Species specific vulnerability to increased drought in temperate and Mediterranean floodplain forests

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ABSTRACT

Floodplain forests are sensitive to climate warming and increased drought, as showed by recent oak (*Quercus robur*) dieback and mortality episodes. However, a comprehensive comparison of coexisting tree species under different climate settings or biomes are lacking. Herein, we compared growth rates, growth responses to climate and drought severity, and modeled climate mediated growth of oak and three coexisting tree species (ash, *Fraxinus angustifolia*; alder, *Alnus glutinosa*; elm, *Ulmus minor*). Two floodplain forests subjected to cooler (temperate climate, Ticino) and warmer (Mediterranean climate, Bosco Pantano) conditions in northern and southern Italy, respectively, were analyzed. Ash seemed to be the most sensitive to drought, particularly at the Mediterranean site where oak and elm growth were also negatively affected by water shortages. Alder appeared to be the least sensitive species in terms of growth variability to drought under both temperate and Mediterranean climate conditions. Furthermore, the growth model revealed the influence of soil moisture in spring and summer on the constrained growth of ash and oak and illustrated how oak growth could be severely reduced during drastic hotter droughts. Alder seemed to be the most drought-resistant species under both environmental conditions. These results could represent the first attempts in documenting the ecological consequences of drought in terms of projected climate trends in less investigated Mediterranean floodplain forests. Furthermore, these results highlight how climate and tree-ring data combined with growth models could be useful tools to detect early warning signals of growth decline and impending dieback in floodplain forests in response to dry spells.

1. Introduction

Floodplains and riparian forests are among the most diverse and endangered terrestrial ecosystems threatened by several pressures and stressors that pose a risk to their persistence (Stella and Bendix, 2019). These biodiversity hotspots are vulnerable to land conversion, dam building, and groundwater extraction, which alter the habitats, modify the seasonal flood regime and available soil water pools, and reduce growth performance (Skiadaresis et al., 2019; Šenfeldr et al., 2021). Flood regimes of many floodplains and riparian forests have been modified, making them more vulnerable and dependent on precipitation, particularly in stressed dryland regions (Rohde et al., 2021). Climate warming, increased evapotranspiration rates, and invasive pathogens may increase the risk of growth decline, canopy dieback, and extensive mortality (Stella et al., 2013; Stojanović et al., 2015; Colangelo et al., 2018b; Mikac et al., 2018). Alternatively, high soil water availability in wet sites could buffer them, particularly the non-phreatophyte species, against drought impacts (Heklau et al., 2019).

Drought stress has negatively impacted floodplains and riparian forests in different biomes that are subjected to historical degradation, such as the European temperate and Mediterranean regions (Valor et al.,

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2020; Šenfeldr et al., 2021). For instance, several droughts have led to a substantial increase in growth sensitivity to temperature and a decrease in river water levels in Croatian pedunculate oak (*Quercus robur* L.; hereafter oak) stands (Mikac et al., 2018). In the case of narrow-leaved ash (*Fraxinus angustifolia* Vahl.; hereafter ash) populations growing in southeastern Europe, their radial growth was reduced by soil water shortages in early summer (Camarero et al., 2021; Rodríguez-González et al., 2021). This negative effect of drought on ash growth was not only observed in warm-dry Mediterranean sites, but also under cooler conditions in temperate sites, and a similar negative response was found for oak (Tumajer and Treml, 2006). Therefore, responses of climate and drought severity in selected floodplain tree species should be compared in temperate and Mediterranean biomes to assess whether these species respond differently to rising temperatures and aridification depending on site climatic conditions.

Herein, we aimed to assess climate-growth relationships in four tree species in two floodplain forests subjected to cooler (temperate climate) and warmer (Mediterranean climate) conditions in northern and southern Italy, respectively. This study also focused on comparing radial growth responses to the observed and projected climate of two major tree species abundant in European floodplain forests, namely oak and ash. These two winter deciduous species share some traits such as relatively shallow roots, ring-porous wood, and water-spending strategies (Köcher et al., 2009). In floodplain forests, the radial growth of non-phreatophyte ash depends on shallow soil water sources (Singer et al., 2013, 2014). Ash species constrain stomatal conductance more than most co-occurring riparian tree species below specific thresholds of soil water availability (Lemoine et al., 2001). This ecophysiological behavior of ash can explain its high growth sensitivity to drought (Camarero et al., 2021).

This study aimed to: (i) quantify the climate trends and growth variability of four coexisting tree species (oak, ash, elm, and alder) in temperate and Mediterranean floodplain forests, (b) evaluate their growth relationships with climate variables and a drought index, and (c) determine the main climatic stressors of floodplain tree species in the two biomes. It is expected that tree growth is negatively affected by warm conditions and summer drought more in the Mediterranean than in the temperate floodplain forest.

2. Materials and methods

2.1. Study sites

We selected two floodplain forests located in northern (Parco Riserva Naturale Orientata La Fagiana, hereafter Ticino), 45.436 °N, 8.825 °E, 102 m a.s.l.) and southern (Bosco Pantano, Basilicata region, hereafter Bosco Pantano) 40.160 °N, 16.680 °E, 6 m a.s.l.) Italy. The northern site is situated in the "Parco Lombardo della Valle del Ticino" in a flat area close to the Ticino River, occupying a forest area of ca. 500 ha, located about 30 km west of Milan city. The main tree species in the study forest were the pedunculate oak (*Q. robur* L.), black alder (*Alnus glutinosa* (L.) Gaertn), elm (*Ulmus minor* Mill.), manna ash (*Fraxinus ornus* L.), hornbeam (*Carpinus betulus* L.), black locust (*Robinia pseudoacacia* L.). Mean oak density and basal areas were 179 individuals ha⁻¹ and 18.8 m² ha⁻¹, respectively. Oak is one of the European tree species more sensitive to drought. According to local reports, the Ticino oak forest showed recent drought-induced decline symptoms since the early 2000s (shoot dieback, leaf loss and withering, epicormics shoots, growth decline etc.). Annual oak mortality in this study area shifted from 5 to 10% from 2004 to 2006 (Colangelo et al. 2018a). According to climate data from the Abbiategrasso station (45.398° N, 8.913° E, 122 m a.s.l.; period 1961–2020, located at 5 km from the sampling site), the climate in the study area was temperate and humid, with a mean annual temperature of 12.8°C and annual total precipitation of 1104 mm. The wettest and driest months were October (122 mm) and January or July (59–60 mm), respectively. January (0.8 °C) and July (24.6°C) were the coldest and

warmest months, respectively. The mean annual water balance is 306 mm (period 1961–2020). The study area was characterized by the presence of a highly permeable Upper Po Plain shallow aquifer formed by gravel and sand deposits over clay deposits. Since 1980, the water table depth measured in Abbiategrasso showed no significant variation except for punctual increases in 1999, 2004, and 2006 (Colangelo et al., 2018a).

The southern site ("Bosco Pantano di Policoro-Herakleia," hereafter Bosco Pantano) is located in the southeastern sector of the Basilicata region along the Ionian coast and includes the final tract and mouth of the Sinni River. According to the European Commission Habitats Directive, this site has communal importance and is a high conservation value Mediterranean flood-plain forest. Here, the oak forms a remnant population constituting part of the species' southernmost distribution limit in Europe. Indeed, this site (approximately 150 hectares) is a relict of a larger old growth forest destroyed by unrestricted exploitation occurred during 1950s aiming to gain new lands for crops and fruit orchards. Here, after the 1950s, the human pressure was limited to very few cuts leaving this area almost undisturbed.

The site is a hygrophilous forest located along waterways and it is protected from the coast by several dunes. The dominant tree species are narrow-leaved ask, black alder, elm, and white poplar (*Populus alba* L.) with limited presence of pedunculate oak. Currently, the vegetation is undergoing a severe decline because of climate change and the construction during the 70s of a dam along the Sinni River which has significantly reduced the water flows and lowered the water table depth. As a consequence, the density of tree individuals is reduced considerably especially for pedunculate oak, that is considered the most important and emblematic species in Bosco Pantano. Indeed, the mean oak density and basal area are 0.7 individuals ha⁻¹ and 0.1 m² ha⁻¹, respectively, considering the entire stand of 150 hectares. Indeed, the environment is becoming increasingly hostile for hygrophilous species with progressive replacement with meso-xerophytic species. Indeed, the presence of a tree vegetation layer is identified by a patchy distribution where tree species coexist in a rich shrub layer. The climate in this area is Mediterranean (data from "Nova Siri Scalo" station, 40.133 °N, 16.637 °E, 9 m a.s.l.; period 1961–2020, located 7 km from the sampling site) with a mean temperature of 16.8°C and total annual precipitation of 557 mm. The wettest and driest months are November (84 mm) and July (12 mm), respectively. January (8.3 °C) and July (26.9 °C) were the coldest and warmest months, respectively. The mean annual water balance is 507 mm (period 1961–2020). In this area, outcrops of coarse sand appear to be mixed with gravel. Soils were basic, slightly saline, and distinguished by fine-textured alluvial sediments (clays and silts).

2.2. Climate data

Monthly climate data (mean temperature, precipitation) for the period 1970–2020 were obtained from the 0.10°-gridded (~10.0 km) E-OBS ver. 22.0 climate dataset was subjected to previous quality checks and homogeneity tests (Cornes et al., 2018). We selected this dataset because local meteorological stations provide only not validated raw data, plenty of missing values, while gridded climate network provides long and homogenous validated records. Changes in drought severity were assessed by downloading the Standardized Precipitation Evapotranspiration Index (SPEI) from the Global Drought Monitor webpage (http://spei.csic.es/index.html). The SPEI is a multiscale drought index that considers effects of temperature and evapotranspiration on water availability and shows negative and positive values, which represent dry and wet conditions, respectively (Vicente-Serrano et al., 2010). We obtained 1- to 20-month long monthly SPEI series to assess growth responses to droughts of different duration, timing and intensity.

We calculated linear slopes of climate variables having the strongest associations with tree growth, considering ensemble climate projections for the two sites for 2022-2099 (see Table S1). Subsequently, we selected the high-emission RCP8.5 scenario and used the climate data provided

by the CORDEX-EUR 11 (0.11 °resolution, ~12.5 km) regional climate models (Jacob et al., 2020).

2.3. Site selection, field sampling and tree-ring width data

For the Bosco Pantano site, we identified patches with the most homogeneous characteristics in terms of specific composition, age, structural stand and site conditions. These patches have been used as replicates to sample cores on the four targeted tree species. In the case of the temperate site (Ticino), although the surface area was wider comparing to Bosco Pantano, the sampling area was chosen in order to be representative of the neighboring patches areas where the four species selected for this study were co-occurring, in order to compare the Mediterranean site with a site having contrasting climatic characteristics. Although the two experimental sites are very close to the human settlements there are law restrictions from the Italian Authorities that prevent a human direct impact. Nevertheless, along the river Sinni in the Mediterranean site, indirect impact still remain, due to the dam construction that reduced the frequency of historical flooding that ensured a constant fed of this lowland forest before the 1950s. Since we focused our analyses on a recent period (1980-2016), we consider human influences were of limited impact.

In the field, we randomly sampled almost dominant and healthy trees of all four species at each site (Table 1). We measured the diameter at breast height (Dbh, measured at 1.3 m) and tree heights using tape and a Vertex hypsometer (Vertex IV/360°, Haglöf, Sweden), respectively. Two cores per tree at breast height (1.3 m) were extracted, taken in opposite directions using a Pressler increment borer (Haglöf, Sweden) for dendrochronological analyses.

Wood samples were air-dried, and surfaces of cores were cut using a sledge core microtome to clearly distinguish ring boundaries (Gärtner and Nievergelt, 2010). Tree rings were visually cross-dated, and tree-ring widths were measured to the nearest 0.01 mm using a binocular microscope coupled to a computer with the LINTAB™ package (Rinntech, Heidelberg, Germany). The COFECHA program (Holmes, 1983) was used to evaluate the visual cross-dating of the tree-ring series.

To estimate tree age at 1.3 m, when a core did not reach the pith, the total missing radius and the number of missing rings were estimated by interpolating the distance to the pith using the curvature of the innermost rings of the sample. We first removed age- and size-related long-term trends of the tree-ring width series by converting the raw tree-ring width series into ring-width indices (TRWi) to evaluate climate-growth relationships. This was done by fitting a 30-year spline to raw data to preserve high-frequency growth variability and then dividing observed by fitted values to obtain dimensionless, standardized ring-width indices (Fritts, 1976). Additionally, we removed the first-order autocorrelation of each series by fitting autoregressive models and obtaining the residual

series. Finally, a bi-weighted robust mean was computed to obtain the mean residual chronology (TRWr) for each tree population (Speer, 2010).

The statistical features of each TRWi chronology were evaluated by calculating the mean and first-order autocorrelation (AC1) of the ring-width data, mean sensitivity (MS, which assesses the year-to-year relative differences in growth between consecutive rings), and expressed population signal (EPS) (Fritts, 1976). This statistics defines how good chronologies represent a theoretical, infinitely replicated chronology (Wigley et al., 1984).

2.4. Climate-growth relationships and statistical analyses

We quantified the climate-growth associations for the periods of 1980–2016 using Pearson correlations. This period was selected because it was the best replicated and common period to all sites and species. Indeed, in Ticino some series ended in 2016, whereas in Bosco Pantano some individuals were young and their series started in 1980.

Correlations were calculated considering monthly climate variables (mean temperature and precipitation) and the window of analysis was from October of the year prior the ring formation to September of the same (late growing season) of the aforementioned years. Correlations were calculated using the mean TRWr series of all trees (residual chronologies). Analogously, we also calculated Pearson correlation between chronologies and 1- to 20-month long monthly SPEI values.

We fitted multiple linear regressions to predict the growth rates (residual chronologies, response variables) of ash and oak as a function of monthly temperature and precipitation data, considering the common period of 1980-2016. We focused on ash and oak chronologies because they were replicated the best according to the EPS (Table 2) and considered the common period of 1980-2016 in models. Regression models were selected by minimizing the Akaike information the criterion (Burnham and Anderson, 2002).

We calculated 20-year moving correlations overlapped by one year between selected species and climate variables that were significantly correlated with TRWi to assess whether climate-growth relationships changed over time. This was performed to compare different drought tolerance strategies of ash and oak. Furthermore, we also calculated 20-year moving Pearson correlations shifts every year for the period 1980-2016 between ash and oak chronologies to assess the extent of their coupling throughout time. Tree-ring analyses were performed using the dplR package (Bunn, 2008) in the R environment (R Development Core Team, 2021).

2.5. VS-lite forward growth model

We used the VS-lite model to assess differences in climatic controls of tree growth and to simulate climate limitations of radial growth related to soil moisture in the two study sites. This model accounts for nonlinear relationships between growth and climate factors. Additionally, we focused on ash and oak chronologies and considered the common period of 1980-2016. The model is based on the principle of limiting factors affecting tree ring formation (Vaganov et al., 2006) and simulates anomalies of the TRWi based on the minimum growth response to temperature (gT) and soil moisture (gM) at a monthly scale (Tolwinski-Ward et al., 2011, 2013). Insolation (gE) was estimated using the site latitude.

The VS-lite model determines for each month and year partial growth rates (unitless variable, range 0-1) of temperature (gT), soil moisture (gM) and photoperiod (gE, estimated from site latitude). Partial growth rates represent the radial growth potential under given climatic conditions or solar radiation. Climatic partial growth rates of temperature and soil moisture are defined as piece-wise linear functions of monthly temperatures and soil moisture, whereas the photoperiod partial growth rate is defined as the ratio of daylength to daylength of the summer solstice. For each month, the lowest of climatic partial

Table 1
Size and age of sampled trees. Values are means ± SD.

Species	Site	Diameter at 1.3 m (cm)	Height (m)	Age at 1.3 m (years)
Alnus glutinosa	Ticino	40.4 ± 9.9	12.8 ± 1.9	51 ± 19
	B. Pantano	40.9 ± 13.7	15.4 ± 2.2	46 ± 5
Ulmus minor	Ticino	20.8 ± 4.1	8.9 ± 1.7	40 ± 8
	B. Pantano	26.8 ± 8.6	9.8 ± 2.4	38 ± 4
Fraxinus angustifolia	Ticino	35.8 ± 7.0	13.0 ± 1.8	54 ± 14
	B. Pantano	49.3 ± 9.8	19.2 ± 2.2	57 ± 7
Quercus robur	Ticino	52.4 ± 9.5	23.7 ± 6.4	77 ± 13
	B. Pantano	45.1 ± 18.9	18.7 ± 5.0	69 ± 20

Table 2
Number of sampled trees and processed cores and related tree-ring width variables. Variables' abbreviations are: AC1, first-order autocorrelation of ring-width data; MSx, mean sensitivity of standard ring-width indices, EPS, Expressed Population Signal. Statistics correspond to the common period 1980–2016.

Species	Site	No. trees (cores)	Period	Tree-ring width (mm)	AC1	MSx	EPS
A. glutinosa	Ticino	11 (21)	1922–2016	2.78 ± 1.79	0.71	0.37	0.82
	B. Pantano	10 (20)	1965–2018	2.95 ± 2.03	0.73	0.36	0.63
U. minor	Ticino	11 (22)	1970–2017	2.24 ± 1.15	0.63	0.34	0.74
	B. Pantano	13 (26)	1980–2018	4.14 ± 1.89	0.42	0.34	0.72
F. angustifolia	Ticino	12 (23)	1921–2017	3.13 ± 1.61	0.70	0.27	0.85
	B. Pantano	11 (21)	1950–2018	3.38 ± 2.14	0.76	0.29	0.88
Q. robur	Ticino	14 (27)	1916–2016	2.70 ± 1.30	0.68	0.27	0.92
	B. Pantano	12 (25)	1906–2020	3.07 ± 1.65	0.77	0.25	0.85

growth rates is retained for the rest of simulations (following Liebigs' law of minimum and assuming the cambial activity is controlled by the most limiting environmental variable) and then multiplied by the respective partial growth rate to photoperiod into integral growth rates. Integral growth rates represent a proxy of radial growth given by overall forcing of climatic conditions and solar radiation. Annual values of integral growth rates are the final output and they can be compared with observed growth rates (TRWi). The model inputs are monthly mean temperature and total precipitation, the ring-width chronology (TRWi), and site coordinates. The outputs are simulated growth rates which are compared with observed growth rates (TRWi) using Pearson correlation coefficients (r).

We used Bayesian estimations to simulate growth rates using two parameters: first, the threshold below which growth will not occur (T1 for temperature and M1 for soil moisture), and second, the threshold above which growth is not limited by these climate factors (T2 for temperature and M2 for soil moisture; see Table S2). Growth responses to temperature (gT) and soil moisture (gM) were simulated by calibrating these key parameters.

We simulated VS-lite chronologies for the period 1980–2016 using the calibrated posterior parameter estimate for each tree species and also considered specific simulations of gM for that period and in two specific dry years (2003 in Ticino and 1992 in Bosco Pantano). We also compared the gM values estimated for the growing season (April–October). Mann-Whitney U tests were used to compare the mean gM values calculated for 1980–2016 with those of dry years.

We evaluated the assumption of uniform priors for the growth function parameters (with independent and normally distributed errors for TRWi values) over 13,000 iterations using three parallel chains and a white Gaussian noise model error (Tolwinski-Ward et al., 2013). We first adjusted the gT and gM parameters and then performed the Bayesian calibration. We used a Gaussian-like likelihood function and assumed a constant standard deviation for the Gaussian likelihood function. There was burn-in to let the Markov Chain Monte Carlo (MCMC) simulations to stabilize, and the chain convergence was also checked (Gelman and Rubin, 1992). A Gibbs sampler was used for the MCMC chain in the Bayesian calibration and the burn-it length was 100.

The VS-lite model uses the empirical leaky bucket hydrology model to estimate monthly soil moisture from temperature and total precipitation (Huang et al., 1996). However, the model does not explicitly account for the phreatic water uptake. Finally, we compared the observed and simulated chronologies in the two study cases using Pearson correlation coefficients.

3. Results

3.1. Climate trends and variability

According to our results, temperatures have been rising steadily since the 1970s in both study sites, albeit more rapidly in Ticino (slope 0.08 °C yr^{-1}, $p < 0.01$) than in Bosco Pantano (slope 0.06 °C yr.$^{-1}$, $p < 0.05$) with peaks in 1990, 1994, 1997, 2003, 2006, 2007, and 2015–2016 (Fig. 1). Some of these warm episodes corresponded to

severe droughts, including 2003 in Ticino and 1997 in Bosco Pantano. The years with the lowest precipitation were 2007 in Ticino (544 mm) and 2003 in Bosco Pantano (243 mm).

Since 1950, the driest decades have been in the 1990s and the 2000s. From 2010 onwards, the SPEI tended to decrease in Ticino (slope = -0.18 yr^{-1}, $p = 0.01$); however, this tendency towards drier conditions was not observed in Bosco Pantano. According to the SPEI, 1992 and 2003 were among the driest years in Bosco Pantano and Ticino, respectively. The 2003 drought in Ticino was mainly due to very warm conditions from May to August (+5.2 °C above the long-term average) and low precipitation (-170 mm below the long-term average), whereas the 1992 drought in Bosco Pantano was mainly caused by a low amount of precipitation from May to August (-170 mm below the long-term average).

3.2. Size and growth variability

The highest and thickest-stem sampled trees corresponded to oaks and ash in Bosco Pantano, whereas elms were the smallest and youngest trees at both sites (Table 1). The oldest trees were oaks in Ticino.

Elm was the fastest-growing species at the Pantano site (4.1 mm yr^{-1}), followed by ash (3.4 mm yr^{-1}); however, elm had the lowest growth at Ticino (2.2 mm yr^{-1}). Alders and oaks demonstrated intermediate growth rates (2.7–3.1 mm yr^{-1}). The highest first-order autocorrelation values corresponded to ash, oak, and alder, whereas the highest mean sensitivity values corresponded to alder and elm. The lowest EPS values were found for alder and elm in Bosco Pantano, whereas the highest EPS values were reported for ash in Bosco Pantano and oak in Ticino (Table 2).

In Bosco Pantano, the 2012 was characterized by a severe growth drop (–23.9% compared to 2011), particularly in the case of elm (–41.9%) and alder (–26.5%) (Fig. 2). The year 2017 experienced another growth reduction (–25.4%) at this site compared to that in the previous year; however, this time, the strongest growth loss occurred in ash (–35.0%). In dry season of 1992, oak and ash showed relative growth reductions of 32.1% and 38.4%, respectively, compared with those of the previous year.

All species had diminished growth during the 2003 drought, but the reductions were stronger in Ticino (–24.5% mean reduction with respect to 2002) than in Bosco Pantano (–14.9%) (Fig. 2). Taking into account the different species, the 2003 growth reduction was the highest in elms from Ticino (–38.2%) and alders from Bosco Pantano (–40.5%). In this year, oak and ash showed relative growth reduction of 16.2% and 21.9%, respectively.

In Ticino, elm and oak chronologies were positively correlated ($r = 0.43$, $p = 0.009$). In Bosco Pantano, the ash chronology was positively correlated with elm ($r = 0.43$, $p = 0.029$) and oak ($r = 0.32$, $p = 0.045$) chronologies.

3.3. Growth responses to climate and drought

In Ticino, alder grew less as the prior October temperature increased, whereas warmer January-February conditions enhanced elm growth
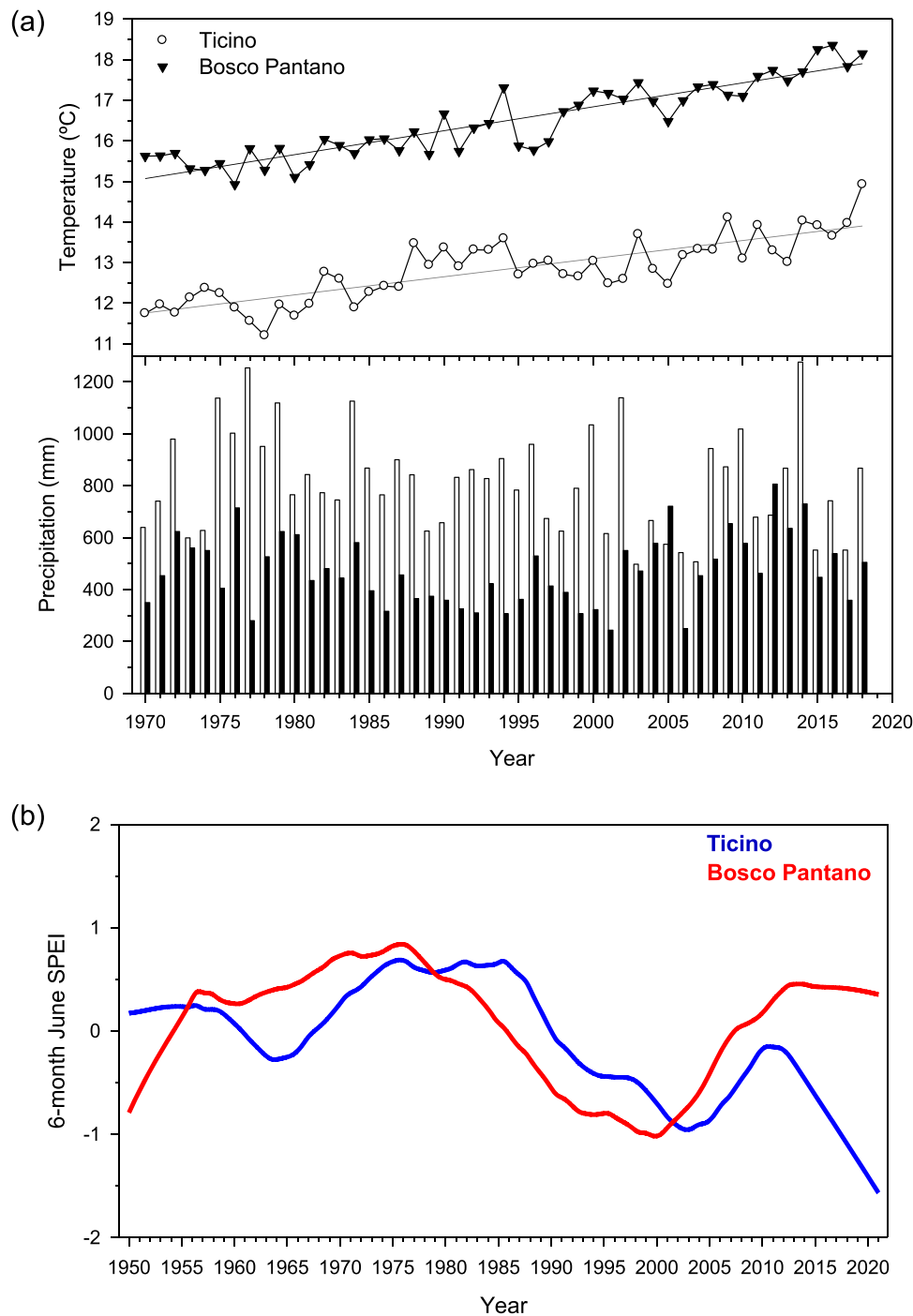
Fig. 1. (a) Annual climate data in the two study floodplain forests (Ticino, Bosco Pantano) and (b) patterns and trends of drought severity according to the 6-month June SPEI (period 1950-2021). In plot (a) linear regressions indicate significant (*p* < 0.05) slopes of temperature trends. In plot (b) smoothed functions correspond to loess fits with 0.2 of sampling proportion.

(Fig. 3a, c). Ash growth responded negatively to high temperatures in March and July, but wet conditions in February, April, and July improved their growth. In contrast, wet March conditions were associated with lower oak growth.

In Bosco Pantano, warm May conditions reduced ash and oak growth (Fig. 3b, d). The warm July conditions constrained elm growth. Ash responded positively to wet January conditions, while elm responded positively to wet May conditions. Finally, wet conditions in previous November and current September were associated with lower growth rates in the alder.

The selected multiple linear regressions showed that ash growth was

constrained by warm July and May conditions in Ticino and Bosco Pantano (Table 3). At both sites, prior winter precipitation enhanced ash growth, as well as for oaks in Ticino. In Bosco Pantano, warm January conditions improved ash and oak growth. In the case of oak, wet conditions in March and warm conditions in May reduced its growth in Ticino and Bosco Pantano, respectively.

Regarding associations between ring-width indices and SPEI, in Ticino we only found significant (*p* < 0.05) positive correlations with ash and 6-month SPEI values, which peaked in July (Fig. 4a). However, in Bosco Pantano, significant correlations were observed for ash, oak, and elm (Fig. 4b). Elm and oak responded to short- and mid-term
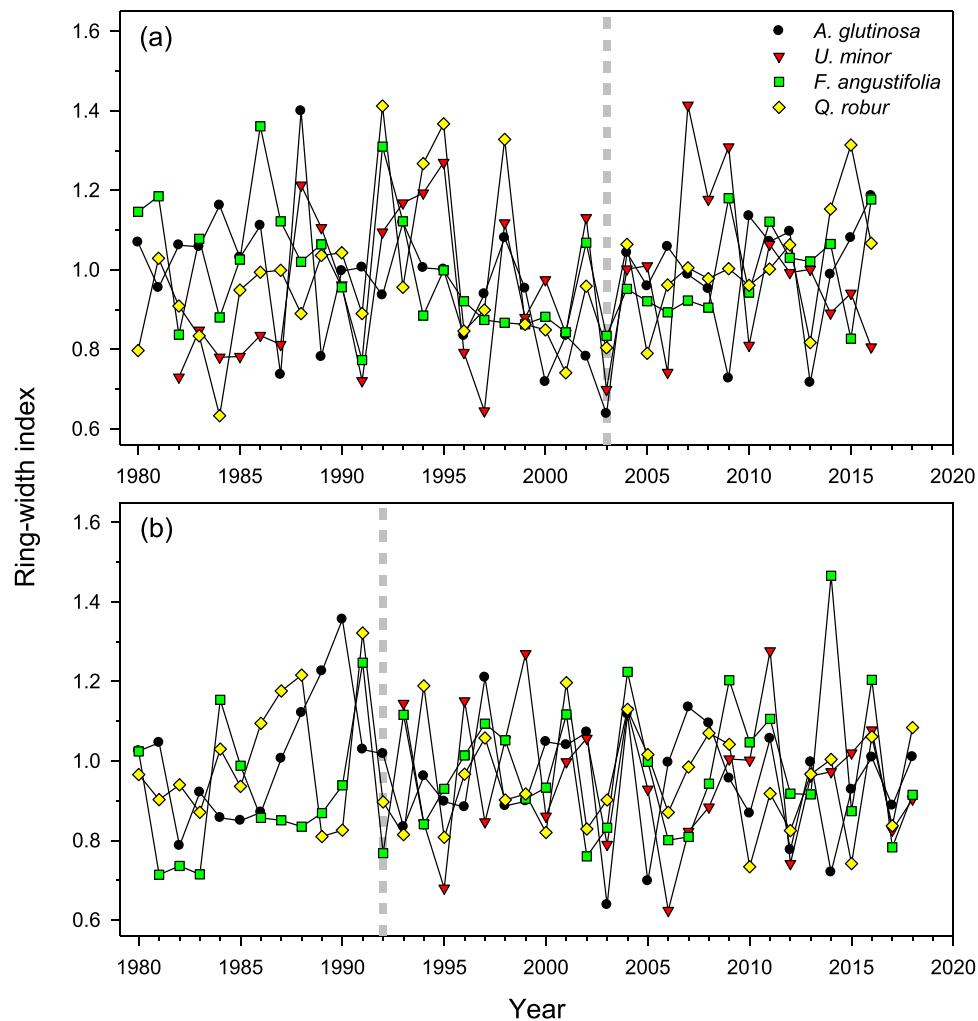
Fig. 2. Tree-ring width chronologies of the four study species in the two floodplain forests located in northern (a, Ticino) and southern (b, Bosco Pantano) Italy. The best-replicated and common period is presented in each site (1980–2016 and 1980–2018, respectively). The vertical dashed lines indicate major droughts (2003 in Ticino and 1992 in Bosco Pantano).

droughts (2- to 7-month SPEI), with correlations peaking in May-July and January-March, respectively. Ash showed the highest SPEI-growth correlations with responses to short- and long-term drought during most months, reaching a maximum correlation coefficient ($r = 0.59$) for 2-month SPEI January values. Overall, ash growth was sensitive to drought during the growing season (spring, summer) in both study sites, whereas ash and oak also responded to early growing-season droughts in Bosco Pantano. However, elm responded to droughts during the growing season in this site.

The moving correlations between selected climate variables and oak and ash ring-width indices exhibited that oak growth in Ticino became more dependent on February precipitation, whereas the negative influence of July temperature on ash growth remained quite stable (Fig. 5). In Bosco Pantano, the positive influence of January temperature on oak growth remained steady, whereas the May temperature tended to increase their importance as negative driver of ash growth.

3.4. Characterizing the climatic stressors of growth using the VS-Lite model

The VS-Lite model was able to capture growth variability in three out of the four chronologies considered, except in the case of the oak in Bosco Pantano, where observed and simulated series of ring-width indices had a non-significant correlation ($r = 0.26$) (Table 4). In contrast, the model produced a simulated ash chronology for this site

that was related to the observed chronology ($r = 0.46$).

According to the VS-Lite model, growth limitations due to soil moisture were the strongest for ash in Bosco Pantano, particularly during the dry year of 1992 (Fig. 6), followed by ash in Ticino. The simulated gM values were lower during the growing season (April to October) in both ash populations than those in the oak ones. Notably, during the dry years, the gM values of both oak populations decreased from July to October in Ticino and from June to November in Bosco Pantano, indicating severe drought stress in the late summer. In the case of Ticino, the oak gM summer values during the 2003 drought overlapped with the ash mean gM values, indicating similar drought stress.

4. Discussion

We found the strongest growth response to drought in the Mediterranean floodplain forest, specifically in the case of ash and oak, as well as in elm. Warmer spring conditions are becoming a major stressor of oak and ash growth, and this may continue in view of projected climate trends for the 21st century. However, this does not mean that tree species inhabiting the temperate floodplain forest in Ticino were not sensitive to water shortages, as shown by their strong growth drops in response to the severe 2003 summer heatwave and drought. The VS-Lite simulations suggest that such extreme climate events can lead to summer drought stress in oaks similar to that experienced by ash at this site. Severe droughts can also constrain oak growth at the Mediterranean site Bosco
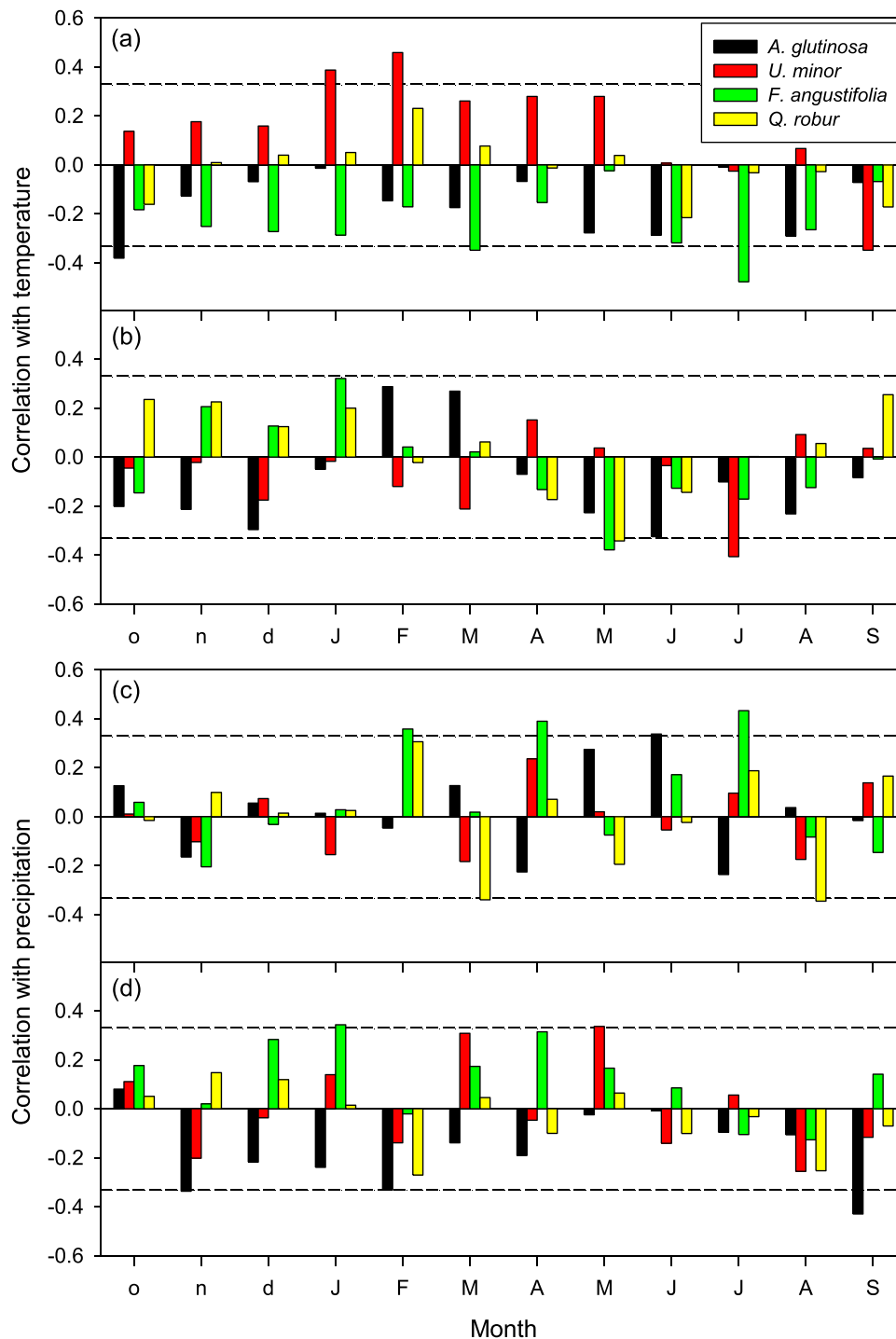
Fig. 3. Climate-growth relationships in the Ticino (a, c) and Bosco Pantano (b, d) study sites. Bars are Pearson correlations obtained by relating species' ring-width chronologies and monthly mean temperature (a, b) and total precipitation (c, d). Dashed horizontal lines show the 0.05 significance levels. In lower case the months of the year preceding the ring formation, in capital letters the months of the same year.

Pantano; whist, low soil moisture in late summer and early autumn constrains the growth of ash more than that of oak. However, we recon that the missing of data on soil characteristics and soil water availability may limit our inferences based on precipitation data on drought-intolerant tree species with access to the phreatic water table. Indeed, investigating phreatophytic tree species without accounting for water holding capacity, lateral flow or deep soil water uptake may lead to an overestimation of drought impacts. Regrettably, currently there are no long-term series of soil water availability or other proxies (e.g., changes in water table depth) in the study site.

In Ticino, the 2003 drought also reduced the number and lumen area of oak vessels the following year, leading to a decrease in potential hydraulic conductivity and stem wood production (Nola et al., 2020). The reduction in lumen area in response to drought concurs with the water-spending strategy of deciduous oak species that maintain high photosynthesis rates despite water shortage, increasing the risk of damage due to hydraulic failure (Cavender-Bares and Holbrook, 2001). Lastly, tree-ring width statistics such as first-order autocorrelation were similar to the values reported in floodplain ash and oak stands, supporting our analyses (Šenfeldr et al., 2021).

Table 3

Selected multiple linear regressions fitted to four residual chronologies of two study species (*F. angustifolia, Q. robur*) as a function of monthly climate variables (T, mean temperature; Pr, total precipitation), and considering the common period 1980-2016 in the two study sites. Months are abbreviated by their first three letters. Intercepts and selected climate predictors were significant ($p < 0.05$). Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Species	Site	Parameter estimates	R^2
F. angustifolia	Ticino	$y = 1.9513 - 0.0403\,TJul + 0.0008\,PrFeb$	0.36**
	B. Pantano	$y = 1.3673 + 0.0470\,TJan - 0.0413\,TMay + 0.0569\,PrJan$	0.41***
Q. robur	Ticino	$y = 1.1293 + 0.0015\,PrFeb - 0.0010\,PrMar - 0.0023\,PrAug$	0.42***
	B. Pantano	$y = 1.5050 + 0.0353\,TJan - 0.0308\,TMay$	0.21*

Cumulative stress due to consecutive hotter droughts (heatwaves coinciding with low precipitation) could affect tree growth in temperate floodplain forests (Schnabel et al., 2022). Our findings agree with those of previous research demonstrating the high radial growth sensitivity of ash species to drought (Camarero et al., 2021), which confirms that this species is vulnerable to the drying of upper unsaturated soil horizons (Sánchez-Pérez et al., 2008; Singer et al., 2013, 2014). The correlations between SPEI and ash growth found in Ticino also agree with the findings of a previous study conducted in a nearby stand (Rodríguez-González et al., 2021). Our results support the forecasts proposed by Šenfeldr et al., (2021), who predicted a higher vulnerability for ash than for oak in response to increased drought stress due to global warming. However, ash may also exhibit a high growth resilience. Comparatively, oak was less sensitive to drought and low soil moisture, as shown by the results of VS-Lite simulations. This concurs with the ability of oak to downregulate sap flow with decreasing soil moisture, thus avoiding water loss better than ash (Brinkmann et al., 2016; Kowalska et al., 2020; Schnabel et al., 2022). It was also found a high stomata responsiveness to vapour pressure deficit in oak (Martinez-Vilalta et al. 2014; Urli et al., 2015; Garcia-Forner et al. 2017).

Alder and elm form diffuse- and ring-porous wood types, respectively, which means an earlier growth start and a longer growing season in the case of elm, which produces the first earlywood vessels after bud burst and before leaf expansion occurs (Suzuki et al., 1996; Kitin and Funada, 2017). Alder and elm are considered relatively isohydric, water-saving species with high stem capacitance to buffer negative water potentials under decreasing soil water content (Meinzer et al., 2009, 2017). However, long periods of dry shallow soils may lead to drought-triggered dieback and mortality, as found in *Ulmus sibirica* (Koepke et al., 2010). In addition, wet and cool conditions improved alder growth in the Mediterranean and temperate sites, respectively, confirming that this species is sensitive to the growing season climate and abrupt changes in hydrological conditions (Douda et al., 2009; Valor et al., 2020). Low water-use efficiency could make alder dependent on shallow-soil and phreatic water sources and less responsive to long-term droughts compared with tree species, which are more dependent on deeper and fluctuating soil water sources (Nadal-Salda et al., 2017; Valor et al., 2020). The low water-use efficiency of alder may make it more vulnerable to drought stress, but such vulnerability may be reduced by accessing the deep soil phreatic water (e.g., Claessens et al., 2010). If such phreatic and deep water supply would diminish under global warming, alder would become even more responsive than other coexisting species to drought stress. In the case of elms, their younger age was due to the Dutch elm disease, which kills larger and older individuals (Pita et al., 2018). This age effect may influence climate-growth associations because younger and smaller trees may be less sensitive to climate variability in hardwood species (Colangelo et al., 2021). Nevertheless, elm growth was reduced by dry spring conditions at the Mediterranean site, and also by cold late-winter conditions at the temperate site. In addition, spring dry conditions

associated with higher temperatures can stimulate growth, as illustrated by oak in Ticino, which may be explained by warm conditions that increase vessel size and hydraulic conductivity (Tumajer and Treml, 2006).

In temperate floodplain forests, exceptionally warm springs may increase productivity if water and nutrients are available, whereas summer droughts can reduce carbon uptake due to soil moisture depletion (Kowalska et al., 2020). Ash is reported to have a high nutrient-use efficiency, which may explain the more abrupt growth decrease during a single drought compared to oak (Kazda et al., 2000). Therefore, more frequent hotter droughts would negatively impact growth in ash more than in oak; however, the impacts on carbon uptake may differ unless a critical threshold of soil moisture is reached and this triggers dieback and mortality (Colangelo et al., 2018a).

Although ash is reported to mainly use water from shallow soil layers when the soil water supply is high (Singer et al., 2013), the water uptake can be extended to deeper soil layers under dry conditions (Brinkmann et al., 2019). However, longer droughts could reduce soil moisture in the late growing season and constrain ash growth or lead to a delayed latewood formation under warmer conditions. Changes in the period of wood formation in response to more lasting summer droughts should be further investigated in ash and other riparian tree species. Such plastic behavior and differences among coexisting species in terms of hydraulic and photosynthetic traits or water-uptake soil depths could also mitigate drought stress in diverse floodplain forests through complementary effects (Sánchez-Pérez et al., 2008). Additionally, microenvironmental conditions can modulate tree responses to drought in floodplain forests. For instance, in a temperate floodplain forest, oak growth was positively influenced by temperature during the growing season, but negatively affected by drought in drier sites located outside the flood area (Tumajer and Treml, 2006). Therefore, the water level is another important driver of ash and oak growth in seasonally flooded forests (Šenfeldr et al., 2021), and recent dieback episodes are often the result of long-term declines in water levels and increased drought stress (Stojanovič et al., 2015).

Our study has several positive points we would like to highlight: (i) we show the value of exploring the climate sensitivity based on field data of understudied ecosystems such as floodplain forests and underlooked tree species (e.g., ash), and (ii) we emphasize the importance of soil water dynamics determining the sensitivity to drought of these forests.

Floodplain forests are subject to multiple climatic threats. As Nola et al., (2020) suggested, the lower performance of temperate floodplain oak stands after drought jeopardizes their future performance, and dry spells may favor their replacement by invasive, more drought-tolerant species, such as black locust (*Robinia pseudoacacia* L.) and red oak (*Quercus rubra* L.). Overall, the red oak has deep-penetrating root systems, enabling them to maintain relatively high pre-dawn water potentials during drought (Abrams et al., 1990). Also, black locust has been projected to outcompete ash under global warming, due to an enlarged growing season and its ability to plastically access the phreatic water table, which provides it with an advantage under water shortage conditions in relation to ash (Nadal-Sala et al., 2019). Šenfeldr et al., (2021) concluded that increasing groundwater levels by managing river hydrological systems, particularly during dry periods, and promoting mixed, structurally diverse stands would reduce the vulnerability of drought-prone floodplain ash stands. Indeed, tree-ring analyses and growth models can be used to detect early warning signals of impending dieback in floodplain forests in response to drought. Early detection of stress might be used to guide forest managers through health assessments and improve tools for hydrologic remediation or floodplain forest restoration to reduce drought stress (Middleton and Souter, 2016). These measures should be implemented for oak stands currently showing drought-related dieback, as observed in some Ticino areas (Colangelo et al., 2018a), but also drought-sensitive ash populations.
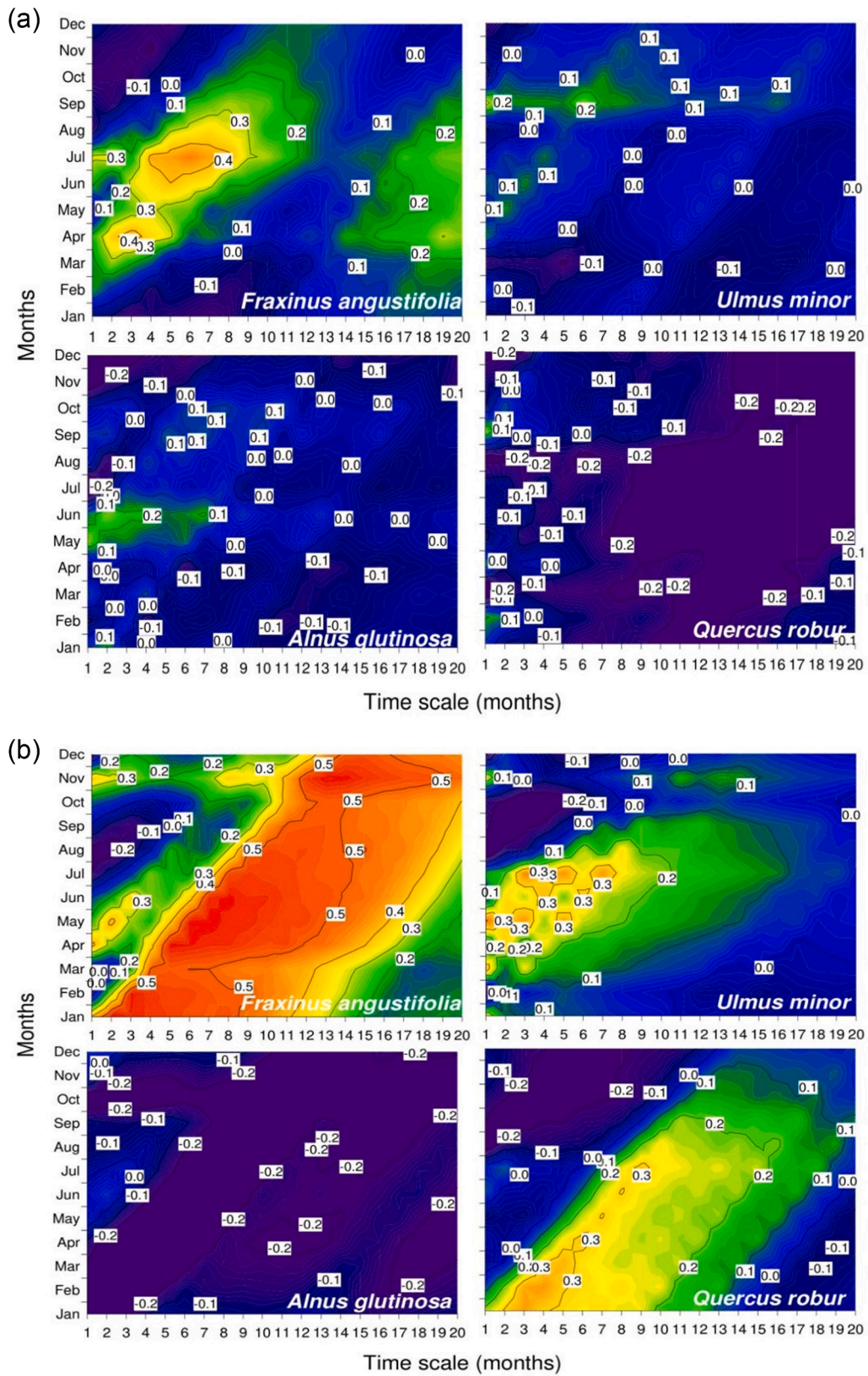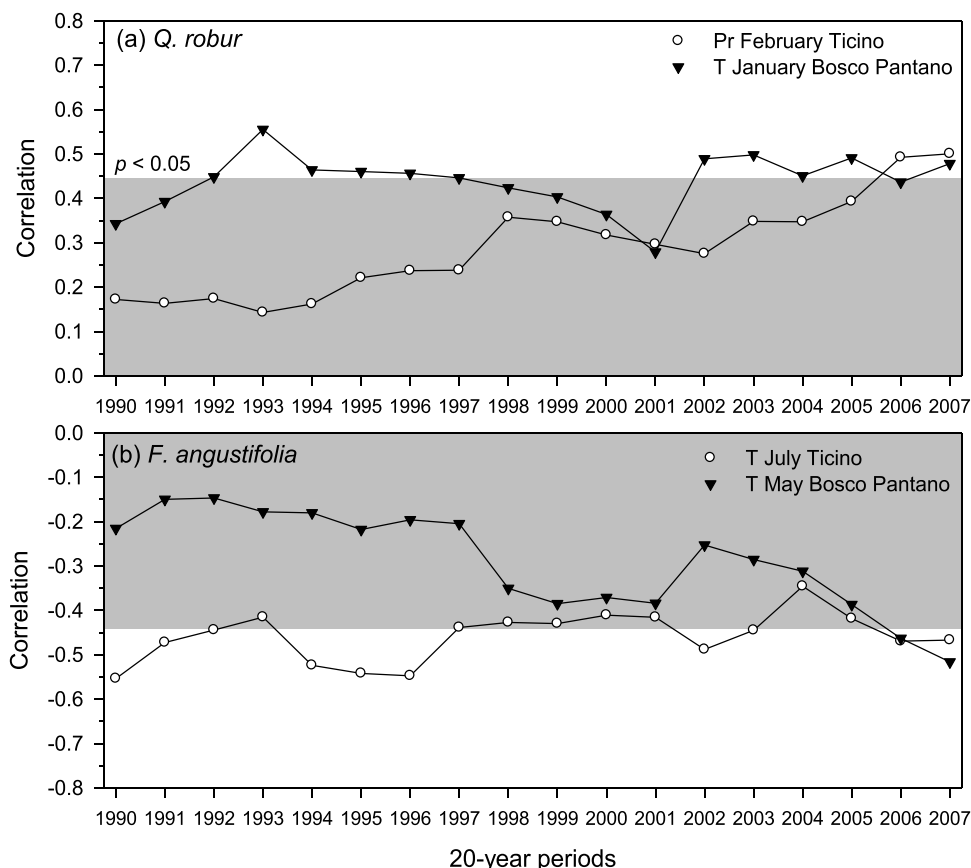
Fig. 4. Drought-growth relationships in the Ticino (a) and Bosco Pantano (b) study sites based on Pearson correlations (color scale) calculated by relating species' ring-width chronologies and monthly values (y axes) of the SPEI drought index calculated at several time scales, specifically from 1 to 20 months (x axes).

Fig. 5. Moving Pearson correlations calculated by relating the oak (a, *Q. robur*) and the ash (b, *F. angustifolia*) ring-width chronologies and selected monthly climate variables (T, mean temperature; Pr, precipitation) in the Ticino and Bosco Pantano study sites. The symbols located outside the grey boxes indicate significant ($p < 0.05$) correlations.

Table 4

Statistics of the VS-Lite model fits including the correlation calculated by relating observed and simulated ring-width series for the common period 1980-2016. Their correlation significance levels (p) are given between parentheses. The last four columns show the function describing growth limitation for soil moisture (gM) calculated for the common period 1980–2016 (mean $\pm$ SD) and for dry years (2003 in Ticino and 1992 in Bosco Pantano; see Figs. 1 and 6). The gM functions were calculated for the whole year and for the growing season (April-October). Note that lower gM values indicate stronger growth limitation by low soil moisture levels. Different letters indicate significant ($p < 0.05$) differences in gM between the 1980–2016 period and the dry year for each species according to Mann-Whitney tests.

Tree species	Site	r (p)	gM 1980-2016		gM-dry year	
			Year	April-October	Year	April-October
F. angustifolia	Ticino	0.34 (0.05)	0.79 $\pm$ 0.09	0.76 $\pm$ 0.11a	0.70 $\pm$ 0.27	0.52 $\pm$ 0.19b
	B. Pantano	0.46 (0.01)	0.38 $\pm$ 0.18a	0.29 $\pm$ 0.17a	0.15 $\pm$ 0.11b	0.11 $\pm$ 0.10b
Q. robur	Ticino	0.35 (0.04)	0.97 $\pm$ 0.02	0.97 $\pm$ 0.03	0.89 $\pm$ 0.19	0.81 $\pm$ 0.21
	B. Pantano	0.26 (0.11)	0.98 $\pm$ 0.04	0.96 $\pm$ 0.05	0.88 $\pm$ 0.17	0.82 $\pm$ 0.20

5. Conclusions

Comparisons of radial growth responses to climate and drought among four species coexisting in temperate and Mediterranean flood-plain forests revealed high sensitivity of ash to drought at both sites; oak and elm were also sensitive to drought at the Mediterranean site,

whereas alder was less sensitive to both climatic conditions. By applying a growth model, we identified the major limitation imposed by low soil moisture during the growing season on ash growth, but also detected that oak growth could be severely impaired by extremely dry conditions in late summer. This non-linear response to low soil-moisture thresholds could explain the dieback and mortality episodes observed in oak stands in the temperate study site.

The negative relationship found between spring temperatures and oak growth at the Mediterranean site and 21st−century climate projections may indicate that these relict populations would be further threatened by climate warming, although more experimental data are needed to strengthen these conclusions.

Certainly, the multiple anthropogenic pressures on floodplain forests demand for additional studies including more sites and tree species to better understand their responses to long-term changes in land use and climate. Indeed, in order to have more specific information on post-drought stand dynamics, it would be necessary to carry out specific monitoring and measure or reconstruct variables responsive to drought such as wood anatomy, non-structural carbohydrate concentrations and nutrient availability.

Further, we are also aware on the main shortcomings of the study, including: (i) the existence of confounding factors and limitations such as different climate and hydrological conditions, and (ii) the limited scope of representativeness for extracting general conclusions on the compared biomes (temperate vs. Mediterranean floodplain forests) or tree species (e.g., oak, ash).

Declaration of Competing Interest

The authors declare that they have no known competing financial
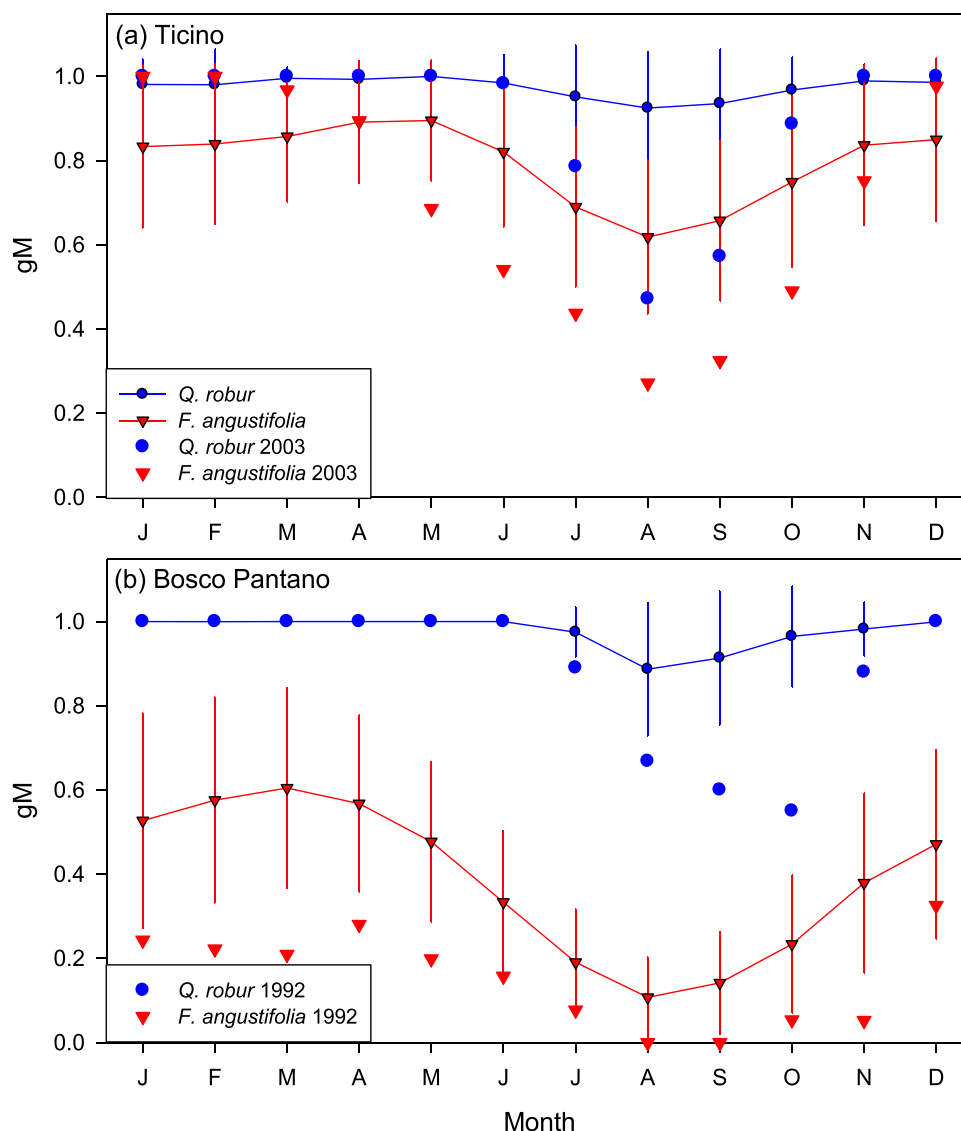
Fig. 6. Simulated growth limitations of *Q. robur* and *F. angustifolia* in the Ticino (a) and Bosco Pantano (b) study sites related to soil moisture (gM). Departures from gM = 1 indicate growth is limited by low soil moisture. Values are means ± SD (symbols with lines) for the common period 1980–2016. Symbols without lines indicate extreme conditions for dry years leading to growth reduction (2003 in Ticino and 1992 in Bosco Pantano).

interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.109238.

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