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Cork-ring width responds to climate depending on local site dryness

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ABSTRACT

Cork, the bark of cork oak (*Quercus suber*), is a major non-wood forest product in the Mediterranean Basin, but its future production will depend on forecasted warmer and drier conditions. The comparison of topographically contrasting sites, subjected to different soil water availability, may be used as an analogous situation to projected aridification. We quantified cork and wood production and cork responses to climate variability and drought indices at dry (slope ridge) and wet (valley bottom) sites located in a relict cork oak population in north-eastern Spain. We also calculated intrinsic water-use efficiency cork (iWUE) by analysing C isotope ratios ($\delta^{13}C$) in annual cork samples. In the wet site, tree- and cork-rings were wider than in the dry site, where cork $\delta^{13}C$ and iWUE were higher, particularly during moderate droughts. Cork and radial growth covaried in both sites and the slopes of their linear regressions were similar between dry and wet sites. In the dry site, cork width increased as June-July soil moisture did, whereas cork iWUE decreased as May soil moisture increased. Moist soil conditions in the prior October and March also enhanced cork growth at both sites, whilst wet prior winter conditions reduced cork iWUE at the dry site. Our findings show how cork production depends on local soil water availability. Cork $\delta^{13}C$ can be used and combined with wood information to trace the physiological status of cork oak trees in response to drought stress.

1. Introduction

The Mediterranean Basin is a climate change hotspot subjected to increasingly warmer conditions (Lionello and Scarascia, 2018). In this region, forecasted drying would lead to more arid conditions and negatively impact forests ecosystem services including the provision of non-wood products such as cork (Aronson et al., 2009). Cork is the bark of cork oak (*Quercus suber* L.) that is traditionally stripped from the trunks of mature trees at intervals spanning 8–14 years (Pereira, 2007). This oak species has a wide distribution area (ca. 2.5 million ha) and a high socio-economic and ecological relevance in the region with Portugal and Spain being the largest cork producers worldwide, accounting for 58 % and 20 % of exports, respectively (ITC (ITC (International Trade Center)), 2023). Under current management practices, climate warming may result in a 20 % decrease in cork production by 2100 (Palma et al., 2015). In addition, climate warming can also impact cork quality, which depends on factors such as cork thickness and porosity, among others (Sánchez-González et al., 2023). Furthermore, hotter droughts may threaten some relict cork oak populations rising mortality rates (Sánchez-Cuesta et al., 2021).

The cork oak is an evergreen, drought-avoiding tree species with diffuse-porous wood widely distributed in the western Mediterranean basin on sites with acidic soils, often poor in nutrients, where it is frequently managed for cork production (David et al., 2007; Kurz-Besson et al., 2014). It is considered a water-saving (isohydric) species with a dimorphic rooting system that allows access to shallow and deep water soil reserves (David et al., 2013). It forms annual cork and growth rings (Pereira, 2007). The phellogen of cork oak remains active from early April up to November, and its division rate peaks around June showing low cork growth rates during summer (Graça and Pereira, 2004). The cambial activity extends from March to October, with radial growth rates reaching maximum values June and July (Costa et al., 2002).

The interest in quantifying long-term cork oak vulnerability to climate warming has motivated several studies on cork-width responses (Camarero et al., 2024b; Caritat et al., 1996, 2000; Costa et al., 2016, 2022a, 2022b; Ferreira et al., 1998; Ghalem et al., 2018; Leite et al., 2018, 2019; Oliveira et al., 2016) and ring-width responses to climate variables and drought indices (Costa et al., 2002, 2003; Camarero et al.,

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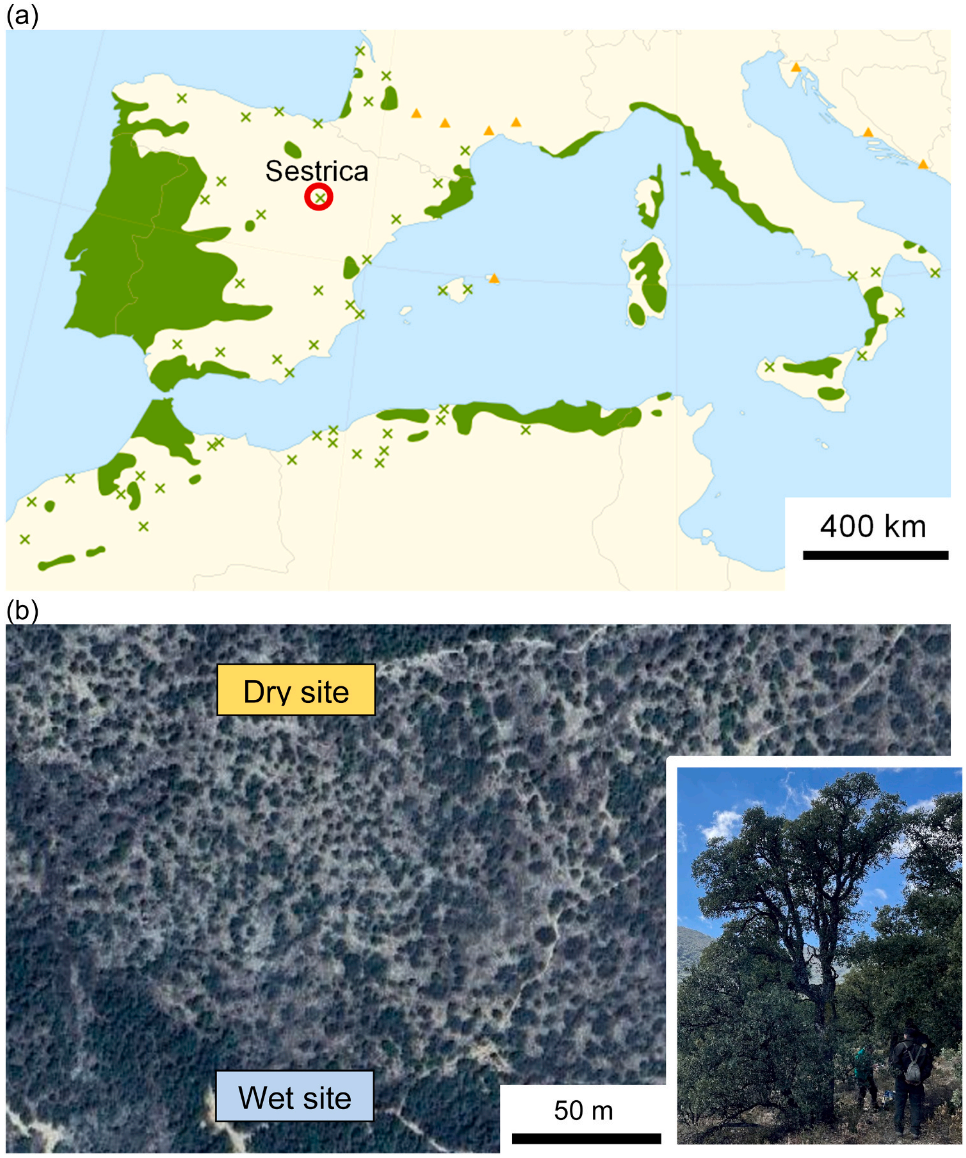

Fig. 1. Map of the *Quercus suber* distribution area (green areas) in the western Mediterranean Basin (crosses indicate native isolated populations and triangles indicate introduced and naturalized populations; modified from Caudullo et al. (2017) showing the location of the study site (Sestrica). (b) Aerial photograph and location of sampled dry and wet sites and view of a tree sampled in the dry site.

2024a, Rubio-Cuadrado et al., 2024). A few of these studies also analyzed C isotope ratios ($\delta^{13}C$) in cork (Costa et al., 2022a) or wood (Rubio-Cuadrado et al., 2024) rings, as this is a robust proxy of intrinsic water-use efficiency (iWUE; McCarroll and Loader, 2004). Stable C isotopes signatures in cork rings may reflect the trees' physiological status and provide complementary information to that obtained from tree-ring and cork-width series under variable Mediterranean environments (Costa et al., 2022). However, no studies have compared these three proxies (ring width, cork width and iWUE) in the same forest, to the best of our knowledge, by analysing how cork and wood growth covary as a function of climate variability. It was suggested that cork growth was less sensitive to climate fluctuations than wood growth (Costa et al., 2002), but subsequent studies seem to refute this hypothesis (e.g. Caritat et al., 2000). Furthermore, the within-site variability in cork oak responses to climate has been rarely considered, despite different slope aspects, locations along a slope and slope steepness determine local temperature ranges, evapotranspiration rates and the access to different soil water pools in this species (Mendes et al., 2016). Such local variability may affect cork and wood formation and cork iWUE, but this has not been investigated yet.

Here, we aimed to quantify cork and wood responses to climate variability and drought stress by analysing width changes in annual cork and tree rings and cork iWUE in two stands located in nearby dry (slope ridge) and wet (valley bottom) sites. We selected a relict cork oak population located near the Sestrica village, in North Eastern Spain. There, both wood and cork production are constrained by dry conditions during spring (Camarero et al., 2024a, 2024b), so cork persistence could be threatened in the future under forecasted aridification.

We hypothesize that (i) cork and wood production will be lower at the dry site, where they are more constrained by lower soil water availability, and (ii) cork iWUE will be higher. We also expect a stronger cork-ring width responsiveness to climate and drought severity at the dry site.

Table 1
Characteristics measured in sampled trees and processed wood and cork samples. The ring and cork values correspond to the period 2007 −2021 (n = 15 years). Values are means ± SE. Different letters indicate significant differences between sites according to t tests.

Site	No. sampled trees	Diameter at 1.3 m (cm)	Age (years)	Tree-ring width (mm)	Cork-ring width (mm)	Cork $\delta^{13}C$ (‰)	Cork iWUE (μmol mol^{-1})
Dry	12	29.2 ± 1.1a	72 ± 4a	1.35 ± 0.05a	0.54 ± 0.03a	−27.98 ± 0.08b	76.62 ± 0.86b
Wet	10	36.5 ± 1.6b	66 ± 3a	1.83 ± 0.12b	1.10 ± 0.07b	−28.25 ± 0.09a	73.50 ± 0.96a

2. Material and methods

2.1. Study site

The Sestrica "alcornocal" (*Quercus suber* L. forest) is a relict cork oak population located in the Spanish Iberian System where it occupies ca. 294 ha (Fig. 1a). The stand basal area and density are 12.2 m^2 ha^{-1} and 420 stems ha^{-1}, respectively. There, two sites where *Q. suber* was dominant (it accounted for 72 % of the total basal area), but showing contrasting geomorphology, were selected for sampling. The dry and wet sites are located on a slope ridge (1.6363° W, 41.5061° N, 886 m a.s. l.) and near a valley bottom (1.6398° W, 41.5025° N, 766 m a.s.l.), respectively (Fig. 1b). The horizontal distance between the two sites is 280 m. Both sites are located in slopes facing E-SE, but the ridge has a steeper slope (20–30°) than the valley bottom (0–10°).

Vegetation reflects the change in slope steepness and location along the slope with a higher abundance of *Pinus pinaster* Ait. and *Quercus ilex* L. in the dry site and *Arbutus unedo* L. and *Acer monspesulanum* L. in the wet site. The understory is dominated by *Juniperus oxycedrus* L., several *Cistus* (*C. populifolius* L., *C. laurifolius* L., *C. salviifolius* L.) and *Erica* (*E. arborea* L., *E. scoparia* L.) species, other shrubs (*Lavandula pedunculata* Cav., *Helichrysum italicum* (Roth.) G. Don., *Genista Scorpius* (L.) D.C.) and vines (*Lonicera etrusca* L. Santi, *Hedera helix* L.). The cover of *Q. suber* increases at the wet site where tree height is also higher than in the dry site, approximately 90 vs. 60 % and 9 vs. 7 m, respectively (see also the diameters in Table 1). Soils are rocky, sandy and acid (inceptisol type), and developed on quartzites.

According to data from the Illueca meteorological station (Spanish Meteorological Agency −AEMET, 1.63° W, 41.53° N, 605 m), located at 3.8 km from the study site, the climate conditions in the area are Mediterranean with continental influence. The mean annual temperature is 11.4 °C and the total annual precipitation is 490 mm. Spring accounts for 30 % of the annual precipitation and there is a clear summer drought lasting from July to September (see climate water balance in Fig. S1). The estimated annual water balance is ca. –300 mm.

The forest is privately owned and scarcely managed with the last cork harvest (debarking) being done in 2005. Oak forests in the study area were traditionally managed as coppice stands until the 1960s when massive migration of rural population to cities occurred.

2.2. Climate data and drought indices

Due to the lack of long and homogeneous climate records near the study area, we used 0.1°-gridded monthly climate data (mean maximum and minimum temperatures, total precipitation) corresponding to the E-OBS climate dataset version 28.0e (Cornes et al., 2018). We also obtained 0.1°-gridded monthly soil moisture data at 0–10 cm depth were also obtained for the period 1982–2018 based on land surface model simulations with precipitation-based forcing (Rodell et al., 2004).

To assess changes in drought severity and duration at regional and local scales we used Standardized Precipitation Evapotranspiration Index (SPEI) monthly and weekly data gridded at 0.1° and 1.1 km^2 resolutions, respectively. The 0.1° SPEI data were calculated from monthly temperature and precipitation obtained from the 0.1° grid, whereas the 1.1 km^2 SPEI data were downloaded from the Spanish Drought Monitor website (https://monitordesequia.csic.es/). The SPEI is a multi-scalar drought index calculated on cumulative climate water balances which depend on temperature and precipitation (Vicente-Serrano et al., 2010). Negative and positive SPEI values correspond to dry and wet conditions, respectively. In both cases, we considered SPEI values calculated at several time scales, specifically considering 1-, 3-, 6-, 9- and 12-month long scales. Lastly, 0.5°-gridded monthly data of the self-calibrating Palmer Drought Severity Index (scPDSI), which accounts for long- to mid-term regional drought effects (Wells et al., 2004), were also obtained from the Climate Explorer webpage (https://climexp.knmi.nl/). The scPDSI was calculated assuming that soils had a water holding capacity lower than 20 mm.

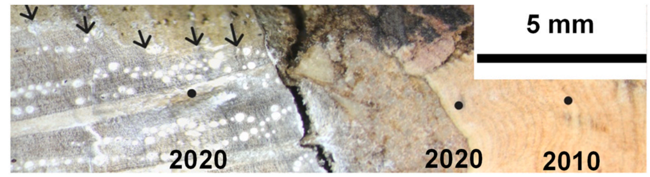

Fig. 2. A view of a *Q. suber* cross-section showing tree-ring (arrows, left part of image) and cork-ring boundaries (right part of the image). Vessels are filled with chalk dust. Points indicate decades.

2.3. Field sampling

First, we selected 12 and 10 mature, apparently healthy cork oak trees for sampling in the dry and wet sites, respectively (Table 1). Second, the diameter of all sampled trees was measured at 1.3 m using tapes. Third, cork samples were extracted using a 10-mm Pressler increment borer, whereas cores were obtained using a 5-mm Pressler increment borer (Haglöf, Sweden). In both cases, two radial cores of wood and cork were sampled per tree at close stem locations and at 1.0 −1.3 m height.

2.4. Cork and core processing

Cork and wood samples were processed using dendrochronological techniques (Fritts, 1976). First, wood and cork samples were air-dried, and cross-sections were cut using a sledge microtome (Gärtner et al., 2015). To improve the contrast of vessels and highlight ring boundaries, vessels were filled with chalk dust. Then, both cork and wood cross-sections were visually cross-dated under the binocular scope and scanned at 1200 dpi (Epson Expression 10000XL). The widths of cork and wood rings were measured with a 0.001 mm resolution along two radii per tree (see Fig. 2) using the CooRecorder software (Larsson and Larsson, 2018). The visual cross-dating was checked using the COFECHA software, which calculates moving correlations between individual series and the mean site series (Holmes, 1983). Tree age at 1.3 m was estimated by counting the number of rings along the oldest core of each tree whenever it reached the pith or presented curved, innermost rings.

To calculate climate- or drought-cork or wood relationships, the individual cork-ring-width series were converted into indexed cork- and ring-width series through standardization and detrending (Fritts, 1976). These procedures allow removing size-related trends in cork- or ring-width data and emphasize high-frequency variability. We fitted negative linear or exponential functions to individual cork- and ring-width series and obtained cork- and ring-width indices by dividing observed values by fitted values. Then, autoregressive models were fitted to remove the first-order autocorrelation of the series of

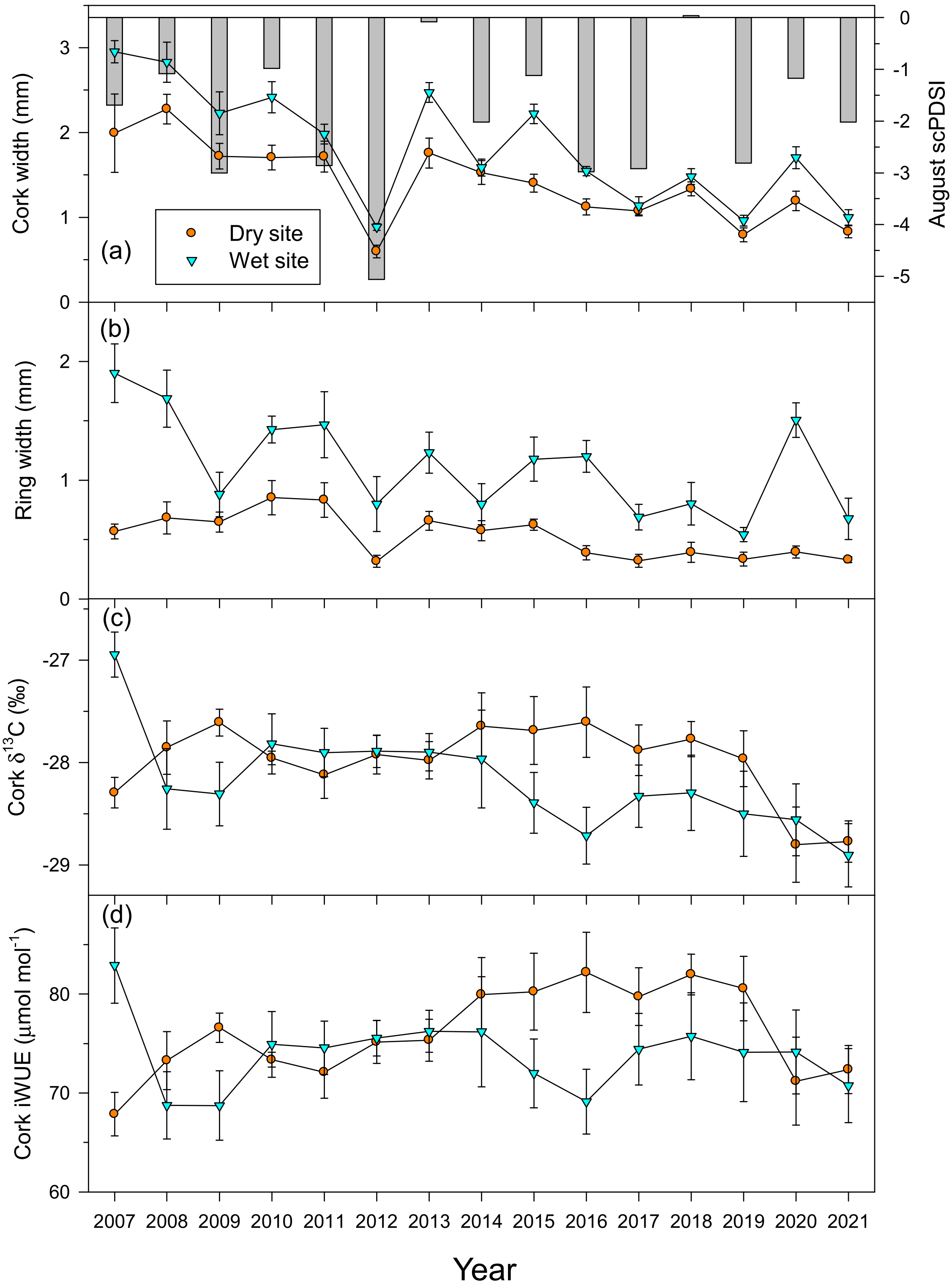

Fig. 3. Cork and ring variables measured for the period 2007 −2021 in wet and dry sites: (a), cork width; (b), ring width; (c), cork $\delta^{13}C$, and (d), cork iWUE. Values are means ± SE. The August scPDSI is shown in plot (a) (grey bars, right *y* axis).

dimensionless indices. The resulting pre-whitened individual series were averaged using a bi-weight robust mean to obtain mean residual cork- and ring-width series for each site (Fritts, 1976). These procedures were done using the dplR package (Bunn, 2008, 2010; Bunn et al., 2024) in the R statistical software (R Development Core Team, 2024).

Robust cork- and ring-width mean series for the dry and wet sites were built for the common, best-replicated period (2007–2021, n = 15 years). In the study site, we previously developed and analysed, well-replicated site mean series (chronologies) of annually resolved cork and ring-width series for the periods 2008–2021 and 1968–2021, respectively, without distinguishing dry and wet sites (Camarero et al., 2024a, b). In these studies, we found that ring (1.71 mm) and cork widths (3.06 mm) were intermediate as compared with other cork oak forest, and cork porosity was quite low (4.4 %), indicating a good cork quality in Sestrica trees.

2.5. Cork $\delta^{13}C$ analyses and calculation of iWUE

Cork $\delta^{13}C$ measurements were used to estimate cork iWUE. Annual cork samples were separated under the binocular using scalpels. This was done for four trees from the dry site and five trees from the wet site considering the common 2007 –2021 period. For $\delta^{13}C$ analyses, wood samples are usually milled and homogenised using ball mills. However, this was not feasible for cork due to its porous and elastic texture. Therefore, these samples were carefully cut into very small pieces. Cork aliquots (0.8–1.2 mg) were weighed on a microbalance (AX205 Mettler Toledo, OH, USA) into tin foil capsules. In total, we analysed 56 and 69 samples from the dry and wet sites, respectively.

Isotope analyses were carried out at the Stable Isotope Laboratory of the University of Almería (Almería, Spain). Encapsulated cork samples were combusted to CO_2 with a combustion module (CM) coupled to a cavity ring-down spectroscopy (CRDS) System (G2201-I Analyzer, Picarro), achieving a flash combustion at temperatures of 1700–1800 °C. The released CO_2 was transferred to a Picarro Liaison A0301 interface and inputted into CRDS for analysis. The $\delta^{13}C$ values were referenced to the Vienna PeeDee Belemnite (V-PDB) scale. Sugarcane, acetanilide, and urea were used as working reference standards for consecutive δ^{13} C analyses of the wood samples, covering a wide calibration range from −11.9 ‰ to −44.3 ‰. These working reference standards were initially calibrated against the USGS (USGS-40 l-Glutamic acid) and IAEA standards (IAEA-603 and NBS-18 calcites). Based on analyses of standards, the precision ranged between 0.01 and 0.17 ‰ ($n = 8$) and, in terms of accuracy, the $\delta^{13}C$ error ranged from − 0.28 ‰ to 0.66 ‰.

We calculated iWUEi using the following framework. First, to account for changes in $\delta^{13}C$ of atmospheric CO_2 (Ca), we calculated C isotope discrimination in cork ($\Delta^{13}Cc$) from $\delta^{13}Ca$ and cork $\delta^{13}Cc$ following Farquhar and Richards (1984):

$$\Delta^{13}Cc = (\delta^{13}Ca - \delta^{13}Cc) / (1 + \delta^{13}Cc/1000) \quad (1)$$

The Ca and $\delta^{13}Ca$ values were obtained from Belmecheri and Lavergne (2020). Second, we calculated cork iWUE (in μmol H_2O mol^{-1} CO_2) following Farquhar et al. (1982):

$$iWUE = Ca\ [1 - (Ci / Ca)]\ 0.625 \quad (2)$$

where Ci is the CO_2 concentration in the sub-stomatal cavity of leaves, and 0.625 is the relation among the conductance of H_2O compared to the conductance of CO_2. To determine Ci we used the equation proposed by Francey and Farquhar (1982):

$$Ci = Ca\ (\delta^{13}Cc - \delta^{13}Ca + 1)/(b - a)] \quad (3)$$

where a is the diffusion fractionation across the boundary layer and the stomata (+4.4 ‰) and b is the Rubisco fractionation (+27.0 ‰).

2.6. Statistical analyses

Several variables (tree diameter, cork and ring widths, correlation between individual ring- and cork-width series, cork $\delta^{13}C$ and iWUE) were compared between the two sites using t tests between the two sites after log-transforming for achieving normality. Log-transformed annual cork- and ring-widths measured in the trees of the dry and wet sites were related using ordinary least squares regression (Kilmer and Rodríguez, 2017). An ANCOVA was used to compare the slopes of these fits between the wet and dry sites.

To assess cork and wood responses to climate variability and drought severity, Pearson correlations were calculated between series of cork- and ring-width indices and monthly climate variables (mean maximum and minimum temperatures, precipitation, soil moisture) or drought indices (1-month long SPEI, scPDSI). This was done using the treeclim R Package (Zang and Biondi, 2015). We selected the 1-month SPEI because it produced the largest correlations with cork variables in preliminary analyses. The climate window of these analyses spanned from the prior to the current September. In the case of SPEI weekly data, we also calculated correlations between cork-ring indices or iWUE with 1- (SPEI 1), 3- (SPEI 3), 6- (SPEI 6), 9- (SPEI 9) and 12-month (SPEI 12) long SPEI values to pinpoint the intra-annual window of cork response to drought severity.

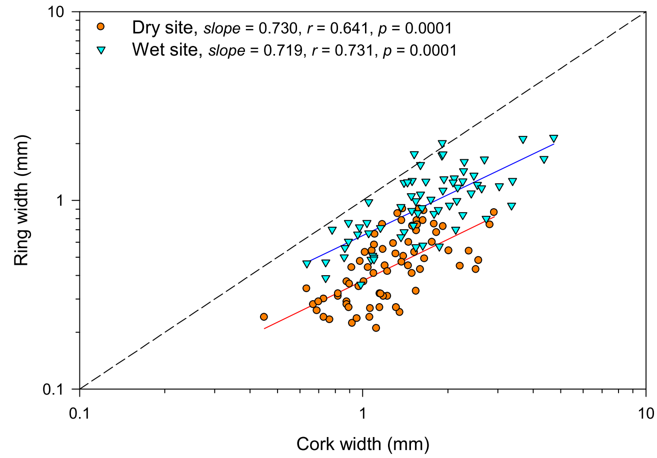

Fig. 4. Relationships between annual cork and ring widths observed at the individual level at the dry (orange circles, red line) and wet (blue triangles and line) sites. The lines show linear regressions between both variables and the corresponding statistics are shown. The dashed line shows the $x = y$ relationship.

3. Results

3.1. Differences in wood and cork growth between the wet and dry sites

At the dry site, tree diameter, cork and ring widths were lower than at the wet site (Table 1; Fig. 3 and **S2**). Cork $\delta^{13}C$ and, consequently, cork iWUE were higher at the dry site. Tree age did not differ significantly between sites ($t = 1.01$, $p = 0.35$).

The selected functions to remove cork- or ring-width trends were mostly negative linear functions. Linear functions were selected in 93 % and 65 % of cork- and ring-width series, respectively. Since first-order autocorrelations were significant (mean ± SD values of first-order autocorrelations of cork and ring widths were 0.42 ± 0.29 and 0.63 ± 0.20, respectively), autoregressive models fitted to standard indices allowed removing most of their effects and obtaining pre-whitened, residual indices.

The mean correlation between individual cork-width series (period 2007 –2021) was lower in the dry (mean $r \pm SE = 0.59 \pm 0.01$) than in the wet (0.78 ± 0.03) sites ($t = -5.93$, $p = 0.001$). In contrast, the mean correlation between ring-width series was higher in the dry (0.49 ± 0.03) than in the wet site (0.45 ± 0.10), but differences were not significant in this case ($t = 0.28$, $p = 0.78$).

3.2. Relationships between cork and wood growth

At the individual level, we found that log-transformed cork and ring widths were positively correlated at the dry and wet sites (Fig. 4). The linear regressions fitted for both variables showed similar slopes at both sites (ANCOVA, $F = 0.01$, $p = 0.93$). Cork iWUE was only slightly and negatively related to ring width at the dry site ($r = -0.14$, $p = 0.37$, $n = 41$).

3.3. Climatic constraints of cork production and iWUE

Correlations between cork growth indices and temperature were

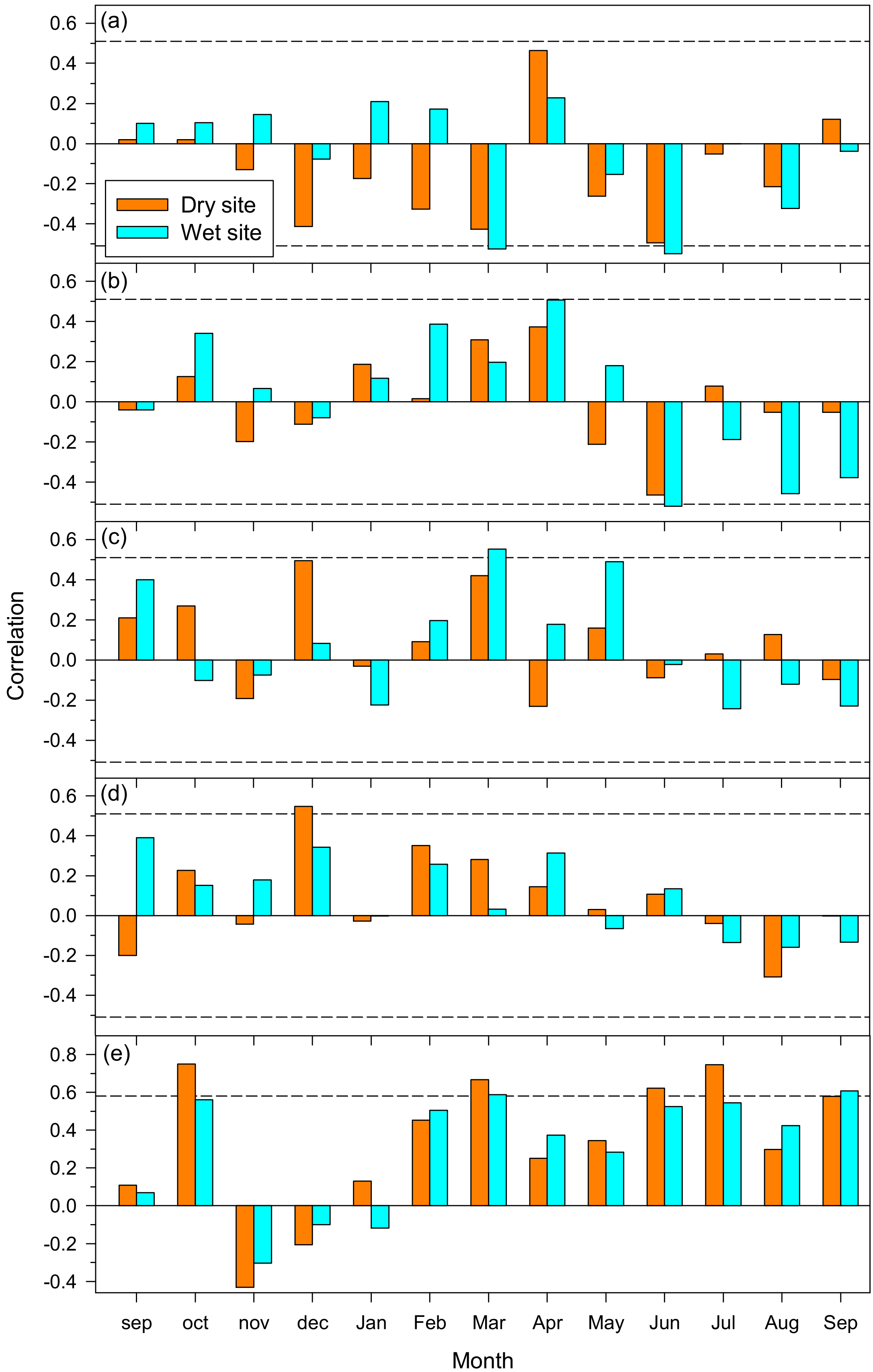

Fig. 5. Relationships between cork width-indices measured for the dry and wet sites and monthly climate variables (a, mean maximum temperature; b, mean minimum temperature; c, total precipitation; d, 1-month SPEI; e, soil moisture). The horizontal dashed lines show the 0.05 significance levels.

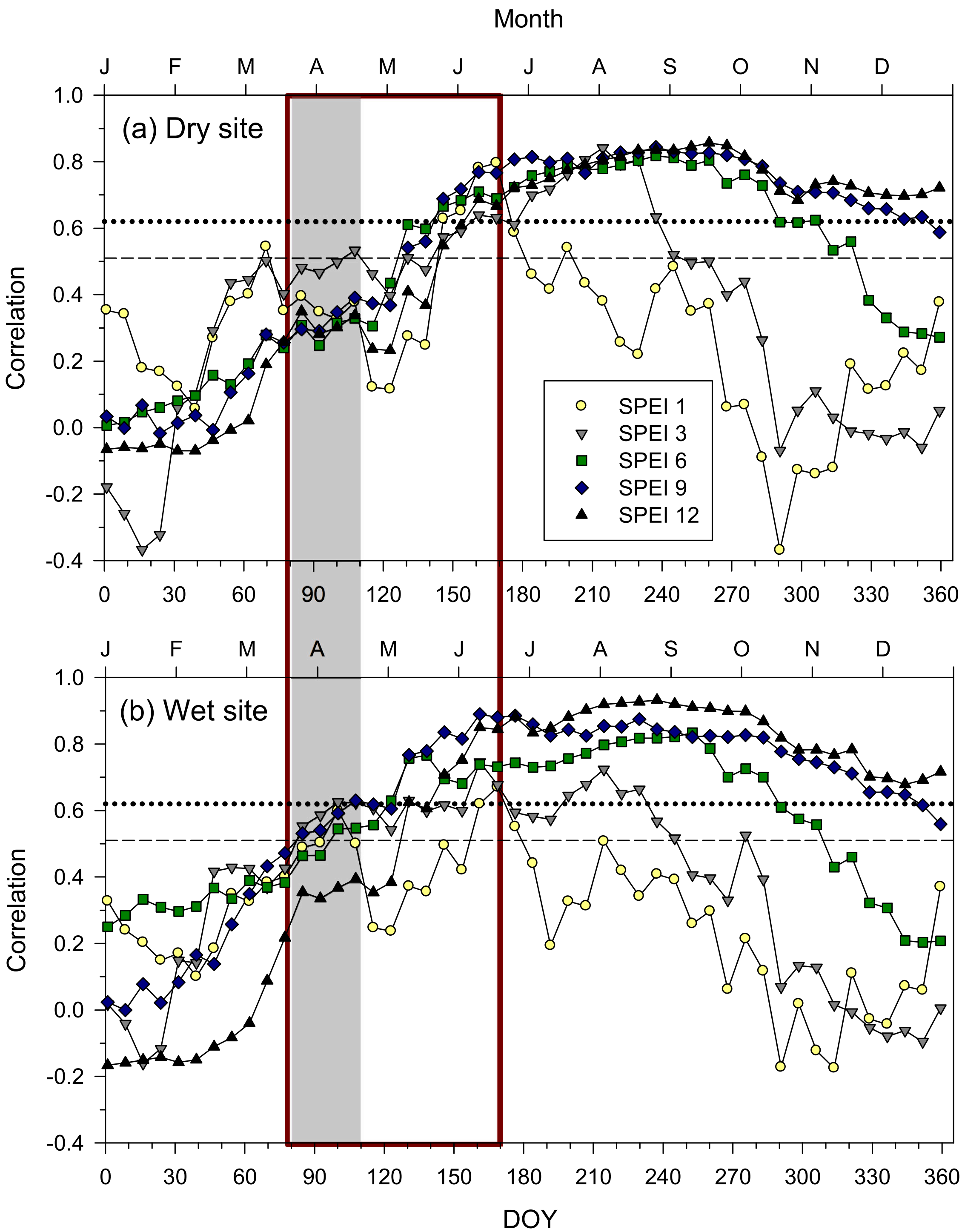

Fig. 6. Correlations between the series of cork ring-width indices from the (a) dry and (b) wet sites and weekly SPEI values. SPEI values were aggregated in 1- (SPEI 1), 3- (SPEI 3), 6- (SPEI 6), 9- (SPEI 9) and 12-month (SPEI 12) long scales. The horizontal and dotted dashed lines show the 0.05 and 0.01 significance levels, respectively. DOY is the day of the year. The dark red box highlights the period of cork formation and the grey box indicates the onset of the cork growth.

negative, only in the wet site and only in the spring and summer (Fig. 5). Correlations of cork growth indices with March precipitation were positive and significant in in the wet site. Correlations of cork growth indices with 1-month SPEI were positive with the prior December only in the dry site. Correlations between cork growth indices and soil moisture were positive in both sites in prior autumn and in current spring and. The positive correlations between cork ring-width indices and the scPDSI were significant from May to September and reached maximum values in August at the wet site (Fig. S3). In the case of weekly SPEI values, the positive correlations with cork-width indices gradually increased from April to June and these coefficients reached maximum values in August, specifically for 12-month long SPEI values and in the wet site (Fig. 6).

Correlations between cork iWUE and prior-autumn temperature and prior-December precipitation were positive in the wet site (Fig. 7 a, b, c). Correlations of cork iWUE with August 1-month SPEI were positive in the wet site (Fig. 7d). Correlations between cork iWUE and May soil moisture were negative, but only in the dry site (Fig. 7e). Negative

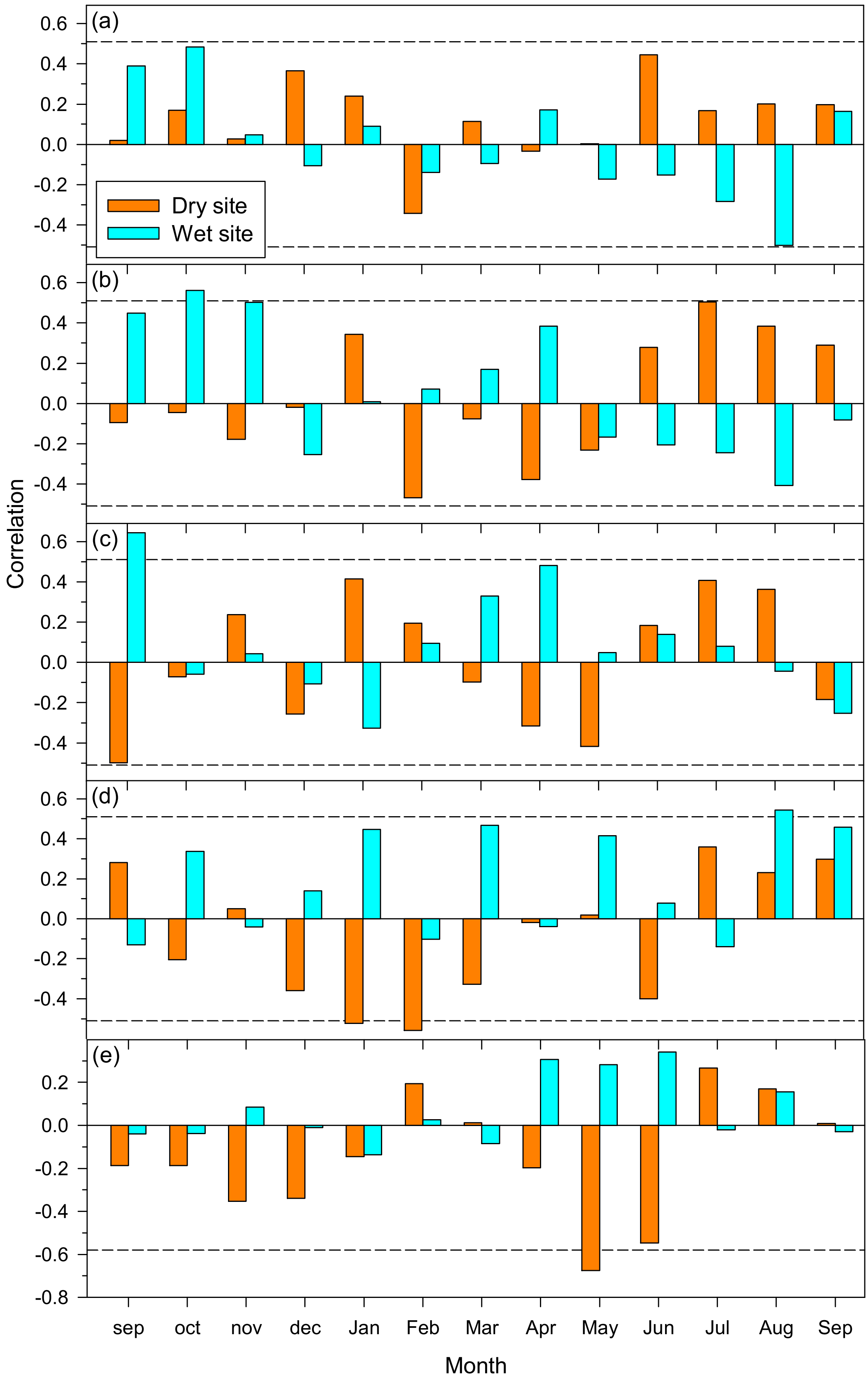

Fig. 7. Relationships between cork iWUE measured for the dry and wet sites and monthly climate variables (a, mean maximum temperature; b, mean minimum temperature; c, total precipitation; d, 1-month SPEI; e, soil moisture). The horizontal dashed lines show the 0.05 significance levels.

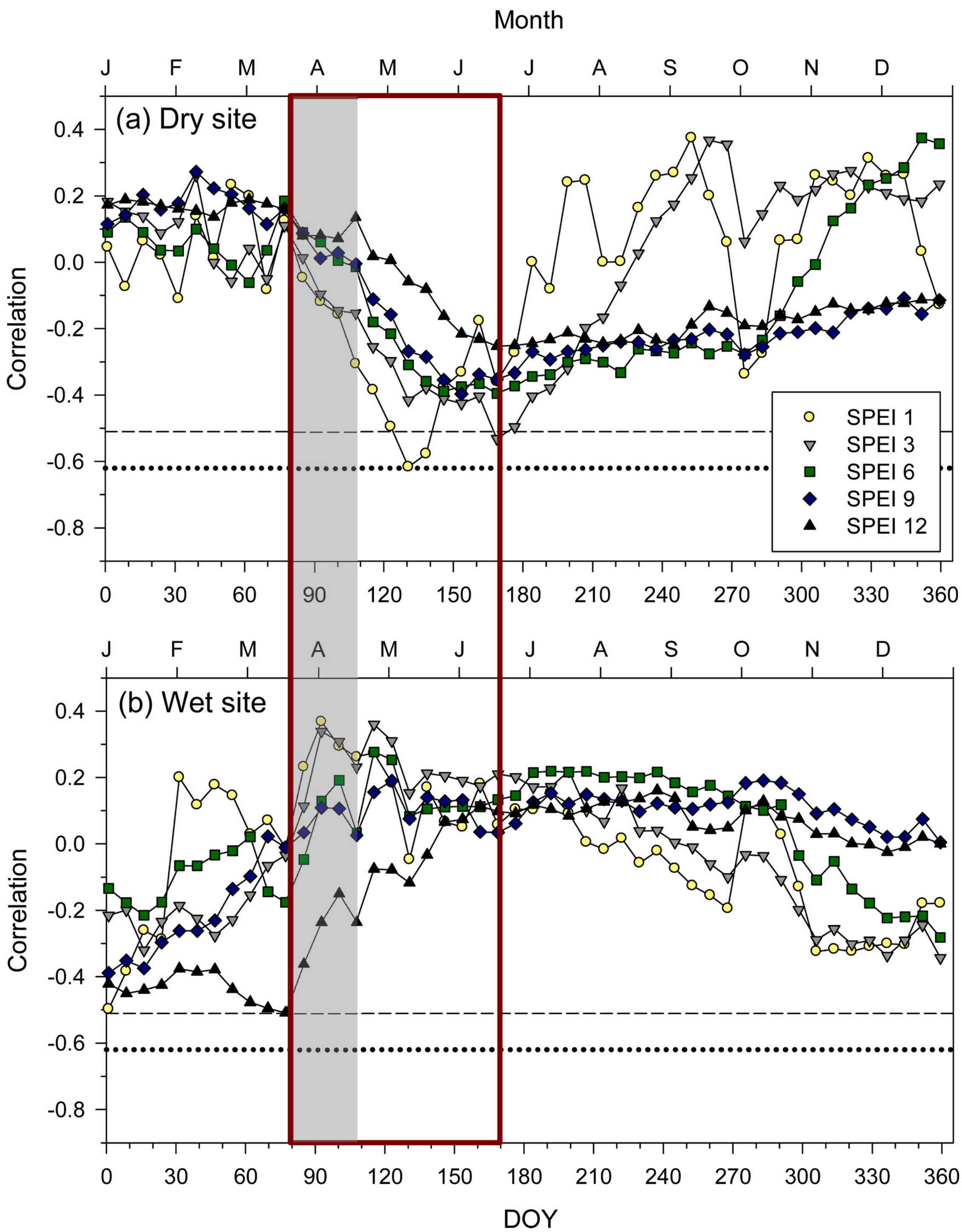

Fig. 8. Correlations between the series of cork iWUE from the (a) dry and (b) wet sites and weekly SPEI values. SPEI values were aggregated in 1- (SPEI 1), 3- (SPEI 3), 6- (SPEI 6), 9- (SPEI 9) and 12-month (SPEI 12) long scales. The horizontal and dotted dashed lines show the 0.05 and 0.01 significance levels, respectively. DOY is the day of the year. The dark red box highlights the period of cork formation and the grey box indicates the onset of the cork growth.

correlations between weekly 1-month SPEI values and cork iWUE reached a minimum value in the dry site in early May (Fig. 8).

4. Discussion

As hypothesized, cork and wood production were lower in the dry site and iWUE was higher, indicating that phellogen dynamics are constrained by low soil water availability. The findings also confirm that topography and site conditions greatly modulate cork formation in seasonally dry mountainous regions. Our results did not support that the cork-wood covariation and cork responsiveness to climate and drought were higher at the dry site, except when considering soil moisture. Cork iWUE and weekly SPEI values were also more negatively related in the dry site than in the wet site. In contrast, the wet site showed higher cork-width sensitivity to precipitation, scPDSI and weekly SPEI.

These discrepancies may be explained by at least two reasons. First, we used different climate datasets with different spatial (0.5°, 0.1°, 1.1 km^2) and temporal (month, week) resolutions which are a source of uncertainty. Further research should carry out similar analyses in other sites where long-term local climatic data are available at the stand scale (e.g. 1 ha). Second, the study area is topographically complex and is subjected to a severe summer drought that constrains wood and cork production. Trees from the wet site showed a higher cork width and also a higher year-to-year variability in cork width (coefficient of variation, CV = 46 %) than the trees from the dry site (CV = 39 %), which explains the stronger coupling of some climate variables (temperature, precipitation, scPDSI, weekly SPEI) with cork growth indices of the former. Interestingly, cork iWUE responded more to soil moisture and short droughts (1-month SPEI), in absolute terms, in trees from the dry site, suggesting that it may be a more integrative proxy of drought stress than cork width. The response to soil moisture was also stronger for cork width of trees from the dry site. Therefore, soil moisture should be routinely measured to better disentangle cork responses to water shortage. We acknowledge the limitation of using modelled soil moisture for shallow depths given that cork oak has a dimorphic root systems and may exploit different soil water pools, thus relying mostly on deep soil water pools for secondary growth (David et al., 2013).

The major contributions of this study compared to previous work based on different cork oak populations (e.g., Camarero et al., 2024a, 2024b) is that it shows that: (i) ring and cork width covary, and (ii) cork growth and iWUE change in response to local topography and climate conditions within the same population. A novel insight of this study is showing how cork and wood production depend on local soil water availability which have implications for managing cork oak stands in mountain areas.

Overall, our findings reveal how cork and wood production respond differently to drought along distinct locations along the slope. However, cork iWUE was higher during some years (2007, 2010 −2013, 2020, and 2021) in trees from the wet site, albeit this difference was significant ($p < 0.05$) only in 2007. It is possible that long, chronic drought stress would explain the similar cork iWUE values in dry and wet sites during some dry periods such as 2009 −2012 or 2020 −2021. In the case of 2007, ontogenetic effects could be responsible of the high cork iWUE values observed in the wet site.

There may be potential effects of the different chemical composition of cork compared to those in wood regarding the interpretation of iWUE cork and its correlations with climate. Wood is mostly made of cellulose (40 %), hemicellulose (25 %) and lignin (20 %), whereas cork is mainly made of suberin (41 %), lignin (22 %), and hemicellulose (18.2 %; Pereira, 1988). Fractionation processes cause lignin to be depleted in ^{13}C, but lignin and cellulose show comparable environmental signals in the case of tree rings (Loader et al., 2003). Further research should explicitly compare cork and wood iWUE series to disentangle their climatic signals in cork oak forests.

In general, the presented findings are consistent with previous research. Warm-dry conditions from late spring to early summer have been found to constrain cork production (Caritat et al., 1996, 2000; Costa et al., 2022b) through soil dryness (Camarero et al., 2024b), whereas previous wet winter conditions enhanced it (Ferreira et al., 1998). Short- to mid-term (2 −16 months) summer droughts also reduced cork growth (Oliveira et al., 2016). Here, we gained detail on this analysis by considering monthly and weekly SPEI values and found how drought negatively impacts cork growth indices since June and for 1- to 9-month long SPEI values. The cork-width responses to summer and early-autumn dryness could be due to a second cork growth flush after the dry summer leading to a facultative bimodal pattern (Caritat et al., 2000), analogous to that observed in the xylem for some Mediterranean evergreen oak species such as *Quercus ilex* L. (Campelo et al., 2018).

Cork iWUE responded more to short droughts starting in May which concurs with the phellogen phenology and the drought-avoidance strategy of cork oak. Our cork δ^{13}C data range is slightly wider (range −29.9 – −26.6 ‰) than that published by Costa et al. (2022a) for samples from wetter (annual precipitation between 500 and 800 mm) Portuguese open cork woodlands (-27.3 – −26.8 ‰). In their study, negative relationships were found between cork δ^{13}C and temperature, which could be due to opposite trends in both variables or to a lower sensitivity of photosynthesis to water shortage as compared with cork formation, but in our case cork iWUE depended on drought severity and soil moisture suggesting a tight stomatal control under low water availability.

5. Conclusions

This study linked wood and cork production in cork oak. Cork and ring widths were tightly related at two nearby but topographically different dry and wet sites. Moreover, cork and wood production were lower at the dry site, whereas cork iWUE was higher. We evidenced that cork formation and iWUE are very sensitive to drought stress and low soil moisture availability in spring and summer, particularly in the dry site. These results have implications for management because cork oak trees from wet sites could become more stressed by drought under forecasted warmer and drier conditions.

CRediT authorship contribution statement

Colangelo Michele: Writing – review & editing, Visualization, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Camarero J. Julio:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Fernández-Cortés Angel:** Writing – review & editing, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2025.126339.

Data availability

Data will be made available on request.

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