

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

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Received 22 February 2005; received in revised form 25 August 2005; accepted 23 September 2005

Available online 9 December 2005

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.

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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)	POH0	PIH0	P2H0
Spring 1988 (H1)	POH1	PIH1	

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:

$$F_{ik} = \sum P_{ij'k}, \quad j' = 1, 2, 3, 4, 5$$

or, for any 1 year:

$$F'_{ik} = \sum P_{ij'k}, \quad j' = 1, 2, 3, 4, 5$$

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

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

where n is the total number of species recorded in the data set. Similarly, species richness was defined for each of the plant functional types (plant functional groups).

The above-ground biomass on herbaceous sward patches between the *S. spinosum* shrubs was sampled in April at the end of each growing season. Five 25 cm × 25 cm quadrats were placed at random in each plot and all plant biomass down to ground level was harvested, oven dried at 75 °C and weighed.

Plant functional groups among the Mediterranean vegetation that characterized the experimental site were defined mainly according to life history, stature, and gross taxonomical features, and a total of nine plant functional groups were so defined. Herbaceous species were grouped into annual and perennial species, of which the annual species included annual grasses, annual legumes and annual forbs, and the perennial ones included: perennial grasses and perennial forbs. Woody species were divided into shrubs plus dwarf shrubs, climbers and trees. Geophytes formed one plant functional group. The population of trees in the study area was very small and their presence was not considered in the study. The effects of phosphorus fertilizer and herbicide treatments on overall species richness and on the species richness within each plant functional group were analysed by general linear model (GLM) procedures (SAS, 1994). A separate model for each year included block, phosphorus, herbicide, and the phosphorus × herbicide interaction as factors. An overall model for all years, which used repeated measures of analysis of variance (ANOVA), included the same factors plus year and block effects. The association between phosphorus treatments and frequency of each species in the H0 (no herbicide) treatments was evaluated with a χ^2 -test for independence (SAS, 1994). Similarly, the association between herbicide treatments and the frequency of each species in the P0 (no-phosphorus) treatment was tested. To prevent the introduction of random-sampling artifacts, species that occurred in less than 25% of the plots [$(F_{ik'} + F_{ik'') < 13$, $k' = P0 + P1$, $k'' = H0 + H1$] in either test were excluded from this analysis.

3. Results

During the experiment a total of 155 species were recorded at the site: 10% annual grasses, 5% perennial

Table 1

Means (and standard deviations) of overall species richness per 10 m × 10 m quadrat in the various treatments during the experimental period 1989–1993

Year	Treatment				
	POH0	PIH0	POH1	PIH1	P2H0
1989	27 (3.3)	28 (4.8)	25 (2.5)	26 (1.4)	31 (2.2)
1990	35 (3.7)	36 (6.5)	33 (4.0)	35 (3.3)	36 (2.9)
1991	35 (3.4)	39 (2.9)	40 (6.8)	41 (5.8)	45 (2.5)
1992	39 (6.3)	38 (4.9)	43 (1.6)	43 (3.9)	44 (4.1)
1993	43 (6.3)	43 (5.4)	47 (4.4)	48 (5.1)	46 (6.0)
1989–1993	36 (7.3)	37 (7.2)	37 (8.9)	39 (8.4)	40 (3.6)

P0 and H0: control; P1: P fertilization (4.5 g P m⁻²); P2: P fertilization (9 g P m⁻²); H1: herbicide application.

grasses, 26% annual legumes, 32% annual forbs, 7% perennial forbs, 8% shrubs + dwarf shrubs, 5% geophytes, 2% climbers and 5% trees. Annuals represented 68% of all species recorded. The annual grasses were *Avena sterilis* L., *Brachypodium distachyon* (L.) P. Beauv. and *Crithopsis delileana* (Schult. and Schult.f.) Roshev., and the dominant perennial grasses were *Hordeum bulbosum* L. and *Dactylis glomerata* L. The annual legumes comprised *Trifolium stellatum* L., *T. resupinatum* L. and *Scorpiurus muricatus* L. Amongst the 49 annual forbs the most common species were *Linum pubescens* Banks and Sol., *L. nodiflorum* L., *Hedypnois rhagadioloides* (L.) F.W. Schmidt and *Plantago cretica* L., and the dominant perennial forbs were the thistle *Eryngium creticum* Lam. and *Helichrysum sanguineum* (L.) Kostel. The main geophyte species present at the site was *Ornithogalum narbonense* L. *S. spinosum* and *Calicotome villosa* (Poir.) Link were the dominant dwarf shrubs, and these two shrub species, together with the annuals constituted more than 97% of the total plant cover (Henkin et al., 1999).

Phosphorus application showed no significant effect on overall species richness in this study (Table 1), but it significantly increased the species richness of annual legumes in all years (Tables 2 and 3 and Fig. 1). Compared with the control treatment, species richness of annual legumes in the PIH0 treatment (4.5 g m⁻²) increased by 17, 43, 53, 37 and 19%, respectively in the five successive years. The increased richness in legume species was even greater when the phosphorous concentration was doubled (P2H0),

Table 2

Means (and standard deviations) of species richness of main plant functional types per 10 m × 10 m quadrat in the various treatment during the 1989–1993

Plant functional type	Treatment				
	POH0	PIH0	POH1	PIH1	P2H0
Annual grasses	4.6 (1.9) a	4.9 (1.6) a	5.0 (1.7) a	4.8 (1.9) a	4.3 (2.3) a
Annual forbs	11.2 (3.7) a	10.6 (3.1) a	13.1 (3.2) a	12.9 (2.7) a	11.1 (3.3) a
Annual legumes	7.9 (2.9) c	12.0 (2.7) b	8.0 (3.1) c	12.0 (2.8) b	15.1 (2.3) a
Perennial grasses	4.1 (0.9) a	3.3 (1.0) a	4.0 (1.0) a	3.5 (1.2) a	3.3 (0.9) a
Perennial forbs	1.3 (1.1) a	0.8 (0.6) a	1.2 (0.9) a	1.4 (0.9) a	0.8 (0.9) a
Shrubs and dwarf shrubs	4.7 (1.65) a	3.8 (1.4) ab	3.2 (1.8) b	2.7 (1.7) b	4.6 (1.3) a

Treatments bearing the same letter are not significantly different at $P < 0.05$. P0 and H0: control; P1: P fertilization (4.5 g P m⁻²); P2: P fertilization (9 g P m⁻²); H1: herbicide application.

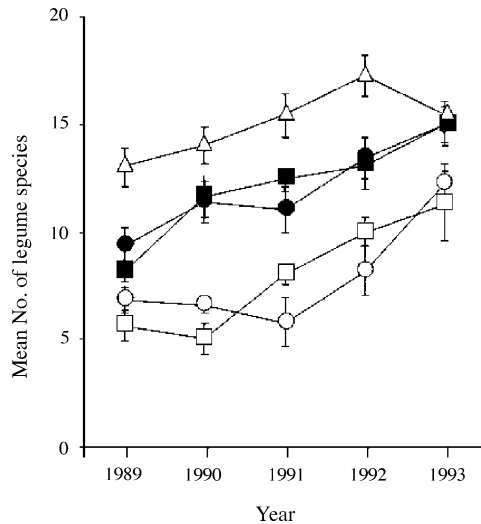


Fig. 1. The effects of phosphorus and herbicide applications on annual legume richness. Treatments: control (○), herbicide (□), medium phosphorus enrichment (4.5 g P m^{-2} , ●), herbicide + medium phosphorus enrichment (■), high phosphorus enrichment (9.0 g P m^{-2} , △).

with increases of 48, 53, 62, 52 and 21%, respectively. On average, phosphorus application increased the species richness of annual legumes by 41%. Species richness of these plant functional groups in the control treatment (P0H0) increased from 2.6 to 6.0 and from 8.2 to 12.0, respectively, during the 5 years of the study. Species richness of perennial grasses was not affected by phosphorus enrichment, except for a significant decrease in 1992 (Table 3), but the effect was not significant in the overall analysis (Table 3). Shrub species richness was not affected by phosphorus application during the 5 years of the study, but there was a continuous increase in the course of time (Table 3); this was mainly a reflection of the gradual recovery of prickly burnet after the fire and shrub control. Among the remaining plant functional groups (perennial forbs, climbers and geophytes) no significant effects of phosphorus enrichment were found.

Species richness among shrubs was significantly reduced by the herbicide treatment (Tables 2 and 3): the average

Table 4

Number of individual species^a (excluding trees) with significant ($P < 0.05$) responses of their frequency to phosphorus and herbicide application at the Ein Yaaqov site

		Phosphorus response			Total
		P+	P0	P–	
Herbicide response	H+	1 (1.6)	4 (6.3)	0 (0)	5 (7.8)
	H0	16 (25.0)	31 (48.4)	4 (6.3)	51 (79.7)
	H–	1 (1.6)	5 (7.8)	2 (3.1)	8 (12.5)
	Total	18 (28.1)	40 (62.5)	6 (9.4)	64 (100)

P–, H–: frequency reduced by phosphorus or herbicide effect, respectively. P+, H+: frequency increased by phosphorus or herbicide effect, respectively. P0, H0: no frequency response for phosphorus or herbicide application. Data represent numbers of species in each group and percentages of the total species tested (in brackets).

^a Species with a frequency greater than 25% ($F_{ik} > 6$).

number of shrub species during the 5-year study declined from 4.7 to 3.2 and, concurrently, the species richness of annual forbs increased from 11.2 to 13.1. Species richness of annual legumes, grasses, climbers and geophytes was not affected by the herbicide treatment (Tables 2 and 3). No significant interaction between herbicide and fertilizer treatments in their effects on species richness was found in any plant functional group.

The frequencies of several individual species showed significant responses to the phosphorus and/or herbicide treatments. A cross-classification of the 64 species with frequencies of at least 25%, into phosphorus- and herbicide-responsive groups within plots ($F_{ik} > 6$), showed that 28% of them responded positively to phosphorus applications by increasing their frequency (Table 4) whereas 9% responded negatively; 8% responded positively and 13% negatively to herbicide application (Table 4). The remaining species showed no significant responses to the herbicide or phosphorus application (80 and 62%, respectively). Among the species that responded positively to phosphorus fertilizer applications, 78% (14 of 18 spp.) were annual legumes; within this group, the most important ($P < 0.01$) were *Trifolium subterraneum* L., *T. echinatum* M.Bieb., *T.*

Table 3

Results of two-way and repeated measures ANOVA (P values) for functional groups over the 5-year study

Year	Shrubs		Perennial grasses		Annual legumes		Annual forbs		Total perennials		Total annuals	
	H	P	H	P	H	P	H	P	H	P	H	P
1989	0.0001	–	–	–	–	0.0017	–	–	–	–	–	–
1990	0.0004	–	–	–	–	0.0001	–	–	–	0.0402	–	0.0149
1991	0.0444	–	–	–	0.0383	0.0001	–	–	–	0.0481	–	0.0208
1992	0.0421	0.0202	–	0.0141	–	0.0002	0.0112	–	–	0.0113	–	–
1993	0.0431	–	–	–	–	0.0172	–	–	–	0.0312	–	–
Overall analysis	0.0022	–	–	–	–	0.0001	0.0177	–	–	0.0148	–	0.0055
	0.0001	–	–	–	0.0001	–	0.0001	–	–	0.0001	–	0.0001

Phosphorus application (P), herbicide application (H). Only significant values ($P < 0.05$) are presented. Results for climbers, perennial forbs, geophytes, annual grasses and all types were not included in this presentation as no significant differences were found. No significant $P \times H$ interactions or block effects were found, therefore, their results were not included, to aid clarity of presentation.

Table 5
Classification of species^a by significant responses ($P < 0.05$) to phosphorus and herbicide application at the Ein Yaagov site

	P+	P0	P-
H+	<i>Anthemis bormmuelleri</i>	<i>Biscutella didyma</i> , <i>Lagoecia cuminoideis</i> , <i>Theligonium cynocrambe</i> , <i>Vallerianaella vesicaria</i>	
H0	<i>Bromus alopecurus</i> , <i>Carduus argentatus</i> , <i>Lathyrus aphaca</i> , <i>Medicago polymorpha</i> , <i>Medicago rotata</i> , <i>Stachys distans</i> , <i>Torilis tenella</i> , <i>Trifolium campestre</i> , <i>Trifolium echinatum</i> , <i>Trifolium pilulare</i> , <i>Trifolium purpureum</i> , <i>Trifolium resupinatum</i> , <i>Trifolium subterraneum</i> ^b , <i>Trifolium stellatum</i> , <i>Vicia palaestina</i> , <i>Vicia peregrina</i>	<i>Aegilops geniculata</i> , <i>Astragalus epiglottis</i> , <i>Avena sterilis</i> , <i>Brachypodium distachyon</i> , <i>Bromus madriensis</i> , <i>Catananche lutea</i> , <i>Catapodium rigidum</i> , <i>Centaurea iberica</i> , <i>Clypeola jonthlapsi</i> , <i>Convolvulus arvensis</i> , <i>Coronilla scorpioides</i> , <i>Crepis aspera</i> , <i>Crithopsis delileana</i> , <i>Dactylis glomerata</i> , <i>Eryngium creticum</i> , <i>Galium judaicum</i> , <i>Hedypnois cretica</i> , <i>Hordeum bulbosum</i> , <i>Linum nodiflorum</i> , <i>Linum pubescens</i> , <i>Lolium rigidum</i> , <i>Lotus peregrinus</i> , <i>Ornithogalum narbonense</i> , <i>Picris altissima</i> , <i>Piptatherum blancheum</i> , <i>Polygala monspeliaca</i> , <i>Salvia fruticosa</i> , <i>Scorpiurus muricatus</i> , <i>Sherardia arvensis</i> , <i>Trifolium scabrum</i> , <i>Uruspermum picroideis</i>	<i>Anagallis arvensis</i> , <i>Plantago cretica</i> , <i>Poa bulbosa</i> , <i>Stipa bromioides</i>
H-	<i>Medicago coronata</i>	<i>Calicotome villosa</i> , <i>Crupina crupinastrum</i> , <i>Hymenocarpus circinnatus</i> , <i>Linum strictum</i> , <i>Sarcopoterium spinosum</i>	<i>Cistus creticus</i> , <i>Fumana arabica</i>

P-, H-: richness reduced by phosphorus or herbicide effects, respectively. P+, H+: richness increased by phosphorus or herbicide effects, respectively. P0, H0: no response to phosphorus or herbicide application.

^a Only ubiquitous species with frequency greater than 25% (trees were not included).

^b Overall frequency less than 25% but with a dramatic increase from 0% in the control to 36% in the P+ treatments.

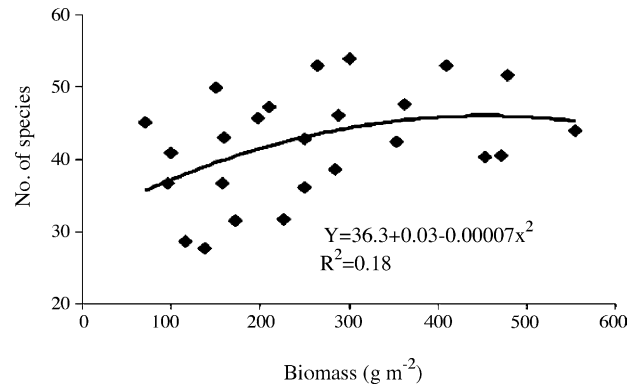


Fig. 2. Correlation between species richness and biomass production of all annual species.

resupinatum L., *Vicia palaestina* Boiss. and *Medicago coronata* (L.) Bartal. (Table 5). No annual legume decreased in frequency as a result of phosphorus applications.

The only species that increased because of herbicide treatment were forbs (Table 5), whereas the eight species that responded negatively to the herbicide application included four shrubs, two annual legumes and two annual forbs (Table 5).

A significant positive correlation ($P = 0.0407$, Fig. 2) between species richness and the biomass production was found in annual species: the species richness increased with increasing primary productivity in the various treatments. This positive correlation was even more significant ($P = 0.0010$) when annual legumes were considered separately. The greatest number of legume species was found in the most productive plots.

4. Discussion

The vegetation in most plant functional groups showed relatively small amplitudes of change in species richness after selective herbicide (2,4-D) and enhancement of resources availability by phosphorus enrichment. In terms of functional composition, the vegetation of this community appeared to be remarkably stable even under severe habitat manipulation, a finding that matches those of previous studies of Mediterranean vegetation (Lavorel et al., 1999; Sternberg et al., 2000). The main “responsive groups” (Lavorel et al., 1999) were annual legumes and shrubs.

Other studies in similar areas in Galilee, Israel (Ofer and Seligman, 1969; Henkin et al., 1996, 1998), and around the world (Osman et al., 1991, 1999) have shown that the addition of phosphorus significantly increased herbaceous biomass and cover of annual legumes. Wilson et al. (1996) found a decrease in species richness in plots where phosphorus had been applied but in the present study no significant change in overall species richness was found. In the present study, opposite results were obtained as species

richness of annual legumes significantly increased following phosphorus application.

In addition to reducing the shrub cover, the herbicide application caused a significant decrease in richness of shrubs. The opening of areas formerly dominated by shrubs facilitated the colonization by and establishment of annual forbs (five species) that were favored by the disturbance. Moreover, the removal of the shrubs probably released annual species from competition for light and water, and thereby inhibited recolonization of the dominant shrubs (Halpern, 1988; Sternberg et al., 1999), while increasing spatial heterogeneity (Collins and Barber, 1985). Annual forbs and annual legumes were the dominant plant functional groups in the vegetation (Fig. 1), and these were the most responsive to manipulation. Similar to the present findings, Hadar et al. (1999) showed that clearing of shrubs in Mediterranean shrubland had positive effects on legumes abundance.

Among the plant functional groups, species richness was highest among the annual forbs (Table 2), and the frequencies of these species decreased as a result of phosphorus application. *P. cretica* (annual forb, Table 5), is commonly considered an indicator species of phosphorus deficiency in the soil (Danin, pers. commun.). This small plant, under more fertile conditions was easily overcome by competition from larger plants that responded positively to phosphorus enrichment (Henkin et al., 1998).

Herbicide application was also beneficial to other annual forbs (Table 5). The opening of new sites for colonization enabled them to become established in areas previously occupied by dominant shrubs. A notable result of the present study was the recognition of the large number of species that showed no significant response to either disturbance by the herbicide or to phosphorus enrichment (Table 5). Such stability in the face of disturbance evidently derives from the life history attributes of the dominant species (Noble and Gitay, 1996). It appears to indicate that there is very little niche differentiation on the site and that species richness is a poor indicator of functional richness (Diaz and Cabido, 2001). Persistence under disturbance is facilitated by plant morphological traits, such as the underground bud position in geophytes and hemicryptophytes. Annuals, the main life form in the study area, persist as seeds in soil cracks and soil seed banks, and as standing litter, and these species germinate in open areas around the shrub canopy. Furthermore, annuals, especially legumes, are “adapted” to the unpredictability of their environment through an escape strategy based on the production of dormant seeds (Kigel, 1995; Sternberg et al., 2003).

Acknowledgments

The project was funded by the Ministry of Agriculture and Rural Development, Israel and Northern R and D, Israel.

Thanks are extended to anonymous reviewers for helpful comments.

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