



Free behind bars: Effects of browsing exclusion on the growth and regeneration of *Zelkova abelicea*

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ABSTRACT

Caprine overbrowsing is a main threat to trees of pastoral mountain woodlands in the Mediterranean region of Europe. In this study, we assess the impact of browsing exclusion on the growth and regeneration of the endangered *Zelkova abelicea*, a Paleogene relict tree endemic to Crete (Greece). Shoot elongation, height growth and natural regeneration were monitored during two to five years in 31 fenced plots across the distribution range of the species. We found that in the absence of browsing pressure, *Z. abelicea* produces shoots on average two times longer than when browsed, therefore clearly demonstrating the negative impact of current browsing pressure on the growth performance of the species. Shoot elongation and height growth were maximal in most plots during the first two years following fencing, after which growth rates decreased. The proportion of trees that reached a height considered out of reach of caprine browsing had more than doubled already after four years, although this was dependent on initial tree height. Shoot elongation and height growth were positively correlated with tree height, and smaller trees took more time to reach a specific height. Seedlings were only found in three fenced plots as well as in two control browsed areas during a single year and only in western Crete. This underlines the possible strong and concerning impact of climatic factors on seed formation as well as on seedling growth and survival, although site specificities such as stand structure and micro-topography should also be considered. Our findings have important implications for conservation actions, as they can help choose which stands and which individuals to fence in priority for efficient long-term conservation.

1. Introduction

Crete has a very long history of browsing. Even before the introduction of domesticated goats in the early Neolithic, a diverse community of wild browsers, e.g. several deer species, a dwarf elephant and a dwarf hippopotamus existed on Crete (Papanastasis, 1998, Rackham and Moody, 1996, Van der Geer et al., 2006). The probable strong browsing pressure induced by these wild browsers led numerous, mainly endemic, plants on Crete to develop specific adaptations to browsing (e.g. spines, unpalatable twigs, prostrate growth habit, high regeneration

potential, poisonous compounds) or to shift their ranges to inaccessible places such as cliffs, already before the Neolithic introduction of domestic goats (Papanastasis, 1998, Rackham and Moody, 1996).

Small-sized, long-established and more or less extensive and sustainable pastoralism was carried out during centuries on Crete, shaping the landscape and ecosystems (Hill et al., 1998, Ispikoudis et al., 1999, Kosmas et al., 2015, 2016, Lorent et al., 2009). During the 20th century, due to the socioeconomic changes that shook Europe after the Second World War, pastoralism drastically changed on Crete. Although the number of farms decreased, more intensive practices arose, and the

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number of sheep and goats increased almost exponentially, even more so after the adhesion of Greece to the European Union in 1981 and the access to subsidies delivered to farmers per animal (Bauer and Bergmeier, 2011, Hill et al., 1998, Hostert et al., 2003, Ispikoudis et al., 1993, Kizos et al., 2014, Kosmas et al., 2016, Lyrantzis, 1996, Lorent et al., 2009). At the same time, there has been a strong development of roads in the mountains, also supported by European Union subsidies, making remote areas easier to access and to bring bigger flocks (Hill et al., 1998, Hostert et al., 2003). Some sort of traditional transhumance is still practiced nowadays as flocks are moved from lowland overwintering areas to summer mountain pastures in spring. However, these flocks are composed of much more animals, often surpassing the carrying capacity of the local rangelands, and are often left for longer time stretches to roam freely in specific areas from spring to autumn (Ispikoudis et al., 1993). This uncontrolled overstocking, overbrowsing and partial abandonment of transhumance for semi-permanent pastures has led to rapid and intense landscape deterioration in many places in Crete (Ispikoudis et al., 1993, Papanastasis, 1998). Unsustainable browsing and grazing practices are one of the most important causes of landscape degradation on Crete (Kairis et al., 2015). Overbrowsing as well as underbrowsing becomes clearly detrimental to the conservation of local landscapes when occurring over decades (Papanastasis, 1998). It is not the presence of flocks that is detrimental to the Mediterranean landscape and vegetation, but a lack of sustainable management of the flocks themselves in terms of stocking density (i.e. number of animals per surface per time), herd movement, etc. (Papanastasis, 1998). In fact, pastures and rangelands with low and moderate livestock densities are considered as important priority habitats in Europe (Kairis et al., 2015). Overbrowsing occurs when there are not only changes in the local vegetation structure but also a loss of animal productivity (Wilson and Macleod, 1991). In recent times in Crete, research does not point towards less animal productivity when the landscape is degraded due to unsustainable browsing practices. This is due to the fact that oftentimes the dependency to and use of external feed or fodder is increased in order to compensate the loss of vegetation (Kizos et al., 2014, Kosmas et al., 2015, Lorent et al., 2009).

Zelkova abelicea Lam. (Boiss.) (Ulmaceae) is one of three endemic tree species to Crete (Cambria et al., 2019, Médail et al., 2019, Villar et al., 2015). This Paleogene relict is found only in the mountainous regions of the island above 900 m a.s.l. where it grows in places that are rather cool and not too xeric such as north-facing slopes or in and around dolines. The species is also found growing on scree slopes and in or around seasonal riverbeds as well as at high elevations on south-facing slopes. It forms scattered and isolated stands, with *Acer sempervirens* L., *Quercus coccifera* L. and occasionally *Cupressus sempervirens* L. (Bauer and Bergmeier 2011, Egli 1997, Fazan et al., 2012, Goedecke and Bergmeier, 2018, Sarlis, 1987, Søndergaard and Egli, 2006). Most individuals are found in a stunted dwarfed form due to overbrowsing by goats, with multiple stems and very slow growth. Such individuals can survive for centuries under this dwarfed form (Fazan et al., 2012). However, they cannot produce flower nor fruit. Arborescent, up to 15–20 m of height, fruiting individuals are much rarer and represent ca. 5% of all known individuals. Some stands are even composed entirely of dwarfed individuals. The species propagates easily by vegetative root suckers, especially when erosion or disturbance occurs (Egli, 1997, Fazan et al., 2012, Kozłowski et al., 2014, 2018, Søndergaard and Egli, 2006). *Zelkova abelicea* is classified as endangered (EN) on the IUCN Red List (Kozłowski et al., 2012). Unsustainable pastoral activities pose the most important threats to the species. In fact, most populations are found in heavily browsed areas. Overbrowsing by goats as well as trampling by numerous sheep or goats prevent seedlings from establishing and dwarfed individuals from growing tall and fructifying. Climatic and edaphic factors may also play a role in influencing plant growth and seedling establishment (Bauer and Bergmeier, 2011, Egli, 1997, Kozłowski et al., 2012, Sarlis, 1987). Previous studies pointed out that seeds germinate very slowly and need cold stratification for several

months and are therefore very sensitive to climate fluctuations as well as climate change (Fournaraki and Thanos, 2002).

Z. abelicea is emblematic of the Cretan mountains, and the largest trees are often found growing next to abandoned shepherd huts. In the past, trees were pollarded and leaves used for forage (Bauer and Bergmeier, 2011, Rackham and Moody, 1996). The wood of *Z. abelicea* was and still is considered the best to make traditional shepherd sticks, i.e. so-called “katsounes”. This practice continues today although it is now illegal because *Z. abelicea* is protected by the Greek State, forbidding the use and collection of any of its parts (Fournaraki and Thanos, 2006, Rackham and Moody, 1996).

Since 2014, a project for the conservation of *Z. abelicea* has been carried out on Crete with different conservation actions (see: www.abelisia.gr and www.zelkova.ch). One of these actions led to the installation of permanent fenced plots throughout the distribution range of the species, with a complete exclusion of browsing and a yearly monitoring to assess tree growth. In this paper, we 1) investigate the effects of browsing exclusion within these permanent plots during several consecutive years on the growth and regeneration of *Z. abelicea* and 2) compare annual growth within the fenced plots with the growth of *Z. abelicea* in control non-fenced, browsed areas.

2. Material and methods

2.1. Sampling procedure and data collection

Within the scope of the project for the conservation of *Z. abelicea*, 31 plots containing dwarfed *Z. abelicea* individuals were fenced in twelve study areas throughout the whole distribution range of the species (Fig. 1). Only Mount Psiloritis which contains a single known *Z. abelicea* population was not included in the study because no agreement was reached with local land users regarding fencing procedures. The plots were established in order to exclude caprine and ovine browsing and trampling and to allow regrowth of *Z. abelicea* individuals, seedling establishment and development of a non-browsed plant community (Fig. 2A and 2B). Plots were established gradually every autumn between 2014 and 2017, and monitored annually until 2019, leading to two to five years of data collection per plot. Chronology of plot establishment can be found in Table 1. Plots were very diverse in terms of plot surface, number of *Z. abelicea* individuals, initial tree height and altitude (Tables 1 and 4). They are probably also diverse in terms of browsing pressure, however, precise stocking densities, flock composition (i.e. proportion of goats), length of browsing period or browsing history are unknown. The available data for the whole island, without considering seasonal patterns of flock transhumance, show that in 2019, there was a total of 2,301,679 goats and sheep on Crete, of which 23% are goats (ELSTAT, 2021a). This amounts to a total stocking density of 5 animals/ha, or 1.15 goats/ha when considering forest areas and pastures (i.e. 461120 ha, ELSTAT, 2021b). To our knowledge, all of the mountain woodlands composed of *Z. abelicea* trees and shrubs included in this study are important pastures or browsing areas for goats and sheep. Although more precise census data are lacking, they are most likely under strong browsing pressure. Previous studies in other areas of Crete have shown that stocking densities greatly surpass (up to 20 times more) the carrying capacity of the local rangelands (Ispikoudis et al., 1993, Kairis et al., 2015, Kosmas et al., 2016, Lyrantzis 1996, Menjli and Papanastasis, 1995, Papanastasis et al., 2002). The only wild browser of Crete is the agrimi goat (*Capra aegagrus cretica*). The main population of agrimi is found nowadays only in the Levka Ori in western Crete, although individuals were introduced on several satellite islets for conservation purposes (Geskos, 2013, Horwitz & Bar-Gal, 2006). However, its potential impact on *Z. abelicea* is most probably marginal or null compared to that of domestic goats since the estimated agrimi population size on Crete is of ca. 1000 individuals (Geskos, 2020). In every plot, for every *Z. abelicea* individual, the length of the longest shoot (Fig. 2C) produced during the year (hereafter named as shoot length, and possibly

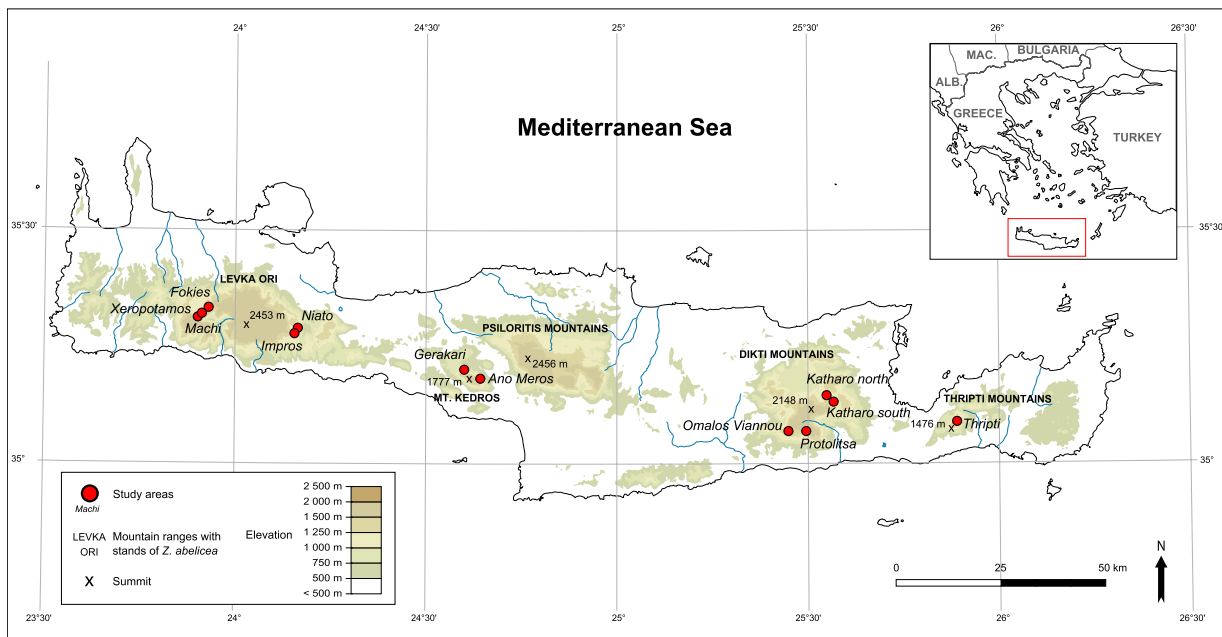


Fig. 1. Location of the study areas in the mountains of Crete (Greece).

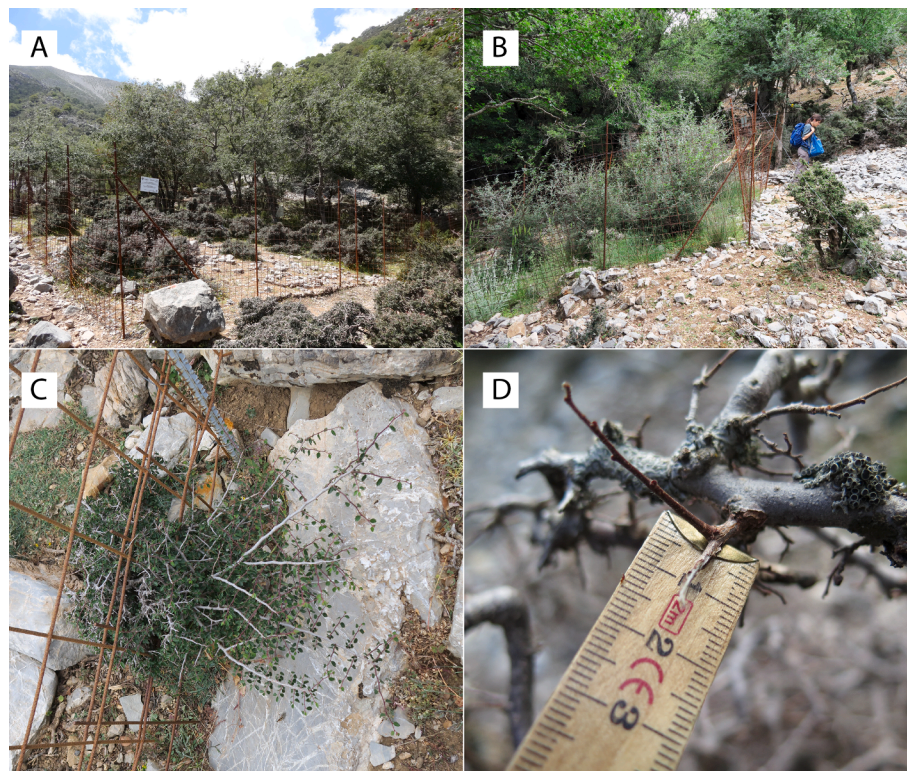


Fig. 2. A. Dwarfed browsed individuals of *Z. abelicea* in the foreground and tree type individuals in the background enclosed within a fenced plot. B. Differences in growth and vegetation inside and outside of a fenced plot four years after fencing. C. Dwarfed *Z. abelicea* producing long non-browsed shoots within a fenced plot (right) but with minute growth in browsed areas outside of the plot (left). D. Annually produced shoots on a browsed *Z. abelicea*.

different from year to year depending on yearly growth) 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. For trees

higher than 2 m, growth parameters were visually estimated. Additionally, in October 2019, the length of the longest shoot and tree height were also measured in each of the twelve study areas on a total of 120 (10 per area) control non-fenced and subject to browsing *Z. abelicea* individuals (Fig. 2D). These sampled individuals were located in the

Table 1

Characteristics of fenced plots and control non-fenced areas. T0: year of establishment of plot. Nb. of *Z. abelicea* trees: number of individuals with full records. F: fenced, C: control non-fenced. Damage: occurrence of 1st damage: SP: spring, SU: summer, WI: winter. H: human induced. N: natural causes such as rockfall or snow, A: animal influence.

Mountain range	Area	Plot ID	Altitude (m a.s.l.)	T0	Plot size (m ²)	Nb. of <i>Z. abelicea</i> trees	F/C	Damage	
Levka Ori	West	Xeropotamos	XER1	1270	2014	10	2	F	SP 2017H
			XER2	1220	2014	20	8	F	SP 2017H
			XER3	1243	2014	70	6	F	SU 2016H
			XER	1230	–	–	10	C	–
		Machi	KAL1	1171	2014	25	14	F	–
			KAL2	1195	2014	18	7	F	–
			KAL	1170	–	–	10	C	–
		Fokies	POR1	1071	2014	39	18	F	WI 2015/16N
			POR2	1140	2014	37	7	F	–
	POR		1070	–	–	10	C	–	
	East	Niato	NIA1	1220	2014	36	2	F	–
			NIA2	1219	2014	32	5	F	–
			NIA3	1211	2014	21	3	F	–
			NIA4	1221	2014	19	3	F	–
			NIA	1215	–	–	10	C	–
		Impros	IMB1	1178	2015	34	24	F	–
			IMB2	1172	2015	21	8	F	–
			IMB3	1178	2015	21	11	F	–
			IMB	1178	–	–	10	C	–
Kedros	Gerakari	GER1	1255	2015	33	9	F	–	
		GER2	1257	2015	26	7	F	SU 2016A	
		GER	1255	–	–	10	C	–	
	Ano Meros	ANME1	998	2015	12	1	F	SU 2016N	
		ANME2	986	2015	37	7	F	–	
		ANME	995	–	–	10	C	–	
Dikti	North	Katharo north	KATH1	1177	2016	38	14	F	–
			KATH2	1201	2016	67	27	F	–
			KATH12	1200	–	–	10	C	–
		Katharo south	KATH3	1149	2016	24	7	F	WI 2016/17H
			KATH4	1153	2016	59	6	F	–
			KATH34	1150	–	–	10	C	–
	South	Omalos Viannou	VIAN1	1324	2015	23	3	F	–
			VIAN2	1327	2015	22	10	F	–
			VIAN3	1309	2015	15	8	F	–
			VIAN	1325	–	–	10	C	–
		Protolitsa	PROT1	1637	2015	19	11	F	–
			PROT2	1619	2015	20	14	F	–
			PROT3	1593	2015	19	6	F	–
PROT	1620	–	–	10	C	–			
Thripti	Thripti	THR1	1152	2017	95	19	F	–	
		THR2	1152	2017	88	28	F	–	
		THR3	1155	2017	105	25	F	–	
		THR	1154	–	–	10	C	–	

immediate vicinity (<30 m of distance) of the fenced plots.

Natural regeneration of *Z. abelicea*, sexually through seedlings or vegetatively through root suckers, was also monitored in every plot and external area every spring between 2015 and 2019. Seedling and root sucker presence and number were recorded and counted.

2.2. Selection of fenced plots and trees for analysis

Disturbances such as intentional or nature-induced destruction of fences with subsequent browsing occurred in seven plots at different times (Table 1). 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, died or was not previously noticed. Such trees were also excluded from further analyses. Therefore, a total of 271 trees with full records (or 320 when also counting the 49 trees with full records included in the disturbed plots) found within the fenced plots were analyzed. Plots contained on average 10 *Z. abelicea* individuals, but with a wide range between one and 28 trees (Table 1).

2.3. Analyses

Statistical analyses were carried out using R (R Core Team, 2020, version 4.0.2.). Average shoot length, tree height and annual height change and standard deviations were computed. Significance in differences in shoot length between fenced plots and control non-fenced areas were assessed using a Wilcoxon rank sum test (`wilcox.test`, package `stats`, Hollander and Wolfe, 1973) for 2019, the only year for which data were available for the control non-fenced plots. Correlations between shoot length and time after fencing as well as for height growth and time after fencing were done using Spearman's rank correlation (`cor.test`, package `stats`, Hollander and Wolfe, 1973) in order to show the general direction of shoot or height changes depending on time. Further correlations were made between shoot length, tree height and height changes also using Spearman's rank correlation. The browsing height that goats can reach strongly varies amongst authors with a range of heights between one and two meters depending on goat variety, whether or not bipedal browsing (i.e. rise up on hind legs) was considered, and vegetation type, i.e. dense growing or large shrubs are more difficult to browse up high unless they can be climbed upon (e.g. Foroughbakhch et al., 2013, Harrington, 1979, Nastis, 1997, Ouédraogo-Koné et al., 2006, Platis and Papanastasis, 2003, Sanon et al., 2007, Skarpe et al., 2007, Webb et al., 2004).

In the present study, *Z. abelicea* individuals measuring > 200 cm are considered as being tall enough to escape browsing. Although browsing probably sporadically occurs above that height, we consider such individuals as having a strong likelihood of escaping browsing based on our field observations and browsing height thresholds given in the literature cited above.

3. Results

3.1. Shoot lengths

Shoot lengths per time in non-disturbed fenced plots as well as in control non-fenced areas are given in Table 2 and Fig. 3, while individual plot data are found in Appendix A, Table A.1 and Fig. A.1. In 2019 (only year for which data is available for both the control unfenced plots and fenced plots) shoots in undisturbed fenced plots were on average 1.85 times longer than shoots in control non-fenced areas, with values varying between 1.10 and 4.10 times longer, depending on locality. Shoot length is significantly ($p < 0.1$) longer in non-disturbed fenced plots compared to control non-fenced areas in 2019 for most plots, except for three plots (Table 3). Correlations between shoot length and increasing time after fencing are also found in Table 3. Overall in non-disturbed fenced plots, there is no significant correlation (ρ : -0.02 , $p > 0.1$) between shoot lengths and time after fencing. However, when considered individually, for a majority (12 plots) of non-disturbed plots there is a significant ($p < 0.1$) and mostly strong negative correlation between shoot length and increasing time after fencing, while six plots show negative but non-significant correlations. Only six plots show positive trends but only two are significant ($p < 0.1$). Shoot length was positively correlated with tree height (ρ : 0.54 , p -value < 0.001), with taller trees generally producing longer shoots.

3.2. Height changes

Average tree height and height changes per time for non-disturbed fenced plots as well as for control non-fenced areas are found in Table 2. Trees in fenced plots had heights in T0 comprised between 6 and 330 cm, whereas trees in control non-fenced areas measured between 20 and 175 cm. Strong variations occurred between trees in terms of height change, as the highest annual growth change amounted to 80 cm while the minimum was 0 cm. Table 4 and Fig. A.2 in Appendix A give detailed results for every fenced plot. In 2019 at the end of the study period, trees had on average grown 34.36 ± 30.80 cm with variations between 0 and 148 cm depending on individual tree. Height changes were overall not significantly correlated with time after fencing (similarly to shoot lengths) (ρ : 0.02 , $p > 0.1$). However, when fenced plots were considered individually, height changes were negatively correlated with time after fencing in a majority of (non-disturbed) plots, either significantly ($p < 0.1$) for 12 plots or not significantly ($p > 0.1$) in four plots (Table 4). Significant ($p < 0.1$) positive values were found in one single plot, while the remaining seven plots have positive but not significant ($p > 0.1$) values (Table 4). In addition, height changes were

Table 2

Growth characteristics per time for non-disturbed fenced plots and control non-fenced areas. Average, minimum and maximum shoot lengths, average tree height and height change and number of plots and trees are given.

Fencing	Time	Shoot length (cm)			Height (cm)		Nb plots	Nb trees
		Average	Min	Max	Average	Change		
Fenced	T0	–	–	–	78.40 ± 54.84	–	24	271
	T1	20.61 ± 17.92	1	105	88.73 ± 58.24	10.33 ± 12.16	24	271
	T2	18.58 ± 12.38	3	57	99.81 ± 61.69	11.08 ± 10.23	24	271
	T3	15.41 ± 8.86	3	45	124.31 ± 65.89	9.63 ± 8.91	21	199
	T4	16.46 ± 8.28	3	48	131.65 ± 73.34	7.82 ± 6.60	18	152
	T5	17.24 ± 4.54	8	30	200.22 ± 58.10	9.83 ± 4.23	7	41
Non-fenced	–	6.83 ± 2.65	3	16	83.14 ± 37.34	–	12	120

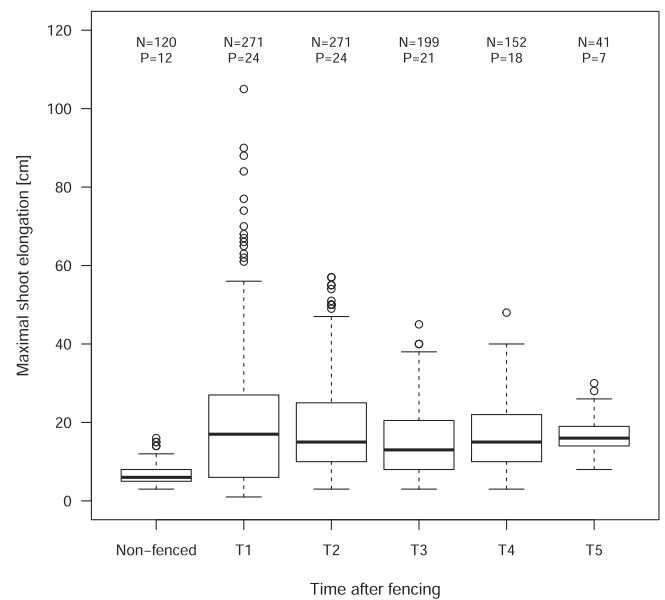


Fig. 3. Shoot length in non-disturbed fenced plots one to five years after fencing (T1 to T5) and in control non-fenced areas. N: number of trees, P: number of fenced plots or control non-fenced areas.

positively correlated with tree height (ρ : 0.44 , p -value < 0.001) showing that taller trees had a tendency to grow more per year.

The percentage of trees in T0 (in non-disturbed plots) that reached the 200 cm threshold at which the browsing likelihood is considered low was 4%, although strong variations (0–43%) between plots exist (Table 4). In 2019 (i.e. plots having been fenced two (T2) to five (T5) years depending on locality), at the end of the study, 10% of trees (in non-disturbed plots) measured > 200 cm, with strong variations (0–67%) amongst plots (Table 4).

3.3. Homogenous number of trees through time

The number of plots per time varied (i.e. 24 plots in T1, but only 7 plots in T5) due to the fact that the plots were established gradually between 2014 and 2017. This non-homogeneous number of plots through time may influence also our results. Therefore, we made the same analyses of shoot length and height changes over a homogeneous dataset including only plots that had complete data from T1 to T4 (18 plots, 151 trees). We found similar results (Table 5) to those obtained when including all non-disturbed plots over the whole five year of the study. Indeed, shoot length here was also maximal during the first and/or second year after fencing after which it decreased (Appendix A, Fig. A.3). Average height and height changes per time are also given in Table 5: after four years of fencing, trees had grown on average 45.32 cm (range: 0–140 cm). The percentage of trees in T0 that measured >200 cm was 6%. In T1 it amounted to 10%, in T2 it rose to 11%, in T3 it

Table 3

Levels of significance of Wilcoxon rank sum test between shoot length in fenced plots and control non-fenced areas in 2019. Spearman's rank correlation rho between shoot length and time after fencing with significance levels are also given. Levels of significance: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.1$. ^d plots in which disturbance occurred.

Fenced	Non-fenced	T2	T3	T4	T5	Rho
XER1 ^d	XER	-	-	-	* ^d	-0.56 ^d *
XER2 ^d	XER	-	-	-	*** ^d	-0.75 ^d ***
XER3 ^d	XER	-	-	-	*** ^d	-0.41 ^d ***
KAL1	KAL	-	-	-	***	-0.80***
KAL2	KAL	-	-	-	***	-0.92***
POR1 ^d	POR	-	-	-	*** ^d	-0.55 ^d ***
POR2	POR	-	-	-	***	-0.75***
NIA1	NIA	-	-	-	*	0.12
NIA2	NIA	-	-	-	**	-0.29
NIA3	NIA	-	-	-	0.61	-0.48*
NIA4	NIA	-	-	-	*	-0.43
IMB1	IMB	-	-	**	-	-0.06
IMB2	IMB	-	-	***	-	-0.47**
IMB3	IMB	-	-	***	-	-0.53***
GER1	GER	-	-	***	-	-0.44**
GER2 ^d	GER	-	-	0.52 ^d	-	-0.46 ^d ***
ANME1 ^d	ANME	-	-	0.14 ^d	-	-1 ^d
ANME2	ANME	-	-	***	-	0.23
VIAN1	VIAN	-	-	**	-	-0.51*
VIAN2	VIAN	-	-	***	-	-0.52***
VIAN3	VIAN	-	-	*	-	0.45**
PROT1	PROT	-	-	***	-	-0.06
PROT2	PROT	-	-	**	-	0.03
PROT3	PROT	-	-	0.96	-	-0.09
KATH1	KATH12	-	***	-	-	0.28*
KATH2	KATH12	-	***	-	-	-0.63***
KATH3 ^d	KATH34	-	** ^d	-	-	-0.27 ^d
KATH4	KATH34	-	**	-	-	-0.76***
THR1	THR	**	-	-	-	-0.32*
THR2	THR	0.53	-	-	-	0.05
THR3	THR	***	-	-	-	-0.20

reached 13% and in T4, 15% of individuals were over 200 cm.

3.4. Fenced plots with disturbance

Disturbances, with recorded signs of subsequent browsing, occurred in 7 fenced plots at different times after establishment of the fences (Table 1). Despite these disturbances, shoot lengths were significantly ($p < 0.1$) longer in XER1, XER2, XER3, POR1 and KATH3 plots compared to control external plots in 2019 and a significant ($p < 0.1$) negative correlation between shoot length and time after fencing was also visible for four of these five plots, and only not significant ($p > 0.1$) for KATH3. Both GER2 and ANME1 have shoot lengths that are not significantly ($p > 0.1$) longer than shoots in browsed areas, although both show a negative correlation between shoot length and passing time, but significant ($p < 0.1$) only for GER2 (Table 3 and Appendix A, Fig. A.1). Average height changes between T0 and the last year of measurement were positive for all of the disturbed plots, although some individual trees showed negative values (i.e. they were smaller than in T0) in XER1, XER3 and GER2 (Table 4). Correlation between height growth changes and time after fencing were significant ($p < 0.1$) and negative only for POR1. For all other plots they were non-significant, either negative (XER1, XER2) or positive (XER3, GER2, ANME1, KATH3). The proportion of trees that reached 200 cm during the last year of measurement was either similar to T0 and had not changed (POR1, ANME1, KATH3) or had increased (XER1, XER2, XER3, GER2).

3.5. Natural regeneration

In 2018, two, three and twenty seedlings were found in three fenced plots (KAL2, XER2 and XER3, respectively), in open areas or under shrub cover and three and thirty seedlings were found in two external areas

(KAL and XER, respectively). Seedlings were found mainly, but not exclusively, growing under shrubs or in between loose rocks, only in Machi and Xeropotamos in western Crete, but none were found to have survived in 2019. Although no new seedlings were recorded in 2019 within the study sites, the presence of new seedlings was noted from adjacent areas to the above-mentioned study sites. No new vegetatively propagated (suckers) individuals were recorded within the studied sites.

4. Discussion

Goats are known to reduce or limit woody plants or tree growth (Bashan and Bar-Massada 2017, Elias and Tischew 2016, Gizicki et al., 2018, Hester et al., 2006, Madèra et al., 2019, Mancilla-Leytón et al., 2013, Rooke 2003). In our study, we clearly show that this was also the case here. *Z. abelicea* individuals in fenced plots where browsing was excluded produced significantly (on average two times) longer shoots than individuals in areas where browsing occurred. Furthermore, in some plots, some trees grew over 100 cm in height since they were fenced (Table 4), showing the potential of the species to grow when given the opportunity. This unambiguously demonstrates the strong impact that current browsing has on the growth of *Z. abelicea* in the Cretan mountains. Most plots showed a maximal shoot elongation and height growth during the first two years after browsing exclusion, with stronger growth variations between individuals within the first year compared to the second. Subsequent years involved less growth, while staying high. The reasons behind this phenomenon are still unclear and could be linked with tree physiology or energy reserves, and we do not yet have sufficient perspective to see if this trend will continue with passing years. Tsiourlis (1998) found that *Q. coccifera* produced more biomass the first year after browsing exclusion, with decreasing values thereafter and a possible stabilization after the third year, although the study did not include subsequent years to validate this assumption. Konstantinidis et al. (2005) observed that *Q. coccifera* produced longer shoots in the first two years after a fire event and then has a slower growth. In burnt shrubs, this increased growth during the first few years after disturbance is due to the mobilization of energy reserves (Bowen and Pate, 1993).

It is possible that a similar phenomenon happens when *Z. abelicea* is not browsed anymore. However, the removal of browsing is not a trigger event similar to fire, except if we consider the absence of browsing or browsing induced chemical reactions as being a trigger. Moreover, since the plots were fenced at different times over the course of four separate years, such a reaction can most probably not be imputed to interannual climatic fluctuations. It is not impossible that this pattern could be linked to the way sampling was done, since shoot length was always measured on the longest annually produced shoot and thus not always on the same shoot, although the fact that this pattern seems to happen throughout most plots and over several years tends to exclude this hypothesis.

As the large standard deviations clearly point out, shoot lengths within the fenced plots were much more variable than in the control non-fenced areas. Height changes and shoot lengths were also more variable the first year after fencing than in subsequent years. This points towards the fact that in browsed areas, growth is mainly regulated by browsing pressure (Fazan et al., 2012), whereas in fenced plots where browsing is not a limiting factor anymore, other factors either specific to the tree or to the site (e.g. tree height, energy reserves, micro-climate, soil, resource competition, etc.) may play a major role and individual trees and plots show a wide range of variability to browsing removal.

In addition, we demonstrate that protection against browsing over several consecutive years allows prostrate, shrubby dwarfed *Z. abelicea* individuals to grow enough to reach a height considered as sufficient to escape most browsing by goats. Although this strongly depends on the initial height of the individuals and the growth rate of their shoots, the number of trees taller than 200 cm was 2.5 times larger already after 4 years of fencing, while in some specific plots (e.g. KAL1, KAL2, NIA3,

Table 4

Average (with standard deviation), minimum and maximum height changes between T0 and the last time of measurement (Tx) for every fenced plot. Proportion of trees higher than 200 cm in T0 and Tx. Spearman's rank correlation rho between height change and time after fencing with significance levels are also given. Levels of significance: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.1$. Average height (with standard deviation) at T0 when the plot was established. Last time of measurement (Tx). ^d plots in which disturbance occurred.

Plot	Height change T0-Tx (cm)			Prop trees > 200 cm		Rho	Height at T0 (cm)	Tx
	Mean	Min	Max	T0	Tx			
XER1 ^d	35.50 ± 29.0 ^d	-56 ^d	55 ^d	0.00	0.50	-0.36 ^d	143 ± 10	T5
XER2 ^d	72.88 ± 53.0 ^d	24 ^d	91 ^d	0.00	0.25	-0.31 ^d	92 ± 50	T5
XER3 ^d	17.79 ± 20.6 ^d	-6 ^d	87 ^d	0.00	0.05	0.00 ^d	92 ± 43	T5
KAL1	96.21 ± 19.0	64	122	0.14	0.57	-0.28*	126 ± 65	T5
KAL2	96.14 ± 24.9	64	134	0.00	0.57	-0.31*	126 ± 49	T5
POR1 ^d	58.63 ± 27.3 ^d	11 ^d	118 ^d	0.00	0.00	-0.33 ^d ***	59 ± 21	T5
POR2	74.57 ± 21.2	43	95	0.00	0.00	-0.31*	62 ± 23	T5
NIA1	54.00 ± 19.8	40	68	0.00	0.00	0.31	131 ± 21	T5
NIA2	69.80 ± 15.4	53	86	0.00	0.20	-0.41*	118 ± 38	T5
NIA3	48.33 ± 32.1	12	73	0.33	0.67	0.20	186 ± 98	T5
NIA4	91.00 ± 54.2	40	148	0.33	0.67	-0.74**	101 ± 96	T5
IMB1	15.67 ± 12.9	0	47	0.00	0.00	0.02	39 ± 25	T4
IMB2	57.25 ± 15.4	28	78	0.00	0.00	-0.68***	76 ± 16	T4
IMB3	66.00 ± 16.8	22	85	0.00	0.00	-0.73***	59 ± 17	T4
GER1	69.30 ± 16.2	38	90	0.11	0.33	-0.35*	118 ± 67	T4
GER2 ^d	5.44 ± 7.80 ^d	-3 ^d	18 ^d	0.33	0.43	0.07 ^d	156 ± 77	T4
ANME1 ^d	8.00 ± 0.00 ^d	8 ^d	8 ^d	0.00	0.00	0.77 ^d	175 ± 0	T4
ANME2	36.29 ± 43.3	0	108	0.43	0.57	0.16	177 ± 84	T4
KATH1	13.00 ± 5.1	6	23	0.07	0.07	0.25	111 ± 50	T3
KATH2	25.67 ± 8.4	5	41	0.00	0.04	-0.36***	87 ± 38	T3
KATH3 ^d	26.86 ± 7.93 ^d	20 ^d	42 ^d	0.00	0.00	0.10 ^d	70 ± 29	T3
KATH4	40.83 ± 8.1	31	50	0.17	0.17	-0.66**	146 ± 35	T3
VIAN1	77.67 ± 7.0	71	85	0.00	0.00	-0.74**	86 ± 40	T4
VIAN2	35.30 ± 12.3	15	57	0.00	0.00	-0.10	78 ± 40	T4
VIAN3	13.50 ± 4.2	9	22	0.00	0.00	-0.29	54 ± 41	T4
PROT1	30.36 ± 9.3	14	48	0.09	0.09	0.04	99 ± 83	T4
PROT2	15.43 ± 11.8	0	38	0.00	0.00	0.16	62 ± 30	T4
PROT3	28.17 ± 6.6	18	36	0.00	0.00	0.45*	73 ± 37	T4
THR1	19.16 ± 10.9	1	42	0.00	0.00	-0.19	64 ± 40	T2
THR2	6.71 ± 6.7	0	28	0.00	0.00	0.38**	41 ± 17	T2
THR3	14.88 ± 9.1	3	37	0.00	0.00	-0.15	38 ± 13	T2

Table 5

Growth characteristics per time for the 151 trees in 18 fenced plots with homogenous data from T1 to T4. Average shoot length, average tree height and height change are given.

Time	Average shoot length (cm)	Height (cm)	
		Average	Change
T0	-	86.74 ± 60.78	-
T1	25.03 ± 21.26	98.99 ± 63.82	12.25 ± 14.72
T2	24.03 ± 13.82	113.61 ± 67.19	14.62 ± 12.22
T3	17.15 ± 9.31	124.19 ± 70.51	10.58 ± 9.39
T4	16.51 ± 8.29	132.06 ± 73.41	7.87 ± 6.60

NIA4, ANME2), over 50% of individuals had reached that height at the end of the study period in 2019. These findings are highly important for conservation practitioners or rangeland managers, as they can help to estimate how many years will be needed to reach a sufficient height depending on tree size and locality, or which stands to select in priority to reach a desired height the quickest possible. In addition, it is crucial for the natural regeneration through seed of *Z. abelicea* for trees to reach a height at which flowering and fruiting branches are out of reach of goats. Indeed, overbrowsed individuals do not produce flowering shoots (Kozłowski et al., 2014). Increasing the number of potentially fruiting trees will in turn increase the number of fruit produced and thus improve the chances of natural regeneration through seedlings.

Most plots in which disturbance (i.e. browsing by goats after fencing) occurred showed an increase in average shoot length despite browsing. Only in two plots (GER2 and ANME1) shoot lengths were not significantly different from shoots in browsed areas (Table 3). However, it is difficult to assess if the non-significant shoot elongations within these disturbed plots are a consequence of a browsing disturbance or due to

tree or site-specific characteristics (e.g. micro-climate, soil, competition, energy reserves, etc.). Height increased in all of the plots with disturbance between T0 and the last time they were measured, although in three plots (XER1, XER3, GER2), some individuals lost height (Table 4), indicating that browsing damage surpassed tree growth. The negative correlation of shoot growth and height change with time after fencing was also not as clear in disturbed fenced plots compared to undisturbed fenced plots.

In undisturbed fenced plots, shoot and height elongation were positively correlated with tree height and were found to be very different amongst sites. There seems to be important growth differences (both in terms of shoot length and height change) between plots. Some of these variations are probably imputable to the fact that individuals within the plots have different initial heights, or to the fact that individual *Z. abelicea* trees could possibly react differently to browsing removal depending on their age, energy reserves, competition, etc. However, some plots showed very slow growth (i.e. NIA1, ANME2, VIAN3, PROT2, PROT3 and THR2 in T1, VIAN3 and THR2 in T2, NIA4 and PROT2 in T3, PROT3 in T4 and NIA3 in T5), with no significant differences with the control non-fenced areas, unlike the majority of plots. Further investigations should be carried out to see if these differences and slow growth rates are due to differences in initial tree height or spatial structure of plant communities (i.e. does tree density or competition influence growth rates?), location (i.e. to what extent do geographical parameters such as climate, soil chemical and physical properties or altitude influence growth?) or past browsing pressure (i.e. stocking rate and seasonality of browsing) and flock composition (goats vs. sheep ratio).

The rarity of natural regeneration through seedling recruitment both in fenced plots and control unfenced plots in most years and sites can be regarded as concerning. This phenomenon was already noticed by Egl

(1997) both in fenced unbrowsed as well as browsed areas. The impact of browsing domesticated flocks has very often been regarded as a crucial negative factor hampering tree seedling establishment in Mediterranean habitats, and with this respect, the facilitating role of shrub cover has been largely recognized. Several studies (e.g. Baraza et al., 2006, Di Pasquale and Garfi, 1998, Tiscar-Oliver, 2015), have clearly demonstrated that thorny or unpalatable shrubs can act as physical barriers protecting seedlings and saplings from herbivory and trampling. Moreover, the role of shrub cover on seedling establishment and growth can be diverse and complex by providing a favorable micro-habitat against extreme solar irradiation, photo-inhibition and desiccation (Castro et al., 2004, Rodríguez-García et al., 2011, Rühl et al., 2006, Tiscar-Oliver, 2015). In our study, we did not focus specifically on the interactions between *Z. abelicea* and shrub cover. However, we did observe that seedlings in fenced plots were found both in open gaps and under shrub cover, whereas in external, browsed areas most seedlings were found in more protected locations, such as below the canopy of the neighboring shrubs or in between loose rocks, and were absent from more open areas probably due to herbivory. Furthermore, since in our study, seedlings were also found in external areas, the absence of recruitment through seedlings cannot be solely imputed to over-browsing. Indeed, the absence of seedlings in all sites and years except for three fenced and two control areas in 2018 and adjacent areas in 2019 in western Crete points towards a strong influence of some other factor on seedling survival, or seed soundness, regardless of the browsing status. We hypothesize that climatic conditions possibly play an important role in *Z. abelicea* seedling survival alongside browsing pressure, as was already noted by Egli (1997). Fruit production in *Z. abelicea* as well as the proportion of fruits containing a viable embryo seem to strongly fluctuate depending on the year and site (personal observations, Egli, 1997, Fournaraki and Thanos, 2002, 2006, Søndergaard and Egli, 2006), which in turn will influence the presence of seedlings. In addition, one must also consider site specificities (e.g. micro-topography or stand structure and dynamics) that could influence the occurrence and survival of seedlings. Some of the studied sites (e.g. Thripti) are characterized by the absence of individuals above 2 m (i.e. that are able to produce fruit), whereas others (e.g. Protolitsa) have fruiting individuals but are found on steep stony slopes unfavorable to soil retention and the establishment of seedlings. The fact that no surviving seedlings were found again in 2019, even in the fenced plots, and that seedlings were not found in any other site raises concern for the long-term conservation and genetic diversity of the species. Furthermore, no new suckers were found in our study. However, this is not surprising since suckering appears mostly after disturbance events affecting roots such as fire or erosion (Egli, 1997, Fazan et al., 2012). Thanks to its capacity to profusely re-sprout through root suckers after disturbance events, *Z. abelicea* can propagate and survive asexually in the absence of naturally produced seedlings, but the genetic diversity will be impoverished.

With the *Z. abelicea* conservation project, it is the first time that so many areas containing *Z. abelicea* individuals and spread out through most of the distribution area of the species were fenced, and for such a long span of time. At the time of submission of this article, the oldest plots have been fenced for 6 consecutive years. Although some plots did suffer from anthropogenic disturbances, most did not, and this success can be imputed to the small size of the fenced plots, and more importantly, to the involvement and information of local people in and about the *Zelkova* project, a crucial prerequisite for success in conservation projects (Tisdell, 1995, Elbroch et al., 2011).

5. Conclusions

This study shows the strong impact of current browsing pressure on the growth of *Z. abelicea* in the mountains of Crete (Greece). Both shoot length and height clearly increased when browsing was removed. Shoots were on average two times longer in fenced plots than in browsed areas.

Interestingly, growth was maximal during the first two years after fencing, and was lower in subsequent years. Although growth rates strongly depended on initial tree height, the proportion of trees that had reached a height considered sufficient to escape browsing had more than doubled after four years of fencing. Natural regeneration through seedlings was found in the study sites only for one year and localized in two specific areas in western Crete and raises concerns about the influence of climatic variables on seed production, viability and seedling survival. Spatial differences in natural regeneration as well as in growth seem to exist between plots and should be further investigated. Our results have important conservation implications and can be used in the future in order to choose which *Z. abelicea* stands to protect in priority depending on conservation goals and available time.

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. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.118967>.

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