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# Drought limits tree growth more than greenness and reproduction: insights from five case studies in Spain

J. Julio Camarero [a,*], Álvaro Rubio-Cuadrado [b], Ester González de Andrés [a], Cristina Valeriano [a], Manuel Pizarro [a], J. Bosco Imbert [c], Yueh-Hsin Lo [c], Juan A. Blanco [c]

[a] Instituto Pirenaico de Ecología (IPE-CSIC), Avda, Montañana 1005, Zaragoza, E-50192, Spain
[b] Departamento de Sistemas y Recursos Naturales, Escuela Técnica Superior de Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, Madrid, 28040, Spain
[c] Institute for Multidisciplinary Research in Applied Biology (IMAB), Detp. Science, Public University of Navarra (UPNA), Pamplona, 31006, Spain

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ABSTRACT

Droughts impact forests by influencing various processes such as canopy greenness, tree growth, and reproduction, but most studies have only examined a few of these processes. More comprehensive assessments of forest responses to climate variability and water shortages are needed to improve forecasts of post-drought dynamics. Iberian forests are well-suited for evaluating these effects because they experience diverse climatic conditions and are dominated by various conifer and broadleaf species, many of which exhibit masting. We assessed how greenness, evaluated using the normalized difference vegetation index (NDVI), tree radial growth, and seed or cone production responded to drought in five tree species (three conifers: silver fir (*Abies alba*), Scots pine (*Pinus sylvestris*), and stone pine (*Pinus pinea*); two broadleaves: European beech (*Fagus sylvatica*) and holm oak (*Quercus ilex*) inhabiting sites with different aridity. We correlated these data with the standardized precipitation evapotranspiration index (SPEI) using the climate window analysis (*climwin*) package, which identifies the most relevant climate window. Drought constrained growth more than greenness and seed or cone production. Dry conditions led to high seed or cone production in species found in cool, moist sites (silver fir, beech, and Scots pine). We also found negative associations of cone production with summer SPEI in the drought-tolerant stone pine, which showed lagged growth−cone negative correlations. However, in the seasonally dry holm oak forests, severe droughts constrained both growth and acorn production, leading to a positive correlation between these variables. Drought impacts on greenness, growth, seed, and cone production depended on species phenology and site aridity. A negative correlation between growth and reproduction does not necessarily indicate trade-offs, as both may be influenced by similar climatic factors.

## 1. Introduction

The Mediterranean Basin is a climate change hotspot subjected to significant warming and drying trends from winter to spring, reducing soil moisture during the growing season (Tuel and Eltahir, 2020, 2021). The Spanish mainland exemplifies this aridification trend, with decreasing winter-spring rainfall leading to drought in northern and western Iberia (Gonzalez-Hidalgo et al., 2024). However, the effects of drought on canopy greenness, tree growth, and reproduction in Iberian forests remain poorly understood despite some studies separately addressing some of these three processes (Mutke et al., 2005; Espelta et al., 2008; Montserrat-Martí et al., 2009; González de Andrés et al., 2014; Gazol et al., 2018; Peña-Gallardo et al., 2018; Khoury and Coomes, 2020; Garcia-Barreda et al., 2021, 2023; Lucas-Borja and Vacchiano, 2018; Shestakova et al., 2021). Furthermore, drought stress may affect greenness, growth, and seed or cone production differently due to variations in their timing (Camarero et al., 2015a; González de Andrés et al., 2019; Garcia-Barreda et al., 2021, 2023).

Under future climate scenarios, rising temperatures could lead to earlier flowering, more severe spring-summer droughts, and warmer, drier autumns, further constraining seed production in key Mediterranean tree species such as evergreen oaks (Pérez-Ramos et al., 2010;

* Corresponding author.
*E-mail address:* jjcamarero@ipe.csic.es (J.J. Camarero).
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Fernández-Martínez et al., 2012). Iberian forests provide an ideal setting for assessing drought impacts on forest greenness, tree growth, reproduction and regeneration, as they encompass a wide range of climate conditions—from temperate to Mediterranean—and host diverse tree species, including conifers (e.g., pines, firs) and broadleaves (e.g., European beech, oaks), many of which exhibit masting behavior. Some of these masting species, such as stone pine (*Pinus pinea* L.), also produce commercially valuable seeds (Mutke et al., 2005).

Climate variability influences tree growth and seed production (Caignard et al., 2017; Bogdziewicz et al., 2020a, 2020b), which is crucial for understanding forest dynamics and potential shifts in resource allocation between these processes (Koenig, 2021; Qiu et al., 2022). Some studies have reported trade-offs between seed or cone production and radial growth, suggesting resource limitations (e.g., Eis et al., 1965; Piovesan and Schirone, 2000; Kelly and Sork, 2002; Drobyshev et al., 2010; Plavcová et al., 2022). However, climatic factors such as temperature and drought can also drive variability in seed production and growth. For example, high reproductive effort during mast years is associated with lower growth in European beech (*Fagus sylvatica* L.), yet this pattern is linked to warm summer conditions in the preceding year, highlighting lagged climate effects on growth (Hacket-Pain et al., 2018). Climatic influences may act in complementary or opposing ways. For instance, wet conditions promoted tree growth but reduced acorn production in five Californian oak species (Knops et al., 2007). According to the "resource budget" hypothesis (Isagi et al., 1997), large seed crops should be preceded by periods of high greenness, elevated growth rates, and abundant stored reserves (Sork et al., 1993; Camarero et al., 2010). In such cases, droughts could synchronize interannual variability in growth and reproduction by acting as climatic cues for abundant seed or cone production (Wion et al., 2020). Alternatively, drought stress may amplify trade-offs between growth and reproduction (Hacket-Pain et al., 2017; Bogdziewicz et al., 2020a), suggesting that tree populations in dry regions experience stronger trade-offs (Mutke et al., 2005; Gonzalez et al., 2023). However, populations from cooler, wetter regions often show more pronounced responses to drought years (Lauder et al., 2019). This makes Spanish forests a suitable system for studying how trade-offs between greenness, growth, and reproduction vary under drought stress.

Remote sensing techniques, including reflectance-based indices such as the Normalized Difference Vegetation Index (NDVI), are widely used to assess changes in forest greenness at various spatial scales (Huete et al., 2002). The NDVI has been shown to respond to drought severity in Iberian forests, complementing growth data (Peña-Gallardo et al., 2018). A main knowledge gap is determining how climate variability, particularly drought stress, impacts forest greenness, tree growth, and reproduction and how these impacts affect trade-offs between these processes.

In this study, we aim to relate drought conditions to canopy greenness (NDVI), a proxy for carbon sources, as well as radial growth (tree-ring width) and seed or cone production, two major carbon sinks. We selected five forests in Spain, dominated by three major conifer species and two broadleaves, to account for biogeographic, ecological, and climatic gradients—particularly site aridity.

Because allocation to growth and reproduction depends on climate conditions during key phenological stages (e.g., reproductive bud formation, leaf flush, shoot elongation, xylem and seed development, and cone ripening; Garcia-Barreda et al., 2021), we hypothesize that (1) drought will differentially affect greenness, growth, and reproduction based on their phenological timing, and (2) the magnitude of these impacts will vary across tree species. Specifically, we expect drought to have a stronger effect on conifer greenness and growth in the driest sites, whereas broadleaves may exhibit greater resilience (Anderegg et al., 2015).

## 2. Material and methods

### 2.1. Study sites and reproductive phenology of tree species

We selected five sites subjected to contrasting climate conditions and where long enough series of tree growth and seed production were available (Table 1 and Figs. S1 and S2). In the two wettest and coolest sites located in the western Spanish Pyrenees and subjected to temperate conditions (Gamueta and Las Eras), we used data for silver fir (*Abies alba* Mill.), whereas in another warmer and drier Pyrenean site subjected to temperate continental conditions (Aspurz), data were available for Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.). The holm oak (*Quercus ilex* L.) was studied at a site (Arascués) situated in northeastern Spain and subjected to Mediterranean continental conditions with a marked summer drought. Finally, in the warmest and driest Mediterranean continental site located in central Spain (Almorox), stone pine (*P. pinea*) was studied. In the case of silver fir and beech, study sites were located near the southwestern distribution limit of the species in Europe (Fig. S1).

The Gamueta site showed a structure corresponding to an old-growth, uneven mixed (beech-fir) forest, whereas the forest structure in the Las Eras site corresponded with a young, pure silver fir forest (Molina-Valero et al., 2020). Some selected stands of these forests were logged in the 1950s (Camarero et al., 2011). The Aspurz site is a relatively young mixed forest with beech gradually replacing pine (González de Andrés et al., 2019). The Arascués site is a formerly coppice, pure holm oak stand. Finally, the Almorox site is a relatively open, old stone pine stand, with holm oak and Mediterranean shrubs in the understory, showing recent drought-induced dieback and mortality (Moreno-Fernández et al., 2022). All sites are located on basic soils, except Aspurz and Almorox sites. The three wettest sites (Gamueta, Las Eras, and Aspurz) show well-developed deep soils, whereas rocky, thinner soils predominate in the two driest sites (Arascués and Almorox).

The five study species are wind-pollinated and represent major taxonomic families among conifers (Pinaceae) and broadleaves (Fagaceae). They are monoecious species with unisexual flowers showing low tolerance to shade, except silver fir and beech, which are considered shade-tolerant species. Holm oak and stone pine are the two species most tolerant to drought stress, albeit both have shown recent dieback processes linked to aridification (Camarero et al., 2015a; Moreno-Fernández et al., 2022).

Regarding the timing of reproductive processes, silver fir, and Scots pine take two growing seasons from bud differentiation to seed ripening and dispersal, which occur in September–November (Garcia-Barreda et al., 2021). In contrast, stone pine takes three years from floral bud differentiation to seed maturity, with seeds being fully ripe in October and November (Mutke et al., 2005). In the case of holm oak and beech, flowers are produced in April and May, and fruits ripen in October and November of the same year (Montserrat-Martí et al., 2009; Hacket-Pain et al., 2017).

### 2.2. Drought index

We used homogeneous, 1.1-km$^2$ gridded monthly climate data of the Standardized Precipitation Evapotranspiration Index (SPEI), which is used to evaluate the severity and duration of drought (Vicente-Serrano et al., 2010, 2017). Monthly SPEI series (1- to 24-month scales) were obtained from the CSIC drought monitor webpage (https://monitordesequia.csic.es/) considering the period 1970–2022. Positive and negative SPEI values indicate wet and dry conditions corresponding to positive and negative climate water balances (calculated as the difference between precipitation and potential evapotranspiration), respectively (Vicente-Serrano et al., 2010).

### 2.3. NDVI series

The NDVI measures the difference between near-infrared light, which vegetation strongly reflects, and red light, which vegetation absorbs (Huete et al., 2002). To obtain the NDVI series for the study sites, we used Google Earth Engine (GEE) and implemented the best available pixel compositing method, which creates annual image composites by

**Table 1**
Geographical features, study tree species, and climatic conditions of the five study sites.

| Site | Latitude (° N) | Longitude (° W) | Elevation (m a.s.l.) | Tree species | Mean annual temperature (°C) | Mean annual minimum temperature (°C) | Mean annual maximum temperature (°C) | Total annual precipitation (mm) | De Martonne aridity index[a] |
|---|---|---|---|---|---|---|---|---|---|
| Gamueta | 42.885 | 0.800 | 1348 | *Abies alba* | 6.1 | 0.1 | 11.7 | 1550 | 96.3 |
| Las Eras | 42.877 | 0.806 | 1320 | *Abies alba* | 6.2 | 0.1 | 11.6 | 1540 | 95.1 |
| Aspurz | 42.748 | 1.089 | 642 | *Pinus sylvestris* and *Fagus sylvatica* | 11.5 | 5.8 | 17.3 | 960 | 44.7 |
| Arascués | 42.240 | 0.450 | 643 | *Quercus ilex* | 13.3 | 7.6 | 19.1 | 628 | 27.0 |
| Almorox | 40.287 | 4.379 | 636 | *Pinus pinea* | 14.8 | 8.8 | 21.0 | 582 | 23.5 |

Note.
[a] The De Martonne aridity index (DMI) is calculated as $DMI = P/(T + 10)$, where $P$ is the annual precipitation total (mm) and $T$ is the mean annual air temperature (°C). Very humid conditions correspond to $DMI > 35$, whilst semi-humid and Mediterranean conditions correspond to $24 \leq DMI < 28$ and $20 \leq DMI < 24$, respectively.

integrating data from multiple sensors and available Landsat satellite images (White et al., 2014). Selected images were atmospherically corrected based on surface reflectance values and correspond to a 105-day window centered on June 15 (day of year (DOY): 166), which corresponds to the greenness peak in the growing season (DOY: 60–273). We also applied gap-filling procedures to address missing data and implemented a "Despike" algorithm to remove outliers and anomalies above-defined thresholds (Rouse et al., 1974). This algorithm was parameterized with the following settings: target day = June 15, range of days = 105, cloud threshold = 40%, scan line corrector failed (SLC-off) penalty = 0.7, opacity score range = 0.2–0.3, maximum cloud distance = 1500 m, threshold = 0.65, and start and end years from 1984 to 2023. The monthly NDVI series were extracted for the period 1986–2022 and considering a spatial resolution of 30 m. In the silver fir sites, some years (2003 and 2010) were missing due to elevated cloudiness during the growing season. These processes were done using the GEE-based Landtrend-CSIC application (https://landtrend.csic.es/; Pizarro, 2024).

### 2.4. Tree-ring width series

For each site and species, we sampled between 27 and 152 mature, dominant trees located 5–15 m apart and measured their diameter at 1.3 m (diameter at breast height (dbh); Table S1). They were sampled in different years to quantify radial growth variability using dendrochronology (Fritts, 1976). Two cores were sampled at 1.3 m from each tree in opposite directions and perpendicular to the maximum slope using a 5-mm Pressler increment borer. Cores were air-dried, glued onto wooden supports, and carefully sanded until ring boundaries were conspicuous. Then, annual rings were visually cross-dated and measured with a precision of 0.01 mm using a binocular microscope coupled to a computer with the LINTAB package (Rinntech, Germany). The COFECHA program was used to evaluate the visual cross-dating of tree-ring width data (Holmes, 1983).

Since the ring-width series contain long-term trends due to non-climate factors such as stand dynamics or ontogenetic changes, we obtained standardized and detrended ring-width indices using the dplR package (Bunn, 2010; Bunn et al., 2016) in R statistical software (R Core Team, 2023). We fitted a 30-year cubic smoothing spline to each ring-width series and divided them by the fitted spline. The resulting detrended series of indices were pre-whitened, fitting an autoregressive time series model (AR1 model). Lastly, a mean series of ring-width indices for each site and species (chronology) was calculated using bi-weight robust means. The statistical quality of each chronology was checked by calculating the expressed population signal (EPS) (Wigley et al., 1984). In all cases, EPS was higher than 0.85, confirming a high coherence and good replication for all chronologies (Table S1). Not updated tree-ring series of the study sites have been previously published (Camarero et al., 2011, 2015a; Garcia-Barreda et al., 2021, 2023; Moreno-Fernández et al., 2022; Primicia et al., 2013; Cardil et al., 2018).

### 2.5. Data on seed or cone production

Several methodological approaches were used to quantify seed and cone production based on trap collections or visual estimates of canopy seed or cone production made in autumn. At each of the two silver fir sites, seeds were annually collected from 36 seed traps located within 900 $m^2$ square plots situated in each stand (González de Andrés et al., 2014). Traps (0.014 $m^2$ in area and 1 m in height) were placed along a 5-m regular grid. Seed counts started in 2001 and 2005 in Gamueta and Las Eras, respectively, and data until 2022 were considered (Table 2). In Aspurz, seed cones and beech fruits were also annually collected in traps and counted (2005–2020). Here, nine circular traps (0.283 $m^2$ in area and 1 m in height) were randomly distributed in each of three plots (30 m × 40 m), and above-ground litterfall was collected monthly from August to November when the litter fall peak occurs (Blanco et al., 2006). The collected cones or nuts were counted and summed for every year. In the holm oak forest, the acorn harvest was annually estimated (2003–2022) in 150 trees located in three nearby stands 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). Finally, in the case of stone pine, we used annual nut harvests of the study forest (1,437 ha) recorded in the management plans during 1986–2002 with missing data in 2000 and 2001 (Prieto, 2011). The fruits of this species are economically valuable, and this explains the existence of a local series of cone yields ($kg \cdot ha^{-1}$) harvested each year (e.g., Mutke et al., 2005). Readers can consult further details on these methods in studies that have been previously published and used part of the seed production presented here (Camarero et al., 2015a; González de Andrés et al., 2019; Garcia-Barreda et al., 2021, 2023).

### 2.6. Correlation and climwin analyses relating SPEI, NDVI, growth, and reproduction

After checking the normality of variables using the Shapiro-Wilk test, we used Pearson correlations ($r$) to assess the relationships between monthly values of the SPEI drought index and the measures of greenness (NDVI), radial growth (ring-width indices), and seed or cone production. Seed and cone production was previously standardized, and $\log(x + 1)$ was transformed. The significance levels of correlations were corrected by accounting for the presence of temporal autocorrelation following the method proposed by Mudelsee (2003), which is based on a non-parametric stationary bootstrap that calculates an average block length proportional to the maximum estimated persistence time of data. These correlations were calculated considering monthly SPEI values (from January to December) and SPEI timescales ranging from 1 to 24 months. We highlighted the months and timescales when maximum correlation coefficients, in absolute terms, were obtained. Lastly, cross-correlations were also calculated to detect lagged relationships

**Table 2**
Temporal scale, month, and maximum correlation (in absolute terms) were found when relating the SPEI drought index vs. NDVI, tree growth (ring-width indices), and seed or cone production. Significance levels of correlations are abbreviated as follows: *$p \leq 0.05$, **$p \leq 0.01$, and ***$p \leq 0.001$.

| Site | Tree species | Variable | Period with data (year) | Temporal scale (month) | Month | $r$ |
|---|---|---|---|---|---|---|
| Gamueta | *A. alba* | NDVI | 2001–2022 (22) | 2 | Aug. | 0.73*** |
| | | Growth | | 5 | Nov. | 0.78*** |
| | | Seed | | 2 | Aug. | −0.43* |
| Las Eras | *A. alba* | Growth | 2005–2022 (18) | 3 | Sep. | 0.74*** |
| | | Seed | | 2 | Aug. | −0.39 |
| Aspurz | *P. sylvestris* | NDVI | 2005–2020 (15)[a] | 6 | Nov. | 0.41 |
| | | Growth | | 1 | Jul. | 0.75*** |
| | | Cone | | 21 | Jul. | −0.69*** |
| | *F. sylvatica* | Growth | 2005–2020 (15)[a] | 23 | Jul. | 0.87*** |
| | | Seed | | 4 | Oct. | −0.60* |
| Arascués | *Q. ilex* | NDVI | 2003–2022 (20) | 21 | Jul. | 0.61*** |
| | | Growth | | 11 | Jun. | 0.66*** |
| | | Seed | | 20 | Dec. | 0.72*** |
| Almorox | *P. pinea* | NDVI | 1986–2002 (15)[b] | 1 | Mar. | 0.54* |
| | | Growth | | 13 | Dec. | 0.65*** |
| | | Cone | | 20 | Feb. | −0.70*** |

Note.
[a] Data for 2006 are missing.
[b] Data for 2000–2001 are missing.

between growth indices and seed or cone production.

The correlation analyses were refined using the R package *climwin,* which allows detecting optimum climate windows, i.e., the most parsimonious model with the highest predicting capacity, and the type of relationship between the climate (SPEI) and the response biological variables (NDVI, growth indices, and seed or cone production) (Bailey and van de Pol, 2016; van de Pol et al., 2016). The package *climwin* has also been successfully applied to assess climate–growth relationships (Rubio-Cuadrado et al., 2022). Four functions (linear, quadratic, cubic, and inverse) were used to relate the climate and response. The corrected Akaike information criterion (AICc) was used to select the most parsimonious models following an information-theoretic approach (Burnham and Anderson, 2004). Then, the difference between the AICc of the selected model and that of the null model was calculated (ΔAICc). The large number of fitted models, due to the use of the different functions and the testing of all possible climate windows with monthly resolution, increases the possibility of obtaining models with low ΔAICc by chance. To address the statistical problem of multiple testing, randomization tests were performed on fitted models using 1,000 repetitions. The randomization test determines the expected distribution of ΔAICc values in a data set where no response to climate exists and provides a probability value ($p$), which determines the likelihood that the ΔAICc value of the selected model has occurred by chance (van de Pol et al., 2016). As randomization tests require high computational power, the analyses were done using the "Magerit-3" high-performance computer of Universidad Politécnica de Madrid (www.cesvima.upm.es, Madrid, Spain).

## 3. Results

### 3.1. Relationships between NDVI, growth indices, and seed or cone production

Some years (e.g., 2005; Figs. 1 and S3) with low growth indices in Scots pine and holm oak and a lack of seed production in holm oak corresponded to severe droughts. In addition, drops in NDVI of stone pine were also observed during dry years (Fig. S4).

We found a positive correlation between NDVI and seed production in holm oak, but it was not significant ($r = 0.44$, $p = 0.089$). No significant correlations were found between the NDVI and growth indices, except in beech between the growth of the previous year ($t - 1$) and NDVI of year $t$ ($r = 0.60$, $p = 0.018$).

In silver fir from Gamueta, growth indices of the year ($t - 1$) negatively correlated to seed production of the year $t$ ($r = -0.42$, $p = 0.057$). In Scots pine, growth and cone production were negatively related ($r = -0.52$, $p = 0.045$), whereas they were positively related in holm oak ($r = 0.65$, $p = 0.003$). In stone pine, 3-year lagged negative relationships were found between cone production year ($t - 3$) and growth indices of year $t$ ($r = -0.64$, $p = 0.012$; Fig. S5).

### 3.2. Relationships between drought severity, NDVI, growth, and seed or cone production

The SPEI series showed negative temporal trends in the silver fir and holm oak sites corresponding to aridification trends ($r = -0.67$, $p = 0.0005$). The October 12-month SPEI series, corresponding to the water year, detected severe droughts (SPEI $< -1.25$) affecting all sites in 2002, 2005, 2012, 2019, and 2022 (Fig. S3).

The highest correlations ($r = 0.74$–$0.87$) were found between the SPEI and the growth indices of species inhabiting the wet-cool sites (silver fir, beech, Scots pine; Table 2 and Figs. 2–4). They were followed by SPEI–growth correlations ($r = 0.65$–$0.66$) of species from dry-warm sites (holm oak, stone pine; Table 2, Figs. 5 and 6). In the two wettest silver fir sites, NDVI−SPEI and growth−SPEI correlations peaked in autumn at short time scales (2–5 months), whereas they did it in spring and summer at long scales (4–23 months) in other sites.

The strongest SPEI–NDVI correlation was found in silver fir ($r = 0.73$), followed by holm oak. Regarding reproduction, we found negative associations of seed and cone production with SPEI in all species and sites except holm oak ($r = 0.72$), i.e., wetter conditions enhanced acorn production in this case with correlations peaking in winter and at long time scales. The lowest correlations between SPEI and reproduction data (cone or seed series) were found for stone pine ($r = -0.70$) and Scots pine ($r = -0.69$), peaking in winter and summer at long time scales, followed by beech ($r = -0.60$) and silver fir in Gamueta ($r = -0.43$), i.e., drier conditions enhanced seed or cone production in these cases. In this last site, the temporal scale (2 months) and month (August) corresponding to the maximum absolute correlations between SPEI and NDVI (or reproduction) were the same. In the case of beech, correlations between SPEI and seed production also peaked at short time scales but in autumn.

### 3.3. Climwin analyses

In general, most selected models were not linear (Tables 3 and S3; see also Fig. S6). According to AICc, the most informative models corresponded to growth and seed data, particularly for silver fir and beech, whereas NDVI responded less to the SPEI (Table 3). The nonlinear SPEI–seed relationships increased the correlation coefficients obtained with *climwin* as compared with simple correlations, which showed

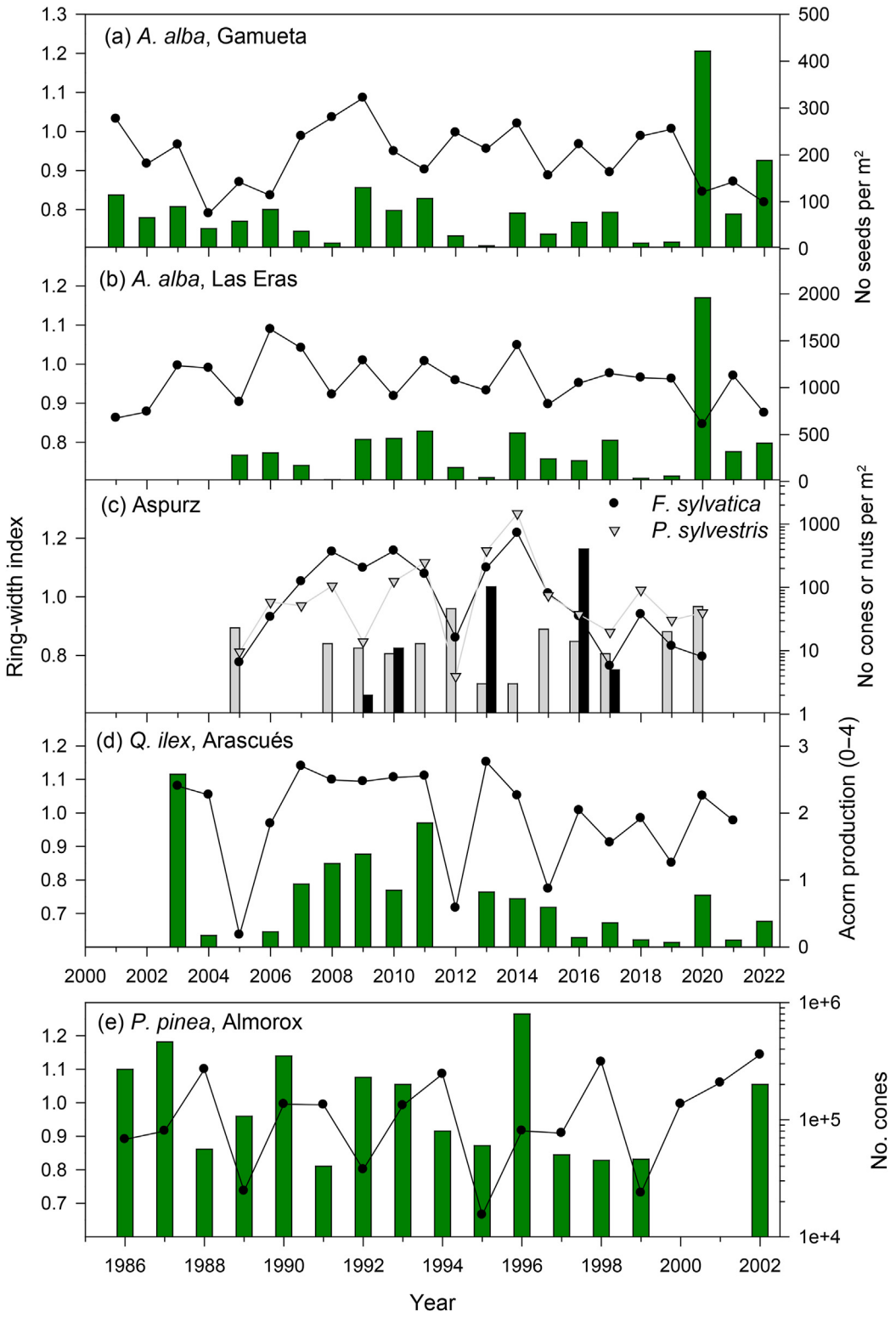



**Fig. 1.** Series of growth indices (lines with symbols, left *y*-axes) and seed or cone production (bars, right *y*-axes) in the five study sites. Note the log scales in some cases.

stronger SPEI–growth relationships (Tables 2 and 3). In other words, SPEI–growth relationships were mostly linear (Tables 3 and S2), and this explains the similar results of correlations and *climwin* analyses in the case of this variable.

The SPEI and NDVI showed linear relationships, except in the wet Scots pine site and also in the dry stone pine site, where, again, the maximum NDVI values were found for intermediate SPEI values ranging from −1 to 1 (Fig. S6). In the cool-wet silver fir sites, the summer (from June to August) SPEI is the most important driver of NDVI, whereas this occurs in early spring in the case of the dry stone pine site (Table 3). All species showed direct and positive relationships between SPEI and growth indices, except stone pine, which presented optimum growth

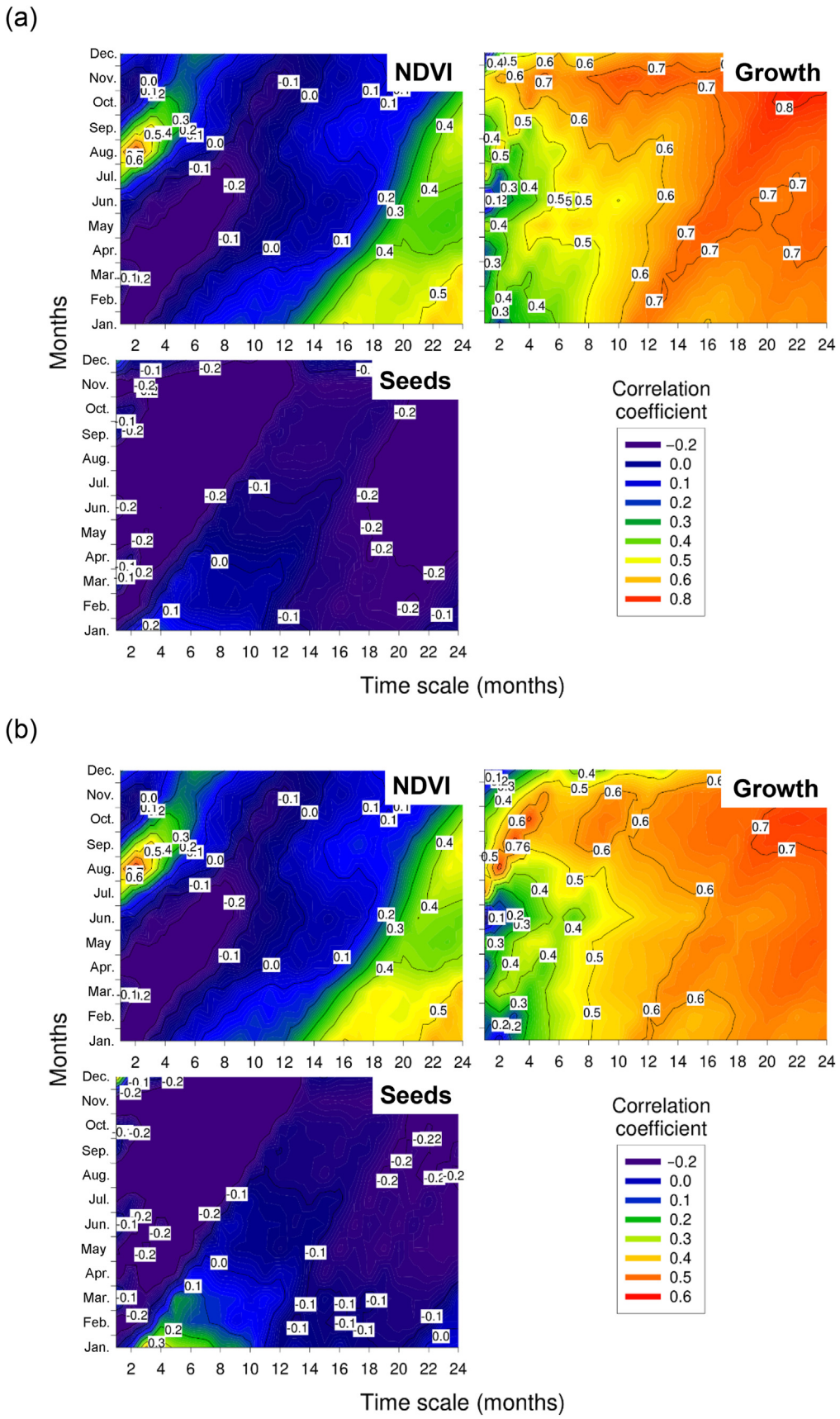



**Fig. 2.** Relationships of the SPEI with NDVI, growth indices, and seed production of silver fir in **(a)** Gamueta and **(b)** Las Eras study sites. The *x* and *y* axes show the SPEI time scale (1–24 months) and months, respectively.

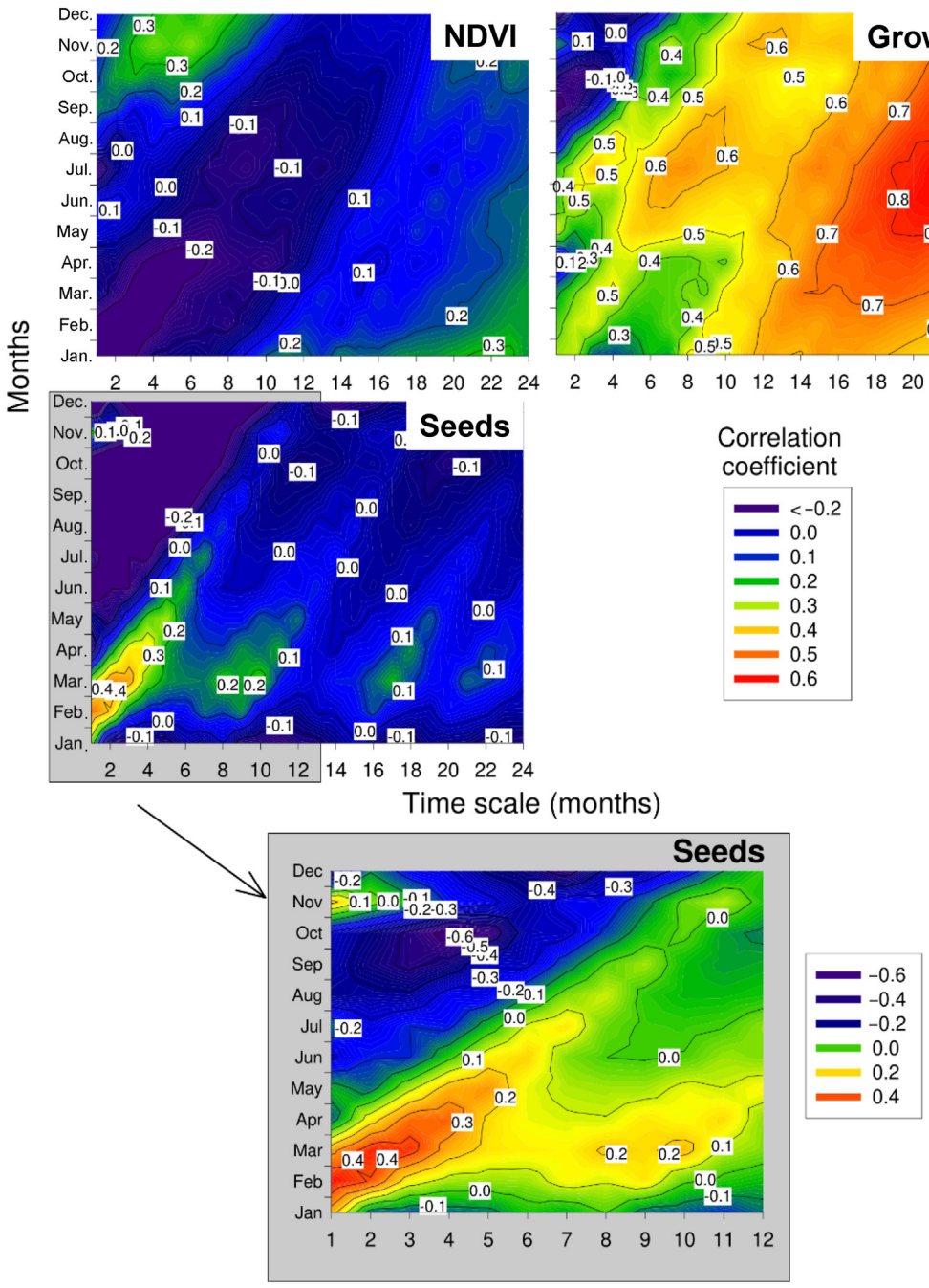



**Fig. 3.** Relationships of the SPEI with NDVI, growth indices, and seed production of European beech in Aspurz. The *x* and *y* axes show the SPEI time scale (1–24 months) and months, respectively. The lowermost plot zooms out the correlations from 1 to 12 months.

values for intermediate SPEI values.

*Climwin* analyses revealed that silver fir, beech, and Scots pine showed the highest cone or seed production during dry years (Table 3 and Fig. S6). In stone pine, the nonlinear relationship showed that cone production was high not only during the driest years but also during the wettest years, being low during years with intermediate SPEI values. In holm oak, acorn production increased during wet years following a quadratic function. In this species, and also in Scots pine, the prior-year climate conditions influenced the reproductive effort, whereas in the other tree species, the current-year climate conditions were the main driver of seed or cone production. The influence of the SPEI during the year of seed or cone production occurred either in winter (stone pine), spring-summer (beech), or summer (silver fir).

## 4. Discussion

### 4.1. Drought as a major climatic cue for tree reproduction

Drought is a major stressor for forests worldwide, exerting lasting negative effects on tree growth (Anderegg et al., 2015) and reducing seed and cone production in seasonally dry (Espelta et al., 2008; Pérez Ramos et al., 2010; Garcia-Barreda et al., 2023) and mesic temperate forests (Pesendorfer et al., 2020; Garcia-Barreda et al., 2021). This study supports the resource-matching hypothesis, which posits that fruit production responds to annual environmental variability through climate cueing (Kelly and Sork, 2002; Pearse et al., 2016). Our findings align with prior research highlighting the key role of climate variability in fruit

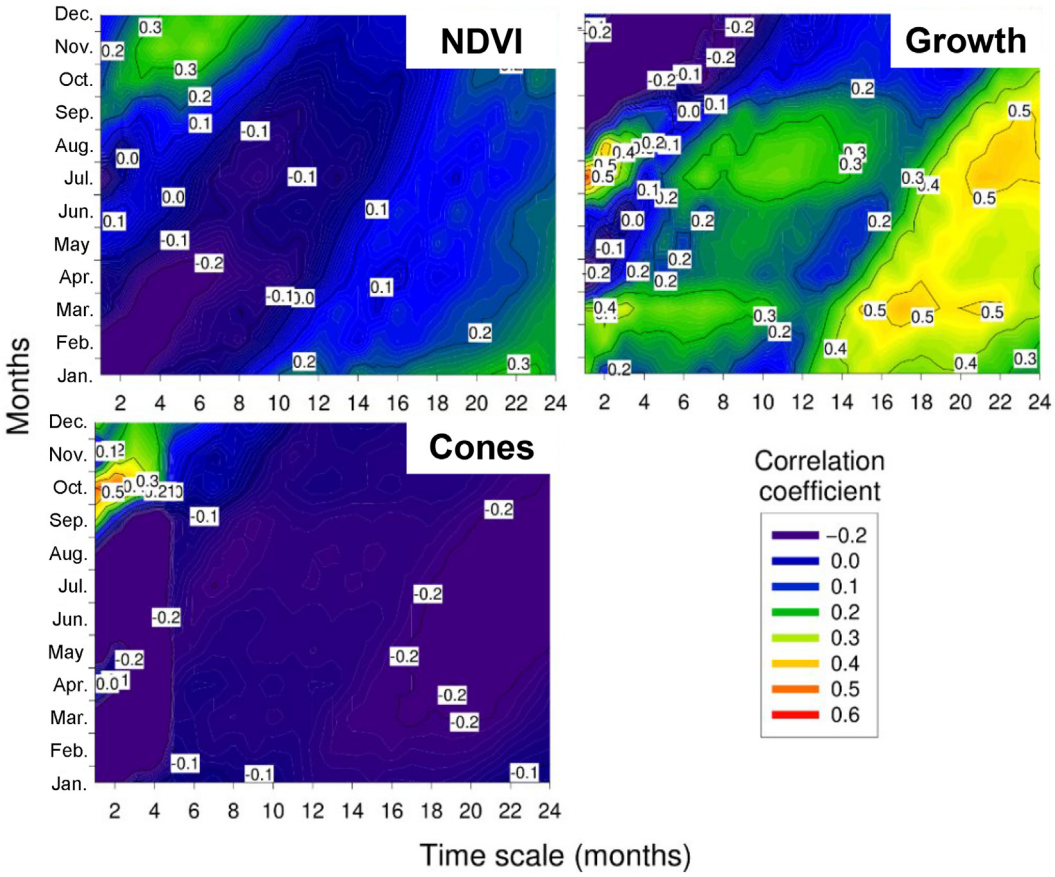



**Fig. 4.** Relationships of the SPEI with NDVI, growth indices, and cone production of Scots pine in Aspurz. The *x* and *y* axes show the SPEI time scale (1–24 months) and months, respectively.

production and canopy cover (Vergotti et al., 2019). However, unlike previous studies, we did not detect trade-offs between growth and reproduction in evergreen species, except for stone pine, which exhibited a lagged (3-year-long) negative correlation between reproduction and growth.

In the studied Iberian forests, both NDVI and growth responded to water availability, with growth showing a stronger response, consistent with previous findings (Gazol et al., 2018; Peña-Gallardo et al., 2018; Khoury and Coomes, 2020). This could be due to the direct effects of drought on cell turgor and cambial activity (carbon sinks) or indirect effects on carbon assimilation (photosynthesis). In general, growth is more constrained by drought stress than photosynthesis (Körner, 2015), which may explain why NDVI responses are more complex, reflecting changes in cover and greenness.

Tree species in cool-wet sites (silver fir, beech, and Scots pine) exhibited high seed or cone production during dry years, suggesting these droughts were not severe enough to limit growth or reproduction (Primicia et al., 2013; González de Andrés et al., 2014). In beech, a one-year lagged positive correlation between growth and NDVI suggests legacy effects of wet conditions enhancing wood production and carbohydrate reserves. Warm, dry summers are known to cue masting in beech, with seed production peaking in years following warm summers and springs (Hacket-Pain et al., 2018; Nussbaumer et al., 2018). However, in Polish temperate forests, where atmospheric water demand is low, beech seed production declined after summer droughts (Pesendorfer et al., 2020). From a management perspective, although droughts may trigger high seed production in wet sites, recruitment success may still be low under water shortages, limiting regeneration.

In silver fir and Scots pine, negative correlations between growth indices and cone production may be explained either by potential trade-offs or by inverse responses to climatic factors. In fir species, the resource-switching model suggests that under deteriorating conditions, resources shift from growth to reproduction, increasing nutrient-use efficiency (Kelly and Sork, 2002). While this may lead to trade-offs, we did not observe them in silver fir, possibly due to mismatches between climatic drivers and the timing of growth and reproduction (Garcia-Barreda et al., 2021).

In the case of Scots pine, severe droughts reduced growth but triggered heavy cone production (Martínez-Alonso et al., 2007). In the Mediterranean Scots pine forests of southeastern France, both growth and cone production were negatively affected by water shortages in the current and previous years, as cone-setting depends on buds formed the year before (Thabeet et al., 2009). Fruiting in these forests was constrained by dry spring-summer conditions, while growth and reproduction were enhanced by prior winter-to-spring precipitation.

Climate variability directly influences resource acquisition and growth (Smaill et al., 2011) while indirectly driving flowering and seed maturation, shaping spatial and temporal seed production patterns (Pearse et al., 2017). Drought may cue masting but can also lead to crop failure (Koenig et al., 2015). This explains why severe winter-to-summer droughts led to simultaneous declines in growth, NDVI, and acorn production in holm oak forests, in agreement with previous research (Pulido and Díaz, 2005; Espelta et al., 2008; Ogaya and Peñuelas, 2007; Pérez Ramos et al., 2010; Sánchez-Humanes and Espelta, 2011; Garcia-Barreda et al., 2023). Despite this, holm oak showed no clear trade-offs between growth and reproduction, except for reduced nitrogen concentrations in leaves of acorn-bearing shoots (Alla et al., 2012). In this species, high spring temperatures advanced flowering and increased airborne pollen, while high yields were associated with wet springs (García-Mozo et al., 2007; Fernández-Martínez et al., 2012). Similar trends were observed in

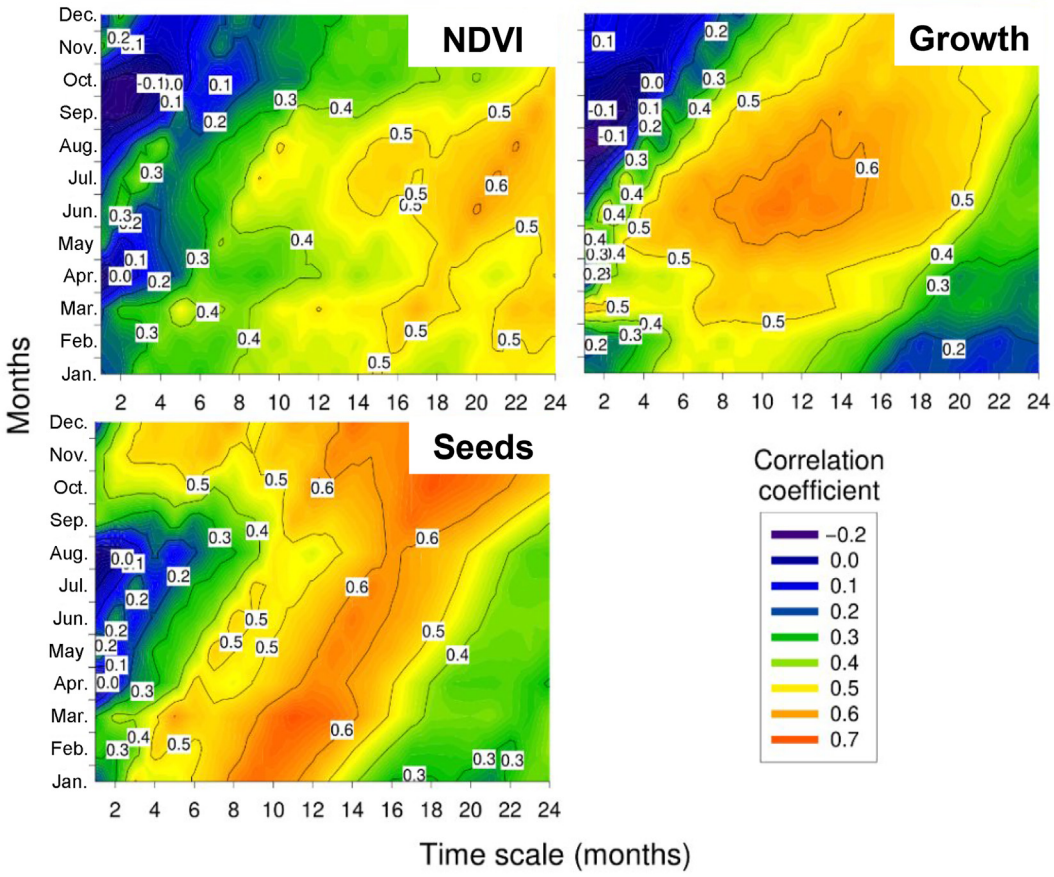



**Fig. 5.** Relationships of the SPEI with NDVI, growth indices, and seed production of holm oak in Arascués. The *x* and *y* axes show the SPEI time scale (1–24 months) and months, respectively.

Mediterranean oaks from Spain and California, USA (Koenig et al., 1996; Fernández-Martínez et al., 2012), whereas in European temperate oaks, warm springs were the main cue for masting (Nussbaumer et al., 2018). These findings suggest that negative growth–reproduction correlations do not necessarily indicate resource trade-offs, as both can be driven by the same climatic cues.

Significant growth–reproduction relationships do not necessarily involve trade-offs. First, associations between fruit production and growth can emerge if similar climate conditions promote or constrain both (Despland and Houle, 1997; Piovesan and Adams, 2001; Drobyshev et al., 2010; Żywiec and Zielonka, 2013). Second, alternating high and low fruiting years (Stevenson and Shackel, 1998) could also explain why high seed crops coincide with reduced growth in subsequent years, as seen in silver fir and Scots pine, possibly due to nutrient or carbohydrate depletion (Sala et al., 2012; Plavcová et al., 2022).

### 4.2. Drought impacts on greening, growth, and reproduction depend on site aridity

Our findings confirm that forest processes such as greening, growth, and seed/cone production are constrained by severe droughts (hypothesis 1) and that these impacts vary by species and site aridity (hypothesis 2). However, the temporal scales and relationship types (linear vs. nonlinear) must be explicitly considered (Camarero et al., 2015b; Pasho et al., 2011). Stone pine exemplified these nonlinear responses, showing peak growth at intermediate SPEI values, suggesting that its productivity is the highest under warm, moderately wet conditions. This implies that both xylem and cone development in this drought-tolerant species are limited by winter-to-spring water shortages and high evapotranspiration, while excessive spring humidity and cloud cover may also restrict cambial activity (Liphschitz et al., 1984; Campelo et al., 2006; Mazza et al., 2014; Natalini et al., 2016; Calama et al., 2019). Growth–SPEI relationships were mostly linear, while SPEI–seed/cone production relationships were better captured using nonlinear models.

Increasing aridity is reducing cone production in several pine species across seasonally dry regions, such as the southwestern USA and Spain (Forcella, 1981; Mutke et al., 2003; Garcia-Barreda et al., 2021; Gonzalez et al., 2023). In stone pine, kernel yield declines have been linked to drought and biotic stressors like the invasive seed bug *Leptoglossus occidentalis*, which has affected Spanish populations (Calama et al., 2020). A three-year lagged negative correlation between cone yield and radial growth has been observed in northwestern Spain (Garcia-Barreda et al., 2021), a pattern we confirmed in central Spain, suggesting robustness in agreement with other studies (Shestakova et al., 2021).

### 4.3. Caveats and limitations of the study

While our use of diverse methodological approaches and limited site replication—except in silver fir—introduces some uncertainty, we are confident in the robustness of our findings. For example, seed series from the two silver fir sites showed strong correlations ($r = 0.94$, $p < 0.001$). Despite limitations in dataset length, consistent temporal patterns across species suggest meaningful ecological trends rather than artifacts. Future research should examine multiple sites across aridity gradients for widespread species like Scots pine and leverage retrospective analyses (e.g., cone scar records; Gonzalez et al., 2023) to further explore growth–reproduction trade-offs and seed viability under climate change. Longer growth and reproduction time series would add robustness to our conclusions.

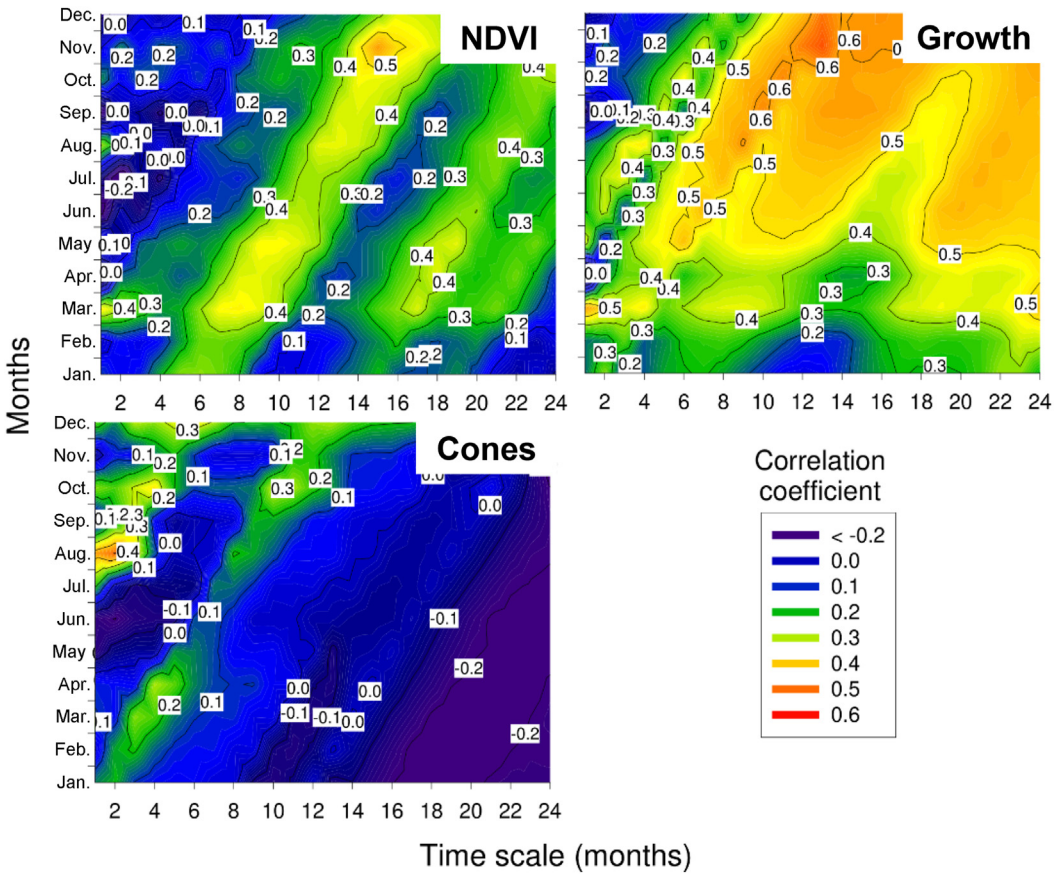



**Fig. 6.** Relationships of the SPEI with NDVI, growth indices, and cone production of stone pine in Almorox.

**Table 3**
Output of *climwin* analyses relating the SPEI drought index vs. NDVI, tree growth (ring-width indices), and seed or fruit production. The climate window indicates the first and last month of climate influence (e.g., 3–5 means March–May).

| Site | Tree species | Variable | SPEI scale (months) | Function type | Δ AICc | Climate window | *p* | $R^2$ | *r* | *n* |
|---|---|---|---|---|---|---|---|---|---|---|
| Gamueta | *A. alba* | NDVI | 2 | Inverse | −11.98 | 8–8 | 0.001 | 0.64 | 0.80 | 146 |
| | | Growth | 22 | Inverse | −24.48 | 11–11 | 0.001 | 0.71 | 0.84 | 166 |
| | | Seed | 1 | Cubic | −25.01 | 7–8 | 0.001 | 0.79 | 0.89 | 97 |
| Las Eras | *A. alba* | NDVI | 2 | Inverse | −11.98 | 8–8 | 0.001 | 0.64 | 0.80 | 146 |
| | | Growth | 1 | Inverse | −20.99 | 7–10 | 0.001 | 0.66 | 0.81 | 145 |
| | | Seed | 1 | Cubic | −10.46 | 7–8 | 0.001 | 0.68 | 0.82 | 97 |
| Aspurz | *P. sylvestris* | NDVI | 3 | Linear | −1.22 | 9–11 | 0.065 | 0.22 | 0.47 | 3 |
| | | Growth | 1 | Linear | −11.0 | 7–7 | 0.001 | 0.56 | 0.75 | 1 |
| | | Cone | 21 | Cubic | −10.5 | 9–9 | 0.001 | 0.74 | 0.86 | 117 |
| | *F. sylvatica* | Growth | 22 | Inverse | −22.39 | 7–7 | 0.001 | 0.78 | 0.88 | 166 |
| | | Seed | 5 | Cubic | −39.92 | 9–10 | 0.001 | 0.98 | 0.99 | 101 |
| Arascués | *Q. ilex* | NDVI | 20 | Inverse | −5.92 | 6–6 | 0.006 | 0.43 | 0.66 | 164 |
| | | Growth | 11 | Inverse | −10.28 | 6–6 | 0.001 | 0.45 | 0.67 | 155 |
| | | Seed | 19 | Quadratic | −11.89 | 11–11 | 0.001 | 0.59 | 0.77 | 67 |
| Almorox | *P. pinea* | NDVI | 1 | Quadratic | −4.90 | 3–3 | 0.010 | 0.44 | 0.66 | 49 |
| | | Growth | 1 | Quadratic | −15.63 | 1–5 | 0.001 | 0.64 | 0.80 | 49 |
| | | Cone | 1 | Quadratic | −7.83 | 1–2 | 0.003 | 0.63 | 0.79 | 49 |

## 5. Conclusions

Drought had varying impacts on canopy greenness, radial growth, and seed or cone production across the five studied tree species. The extent to which water shortages influenced these processes depended on species-specific responses to climate, shaped by site aridity and growth and reproductive phenology. Radial growth was more sensitive to drought than canopy greenness or seed and cone production. While dry conditions acted as climate cues, triggering high seed or cone production in species from the wettest sites (silver fir, beech, and Scots pine), they reduced cone or acorn yields in those from the driest sites (stone pine and holm oak). In holm oak, both growth and acorn production declined significantly during severe droughts, highlighting potential risks to the long-term persistence and regeneration of some tree species or populations under projected aridification.

## CRediT authorship contribution statement

**J. Julio Camarero:** Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Álvaro Rubio-Cuadrado:** Writing – review & editing, Visualization, Validation,

Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Ester González de Andrés:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Cristina Valeriano:** Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Manuel Pizarro:** Writing – review & editing, Software, Methodology, Formal analysis, Data curation. **J. Bosco Imbert:** Writing – review & editing, Supervision, Software, Resources, Methodology, Investigation, Data curation. **Yueh-Hsin Lo:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Data curation. **Juan A. Blanco:** Writing – review & editing, Supervision, Software, Resources, Methodology, Investigation, Conceptualization.

## Data availability

Data are available on reasonable request to the first author.

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## 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.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2025.100329.

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