



Imprisoned in the Cretan mountains: How relict *Zelkova abelicea* (Ulmaceae) trees cope with Mediterranean climate



Laurence Fazan^{a,b,*}, Sébastien Guillet^{a,c}, Christophe Corona^d, Gregor Kozłowski^{b,e}, Markus Stoffel^{a,c}

^a Institute for Environmental Sciences, University of Geneva, Boulevard Carl Vogt 66, CH-1205 Geneva, Switzerland

^b Department of Biology and Botanical Garden, University of Fribourg, Chemin du Musée 10, CH-1700 Fribourg, Switzerland

^c Dendrolab.ch, Department of Earth Sciences, University of Geneva, Rue des Maraichers 13, CH-1205 Geneva, Switzerland

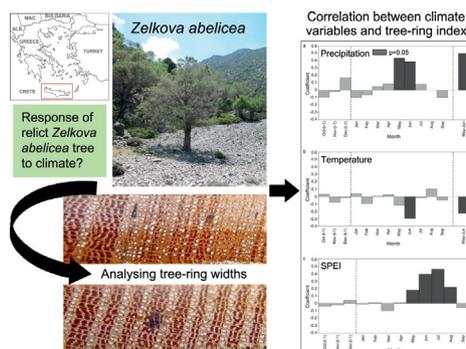
^d GEOLAB UMR CNRS 6042, Rue Ledru 4, FR-63057 Clermont-Ferrand Cedex 1, France

^e Natural History Museum Fribourg, Chemin du Musée 6, CH-1700 Fribourg, Switzerland

HIGHLIGHTS

- We established the first ever centennial chronology for a broadleaved tree on Crete.
- *Zelkova abelicea* is most sensitive to precipitation and drought in May–June.
- No growth change can be related to the increase in dry conditions of the past decades.
- *Z. abelicea* has a high capacity to withstand changing environmental conditions.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 6 December 2016

Received in revised form 5 April 2017

Accepted 7 April 2017

Available online xxx

Editor: Elena Paoletti

Keywords:

Dendroclimatology

Dendroecology

Drought stress

Relict endangered tree

Zelkova abelicea

Crete

ABSTRACT

We investigate the sensitivity of the relict, endemic Cretan tree species *Zelkova abelicea* (Lam.) Boiss. (Ulmaceae) to several climate variables (temperature, precipitation and drought). For this purpose, we establish the first centennial tree-ring chronology for the species, and the first ever tree-ring chronology for a broadleaved species on Crete. We demonstrate the strong sensitivity of *Z. abelicea* towards precipitation and drought in late spring to early summer and the absence of a significant response to abundant precipitation occurring during winter or early spring. Whereas the late spring sensitivity is strong and consistent through time, the species seems to be experiencing a loss of signal towards early summer conditions since the 1970s, interpreted as an earlier cessation of cambial activity due to the increase in summer drought conditions on Crete. However, despite a reduced vegetative period, no significant decrease in radial growth of *Z. abelicea* was observed in the tree-ring series for the last decades, thus highlighting the capacity of *Z. abelicea* to withstand changing environmental conditions.

© 2017 Elsevier B.V. All rights reserved.

* Corresponding author at: Department of Biology and Botanical Garden, University of Fribourg, Chemin du Musée 10, CH-1700 Fribourg, Switzerland.

E-mail addresses: laurence.fazan@unifr.ch (L. Fazan), sebastien.guillet@unige.ch (S. Guillet), christophe.corona@univ-bpclermont.fr (C. Corona), gregor.kozlowski@unifr.ch (G. Kozłowski), markus.stoffel@unige.ch (M. Stoffel).

1. Introduction

The genus *Zelkova* (Ulmaceae) comprises 6 extant tree species (Kozłowski and Gratzfeld, 2013). The taxon was an important component

of northern hemispheric forests during the Paleogene (Mai, 1995; Milne and Abbott, 2002). The members of the genus nowadays show important disjunctions, which is characteristic of relict trees. Three species are currently found in eastern Asia (*Z. serrata*, *Z. schneideriana*, *Z. sinica*), one in the Transcaucasian region (*Z. carpinifolia*) and two in the Mediterranean region (*Z. sicula*, *Z. abelicea*) (Kozłowski and Gratzfeld, 2013). The three east Asian and the Transcaucasian species still grow mostly in mesophilous conditions (Kozłowski and Gratzfeld, 2013; Kvavadze and Connor, 2005), similar to the warm and humid conditions with little seasonal contrast (Mai, 1989; Milne, 2006; Wolfe, 1978) experienced by the ancestral taxon during the Paleogene. The two Mediterranean species, by contrast, occur in more arid and seasonally contrasted climates and have withstood important climatic and environmental changes in the past (Kozłowski and Gratzfeld, 2013).

Zelkova abelicea (Lam.) Boiss. is of particular scientific interest as it is the only endemic tree species of the Greek island of Crete (Fielding and Turland, 2005), where it is found solely in the mountains, mainly on north-facing slopes and in areas where soil conditions and humidity are favorable (Fazan et al., 2012). Moreover, the species is classified as endangered in the IUCN Red List of Threatened Species (Kozłowski et al., 2012) and holds a very strong patrimonial value, as traditional shepherd canes (katsounes) are preferentially made with its hard and durable wood (Fournaraki and Thanos, 2006).

The main threats faced by the species are intensive pastoralism (mainly browsing and the effects of the presence of numerous animals such as trampling and soil erosion) and wildfires (Kozłowski et al., 2012). Additional threats also come from wood cutting, road construction, land-use changes, and potential anthropogenic modifications of local groundwater regimes (Egli, 1997; Fazan et al., 2012; Fournaraki and Thanos, 2006; Kozłowski et al., 2012, 2014; Sarlis, 1987; Søndergaard and Egli, 2006). The species is protected under Greek law, forbidding the collection and export of any plant material (Fournaraki and Thanos, 2006), and the pressure on and the use of forest resources in general have greatly diminished on Crete since the 1960s (Arvanitis, 2011). Additionally, a conservation project for *Z. abelicea* has been initiated in 2014 to protect the species and to promote regeneration of forest stands, growth of seedlings and browsed individuals, to maintain old specimens and to preserve the genetic variability of the species by coupling different in situ and ex situ measures and by raising public awareness (Project Zelkova, 2017).

Although conservation projects have been initiated and measures taken to regulate disturbance factors linked with human presence such as browsing flocks or wood cutting, the impacts of climate change on the species remain poorly understood.

Since the 1960s, the Mediterranean area has been subject to a rise of temperatures, especially during the summer season (Giorgi and Lionello, 2008; Luterbacher et al., 2006). For precipitation, the situation shows more spatial variability (Kostopoulou et al., 2014). However, decreases in precipitation have been recorded for the Eastern Mediterranean area, and notably for the Greek islands (Kostopoulou and Jones, 2005; Kostopoulou et al., 2014; Sarris et al., 2007). For the 21st century, climate models predict a continuation of the increase in temperature but show more mitigated results towards a continuation of precipitation decrease (Kostopoulou et al., 2014).

Moreover, the mountains of the Mediterranean are very vulnerable to climatic changes which may lead to the reduction of species and to habitat changes (Kovats et al., 2014; Nogués-Bravo et al., 2008).

In this context, understanding the sensitivity of an endangered Paleogene relict such as *Z. abelicea* to the current climate as well as its reaction to climate change is important for the implementation of conservation measures. For this purpose, we (i) have established a century long tree-ring chronology for *Z. abelicea*, and (ii) use tree-ring series to investigate the response of *Z. abelicea* to climatic parameters and (iii) to detect any potential shifts in climate/growth relationships. This study is innovative for Crete and presents a challenge, as very little dendroclimatological research has been carried out on the island (e.g. Sarris et al., 2011; Touchan et al., 2014, both focused on *Pinus halepensis* subsp. *brutia*).

Furthermore, most forest stands have experienced strong and century-long human impacts such as browsing, pollarding or fire (Arvanitis, 2011; Atherden and Hall, 1999; Rackham and Moody, 1996) that may interfere with the climate signal present in the tree-rings.

2. Material & methods

2.1. Study species

Z. abelicea is a ring-porous deciduous broadleaved tree of the Ulmaceae family found between 900 and 1800 m a.s.l. in all 5 main mountainous regions of Crete (Appendix A, Fig. S1). It is characterized by a very fragmented distribution with <100 known stands and a predominance of stands in the Levka Ori and Dikti Mountains and with only 1 extant known stand from the Psiloritis and Thripti areas, respectively (Kozłowski et al., 2014).

The species grows in scattered populations either as monospecific stands or intermixed in open forests with *Acer sempervirens*, *Quercus coccifera* or *Cupressus sempervirens*. Trees grow preferentially in north-facing areas or on the edges of karstic poljes; in areas with deep eutric or dystric cambisol soils with an adequate water supply. The species can also be found on scree slopes, along thalwegs, in or around ephemeral riverbeds, on south-facing slopes preferentially at high altitudes (>1500 m a.s.l.) as well as on slopes with rock outcrops and limited soil (Egli, 1997; Fazan et al., 2012; Søndergaard and Egli, 2006).

The large majority of individuals grow as dwarfed shrubs <2 m high, while only 5% of the individuals are arborescent, “normal growing” trees. Morphology is mainly driven by browsing pressure with individuals staying stunted for decades to centuries before they are able to escape browsing (Fig. 1a) (Fazan et al., 2012; Kozłowski et al., 2014).

The species has a short growing season compared to other tree species growing in the region, leafing out only in mid-May, a typical behavior for a ring-porous species (Sperry et al., 1994; Wang et al., 1992), and losing its leaves already in October (Egli, 1997 and personal observations).

Tree-ring widths in *Z. abelicea* individuals vary between 0.13 and 3.5 mm (Fazan et al., 2012), and usually have a single row of large early-wood vessels, a feature common to all *Zelkova* species (Wheeler and Manchester, 2007), followed by several rows of latewood vessels. Some tree-rings are so narrow that they are formed almost entirely of early-wood vessels, with very little latewood vessels, which can make them difficult to distinguish from their neighbors, or are not formed on the entire circumference resulting in locally missing tree-rings. Tiny tree-rings occur mainly in browsed individuals but can also be found in disturbed arborescent individuals (Fig. 1b) (see also Fazan et al., 2012).

2.2. Sampling sites and sampling strategy

In this study, three stands (OMA, KAL, XER) were sampled from the southern and south-eastern sides of the Omalós polje in the Levka Ori in western Crete between 1120 and 1400 m a.s.l. (Table 1 & Appendix A, Fig. S1). At these sites, mean annual temperature and total precipitation computed from the local Samaria weather station for the available period (2008–2016) are 11.8 °C and 1612 mm, respectively (Fig. 2) (35.3°N, 23.91667°E, 1250 m a.s.l. NOAA, 2016), whereas Ghosn et al. (2010) report 9.3 °C and 1094 mm for the Omalós polje for the period 1994–2002. Drought occurs during the summer (June–August account for <1% of the annual rainfall) whereas most of the precipitation falls in late autumn and winter (November–March account for 91% of the annual rainfall) (Fig. 2).

A total of 181 increment cores from 90 trees (preferentially two cores per tree) were taken (Table 2), using a Suunto increment borer, between 40 and 120 cm above the root collar so as to maximize the number of available tree-rings. Cores were preferentially taken on the sides of the trunk that were perpendicular to the general slope direction so as to minimize the impact of tension wood. Trees were selected with respect to their age (oldest possible), state (no visible wounds, rotting,

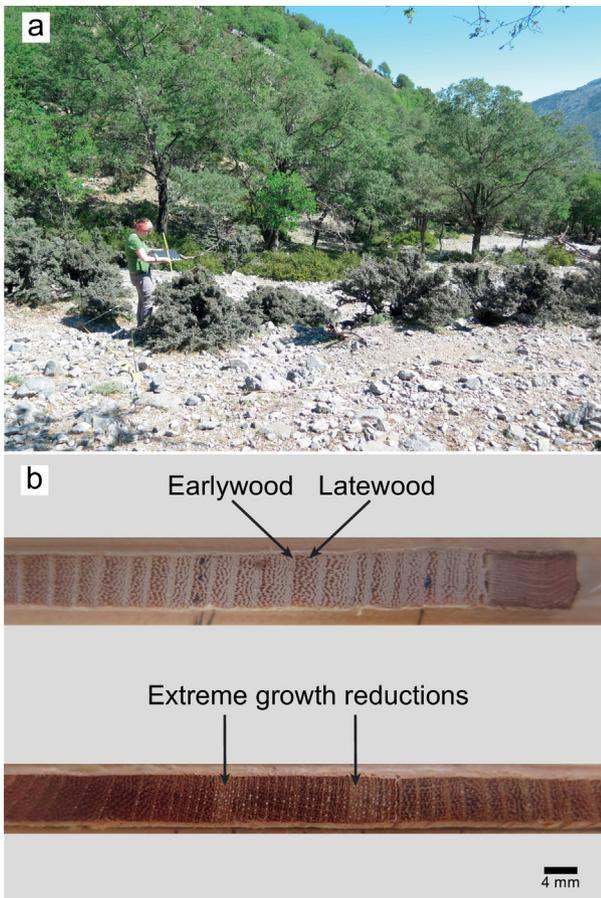


Fig. 1. a) Browsed, dwarfed *Z. abelicea* individuals in the foreground and normal growing individuals in the background, and b) typical ring-porous tree-rings in a normal growing tree and areas of extreme growth reduction with narrow rings in a normal growing tree.

hollowness, tilting) and height (tall enough to not have experienced browsing for several decades).

2.3. Sample preparation and analysis

Samples were analyzed and data processed following standard dendrochronological procedures (Bräker, 2002). Tree-rings were then counted and tree-ring widths measured using a digital LINTAB5 (resolution 1 μm) positioning table connected to a Leica stereomicroscope and TSAP-Win Scientific Software (Rinntech, 2014).

Individual tree-ring series coming from the same tree were crosschecked visually and statistically using TSAP-Win (Rinntech, 2014) and Cdendro (Larsson, 2003) to check for potential counting errors or missing tree-rings and were then corrected if necessary.

Correctly crosschecked individual tree-ring series were averaged into a single mean tree-ring series per tree. In a further step, mean tree-ring series of different trees were crossdated with one another and again checked for counting errors or missing tree-rings. Finally, crossdating and measurement accuracy were checked using COFECHA (Holmes, 1983).

Table 1
General characteristics of the sampling sites.

Site	Latitude (°N)	Longitude (°E)	Altitude (m a.s.l.)	Slope (°)	Aspect	# trees (cores)
OMA	35.315667	23.911861	1195–1230	15–30	W-NE	30 (59)
KAL	35.319028	23.919028	1125–1200	12–28	E-NW	30 (61)
XER	35.309972	23.902778	1185–1400	0–30	W-E	30 (61)

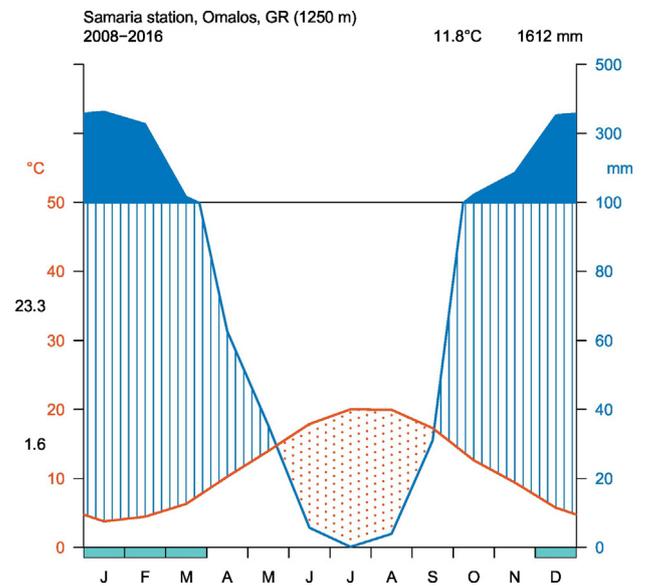


Fig. 2. Ombrothermic diagram for the Samaria weather station for the period 2008–2016. The red line represents mean monthly temperature, the blue line mean monthly precipitation totals. Light blue squares along the horizontal axis indicate months in which daily temperatures may fall below 0 °C but for which mean monthly minimum temperatures exceed 0 °C. The red dotted area indicates dry months – defined, according to the classification developed by Bagnouls and Gaussen (1953) as months in which total precipitation (mm) is equal to or lower than twice the mean monthly temperature (°C) ($P < 2T$). The minimum and maximum mean temperatures of the coldest, respectively warmest months are indicated on the left of the diagram. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.4. Detrending and tree-ring chronology building

Mean tree-ring series were detrended using ARSTAN (Cook, 1985; Cook and Krusic, 2005) to eliminate non-climatic trends (e.g. age related growth trends) and to maximize climatic information. We used the Friedman super smoother method (Friedman, 1984) which is used to model the growth of trees experiencing strong disturbance or competition (Edvardsson et al., 2012; Fang et al., 2010; Leland et al., 2013). The alpha value was left to the default value of 5. To account for the decreasing number of tree-ring series back in time, we used the method developed by Osborn et al. (1997) which stabilizes the variance of the final tree-ring chronology. Three tree-ring chronologies (standard, residual and arstan) were obtained through ARSTAN and each is a biweight robust mean of the mean tree-ring series which were individually detrended (Cook, 1985). The running EPS (expressed population signal) and running interseries correlation (running rbar) were calculated using a 40-year window with an overlap of 39 years in order to express the quality, reliability and strength of the common signal in the tree-ring chronology (Wigley et al., 1984). The commonly accepted EPS threshold above which a tree-ring chronology is considered reliable is 0.85 (Wigley et al., 1984).

Descriptive statistics of the raw tree-ring chronologies were computed with COFECHA (Holmes, 1983): mean tree-ring series length in years, mean tree-ring series growth rate, mean sensitivity which shows the mean change in tree-ring width from one year to another and indicates if the trees are complacent (or not) and mean autocorrelation which is a measure of the influence of the growth of the previous year on the tree-ring width of the current year.

2.5. Correlation functions

Bootstrapped correlation functions were computed using the program DENDROCLIM 2002 (Biondi and Waikul, 2004) between the

Table 2
Descriptive statistics for the raw tree-ring chronologies of the three sampling sites (OMA, KAL, XER) and the overall mean raw tree-ring chronology (MSL: mean tree-ring series length; MGR: mean growth rate; MSE: mean sensitivity; AC: autocorrelation).

	# trees (cores)	Time span	MSL (min–max) (yr)	MGR (mm/yr)	MSE	AC
OMA	27 (52)	1821–2012	113 (35–192)	1.16 ± 0.659	0.345	0.601
KAL	25 (50)	1779–2012	81 (30–234)	1.41 ± 0.668	0.302	0.634
XER	22 (43)	1883–2012	78 (46–130)	1.51 ± 0.747	0.315	0.640
All	74 (145)	1779–2012	92 (30–234)	1.32 ± 0.684	0.324	0.621

residual tree-ring chronology in order to minimize the influence of autocorrelation, and the following monthly climatic variables: mean temperature, total precipitation and Standardized Precipitation Evapotranspiration Index (SPEI, Vicente-Serrano et al., 2010). We used a 12-month window going from prior October to current September to encompass the whole current growing season of the species. Only the period for which the residual tree-ring chronology exceeded the 0.85 EPS threshold was taken into account for the analyses.

To assess the stability of the climatic response through time, moving correlation functions were then computed using DENDROCLIM 2002 (Biondi and Waikul, 2004) using a 30-year moving window.

2.6. Detecting trends in tree growth

Temporal trends and their significance in the standard tree-ring chronology were tested with the Mann-Kendall test (Kendall and Gibbons, 1990; Mann, 1945), following the approach proposed by Hannaford et al. (2013) and Ruiz-Villanueva et al. (2016). The Mann-Kendall test is widely used for the analysis of trends in climatologic and hydrologic time series mainly because it is a non-parametric test and does not require the data to be normally distributed.

The Mann-Kendall test was performed after applying a different detrending method to the *Z. abelicea* tree-ring series, namely the adaptive regional growth curve (ARGC) (Nicault et al., 2010). Contrary to the Friedman super smoother method, which mostly preserves high frequency variations, the ARGC standardization has proven efficient to keep long-term fluctuations in tree-ring series and should be more suitable for the assessment of growth trends. We applied the Mann-Kendall test for every possible combination of start and end year over the period for which the standard tree-ring chronology exceeded the 0.85 EPS threshold with a minimum window length of 30 yr.

2.7. Climatic data

Station data from western Crete are sparse. The closest functioning weather station in the mountains is <2 km away from the study area but was only installed in 2008. As a consequence, we decided to use mean monthly temperature and monthly total precipitation gridded data from the Climatic Research Unit (35–35.5°N, 23.5–24°E, CRU, 2014) spanning from 1901 to 2013 with a 0.5° latitude and longitude resolution. We also used the SPEI to investigate the influence of drought on tree growth in the study area. SPEI gridded data with a 0.5° latitude and longitude resolution (1901–2011) were extracted from the Global SPEIbase (Beguería et al., 2010) for the grid cell closest to the study area (35.3193°N, 23.914°E). We used a short time scale 3-month SPEI (i.e. the values of the two preceding and the current month determine the value of a given month), thereby accounting for precipitation as well as potential short-term groundwater storage.

3. Results

3.1. Tree-ring series and tree-ring chronology

A total of 74 (145) trees (cores) were successfully crossdated and kept for further analyses. 16 (36) trees (cores) were found unsuitable for further analyses as they showed strongly perturbed growth or the wood was too rotten to clearly distinguish the tree-rings. Descriptive statistics for the raw tree-ring chronologies of each sampling site as well as the overall mean raw tree-ring chronology are found in Table 2.

The raw and residual overall mean tree-ring chronologies, sample depth, running EPS, and running interseries correlation and are represented in Fig. 3. The EPS exceeds 0.85 between 1913 and 2012 which indicates that the chronology is most reliable for this period. The average

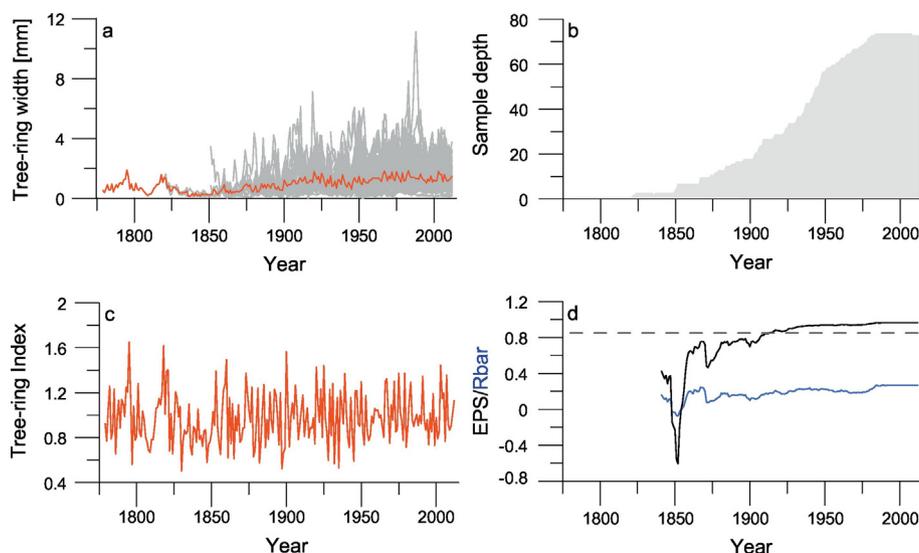


Fig. 3. a) *Z. abelicea* raw tree-ring chronology (red) with individual tree-ring series (grey), b) sample depth, c) residual tree-ring chronology, and d) EPS (black) and rbar (blue) with the 0.85 threshold (dotted line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

EPS for that period is 0.93 and interseries correlation 0.21. 27 trees are necessary to reach an EPS of 0.85.

3.2. Climate growth relationships

Correlation functions are illustrated in Fig. 4. Significant ($p < 0.05$) values are indicated with darker colored bars. The period considered for analysis spanned from 1913 to 2012 for precipitation and temperature and from 1913 to 2011 for the SPEI. All values for the correlation functions are found in Appendix A, Table S1.

A significant positive correlation is observed between the *Z. abelicea* residual tree-ring chronology and current May (0.44) and June (0.39) precipitation (Fig. 4a). When considered together, the correlation is 0.50. The species is negatively correlated with June (-0.29) temperatures (Fig. 4b). Significant values for May through August (0.18, 0.39, 0.46 and 0.22, for each month, respectively) are found for the SPEI (Fig. 4c). The species does not seem to show any sensitivity towards prior winter or early spring conditions or towards conditions occurring at the end of the growing period in autumn.

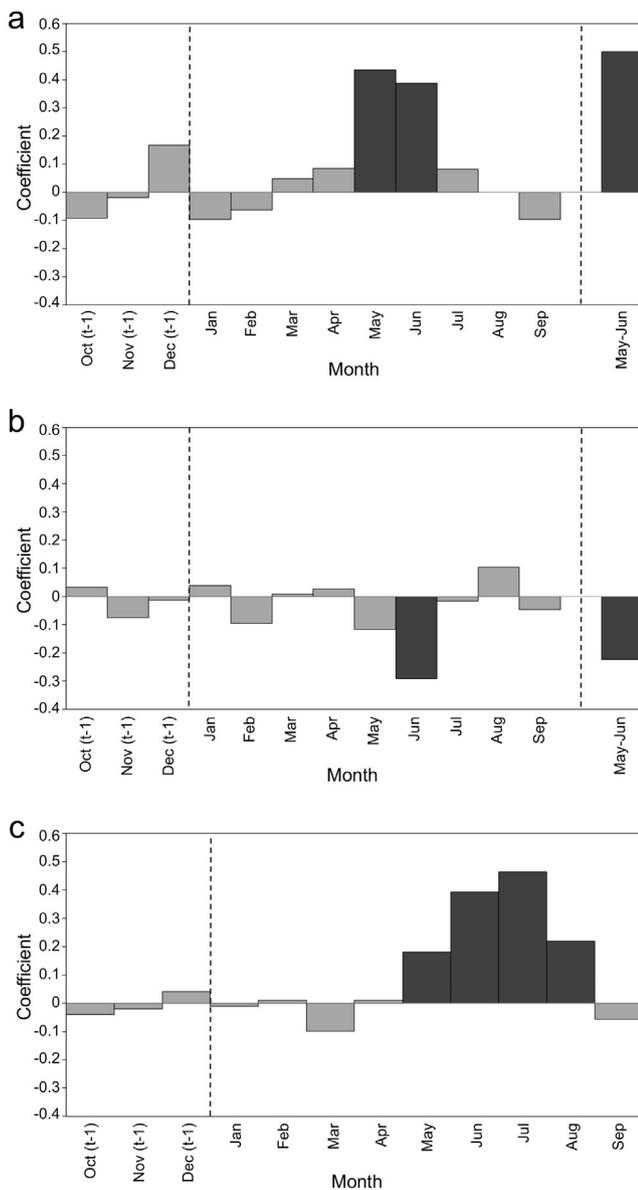


Fig. 4. Correlation functions from prior October to current September between the residual tree-ring chronology and a) precipitation, b) mean temperature and c) 3-month SPEI. Significant ($p < 0.05$) values are indicated with darker colored bars.

3.3. Temporal stability of climatic sensitivity and trends in tree growth

Moving correlation functions are illustrated in Fig. 5. Only significant ($p < 0.05$) values are indicated. The positive correlation with precipitation in May is constant throughout the study period, whereas the correlation with precipitation in June disappears after the mid-1960s (Fig. 5a). June temperatures are temporally stable until the 1970s, thereafter the signal disappears (Fig. 5b). By contrast, the SPEI shows a stable positive signal for July throughout the entire period (Fig. 5c). The multi-temporal trend analysis performed on the ARGChronology (Appendix A, Fig. S2) shows a significant downward trend ($p < 0.05$) for the period 1913–1950/55. Statistically significant positive slopes are observed for the period 1955–1975/80. A shift towards narrower rings is detected during the period 1975/80–2000, but this trend is no longer significant after the year 2000 (Fig. 6).

4. Discussion

4.1. Climatic sensitivity

4.1.1. Complacency and sensitivity towards climate

We were able to crossdate and extract a climatic signal from tree-ring series coming from *Z. abelicea* trees growing in the mountains of Crete despite the past anthropogenic pressure (e.g. pollarding or browsing revealed by the low interseries correlation value) experienced by the trees. In the literature, tree-ring series considered as complacent have sensitivity values < 0.15 , whereas tree-ring series with values > 0.30 are considered as having high sensitivity (Grissino-Mayer, 2001). The mean sensitivity value of 0.324 demonstrates the high sensitivity of *Z. abelicea* tree-rings to year-to-year variability in climate. Moreover, these values are consistent with what can be found for other tree species of the Mediterranean area (e.g. Campelo et al., 2007; Campelo et al., 2010; Cherubini et al., 2003; Garfi, 1997; Lebourgeois et al., 2012; Touchan et al., 2014).

4.1.2. Prior winter to early spring conditions

No signal was found towards prior winter or early spring conditions. This differs with other deciduous species of the Mediterranean which show positive signals towards winter precipitation (e.g. for *Quercus* species: Camarero et al., 2016; Cherubini et al., 2003; Corcuera et al., 2004; Di Filippo et al., 2010). *Quercus* species are known to have roots that reach deep into the ground and may attain profound water reserves (Cherubini et al., 2003) and thus make use of deeply infiltrated winter precipitation. Similarly to *Z. abelicea*, Garfi (1997) found no relationships between winter conditions and *Z. sicula* tree-ring widths in Sicily except for a positive correlation with precipitation occurring shortly before growth resumption. He explains the absence of any signals in *Z. sicula* towards precipitation during most of the winter period as being linked to its superficial root system. The species can only take advantage of water supplementation occurring during the growth period or very shortly before, whereas any earlier precipitation would have been lost to evaporation and runoff or infiltrated too deep in the underground for the species to benefit at the time the tree starts to grow in spring.

4.1.3. Spring temperatures

Z. abelicea does not seem to take advantage of warmer than usual temperatures in early spring that could help initiate an early onset of growth and a potentially longer growing period, and thus, allow wider tree-rings. This could indicate that the date of growth resumption is not influenced solely by environmental factors. This finding is contrary to the reaction of some deciduous *Quercus* species growing in the Mediterranean area and investigated by Tessier et al. (1994). Their study showed that for several species, spring temperatures were positively correlated with tree-ring width, with low temperatures in early spring limiting growth. Gea-Izquierdo and Cañellas (2014) observed that *Q. pyrenaica* trees growing at colder locations only (i.e. higher altitude)

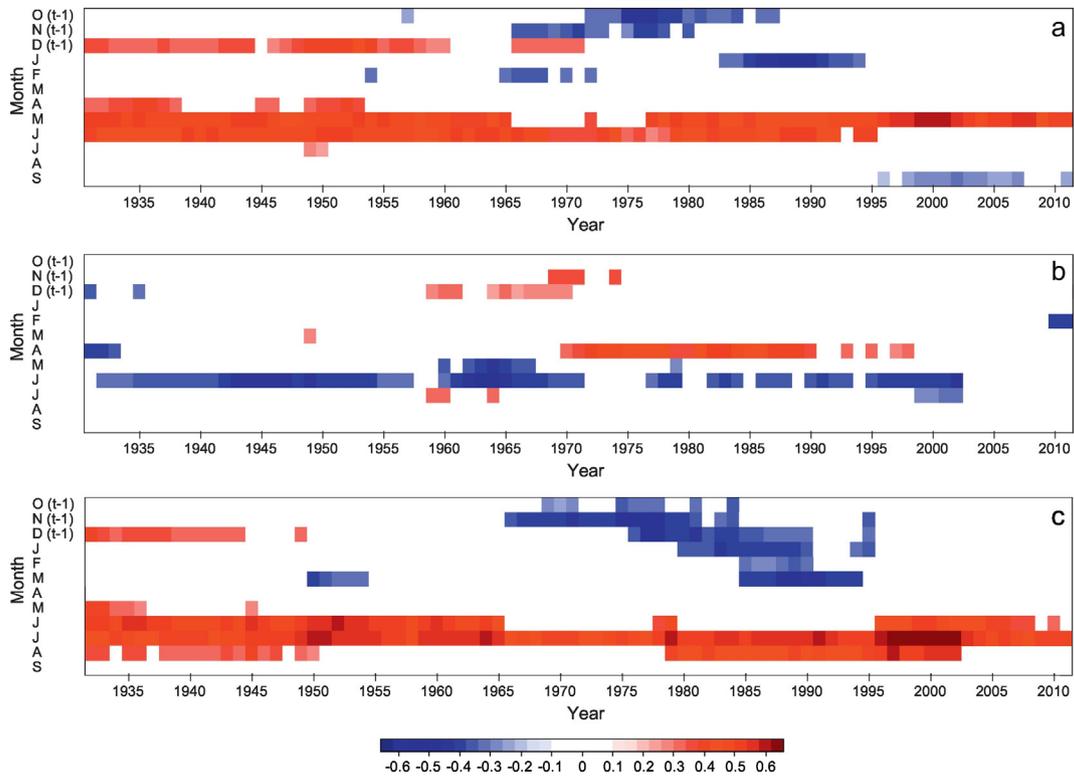


Fig. 5. Moving correlation functions from prior October to current September, representing a) precipitation, b) mean temperature and c) 3-month SPEI. Only significant ($p < 0.05$) values are represented. Red (blue) represents positively (negatively) correlated values. The years indicated on the x-axis show the last year of the considered 30-year window, e.g. 1990 will represent the period 1960–1990. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

were sensitive to spring temperatures. However, Garfi (1997) also found that *Z. sicula* was not influenced by early spring temperatures and explained this rigidity by a genetic predetermination of growth resumption. Moreover, ring-porous tree species are known to produce earlywood cells before the onset of the leaves (Bréda & Granier, 1996; González and Eckstein, 2003; Hinckley and Lassoie, 1981). Earlywood formation thus relies mainly on carbon reserves in the tree (Barbaroux and Bréda, 2002) rather than on climatic conditions at the onset of growth.

4.1.4. Precipitation of late spring to early summer

In our study, the growth of *Z. abelicea* is mainly influenced by precipitation in May and June of the year of radial growth. A rainfall surplus in late spring to early summer tends to produce wider tree-rings. Similarly, rainfall deficits for the same period are related to narrower tree-rings. June temperatures also play a role (i.e. negative correlation) in radial growth, a process which is probably linked with evapotranspiration processes. This hypothesis is further supported by the positive correlations between the residual tree-ring chronology and May to August

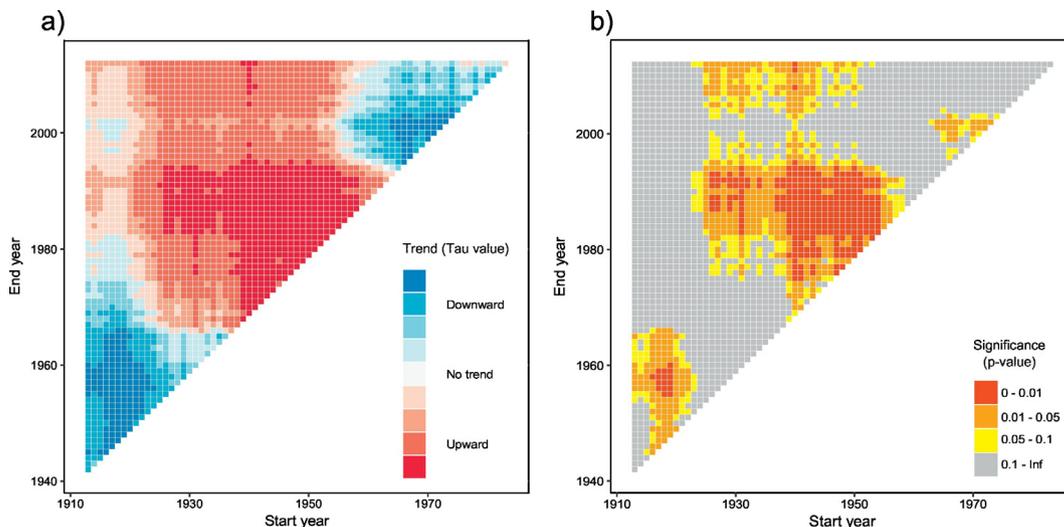


Fig. 6. a) Multi-temporal trend analysis of the ARGC *Z. abelicea* tree-ring chronology for the period 1913–2012. Blue and red cells correspond to negative and positive Tau values, which indicate growth release or suppression, respectively, b) This plot shows the significance (p -values) of the trends. Each cell represents a period of minimum 30 years on which the analysis is done. The lowest cell of the first column shows the period 1913–1942, the cell above the period 1913–1943. The lowest cell on the 2nd column shows the period 1914–1943, whereas the unique cell of the last column shows the period 1983–2012. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

SPEI index which reflect the high sensitivity of the species to drought conditions occurring during the previous 3 months. A similar response towards late spring-early summer precipitation and/or drought has also been found in *Z. sicula* and numerous other species growing in the Mediterranean (e.g. Campelo et al., 2009; Cherubini et al., 2003; Di Filippo et al., 2010; Garfi, 1997; Lebourgeois et al., 2012; Nijland et al., 2011; Tessier et al., 1994; Touchan et al., 2014). No study has been carried out so far to investigate the precise period in which Mediterranean *Zelkova* species form tree-rings and their relationship with precipitation. However, several authors studying deciduous ring-porous *Quercus* species growing in a Mediterranean environment have shown the importance of precipitation in late spring and early summer on tree-ring width formation (e.g. Camarero et al., 2016; Di Filippo et al., 2010; Tessier et al., 1994). The water balance at that period is of major importance for the growth of deciduous ring-porous *Quercus* species because most of the latewood is formed at that time (Di Filippo et al., 2010). In ring-porous trees, variations in tree-ring widths are mainly determined by fluctuations in the amount of latewood produced (Corcuera et al., 2004). Thus precipitation quantities during this period have a very strong influence on tree-ring widths.

4.1.5. Absence of signal towards summer and autumn conditions

Z. abelicea does not react to climatic conditions occurring during most of the summer period (July–September). It is probable that cambial activity is reduced to a minimum during the dry and hot summer and radial growth is reduced or inhibited due to the lack of water resources during the summer drought period. When drought conditions prevail already in May–June, cambial growth will cease very quickly, inducing a narrower tree-ring. From a physiological perspective, the water deficit combined with high temperatures and the presence of large earlywood vessels typical of ring-porous trees can lead to embolism and vessel cavitation which in turn can reduce tree vitality and thus influences negatively tree-ring width (Di Filippo et al., 2010). Garfi (1997) found similar results for *Z. sicula*. Furthermore, other studies have shown that broadleaved trees growing in a Mediterranean climate have reduced cambial activity during the dry and hot summer (e.g. Akkemik et al., 2006; Cherubini et al., 2003; Di Filippo et al., 2010).

Z. abelicea did not show any correlation with climatic parameters at the end of the summer before the onset of dormancy that could indicate growth resumption. Moreover, no anatomical characteristics (e.g. false tree-rings/intra-annual density fluctuations) that would suggest re-growth were visible. Garfi (1997) found that *Z. sicula*, on the contrary, had a correlation with autumnal climatic conditions, reflecting a reactivation of the cambium after the limiting summer conditions had ceased, and before the onset of winter dormancy. This reactivation is visible in the tree-ring series by a false tree-ring, and on an eco-physiological level by new shoots and leaves. In the aforementioned study, temperature (23 °C) and precipitation (63 mm) in September, at the end of the summer season, are both higher compared to the situation of *Z. abelicea* on Crete (17.11 °C and 31 mm in September for the Samaria weather station, NOAA, 2016). The absence of cambial reactivation in *Z. abelicea* could therefore be linked to the fact that when moisture conditions become optimal enough for growth again, mean temperatures are already too low and leaf senescence mechanisms and preparation for dormancy have already initiated.

4.2. Stability of climatic sensitivity through time

The temporal stability of the May precipitation signal in the moving correlation functions shows that the sensitivity of the species has not changed throughout the past century. However, the loss of the June precipitation and temperature signals since the mid-1960 and early 1970s could be an indication that the species is experiencing an earlier onset of dry and hot summer conditions and thus stops its activity earlier than before, already in June, in order to face the summer drought conditions. These signal losses and their appearance since the mid-1960s and early

1970s, are corroborated with data on local climatic changes and in particular the increase in summer drought conditions that have been observed for Crete since the 1970s (Chartzoulakis and Psarras, 2005; Sarris et al., 2011 and references therein). However, we only found limited evidence of radial growth decrease that could suggest that *Z. abelicea* trees are suffering from increasing drought conditions since the 1970s. The Mann-Kendall test (Fig. 6) shows that there is a statistically significant trend towards narrower tree-rings after the 1970s, but the trend lessens and is no longer significant after 2000 and is not found for the most recent years. This differs from results of Sarris et al. (2011) on *Pinus halepensis* growing in lowland Crete, who distinctly showed that tree-ring widths have decreased since the 1970s in connection with the diminution in rainfall and stated that trees have increased their dependency towards deep water reserves. In this respect, our preliminary findings highlight the capacity of *Z. abelicea* to cope with increasing summer drought conditions. However, these results call for more investigations as (i) they were only derived from one population from the mountains of western Crete and should be replicated to other mountain ranges on Crete; (ii) the absence of reaction of *Z. abelicea* towards current climate changes could come from the larger amounts of annual precipitation that fall in the Cretan mountains (>1500 mm/yr) as opposed to the lowlands (<300 mm/yr) (NOA, 2016; Rackham and Moody, 1996; Vrochidou and Tsanis, 2012); (iii) the cessation of the exploitation of *Z. abelicea* trees for wood and fodder in the mountains of Crete since the 1960s and the co-occurring climate change may influence and counteract the climatic signal contained in the tree-rings; (iv) although tree growth does not seem to be influenced by changing climatic conditions, the increased drought conditions may affect negatively forest regeneration by lowering seed germination rates and seedling or sapling survival.

5. Conclusions

This study has demonstrated the feasibility of extracting dendroclimatic signals from trees that have experienced intense anthropogenic disturbances in the past. We were also able to establish the first centennial tree-ring chronology for *Z. abelicea*, which is also the first tree-ring chronology for a broadleaved tree on Crete.

Our analyses show that radial growth of *Z. abelicea* is significantly correlated to drought conditions in May and June. Since the species showed no signal towards summer conditions, we hypothesize that its cambial activity is reduced to a minimum during that period in order to cope with the water deficit conditions during the summer months. Moreover, *Z. abelicea* does not seem capable of taking advantage of less limiting conditions at the beginning (e.g. abundant winter precipitations) or the end of the growing season as observed for *Z. sicula* on Sicily. However, additional studies on groundwater regimes and water accessibility should be undertaken to clarify this aspect.

The climatic sensitivity of the species is stable throughout the 20th century for most of the climatic parameters. A loss of sensitivity towards June conditions since the 1970s is interpreted here as an earlier onset of reduced summer activity. This evolution is consistent with the changes in climate that have been noticed since the 1970s for Crete, namely an intensification of summer drought conditions. At the same time, the absence of any significant decrease in tree-ring series suggests the ability of *Z. abelicea* to maintain its wood production despite a reduced growing season and demonstrates the capacity of the species and of relict trees, in more general terms, to withstand severe environmental changes, which is promising for the long-term conservation of the species.

Acknowledgements

We thank Léa Leuzinger and Pierre-Emmanuel Du Pasquier for their help in the field, Stergios Pirintzos for his assistance in obtaining sampling and export permits, Salvatore Pasta for his pertinent comments on the manuscript as well as the anonymous reviewers who greatly

helped to improve a previous version of the manuscript. Permission to sample trees and export material was granted by the Greek Ministry of the Environment, permits no. 172927/1881 and no. 1162. Fieldwork was supported through a student grant from the Fondation Ernst et Lucie Schmidheiny (Geneva) and through private funds in the scope of the *Zelkova* project.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.scitotenv.2017.04.047>.

References

- Akkemik, Ü., Çınar, Yılmaz H., Sevgi, O., 2006. Cambial activity of the sessile oak (*Quercus petraea*) in Belgrade Forest, Istanbul. *Turk. J. Agric. For.* 30, 429–438.
- Arvanitis, P., 2011. Traditional Forest Management in Psiloritis, Crete [c. 1850–2011]: Integrating Archives, Oral History and GIS. PhD thesis, University of Nottingham (346pp.).
- Atherden, M.A., Hall, J.A., 1999. Human impact on vegetation in the White Mountains of Crete since AD 500. *The Holocene* 9 (2):183–193. <http://dx.doi.org/10.1191/095968399673523574>.
- Bagnouls, F., Gaussen, H., 1953. Saison sèche et indice xérothermique. *Bulletin de la Société d'histoire naturelle de Toulouse*. 88, pp. 193–240.
- Barbaroux, C., Bréda, N., 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiol.* 2:1201–1210. <http://dx.doi.org/10.1093/treephys/22.17.1201>.
- Beguéría, S., Vicente-Serrano, S.M., Angulo-Martínez, M., 2010. A multiscalar global drought dataset: the SPEIbase - a new gridded product for the analysis of drought variability and impacts. *Bull. Am. Meteorol. Soc.* 91:1351–1354. <http://dx.doi.org/10.1175/2010BAMS2988.1>.
- Biondi, F., Waikul, K., 2004. DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Comput. Geosci.* 30 (3):303–311. <http://dx.doi.org/10.1016/j.cageo.2003.11.004>.
- Bräker, O.U., 2002. Measuring and data processing in tree-ring research – a methodological introduction. *Dendrochronologia* 20:203–216. <http://dx.doi.org/10.1078/1125-7865-00017>.
- Bréda, N., Granier, A., 1996. Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand (*Quercus petraea*). *Ann. Sci. For.* 53, 521–536.
- Camarero, J.J., Sangüesa-Barreda, G., Vergarechea, M., 2016. Prior height, growth and wood anatomy differently predispose to drought-induced dieback in two Mediterranean oak species. *Ann. For. Sci.* 73 (2):341–351. <http://dx.doi.org/10.1007/s13595-015-0523-4>.
- Campelo, F., Gutiérrez, E., Ribas, M., Nabais, C., Freitas, H., 2007. Relationships between climate and double rings in *Quercus ilex* from northeast Spain. *Can. J. For. Res.* 37 (10): 1915–1923. <http://dx.doi.org/10.1139/X07-050>.
- Campelo, F., Nabais, C., García-González, I., Cherubini, P., Gutiérrez, E., Freitas, H., 2009. Dendrochronology of *Quercus ilex* L. and its potential use for climate reconstruction in the Mediterranean region. *Can. J. For. Res.* 39 (12):2486–2493. <http://dx.doi.org/10.1139/X09-163>.
- Campelo, F., Nabais, C., Gutiérrez, E., Freitas, H., García-González, I., 2010. Vessel features of *Quercus ilex* L. growing under Mediterranean climate have a better climatic signal than tree-ring width. *Trees* 24:463–470. <http://dx.doi.org/10.1007/s00468-010-0414-0>.
- Chartzoulakis, K., Psarras, G., 2005. Global change effects on crop photosynthesis and production in Mediterranean: the case of Crete, Greece. *Agric. Ecosyst. Environ.* 106: 147–157. <http://dx.doi.org/10.1016/j.agee.2004.10.004>.
- Cherubini, P., Gartner, B.L., Tognetti, R., Bräker, O.U., Schoch, W., Innes, J.L., 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. *Biol. Rev.* 78:119–148. <http://dx.doi.org/10.1017/S1464793102006000>.
- Cook, E.R., 1985. A Time Series Analysis Approach to Tree Ring Standardization. PhD thesis, University of Arizona (171pp.).
- Cook, E.R., Krusic, P.J., 2005. Program ARSTAN. A Tree-ring Standardization Program Based on Detrending and Autoregressive Time Series Modeling, With Interactive Graphics. Tree-Ring Laboratory Lamont Doherty Earth Observatory of Columbia University, Palisades, NY.
- Corcuera, L., Camarero, J.J., Gil-Pelegrín, E., 2004. Effects of a severe drought on growth and wood anatomical properties of *Quercus faginea*. *IAWA J.* 25 (2):185–204. <http://dx.doi.org/10.1163/22941932-90000360>.
- CRU, 2014. University of East Anglia Climatic Research Unit (CRU). Harris I., Jones P. CRU TS3.22. Climatic Research Unit (CRU) Time-Series (TS) Version 3.22 of High-resolution Gridded Data of Month-by-month Variation in Climate (Jan. 1901–Dec. 2013). NCAS British Atmospheric Data Center <http://dx.doi.org/10.5285/18BE23F8-D252-482D-8AF9-5D6A2D40990C> (website consulted on 11.02.2015).
- Di Filippo, A., Alessandrini, A., Biondi, F., Blasi, S., Portoghesi, L., Piovesan, G., 2010. Climate change and oak growth decline: dendroecology and stand productivity of a Turkey oak (*Quercus cerris* L.) old stored coppice in Central Italy. *Ann. For. Sci.* 67 (7):706. <http://dx.doi.org/10.1051/forest/2010031>.
- Edvardsson, J., Linderson, H., Rundgren, M., Hammarlund, D., 2012. Holocene peatland development and hydrological variability inferred from bog-pine dendrochronology and peat stratigraphy – a case study from southern Sweden. *J. Quat. Sci.* 27 (6): 553–563. <http://dx.doi.org/10.1002/jqs.2543>.
- Egli, B., 1997. A project for the preservation of *Zelkova abelicea* (Ulmaceae), a threatened endemic tree species from the mountains of Crete. *Bocconea* 5 (2), 505–510.
- Fang, K., Gou, X., Peters, K., Li, J., Zhang, F., 2010. Removing biological trends from tree-ring series: testing modified Hughschiff curves. *Tree-Ring Res.* 66 (1):51–59. <http://dx.doi.org/10.3959/2008-18.1>.
- Fazan, L., Stoffel, M., Frey, D.J., Pirintzos, S., Kozłowski, G., 2012. Small does not mean young: age estimation of severely browsed trees in anthropogenic Mediterranean landscapes. *Biol. Conserv.* 153:97–100. <http://dx.doi.org/10.1016/j.biocon.2012.04.026>.
- Fielding, J., Turland, N., 2005. Flowers of Crete. Royal Botanic Gardens, Kew.
- Fournaraki, C., Thanos, C.A., 2006. *Zelkova abelicea*, the Unique Endemic Tree of Crete and Its Conservation. 1. ENSCONEWS, pp. 14–16.
- Friedman, J.H., 1984. A variable span smoother. Technical Report 5. Laboratory for Computational Statistics, Department of Statistics, Stanford University, Stanford, California (32 pp.).
- Garfi, G., 1997. Première Contribution à l'étude de *Zelkova sicula* (Ulmaceae), une Relique de la Flore Tertiaire, Endémique de la Sicile Sud-orientale. Phd thesis. Université d'Aix-Marseille III (263 pp.).
- Gea-Izquierdo, G., Cañellas, I., 2014. Local climate forces instability in long-term productivity of a Mediterranean oak along climatic gradients. *Ecosystems* 17 (2):228–241. <http://dx.doi.org/10.1007/s10021-013-9719-3>.
- Ghosh, D., Vogiatzakis, I.N., Kazakis, G., Dimitriou, E., Mousoulis, E., Maliaka, V., Zacharias, I., 2010. Ecological changes in the highest temporary pond of western Crete (Greece): past, present and future. *Hydrobiologia* 648 (1):3–18. <http://dx.doi.org/10.1007/s10750-010-0143-9>.
- Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. *Glob. Planet. Chang.* 63:90–104. <http://dx.doi.org/10.1016/j.gloplacha.2007.09.005>.
- González, I.G., Eckstein, D., 2003. Climatic signal of earlywood vessels of oak on a maritime site. *Tree Physiol.* 23:497–504. <http://dx.doi.org/10.1093/treephys/23.7.497>.
- Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* 57 (2), 205–221.
- Hannaford, J., Buys, G., Stahl, K., Tallaksen, M., 2013. The influence of decadal-scale variability on trends in long European streamflow records. *Hydrol. Earth Syst. Sci.* 17, 2717–2733.
- Hinckley, T.M., Lassoie, J.P., 1981. Radial growth in conifers and deciduous trees: a comparison. *Mitt. Forstl. Bundesversanst. Wien.* 142, 17–56.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.
- Kendall, M.G., Gibbons, J.D., 1990. Rank Correlation Methods. fifth ed. Oxford University Press, London & New York (260pp.).
- Kostopoulou, E., Jones, P.D., 2005. Assessment of climate extremes in the Eastern Mediterranean. *Meteorol. Atmos. Phys.* 89:69–85. <http://dx.doi.org/10.1007/s00703-005-0122-2>.
- Kostopoulou, E., Giannakopoulos, C., Hatzaki, M., Karali, A., Hadjinicolaou, P., Lelieveld, J., Lange, M.A., 2014. Spatio-temporal patterns of recent and future climate extremes in the eastern Mediterranean and Middle East region. *Nat. Hazards Earth Syst. Sci.* 14: 1565–1577. <http://dx.doi.org/10.5194/nhess-14-1565-2014>.
- Kovats, R.S., Valentini, R., Bouwer, L.M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M., Soussana, J.F., 2014. Europe. In: Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge and New York, pp. 1267–1326.
- Kozłowski, G., Gratzfeld, J., 2013. *Zelkova* – An Ancient Tree. Global Status and Conservation Action. Natural History Museum Fribourg (60pp.).
- Kozłowski, G., Frey, D., Fazan, L., Egli, B., Pirintzos, S., 2012. *Zelkova abelicea*. The IUCN Red List of Threatened Species. Version 2014.2. <http://www.iucnredlist.org/details/30319/0> (website consulted on 14.06.2014).
- Kozłowski, G., Frey, D., Fazan, L., Egli, B., Bétrisey, S., Gratzfeld, J., Garfi, G., Pirintzos, S., 2014. The Tertiary relict tree *Zelkova abelicea* (Ulmaceae): distribution, population structure and conservation status on Crete. *Oryx* 48 (1):80–87. <http://dx.doi.org/10.1017/S0030605312001275>.
- Kvavadze, E.V., Connor, S.E., 2005. *Zelkova carpinifolia* (Pallas) K. Koch in Holocene sediments of Georgia – an indicator of climatic optima. *Rev. Palaeobot. Palynol.* 133: 69–89. <http://dx.doi.org/10.1016/j.revpalbo.2004.09.002>.
- Larsson, L.A., 2003. CDendro: Cybis Dendro Dating Program. Available at www.cybis.se.
- Lebourgeois, F., Mérian, P., Courdier, F., Ladier, J., Dreyfus, P., 2012. Instability of climate signal in tree-ring width in Mediterranean mountains: a multi-species analysis. *Trees* 26 (3):715–729. <http://dx.doi.org/10.1007/s00468-011-0638-7>.
- Leland, C., Pederson, N., Hessel, A., Nachin, B., Davi, N., D'Arrigo, R., Jacoby, G., 2013. A hydroclimatic regionalization of central Mongolia as inferred from tree rings. *Dendrochronologia* 31 (3):205–215. <http://dx.doi.org/10.1016/j.dendro.2012.11.003>.
- Luterbacher, J., et al., 2006. Mediterranean climate variability over the last centuries: a review. In: Lionello, P., Malanotte-Rizzoli, P., Boscolo, R. (Eds.), *The Mediterranean Climate: An Overview of the Main Characteristics and Issues*. Elsevier, Amsterdam, pp. 27–148.
- Mai, D.H., 1989. Development and regional differentiation of the European vegetation during the Tertiary. *Plant Syst. Evol.* 162 (1):79–91. <http://dx.doi.org/10.1007/BF00936911>.
- Mai, D.H., 1995. Tertiäre Vegetationsgeschichte Europas. Methoden und Ergebnisse, Gustav Fischer, Jena, Germany.

- Mann, H.B., 1945. Nonparametric tests against trend. *Econometrica* 13 (3):245–259. <http://dx.doi.org/10.2307/1907187>.
- Milne, R.I., 2006. Northern hemisphere plant disjunctions: a window on Tertiary land bridges and climate change? *Ann. Bot.* 98:465–472. <http://dx.doi.org/10.1093/aob/mcl148>.
- Milne, R.I., Abbott, R.J., 2002. The origin and evolution of Tertiary relict floras. *Adv. Bot. Res.* 38:281–314. [http://dx.doi.org/10.1016/S0065-2296\(02\)38033-9](http://dx.doi.org/10.1016/S0065-2296(02)38033-9).
- Nicault, A., Guiot, J., Edouard, J.L., Brewer, S., 2010. Preserving long-term fluctuations in standardisation of tree-ring series by the adaptive regional growth curve (ARGC). *Dendrochronologia* 28 (1):1–12. <http://dx.doi.org/10.1016/j.dendro.2008.02.003>.
- Nijland, W., Jansma, E., Addink, E.A., Domínguez, Delmás M., De Jong, S.M., 2011. Relating ring width of Mediterranean evergreen species to seasonal and annual variations of precipitation and temperature. *Biogeosciences* 8:1141–1152. <http://dx.doi.org/10.5194/bg-8-1141-2011>.
- NOA, 2016. National Observatory of Athens. Samaria Forest Weather Station (Μετεωρολογικός σταθμός Δρυμού Σαμαριάς Χανίων). <http://penteli.meteo.gr/meteosearch/> (website consulted on 25.09.2016).
- Nogués-Bravo, D., Araújo, M.B., Lasanta, T., López-Moreno, J.I., 2008. Climate change in Mediterranean mountains during the 21st century. *Ambio* 37 (4):280–285. [http://dx.doi.org/10.1579/0044-7447\(2008\)37\[280:CCIMMD\]2.0.CO;2](http://dx.doi.org/10.1579/0044-7447(2008)37[280:CCIMMD]2.0.CO;2).
- Osborn, T.J., Briffa, K.R., Jones, P.D., 1997. Adjusting variance for sample-size in tree-ring chronologies and other regional mean timeseries. *Dendrochronologia* 15, 89–99.
- Project Zerkova, 2017. Project Zerkova Website. <http://www.zerkova.ch> (website consulted on 12.01.2017).
- Rackham, O., Moody, J., 1996. *The Making of the Cretan Landscape*. Manchester University Press, Manchester (237pp.).
- Rinntech, 2014. TSAP-Win Scientific© - Time Series Analysis and Presentation for Dendrochronology and Related Applications. http://www.rinntech.de/images/stories/PDF/TSAPWin_brochure.pdf (website consulted on 11.06.2014).
- Ruiz-Villanueva, V., Stoffel, M., Wyzga, B., Kundzewicz, Z.W., Czajka, B., Niedzwiedz, T., 2016. Decadal variability of floods in the northern foreland of the Tatra Mountains. *Reg. Environ. Chang.* 16 (3):603–615. <http://dx.doi.org/10.1007/s10113-014-0694-9>.
- Sarlis, G.P., 1987. *Zelkova abelicea* (Lam.) Boiss., an endemic species of Crete (Greece). *Webbia* 41 (2):247–255. <http://dx.doi.org/10.1080/00837792.1987.10670412>.
- Sarris, D., Christodoulakis, D., Körner, C., 2007. Recent decline in precipitation and tree growth in the eastern Mediterranean. *Glob. Chang. Biol.* 13:1187–1200. <http://dx.doi.org/10.1111/j.1365-2486.2007.01348.x>.
- Sarris, D., Christodoulakis, D., Körner, C., 2011. Impact of recent climatic change on growth of low elevation eastern Mediterranean forest trees. *Clim. Chang.* 106 (2):203–223. <http://dx.doi.org/10.1007/s10584-010-9901-y>.
- Søndergaard, P., Egli, B.R., 2006. *Zelkova abelicea* (Ulmaceae) in Crete: floristics, ecology, propagation and threats. *Willdenowia* 36, 317–322.
- Sperry, J.S., Nichols, K.L., Sullivan, J.E.M., Eastlack, S.E., 1994. Xylem embolism in ring-porous, diffuse-porous and coniferous trees of Northern Utah and Interior Alaska. *Ecology* 75 (6):1736–1752. <http://dx.doi.org/10.2307/1939633>.
- Tessier, L., Nola, P., Serre-Bachet, F., 1994. Deciduous *Quercus* in the Mediterranean region: tree-ring/climate relationships. *New Phytol.* 126, 355–367.
- Touchan, R., Anchukaitis, K.J., Shishov, V.V., Sivrikaya, F., Attieh, J., Ketmen, M., Stephan, J., Mitsopoulos, I., Christou, A., Meko, D.M., 2014. Spatial patterns of eastern Mediterranean climate influence on tree growth. *The Holocene* 24 (4):381–392. <http://dx.doi.org/10.1177/0959683613518594>.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J. Clim.* 23:1696–1718. <http://dx.doi.org/10.1175/2009JCLI2909.1>.
- Vrochidou, A.E.K., Tsanis, I.K., 2012. Assessing precipitation distribution impacts on droughts on the island of Crete. *Nat. Hazards Earth Syst. Sci.* 12:1159–1171. <http://dx.doi.org/10.5194/nhess-12-1159-2012>.
- Wang, J., Ives, N.E., Lechowicz, M.J., 1992. The relation of foliar phenology to xylem embolism in trees. *Funct. Ecol.* 6 (4):469–475. <http://dx.doi.org/10.2307/2389285>.
- Wheeler, E.A., Manchester, S.R., 2007. Review of the wood anatomy of extant Ulmaceae as context for new reports of later Eocene *Ulmus* woods. *Bull. Geosci.* 82 (4), 329–342.
- Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Clim. Appl. Meteorol.* 23:201–213. [http://dx.doi.org/10.1175/1520-0450\(1984\)023<0201:OTAVOC>2.0.CO;2](http://dx.doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2).
- Wolfe, J.A., 1978. A paleobotanical interpretation of Tertiary climates in the northern hemisphere: data from fossil plants make it possible to reconstruct Tertiary climatic changes, which may be correlated with changes in the inclination of the earth's rotational axis. *Am. Sci.* 66 (6), 694–703.