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Using wood rings to determine age and climate constraints of grapevine (*Vitis vinifera*) radial growth

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Summary – Grapevine (*Vitis vinifera*) is the most widely cultivated and economically relevant crop in the world, but its productivity is menaced by aridification in some wine-growing regions such as the Mediterranean Basin. The impacts of climate on vines depend on regional conditions, cultivar, and vine age, among other factors. Hence, a better understanding of vine radial-growth responses to climate in different regions is sorely needed. First, we related climate data and drought severity with a long-term series of vine leaf unfolding from NE Spain to test if climate warming is advancing the onset of the growing season. Second, we used growth rings to estimate age and quantify climate-growth relationships of vines using dendrochronology. Three sites from different designations of origin and vine varieties were studied: Logroño in northern Spain (La Rioja, Tempranillo), San Martín del Río in northeast Spain (Calatayud, Garnacha) and Anzi in southern Italy (Aglianico, Aleatico). Vine leaf unfolding occurred earlier as winter-spring conditions were warmer and drier. Vine ages ranged between 16 (Logroño, Anzi) and 56 years (S. Martín del Río), and growth rates declined in the two youngest grapevines. Ring widths varied between 1.19 (S. Martín del Río) and 1.80 mm (Logroño), with Anzi showing intermediate values (1.37 mm). February precipitation enhanced vine growth in San Martín del Río (r = 0.64) and Anzi (r = 0.49), whereas the correlation with soil moisture peaked in March in San Martín del Río (r = 0.83). Vine growth rates positively responded to September minimum temperatures in San Martín del Río (r = 0.51) and Logroño (r = 0.50). Garnacha cultivar in San Martín del Río showed the highest responsiveness to water availability. Therefore, similar old grapevines from continental, seasonally dry areas could be the most negatively affected by future warmer and drier climate conditions.

Keywords – Dendro-viticulture, drought, Garnacha, growth ring, vine cultivar, vineyard.

Introduction

Grapevine is a major and iconic crop in regions with a Mediterranean climate where wine production provides important economic and cultural benefits (Keller 2015). Several climate models indicate that climate warming may lead to the loss of about 20% of viticulture areas by the late 21st century, with countries traditionally producing high-quality wines such as Spain and Italy being severely impacted and losing grapevine-producing areas (Hannah *et al.* 2013; Sgubin *et al.* 2023). *Vitis* species are climbing vines, often found in riparian habitats, with the grapevine (*Vitis vinifera* subsp. *vinifera* L.) showing a prominent economic importance in Mediterranean areas (Keller 2015). However, vine cultivation may be disproportionately affected by aridification in the Mediterranean Basin, as this region is prone to the negative impacts of climate extremes such as droughts (Ali *et al.* 2022).

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Conditions required for grapevine cultivation and high-quality wine production depend on several climatic variables including temperature and precipitation (Jones *et al.* 2005; Jones & Alves 2012). Temperature is critical for the development of important phenological phases such as bud break, leaf unfolding and fruit maturity (García de Cortázar-Atauri *et al.* 2017), and thermal conditions also affect vine physiology, fruit composition, and wine quality (Coombe 1987; Jones 2006). Rainfall amount is also critical since dry conditions can reduce grape productivity in the absence of irrigation (Moutinho-Pereira *et al.* 2004), whilst excessive precipitation reduces wine quality and increases the incidence of pests (van Leeuwen *et al.* 2019). In general, it is considered that climate warming will advance vine leaf phenology and increase the water demand (Hannah *et al.* 2013). However, how these changes relate to vine xylem growth is understudied. In addition, vine xylem responses to environmental conditions depend on the cultivar and pedoclimatic conditions (Schultz 2003; Roig-Puscama *et al.* 2021).

Spain and Italy are among the main wine producers and accounted for 33% of wine production in the world in 2021 (OIV 2022). In Spain, it is estimated that almost one-quarter of the vineyards (ca. 235 000 ha) are very exposed to climate warming, which could also lead to the loss of old grapevines belonging to rare cultivars. Such old vines are being increasingly appreciated by winegrowers because they are considered to be more tolerant to drought due to their deeper roots and allow the production of high-quality, distinctive, and expensive wines (Grigg *et al.* 2018). Furthermore, increasing cultivar diversity, including old vines, could also buffer potential losses of winegrowing regions under climate warming (Wolkovich *et al.* 2018; Morales-Castilla *et al.* 2020). Therefore, some of Spain's main designations of origins have put in new legislation to define grapevine age as part of superior classification levels. For instance, the new "Viñedo Singular" category in La Rioja (northern Spain) requires the grapevines to be at least 35 years old. Nevertheless, many old vines are uprooted and replaced by young productive vines (Lasanta *et al.* 2016), despite grapevines reaching a maximum age of 80–120 years (Vršič *et al.* 2011; Keller 2015).

Despite the interest in climate warming impacts on grapevine performance, there is scarce long-term data on vine age, ring growth, and wood anatomy and how they respond to climate variability (Roig-Puscama *et al.* 2021; Damiano *et al.* 2023). The study of annual growth rings in vines using dendrochronology (dendro-viticulture) would help answer how grapevine growth depends on age and how it responds to regional climate variability and aridification (Tyminski 2013; Maxwell *et al.* 2016).

Vines are considered vulnerable to drought stress (Matthews *et al.* 1987; Lovisolo *et al.* 1998; Pellegrino *et al.* 2005; Jacobsen *et al.* 2015). Such vulnerability is partially related to its bimodal distribution of vessel diameters (Carlquist 1985), with wide vessels being more hydraulically efficient but also more vulnerable to embolism than narrow vessels formed in the late growing season (Pratt 1974; Shtein *et al.* 2017; Munitz *et al.* 2018; Brandes *et al.* 2022; but see Bouda *et al.* 2019). Therefore, drier conditions are expected to induce a loss of hydraulic function and a reduction in radial growth, particularly in cultivars from the most arid sites or growing on shallow or rocky soils. Ring-width data allow quantifying the magnitude of the vine response to droughts of different severity or duration.

In vine, cambial activity begins about 14 days after bud break (Bernstein & Fahn 1960) and new leaves are formed ca. 60 days after bud break (Romero *et al.* 2010). Current-year vessels are functional at least 54 days after bud break (Jacobsen *et al.* 2015), when canopy development has almost finished, whereas radial growth rates peak from early April to mid-May (Matthews *et al.* 1987). These phenological phases indicate that leaf and xylem phenology may be coupled but respond differently to climate warming. Comparing series of leaf phenology and ring width would allow checking if warmer conditions trigger earlier unfolding dates and enhance grapevine growth.

Here, we study growth rings of old grapevines corresponding to different designations of origin and growing under different climate and soil conditions in vineyards located in northern Spain, northeastern Spain, and southern Italy, respectively. Our specific objectives are: (i) to relate climate data and a drought index to leaf unfolding dates to test if climate warming is leading to an earlier start of the growing season, which could be linked to enhanced growth, (ii) to estimate the ages of sampled vines, and (iii) to assess climate-growth relationships using climate variables (temperature, precipitation). Combining growth and phenology data strengthens our approach since phenology plays a major role in the tolerance to climate warming of vines (García de Cortázar-Atauri *et al.* 2017).

Material and methods

Study designations of origin

We selected three old grapevines located in three designations of origin: Logroño in "La Rioja" region (northern Spain), San Martín del Río in "Calatayud" region (northeastern Spain), and Anzi in "Aleatico" region (southern Italy), respectively (Fig. A1 in the Appendix). Regarding pruning management, it was similar in all sites, but the training system differed with vertical shoot position and double Guyot systems in the Spanish and Italian grapevines, respectively. In studies on grapevine responses to drought, the Garnacha cultivar was among the most efficient and produced the smallest leaves when subjected to strong water limitation (Gómez del Campo *et al.* 2003).

The three study grapevines experience a Mediterranean climate characterized by warm and dry summers (Fig. A2 in the Appendix). However, climate conditions change among sites. The wettest site is Anzi with 815 mm of total annual precipitation, followed by San Martín del Río (422 mm) and Logroño (411 mm) (Fig. A3 in the Appendix). The highest mean maximum temperature (30.1°C) is recorded in July in San Martín del Río, followed by Logroño (29.6°C) and Anzi (28.3°C). The lowest mean minimum temperature (−1.2°C) is recorded in January, also in San Martín del Río, followed by Anzi (−0.6°C) and Logroño (2.1°C). Therefore, San Martín del Río is the most continental site. In Logroño, soils are basic with a silty loam texture. In San Martín del Río, soils are acid and stony, developed on slates, with a clay texture. In the Italian site, soils are basic and sandy. The main grapevine varieties in the study sites are Tempranillo, Garnacha, and Aleatico in the Logroño, San Martín del Río, and Anzi study sites, respectively (Table 1). According to local managers, grapevines were not grafted.

Field sampling

Sampling was carried out from July-August 2020 to June 2021. In each site, we took a basal cross-section of 15–25 vines showing crooked, multiple stems, two aspects associated with old individuals (Vršič *et al.* 2011). We further checked this information with local managers and owners who confirmed that grapevines were planted more than 15 years ago. Usually, some of the sampled vines showed rotten pith or heartwood and we discarded them keeping 8 to 23 individuals per site for dendrochronological analyses (Table 1).

Climate and SPEI data

Climate data from local stations were used to describe the climatic conditions of the study sites (Fig. A2 in the Appendix), but they were not long enough for analysing climate-growth relationships. Due to the lack of long-term homogeneous climate series near the three study sites, we used daily and monthly climate data (mean maximum and minimum temperatures, total precipitation) from the 0.1°-gridded E-OBS ver. 27.0e dataset considering the period 1960–2020 (Cornes *et al.* 2018). Daily and monthly temperature data corresponded to averages of hourly and daily data, respectively, whereas daily and monthly precipitation data corresponded to summed hourly and daily data, in that order, used in Europe in similar tree-ring analyses (usually considering forest tree species) and it is available at different spatial resolutions or grids (0.1, 0.25 and 0.5°). This is a complete, clean, and homogeneous climate dataset that has been used in previous studies relating climate variables and phenology or growth data (Valeriano *et al.* 2023). We also obtained monthly data of shallow (0–10 cm) soil moisture (period 1980–2018) from the 0.1°-gridded Land Data Assimilation Systems dataset (Rodell *et al.* 2004). Lastly, we obtained weekly data of the Standardized Precipitation Evapotranspiration Index (SPEI) at 1-month long scales (period 1961–2020) for the Spanish site to assess if leaf unfolding responded to drought severity. These data correspond to the 1.1 km^2-gridded Spanish SPEI dataset (Vicente-Serrano *et al.* 2017). The SPEI has positive and negative values for wet and dry conditions, respectively, and it is calculated as a function of a cumulative water balance considering precipitation and atmospheric evaporative demand. The SPEI data are available online at http://monitordesequia.csic.es/.

Table 1. Main features of the three study grapevines. The number of measured series correspond to the cross-dated and measured radii.

Site	Latitude	Longitude	Elevation (m a.s.l.)	Variety	No. sampled individuals	No. measured series
Logroño	42.446°N	2.515°W	453	Tempranillo	23	47
San Martín del Río	41.052°N	1.425° W	938	Garnacha	8	16
Anzi	40.463°N	15.965°E	704	Aleatico	21	29

Data on leaf unfolding date

Data on grapevine leaf unfolding dates were available from a site located in northeastern Spain (Cardedeu, 41°34′N, 2°21′E). Phenological data were taken from 1953 to 2000, but they were available only for 28 years since data were missing for 1957–1968, 1970–1971, 1975–1979 and 1985 (Peñuelas *et al.* 2002). Phenological events were recorded with an estimated accuracy of ±1 day. At least six individual plants per species were monitored and the phenophase was recorded once the whole plant had reached the functional phenological stage.

Dendrochronological methods

Wood cross-sections were air-dried and carefully sanded with sandpapers of different grains until rings were clearly visible. Then, they were visually cross dated under the binocular scope and scanned at 1200 dpi (Epson Expression 10 000XL). The ring widths were measured with a 0.001 mm resolution along two radii per sample using the CooRecorder software (Larsson & Larsson 2018). The visual cross-dating was checked using the COFECHA software which calculates moving correlations between individual tree-ring width series and the mean site series of ring widths (Holmes 1983). Age was quantified by counting the number of annual growth rings from bark to pith along the two cross-dated and measured radii of each section. In most cases, particularly for vines older than 20 years, the pith was rotten. In those individuals, we calculated the theoretical age by fitting a concentric template and estimated the number of missing rings assuming a similar growth rate as in the innermost rings (Norton *et al.* 1987).

To calculate climate–growth relationships, the individual ring-width series were converted into indexed ring-width series through standardization and detrending (Fritts 1976). These procedures allow removing size-related trends in ring-width data and emphasize high-frequency growth variability. We fitted 12-year cubic smoothing splines with a 50% frequency response cut-off to individual ring-width series and obtained ring-width indices by dividing observed by fitted values. The length of the spline was selected to retain high-frequency (annual to decadal) growth variability. Then, we fitted autoregressive models to remove most of the first-order autocorrelation in a series of dimensionless ring-width indices. The residual or pre-whitened individual series were averaged using a bi-weight robust mean to obtain mean residual series for each site (Fritts 1976). These procedures were done using the dplR package (Bunn 2010) in R (R Development Core Team 2023).

Lastly, we calculated several statistics for the common, best-replicated period (2000–2020). This period was defined based on the values of the Expressed Population Signal (EPS) and we considered the best-replicated period with EPS $\geqslant$ 0.85 as the one in which the calculated chronologies approached the theoretically perfect chronologies (Wigley *et al.* 1984). We also characterized the mean site chronologies by calculating the mean and standard ring-width values, the mean first-order autocorrelation of ring widths (AR1), which accounts for year-to-year persistence in growth, the mean interseries correlation (rbar), and the correlation with the mean site series (Briffa & Jones 1990).

Statistical analyses

To calculate climate-growth relationships, the site mean series or chronologies of ring-width indices were related to monthly climate data (mean maximum and minimum temperatures, total precipitation, soil moisture, SPEI) using the Treeclim R package (Zang & Biondi 2015). The window of analysis was from September of the year previous to growth to September of the growth year and the considered period was 2000–2020. Ordinary least squares regressions were also fitted between daily climate data (mean minimum and maximum temperatures, total precipitation) and series of ring-width indices. Analogously, leaf unfolding dates were also related to monthly climate data (from the previous October to the current April) and weekly SPEI data (considering 1-month SPEI data), to evaluate the climate drivers of leaf unfolding.

Results

Phenology of leaf unfolding

On average, vine leaf unfolding started the 13th of April (DOY, mean ± SD 104 ± 12) ranging between the 16th March (DOY 76) and the 2nd May (DOY 123). Leaf unfolding occurred earlier as maximum temperatures from February to April and minimum temperatures and radiation from February to March increased (Fig. 1). Wet conditions from March to early April were linked to delayed leaf unfolding.

Growth rate and age

The oldest vine (56 years) was sampled in San Martín del Río (Fig. A4 in the Appendix), where the mean age was significantly ($p < 0.05$) higher than in the other two sites (Table 2). These two sites showed significant negative trends in growth (Kendall $\tau = -0.44$ in Logroño; $\tau = -0.67$ in Anzi; $p < 0.01$ in both cases), whereas this was not the case in San Martín del Río ($\tau = -0.05$; Fig. 2). This is an age-based growth decrease because the detrended ring-width series did not show this trend. No significant correlation was found among the site series of ring-width indices suggesting different patterns in year-to-year growth variability.

The mean ring width was higher in Logroño (1.80 mm) than in the other two sites (Anzi, 1.37 mm; San Martín del Río, 1.19 mm). The highest first-order autocorrelation was found in San Martín del Río, whereas the highest correlation with the mean site series and EPS was found in Anzi. The age of grapevines and the mean ring width were negatively associated and the best fit corresponded to a power function (ring width = 14.195 age$^{-0.71745}$; Fig. A4 in the Appendix).

Responses to climate variables and drought severity

Vine growth was enhanced by high February precipitation in the case of San Martín del Río and Anzi (Fig. 3). Cool conditions from February to March also improved growth in San Martín del Río, while high minimum September temperatures of the current year did it in San Martín del Río and also in Logroño. However, high minimum temperatures in the previous December were related to low growth indices in Anzi.

In the case of the monthly SPEI data, grapevine growth indices mainly responded to 1-month April SPEI values (San Martín del Río, $r = 0.59$, $p < 0.01$; Logroño, $r = 0.44$, $p < 0.05$) and May (Anzi, $r = 0.54$, $p < 0.01$). In San Martín del Río and Anzi, significant correlations were also found for 2-month SPEI values of the same months (April, May). Overall, vines from San Martín del Río were the most sensitive to winter-spring water availability because elevated soil moisture from January to March enhanced growth there (Fig. 4). In contrast, wet soil conditions in the previous December were negatively correlated with growth indices in Logroño.

Correlations between daily climate data and ring-width indices were in agreement with those found using monthly climate data (Fig. A5 in the Appendix). This was the case of the positive relationships between ring-width indices and mid-September minimum temperatures in Logroño (Fig. 5) or early-February precipitation in Anzi (Fig. 6). However, analyses based on daily climate data also uncovered some new relationships such as the positive association between ring-width indices and late-March minimum temperatures in San Martín del Río (Fig. 7).

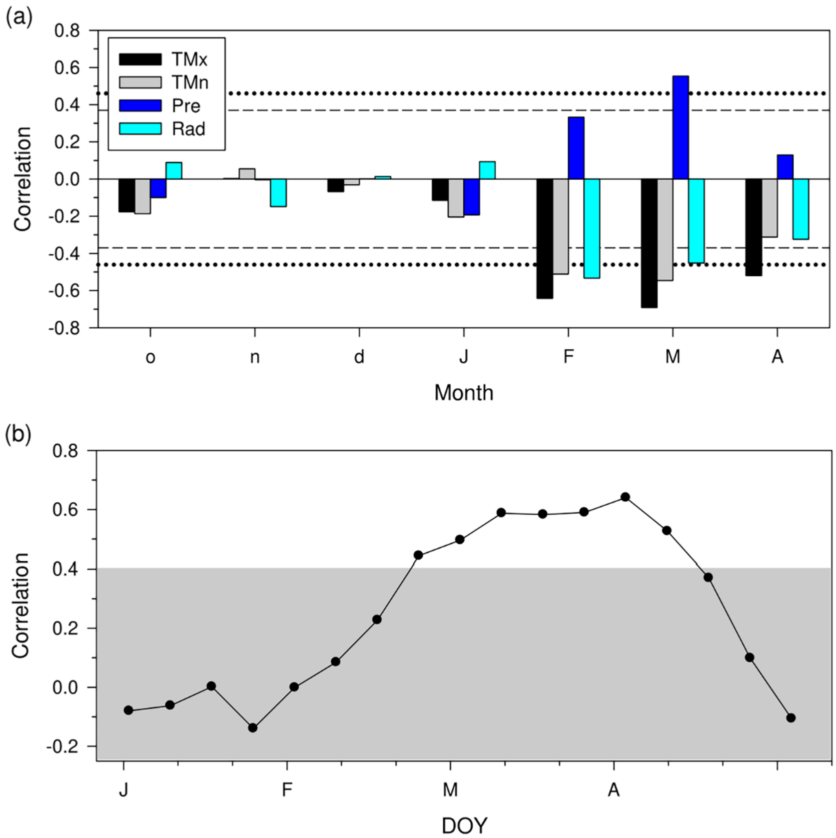

Fig. 1. Relationships found between (a) monthly climate data or (b) weekly SPEI data and leaf unfolding phenology in the Cardedeu site. The SPEI data were calculated considering 1-month cumulative water balance data. In plot (a), lowercase and uppercase letters indicate months of the previous and current years. Abbreviations: TMx, mean maximum temperature; TMn, mean minimum temperature; Pre, total precipitation; Rad, mean radiation. Horizontal dashed and dotted lines show the 0.05 and 0.01 significance levels, respectively. In plot (b), values located outside the grey box are significant ($p < 0.05$).

Table 2. Ring-width statistics of the three study grapevines.

Site	Period	Age (years)	Ring width (mm)	SD	AR1, first-order autocorrelation	Correlation with the mean site series	rbar	EPS, Expressed Population Signal
Logroño	1992–2020	21 ± 4b	1.80 ± 0.41a	0.97 ± 0.34	0.43 ± 0.26	0.52 ± 0.13	0.40	0.86
San Martín del Río	1962–2020	33 ± 6a	1.19 ± 0.32b	0.63 ± 0.30	0.53 ± 0.28	0.49 ± 0.14	0.36	0.85
Anzi	1987–2020	23 ± 4b	1.37 ± 0.45b	0.83 ± 0.39	0.45 ± 0.27	0.53 ± 0.12	0.42	0.88

Values are means ± SD. The statistics (ring width, SD, AR1, correlation with mean site series, rbar and EPS) were calculated for the common, best-replicated period 2000–2020. Different letters indicate significant ($p < 0.05$) differences between sites according to Mann–Whitney tests.

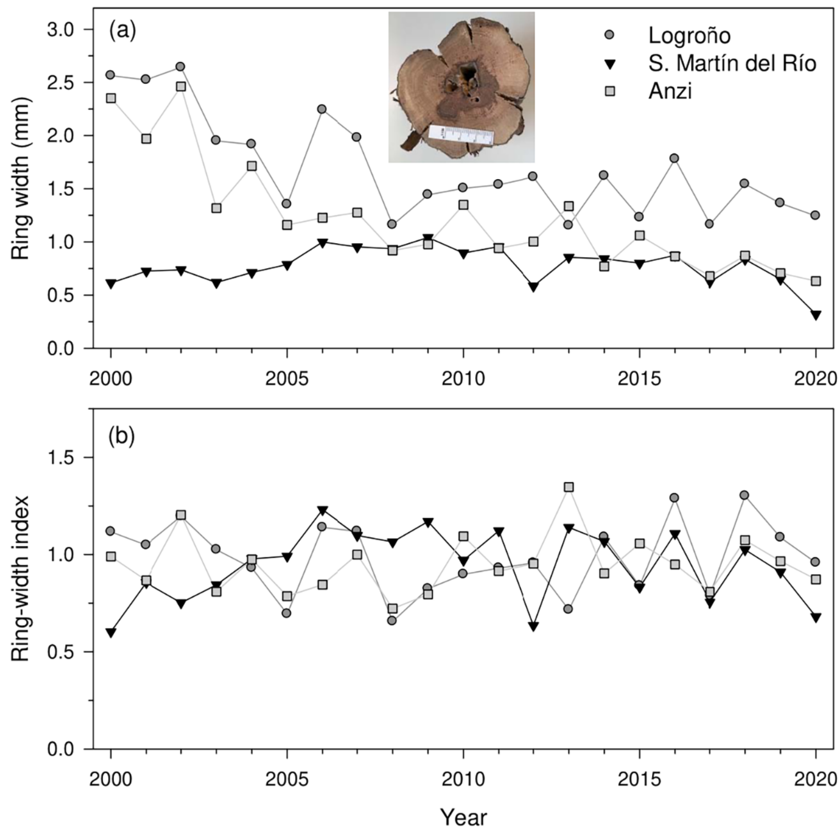

Fig. 2. Mean series of ring-width (a) and ring-width indices (b) of the three study grapevines. Series are presented for the common, best-replicated 2000–2020 period. In plot (a) the inset shows one of the cross-dated and measured vine cross-sections from Anzi.

Discussion

Warmer spring conditions seem to trigger an earlier onset of leaf unfolding in vines, in agreement with previous findings in other areas (García de Cortázar-Atauri *et al.* 2017; Koch & Oehl 2018; Alikadic *et al.* 2019). According to Peñuelas *et al.* (2002) the grapevine leaf unfolding advanced 17.4 days from the 1950s to 2000 in response to warmer conditions from January to April. However, an earlier leaf flushing is not necessarily related to enhanced radial growth in seasonally dry areas where an earlier budburst can affect plants facing dry winter-spring conditions (Camarero *et al.* 2022). Several recent papers have found that photosynthesis, the growing season, and the annual amount of growth are not in sync in trees, especially during drought (Cabon *et al.* 2022; Dow *et al.* 2022; Kannenberg *et al.* 2022). According to our data, growing season length does not seem to change the amount of growth in vines as has been found in trees.

Vine radial growth is positively correlated with high soil moisture levels and low drought severity from winter to spring. This is the period when soil recharge happens in seasonally continental dry sites such as the San Martin del Río site. Here, the oldest vine individuals were also found. The dryness of this site and the elevated age of sampled vines may explain the high responsiveness to precipitation and soil moisture in the previous winter. Remarkably, we found a tight relationship between vine diameter and age in the San Martin del Río site, where diameter explained 73% of age variability (Fig. A4b in the Appendix). This could be due to the wide age range we found in this vineyard (22–56 years).

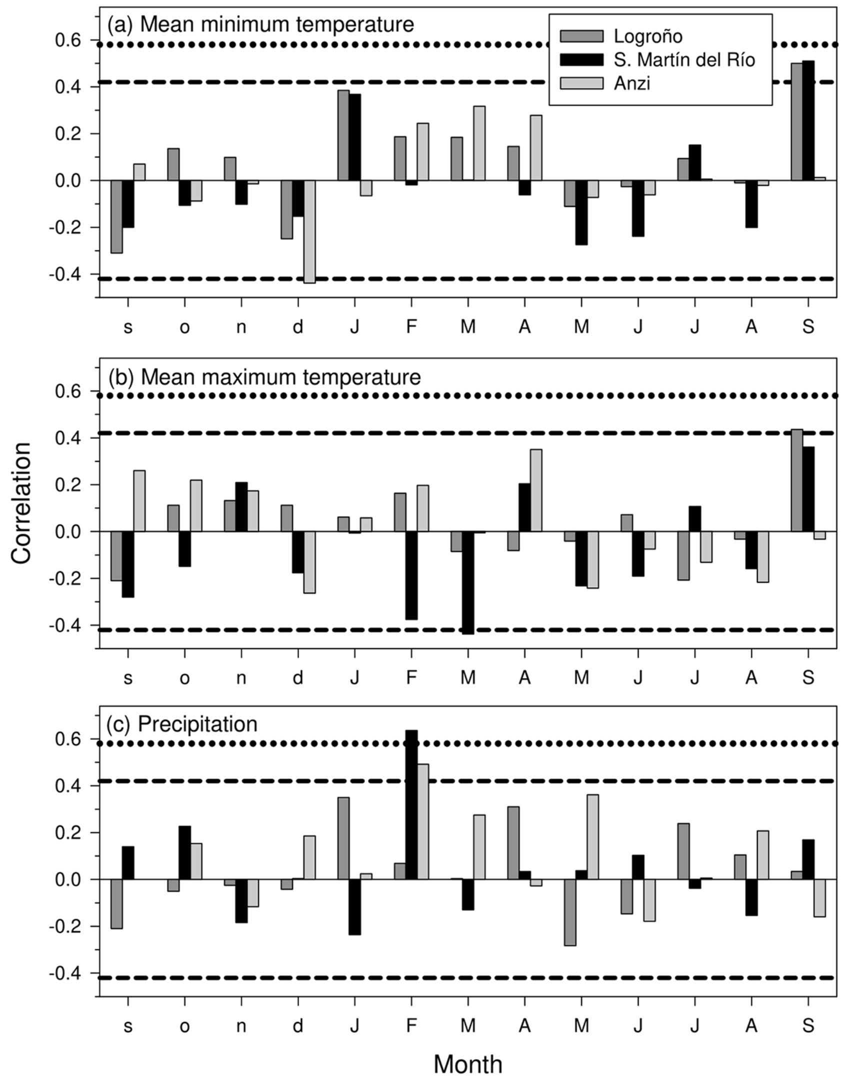

Fig. 3. Climate-growth relationships based on the correlations calculated between site series of ring-width indices and monthly climate variables (a, mean minimum temperature; b, mean maximum temperature; c, total precipitation). Correlations were calculated from the previous to the current September. Months corresponding to the prior and current years are abbreviated by lower- and uppercase letters, respectively. Horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively.

The positive response of vine growth indices to September temperatures in Logroño and San Martín del Río may correspond to a second period of xylem formation in autumn, after the main spring growth peak, which suggests a facultative bimodal growth strategy as has been found for other Mediterranean tree and shrub species (Camarero *et al.* 2010). This idea could be further examined by obtaining and analyzing long-term series of automatic dendrometer data in the field. In Anzi, warm nights in December could lead to higher respiration rates, reducing reserves such as non-structural carbohydrates, and leading to lower growth rates in spring (Schnitzer & van der Heijden 2019).

Lianas, including vines, show several xylem traits conferring resistance to tension-induced cavitation such as long and dimorphic vessels and small pit diameters, ensuring both hydraulic efficiency and safety (Carvalho *et al.* 2015). These and other traits (e.g., vulnerability segmentation and leaf shedding) may allow vines to show fast growth rates

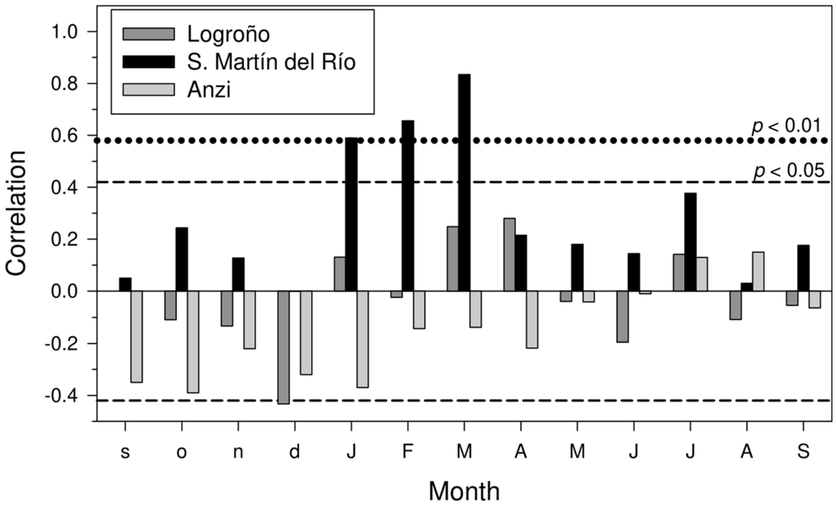

Fig. 4. Relationships between monthly soil moisture and site series of ring-width indices. Correlations were calculated from the previous to the current September. Months corresponding to the prior and current years are abbreviated by lower- and uppercase letters, respectively. Horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively.

without compromising resistance to cavitation under drought (Charrier *et al.* 2018; van der Sande *et al.* 2019). The ability to grow during the dry season may also be related to the amount and use of stores such as non-structural carbohydrates (Schnitzer & van der Heijden 2019), but our analyses did not find any significant relationships between growth indices and summer climate in vines. Consequently, the role played by winter precipitation and low evapotranspiration rates to recharge soil moisture prior to cambium reactivation in spring seems to be critical in continental sites such as San Martín del Río.

In vines, radial growth may be a more comprehensive proxy of long-term changes in soil moisture as compared to short-term ecophysiological proxies such as soil water potential or gas exchange variables (stomatal conductance and photosynthesis rates) (Gambetta *et al.* 2020). As drought develops, tissue expansion is the most sensitive indicator of diminished water status (Hsiao 1973), and cambial activity integrates water deficit effects on growth over the previous and current growing seasons (Fritts 1976). Furthermore, several components of vegetative growth in grapevines (e.g., internode extension, leaf expansion and elongation of tendrils) are easy to measure and related to changes in soil water potential, crop yield and grape quality (Hardie & Martin 2000; Pellegrino *et al.* 2005). Therefore, these measures of vegetative growth could be recorded over several years and compared with grapevine crops and retrospective xylem variables such as ring width or vessel lumen area (De Micco *et al.* 2018). For instance, it could be tested if narrow rings correspond to reduced leaf areas and decreasing grape production because of excessive fruit exposure to elevated temperatures (Jackson & Lombard 1993).

The xylem anatomy of vines and changes in radial growth reflect the responses to soil water availability but also depend on the cultivar considered (De Micco *et al.* 2018; Roig-Puscama *et al.* 2021). There are differences between varieties in their sensitivity to drought stress with some of them (e.g., Tempranillo) showing a low water-use efficiency and a poorer adaptation to withstand warm and dry stressful conditions (Medrano *et al.* 2003). In contrast, the responsive Garnacha cultivar should show a high water-use efficiency to tolerate water deficit including isohydric (water-saving) behavior (Schultz 2003; Charrier *et al.* 2018). Isohydry would reflect a strong stomatal control of transpiration rate resulting in small fluctuations in leaf water potential (Tardieu & Simonneau 1998). Contrastingly, fast-growing varieties such Tempranillo (Logroño site) could follow anisohydric (water-spending) strategies and exhibit less stomatal control over evaporative demand and soil moisture, allowing large fluctuations in leaf water potential and also contribute to heat dissipation (Soar *et al.* 2009).

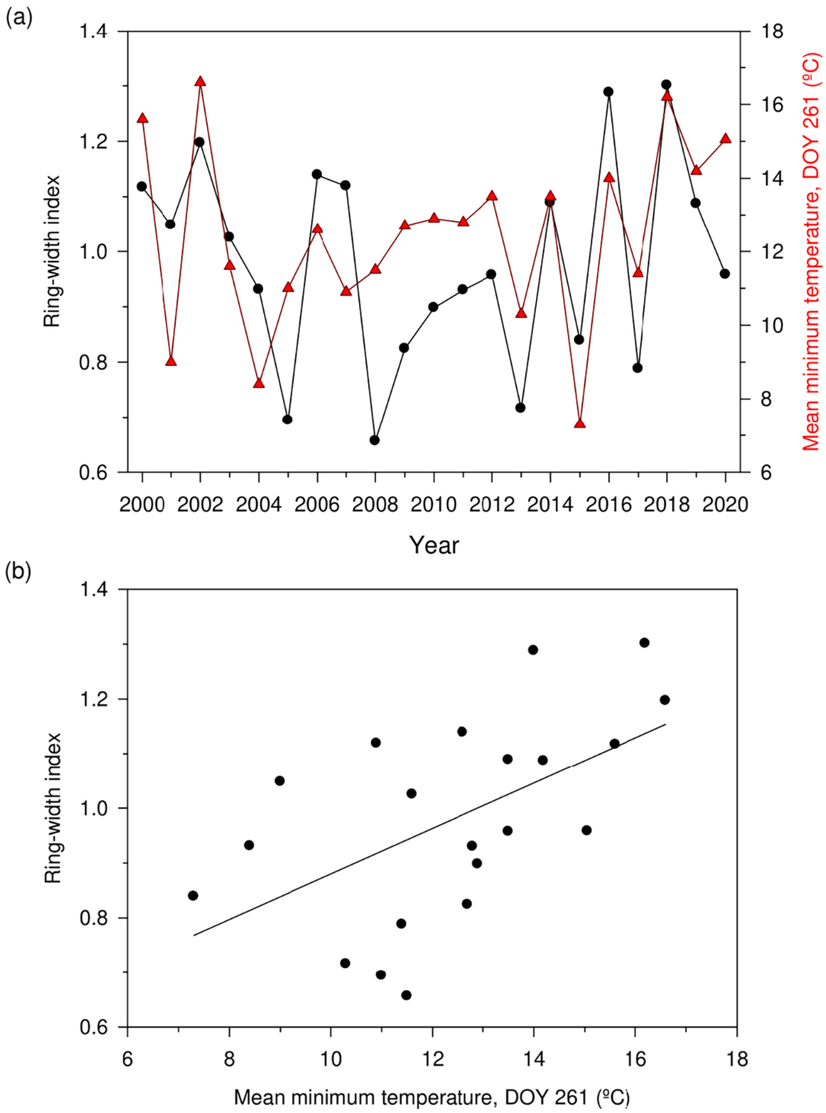

Fig. 5. Relationships (Pearson correlations) between daily mean minimum temperatures (red line) of the day of year (DOY) 261 (17 September) and ring-width indices (black line) in Logroño (see also Fig. A5 in the Appendix). The plots show (a) the temporal series of both variables and (b) a scatter relating them. The summary statistics of the linear regression ($y = 0.465 + 0.041x$) are $r^2 = 0.31$ and $p = 0.012$.

Three caveats should be considered regarding our study. First, there are notable differences between study sites which limit our comparisons. For instance, the leaf phenology data were taken in a site (Cardedeu) which is not located in a major designation of origin area. In addition, grapevine productivity depends also on many pedo-climatic factors and cultivation management. So, more precise information on the role played by soil in the regulation of water availability should be considered in future studies on grapevine growth and hydraulic architecture (Roig-Puscama *et al.* 2021). Second, the soil moisture data were downloaded from the Land Data Assimilation Systems rather than measured on-site. Future research based on long-term series of soil moisture such as those available at the International Soil Moisture Network (Dorigo *et al.* 2021) would strengthen the robustness of similar findings. Our findings probably reflect regional rather than local vine responses to climate given that we lacked on-site climatic

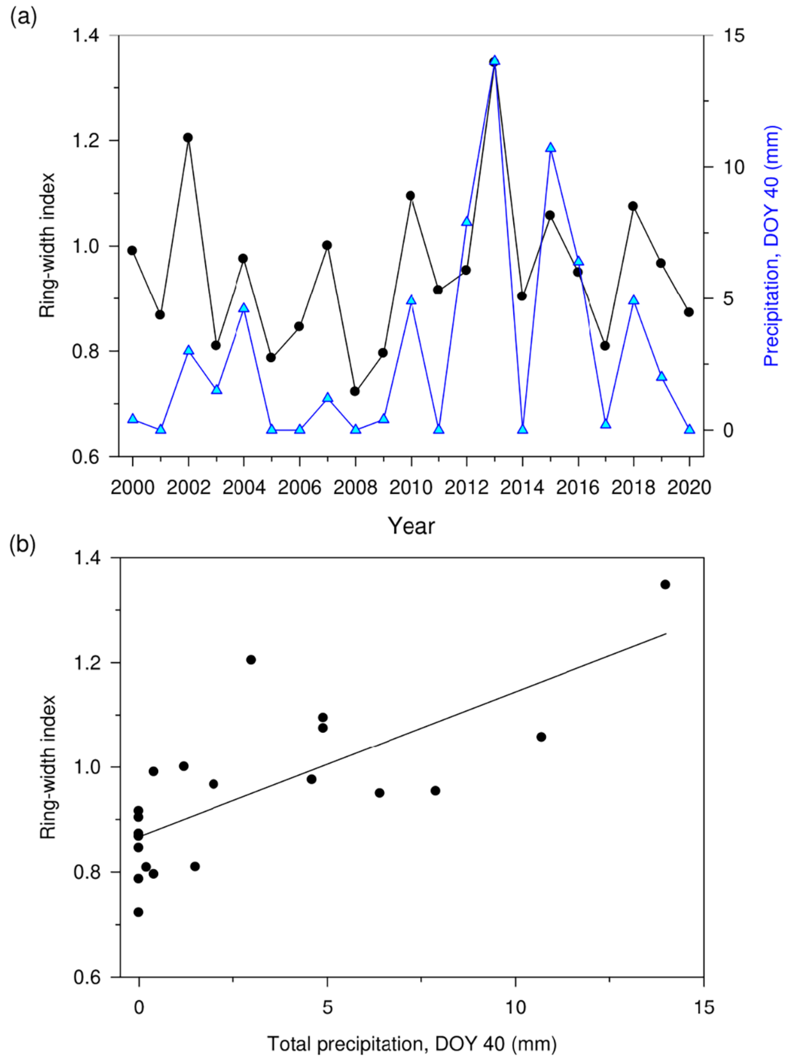

Fig. 6. Relationships (Pearson correlations) between daily precipitation (blue line) of the day of year (DOY) 40 (9 February) and ring-width indices (black line) in Anzi (see also Fig. A5 in the Appendix). The plots show (a) the temporal series of both variables and (b) a scatter relating them. The summary statistics of the linear regression ($y = 0.867 + 0.028x$) are $r^2 = 0.55$ and $p = 0.0004$.

measurements. Third, growth (ring width) data should be complemented with wood anatomy parameters which are strong proxies of changes in water transport efficiency and safety in grapevine (Bouda *et al.* 2019; Brook *et al.* 2020; Roig-Puscama *et al.* 2021; Damiano *et al.* 2023).

This study illustrates how dendrochronological methods applied to vine (dendro-viticulture) could be further used to improve our knowledge of climate stressors of grapevine growth to make grapevine management more water-use efficient (Tyminski 2013; Maxwell *et al.* 2016).

To conclude, vine radial growth positively responded to wet-cool conditions and high soil moisture levels from late winter to early spring in the continental-dry San Martín del Río site corresponding to the Garnacha cultivar. In this site, we found the lowest growth rate and the oldest vines, which were 56 years old, whereas in the other sites, growth rates were higher and declined as vines aged. Vine ages were probably higher but pith rotting complicated age estimation. Old vine individuals of cultivars that endure water deficit (e.g., Garnacha) should be further investigated

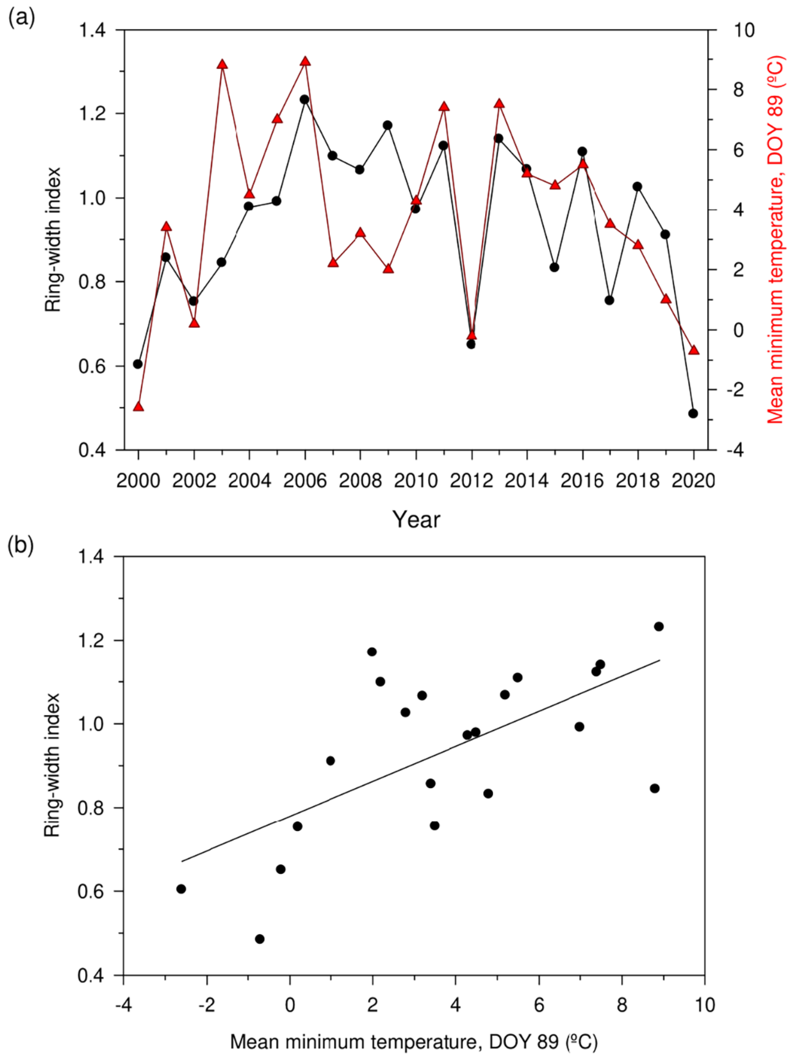

Fig. 7. Relationships (Pearson correlations) between daily mean minimum temperatures (red line) of the day of year (DOY) 89 (29 March) and ring-width indices (black line) in *San* Martín del Río. The plots show (a) the temporal series of both variables and (b) a scatter relating them. The summary statistics of the linear regression ($y = 0.779 + 0.042x$) are $r^2 = 0.43$ and $p = 0.0011$.

as genetic sources of drought tolerance. Vine varieties showed different growth responses to monthly and climate variables. Estimating vine age and establishing climate-growth relationships are necessary steps to forecast future winegrape yields and to prepare management plans considering increased aridification.

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Appendix

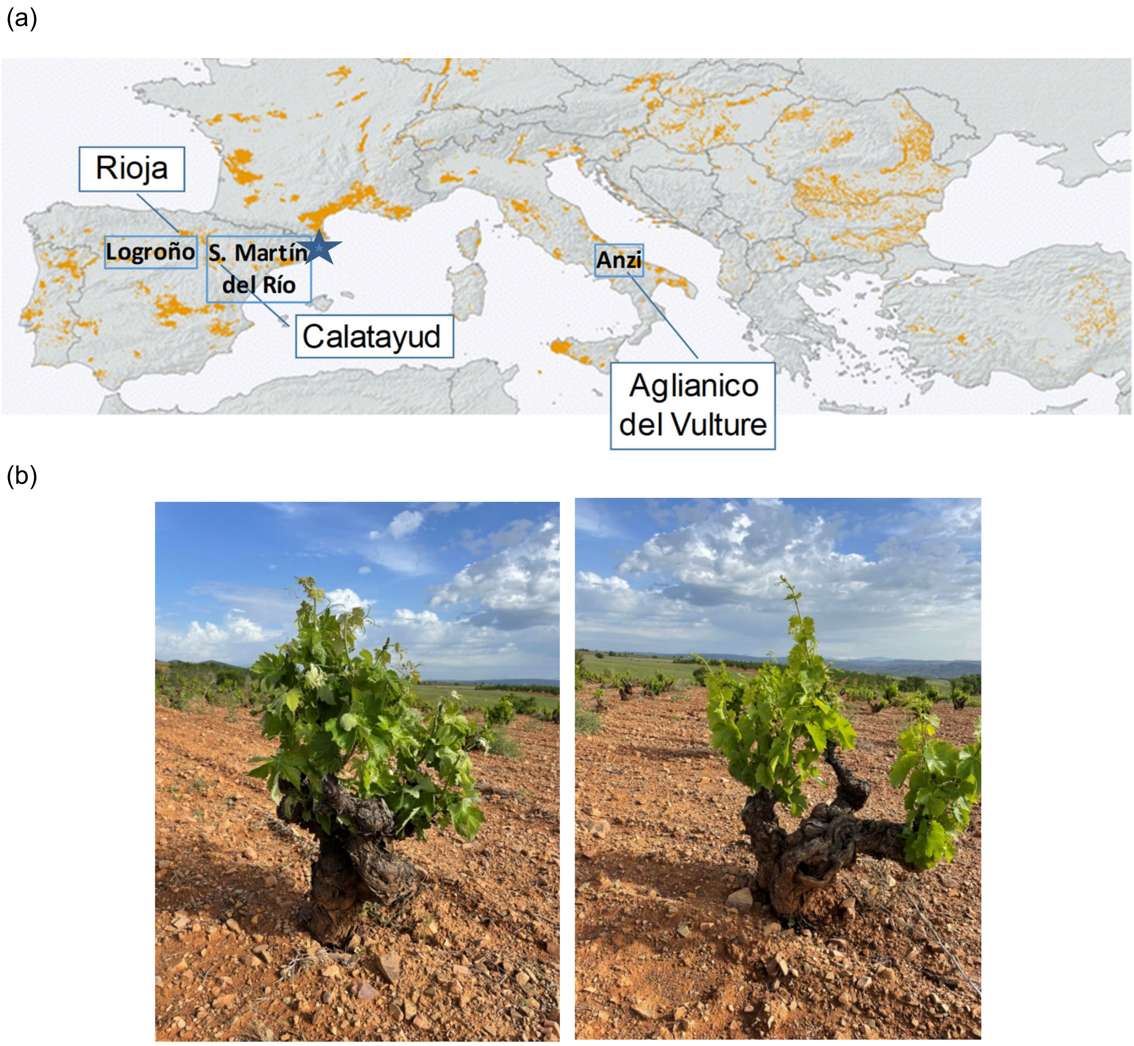

Fig. A1. (a) Map showing the main distribution of grapevines in southern Europe (yellow patches) highlighting the three study designations of origin (wine regions). The three study grapevines are indicated with bold characters. The star shows the location of the site from north eastern Spain with leaf unfolding data (Cardedeu). (b) View of two old grape vines located in San Martín del Río, north eastern Spain.

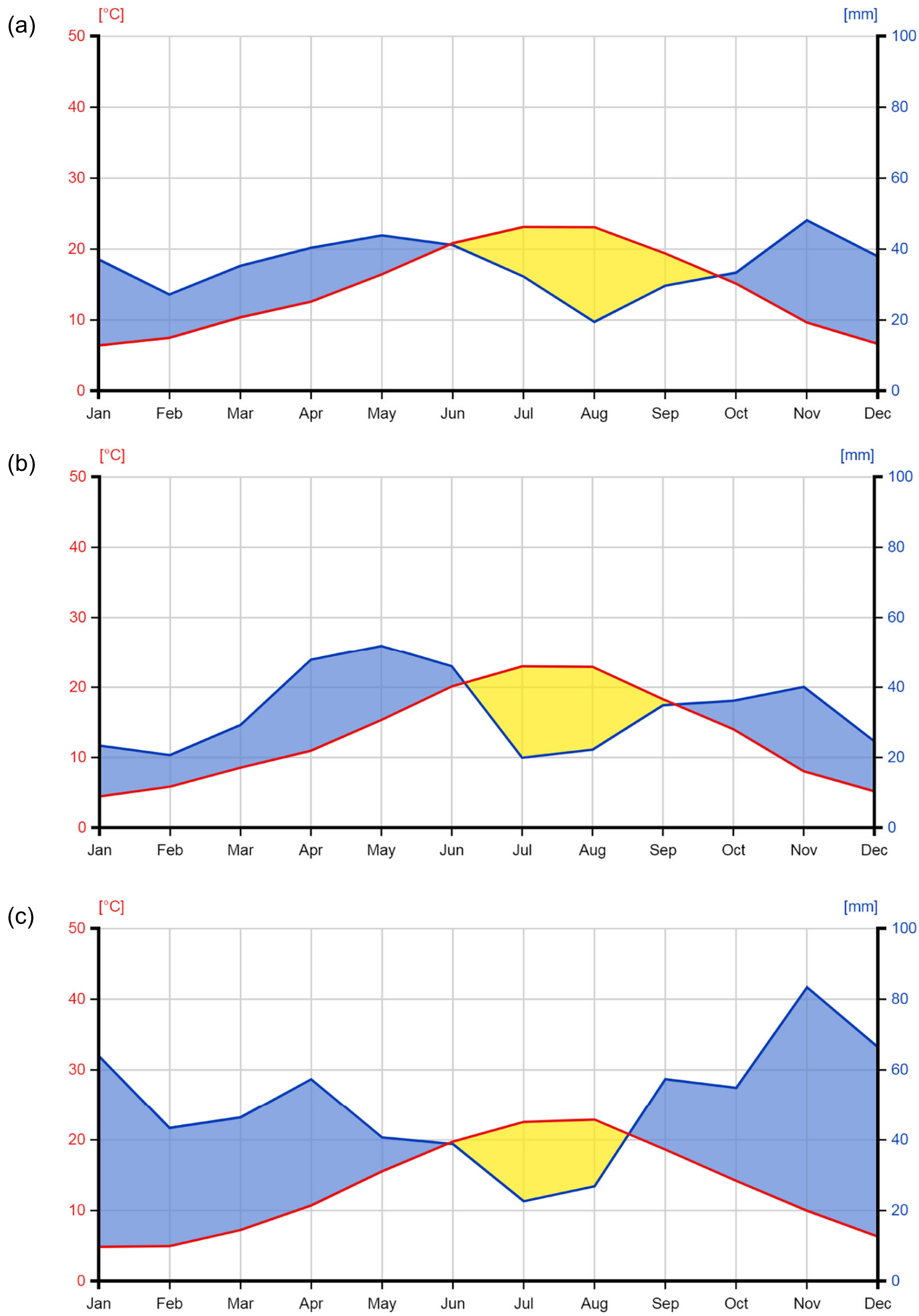

Fig. A2. Climate diagrams of the three meteorological stations used for the (a) Logroño (Logroño station, 42.45°N, 2.33° W, 353 m, period 1950–2020), (b) San Martín del Río (Daroca station, 41.11°N, 1.41°W, 779 m, period 1950–2020) and (c) Anzi (Laurenzana station, 40.46°N, 15.97°E, 704 m, period 2000–2020) study sites. Climate diagrams were created with the ClimateCharts.net webpage (Zepner L, Karrasch P, Wiemann F, Bernard L. 2021. ClimateCharts.net — an interactive climate analysis web platform, *Int. J. Digital Earth* 14(3): 338–356. DOI: 10.1080/17538947.2020.1829112.

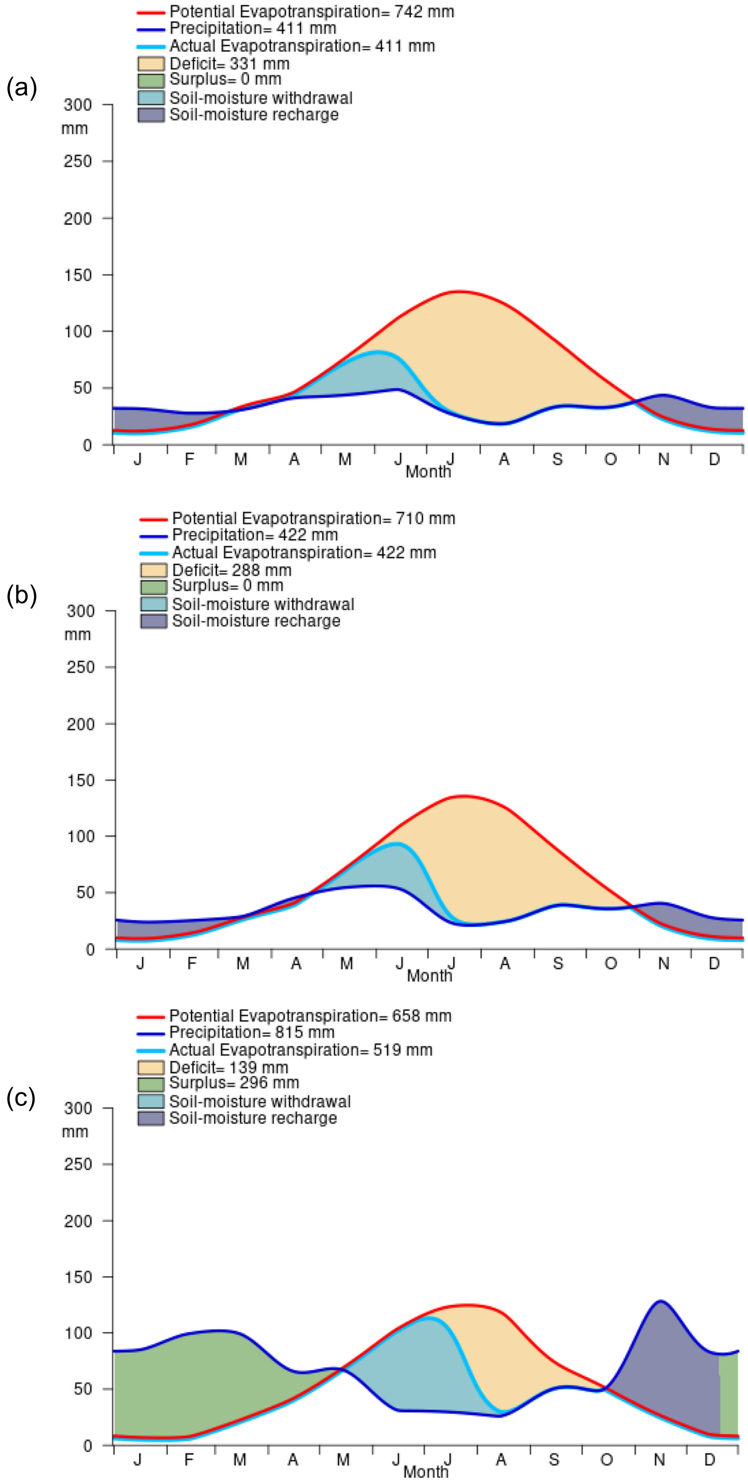

Fig. A3. Climate water balances for the (a) Logroño, (b) San Martín del Río and (c) Anzi sites.

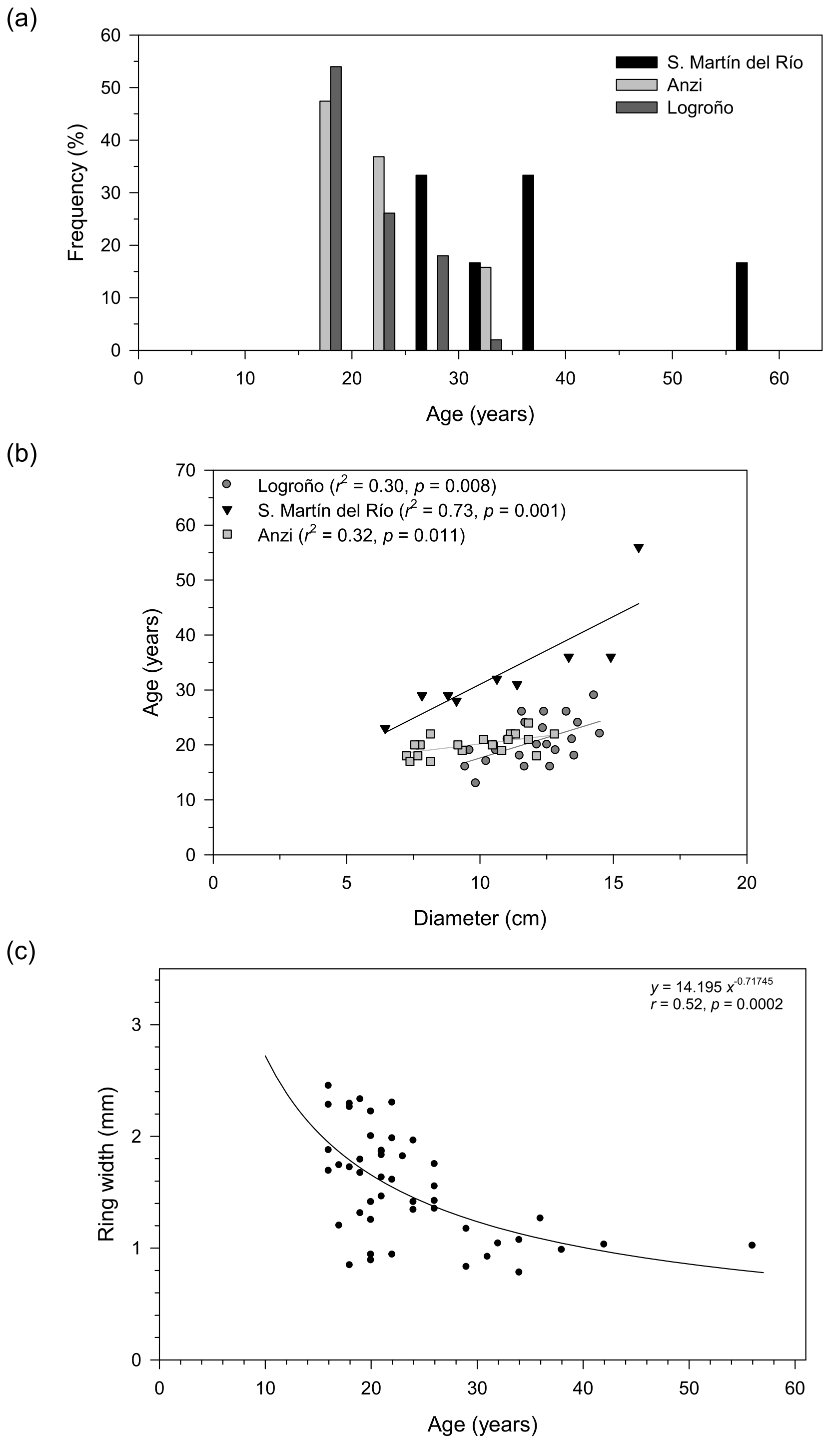

Fig. A4. (a) Relative frequency of sampled grape vines according to their age considering 5-year age classes. (b) Linear regressions relating grapevine stem diameter and age in the three study sites. The statistics show the amount of explained variance (r^2) and its probability level (p). (c) Power function relating vine age and mean ring width.

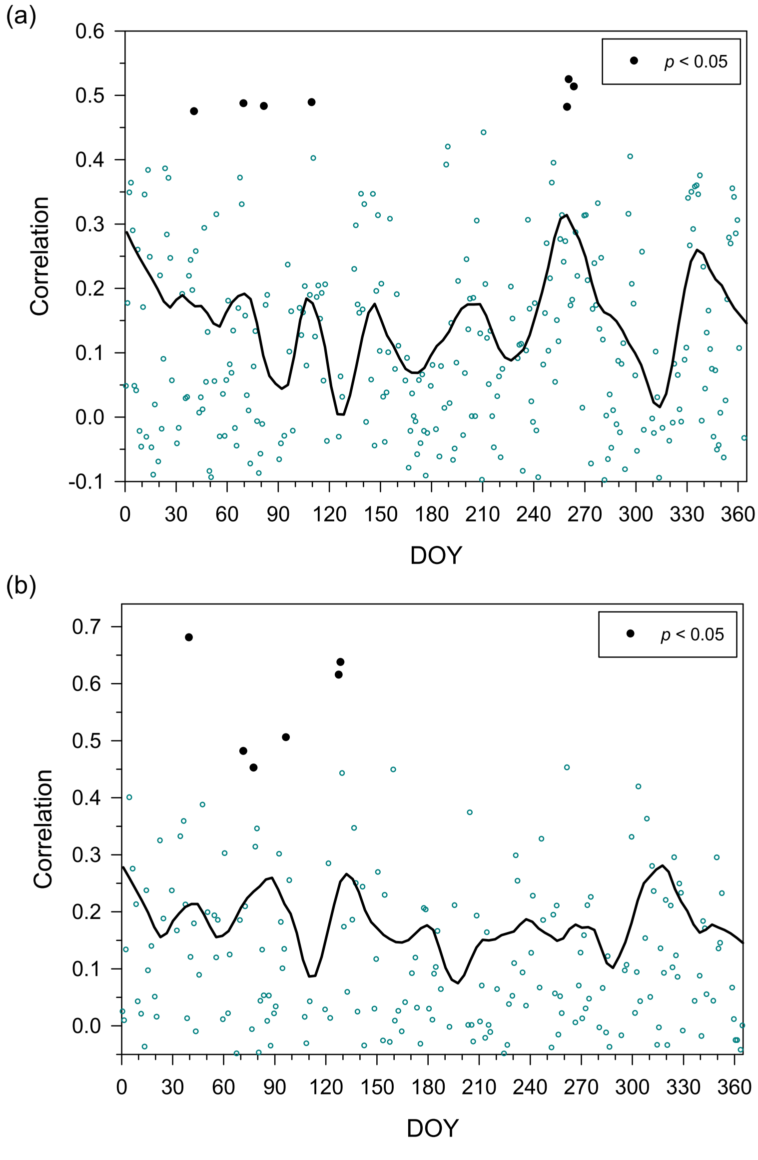

Fig. A5. Relationships (Pearson correlations) between vine ring-width indices and (a) daily mean minimum temperatures in Logroño and (b) precipitation in Anzi. The filled symbols indicate significant ($p < 0.05$) correlations. The line shows smoothed correlation values based on a 1-degree polynomial loess function (with 0.1 sampling proportion).