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Species richness in relation to phosphorus and competition in a Mediterranean dwarf-shrub community

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Abstract

Changes in species richness and productivity in a Mediterranean dwarf-shrub community were documented during 5 years following treatments intended to improve soil fertility and reduce shrub cover. Five treatments, replicated five times, were tested: (a) shrub cover reduction by selective herbicide application; (b) application of medium levels of phosphorus; (c) application of high doses of phosphorus; (d) a combined herbicide and phosphorus application; (e) an untreated control. Species were classified into nine functional groups according to life cycle, growth form and taxonomy: trees, shrubs, climbers, geophytes, perennial and annual grasses, annual legumes, perennial and annual forbs. The perennial and annual grasses, climbers, perennial forbs and geophytes showed no significant response to any treatment. Phosphorus application significantly increased the productivity and the richness of annual legume species, while herbicide treatment significantly reduced the frequency and richness of shrubs and increased those of annual forbs. Greater biomass production did not lead to a decrease in species richness; on the contrary, it was positively related to greater species richness, especially of the legume component.

Keywords: Annual legumes; Disturbance; Plant functional types; Resilience; Shrub encroachment; Soil nutrients

1. Introduction

The high species richness of the Mediterranean basin flora reflects the complexity of the habitat, caused by intensive human activity over millennia (Naveh, 1990; Lev Yadun et al., 2000). The long history of human intervention in the Mediterranean area has produced a much richer flora (including several different ecotypes) than in other Mediterranean-type regions of the world (Shmida, 1981; Noy-Meir, 1990). Traditional land utilization and interventions, including logging, bush clearing for cultivation, grazing and fire have not only added diversity to the landscape but have also induced a more complex web of nutrient and genetic flows (Mooney and Hobbs, 1994).

Diversity in Mediterranean ecosystems has been studied in relation to grazing (Noy-Meir et al., 1989; Hadar et al., 1999; Sternberg et al., 2000), clearing and herbicide applications (Sternberg et al., 1999) and environmental gradients ('beta diversity') (Puerto et al., 1990).

Most Mediterranean grasslands are on soils deficient in one or more plant nutrients (Seligman, 1996). Pasture production is poor in areas of low soil phosphorus availability and high cover of *Sarcopoterium spinosum* (L.) Spach (Henkin et al., 1998). Whereas phosphorus addition can cause a burst of productivity with an increase in plant cover of legume species (Osman et al., 1991, 1999; Henkin et al., 1998), little is known on how changes in productivity affect species richness,

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particularly in Mediterranean environments (Debussche et al., 1996). As a rule, high productivity tends to reduce species diversity (Tilman and Pacala, 1993; Janssens et al., 1998), especially when it is caused by nitrogen enrichment (Foster and Gross, 1998), but the effects of phosphorus enrichment are less well understood (Henkin et al., 1998).

It has been recognized that species with similar biological traits have similar responses to changes in habitat conditions (Gitay and Noble, 1997), and McIntyre et al. (1999) suggested that a set of traits could be used to compare functional responses of vegetation to disturbance. This approach enabled the relevant plant functional traits to be selected so that plants could be grouped according to plant functional types (plant functional groups) (Lavorel et al., 1997; Diaz et al., 1999). Moreover, species can be grouped into ''response types'' according to their response to an environmental factor such as availability of resources or disturbance regime (Diaz and Cabido, 2001; Lavorel and Garnier, 2002).

Within the general goal of increasing pasture productivity, the particular aim of the present study was to examine the responses of a mixed community of shrubs and herbaceous species to nutrient enrichment and dominant shrub removal, as expressed in the effects on species richness and species composition within and between plant functional types.

2. Materials and methods

The study site was located near Ein Yaaqov, 15 km east of the Mediterranean coastline in western Galilee, Israel (longitude 35°15′E; latitude 33°01′N; elevation 500 m.a.s.l.); its average annual precipitation was 798 mm. The soil was a terra-rossa, Xerochrepts, Haploxeroll (Dan et al., 1975; Soil Survey Staff, 1975) overlying Turonian hard limestone. The rangeland was typical Mediterranean 'batha' vegetation (dwarf shrubs, grasses and herb associations) dominated by prickly burnet dwarf-shrub (*S. spinosum*) (Zohary, 1973). Patches of relatively deep soil (occasionally as deep as 70 cm), some of them on abandoned terraces, were interspersed among rock outcrops. These gaps between the shrubs were dominated by herbaceous vegetation. The concentration of bicarbonate-extractable P in the terra-rossa soil at the study site was relatively low and limited the productivity of the site (Henkin et al., 1998). The terraces have not been cultivated for at least 50 years, but in the past were heavily grazed by goats. Since 1986 only beef cattle have grazed on the site, from the end of the growing season in spring and throughout the dry summer. The study was conducted in an enclosure protected from grazing during the winter/spring growing season. The present nomenclature follows Feinbrun-Dothan and Danin (1991).

The experiment was established in 1988 in an area of some 3 ha, dominated by *S. spinosum*, with herbaceous vegetation in open gaps between the shrubs. In order to increase pasture production, several treatments were established: (a) shrub removal (H1) by manual-sprayer application of a selective herbicide (2,4-D) as 1% acid equivalent in aqueous solution, in April 1988; (b) and (c) medium and high phosphorus enrichment (4.5 and 9.0 g P m^{-2}—P1 and P2, respectively) applied by hand in the autumn (October) of 1988, as a single application of enriched super-phosphate (25%); (d) a combined herbicide and medium phosphorus application; (e) an untreated control. For full details of the experimental design and treatments, see Henkin et al. (1998). The treatments were applied to 10 m × 10 m plots allocated at random in five replicated blocks. There were five treatment combinations per block, as follows:

Herbicide treatment	Phosphorus fertilization		
	Control (P0)	4.5 g P m^{-2} (P1)	9.0 g P m^{-2} (P2)
Control (H0)	P0H0	P1H0	P2H0
Spring 1988 (H1)	P0H1	P1H1	

The whole area was burnt in the summer (July) of 1988, after the herbicide application and before the phosphorus fertilization. The fire intensity was low, and only the dry structures of the dwarf shrubs were burnt. The herbicide was applied only over the woody vegetation, to kill both above-ground and underground structures.

At the end of each growing season (beginning of May) and before the experimental site was opened for grazing, the vegetation in each of the 10 m × 10 m plots was visually assessed, and all species in each plot were identified and recorded. This procedure was carried out in each of the five replications, each year for five consecutive years (1989–1993).

The presence or absence of species i in replication j' of treatment k was recorded by allocating the value 1 or 0, respectively, to the parameter (P_{ijk}). Consequently, the absolute frequency (F_{ik}) of species i in treatment k (F_{ik}), over the whole 5-year experimental period in all five replications (j') is:

$$F_{ik} = \sum P_{ij'k}, \quad j' = 1, 25$$

or, for any 1 year:

$$F'_{ik} = \sum P_{ij'k}, \quad j' = 1, 5$$

In any 1 year, the species richness (S) in a 10 m × 10 m plot in each treatment was defined as the mean number of species that were recorded in each of the replications x (5) years during the experimental period. Similar parameters were defined for species richness within each plant functional type

$$S_{jk} = \sum P_{ijk}, \quad i = 1, n$$