
Volume 261, issue 1, 1 January 2011
ISSN 0378-1127
ELSEVIER
Forest Ecology and Management

Forest Ecology and Management 261 (2011) 143–147

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Quercus calliprinos regrowth advantage under grazing in Mediterranean maquis and its management implications

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ARTICLE INFO

Article history:
Received 20 June 2010
Received in revised form
25 September 2010
Accepted 27 September 2010

Keywords:
Deciduous trees
Diversity
Evergreen trees
Grazing
Regrowth
Sclerophyllous vegetation

ABSTRACT

The post disturbance natural succession of the Mediterranean maquis, which turns open and species-rich landscapes into dense, closed stands of sclerophyllous woody vegetation is a principal threat to plant and animal diversity. Therefore, in the absence of traditional agricultural disturbance, active management regimes that include cutting and grazing are proposed to preserve biodiversity. The Mediterranean woody vegetation in Israel is strongly dominated by one species – the evergreen sclerophyllous *Quercus calliprinos* (Kermes oak). We hypothesized that under cutting and grazing, the evergreen *Q. calliprinos* has a relative regrowth advantage over other competing tree species. Here we examined the effect of grazing and the effect of tree structural traits on the regrowth after clear cutting of all trees in our study plots at Mt. Meron LTER site, Israel. All trees were removed from five blocks of 2000 m^2 and each block was divided into two plots, five of which were exposed to grazing livestock while five were wire-fenced and ungrazed. The regrowth rate of *Q. calliprinos* under grazing was higher than that of all other tree species suggesting that in the long-term, under such a conservation management regime, the dominance of the evergreen sclerophyllous *Q. calliprinos* over the deciduous tree species will increase and consequently will decrease plant and animal diversity. Therefore, we conclude that to protect landscape and species diversity in Mediterranean ecosystems dominated by evergreen oaks, when cutting and grazing are applied, special care must be paid to trees that are more negatively affected by such treatment.

Nomenclature: Danin (1998).

1. Introduction

Typical vegetation in Mediterranean-type ecosystems (MTEs) worldwide is characterized by dense forests dominated by short (2–5 m high), multi-stemmed, evergreen, sclerophyllous trees (di Castri et al., 1981). This complex vegetation type is termed 'maquis' in the Mediterranean basin. Under traditional agricultural disturbances, such as cutting and grazing, the Mediterranean maquis is a plant and animal species rich biome (Naveh and Whittaker, 1979). However, in the absence of human interference, the natural succession will turn this open landscape into closed, dense and shady woody vegetation with low biodiversity (Perevolotsky, 2005). Therefore, active management including cutting and grazing, is proposed to prevent tree closure and consequent loss in biodiversity.

Since the early pre-historical period, the Mediterranean maquis has been widely affected by intensive human activities. Fires, cuttings and grazing were the traditional exploitation techniques of the natural woody vegetation, which greatly affected the evolution of plants and the landscape (Naveh, 1990). With the beginning of agriculture, about 10,000 years ago, cutting and grazing became the dominant human activities (Naveh and Carmel, 2004).

Rapid resprouting and regrowth from secondary buds is the main adaptation of Mediterranean trees to major disturbances such as fire, cutting and grazing (Naveh, 1975; Bond and Midgley, 2001). The regrowth rate is commonly affected by tree age, size, aboveground biomass and stem density (Ehleringer and Mooney, 1983; Danell et al., 1985; Malanson and Trabaud, 1988; Bellingham and Sparrow, 2000). Tsiouvaras et al. (1986) showed that as response to repeated clipping of Kermes oak (*Q. coccifera*) canopies, growth rate of twigs had increased and the growth period was extended into the summer, a season in which Kermes oak trees do not normally grow. Carrión et al. (2000) studied the distribution of the evergreen *Q. suber* (cork oak) and concluded that the dense monospecific forests of cork oak in the Iberian Peninsula are the result of human selection and, that in the absence of human intervention, *Q. suber* would develop into mixed forests with other evergreen and deciduous oaks.

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doi:10.1016/j.foreco.2010.09.044

The Mediterranean maquis covers most of the northern and central mountainous region (300–900 m a.s.l.) in Israel. This vegetation includes about 15 evergreen and 15 deciduous tree species (Danin, 2010; Shmida, personal communication), but is strongly dominated by the evergreen sclerophyllous *Quercus calliprinos* Webb, which accounts for 80–90% of the tree coverage (Zohary, 1973). In this paper, we posit the hypothesis that under a management regime that includes cutting and grazing, the evergreen *Q. calliprinos* has a relative advantage in regrowth over its accompanying tree species. We studied the effect of grazing on the regrowth rate after canopy removal of *Q. calliprinos* and three deciduous tree species. We also examined the influence of pre-treatment tree structure on the regrowth rate of *Q. calliprinos* and five deciduous tree species. Our specific predictions were P1: The evergreen *Q. calliprinos* will have a higher regrowth rate than deciduous trees. P2: Cattle grazing will have a smaller negative effect on *Q. calliprinos* than on the deciduous species. P3: Regrowth is species-specific and, in each species regrowth rate will be connected with different structural traits.

2. Materials and methods

2.1. Study site and experimental design

We carried out the research at the Mt. Meron Long-Term Ecological Research site, which was established as part of the Israeli LTER network to study the effect of woody species as landscape modulators along the rainfall gradient in Israel (Shachak et al., 2008; Agra and Ne'eman, 2009). The site is located in northern Israel (35.25°E, 33.15°N), 850 m a.s.l., with mean annual precipitation of 900 mm, falling mainly during the short winter (December to February). The bedrock is limestone covered with terra-rossa soil. The vegetation is a dense maquis, subject to moderate cattle grazing of 0.3 cows ha^{-1} $year^{-1}$, a typical grazing intensity in such areas. The average total vegetation cover was ca. 95%, of which 60% was trees, 15% shrubs, 10% dwarf-shrubs and 10% open patches of herbaceous plants. The dominant tree species *Quercus calliprinos* Webb (constitutes 75% of the individuals and 80% of their coverage), is accompanied in the study area mainly by the following deciduous trees: *Q. boissieri* Reuter (4% of trees and 7% of tree cover), *Pistacia palaestina* Boiss. (5% of trees and 5% of tree cover), *Crataegus aronia* (L.) DC. (7% of trees and 4% of tree cover), *Pyrus syriaca* Boiss. (4% of trees and 2% of tree cover), *Stirax officinalis* L. (2% of trees and 1% of tree cover) and *Prunus ursina* Kostchi (2% of trees and 1% of tree cover).

All trees were removed down to ground from five blocks of 2000 m^2. Each block was divided into two equal (1000 m^2) plots, five of which were exposed to grazing livestock while five were wire-fenced and ungrazed. The research plots were located near hilltops with little or no slope, and heterogeneous in their aspect, vegetation and rock cover.

2.2. Effect of grazing on regrowth rate

To examine the effects of grazing, three growing seasons after canopy removal, we measured the regrowth of randomly sampled *Q. calliprinos* trees and trees of the three other most common species growing in the experiment plots: *Q. boissieri*, *P. palaestina* and *C. aronia*. Sampling effort for each species was determined by analyzing the coefficient of variation (CV) against sample size in the plots.

For each tree, we determined three parameters of the re-growing canopy: (1) canopy height- the highest re-growing shoot; (2) canopy diameter – the average of two diameters (north/south and east/west) of the re-growing canopy; (3) relative horizontal regrowth – canopy diameter divided by the average pre-removal diameter of the species in the plot (according to the data collected before treatment application). Relative horizontal regrowth was calculated to correct the data for the differences in initial canopy size among the various species on their regrowth rates. As grazing was applied at the plot scale, to examine the effect of grazing we used the average of all trees in a plot to test each parameter. Since not all species were present in all blocks, we applied a within-subject two-way mixed model ANOVA (SPSS 17: Mixed model, linear) for unbalanced data for the examination of the effects of grazing, tree species, and their interactions on the three tested parameters (West et al., 2007). We used the block as the independent subject, grazing and tree species as the two within-subject fixed factors.

2.3. Effect of tree structure on regrowth rate

This part of the research was done only in the ungrazed plots. During canopy removal, we permanently numbered all tree stumps with aluminum discs and recorded for each tree, the following data: species, canopy diameter, average of two perpendicular stem diameters and number of stems (>4 cm diameter). One growing season after canopy removal, we randomly selected 182 trees from all the ungrazed plots. For each tree, we determined canopy height as the highest re-growing shoot and canopy diameter as the average of two diameters (north/south and east/west) of the re-growing canopy.

Canopy height and diameter, which represent two different structural parameters of the canopy, responsible for vertical and horizontal growth respectively, were not significantly correlated. Therefore, we separately examined the correlations of canopy height and canopy diameter with number of stems, mean stem diameter, pre-removal canopy diameter, and thickest stem diameter. Because the data did not follow a normal distribution (Kolmogorov–Smirnov test) even after various transformations, we used the non-parametric Spearman correlation tests.

3. Results

3.1. Effect of grazing on regrowth rate

Without grazing, three years after canopy removal the two *Quercus* species were higher than *C. aronia* and *P. palaestina*; under grazing, *C. aronia* was the highest, followed by *Q. calliprinos* and *P. palaestina* was the lowest (Fig. 1a). canopy height was significantly affected by grazing and tree species with no interaction between them (Table 1).

Without grazing, *Q. calliprinos*, *Q. boissieri* and *P. palaestina* had a larger canopy diameter than *C. aronia* trees, while under grazing *Q. calliprinos* had larger canopy diameter than the other three species (Fig. 1b). Canopy diameter was significantly affected by grazing and tree species, with no significant interaction between them (Table 1).

P. palaestina had the largest Relative horizontal regrowth in grazed and in ungrazed plots, but also had the largest decrease under the grazing relative to no-grazing treatment (Fig. 1c). Relative horizontal regrowth of *Q. calliprinos* and of *C. aronia* trees was less negatively affected by grazing than that of *Q. boissieri* and *P. palaestina* (Fig. 1c). Relative horizontal regrowth was significantly affected by grazing and tree species, with no significant interaction between them (Table 1).

3.2. Effect of tree structure on regrowth rate

One year after canopy removal, regrowth parameters of *Quercus calliprinos* trees were positively and significantly correlated with most of their pre-removal parameters (Table 2). canopy diameter

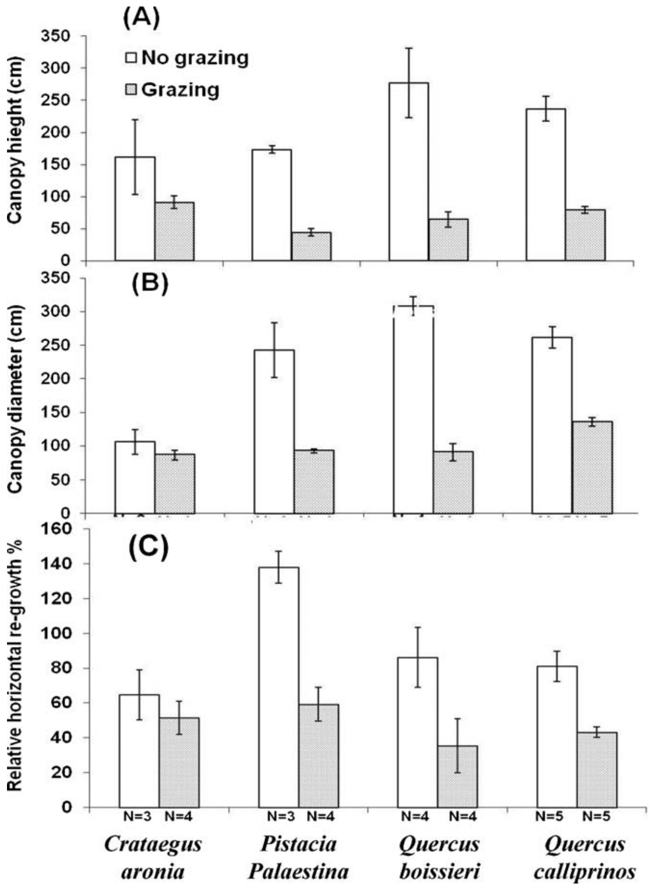

Fig. 1. (A) Mean (±SE) canopy height (per plot), (B) mean (±SE) canopy diameter (per plot) and (C) mean (±SE) Relative horizontal regrowth (mean canopy diameter per plot divided by the mean pre-removal diameter per plot) of the re-growing canopies of *Crataegus aronia, Pistacia palaestina*, *Quercus boissieri* and *Q. calliprinos*, in grazed and in ungrazed plots, three years after canopy removal.

of *Pistacia palaestina* was positively correlated with its pre-removal number of stems ($r_s = 0.711$, $p = 0.021$, $N = 10$), the canopy diameter of *Styrax officinalis* was positively correlated with its pre-removal diameter of the thickest stem ($r_s = 0.900$, $p = 0.037$, $N = 5$) and with its pre-removal average stem diameter ($r_s = 0.975$, $p = 0.005$, $N = 5$) and canopy height of *Crataegus aronia* was negatively correlated with its pre-removal canopy diameter ($r_s = -0.816$, $p = 0.013$, $N = 8$). A total of 181 trees out of 182 trees survived canopy removal, and all 146 trees of the dominant evergreen sclerophyllous *Q. calliprinos* survived.

4. Discussion

4.1. Grazing and regrowth

Contrary to our first prediction, vertical and horizontal regrowth rates of the evergreen *Q. calliprinos* (in the absence of grazing) were not higher or wider than those of the deciduous trees (Fig. 1). This could be due to the fact that deciduous trees may have a more efficient photosynthesis system than evergreen trees (Kikuzawa, 1991), which compensates for their significantly shorter photosynthetic period in Mediterranean-type ecosystems with typical mild winter (Ne'eman, 1993).

In support of our second prediction, under grazing the evergreen *Q. calliprinos* re-growing canopy was the widest of all deciduous species (Fig. 1c), suggesting that evergreen trees are better protected from grazing. The leaves of evergreen trees often contain high amounts of lignin and are spiny, thus decreasing their palatability and digestibility, and thereby further defending them from large herbivores (Kikuzawa, 1991; Bryant et al., 1992). However, the ANOVA model that tested canopy diameter revealed only nearly significant interaction between the effects of the tree species and the grazing. The re-growing canopy of the deciduous oak (*Q. boissieri*) was higher and wider in the absence of grazing, but lower and narrower under grazing than that of the evergreen *Q. calliprinos* (Fig. 1). Evergreen oaks are known to have higher lignin content in their leaves than deciduous oaks (Castro-Díez et al., 1997).

Perevolotsky and Haimov (1992) found similar effects when comparing regrowth rates of *Q. calliprinos* and another evergreen species *Phillyrea latifolia*. When intensive trimming was followed by grazing, the regrowth rate of basal shoots of *Q. calliprinos* was significantly higher than that of *Phillyrea latifolia* (Perevolotsky and Haimov, 1992), implying that *Q. calliprinos* trees have regrowth advantage under grazing not only over deciduous but also over other evergreen species.

The use of Relative horizontal regrowth corrected for the differences in initial widths among trees. Relative horizontal regrowth was significantly affected by grazing and tree species with nearly significant interaction, indicating a species-specific response. *Quer-*

Table 1
Within subject two-way ANOVA (SPSS 17: Mixed Models, Linear) testing the effects of cattle grazing, tree species and their interaction on (A) canopy height (B) canopy diameter and (C) Relative horizontal regrowth of' the re-growing canopies of *Crataegus aronia, Pistacia palaestina*, *Quercus boissieri* and *Q. calliprinos* trees, three years after canopy removal. Significant effects are presented in bold.

Source	Numerator df	Denominator df	*F*	*p*
(A) Canopy height				
Intercept	1	5.523	166.569	<0.001
Grazing	1	5 569	**42.403**	**0.001**
Species	3	4.441	**7.666**	**0.032**
Grazing * species	3	4.569	1.500	0.330
(B) Canopy diameter				
Intercept	1	6.894	306.799	<0.001
Grazing	1	7 322	**40.683**	**<0.001**
Species	3	5 328	**15.160**	**0.005**
Grazing * species	3	5.978	4.571	0.054
(C) Relative horizontal regrowth				
Intercept	1	14.874	286.863	<0.001
Grazing	1	14.874	**29.740**	**<0.001**
Species	3	9.839	**8.049**	**0.005**
Grazing * species	3	9.839	3.519	0.058

Table 2
Spearman correlation coefficients (r_s) between canopy height and canopy diameter of the re-growing *Quercus calliprinos* trees ($N = 146$), one year after canopy removal, and their pre-removal parameters.

		Pre-removal parameters			
		Canopy diameter	Number of stems	Average stem diameter	Diameter of the thickest stem
Canopy height	r_s	0.246	0.367	NS	0.247
	p	0.003	<0.001		0.003
Canopy diameter	r_s	0.473	0.623	0.165	0.311
	p	<0.001	<0.001	0.046	<0.001

NS = no significant correlation.

cus calliprinos Relative horizontal regrowth was less affected by grazing than that of the two other most important species on the site (by percentage cover), *Quercus boissieri* and *Pistacia palaestina* which partially support our second prediction. *Pistacia Palaestina*, leaves are known for their low tannin content and palatability to goats (Kababia, 1998). Although Relative horizontal regrowth of *P. palaestina* remained relatively high in the grazed plots, it differed most from the ungrazed plots; its canopy height under grazing was the lowest, indicating the greatest effect of grazing (Fig. 1). *Crataegus aronia* was found to be less affected by grazing (Fig. 1). The main protection of *C. aronia* is by its aposematic thorns that are a common defense mechanism against grazing by large herbivores, a characteristic of deciduous trees of the Rosaceae such as *C. aronia* and *Pyrus syriaca* (Lev-Yadun and Ne'eman, 2006), which are frequent in the *Quercus-Pistacia* association in the higher mountains in Israel (Waisel et al., 1978). However, the relatively high regrowth rate of *C. aronia* under grazing might be due to the fact that the grazing in our experimental plots occurred mainly during summer while the diet of cows grazing in Mediterranean woodland changes between seasons. Cows consume *C. aronia* in late spring but not in the summer, while *Q. calliprinos* and *P. palaestina* are consumed mostly during summer (Brosh et al., 2006). The different responses to grazing of the evergreen and the deciduous oaks, along with the different responses of *P. palaestina* and *C. aronia* demonstrate the variability in the efficiency of the anti-grazing defense mechanisms and suggest that no single plant trait can fully explain the response to grazing.

We found positive correlations between the size of the regrowing canopy of *Q. calliprinos* and most of its pre-removal dimensions (Table 2). These results demonstrate faster regrowth after cutting in large individuals than in small ones. Apparently, larger trees possess higher carbohydrate reserves in their roots, which support their vigorous post-disturbance regrowth (Canadell and Lopez-Soria, 1998; Malanson and Trabaud, 1988; Bond and Midgley, 2001). However, this feature of *Q. calliprinos* was not found in all other species in our study as well as in *Erica australis* (Cruz et al., 2003). The results indicate also the importance of the large number of stems, characteristic of *Q. calliprinos* trees, for post-disturbance survival and regrowth.

In support of our third prediction, we found species-specific differences in post-disturbance regrowth height and diameter growth rates (Fig. 1). The correlations indicate differences in the factors affecting the regrowth rates of the different species. For instance, the canopy diameter of *S. officinalis* correlated with its pre-treatment thickest stem diameter and average stem diameter, but not with the number of stems or canopy diameter. Only canopy diameter of *P. palaestina* correlated with its pre-treatment number of stems, while canopy height was almost constant. canopy height of *C. aronia* correlated negatively with its pre-removal canopy diameter, while no correlations were found for its canopy diameter. *Quercus boissieri* and *P. syriaca* showed no correlation between their regrowth and pre-removal dimensions. The low number of individuals might explain some of the non-significant correlations, but *S. officinalis* yielded significant correlations with only five individuals, thus small sample size was probably not the main cause of the lack of correlations in *Q. boissieri* and *P. syriaca*.

The results demonstrate the impressive resilience of the Mediterranean maquis trees to extreme disturbance, as almost all trees survived canopy removal. Our results indicate that the absolute regrowth rate of the dominant evergreen *Q. calliprinos* after cutting and under grazing is higher than that of its accompanying deciduous species. This attests its higher resilience, which is a clear advantage under the long human disturbance regime in the eastern Mediterranean basin; this trait could even be the result of selection under a long human disturbance regime (Naveh, 1975, 1990). The results suggest that *Q. calliprinos,* under the combination of cutting and grazing in Mediterranean maquis has a relative regrowth advantage, increasing its relative cover and dominance, causing a decrease in landscape diversity by further reducing the relatively low cover of deciduous species and other tree species.

4.2. *Management implications*

Closed, dense and shady woody Mediterranean vegetation has lower plant and animal diversity than a heterogeneous one consisting also of open and sunny patches where annual herbaceous pants grow (Naveh and Whittaker, 1979; Tews et al., 2004). Therefore, the current approach of conservation management proposes using cutting, trimming and mainly grazing in Mediterranean maquis areas for preserving high biodiversity, by keeping or creating open patches in the dense maquis (Perevolotsky, 2005). We argue that due to the differential responses of the tree species to grazing, these actions may have a long-term negative effect on landscape and habitat diversity by increasing the relative cover of the evergreen *Q. calliprinos* at the expense of other tree species, mainly the deciduous ones. The canopy of *Q. calliprinos* has a strong negative effect on herbaceous plant species richness (Agra and Ne'eman, 2009), which is the plant life form with the largest contribution to plant diversity in the Mediterranean flora (Naveh and Whittaker, 1979). This negative effect is created because *Q. calliprinos* casts deep shade under its canopy during the entire year and a dense cover of slow decomposing leaf litter (Cornelissen, 1996). In contrast, deciduous trees admit sunlight to the ground during winter, which is the main growing season for herbaceous plants. In general, reduced landscape patchiness could lead to a consequent decrease in species diversity (Bascompte and Rodríguez, 2001).

Increasing the relative cover of evergreen trees in general, and of *Q. calliprinos* in particular, will negatively affect herbaceous species diversity, which runs counter to the aim of biodiversity conservation management regime. Therefore, an appropriate management regime must be implemented. Considering our study case of *Q. calliprinos* in Israel, we assert that to protect landscape and species diversity in Mediterranean ecosystems, when cutting is applied in combination with grazing, special care must be paid to trees other than *Q. calliprinos* that are more negatively affected by such disturbances. For instance, in east Mediterranean maquis, because of seasonal changes in the diet of cattle (Brosh et al., 2006), summer grazing might give a relative advantage to some deciduous tree species.

Acknowledgments

We thank the Israel Science Foundation and the Eshkol Fund, Israel Ministry of Science, for their financial support, the Nature and Park Authority for their permission to establish the LTER plots, A. Amitay for his help in establishing the research plots, L. Blaustein and three anonymous reviewers for their comments and the University of Haifa for awarding a Ph.D. fellowship to H.A.

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