous winter water balance, whereas acorn yield was negatively correlated with the winter NAO, thus suggesting that years of high acorn production are associated with previous cold, wet winters (Camarero, 2011). The fact that the positive correlations between fruit yield and tree-ring width (EW in the case of *P. pinea*) became non-significant when the effect of previous winter water balance was controlled indicates that winter climatic conditions are responsible for the indirect association between tree growth and fruit production in the studied *P. pinea*, *C. sativa* and *Q. ilex* sites (Knops et al., 2007). In other words, a prior wet winter favours both growth and reproduction in these three species.

For these three species, the positive correlation between fruit production and radial growth is connected to climatic conditions in periods when trees accumulate resources. Winter precipitation helps refill soil water reserves and increase nutrient mineralization in dry soils, improving the availability of these resources at the beginning of the growing season (Campelo et al., 2009; Natalini et al., 2016; Waldboth and Oberhuber, 2009). Precipitation has a positive influence on the photosynthesis rates during the growing season (Fernández-Martínez et al., 2015; Vergotti et al., 2019). The positive relationship between winter temperatures and growth in *P. pinea* and *C. sativa* could be hypothetically related to physiological activity during winter or storage of non-structural carbohydrates used to grow in spring (Gimeno et al., 2012). However, for European mesic, deciduous species this correlation has been attributed to an advance of spring leaf flushing and the resulting extension of the growing period (Estiarte and Peñuelas, 2015; Vergotti et al., 2019).

Our results for the *P. pinea*, *C. sativa* and *Q. ilex* stands are consistent with the resource-matching hypothesis, which predicts a positive relationship between reproduction and growth, and point out to winter conditions as the responsible climate signal. However, further analyses at tree level are required to confirm these results, since resource availability operates at the individual level. In this regard, the positive relationship between *Q. ilex* fruit production and ring width at tree level, together with the fact that the predicted relationship is consistent with a linear effect, support the resource-matching hypothesis for *Q. ilex*. Likewise, the positive relationship between *P. pinea* fruit yield and its

ring growth three years before has been recently confirmed at tree level (Shestakova et al., 2021).

In the case of *P. pinea* and *C. sativa* stands, climatic conditions in late spring and early summer were also correlated with both tree growth and fruit yield. Radial growth of both species was positively related to wetter conditions in this period, likely due to improved resources availability when water is limiting or to the extension of the growth period to early summer (Fonti and García-González, 2004; Hreidarsson, 2011; Natalini et al., 2016). Late spring is the period when flower primordia differentiation and pollination occur for both *P. pinea* and *C. sativa* (Table 2). While mild wet weather during late spring could enhance radial growth and development of flower primordia, high air humidity seems to impair pollen dispersal in wind-pollinated species as chestnuts and oaks (García-Mozo et al., 2012; Knops et al., 2007; Serdar et al., 2010).

For the *P. pinea* stand, climatic conditions in autumn were also correlated with both growth and fruit yield. Both radial growth and cone yield were positively correlated with cool, wet conditions in this period, in line with Natalini et al. (2016) and Mutke et al. (2005) results in “Tierra de Pinares” county. Mutke et al. (2005) attributed the correlation with cone yield to the fact that the differentiation of flower primordia inside the terminal bud occurs during this period (Table 2). The importance of autumn water balance is supported by the positive correlation of cone yield with October ENSO, which is positively associated with water balance (Fig. S11).

On the other hand, our results showed several correlations between climate and fruit yield for which no link to growth was detected. The fruit yield of *P. pinea* responded negatively to warm summers 3-4 years before seed dispersal. Mutke et al. (2005) indicated that mild mid summers just after pollination reduced premature conelet abscission in *P. pinea*; our results suggest that mild summers could also help the initial development of buds containing flower primordia. The fruit yield of *C. sativa* responded positively to July water balance and to September warm and dry conditions. Chestnut fruits rapidly enlarge and gain weight during summer and early autumn (Table 2). For *Q. ilex*, whose fruits also enlarge mainly in summer and early autumn, Pérez-Ramos et al. (2010) found that water availability reduced acorn abortion rates, whereas intense precipitations at the end of summer promoted the premature abscission of acorns, which they attributed to the mechanical effect of Mediterranean storms. The relevance of early autumn conditions was also emphasised by Montserrat-Martí et al. (2009), who found a negative correlation of *Q. ilex* acorn production with warm conditions in September. These results show that not all the reproductive phenophases are affected by climatic conditions in the same direction that growth is affected (Knops et al., 2007; Koenig et al., 2020). They also suggest that some reproductive phenophases are more sensitive to climate than others. Moreover, while some vegetative phenophases such as leaf bursting are sensitive to the photoperiod (Körner and Basler, 2010), reproductive phenophases may depend not only on climate but also on population levels of predispersal seed predators and diseases (Shestakova et al., 2021). These factors could explain some of the variance in fruit yield which is not accounted for by climate.

A negative correlation between fruit yield and tree growth the year after seed dispersal was found for *P. pinea*. Negative relationships between reproduction and growth of the same or the following year are usually considered an indication of resource allocation trade-offs (Kelly and Sork, 2002; Żywiec and Zielonka, 2013). However, for *P. pinea* the reduction of growth occurred two years after the main period of cone growth (year $i - 1$), and four years after pollination (year $i - 3$). Mutke et al. (2005) found a 3-year lag negative autocorrelation in *P. pinea* fruit production, which they attributed to cone growth being a strong nutrient sink and reducing tree vigour and formation of new terminal buds in late spring. These buds develop into either lateral shoot buds or flower primordia the following year. Therefore, the lagged, negative correlation between reproduction and growth in *P. pinea* would be related to the delayed effect of the resource depletion caused by a bumper crop (Calama et al. 2011).

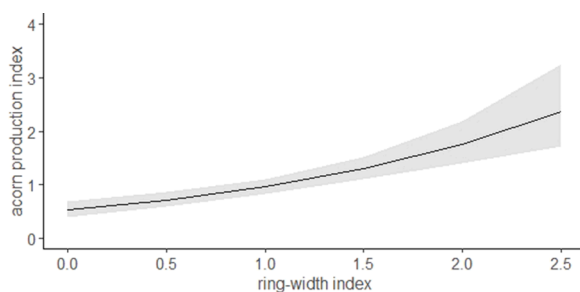


Fig. 3. Predicted relationship (mean and 95% confidence band) of *Q. ilex* fruit yield index at tree level as a function of ring width index.

We did not find any significant correlation between *A. alba* growth and seed production, in contrast to the other three studied species and to the negative correlation found by Davi et al. (2016) for *A. alba* in the southwestern Alps. In our study, tree-ring width responded negatively to warm conditions during the summer and early autumn of the year before ring formation, a relationship probably linked to changes in the dynamic of carbohydrate storage and late-summer drought stress (Camarero et al., 2011; Maxime and Hendrik, 2011). Besides, seed production responded negatively to warm conditions during late autumn and winter, which might entail higher metabolic costs for the tree by an early onset of the growing season and flowering (Fernández-Martínez et al., 2017). Resource switching has frequently been reported in fir species (Kelly and Sork, 2002). Vergotti et al. (2019) attributed the trade-off they observed to the contrasting effect of winter temperature on *A. alba* canopy development and seed production. However, in our study site tree-ring width showed low sensitiveness to winter conditions, similarly to that found in other Spanish and French sites (Gazol et al., 2015; Maxime and Hendrik, 2011).

In addition, our results indicated that seed production of the *A. alba* stand responded positively to a warm and dry May, similarly to that found by Fernández-Martínez et al. (2017), whereas growth responded negatively to dry May conditions reducing cambium activity which peaks in spring (Camarero et al. 2011). This is the period for *A. alba* pollination, which is limited by the short dispersal distances of pollen (Poska and Pidek, 2010). Pollen release to the atmosphere and pollen dispersal are likely to improve with warm, dry weather (García-Mozo et al., 2012). Thus, in our study site there is: (i) limited overlap between the periods in which climate influences radial growth and fruit production, and (ii) a contrasting effect of late spring conditions on radial growth and pollen dispersal.

A shortcoming of this study is that only 20 years of fruiting data were available for *Q. ilex* and *A. alba*, thus limiting the inference on climate impacts on fruit production. Different kinds of fruit production data are used for these stands (semi-quantitative assessments for *Q. ilex* and seed numbers instead of cone biomass for *A. alba*), thus introducing another source of variation.

While we found some results consistent with resource matching, no responses consistent with the resource-budget or the resource-switching hypotheses were found. Despite this, a few instances in which climate had contrasting effects on growth and fruiting were observed. These linkages explained part of the variance in fruit yield at stand level, although they seem to be obscured by the effect of winter water balance on fruiting and growth.

5. Conclusions

We found that at stand level the annual tree-ring width positively correlated with the fruit yield of the xeric *P. pinea*, *C. sativa* and *Q. ilex* forest sites. We confirmed this relationship at tree level for *Q. ilex*. Winter climatic conditions associated with increased growth played a relevant role in driving inter-annual fruiting variability, these linkages being consistent with the resource-matching hypothesis. Besides, we found several species-specific climate-fruiting correlations that were not observed for tree growth but rather matched key phenological events, indicating their sensitiveness to climatic conditions: the flowering (and the subsequent fruit set) and the final period of fruit growth and ripening for the *C. sativa* stand, and flower bud induction and flowering for *P. pinea*. Contrastingly, for the mesic *A. alba* stand no positive ring width – fruit production correlation was found, likely due to the scarce overlap of the climatic variables affecting growth and reproduction, as well as the contrasting effect of late-spring climatic conditions on growth and reproduction. Together these findings support the hypothesis that climate plays a major role as a proximate cause of fruiting potential in Mediterranean forest ecosystems, either increasing resource availability, photosynthetic capacity or directly affecting sensitive reproductive phenophases. Therefore, understanding the linkages between climate

and tree reproduction in Mediterranean Europe could be critical in a context of global warming. Our study shows that dendroecological studies can help disentangle these linkages, particularly by pinpointing climatic signals, while taking into consideration the role played by species-specific reproductive phenology traits.

Declaration of Competing Interest

None.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2021.108493.

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