Applied Vegetation Science **18** (2015) 261–271

Managing cattle grazing and overstorey cover for the conversion of pine monocultures into mixed Mediterranean woodlands

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Keywords
Exclosures; Natural regeneration; *Pinus brutia*; *Pistacia lentiscus*; *Quercus ithaburensis*; Silviculture; Thinning; Understorey

Nomenclature
Feinbrun-Dothan & Danin (1991)

Received 29 April 2014
Accepted 25 October 2014
Co-ordinating Editor: David Ward

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Abstract

Question: A large proportion (70%) of coniferous forest area in Israel is used for livestock grazing. Recently, the possibility of managing these monospecific plantations to form mixed conifer–broad-leaved woodlands via natural regeneration processes has been considered. In light of this we pose the question, how does the interaction of cattle grazing and overstorey thinning (hereafter, thinning) affect natural regeneration in east Mediterranean pine plantations?

Location: Menashe region, Mediterranean Israel (rainfall = 600 mm·yr^{-1}).

Methods: The experiment was carried out in a mature (50 yr) *Pinus brutia* plantation. Ten plots (0.25 ha) were selected, representing thinned (five plots, ≈100 trees·ha^{-1}, leaf area index, LAI≈3) and non-thinned (five plots, ≈230 trees·ha^{-1}, LAI≈6) forest patches. Paired 100-m^2 subplots were positioned within each plot, one of which was fenced to exclude cattle grazing while the other remained available for grazing. Recruitment, growth and shoot water potential of pines and broad-leaved tree species were measured after 10 yr of grazing exclusion.

Results: The density of newly emerged (up to 3-mo-old) pine seedlings was decreased by thinning but not affected by grazing. However, pine sapling (established seedlings) density and height were increased by thinning and decreased by grazing. Sapling density of the dominant native oak *Quercus ithaburensis* was reduced by both thinning and grazing. Thinning enhanced the growth of *Q. ithaburensis* saplings while grazing restricted their height. Grazing and thinning had no significant effect on the total sapling density of broad-leaved tree species, but grazing restricted their height and reduced species richness. Grazing reduced topsoil water content in non-thinned plots but had no effect in the thinned plots. Grazing increased the water potential of pine seedlings while thinning reduced it. Both grazing and thinning had no effect on the water potential of mature *Pistacia lentiscus* shrubs.

Conclusions: Natural regeneration within east Mediterranean pine plantations is limited by both dense overstorey cover and cattle grazing. While grazing exclusion is necessary for the establishment and early growth of recruits, reintroduction of grazing at later phases may facilitate the development of young forests by controlling competition.

Introduction

First-generation forest plantations, the result of an afforestation enterprise carried out over the last 80 yr, are distributed within the Mediterranean zone of Israel over ca. 100 000 ha. These forests are primarily composed of pine species, of which the most common are the native *Pinus halepensis* Mill. and exotic *Pinus brutia* Ten. Both species were proven highly suitable for afforestation in degraded water-limited Mediterranean habitats (Oliet et al. 2002; Esen et al. 2003). Planted pine forests in Israel are multifunctional; they are managed to provide a variety of benefits, of which wood production is of minor importance (Osem et al. 2008). Livestock grazing is an important form of land use in these plantations. While forest areas providing forage and husbandry are beneficial to livestock economy, grazing is considered highly useful as a means of fuel load control and fire hazard reduction (Ne'eman et al. 1997).

Recently, as many of the first-generation pine plantations in Israel approach the end of their life span, the issue of regenerating these forests based on natural regeneration processes has become central (Osem et al. 2008, 2009). As both pine species as well as a variety of native broad-leaved species are regenerating quite vigorously (Osem et al. 2009, 2013; Hibsher et al. 2013) in the understorey of the pine plantations, the opportunity for converting these simply structured monocultures into mixed broad-leaved–conifer woodlands is being seriously considered (Osem et al. 2008). However, very little is known about the impacts of livestock grazing on natural regeneration processes in Mediterranean pine forests.

Large mammalian herbivores have been recognized as an integral part of forest systems, and have a profound effect on their structure and dynamics (Hester 2000). As grazers actively select preferred plant species (Noy-Meir et al. 1989; Osem et al. 2004), the regeneration and development of plant species in the forest understorey may either be hampered directly through consumption and physical damage (Zamora et al. 2001; Kuiters & Slim 2002; Carmona et al. 2013), or may be promoted indirectly as a result of competition release (Belsky & Blumenthal 1997; Posada et al. 2000; Darabant et al. 2007; Khishigjargal et al. 2013). Grazing effects on natural regeneration may also be the outcome of soil disturbance (e.g. soil compaction; Trimble & Mendel 1995; Hamza & Anderson 2005), redistribution of nutrients (Bokdam & Gleichman 2000) as well as seed dispersal (Gill & Beardall 2001; Cosyns et al. 2005). Therefore, grazing may have profound consequences with regard to the composition and spatial arrangement of natural regeneration in forests.

The impacts of livestock grazing on natural vegetation systems of the Mediterranean have been addressed quite extensively (see e.g. Noy-Meir et al. 1989; Osem et al. 2004). Much less attention has been directed towards Mediterranean forest plantations in general and their regeneration and succession in particular. The role of forest overstorey cover in determining processes and feedback loops related to understorey dynamics in east Mediterranean pine forests has been discussed previously (Osem et al. 2013). Manipulation of forest overstorey cover is widely accepted as a principal silvicutural tool in manipulating above- and below-ground resource availability for regeneration and development in the forest understorey (Prévosto et al. 2011; Osem et al. 2013). Within this context, grazing can be seen as an additional factor as well as a silvicultural tool for manipulating the distribution of available resources among the forest understorey components. Moreover, the effect of grazing on natural regeneration may diverge across contrasting resource availability levels, as determined by overstorey canopy cover (Randall & Walters 2011).

First-generation pine plantations being utilized as livestock grazing areas could be considered as novel and unique silvopastoral systems. The development of a silvicutural strategy for regenerating these forests is crucial to their sustainability. Such a strategy would likely combine overstorey and grazing manipulation. However, very little is known about natural regeneration dynamics in east Mediterranean forests and the ways in which this is affected by overstorey cover and grazing.

This study was designed to investigate the interactive effects of cattle grazing and overstorey thinning on natural regeneration in planted Mediterranean pine forests. We focused on the following response variables: (i) *Pinus brutia* regeneration; (ii) broad-leaved tree regeneration; and (iii) soil water availability.

Regeneration of coniferous and broad-leaved tree species in the pine forest understorey was compared across two treatments: grazing exclusion for 10 yr and a grazed control. Paired subplots representing the two grazing treatments were nested within forest plots differing in overstorey canopy cover. Variation in soil water availability was assessed in order to better understand the interactive effects of overstorey cover and grazing on natural regeneration.

Methods

Site

The study was performed in the Mount Horshan Forest area located in the Ramat Menashe region (34°59′58 E, 32°35′14 N) of Israel. The climate is typical east Mediterranean; according to Israel Meteorological Service (IMS) data, average annual rainfall is about 600 mm, concentrated mainly from December to March. The drought season is long, typically about 6 mo with no rain. Daily average temperatures range from 11 °C in winter to 26 °C in summer. The elevation is 170 m a.s.l. Local soils are bright mountain rendzinas, which developed on soft chalk and marl (based on the Geological Survey of Israel). The typical native vegetation in this region is sparse woodland dominated by *Quercus ithaburensis* accompanied by *Quercus calliprinos*, *Pistacia palaestina*, *Pistacia lentiscus* and *Styrax officinalis*. The experiment was carried out in a mature *Pinus brutia* (Cyprus pine) forest. Since the early 1970s this Mediterranean pine species, exotic to Israel, has gradually replaced the native *Pinus halepensis* as the leading conifer

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Doi: 10.1111/avsc.12152

used for afforestation in Israel. Plantations of *P. brutia* have proven highly successful within a wide range of habitat conditions throughout Mediterranean Israel. Vigorous post-fire as well as fire-free natural regeneration has been observed in parts of these plantations (Osem et al. 2013). In order to optimally realize the effects of grazing and overstorey cover on forest regeneration, we selected a forest site with high potential for natural regeneration of *P. brutia* as well as a variety of native broad-leaved tree species. According to forest service documentation, the study area was subjected to controlled cattle grazing since 1990. Based on local foresters' knowledge, this area was under livestock grazing of varying intensity for decades prior to any documentation. Since 1990, cattle stocking rate has increased, gradually reaching a level of 87 grazing days $ha^{-1}\cdot yr^{-1}$ within the last 7 yr including the study period. The herd, a breed mixture of Charolais, Brahma and Baladi, enters the forest area at the beginning of November and forages freely in the area until the end of April.

Experimental structure

A 50-yr-old *P. brutia* plantation (ca. 10 ha) was selected for the study. Average tree DBH and height were 32.5 ± 5.8 cm and 19.1 ± 0.8 m, respectively. The plantation has undergone two comprehensive thinning treatments, one at the age of ≈10 yr and the other at ≈20 yr. Since then a combination of natural mortality and limited silvicultural intervention (sanitation thinning, i.e. removal of dead trees) has resulted in the designated forest area exhibiting a patchy distribution of variable stand structure, ranging in density from four to 30 trees$\cdot ha^{-1}$, stem basal area (BA) of 4–23 $m^2\cdot ha^{-1}$, overstorey leaf area index (LAI) of 1.8–7.5 $m^2\cdot m^{-2}$ and overstorey cover (i.e. canopy projection) from 20% to 95%. The experiment began in the year 2000. Ten 50 m × 50-m plots (0.25 ha) were randomly selected, five of them from thinned forest patches (i.e. thinned plots – thinned within the last 20 yr – average density ≈100 trees$\cdot ha^{-1}$ and canopy projection ≈55%), and the other five from non-thinned patches (i.e. non-thinned plots – average density≈230 trees$\cdot ha^{-1}$ and canopy projection≈95%). In the centre of each plot two 10 m × 10-m subplots were situated; one of them fenced to exclude cattle grazing (ungrazed subplot) while the other remained open (grazed subplot). Thus, the experimental structure represented a split-plot design with thinned/non-thinned as the main plots and grazed/ungrazed as subplots. An area of 10 m × 10 m was practically the largest subplot size that could be attained. This was due to the limited area of thinned/non-thinned plots (50 m × 50 m) and the need to avoid inter-treatment marginal effects by keeping a 15-m buffer zone around the subplot borders. Measurements of recruitment and sapling size, soil moisture and plant water status were conducted during 2009–2010, 10 yr after grazing exclusion (2000).

Measurements

Overstorey characteristics

Stand density, average tree height and DBH were measured separately in each of the ten study plots. Density was determined based on total plot tree count, while height and DBH were measured in a sample of 20% or ten trees at least (the larger of the two). Average density was 233.3 ± 8.9 trees$\cdot ha^{-1}$ in the non-thinned plots and 100.4 ± 13.0 trees$\cdot ha^{-1}$ in the thinned plots. Average tree height and stem diameter were similar among the thinned (18.6 ± 1.18 m and 33 ± 10.1 cm, respectively) and non-thinned plots (19.6 ± 0.43 m and 32.0 ± 1.5 cm, respectively). To account for possible within-plot variation, LAI and canopy projection were measured at the subplot level over three evenly distributed 10-m transects. LAI was determined using the optical tracing radiation and architecture of canopies device (TRAC; Chen et al. 1997), while for overstorey canopy cover (canopy projection) a sighting tube was used (Jennings et al. 1999). Average canopy projection and LAI for the four different treatments were as follows: Non-thinned Ungrazed: 95.56 ± 2.22% and 6.22 ± 0.29; Non-thinned Grazed: 94.45 ± 2.68% and 5.93 ± 0.66; Thinned Ungrazed: 51 ± 6.7% and 2.81 ± 0.82; Thinned Grazed: 58.33 ± 4.20% and 3.1 ± 0.24, respectively. Thus, canopy projection and LAI were approximately twofold larger in the non-thinned than in the thinned plots but did not differ significantly among grazed and ungrazed subplots.

Natural regeneration

Seed rain

In order to account for possible variation in the soil seed bank, the seed rain of *P. brutia* was monitored at plot level in 2009. In each plot, four 40 cm × 67 cm seed traps were placed. The traps were randomly located within each plot and kept at least 10 m away from each other and 15 m from the plot borders. The trap containers were elevated above the ground on a metal pole covered with Rimifoot® glue (R. Jewinn & M. Joffe, Technochemical Factory, Tel-Aviv, Israel) to alleviate seed predation by climbing arthropods. The containers were covered with a metal net to prevent bird and rodent seed predation. The traps were emptied once every 60 d and undamaged seeds counted.

Seedling emergence

The density of newly emerged pine seedlings was measured by counting the total number of individuals in each subplot. The seedling survey was conducted at the end of the emergence season (late winter – March 2010). Winter seedling emergence (i.e. appearance of first seedlings) began in late December. Based on size and appearance, newly emerged *P. brutia* seedlings (up to 3 mo old) are easy to distinguish from saplings that emerged and established in previous years.

Pine recruitment

This survey was carried out in November 2009. Individuals that emerged in previous winters (i.e. had survived at least one dry season – May to October) were considered recruited saplings. The total number of saplings was counted in each subplot (Corona et al. 1998). Saplings were categorized into four height classes: 0–20 cm, 21–100 cm, 101–200 cm, 201–400 cm.

Pine sapling growth

Age vs height curves were established in order to compare patterns of pine sapling growth among treatments. For each grazing × overstorey thinning combination, 20 pine saplings representing the four height classes mentioned above (five individuals for each height class) were sampled. The exact height of each sapling was measured and its age determined via stem ring count at ground surface height.

Broad-leaved tree regeneration

The total number of saplings of each species was counted in each subplot. Saplings were categorized by height class, as described above. Canopy cover of broad-leaved tree saplings was measured within each subplot along three 10-m transects using the line intercept method (Osem et al. 2011).

Water availability

Soil moisture and plant water status were measured in order to assess the effect of grazing and overstorey thinning on water availability to the understorey vegetation. For soil moisture, four soil cores, 5 cm in diameter and 20 cm in depth, were collected in each subplot during late winter (March 2010), late spring (June) and summer (Aug). The soil samples were kept in a cooler and taken to the lab; they were sieved to remove stones and rough organic matter and then weighed prior to and after oven drying (105 °C). Gravimetric soil water content was calculated. For plant water status, predawn water potential was measured using a pressure chamber (PMS Instrument Co., OR, US; Turner 1988). In each subplot, five *P. brutia* seedlings and five twigs from five different mature shrubs of *Pistacia lentiscus* were measured. These measurements were conducted during the summer (Aug). Pine seedlings (5–6 mo old) were assumed to represent the upper 50–60 cm of the soil (Thanos & Doussi 2000), while mature *P. lentiscus* shrubs were assumed to represent deeper soil levels. This shrub species was selected as a representative of the established understorey woody vegetation due to its high abundance of well-developed mature individuals of comparable size over the entire experimental setup.

Statistical analyses

Analyses of variance (ANOVA) were used to analyse variation in regeneration and soil water parameters with respect to overstorey thinning treatments (thinned, non-thinned) and grazing (grazed, ungrazed). In order to adequately address the experimental design (split-plot), a nested statistical model was used (Grazing nested within Thinning). Assumptions for ANOVA were tested through both the Levene and Bartlett tests for homogeneity of variances and the Shapiro-Wilk test for normal distribution of error. Mathematical transformations of data were used when necessary to correct deviations from normality and/or homogeneity of variances. If assumptions for ANOVA were still not met, analyses of variance were conducted using rank-transformed data, as outlined in Conover & Iman (1981). The Tukey-Kramer HSD test was used for *post-hoc* comparisons. For the comparison of age vs height relationship in *P. brutia* saplings growing in the different Thinning × Grazing treatments, an analysis of covariance was applied with Grazing and Thinning as the main explanatory variables, Sapling height as covariate and Age as response variable. Figures throughout the text indicate the average ±SE.

Results

Pine seed rain and seedling density

Pine seed rain fluctuated throughout the study year (2009), ranging from ≈1000 to ≈ 9000 seeds·ha^{-1}·d^{-1}. Yearly average seed rain differed significantly (N = 10, P = 0.045) between the thinned (3050 ± 1108 seeds·ha^{-1}·d^{-1}) and non-thinned (4860 ± 1399 seeds·ha^{-1}·d^{-1}) forest plots. The density of newly emerged pine seedlings in the non-thinned forest plots during late winter (March 2010) was remarkable, reaching 150 000 seedlings·ha^{-1} on average (Fig. 1, Table 1). In the thinned forest plots it was nearly three-fold lower. Newly emerged seedling density was not found to be affected by grazing (Fig. 1, Table 1).

Pine recruitment

Under protection from grazing, pine sapling density was more than three-fold higher in the thinned (31 000 ± 11 000 recruit·ha^{-1}) than in the non-thinned (9500 ± 2500 recruit·ha^{-1}) forest plots. Grazing reduced the density of pine saplings by as much as 85% in the thinned plots and by 25% in the non-thinned ones. When considering height classes, the

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Doi: 10.1111/avsc.12152 © 2014 International Association for Vegetation Science

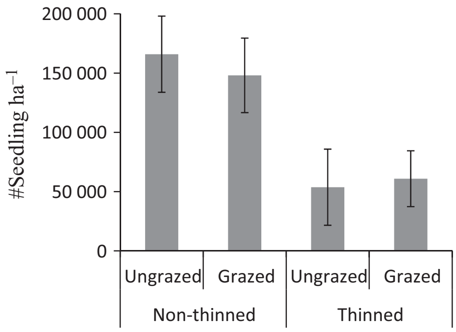

Fig. 1. Density of emerged *Pinus brutia* seedlings in Mount Horshan Forest during late winter (March 2010) as affected by cattle grazing and small-scale overstorey thinning. Bars indicate ±SE, N = 20.

Table 1. Two-way ANOVA (N = 20) of the effect of grazing (grazed, ungrazed) and overstorey thinning (thinned, non-thinned) on the density of newly emerged *Pinus brutia* seedlings during late winter (March) (A); gravimetric soil water content (20-cm depth) during August (B); and predawn twig water potential of *Pinus brutia* seedlings (≈6 mo old) during August (C). Mount Horshan Forest 2010.

Model	Factor	*df*	*F*	*P*
A				
R^2 = 0.59	Grazing	1		n.s.
	Thinning	1	6.09	*
	Graz × Thin	1		n.s.
B				
R^2 = 0.56	Grazing	1		n.s.
	Thinning	1	10.89	**
	Graz × Thin	1	7.13	*
C				
R^2 = 0.48	Grazing	1	13.7	***
	Thinning	1	29.21	****
	Graz × Thin	1		n.s.

*P < 0. 05, **P < 0.01, ***P < 0.001, ****P < 0.0001, n.s., not significant.

effects of overstorey thinning and grazing were even more pronounced. In the non-thinned plots, pine saplings were restricted to the 0–20 cm and 21–100 cm height classes, with grazing causing a moderate decrease in sapling density in these height classes (Fig. 2, Table 2). Pine saplings >1 m were not detected in non-thinned plots regardless of grazing. However, in the thinned plots, under protection from grazing, high sapling densities were found in both the 101–200 cm (ca. 6000 recruit·ha^{-1}) and the 201–400 cm (ca. 2000 recruit·ha^{-1}) height classes. Grazing in the thinned plots practically eliminated the existence of recruits >100 cm (Fig. 2, Table 2). When plotting age vs log height of pine saplings, significant linear relationships emerged in all Thinning × Grazing treatments (Fig. 3). Saplings of the same height were about two

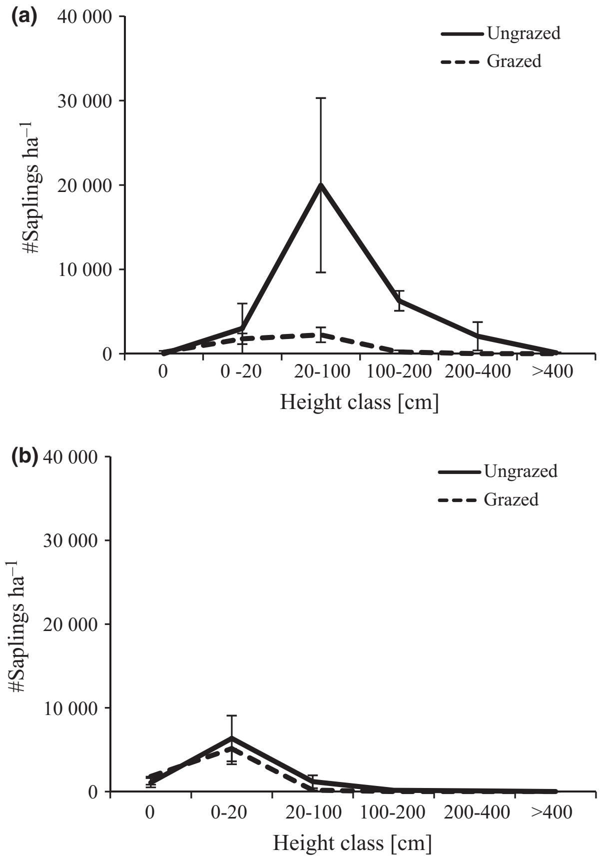

Fig. 2. Density of *Pinus brutia* saplings by height class as affected by cattle grazing in thinned (**a**) and non-thinned (**b**) plots. Mount Horshan Forest, November 2009. Bars indicate ±SE, N = 20.

times older in the non-thinned plots than in the thinned ones. However, no significant effect of grazing was found on the age vs height relationship.

Broad-leaved tree regeneration

Native broad-leaved tree species including *Quercus ithaburensis* (deciduous), *Quercus calliprinos* (evergreen), *Pistacia palaestina* (deciduous), *Rhamnus alaternus* (evergreen), *Styrax officinalis* (deciduous), *Phillyrea latifolia* (evergreen) and *Ceratonia siliqua* (evergreen) were found throughout the entire forest understorey, with no significant effect of either grazing or overstorey thinning on their total sapling density (ca. 1000–2400 trees·ha^{-1}). A significant grazing × height class interaction emerged, indicating that the density of broad-leaved saplings from 20 cm to 4 m in height was higher in the ungrazed than in the grazed subplots, while the density of saplings <20 cm was higher in the grazed than in the ungrazed subplots (Fig. 4, Table 2). Altogether, this resulted in the total cover of broad-leaved saplings being more than three-fold larger in the ungrazed than in the grazed (10.32 ± 2.20% vs 3.30 ± 0.92%,

Doi: 10.1111/avsc.12152

Table 2. Three-way ANOVA (N = 20) of the effect of grazing (grazed, ungrazed) and overstorey thinning (thinned, non-thinned) on the density of *Pinus brutia* saplings (A) and broad-leaved tree saplings (B) of different height classes (0–20 cm, 21–100 cm, 101–200 cm, 201–400 cm, >400 cm). Mount Horshan Forest, November 2009.

Model	Factor	*df*	*F*	*P*
A				
R^2 = 0.40	Grazing	1	6.06	*
	Thinning	1		n.s.
	Graz × Thin	1		n.s.
	H class	5	4.88	***
	H class × Graz	5		n.s.
	H class × Thin	5	2.61	*
	H class × Graz × Thin	5		n.s.
B				
R^2 = 0.51	Grazing	1		n.s.
	Thinning	1		n.s.
	Graz × Thin	1		n.s.
	H class	5	4.88	**
	H class × Graz	5	9.44	****
	H class × Thin	5		n.s.
	H class × Graz × Thin	5		n.s.

*P < 0. 05, **P < 0.01, ***P < 0.001, ****P < 0.0001, n.s., not significant.

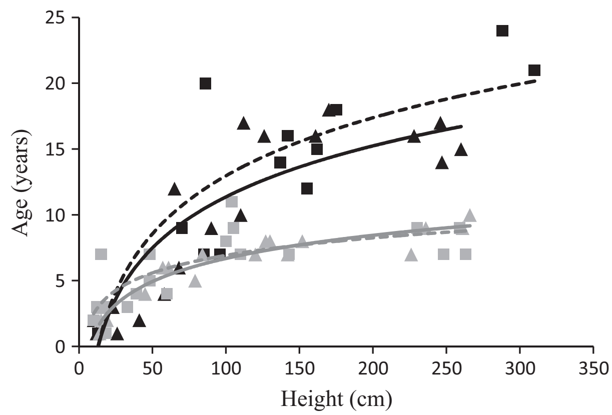

Fig. 3. The relationship between age and height in *Pinus brutia* saplings as affected by cattle grazing and small-scale overstorey thinning. ■ - - non-thinned grazed (N = 20, R^2 = 0.83); ■ - - thinned grazed (N = 20, R^2 = 0.57); ▲ — non-thinned ungrazed (N = 20, R^2 = 0.79); ▲ — thinned ungrazed (N = 20, R^2 = 0.92). Mount Horshan Forest, November 2009.

respectively; R^2 = 0.40, P = 0.01, N = 20) subplots. Broad-leaved sapling species richness was higher in the ungrazed than in the grazed subplots (3.40 ± 0.40 species 100 m^{-2} vs 1.80 ± 0.25 species 100 m^{-2}, respectively; R^2 = 0.40, N = 20, P = 0.008). No effect of overstorey thinning was found on the height distribution, cover or species richness of broad-leaved saplings (Fig. 4, Table 2). We looked separately at the sapling density of each broad-leaved species. The sapling density of *Quercus ithaburensis* was nearly

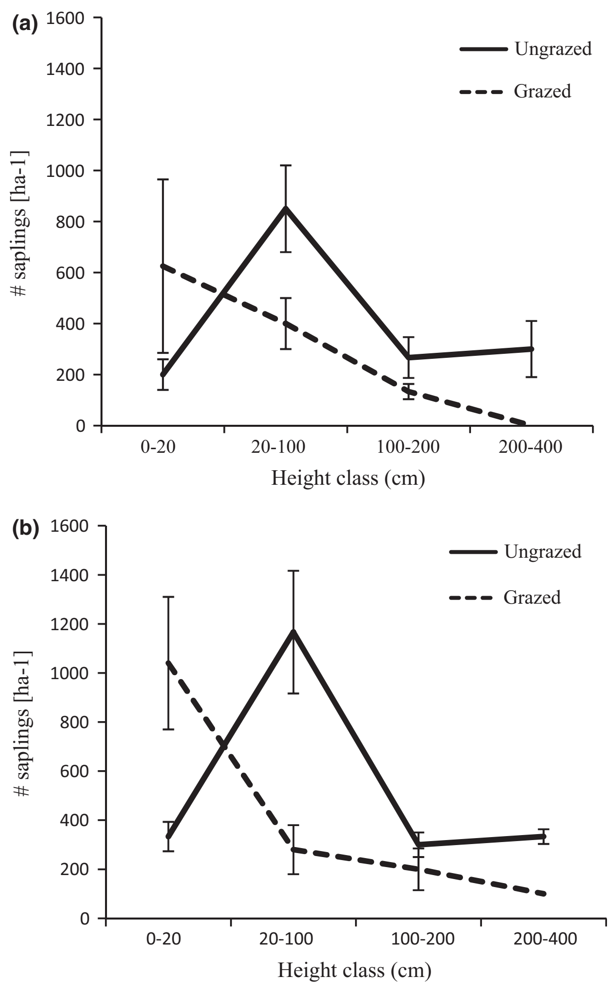

Fig. 4. Density of broad-leaved tree saplings by height classes as affected by cattle grazing in thinned (**a**) and non-thinned (**b**) plots. Mount Horshan Forest, November 2009. Bars indicate ±SE, N = 20.

three-fold larger in the ungrazed than in the grazed subplots (670.00 ± 156.38 trees·ha^{-1} vs 260.00 ± 76.30 trees·ha^{-1}, respectively' R^2 = 0.64, N = 20, P = 0.014). *Q ithaburensis* sapling density was four-fold larger in the non-thinned than in the thinned forest plots (658.33 ± 132.26.70 trees·ha^{-1} vs 175.00 ± 49.10 trees·ha^{-1}, respectively; R^2 = 0.64, N = 20, P = 0.002). No significant effect of grazing or overstorey thinning was found on the sapling density of any of the other broad-leaved tree species.

Soil water

In late winter and mid-spring (March, May), gravimetric soil water content, as measured in the upper 20-cm layer, was unaffected by either grazing or overstorey thinning. However, in late spring (June), an interactive pattern

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emerged; grazing reduced topsoil water content in non-thinned plots but had no effect in the thinned plots (Fig. 5, Table 1). Predawn shoot water potential of 6-mo-old pine seedlings during the summer (August) was significantly lower (more negative) in the thinned than in the non-thinned plots (Fig. 6, Table 1); additionally, it was significantly lower in the ungrazed than in the grazed subplots. Predawn twig water potential of mature *Pistacia lentiscus* shrubs was not affected by overstorey thinning or grazing (Fig. 6).

Discussion

Pine regeneration

In this study, we found the natural regeneration of *P. brutia* was restricted through dense pine overstorey cover and cattle grazing. Our pine seed rain and seedling emergence studies revealed that the restrictive effects of grazing and dense overstorey cover were not related to seed rain or emergence. Grazing had no effect on newly emerged

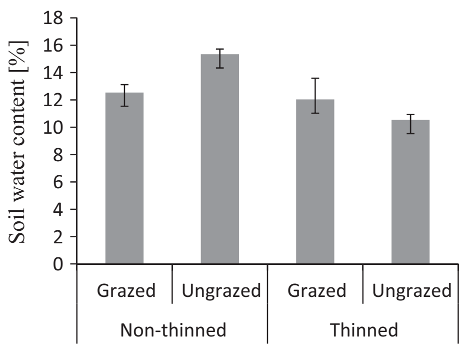

Fig. 5. Gravimetric soil water content (20-cm depth) in Mount Horshan Forest during August 2010 as affected by cattle grazing and small-scale overstorey thinning. Bars indicate ±SE, $N = 20$.

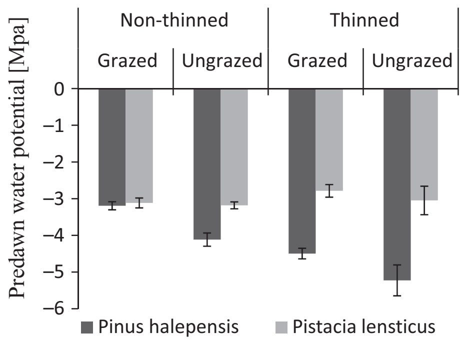

Fig. 6. Predawn shoot water potential of *Pinus brutia* seedlings (≈0.5 yr old) and mature *Pistacia lentiscus* shrubs in Mount Horshan Forest during August 2010 as affected by cattle grazing and small-scale overstorey thinning. Bars indicate ±SE, $N = 20$.

seedling density, while overstorey thinning even reduced seed rain and consequently seedling density. Thus, it might be inferred that both grazing and dense overstorey cover limit pine regeneration by negatively affecting the survival of pine recruits. The importance of seedling survival as a bottleneck for natural regeneration in east Mediterranean *P. halepensis* (a close relative of *Pinus brutia*) forests and the negative effect of dense overstorey cover on the early regeneration phases of this light-demanding species was discussed in previous work (Osem et al. 2013). Similarly, natural regeneration of *Pinus brutia* was found to depend on light availability (Boydak 2004). Here, we report for the first time, a substantial negative effect of cattle grazing on the regeneration of *Pinus brutia* in the forest understorey.

When considering variation in pine sapling age vs height, it became evident that dense overstorey cover inhibits pine sapling growth in the forest understorey. Nevertheless, we were not able to detect any effect of grazing on this relationship. Thus, it is possible that grazing influenced pine regeneration mainly through an acceleration of young recruit mortality. This finding is somewhat contradictory to that of Thanos & Doussi (2000), who considered *Pinus brutia* seedlings 'apparently grazing tolerant.'

Negative effects of grazing on natural regeneration have been found in various forest systems (Kuiters & Slim 2002; McEvoy et al. 2006; Carmona et al. 2013). However, reports of hampered regeneration of pine species caused by grazing are scarce (Zamora et al. 2001). In contrast, positive effects of grazing on pine regeneration have been reported in several forest systems (Belsky & Blumenthal 1997; Darabant et al. 2007). In addition, pine colonization of non-forest areas was promoted through grazing in several ecosystems (Kuiters & Slim 2002; Debain et al. 2005) including natural shrublands in Israel (Osem et al. 2011; Sheffer 2012). These positive grazing effects were mainly attributed to the promotion of pine seedling establishment through the elimination of competing vegetation.

Broad-leaved tree recruitment

The regeneration of native broad-leaved tree species in the understorey of monospecific pine plantations provides an opportunity to manage these systems towards the formation of mixed forests with increased diversity and structural complexity (Osem et al. 2008, 2009). The recruitment of *Quercus ithaburensis*, the dominant broad-leaved tree species in the study area, was significantly reduced through grazing; in agreement with a study conducted in nearby *Q. ithaburensis* woodland (Dufour-Dror 2007). Negative effects of grazing on the regeneration of other oak species were also reported in eastern and western Mediterranean silvo-pastoral systems (Alias et al. 2010; Carmona et al. 2013). However, Tyler et al. (2008)

reported contrasting effects in southern Californian woodlands, where cattle grazing improved the survival of regenerating oaks, while deer browsing reduced sapling survival. In contrast to our findings on pine recruitment, the sapling density of *Q. ithaburensis* was negatively affected through overstorey thinning. The capacity of this oak species to establish and persist in the understorey of mature pine plantations was demonstrated recently (Cooper et al. 2014).

Apart from *Q. ithaburensis*, no effect of grazing or overstorey thinning on the density of broad-leaved tree recruits was found. This indicates that local woodland species have the capacity to regenerate, establish and persist under dense pine overstorey cover as well as under cattle grazing (Vayreda et al. 2013). However, when considering sapling height distribution, it became evident that grazing has constrained growth of regenerating broad-leaved trees. Similar to our findings, Casasús et al. (2007) reported a significant increase in understorey woody biomass following cattle exclusion in a Mediterranean *Pinus nigra* forest in the Pyrenees. Negative effects of grazing on regeneration of Mediterranean broad-leaved tree species were also reported in woodlands of western Crete (Bauer & Bergmeier 2011). In contrast, in a study conducted across forests in Spain, grazing was not found to be an important factor determining the patterns of forest regeneration (Vayreda et al. 2013).

Water relations

In dry environments such as the east Mediterranean, the establishment of plant species is often restricted by water availability. Particularly crucial is the capacity of young recruits to survive the long and dry hot season during the first few years following emergence (Hibsher et al. 2013; Osem et al. 2013). Therefore, effects of grazing and overstorey cover on the water balance are of high relevance for understanding variation in natural regeneration of forests.

Our study revealed a complex picture in which the effects of overstorey thinning and grazing on soil water availability were interactive and variable across seasons and soil depth layers. In the upper soil layers (20 cm), during late spring, overstorey thinning and grazing effects were interactive, likely indicating a delicate balance involving microclimate and evaporative loss, water infiltration and vegetation water uptake. Overstorey thinning may affect topsoil moisture availability through accelerated evaporative loss (Raz-Yaseef et al. 2010; Prévosto et al. 2011; but see Filella & Peñuelas 2003; Maestre & Cortina 2004; Bellot et al. 2004) as well as enhanced understorey transpiration (Simonin et al. 2007; Knapp et al. 2014). Grazing can increase evaporative loss through soil exposure (i.e. litter cover removal; Sayer 2006; Scalon et al. 2013) and also have negative effects on topsoil hydrological properties (Belsky & Blumenthal 1997; Rasa & Horn 2013; Wu et al. 2014). In contrast, it might reduce understorey transpiration through vegetation removal (Frank 2003).

Unlike its complex effect on topsoil moisture, overstorey thinning had a consistent negative effect on predawn shoot water potential of 6-mo-old pine seedlings. This was not expected, since shading was shown to have a negative effect on root development of light-demanding pine species such as *Pinus brutia* (Broncano et al. 1998; Puértolas et al. 2009). Nevertheless, since the thinned forest plots have gone through pronounced understorey development during the last 10 yr or more (i.e. higher densities and larger sizes of regenerating trees in the non-thinned than in the thinned plots), it is likely that the understorey vegetation compensated for and even out-competed the effect of the dense pine overstorey on pine seedlings. Hence, the positive effect of grazing on pine seedling water potential found in our study was most likely the outcome of a reduction in competition through the elimination of understorey vegetation. This is in line with Karl & Doescher (1993), who reported positive effects of cattle grazing on the water status of conifer seedlings in southwest Oregon. We propose that the contrasting effect of grazing on topsoil water content vs pine seedling water status is related to soil depth. The upper soil layers are assumed to be most affected by evaporative loss and are thus more susceptible to soil exposure and disturbance. In deeper soil layers, as represented by the pine seedling water potential (root depth of 6-mo-old pine seedlings $\approx$ 50–60 cm; Thanos & Doussi 2000), water availability is more related to vegetation uptake and thus positively affected by grazing. Finally, when examining the water status of mature *Pistacia lentiscus* shrubs, no effect of overstorey thinning or grazing was detected. Mature individuals of this drought-resistant shrub species likely have well-developed deep root systems, making the effects of small-scale variation in overstorey cover, understorey development and grazing less pronounced. Our work demonstrates the complexity of the water balance in water-limited forests. More study is required to better understand the interactive effects of overstorey structure, understorey structure and soil disturbance on water relations in forests. In such studies it is recommended that manipulations, such as overstorey thinning and grazing exclusion, be applied at larger scales, allowing a more realistic representation of spatial processes.

Conclusions and practical considerations

We offer the following conclusions and practical considerations:

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1 Grazing reduced *Pinus brutia* regeneration mainly through accelerating recruit mortality.
2 Grazing reduced regeneration of the dominant native oak *Quercus ithaburensis* by significantly limiting sapling density and sapling growth in the forest understorey.
3 Grazing restricted the growth of other native broad-leaved tree species but had no effect on their capacity to establish and survive in the forest understorey.
4 Overstorey thinning increased *P. brutia* recruitment and decreased *Q. ithaburensis* recruitment, but had no clear effect on total broad-leaved tree recruitment.
5 Overstorey thinning enhanced *P. brutia* and *Q. ithaburensis* sapling growth but had no clear effect on growth of other broad-leaved tree species.
6 Exclusion of grazing for 10 yr promoted regeneration of pines and broad-leaved trees. As a result, >300 trees·ha^{-1} of broad-leaved saplings have established and crossed the browse line (height >2 m) in both thinned and non-thinned plots. It also led to >2000 trees·ha^{-1} of *P. brutia* saplings that established and crossed the browse line, although this only occurred in the thinned plots.
7 Grazing effect on topsoil moisture was inconsistent but caused an increase in water availability of deeper soil layers, as represented in pine seedling water potential.

Natural regeneration within east Mediterranean pine plantations is limited by both dense overstorey cover and cattle grazing. Thus, for forest renewal, a combination of overstorey thinning (regeneration thinning) and grazing exclusion should be implemented. Following regeneration thinning and depending on site conditions, a period of ca. 10 yr of grazing exclusion should be sufficient for establishment of regenerating pines and broad-leaved trees crossing the browse line (2 m). Understorey thinning should be applied during this period to determine sapling density and species composition. Reintroduced cattle grazing may then facilitate forest development by increasing water availability to target saplings (competition reduction), reducing fire hazard (fuel reduction on the forest floor and vertical separation) and promoting upright growth form of broad-leaved saplings (pruning effect).

Acknowledgements

We thank Maayan Marmelstein for help in the fieldwork, Jaime Kigel for useful advice on the project and the Israeli Forest Service, KKL, for funding this project.

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