

The herb layer restoration potential of the soil seed bank in an overgrazed oak forest

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We investigated the potential contribution of the persistent soil seed bank in post-disturbance restoration of the herb layer in a long-term overgrazed, mixed oak forest (NW Greece). We examined the impacts of grazing on plant richness and density in the soil seed bank in regard to the different dispersal and life strategy types of the herb layer taxa. Soil seed bank was qualitatively and quantitatively analyzed and contrasting plant guilds were defined according to life strategy type and dispersal mode. Soil seed bank differences between a) the upper and lower soil layers and b) plant functional guild pairs (ruderals vs. non ruderals, including typical forest taxa, and physically- vs. animal-dispersed plants) were statistically tested in overgrazed and sporadically grazed plots. Moreover, correlations in soil seed bank species dominance between overgrazed and sporadically grazed plots were examined by Spearman's Rank correlation. The majority of seeds were found in the upper (0-5 cm) soil layer. Seed density in the deeper (5-10 cm) soil layer was rather poor and did not differ significantly between overgrazed and sporadically grazed plots. In the upper soil layer, both seed density and plant species richness were significantly lower in the overgrazed plots. Overgrazing reduced both species richness and seed density of non-ruderal species in general and typical forest herbs in particular, while it did not affect ruderal species richness and density. Plant species richness and seed density of animal-dispersed taxa were reduced by overgrazing while physically-dispersed species were not affected; it is therefore concluded that large herds of grazers fenced in relatively small areas cannot act as efficient dispersal vectors of the former species. Our findings suggest that, upon cessation of grazing, the soil seed bank is rather inadequate to restore the herb layer of overgrazed forest sites.

Key words: life strategy type, dispersal mode, herb layer restoration, grazing, sub Mediterranean forest, wood pasture.

INTRODUCTION

The effects of grazing on forest ecosystems have been investigated mainly in regard to above-ground vegetation. Grazing alters species composition of both tree and herb communities (Rooney, 2009), changes soil chemical properties and soil structure (Binkley *et*

al., 2003), disturbs soil surface (Nomiya *et al.*, 2003), damages low shrub layer and tree shoots (Pépin *et al.*, 2006) and prevents growth of tree saplings and thus forest regeneration in general (Gómez *et al.*, 2003). Among the most significant effects of overgrazing on above-ground vegetation is the reduction of herb and shrub biomass in general (Merrill *et al.*, 2003; Joys *et al.*, 2004; Chaideftou *et al.*, 2009; Bergmeier *et al.*, 2010) and the reduction of herb species richness even of typical forest herbs in particular (Gómez *et al.*,

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2003; Stockton *et al.*, 2005). However the effect of overgrazing on typical forest herb species is less studied at the soil seed bank level (Bossuyt & Hermy, 2001; Godefroid *et al.*, 2006).

Restoration studies in grazed forests focus mostly on tree regeneration (Kuiters & Slim, 2002), referring to the seedlings and saplings of canopy trees as the targets of forest restoration efforts (Tárrega *et al.*, 2006). This is also true for studies using the soil seed bank as a restoration tool (Argaw *et al.*, 1999; Mengistu *et al.*, 2005). In contrast, restoration of the forest herb layer has received less attention including the potential role of the soil seed bank for restoration of the forest herb layer.

The role of seed banks in landscape mosaics and succession was investigated by Beatty (1991), who found that buried seeds originate as persistent remnants from past successional stages or travel by seed dispersal within and between communities. According to Fischer (1987), former successional stages are reflected by buried seeds in forest soils but only weakly.

The floristic significance of soil seed banks has been studied in forest ecosystems with specific emphasis on the growth habits of germinating species (Ashton *et al.*, 1998). Whigham (2004) concluded that increased abundance of white-tailed deer affected negatively woodland herbs, few species of which have been studied in detail. Therefore, there is a significant lack of ecological information needed to conserve and restore species in altered and threatened habitats (Whigham, 2004).

Plant species can be established by soil seed bank, which is fed by seed rain, involving various kinds of diaspore dispersal (Naaf & Wulf, 2007). The question of whether animal-dispersed species are inherently capable of forming a soil seed bank is important for assessing means aiming at restoring grazed woodland ecosystems. Is wood pasture practised at tolerable intensities or should management reduce grazing pressure by, for instance, implementing temporary or permanent grazing exclosures? High degrees of disturbance may lead to an increase of ruderal species in the soil seed bank of grasslands (Wellstein *et al.*, 2007). Schiffman *et al.* (1992) found that seeds of forest herbs were more common than those of ruderals in the soil seed bank. This result was attributed to the scarcity of nearby sources of ruderal and early-successional plants, and the inherently short longevity of seeds of forest species. In forests where controlled grazing is practiced, it would be useful to know which

species are competitors or ruderals and thus tolerate disturbance, irrespective of restoration measures.

The aim of our study is to investigate the potential of the soil seed bank in managing a mixed deciduous oak forest with damaged herb layer, after 30 years of overgrazing. We examine density and species richness of the soil seed bank in overgrazed and sporadically grazed forest sites. Furthermore, we investigate the impact of grazing on plant diversity within the soil seed bank, especially regarding the relative contribution of different plant guilds of the herb layer, classified according to seed dispersal mode and life strategy.

MATERIALS AND METHODS

Study area

The study area is located in Epirus (NW Greece; 40° 02' N, 20° 38' E) and is covered by coppiced sub-Mediterranean mixed oak woods on slightly acidic soils derived from argillite-flysch. Soil texture is clay-loamy to clayey (Tsaliki *et al.*, 2005). The study sites are characterized by *Quercus frainetto*, *Q. pubescens*, *Q. cer-ris*, *Q. trojana*, *Carpinus orientalis* and *Fraxinus ornus*, while *Phillyrea latifolia*, *Cotinus coggygria* and *Juniperus oxycedrus* are also important components of the woody vegetation (Tsaliki *et al.*, 2005). The forests represent subtypes of the south-western Balkanic association *Verbascum glabratum*-*Quercetum frainetto* (*Quercion frainetto*, *Quercetalia pubescentis*) (Bergmeier & Dimopoulos, 2008). The wider study area has been used as non-intensive wood pasture and coppice for centuries.

Altitude of the study sites range between 400 and 700 m a.s.l. The climate is sub-Mediterranean and the dry period lasts from May to early October while annual precipitation was 957 mm (measured for the period March 2006-February 2008). Mean monthly temperatures reach 5°C in winter (December) and 24°C in summer (July) according to the data obtained from the meteorological station established in the study area.

The study area includes an overgrazed woodland area and a sporadically grazed one. The overgrazed woodland area, which covers 112 ha, was fenced 34 years ago and was initially used as a game park. It is subdivided into two parts: 26 ha for wild boar (*Sus scrofa*, ~200 individuals) and 86 ha shared by various ruminants: fallow and red deer (*Dama dama* and *Cervus elaphus*, 400 individuals), roe deer (*Capreolus capreolus*, 50 individuals), mouflon (*Ovis musimon*, 100 individuals) and Cretan goat (*Capra hircus cretica*, 80

individuals). The sporadically grazed woodland area is ungrazed or only sporadically grazed by wild or free-roaming domestic animals. Both woodland areas are largely identical in topography and bedrock.

Thirty years of overgrazing in the game park have resulted in compressed soils, damaged tree bark, roots often protruding from the eroded soil, and in the near absence of herbs and grasses characterizing this forest type. The species composition of the adjacent, sporadically grazed woodland sites was that of a typical sub-Mediterranean forest of the region (Tsaliki *et al.*, 2005; Bergmeier & Dimopoulos, 2008).

Sampling design

In spring 2004 we selected six different plots reflecting different grazing pressure: 3 plots in the overgrazed forest (2 in the ruminant part, 1 in the boar part) and 3 plots in the sporadically grazed forest. Soil core sampling took place in late May 2004 after seed germination in the field had ceased and prior to the production of new seeds and eventual seed rain. This late spring sampling aimed to assess the persistent soil seed bank fraction only (Fenner & Thompson, 2005). Soil cores were sampled from two soil depths: 0–5 cm (upper layer) and 5–10 cm (deeper layer), to assess species richness, density and vertical distribution of the soil seed bank (Thompson, 2000). The use of soil cores of 5 or 10 cm depth is suggested to ensure result comparability (Csontos, 2007).

Within each of the six plots (150 m²), ten subplots (1 m × 1 m) were randomly selected. In each subplot, two soil samples were collected, one for each soil layer (a total of 120 soil samples), using a soil corer of 5 cm in diameter. To exclude seeds that might have accumulated on the soil surface (and thus obtain the soil seed bank in its strict sense) litter was removed before sampling. Each soil sample was bagged, protected from sunlight and transferred to the laboratory. Soil samples were dried and stored in the dark, at ambient temperatures, until late November 2004 to simulate actual field conditions (and potentially satisfy any after-ripening requirements by certain species; Finch-Savage & Leubner-Metzger, 2006). A three-month long, artificial cold stratification (chilling) was then applied where the soil samples were wetted and refrigerated at 3–5 °C, in the dark. Finally, the soil seed bank was quantitatively and qualitatively assessed by using the seedling emergence method (Thompson *et al.*, 1997). Coarse stones and vegetative material (roots and plant fragments) were removed and soil

samples were randomly placed onto metal trays (50 cm × 50 cm, one sample per tray) resulting in a 1.5 cm deep layer to approximate seedling distribution in the field. Using soil samples alone is considered advantageous as it gives simplicity and accuracy (Brown & Oosterhuis, 1981). The trays were placed in a germination incubator under average monthly temperatures ranging from 14 to 22 °C, frequently watered with a fine spray and illuminated for a 10-hour photoperiod daily. Seedling emergence conditions were monitored by data loggers. The first seedlings emerged three days after the start of the germination phase and germination (seedling emergence) lasted for two months.

Emerged seedlings were identified (about 80% of seed bank taxa at species level) and classified (two-way) into diaspore dispersal modes and life strategy types. Diaspore dispersal vectors were: wind, water, vertebrates (either through consumption or external attachment) or ants (according to diaspore type as indicated by Cornelissen *et al.*, 2003; Fenner & Thompson, 2005; based on data from Beattie & Lyons, 1975; Pakeman *et al.*, 2002; Czarnecka, 2005; Kiviniemi, 2008, and our own observations). Different dispersal modes were grouped in two classes: physically-dispersed and animal-dispersed. The latter group comprises species dispersed by all kinds of animals including ants, and the former group those dispersed by wind, water, etc. (Table 1). Plant strategy types were: stress-tolerators, ruderals, competitors or a combination of these (Grime, 2001; Klotz *et al.*, 2002). Different strategy types were also grouped in two major classes: ruderals and non-ruderals, the latter defined as those species that are not (entirely or partly) ruderals (Table 1). Typical forest species were identified using a database of sub-Mediterranean forest plots in Greece (Bergmeier & Dimopoulos, 2008).

Data analysis

Seed density is defined as the abundance of seeds in the soil and was calculated as the mean number of seeds per m² (for the particular soil depth); species richness was calculated as the number of different species in each subplot. Mean and standard deviations were calculated. One-way analysis of variance was performed to test a) the differences in species richness and density of soil seed banks for each dispersal and strategy type guild in overgrazed and sporadically grazed plots for either or both soil depths (0–5 cm and 5–10 cm), and b) the effect of soil depth on

TABLE 1. Herb taxa recorded in the soil seed bank and their features. Life strategy type (after Grime, 2001 and Klotz *et al.*, 2002; related taxa assessed accordingly): S = stress-tolerators, R = ruderals, C = competitors, CS, CR, SR, CSR, are combinations, na = not assigned. Dispersal mode (after citations listed in Table): Wi = wind-dispersed, U = unassisted-dispersed, Wa = water-dispersed; Wi, Wa and U are collectively classified as physically-dispersed (P). A = animal-dispersed (all types), D = animal-dispersed/consumed, At = animal-dispersed/attached, Ant = ant-dispersed. Classification into fruit and diaspore types follows Klotz *et al.* (2002), Cornelissen *et al.* (2003), Fenner & Thompson (2005). Typical forest herb species (according to Bergmeier & Dimopoulos, 2008) are underlined

Taxon	Fruit type/diaspore type	Dispersal mode/Literature	Strategy
<i>Campanula</i> sp.	capsule / seed	P (Wi) / Gondard <i>et al.</i> , 2006	na
<i>Carex flacca</i> Schreb.	nut / nut (utricle)	P (U) / Czarnecka, 2005	CSR
Caryophyllaceae	capsule / seed	W (U)	na
<i>Dactylis glomerata</i> L.	caryopsis / caryopsis	A (At) / Beddows, 1959	CS
<i>Dorycnium hirsutum</i> (L.) Ser.	legume / seed	A (Ant) / Aronne & Wilcock, 1994; Pausas & Verdú, 2008	CS
<u><i>Euphorbia amygdaloides</i> L.</u>	capsule / seed	A (Ant) / Guitián & Garrido, 2006	CS
<i>Galium aparine</i> L.	paired nut / hooked nutlet	A (At) / Strykstra <i>et al.</i> , 2002; Vittoz & Engler, 2007	CR
Gramineae	caryopsis / caryopsis	P / Czarnecka, 2005	na
<u><i>Inula salicina</i> L.</u>	achene / achene (with pappus)	P (Wi) / Chýlová & Münzbergová, 2008	CS
<u><i>Lathyrus laxiflorus</i> (Desf.) O. Kuntze</u>	legume / seed	A (D)	CS
<u><i>Luzula forsteri</i> (Sm.) DC.</u>	capsule / seed	P (Wi) / Gondard <i>et al.</i> , 2006	CSR
<i>Medicago lupulina</i> L.	legume / legume	P (U) / Czarnecka, 2005	CSR
<i>Parietaria judaica</i> L.	nut / nut with perianth	P (Wa) / Cuevas <i>et al.</i> , 2004	CSR
<i>Petrorhagia</i> sp.	capsule / seed	W	SR
<u><i>Silene italica</i> (L.) Pers.</u>	capsule / seed	P (Wi, <i>Silene</i> species) / Gondard <i>et al.</i> , 2006	CSR
<i>Solanum nigrum</i> L.	berry / berry	A (D) / Cuevas <i>et al.</i> , 2004	R
<i>Sonchus asper</i> (L.) Hill	nut / nut with pappus	P (Wi) / Jakobsson & Eriksson, 2003; Cuevas <i>et al.</i> , 2004	CR
<i>Trifolium arvense</i> L.	legume / calyx with legume	P (Wi) / Kiviniemi, 2008	SR
<i>Trifolium campestre</i> Schreb.	legume / calyx with legume	A (D) / Martínez-Ruiz & Marrs, 2007	R
<i>Trifolium physodes</i> Bieb.	legume / calyx with legume	A (D)	CSR
<u><i>Veronica chamaedrys</i> L.</u>	capsule / seed	P (Wi) / Pakeman <i>et al.</i> , 2002; Czarnecka, 2005	CSR
<u><i>Vicia cassubica</i> L.</u>	legume / seed	A (D)	CS
<u><i>Viola alba</i> Besser</u>	capsule / seed	A (Ant) / Beattie & Lyons, 1975; Czarnecka, 2005;	CSR

total seed density and species richness of the soil seed bank. Two-way analysis of variance was performed to test the possible interactions between a) grazing and dispersal type, and b) grazing and strategy type which affect the herb seed bank density and species richness. T-tests were used to determine the effect of dispersal mode, strategy type and typical forest herbs both in the herb seed bank density and species richness. Non-parametric Spearman's Rank correlations were estimated for the seed bank samples, in both soil depths, to assess species dominance differences between overgrazed and sporadically grazed sites.

RESULTS

A total of 28 species was identified in the soil seed bank and 23 (82%) of them were herbs (Table 1), with 8 of them being typical forest herb species. Half of the typical forest species were animal-dispersed, but only one third of the ruderals were animal-dispersed. Non-ruderals comprised 39% of the herb species of the soil seed bank while 61% were (partly or exclusively) ruderals; 57% of all 23 identified herb species were physically dispersed and 43% animal-dispersed.

A total of 116 herbaceous seedlings emerged from the germination experiment, i.e. a total herb density

of 985 seeds m^{-2} . Most of the seeds (696 seeds m^{-2} , 71%,) were found in the upper 5 cm of the soil, while seed density in the deeper soil layer (5-10 cm) was 289 seeds m^{-2} . This difference in seed density between the upper and deeper soil layer was statistically significant ($p < 0.01$).

Seed density in the overgrazed plots was 509 seeds m^{-2} while in the seed bank of the sporadically grazed plots we found a considerably higher density, 1460 seeds m^{-2} (Table 2). In both the upper and deeper soil layers, seed densities in the overgrazed plots were lower than the seed densities in the sporadically grazed plots (Table 2). Overgrazing did not affect significantly either the total seed bank density or species richness in the deeper soil layer (Table 3). In the upper soil layer, mean seed density and species richness significantly decreased with overgrazing (Table 3). Two-way analyses of variance confirmed that overgrazing affected the herb seed bank density and species richness in the upper soil layer, but not in the deeper one (Table 4).

Seeds of typical forest species contributed 52% to the total herb seed bank density. Both density and species richness of typical forest herbs in the seed bank decreased significantly by overgrazing in both the upper and deeper soil layers (Table 3).

TABLE 2. Mean seed bank density (seeds m^{-2}) in the herb seed bank; SD = standard deviations

Dispersal and life strategy type	Soil depth (cm)	Seed bank density (mean \pm SD)	
		Overgrazed	Sporadically grazed
All herbs	0-10	500 \pm 16	1460 \pm 38
	0-5	357 \pm 19	1036 \pm 27
	5-10	153 \pm 25	424 \pm 63
Physically dispersed	0-10	340 \pm 38	832 \pm 59
	0-5	238 \pm 14	509 \pm 49
	5-10	102 \pm 32	323 \pm 63
Animal dispersed	0-10	170 \pm 27	628 \pm 38
	0-5	119 \pm 19	526 \pm 38
	5-10	51 \pm 9	102 \pm 0
Non-ruderals	0-10	153 \pm 16	391 \pm 23
	0-5	85 \pm 14	306 \pm 28
	5-10	68 \pm 5	85 \pm 5
Ruderals	0-10	357 \pm 28	1012 \pm 65
	0-5	272 \pm 14	662 \pm 49
	5-10	85 \pm 27	340 \pm 60
Typical forest herbs	0-10	187 \pm 30	832 \pm 21
	0-5	153 \pm 25	662 \pm 25
	5-10	34 \pm 5	170 \pm 5

TABLE 3. One-way analyses of variance assessing the quantitative and qualitative effects of overgrazing on the soil seed bank in association to contrasting dispersal and life strategy guilds of the herb species

Dispersal and life strategy type	Soil depth (cm)	Seed bank density		Species richness	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
All herbs	0-10	54.069	0.002	15.077	0.018
	0-5	43.243	0.003	19.600	0.011
	5-10	1.600	0.275	0.727	0.442
Physically dispersed	0-10	4.947	0.090	0.450	0.539
	0-5	2.813	0.169	0.750	0.435
	5-10	0.966	0.381	1.000	0.374
Animal-dispersed	0-10	9.851	0.035	11.000	0.029
	0-5	9.290	0.038	17.286	0.014
	5-10	3.000	0.158	0.000	1.000
Non-ruderals	0-10	7.000	0.057	12.500	0.024
	0-5	4.971	0.090	3.571	0.132
	5-10	0.500	0.519	1.000	0.374
Ruderals	0-10	2.114	0.220	5.786	0.074
	0-5	5.813	0.073	6.400	0.065
	5-10	1.510	0.286	9.800	0.035
Typical forest herbs	0-10	30.723	0.005	11.000	0.029
	0-5	21.429	0.010	10.000	0.034
	5-10	32.000	0.005	49.000	0.002

Total herb seed bank density was not significantly different between the plant life strategy types ($t = 2.554, p = 0.051$) (Fig. 1). Ruderal seed density and species richness did not differ significantly with overgrazing (Table 3). Only ruderal species richness of the deeper soil layers differed significantly. Non-ruderal seed abundance did not differ significantly with

overgrazing but only non-ruderal species richness of the herb seed bank differed with overgrazing (Table 3). Plant life strategy appeared in the two-way ANOVA as a factor with influence on the species richness of the herb seed bank even in the deeper soil layers and interacted with the overgrazing factor (Table 4).

Seeds of physically-dispersed species contributed

TABLE 4. Two-way analyses of variance assessing the quantitative and qualitative effects of overgrazing on the soil seed bank detecting the interactions between overgrazing and either strategy type or dispersal mode

Dependent variable	Factor	Total (0-10 cm)		Upper (0-5 cm)		Deeper (5-10 cm)	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Richness	Grazing	12.250	0.008	13.235	0.007	1.800	0.217
	Strategy	12.250	0.008	9.941	0.014	9.800	0.014
	Grazing \times Strategy	1.000	0.347	0.529	0.488	9.800	0.014
Density	Grazing	13.906	0.006	10.368	0.012	1.695	0.229
	Strategy	11.886	0.009	8.192	0.021	1.695	0.229
	Grazing \times Strategy	3.094	0.117	0.800	0.397	1.298	0.288
Richness	Grazing	6.323	0.036	10.316	0.012	0.727	0.419
	Dispersal	0.129	0.729	0.211	0.659	0.182	0.681
	Grazing \times Dispersal	2.065	0.189	3.368	0.104	0.727	0.419
Density	Grazing	12.852	0.007	10.458	0.012	1.438	0.265
	Dispersal	1.984	0.197	0.235	0.641	1.438	0.265
	Grazing \times Dispersal	0.016	0.901	0.418	0.536	0.562	0.475

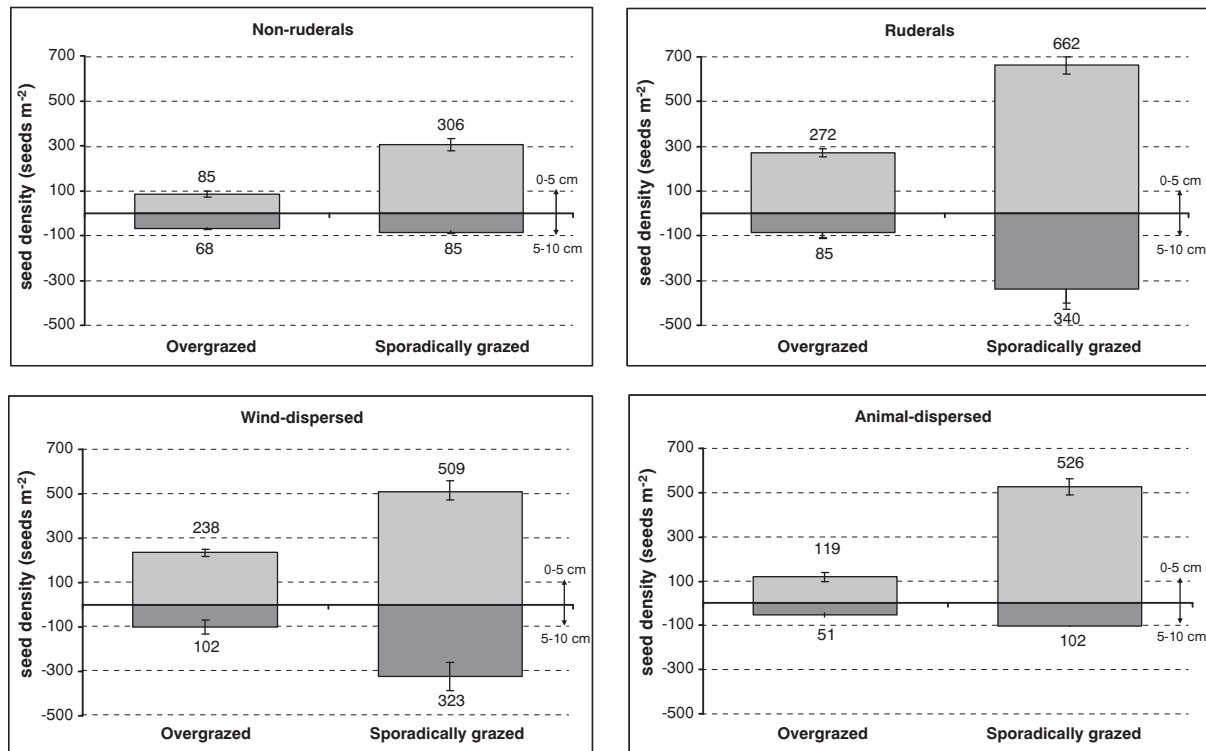


FIG. 1. Soil seed bank density of plants of different dispersal modes and life strategy guilds in overgrazed and sporadically grazed oak forest. Vertical bars represent \pm SE and numbers above and below bars represent mean density (seeds m^{-2}) in the respective sampling layer (0-5 and 5-10 cm deep).

59.5% to the total herb seed bank density (Fig. 1). Physically-dispersed seed density and species richness did not differ significantly with overgrazing in either upper or deeper soil layers. However, both animal-dispersed species richness and seed density decreased significantly with overgrazing in the upper soil layer (Table 3). Mean seed density and species richness of the herb seed bank did not differ between dispersal modes. Two-way ANOVA did not reveal any interaction between overgrazing and seed dispersal in any soil layer (Table 4).

Regarding community structure, species dominance did not change significantly ($r = 0.358$, $p = 0.000$) in either the upper soil layer ($r = 0.469$, $p = 0.000$) or the deeper one ($r = 0.255$, $p = 0.034$). In the control plots, *Euphorbia amygdaloides* (stress-tolerating, competitive forest species, ant-dispersed) and *Trifolium arvense* (stress-tolerating ruderal, wind-dispersed) co-dominated the soil seed bank of the sporadically grazed plots contributing to 19% of the respective soil seed bank. In the overgrazed plots the proportion of these species was only 10% in each soil seed bank. However, *Parietaria judaica* (stress-tolerating, com-

petitive ruderal, water-dispersed) dominated (20%) the soil seed bank of the overgrazed plots, but was absent from the sporadically grazed plots.

DISCUSSION

In our study area, about one third of the identified herb seed bank flora consists of typical forest herbs which contribute to the seed density and follow different strategies to survive and disperse. Seeds of these herbs are retained in the soil seed bank but decline in the overgrazed plots. After thirty years of overgrazing in the game park, the tree canopy is not significantly different from that of the sporadically grazed sites. However, the understorey herb layer significantly decreased in both vegetation cover and species richness (Chaideftou *et al.*, 2009). Thus restoration after cessation of overgrazing needs to focus on the forest herb layer.

The persistent seed bank displayed a characteristic vertical distribution pattern with seed bank abundance and species richness decreasing with soil depth. Such vertical distribution pattern has been observed in forest seed banks (Olano *et al.*, 2002) as well as in

that of grasslands (Funes *et al.*, 2003). The same pattern was observed in both overgrazed and sporadically grazed plots of our study area.

Even though vertical distribution patterns were similar in overgrazed and sporadically grazed plots, total seed bank density and species richness were significantly lower under the pressure of overgrazing, indicating that the restoration potential of this soil seed bank is rather limited. Overgrazing significantly affects the total seed bank in the upper soil layer but not in the deeper soil layer. This limitation of grazing effects to the upper soil layer was also demonstrated by Demel (1998). Regarding the dispersal and life strategy guilds, overgrazing effects on seed bank densities and species richness displayed the same pattern between the upper and deeper soil layers. Therefore, in what follows we shall refer to the total results and not to the upper or deeper soil layers separately.

Overgrazing did not only affect total seed bank density and richness but also the contribution of the different dispersal and life strategy guilds in the seed bank community. Typical forest herb species are shade-tolerant (e.g. *Euphorbia amygdaloides*) and we could expect that such species may be favoured by the well-developed tree canopy of the game park. In our case, overgrazing resulted in a significant decrease of seed bank density and species richness, as well as virtual disappearance of almost all herb species above-ground. Since seeds were no longer produced, an exhaustion of the soil seed bank may have taken place. The decreasing availability of typical forest species in the seed bank indicates its limited potential for short- and mid-term restoration of the herb layer after cessation of grazing.

Several studies in grasslands report that grazing favours ruderal species by increasing their density and/or species richness (e.g., Wellstein *et al.*, 2007). Brunet *et al.* (1996) found that grazing management leads to the establishment of ruderal species from the seed bank while pasture species in ungrazed oak stands did not decrease. In the studied oak forest, overgrazing did not affect the total density or the species richness of ruderals in the seed bank. A possible explanation may refer to the light demanding nature of ruderal species. In grasslands, grazing creates gaps in the vegetation coverage and thus leads to increased ruderal density. In the sampled area, overgrazing did not yet affect canopy structure significantly, and thus light demanding species did not enjoy the advantage that grazing offers in grasslands. The fact that, despite the decrease in total seed bank density, the seed density

of ruderal plants was not affected, may partly reflect the better dispersal ability of this particular guild (most of them are physically-dispersed) over longer distances than the respective of the typical forest herb species.

Seed dispersal mode seems to be less associated with overgrazing in our case study. Animal-dispersed species richness and seed density in the upper soil layer is significantly lower in the overgrazed plots. This may be surprising at first glance since it is documented in the literature that both density and species richness of animal-dispersed species increase with grazing in grasslands (Decocq *et al.*, 2004) and in forests (Heinken *et al.*, 2006). However, the present results may be explained by the fact that the herds grazing in the study area, especially boar digging the soil to feed, are restricted to (fenced in) a limited part of the forest with the result that external sources for animal-dispersed seeds are evidently lacking. So, while wild ranging grazers may act as long distance dispersal vectors for animal-dispersed species and thus enhance animal-dispersed density and species richness, this is not possible for fenced herds. The role of grazing for the restoration of animal-dispersed (excluding ant-dispersed) species richness might be highly dependent on whether the grazers are fenced in, or allowed to roam widely. Thus grazing should not be considered *a priori* as a tool for the restoration of animal-dispersed herbs.

Restoration efforts to maintain animal-dispersal function in the restored forest could possibly include the opening of inner fencings and allowing access to non-forested grassland and scrubland. This might enable grazers to behave as wild rangers and long distance vectors of species as in temperate forests of Europe (e.g. Heinken *et al.*, 2006). Considerable reduction in the numbers of animals in the game park or periodical limitation of their presence might be effective in restoring the herb layer. A similarly effective means could be collecting seeds of herbs from the adjacent woodlands and sowing them in the overgrazed game park with the animals subsequently excluded.

Community structure and dominance hierarchy of the soil seed bank is slightly changed between overgrazed and sporadically grazed plots. Species like *Parietaria judaica* which are abundant in the seed bank of overgrazed plots take advantage of the reduced density of other competing species under overgrazing pressure. Thus the former species increase in dominance in the overgrazed plots. Simultaneously, typical

forest herb species become less frequent (*Viola alba*) or even disappear (*Lathyrus laxiflorus*) under overgrazing pressure.

To sum up, the potential of the persistent soil seed bank to restore plant communities in long-term overgrazed woodland is rather limited. The seed bank has the potential to restore a pioneer community after severe disturbance rather than restore the pre-disturbance community (Dölle & Schmidt, 2009). The management implications of our findings are that if post-grazing restoration relies exclusively on the seed bank, the resulting herb layer will be significantly altered compared to that of an undisturbed forest. Seed banks are dominated by species of disturbed ruderal sites (Dölle & Schmidt, 2009), as ruderals grow rapidly, producing many seeds and have high seed bank persistence adaptations (Thompson *et al.*, 1997; Fenner & Thompson, 2005). Ruderal species will be favoured over non-ruderal species; thus the resulting herb community will be qualitatively and quantitatively enriched in ruderals at the expense of non-ruderals, including typical forest herbs. Therefore, an ecologically sound restoration management should take this into account by favouring non-ruderals, either through direct seeding of the under-represented species or soil transfer.

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