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Understanding the factors influencing the growth of *Zelkova abelicea* in browsing exclosures

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ABSTRACT

The growth of *Zelkova abelicea* (Lam.) Boiss. (Ulmaceae), a tree species endemic to the island of Crete (Greece), was studied within 31 fenced plots protected from browsing during three years after fencing across the entire distribution range of the species. Potential geographic, edaphic, climatic and physiognomic factors that could influence shoot elongation and height increase were investigated for each plot. We found that trees grew twice as much within the same period of time in western and central Crete compared to trees from eastern Crete. In addition, taller trees grew more than shorter individuals. Although some variation was found within the soil parameters, and particularly sites situated on slopes were distinguishable from sites situated in flat dolines, none of the soil parameters was found to be significant in explaining growth differences amongst *Z. abelicea* trees of different mountain ranges. Precipitation and temperature were interpolated for each plot from an existing network of 49 weather stations on Crete. Our analyses showed that the plots were distributed along a longitudinal, westwards increasing gradient in precipitation as well as along an altitudinal gradient in temperature. Our analyses revealed that geographical position on the island, precipitation in June and initial tree height were significant in explaining spatial differences in *Z. abelicea* growth. Our results underline the importance of spring and early summer climatic conditions in determining *Z. abelicea* growth and highlight differences throughout the island.

1. Introduction

Tree growth is known to vary throughout the distribution range of a given species due to a number of factors. These factors may

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include differences related to local climatic conditions, edaphic characteristics, population dynamics (e.g. tree size or age), interspecific competition or differences in herbivore pressure (e.g. Oliveira et al., 1994, Cairns and Moen, 2004, Cotillas et al., 2009, Purves, 2009, Gómez-Aparicio et al., 2011).

On the Greek island of Crete, growth of trees (and more generally of plants) is strongly controlled by (over)browsing until (if ever) they reach a sufficient height and escape herbivore pressure (Fazan et al., 2012, 2021; Zimowski et al., 2014).

Zelkova abelicea (Lam.) Boiss. (Ulmaceae), is one of three tree species endemic to Crete (Villar et al., 2015; Cambria et al., 2019; Médail et al., 2019). This Paleogene relict grows only in the Cretan mountains above 900 m a.s.l., in cool and not too xeric areas such as north-facing slopes, in or around dolines or scree slopes. However, it is also found on south-facing slopes, preferably, but not exclusively at high (>1500 m a.s.l.) altitudes. It grows oftentimes with *Acer sempervirens* L., *Quercus coccifera* L., and occasionally with *Cupressus sempervirens* L., mostly forming scattered and isolated stands (Sarlis, 1987; Egli, 1997; Søndergaard and Egli, 2006; Bauer and Bergmeier, 2011; Fazan et al., 2012; Goedecke and Bergmeier, 2018). The majority of individuals exhibit a stunted dwarfed morphology (Fig. 1A) with multiple stems and very slow growth due to severe browsing by goats (Fazan et al., 2012; Kozlowski et al., 2012). Dwarfed overbrowsed individuals do not produce fruit and can be several hundred years old, indicating almost continuous and long-lasting herbivore pressure (Sarlis, 1987; Fazan et al., 2012). Arborescent, fruiting individuals (Fig. 1B) are much rarer and represent ca. 5% of all known individuals, although proportions are very stand dependent, and most stands are dominated by dwarfed, non-fruiting individuals (Kozlowski et al., 2012). The species, irrespective of its stature, suckers abundantly and hence propagates easily vegetatively, especially when roots are exposed to mechanical damage through soil erosion and/or disturbance (Egli, 1997; Søndergaard and Egli, 2006; Fazan et al., 2012; Kozlowski et al., 2012, 2014, 2018).

Z. abelicea is listed as endangered (EN) on the IUCN Red List (Kozlowski et al., 2012). Unsustainable pastoral activities are a major threat to *Z. abelicea* (Kozlowski et al., 2012) but also more generally the most important cause of landscape degradation on Crete (Kairis et al., 2015). The presence and management of large caprine and ovine flocks prevent seedlings from establishing and dwarfed

Fig. 1. A. Dwarfed and overbrowsed *Z. abelicea* individuals, B. Arborescent fruiting *Z. abelicea* individual, C. Study plot located in the Levka Ori, D. Study plot located in the Dikti Mountains, E. Study plot located on Mt. Thripti.

individuals from growing tall and fructifying. In addition, climate variables such as seasonal precipitation quantity or temperature have been shown to be important factors for controlling growth patterns of *Z. abelicea* individuals that have reached a height sufficient to escape browsing (Fazan et al., 2017).

The impact of browsing on the growth, sexual reproduction and recruitment of *Z. abelicea* is particularly heavy in unprotected areas (Sarlis, 1987; Fazan et al., 2012, 2017, 2021). Fazan et al. (2021) showed that in the absence of browsing, *Z. abelicea* individuals grew on average twice as much as when overbrowsed. However, it remained unknown up to present if trees grew at the same rate throughout the island. Therefore, the goal of this study was to 1. evaluate the growth of *Z. abelicea* individuals in non-browsed fenced plots across the entire distribution range of the species and see if there are significant differences in growth patterns across the island, 2. characterize the fenced plots in terms of tree physiognomic, geographic, edaphic and climatic variables and identify any striking differences, 3. see if any of the above-mentioned variables can explain potential growth differences.

2. Materials and methods

2.1. Sampling procedure and collection of growth and site-specific data

Within the scope of the project for the conservation of *Z. abelicea* (www.abelitsia.gr), 31 plots (Fig. 1C-E) containing overbrowsed *Z. abelicea* individuals were fenced in twelve study areas throughout the whole distribution range of the species (Fig. 2 and see also Table 4). Plots were located in 4 of the 5 mountain ranges containing *Z. abelicea* populations: Levka Ori, Mt. Kedros, Dikti and Thripti Mountains. No plot was established on Mt. Psiloritis due to lack of arrangements with local land users in the area where the sole *Z. abelicea* population of this mountain range is found. The plots were established in order to exclude caprine and ovine browsing and trampling and to allow regrowth and fruiting of *Z. abelicea* individuals, seedling establishment and development of a non-browsed plant community. Site selection for plotting was carried out with respect to several constraints or criteria, including arrangements with local land-users, accessibility, stand structure and topography. Therefore, the morphology, including the initial height, of *Z. abelicea* individuals was variable amongst sites as some plots included well-developed, arborescent trees, i.e. out of the reach of goats (>2 m of height, see Fazan et al., 2021 for details) already at the beginning of the experiment while others contained only overbrowsed, dwarfed *Z. abelicea* individuals. Plot size was also variable, ranging from 10 to 105 m^2 due to the above-mentioned constraints and therefore the number of trees per plot also varied (see also Fazan et al., 2021 for details). Plots were not fenced all at the same time, but gradually between 2014 and 2017, and monitored annually until 2020, leading to three to six years of data collection per plot (for details see Fazan et al., 2021). In every plot, for each *Z. abelicea* individual, the length of the longest shoot produced during the year and tree height were monitored from the time the fences were installed (T0), and thereafter every year (T1, T2, etc.) at the end of the growing season in October or November. Shoot length was not measured in T0. Growth parameters were measured with a centimeter measuring stick. Since plots were established gradually and not all during the same year, growth data are available for all plots only up to T3. Therefore, for the scope of this article, the sum of shoot lengths (hereafter called shoot elongation) from T1 to T3 and the height difference (hereafter called height increase) between T0 and T3 were computed for each *Z. abelicea* individual and averaged over each plot. We found interesting to include both shoot elongation and height increase in our further analyses due to the

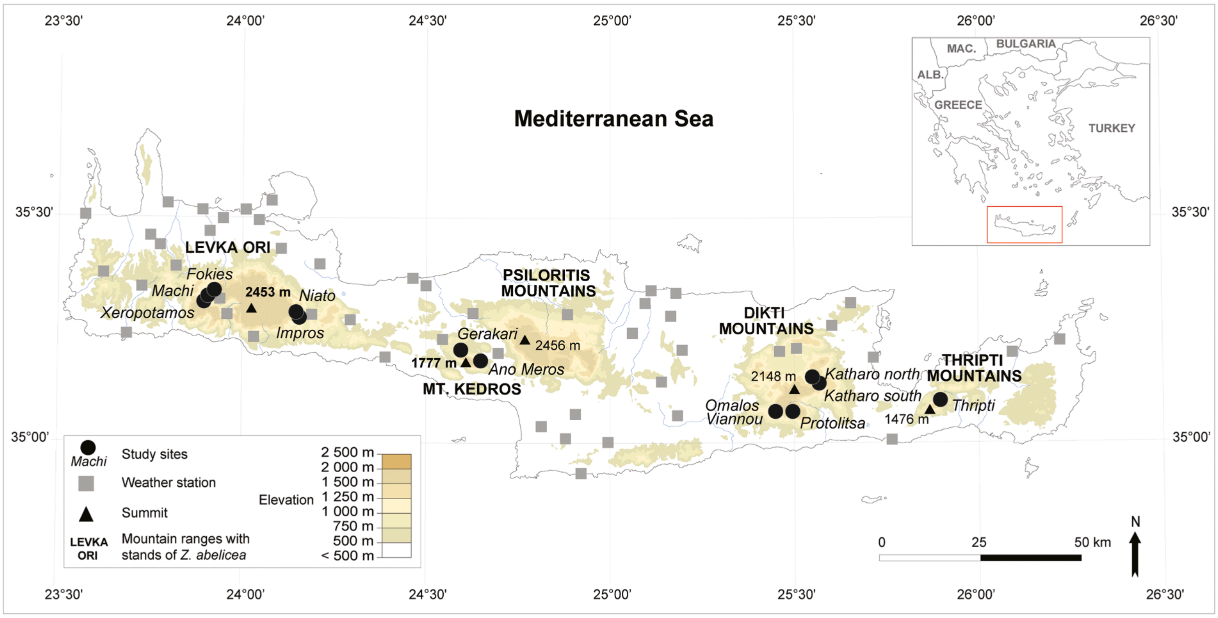

Fig. 2. Location of the 12 study sites (black circles) in which the 31 studied plots are situated, and of the 49 weather stations (grey squares) used for the weather interpolation on the island of Crete (Greece).

Table 1
Average shoot elongation between T1 and T3, height increase between T0 and T3 and average tree height at T0 for each plot. Mean average values for each mountain range are also given. Asterisks (*) indicate plots with disturbance. Mountain averages are computed only on non-disturbed plots for shoot elongation and height increase. The number of trees per plot is also given as well as the sum of trees for all plots per mountain. NA: missing or incomplete data.

Mountain	Plot	Shoot elongation (cm)	Height increase (cm)	Height at T0 (cm)	Nb of trees
Levka Ori	*XER1	85.00	NA	143.00	2
	*XER2	NA	NA	92.38	8
	*XER3	NA	NA	91.89	9
	KAL1	128.00	67.57	126.21	14
	KAL2	144.29	71.71	126.43	7
	*POR1	85.35	38.38	54.92	13
	POR2	80.29	48.29	61.57	7
	NIA1	44.77	26.00	116.33	3
	NIA2	87.20	50.40	117.60	5
	NIA3	67.83	30.75	158.25	4
	NIA4	84.33	80.67	100.67	3
	IMB1	26.87	11.26	36.81	31
	IMB2	78.38	52.00	75.63	8
	IMB3	84.27	62.64	58.91	11
	Average/sum	82.62	50.13	97.19	125
Kedros	GER1	94.11	58.11	117.67	9
	*GER2	NA	5.20	168.40	5
	*ANME1	NA	0.00	175.00	1
	ANME2	65.14	29.14	176.57	7
	Average	79.63	43.63	159.41	22
Dikti	VIAN1	70.58	56.00	147.50	4
	VIAN2	51.80	27.60	77.90	10
	VIAN3	20.26	13.30	51.30	10
	PROT1	44.64	23.64	99.18	11
	PROT2	27.95	11.13	66.20	15
	PROT3	34.17	19.67	72.50	6
	KATH1	20.43	13.00	111.36	14
	KATH2	43.58	25.29	84.79	28
	*KATH3	51.29	26.86	70.29	7
	KATH4	56.67	40.83	146.00	6
	Average	41.12	25.61	92.70	111
Thripti	THR1	44.84	26.95	63.68	19
	THR2	22.66	10.55	38.84	31
	THR3	40.80	19.72	37.68	25
	Average	36.10	19.07	46.73	75

Table 2
Results of the Wilcoxon rank sum test with continuity correction showing the significance of differences in shoot elongation (upper right panel) and height increase (lower left panel) between mountain ranges for undisturbed plots. Significant ($p < 0.05$) values are given in bold.

		Shoot elongation			
Height increase		Levka Ori	Kedros	Dikti	Thripti
	Levka Ori	–	0.35	**< 0.001**	**< 0.001**
	Kedros	0.66	–	**< 0.001**	**< 0.001**
	Dikti	**< 0.001**	**0.03**	–	0.33
	Thripti	**< 0.001**	**0.009**	0.05	–

Table 3
Results of the Wilcoxon rank sum test with continuity correction showing the significance of differences in height at T0 between mountain ranges for all plots. Significant ($p < 0.05$) values are given in bold.

	Levka Ori	Kedros	Dikti	Thripti
Levka Ori	–	**< 0.005**	0.14	**< 0.005**
Kedros	–	–	**< 0.005**	**< 0.005**
Dikti	–	–	–	**< 0.005**
Thripti	–	–	–	–

Table 4
Geographical characteristics of the fenced plots distributed in twelve localities. No aspect is given for NIA plots due to the fact that they were situated on completely flat ground. DD: decimal degrees.

Mountain	Locality	Plot	Latitude (DD)	Longitude (DD)	Altitude (m a.s.l.)	Aspect (°N)	Slope (°)	Heat load
Levka Ori	Xeropotamos	XER1	35.31	23.90	1270	25	9	2.46
		XER2	35.31	23.90	1220	35	17	2.22
		XER3	35.31	23.90	1243	35	10	2.43
	Machi	KAL1	35.32	23.92	1171	306	15	2.63
		KAL2	35.32	23.92	1195	235	22	2.96
	Fokies	POR1	35.35	23.93	1071	40	27	1.93
		POR2	35.34	23.93	1140	50	23	2.04
	Niato	NIA1	35.29	24.15	1220	–	0	2.71
		NIA2	35.29	24.15	1219	–	0	2.71
		NIA3	35.29	24.15	1211	–	0	2.71
		NIA4	35.29	24.15	1221	–	0	2.71
	Impros	IMB1	35.27	24.15	1178	85	13	2.39
		IMB2	35.27	24.15	1172	161	14	2.73
		IMB3	35.27	24.15	1178	350	5	2.62
Kedros	Gerakari	GER1	35.19	24.61	1255	190	23	2.88
		GER2	35.19	24.61	1257	358	25	2.12
	Ano Meros	ANME1	35.19	24.64	998	37	5	2.57
		ANME2	35.19	24.64	986	42	10	2.43
Dikti	Omalos Viannou	VIAN1	35.06	25.47	1324	130	10	2.62
		VIAN2	35.06	25.47	1327	135	9	2.65
		VIAN3	35.06	25.47	1309	191	6	2.79
	Protolitsa	PROT1	35.07	25.51	1637	201	37	2.90
		PROT2	35.07	25.51	1619	195	25	2.91
		PROT3	35.06	25.51	1593	237	23	2.97
	Katharo north	KATH1	35.17	25.54	1177	317	8	2.65
		KATH2	35.17	25.54	1201	252	8	2.82
	Katharo south	KATH3	35.13	25.57	1149	315	17	2.55
		KATH4	35.12	25.57	1153	344	7	2.59
Thripti	Thripti	THR1	35.08	25.89	1152	237	2	2.75
		THR2	35.08	25.89	1152	300	1	2.72
		THR3	35.08	25.89	1155	170	6	2.76

fact that growth in *Zelkova* species occurs following the Troll model (Hallé et al., 1978) with a sympodial and acrotone ramification (Garfì, 1997b) and therefore, maximum growth is not necessarily captured in height increases. In addition, initial tree height (at T0) was also averaged over each plot.

The destruction of fences through human-led or nature-induced events with subsequent browsing occurred in seven plots (XER1, XER2, XER3, POR1, GER2, ANME1, KATH3) at different times. Such plots were excluded from further analyses unless mentioned otherwise. Moreover, for some trees, measurements were missing for one or several years, either because the individual was erroneously not measured, not noticed or died at some point. Such trees were also excluded from further analyses. Therefore, a total of 288 trees with full records between T0 and T3 from 24 fenced undisturbed plots were analyzed. On average, 11 *Z. abelicea* individuals with full records were growing in the plots, but with a wide range between one and 31 trees (Table 1).

For each plot, geographical position (latitude and longitude), altitude, slope and aspect were recorded on the field. In addition, heat load, a unitless index, was computed based on latitude, slope and aspect, following the protocol described by McCune and Keon (2002) in order to get an estimation of how much heat each plot receives. Aspect was shifted by 45° so that southwest slopes have the highest heat load values and northeast slopes have the lowest heat load values (instead of southern, respectively northern oriented slopes, see McCune and Keon, 2002 for details).

2.2. Soil data

Surface soil samples were collected from the upper 35 cm of soil in each of the 31 fenced plots, in spring 2019. The samples were air-dried, ground to pass a 2 mm sieve and analyzed for selected physical and chemical properties. Soil particle size was analyzed following the methods described by Bouyoucos (1962). The relative proportion (%) of sand, silt and clay was used to classify samples into one of 12 soil texture classes following the USDA classification (Soil Science Division Staff, 2017 and see Fig. S3 for more details). PH was measured in a soil/water suspension at a 1:2 ratio, the proportion of organic matter was determined with the wet oxidation method (Walkley and Black, 1934), and electrical conductivity as measured in the saturation paste extract (Rhoades, 1996).

For the available forms of nutrients, nitrate nitrogen NO_3-N was extracted with 1 M potassium chloride. Phosphorus (P) was extracted by 0.5 M sodium bicarbonate (pH 8.5). Phosphorus was then quantitatively determined following the molybdenum blue-ascorbic acid method (Olsen and Sommers, 1982) and determined with Vis-UV spectrophotometry. Exchangeable cations potassium (K) and magnesium (Mg) were extracted with 1 M ammonium acetate (pH 7) (Thomas, 1982) and analyzed by the inductively coupled plasma method (ICP-OES). For trace element determination, the four metals: iron (Fe), copper (Cu), zinc (Zn) and manganese (Mn) were extracted with the DTPA method developed by Lindsay and Norvell (1978) and boron (B) was extracted with the hot water method (Keren, 1996). The soil texture diagram was done in R (version 4.0.2, R Core Team, 2021) with the package soiltexture (Moeys, 2018).

2.3. Interpolated weather data

Weather data (i.e. minimum, maximum and mean daily temperature and total daily precipitation) from October 2014 to September 2020 were uploaded from the 49 Cretan weather stations that had available data for that period, provided by the Environmental Research Institute of the National Observatory of Athens (Lagouvardos et al., 2017) and available online (meteosearch.meteo.gr; and see also Table S1 and Fig. 2). Some stations showed incomplete or missing data for some hours or days and for some variables. In all cases, incomplete or missing values were replaced by “NA” for the full concerned time period. In order to have an estimation of temperature and precipitation at the fenced plots, interpolation was carried out in R using package meteoland (De Cáceres et al., 2018; De Cáceres and Granda, 2021). This package allowed interpolation of the daily station weather data based on the latitudinal, longitudinal and altitudinal position of sites, by taking into account minimum and maximum temperature and precipitation records from nearby known weather stations. The following variables were interpolated: daily mean, maximum and minimum temperature and precipitation sum. Prior to interpolation, optimal parameters α (Gaussian shape parameter) and N (number of stations) were determined for minimum and maximum temperature, precipitation occurrence and precipitation amount (see De Cáceres et al., 2018 and De Cáceres and Granda, 2021 for details). For minimum and maximum temperature, optimal α was 0.5 and N was 49. For precipitation occurrence optimal α was 2.5 and N was 3. For precipitation amount, optimal α was 0.5 and N was 49, showing that all available stations needed to be included in the model in order to best predict precipitation amounts. However, considering the importance of local topographical features, the scarcity of weather stations in some areas and the presumable existence of a longitudinal gradient in precipitation (see e.g. Agou et al., 2019; Goedecke and Bergmeier, 2018; Varouchakis et al., 2018; Vrochidou and Tsanis, 2012), we decided to define N as 10. This way, only the 10 closest weather stations are used to estimate precipitation amounts in a given site (for the sake of comparison, cross validation statistics for the original optimal $N = 49$ can be found in Table S2). Evaluation of the prediction errors for all meteorological variables was carried out by leave-one-out cross validation. The performance of each variable was assessed using mean absolute error (MAE), bias and Pearson’s correlation coefficient (De Cáceres et al., 2018; De Cáceres and Granda, 2021). Interpolations were carried out for each of the 31 fenced plots over the above-mentioned period. The interpolated daily data was then averaged first monthly for mean, minimum and maximum temperature and then annually, or for precipitation first summed monthly and then annually for each fenced plot. Once monthly (for precipitation) or annual (for both precipitation and temperature variables) data were obtained, they were averaged once again over the full period from October 2014 to September 2020, in order to get a single monthly or annual value for every variable.

2.4. Statistical analyses

All statistical analyses were carried out in R. Kruskal-Wallis rank sum tests (kruskal.test, Hollander and Wolfe, 1973) were carried out on the 24 non-disturbed fenced plots in order to look for statistically significant differences in total shoot elongation, total height increase as well as tree height at T0 amongst plots. Pairwise Wilcoxon rank sum tests with continuity correction (pairwise.wilcox.test, package stats, R Core Team, 2021) were carried out on non-disturbed fenced plots to check for and assess significant differences in shoot elongation and height increase, and on all plots to assess significant differences in height at T0 among mountain ranges. In addition, correlations between *Z. abelicea* shoot elongation, height increase and initial tree height were computed with Spearman’s rho (cor.test, package stats, R Core Team, 2021) correlation coefficient.

Principal component analysis (Borcard et al., 2011) was carried out using function rda from package vegan (Oksanen et al., 2019) on the 24 non-disturbed fenced plots separately for the geographic variables (longitude, latitude, altitude, slope, heat load), soil variables (pH, organic matter, electrical conductivity, NO_3-N, P, K, Mg, Fe, Mn, Zn, Cu and B) and interpolated weather data (16 variables: interpolated averaged minimum, mean and maximum annual temperature, averaged sum of annual precipitation and monthly previous October to current September averaged total precipitation) in order to investigate and visualize the different variables and main trends in the data.

In order to see which variables could possibly explain the spatial variation in *Z. abelicea* growth, redundancy analysis (Borcard et al., 2011) was carried out on the 24 non-disturbed fenced plots using function rda from package vegan (Oksanen et al., 2019). Response variables were *Z. abelicea* height increase from T0-T3 and shoot elongation from T1-T3. The variables included in the geographic, soil and interpolated weather datasets described above for principal component analysis were here included as three separate explanatory datasets. In addition, average tree height at T0 was included as a fourth dataset to represent tree physiognomy.

Due to the high number of variables and the occurrence of several separate datasets (i.e. geographic variables, interpolated climatic variables, soil variables and initial tree height), four separate redundancy analyses were carried out on each of the datasets in order to check for significance of each dataset and remove highly collinear variables within a dataset and reduce variable number.

Prior to analysis, response and explanatory variables were standardized to zero mean and unit variance using function decostand (package vegan, Oksanen et al., 2019). Permutation tests were carried out (anova.cca, package vegan, Oksanen et al., 2019) to test the significance ($p < 0.05$) of each of the four redundancy analysis results as well as the canonical axes, with 1000 permutations. Linear dependencies amongst explanatory variables were checked through variance inflation factors (VIFs, vif.cca, package vegan, Oksanen et al., 2019). For datasets that had variables with VIFs above 10, forward selection was performed (forward.sel, package adespatial, Dray et al., 2020). The adjusted R^2 (RsquareAdj, package vegan, Oksanen et al., 2019) of the model containing all potential variables of the dataset was used as a stopping criterion. Through these analyses, a reduced number of variables within the four datasets were found to be significant and were included in the final redundancy analysis. This time, we computed a partial redundancy analysis (Borcard et al., 2011) where *Z. abelicea* growth is explained by the final selected climatic, geographic or soil variables, while at the same time holding initial tree height constant due to its known correlation with tree growth. The adjusted R^2 of the final redundancy analysis, as well as of each dataset alone or in relationship with one another were computed (varpart, package vegan, Oksanen et al., 2019, Borcard et al., 2011) in order to express the explained variance. Significance of the final model was tested again through permutations.

3. Results

3.1. Spatial growth differences

Total shoot elongation and total height increase for each fenced plot, as well as for every mountain are found in Fig. 3 and Table 1. On average, trees in the Levka Ori and Kedros grew two times more than trees from Dikti and Thripti. The Kruskal-Wallis rank sum test showed that significant differences in shoot elongation or height increase do exist (respectively X^2=202.31, df=23, $p < 0.001$; X^2=183.8, df=23, $p < 0.001$) between fenced plots. The pairwise Wilcoxon rank sum test showed in addition that trees from Levka Ori and Kedros have significantly ($p < 0.05$) higher growth (both for shoot elongation and height increase) than trees from Dikti or Thripti (Table 2). Trees from Levka Ori and Kedros showed similar growth in relation to each other, while trees from Dikti and Thripti also showed similar growth in relation to one another.

Tree height at T0 was also found to be significantly different between plots (X^2=139.63, df=23, $p < 0.005$), as well as between mountain ranges (Fig. 4 and Table 3). Trees sampled within the fenced plots on Mt. Kedros were significantly higher at T0 than trees in the three other mountain ranges. Trees in the Levka Ori and Dikti Mountains had a similar height at T0, while trees in the Thripti Mountains were significantly smaller than elsewhere. Furthermore, a positive correlation exists between tree height at T0 and shoot elongation (rho=0.50, $p < 0.001$) as well as for height increase (rho=0.41, $p < 0.001$), indicating that taller trees tend to have a higher growth rate than dwarfed trees, as was already previously pointed out by Fazan et al. (2021).

3.2. Geographical characteristics of plots

Geographical variables for each plot are reported in Table 4. The principal component analysis (Fig. S1) shows that the majority of

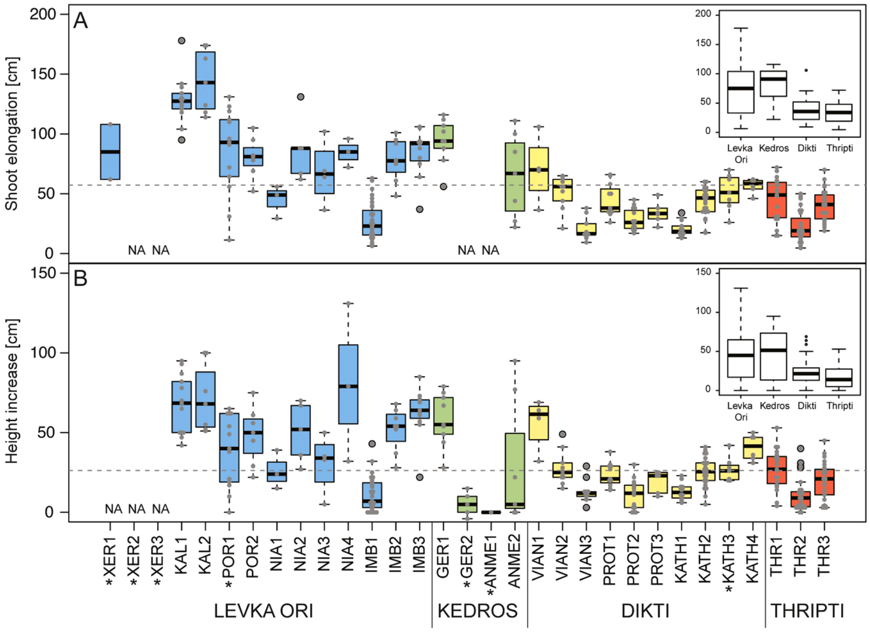

Fig. 3. A. Total shoot elongation from T1 to T3, B. Total height increase from T0 to T3, for each fenced plot. The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range, while values exceeding this threshold are considered as outliers and plotted as open circles. Individual trees per plot are represented by grey dots. The overall median (of undisturbed plots) is expressed by the grey dotted line. * indicate plots with disturbance. The miniatures show boxplots for each mountain range. Plots and mountains are ordered according to their geographical position, going from west to east. Colors show different mountains (blue: Levka Ori, green: Mt. Kedros, yellow: Dikti, red: Thripti).

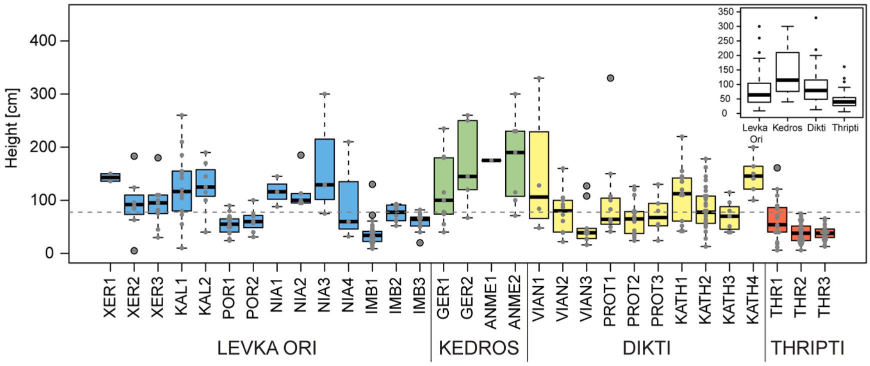

Fig. 4. Initial tree height at the time the fences were established (T0) for each fenced plot. The midlines of the boxplots show the median, the boxes show the 1st and 3rd quartiles and the whiskers extend up to 1.5 times the interquartile range, while values exceeding this threshold are considered as outliers and plotted as open circles. Individual trees per plot are represented by grey dots. The overall median of all plots is represented by the grey dotted line. The miniatures show boxplots for each mountain range. Plots and mountains are ordered according to their geographical position, going from west to east. Colors show different mountains (blue: Levka Ori, green: Mt. Kedros, yellow: Dikti, red: Thripti).

plots is clustered together but clearly organized following their geographical (latitude and longitude) position on the island. The first two axes explain 79% (52% and 27%, respectively) of the variance. Eastern sites are also situated more to the south compared to western plots. In addition, heat load is strongly linked with geographical position, with trees in eastern Crete having a higher heat load index compared to those in western Crete. Protolitsa plots (PROT1, PROT2, PROT3) stand out by their higher than elsewhere altitude.

3.3. Soil characteristics of plots

Soil variables for each plot are found in Table 5. The principal component analysis (Fig. S2) shows that most plots are clustered together and therefore show similarities for most of the pedological variables (Fig. S2A). The first two axes explain 54% (36% and 18%, respectively) of the variance. However, plots from Niato (NIA1, NIA2, NIA3, NIA4) and Thripti (THR1, THR2, THR3) stand out by their higher nutrient content, higher percentage of organic matter, higher electrical conductivity and lower pH than most other sites. Plots from Machi (KAL1, KAL2) and Xeropotamos (XER1, XER2, XER3) have higher P and Zn. Generally speaking, most (but not all) plots in western Crete have higher organic matter content than plots further east (with the exception of Thripti). Soil texture (Table 5 and Fig. S3) varied amongst plots, while some plots in the Levka Ori had a higher silt content than elsewhere, and some plots in Dikti had higher sand content than elsewhere. In addition, plots from Thripti were more homogenous with regards to their clay content compared to the other mountain ranges. The soils within the plots were classified as clay, clay loams, loams, sandy clay loams and sandy loams.

3.4. Weather variability

The performance of each interpolated variable is reported in Table 6. Mean absolute errors for predicted versus observed values were of 2.23 °C for daily minimum temperature and 1.64 °C for maximum temperature, with high correlation coefficients. Bias for minimum temperature was − 0.02 °C and for maximum temperature 0.01 °C. The prediction of temperature ranges resulted in a MAE of 2.25 °C, a correlation coefficient of 0.57 and a bias of 0.03 °C. MAE for annual station rainfall was 1405.93 mm, with a correlation coefficient of 0.66 and a bias of 97.83 mm. The principal component analysis (Fig. S4) showed a clear distinction between plots. The first axis mainly explains precipitation patterns, where plots from western Crete (Levka Ori) and Kedros stand out by their higher than elsewhere precipitation levels for most months, as well as for annual precipitation. Plots from Dikti show intermediate values, while plots from Thripti have lower than elsewhere precipitation. There is a difference between plots from the eastern and western Levka Ori. The eastern Levka Ori plots (Niato and Impros) show higher precipitation levels for all months than the western Levka Ori (Xeropotamos, Machi and Fokies) plots. The latter are more similar to what occurs on Mt. Kedros. In addition, plots from the western Levka Ori seem to have less abundant precipitation values for several months (i.e. October and December of the previous year and April and May of the current year), a pattern which is not visible in the eastern Levka Ori plots. The second axis represents mainly temperature gradients, with the high altitude Protolitsa plots (Mt. Dikti) showing lower than elsewhere temperature and a clear distinction between plots of Mt. Kedros, with the lower lying Ano Meros plots showing higher temperatures than the plots of Gerakari. Plots from eastern Crete seem to have overall lower annual temperatures than those of western Crete. The first two axes explain altogether 92% of the variance (62% and 30%, respectively).

3.5. Relationships between growth and explanatory variables

From the four initial datasets (geographic, physiognomic, soil and interpolated weather), the combined use of permutation tests and forward selection revealed that only longitude, precipitation in June and initial tree height were significant (Fig. 5), and only the

Table 5
Soil characteristics of each fenced plot. Org. mat: organic matter, Text. class: textural class, El. cond: electrical conductivity.

Plot	pH	Org. mat (%)	Texture (%)			Text. class	El. cond (mS/cm)	Nutrients (mg/kg)								
			Sand	Silt	Clay			NO_3-N	P	K	Mg	Fe	Mn	Zn	Cu	B
XER1	7.90	6.50	45.30	44.00	10.70	loam	0.24	2.50	25.00	71.00	64.00	18.50	14.40	8.10	1.10	0.97
XER2	8.30	4.70	61.30	30.00	8.70	sandy loam	0.22	3.60	17.00	65.00	53.00	12.60	9.50	2.90	0.74	0.65
XER3	7.50	4.60	45.30	42.00	12.70	loam	0.41	5.50	12.00	79.00	73.00	16.80	19.10	2.00	0.86	0.70
KAL1	7.80	6.80	38.60	50.00	11.40	silt loam	0.28	4.80	7.00	77.00	88.40	21.80	32.10	5.40	1.40	0.77
KAL2	7.60	11.30	38.60	48.00	13.40	loam	0.18	5.00	9.00	123.00	153.00	17.80	21.40	2.10	2.10	0.91
POR1	7.60	2.30	10.60	32.00	57.40	clay	0.12	0.70	4.00	186.00	190.00	11.60	10.40	0.30	1.20	1.30
POR2	7.50	1.30	10.60	26.00	63.40	clay	0.13	1.10	4.00	165.00	404.00	9.50	12.70	0.38	1.10	0.61
NIA1	7.40	9.40	32.60	32.00	35.40	clay loam	0.12	2.60	7.00	212.00	990.00	21.70	30.20	3.60	1.80	1.00
NIA2	6.10	9.40	32.60	26.00	41.40	clay	0.36	24.00	7.00	264.00	427.00	30.90	58.90	2.20	1.80	0.94
NIA3	6.90	8.40	26.60	28.00	45.40	clay	0.70	4.80	6.00	374.00	807.00	31.90	43.80	2.80	1.90	0.60
NIA4	7.20	6.40	28.60	28.00	43.40	clay	0.48	3.10	5.00	161.00	810.00	25.00	21.90	2.00	2.00	0.74
IMB1	7.30	6.20	22.60	36.00	41.40	clay	0.21	3.40	5.00	194.00	143.00	15.80	54.40	1.30	2.30	0.69
IMB2	7.80	5.30	28.60	44.00	27.40	clay loam	0.26	10.10	6.00	155.00	90.40	13.40	26.30	2.10	1.50	0.87
IMB3	6.90	4.50	42.60	26.00	31.40	clay loam	0.12	12.00	5.00	126.00	102.00	15.60	42.90	0.63	1.00	0.68
ANME1	7.80	2.90	54.60	24.00	21.40	sandy clay loam	0.15	3.80	6.00	111.00	98.40	16.90	27.50	0.69	1.90	0.66
ANME2	8.10	3.10	34.60	30.00	35.40	clay loam	0.16	0.50	13.00	111.00	110.00	18.20	26.30	0.90	3.00	0.56
GER1	7.70	4.70	22.60	30.00	47.40	clay	0.24	5.60	8.00	269.00	224.00	21.00	50.60	1.40	4.00	0.79
GER2	7.90	1.30	4.60	36.00	59.40	clay	0.17	0.50	5.00	441.00	204.00	15.30	30.80	0.54	1.90	0.70
VIAN1	7.70	2.20	43.30	23.00	33.70	clay loam	0.23	3.50	4.00	154.00	98.70	11.90	17.10	0.75	2.60	0.47
VIAN2	7.90	4.40	37.30	26.00	36.70	clay loam	0.23	4.20	6.00	229.00	98.80	16.40	28.70	1.10	2.40	0.58
VIAN3	8.00	2.40	57.30	20.00	22.70	sandy clay loam	0.21	3.70	4.00	117.00	110.00	11.70	15.90	0.58	1.20	0.45
PROT1	7.90	6.40	47.30	28.00	24.70	sandy clay loam	0.30	9.40	9.00	226.00	158.00	12.90	14.90	0.74	1.20	0.69
PROT2	7.60	4.30	37.30	28.00	34.70	clay loam	0.17	6.70	6.00	176.00	202.00	15.40	24.90	0.89	2.50	0.72
PROT3	7.60	3.80	23.30	32.00	44.70	clay	0.19	6.80	5.00	309.00	309.00	13.10	25.30	0.58	2.60	0.79
KATH1	7.60	1.90	13.30	22.00	64.70	clay	0.15	3.70	4.00	150.00	303.00	8.00	12.40	0.31	0.50	0.58
KATH2	7.30	2.80	19.30	24.00	56.70	clay	0.10	2.50	4.00	197.00	316.00	10.40	27.10	0.62	0.66	0.60
KATH3	7.90	1.40	71.30	16.00	12.70	sandy loam	0.12	3.50	5.00	46.70	128.00	13.80	4.50	0.17	1.50	0.46
KATH4	7.70	2.10	65.30	18.00	16.70	sandy loam	0.18	1.70	3.00	74.80	119.00	19.00	6.10	0.30	1.20	0.52
THR1	6.50	5.70	18.60	28.00	53.40	clay	0.13	5.70	8.00	401.00	526.00	26.00	54.40	2.60	2.00	1.10
THR2	7.40	6.70	32.60	22.00	45.40	clay	0.25	3.70	7.00	544.00	968.00	11.60	39.40	4.50	1.30	1.50
THR3	7.20	3.90	18.60	30.00	51.40	clay	0.15	0.50	10.00	313.00	571.00	15.90	40.00	1.70	2.20	0.92

Table 6
Leave-one-out cross validation statistics for the interpolation procedure for the 49 weather stations with available data for the period October 2014 to September 2020. n: number of stations or number of days, r: linear correlation coefficient, MAE: mean absolute error. SD stations: standard deviation of MAE across stations, SD days: standard deviation of MAE across days. Date rainfall: sum of precipitation across stations for each date. Date precipitation stations: number of stations with precipitation events for each date.

Variable	n	r	MAE			Bias		
			Value	SD stations	SD days	Value	SD stations	SD days
Minimum temperature (°C)	84991	0.90	2.23	0.97	0.42	-0.02	2.28	0.07
Maximum temperature (°C)	84972	0.95	1.64	0.83	0.32	0.01	1.56	0.06
Temperature range (°C)	84969	0.57	2.25	1.06	0.67	0.03	2.21	0.09
Station annual rainfall ($mm \cdot yr^{-1}$)	49	0.67	1359.23	1304.88	NA	-4.62	1894.38	NA
Station precipitation days	49	0.47	92.00	80.91	NA	-9.39	122.78	NA
Date rainfall (mm)	1429	0.99	9.44	NA	22.89	-0.12	NA	24.76
Date precipitation stations	1429	0.99	1.15	NA	1.26	-0.21	NA	1.69

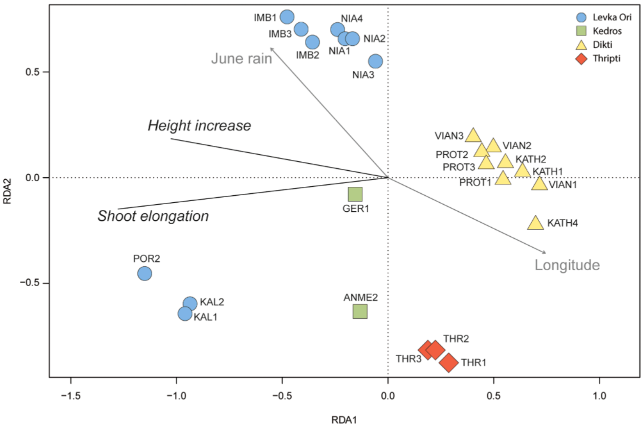

Fig. 5. Partial redundancy analysis correlation triplot of tree growth (shoot elongation and height increase) in the 24 non-disturbed *Z. abelicea* fenced plots explained by geographic (longitude) and climatic (June rain) variables when considering initial tree height as constant. Projecting a plot at right angle on a variable approximates the value of the plot along that variable. Distances amongst plots are not approximations of their Euclidean distance. Plots are distinguished by mountain range through different colors and symbols (blue circle: Levka Ori, green square: Kedros, yellow triangle: Dikti, red diamond: Thripti). Scaling 2 was applied which means that projecting a plot at right angle on a response or explanatory variable approximates the value of the plot along the variable. The angles between response and explanatory variables and between response variables themselves or explanatory variables themselves reflect their correlations (Borcard et al., 2011).

first constrained axis was significant (Table S3). None of the soil variables was found to be significant in the initial redundancy analysis and therefore none were kept for further analyses. The final redundancy analysis explained 52% (adjusted R^2) of the variation in *Z. abelicea* growth. Longitude alone explained 22%, June rain explained 7%, while initial tree height explained 5% (Fig. 6).

4. Discussion

4.1. Size, habit and growth patterns

When protected from browsing, *Z. abelicea* trees were found by Fazan et al. (2021) to grow on average twice as much as their overbrowsed counterparts. Here we revealed in addition a clear difference in both shoot elongation and height increase according to the location of the trees. Both shoot elongation and height increase of protected from browsing *Z. abelicea* individuals from western (Lekva Ori) and central (Mt. Kedros) mountains of Crete was significantly higher, on average two times more, than their eastern (Dikti and Thripti) counterparts.

Our analyses revealed that initial tree height was strongly and significantly positively correlated with both shoot elongation and height increase, as was already shown by Fazan et al. (2021), and that some differences occurred between mountain ranges, with Kedros having significantly taller trees than elsewhere and Thripti having significantly smaller trees. Some of these height variations are most probably related to the sampling procedure (i.e. which trees were fenced), but also to differences in population structure (Kozlowski et al., 2014). Indeed, *Z. abelicea* population structure shows differences amongst sites, with some sites, such as Thripti composed only of dwarfed overbrowsed individuals, whereas other sites have both dwarfed and normal growing trees, in varying proportions (Kozlowski et al., 2014).

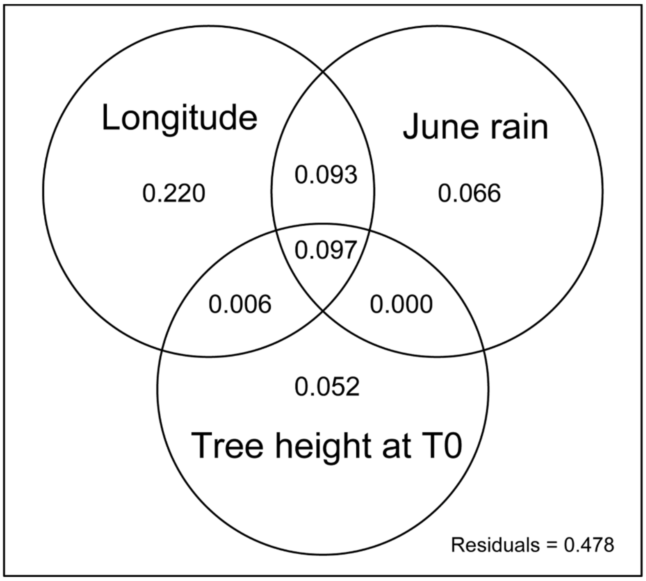

Fig. 6. Variation partitioning of the three different explanatory datasets (physiognomic, geographic and climatic), each containing in our case only one variable (Tree height at T0, longitude and precipitation in June) that were included in the final redundancy analysis. Values represent the adjusted R^2 for each part. The total amount of variation in *Z. abelicea* growth explained by the model is 52%. The intersection between circles shows the part of variation that is explained conjointly by two or more datasets.

4.2. *The role of geography*

Plots containing *Z. abelicea* trees are distributed along a longitudinal as well as latitudinal gradient, due to the geographical position of Crete and its mountains (Fig. 2 and Fig. S1). Therefore, plots in western Crete are situated more to the northwest, those in central Crete are intermediate and those in eastern Crete have a more southeast position. Heat load was found to be higher in the eastern plots compared to the western plots. This could be linked with the fact that eastern plots are located at a slightly lower latitude than western plots. However, the latitudinal difference between the northernmost and southernmost plot is very small and amounts only to 0.29'. Therefore, our finding is most probably linked to the fact that the majority of the investigated plots in eastern Crete have a more southerly aspect than western plots, which means higher heat load values. The three Protolitsa and the three Omalos Viannou plots are indeed located on south facing slopes. However, it cannot be generalized that *Z. abelicea* trees in eastern Crete grow in majority on south-facing slopes since this feature relies strongly on the sampling procedure. To our knowledge, trees situated on north-facing slopes also occur in eastern Crete but were coincidently only rarely sampled in this study. Indeed, Goedecke and Bergmeier (2018), who analysed more records of *Z. abelicea* than those included in the present study, did not find any differences between western and eastern Crete for heat load. In any case, the differences found for heat load in the present article were not significant in explaining growth differences between western and eastern *Z. abelicea* plots.

4.3. *Soil properties*

In this study, we provide information about soil physical and chemical properties and soil nutrient content throughout the range of *Z. abelicea* (with the exception of the population on Mt. Psiloritis) for the first time. Egli (1993) had previously studied in depth the soil characteristics of dolines of Crete, some of which hosted *Z. abelicea* trees, but he did not analyse the nutrient content of soil samples, nor did he consider the *Z. abelicea* sites located on slopes. In our study, soil parameters did not show any striking differences in terms of chemical composition or texture amongst plots. Indeed, most of the plots are clustered in Fig. S2A, showing relatively similar features. However, we did find that plots of Thripti and Niato tend to have a higher nutrient content, higher organic matter content, higher electrical conductivity and lower pH than other plots. These plots have the particularity of being the only sampled plots that are situated in flat karstic poljes or dolines floors (for a precise definition of terms dealing with karstic landscapes, see Egli 1993), at the foot of slopes. All other plots are situated on more or less steep, sometimes terraced, slopes. Dolines are known to receive more nutrients and be moister than slopes (Bátori et al., 2017), through the accumulation of eroded material and runoff. Similarly to what we found in our study, Filibeck et al. (2019) found a positive correlation between slope and pH, with doline bottoms and the foot of slopes having lower pH values than slopes. Steep slopes often have thin soils, little soil accumulation and have surfacing or outcropping limestone, which has a higher pH value (Filibeck et al., 2019). Dolines on Crete are known to have deeper soils with a higher proportion of organic matter compared to adjacent sloped areas (Vogiatzakis et al., 2003). More generally speaking, doline soil in the Mediterranean is often more acidic than slopes, through the accumulation of clay rich, decarbonated soil and wind-blown siliceous material (e.g. Saharan dust) (Filibeck et al., 2019). In addition, plots from the Levka Ori showed slightly higher organic content than plots elsewhere, and the plots from Omalos show higher P and Zn content. Several sites from western Crete seem to have higher silt content than elsewhere, whereas those of Thripti are more homogeneous in terms of clay content. These trends could be linked to differences in the parent material, bedrock, land use or sample selection. However, none of the soil parameters was found to be significant in explaining growth differences amongst *Z. abelicea* trees and further investigations should be undertaken to investigate more these points.

4.4. Weather data variability and climatic patterns

The interpolated weather data allowed a clear distinction between plots according to the rainfall and temperature patterns of nearby weather stations. The model gives a rather precise estimation of temperature. However, results are less precise when it comes to estimating precipitation quantities, and the model gave larger errors. This is most probably imputable to several factors. Firstly, Crete possesses a highly complex topography, which strongly modulates precipitation regimes and places that will receive or not rain. Rainfall is known to be highly variable according to orographic factors, continentality (i.e. distance from the coastline), direction of prevailing winds, topography and aspect (Naoum and Tsanis, 2003). Secondly, the network of weather stations used in this study is rather scanty in some areas (e.g. eastern Crete) and absent from the mountainous areas between 900 and 1800 m a.s.l. where *Z. abelicea* grows. Indeed, only one station is located above 900 m a.s.l., while the median altitude of weather stations used in this study currently lies at 170 m a.s.l. Finally, the model used for interpolation of temperature and precipitation data allows for a correction for altitude only (De Cáceres and Granda, 2021). This explains why plots from Protolitsa (higher altitude than all other plots) stand out (Fig. S4). Indeed, precipitation is known from Crete, and more generally, to increase with rising altitude (e.g. Agou et al., 2019; Naoum and Tsanis, 2003; Varouchakis et al., 2018; Vrochidou and Tsanis, 2012). However, differences in precipitation from windward, north-facing slopes versus leeward, south-facing slopes of Crete have been previously described (Naoum and Tsanis, 2003). Unfortunately, the model used in our study is not complex enough to also include corrections for topography or lee-side effects.

A west to east decreasing precipitation pattern has been highlighted for Crete in general (Agou et al., 2019; Varouchakis et al., 2018; Vrochidou and Tsanis, 2012) as well as along the distribution range of *Z. abelicea* sites, with also an increase in temperature seasonality (Goedecke and Bergmeier, 2018). In our study, when we used the optimal number (according to the model) of 49 stations (i.e. all of the stations with available data for Crete for the concerned period) for the interpolation of precipitation amount, such a trend did not stand out. However, when we limited the number of weather stations to be taken into account for the interpolation of precipitation amount to the closest 10 weather stations (and we could discuss if 10 is already too much, considering the lack of stations situated in the mountainous areas as well as in eastern Crete), such a regional trend became visible (Fig. S4). Indeed, rainfall in most months, as well as annual rainfall were mostly distributed along the first axis of the principal component analysis which mirrors quite well the longitudinal position of the different mountain ranges and the general climatic patterns of the island and shows that the plots in the Levka Ori and Mt. Kedros receive more rain than those from Dikti and Thripti. Minimum, maximum and mean temperature varied instead along the second axis, which was more reflective of the altitudinal distribution of the plots. Our analysis allowed to distinguish well between mountain ranges. However, it is less precise when looking at data within a single mountain range. For example, a striking difference in precipitation records is found in the principal component analysis between plots situated in the western Levka Ori (Fokies, Machi and Xeropotamos) compared to those situated in the eastern Levka Ori (Impros and Niato) which seem to receive a lot more rain than the former. This is mainly due to their geographical proximity, albeit not on the same mountain side and therefore perhaps not being under the same precipitation regime, with a weather station situated at 715 m a.s.l. which shows one of the highest precipitation records of Crete. Therefore, due to the highly complex topography of the mountains, lee-side effects and the scarcity of weather stations in the mountains from the dataset used in this study, we think that at present there is too much uncertainty to assess with certainty and precision the precipitation variability within a given mountain range.

4.5. Major drivers of Zelkova abelicea growth

Although we investigated a fair amount of geographic, physiognomic, edaphic and climatic variables, only few revealed influential in explaining growth differences in *Z. abelicea.* None of the edaphic variables revealed significant in discriminating between *Z. abelicea* growth, showing that although some variability in soil conditions was observed, soil composition does not seem to play a crucial role in influencing *Z. abelicea* growth. Only longitude and rainfall in June, when keeping initial tree height constant, revealed significant in explaining differences in tree growth between plots (Fig. 4). 52% of the variation in the data was explained by the model, while longitude alone, or more generally speaking geographical position on the island since the plots are situated on a west to east line, was the variable which explained the highest proportion of variation (22%). June precipitation explained 7% of the variation in the data while the union of June precipitation and longitude explained a further 9%, pointing towards the fact that both variables explain partly the same structures (i.e. tree growth variations) and that both are correlated.

In Crete, as for most of the Mediterranean region, a large part of precipitation falls during the winter months, with low to null rainfall during the summer season (Agou et al., 2019; Koutroulis et al., 2010, 2013), while only 20% of precipitation is estimated to fall during the springtime (Koutroulis et al., 2013). *Zelkova abelicea* as well as its Sicilian relative, *Z. sicula* Di Pasquale, Garfì & Quézel, seem to not be able to fully exploit the abundant winter precipitation. In fact, during the winter, the deciduous *Zelkova* trees are dormant, and thus most of the winter rainfall is ineffective to growth as it is lost to runoff, infiltrated too deep, or evaporated by the time the trees come out of winter dormancy (Garfì, 1997a; Fazan et al., 2017). Therefore, late spring and early summer precipitation and temperature have been proven to be crucial for the growth of both *Z. abelicea* (Fazan et al., 2017) and *Z. sicula* (Garfì, 1997a). Actually, spring or summer precipitation and temperature are critical for determining growth in the Mediterranean context before the onset of the summer drought period and consequent growth reduction or cessation. Many dendrochronological investigations (e.g. Tessier et al., 1994, Hughes et al., 2001, Cherubini et al., 2003, Griggs et al., 2007, Campelo et al., 2009, Di Filippo et al., 2010, Nijland et al., 2011, Lebourgeois et al., 2012, Touchan et al., 2014, Papadopoulos, 2016, Fyllas et al., 2017) have shown that the growth of several other Mediterranean tree species is correlated positively with late spring or summer water availability and precipitation or negatively with temperature.

Initial tree height was responsible for explaining 5% of the variation found in tree growth but did not co-vary with longitude or June precipitation (0.6%, respectively 0%). Indeed, no longitudinal trend was found in initial tree height. However, significant differences did occur between mountain ranges. The fact that trees from Mt. Kedros are significantly taller than elsewhere, is most probably related to the sampling procedure (i.e. only 4 plots were sampled there and all had an average initial tree height above 100 cm) but it cannot be excluded that this pattern could also be related to differences in browsing pressure and browsing history. Trees from Dikti and Levka Ori displayed a similar height pattern, and both had plots showing a wide variety of initial tree heights (Table 1). Trees from Thripti, however, had significantly smaller initial tree heights than plots from all other mountain ranges. This is consistent with the findings of Kozlowski et al. (2014) who recorded no tall, well-developed trees in Thripti. The fact that trees from Thripti are confirmed to be smaller than elsewhere could be related to climatic constraints on the growth of this easternmost *Z. abelicea* population, as previously mentioned also for shoot elongation.

The fact that longitude was the variable that explained the highest proportion of variance, and not one of the climatic, edaphic or physiognomic variables shows that we were not able to find exactly which variable(s) explain(s) the observed differences in *Z. abelicea* growth between mountain ranges. Precipitation in specific months seem to be a good candidate, as shown above, although longer records and a less scanty network of weather stations would be needed to further investigate this point. Finally, we cannot rule out the roles of genetic variation, browsing history and browsing patterns in influencing *Z. abelicea* growth. Indeed, Christe et al. (2014) showed that *Z. abelicea* trees were genetically different on each mountain range. Although browsing history and patterns were never analyzed for *Z. abelicea* sites, several authors have shown the influence of land use or browsing history on tree growth or stand structure in the Mediterranean (e.g. Chauchard et al., 2007, Cierjacks and Hensen, 2004, Linares et al., 2010, Plieninger, 2007). Therefore, growth patterns may also be determined or influenced by the genetic background of the trees as well as the browsing history and patterns of the different sites.

4.6. Implications for conservation and outlook

When browsing is removed, *Z. abelicea* trees of the Levka Ori and Mt. Kedros grow more than trees from Dikti and Thripti. The former are able to grow on average twice as much in the same amount of time than the latter, and therefore it will take them on average half the time of the latter to grow out of the reach of goats. Some discrepancies do exist amongst plots within a mountain range (e.g. NIA1 and IMB1 plots have very low growth in comparison with all the other Levka Ori plots), which can probably be explained by local site specificities, differences in former land-use management or genetic factors. Nevertheless, the fact that trees from eastern Crete grow at lower rates is important to consider when planning and implementing conservation actions.

In addition, no study has yet investigated why Thripti is currently devoid of fruiting individuals (see also Kozlowski et al., 2014) while they are present in varying amounts in most other sites further west. One could hypothesize that this could be due to the presence of younger, i.e. not yet mature, *Z. abelicea* individuals than elsewhere, which could also be supported by the fact that this population was only discovered by the scientific community during the second half of the 20th century (Kozlowski et al., 2014). However, such an assumption seems unsubstantiated as Christe et al. (2014) show an ancient colonization of Crete by *Z. abelicea,* also in eastern Crete, occurring already before the early Miocene, as well as an absence of effective gene flow mediated by seeds between mountain ranges perhaps already since the Miocene. The remoteness of the site and the rarity of *Z. abelicea* individuals in that area probably explains why the population was discovered only recently. Goedecke and Bergmeier (2018) hypothesize that a gradient of less favourable climatic conditions from west to east explains why populations may be more scattered with a higher proportion of dwarfed trees more to the east. Our results go in that direction by showing that precipitation patterns, and more precisely the seemingly critical precipitation of the month of June decrease eastwards and are the lowest in Thripti, hence affecting the growth rate, the maximum potential size and sexual reproductive ability of trees, in addition to the omnipresent browsing pressure. Therefore, the absence of well-developed, large and/or fruiting individuals (at present) in Thripti can mainly be imputable to constraining environmental conditions and not to higher than elsewhere browsing patterns. For conservation reasons, it is important to assess if it is possible under current (and future) climatic conditions to have sexually reproducing individuals in Thripti, as well as if they once existed in the past. Although it is more than the scope of the current study to answer the first question, Christe et al. (2014) give some clues to answer the second. Indeed, they found high levels of variability in chloroplast markers for each studied population, including Thripti, which indicates that the population is composed of several distinctly genetically different individuals. Such a diversity must have arisen through sexual propagation and not from vegetative, genetically uniform, root suckers, which the species is able to produce profusely (Egli, 1997; Fazan et al., 2012; Kozlowski et al., 2012; Søndergaard and Egli, 2006). This assumption indeed, is consistent with the behaviour of the congeneric *Z. sicula* on Sicily, in which fruiting was observed for the first time even on dwarfed trees, constrained strongly by climatic factors in their current natural range, but only after grazing had been excluded for a few years (Garfì, 1997a).

According to all the issues addressed above, and in the view of a long-term conservation planning, the easternmost populations should deserve a special concern with respect to grazing management. Due to the assumed environmental constraints, at the state of our knowledge, it is not possible to foresee if *Z. abelicea* individuals from Thripti will ever reach the size of fully developed arboreal trees or even grow enough to surpass a browsing height threshold. However, the reorganization of grazing activities towards a greater sustainability, involving sufficiently long periods of protection from browsing pressure on a rotational basis could eventually promote fructification and seedling establishment and therefore allow a demographic increase of those populations and the preservation of the high genetic variability found within the species.

5. Conclusions

Knowing how overbrowsed trees grow across their distribution range when browsing is removed and knowing what factors drive growth are important to consider when planning conservation actions and when looking at grazing management options. In our study, we found that *Z. abelicea* trees from eastern Crete grew twice less in the same period than trees from central and western Crete. These findings were put in relation with precipitation patterns, and in particular the crucial spring and early summer precipitation. Previous studies have also shown the strong influence of overbrowsing on *Z. abelicea* growth overall. In order to avoid the extinction or shrivel of the most marginal stands, and in order to promote regeneration, a drastic shift in the way pastoral activities are currently carried out is necessary. More sustainable and extensive practices would help to maintain population size and promote regeneration while at the same time keeping the high genetic variability found within the species. In the light of our recent findings, special attention should therefore be given to the eastern *Z. abelicea* populations to allow sufficient time and resources for protection or regenerative measures to be effective.

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CRediT authorship contribution statement

LF conceived the study, DG and IR carried out field measurements, TN analyzed soil samples in the laboratory, LF performed the statistical analyses, LF wrote the manuscript, LF, SP, GG and GK reviewed the manuscript. All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02031.

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