

Soil seed banks, habitat heterogeneity, and regeneration strategies in a Mediterranean coastal sand dune

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ABSTRACT

This study investigated the effects of microhabitat characteristics on soil seed bank structure, regeneration strategies, and plant composition in a Mediterranean coastal sand dune in Israel. Three different microhabitats were selected: (a) open patches between shrubs, (b) shrub understorey, and (c) open, disturbed patches in pedestrian trails. In each microhabitat two types of sampling plots were established: (a) seedling removal and (b) control (seedlings not removed). Emerging seedlings in each microhabitat were identified, counted, and removed every two weeks. In the controls, the vegetation was sampled only once at the peak of the herbaceous growing season. At the end of the growing season in plots where seedlings were removed, the upper soil was collected and sieved before seeds set. Viable non-germinated seeds were identified and counted. An estimation of persistent seed banks was obtained for each plot. Species composition, species richness, species diversity, and aboveground biomass by species were estimated. Germination fractions among species and plant functional groups were measured.

Microhabitats differed in soil seed bank density, germination characteristics, above-ground biomass production, and species composition. The open patches between shrubs generally had the highest densities of seeds, seedlings, and mature individual herbaceous plants. Important density differences between total seedlings removed and mature vegetation may indicate strong plant mortality in all microhabitats. Annual and perennial grasses, composites, annual crucifers, and annual forbs produced transient seed banks, while legumes, umbellifers, and perennial forbs had persistent seed banks. Disturbance by public trampling in trails led to low seed and plant densities in this microhabitat. No effects of facilitation of shrubs on the annual vegetation were noted in shrub understorey. Habitat heterogeneity had a strong impact on vegetation structure and regeneration strategies.

Keywords: aboveground biomass, dormancy, germination, plant traits, seedling emergence, plant functional types

INTRODUCTION

Plant recruitment can be affected by habitat patchiness (Fowler, 1988; Lortie and Turkington, 2002), since patches can differ in abiotic conditions, such as water, light, salts, and nutrient availability (Huang and Gutterman, 1999), and through biotic interactions such

as competition, herbivory, and predation (Alpert and Mooney, 1996). Physical and biotic heterogeneity occurs on several spatial and temporal scales across microhabitats. Particularly in stressful environments, the spatial

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proximity between plant species often creates competition for resources that results in net negative effects. In more arid environments, plants can have positive effects on each other, and the relative importance of competition and facilitation may vary inversely along gradients of abiotic stress (Bertness and Callaway, 1994). In poorly developed soils and water-limited environments such as coastal sand dunes, microenvironmental changes provided by nurse plants (e.g., *Retama raetam* (Forssk.) Webb shrubs) or sand burial may benefit the survival and growth of understory species (Pugnaire and Luque, 2001; Franks, 2003). Seedling recruitment is usually higher under the protection of these nurse plants (Castro et al., 2002) and biological diversity is increased (Tewksbury and Lloyd, 2001).

The structural heterogeneity of habitats between shrub understory and open gaps may affect the spatial distribution pattern of seed dispersal and survival, which are considered to be two critical processes influencing seedling establishment and development (Crawford and Young, 1998; Guo et al., 1998). Within this framework, it is generally assumed that Mediterranean annual vegetation is “adapted” to the unpredictability of its environment by an escape strategy based on the production of dormant seeds that persist during periods of limited resource supply (Lavorel et al., 1993). The soil seed bank is conceivably one of the more important long-term refuges for annual plant populations in highly variable environments typical of the Mediterranean and desert regions (Kigel, 1995; Guterman, 2002). In Mediterranean plant communities, seed dormancy maximizes fitness for two main reasons: (a) dormant seeds allow plant populations to persist during unfavorable years, exploiting the average, more favorable conditions, and (b) seed dormancy reduces the variance in fitness response to an unpredictably variable environment (Philippi, 1993). In eastern Mediterranean coastal sand dunes, information about differential germination patterns, species richness, diversity, and biomass production at different spatially heterogeneous microhabitats is scarce.

This study aimed to investigate the effects of microhabitat characteristics on soil seed bank, regeneration strategies, and plant community composition and structure in a Mediterranean coastal sand dune ecosystem. Specific questions of our study were: (a) Does microhabitat heterogeneity affect the structure and composition of the vegetation in a Mediterranean coastal sand dune? (b) Do shrubs facilitate the establishment of annual vegetation under their understory? (c) Are there differential patterns of regeneration among microhabitats? (d) Are microhabitat characteristics and seed persistence correlated?

Understanding the effects of microhabitats on soil seed bank and vegetation structure in Mediterranean coastal sand dunes may contribute to a more efficient management of these fragile areas for conservation.

MATERIAL AND METHODS

The study site

The study site was located in a Mediterranean coastal semistabilized sand dune at the Poleg Stream Nature Reserve, Israel (34°45'N, 32°03'E), which covers an area of 50 ha. The distance from the sea is about 500 m and the altitude ranges between 10–50 m a.s.l. The climate is typical Mediterranean, with a mean annual rainfall of 590 mm, falling mainly in winter–early spring (October to March). At least five months (May to September) of no rainfall characterize this region. The rainfall season covered by the present study (October 2000–April 2001) was relatively dry with 385 mm of rain. Mean maximum temperature reaches 30 °C in July, while the mean minimum temperatures reach 5 °C in January. The soil is sandy regosol with an A-C soil profile (Dan et al., 1970).

The vegetation at the coastal sand dune was a spatially heterogeneous matrix of shrubs and open stabilized patches dominated by herbaceous annual vegetation. There were 90 plant species, with some endemic to the region, e.g., *Rumex rothschildianus* Aarons. Ex Evenari, *Iris atropurpurea* Baker, *Senecio joppensis* Dinsm., and *Lupinus palastinus* Boiss. The vegetation included dominant shrubs, such as *Retama raetam* and *Pistacia lentiscus* L., and perennial and annual herbaceous plants (Kutiel et al., 1979; Kutiel, 1998). Nomenclature follows Feinbrun-Dothan and Danin (1991).

The nature reserve is open to the public, and has a vast number of trails that were spontaneously created by pedestrians during the years. For restoration purposes, some of these trails (including those monitored in this research) were closed to the public a year before the onset of this study.

Experimental design and sampling

Four different sites within the Poleg Stream Nature Reserve, at least 300 m apart, were selected for our study. In each site, we selected three different representative microhabitats: (a) open patches between shrubs, (b) shrub understory, and (c) disturbed, open patches along pedestrian trails. Studies on shrub understory were carried out on the dominant *Retama raetam* individuals of similar size and appearance (mean radius 1.2 m). Within each microhabitat, we established 15 permanent plots of 25 × 25 cm. In each area (including 3

microhabitats) 45 plots were marked, adding up to a total of 180 plots (4 areas \times 45 plots) for the whole study.

Seedling emergence in each microhabitat was monitored in 10 of the 15 established plots, two weeks after the occurrence of the first major rain storm (>10 mm). Sampling was carried out every 2 weeks from November 13, 2000 until March 4, 2001. Emerging seedlings in each plot were identified, counted, and removed at every sampling event until no new germination was observed (mid-March). At the end of the rainfall season and before seed dispersal, we collected the upper 5 cm of the soil (sand) of the 25 \times 25 cm plots where seedling removal was carried out. The soil (sand) was sieved using three different-sized sieves (1 mm, 0.6 mm, and 0.3 mm) and non-germinated seeds were retrieved. From previous measurements it was noted that the seed size of wet seeds of the large majority of the species in the study site was bigger than 0.3 mm. Seeds were identified and counted under a binocular microscope. Undamaged, full, and firm seeds were considered viable. Since no additional seedlings emerged after the last sampling date, the fraction of non-germinated seeds (persistent seed bank) was considered to be the species seed dormancy level under field conditions.

At the peak of the herbaceous growing season (April), the vegetation was sampled in five plots adjacent to the seedling removal plots. The sampling was carried out in each of the three microhabitats at the four different sites. In each plot, the aboveground biomass of the herbaceous vegetation was harvested (primary production). Plants were classified by species, counted, oven-dried at 65 °C for three days, and then weighed. From the vegetation samples we estimated species composition, species richness, species diversity (Shannon–Weaver index), and aboveground biomass for each species.

Plant functional groups

The species were classified into six functional groups according to life cycle and taxonomy (Gitay and Noble, 1997): annual grasses, annual legumes, annual composites, annual crucifers, and annual and perennial forbs (all other dicots). The crucifers were recorded separately because of their occasional dominance in the trails vegetation. Perennial grasses and composites were excluded as they were very sparse.

Statistical analysis

We used analysis of variance (ANOVA) to analyze species and functional group densities of vegetation, seedling, and seed banks between microhabitats and areas (Sokal and Rohlf, 1995). Since the data were usually not distributed normally, we transformed the

dependent variables by using rank-averages and tested for homogeneity of variance before analysis (see Conover and Iman, 1981). We tested differences of seedling distribution patterns among the three microhabitats, and germination using contrasts among the microhabitats (JMP, SAS Institute Inc., 2000) within repeated measures ANOVA.

RESULTS

Soil seed bank characteristic at the site

There were 61 plant species in the soil seed bank. From this, a total of 59 species was also identified as seedlings, while only two species, *Chrysanthemum coronarium* L. (annual composite) and *Osyris alba* L. (shrub), were found only as non-germinated seeds, indicating their potential to persist in the seed bank. The 10 most abundant species accounted for 52% of the total soil seed bank. About 95% of all species were annuals. Overall, the seed bank averaged over all microhabitats was 10.5% annual grasses, 37.2% annual forbs, 2.3% perennial forbs, 30.6% annual legumes, 13.9% annual composites, 3.3% annual crucifers, and 2.2% umbellifers. Seeds of perennial grasses were not found in the soil. Seeds of *Trigonella cylindracea* Desv. (annual legume), *Polycarpon tetraphyllum* (L.) L. (annual forb), and *Cutandia memphytica* (Spreng.) K. Richt. (annual grass) were the dominant species, with almost 21% of the seed bank (7% for each species). The similarity coefficient (Sørensen) for the floristic composition between the vegetation and soil seed bank was high and accounted for 94%.

Soil seed banks and habitat heterogeneity

Both seed bank density and seedlings varied widely with significantly more seeds and species in the open gaps between shrubs compared to the shrub understorey and trails (Fig. 1a,b). Moreover, species diversity (Shannon–Weaver diversity index; H') was equally affected by the spatial heterogeneity patterns as the open gaps showed significantly higher values (1.87 H' ; $F = 11.1$, $p = <0.001$) than shrub understorey (1.44 H') and trails (1.53 H'). No significant differences were observed between shrub understorey and trails.

Soil seed banks, functional groups, and regeneration strategies

Over all microhabitats, almost 20% of the seeds present in the soil did not germinate during the germination season, representing the potential of the persistent seed bank (5,055 vs. 1,263 seeds m^{-2}). Seed persistency was not equally represented among microhabitats. Open

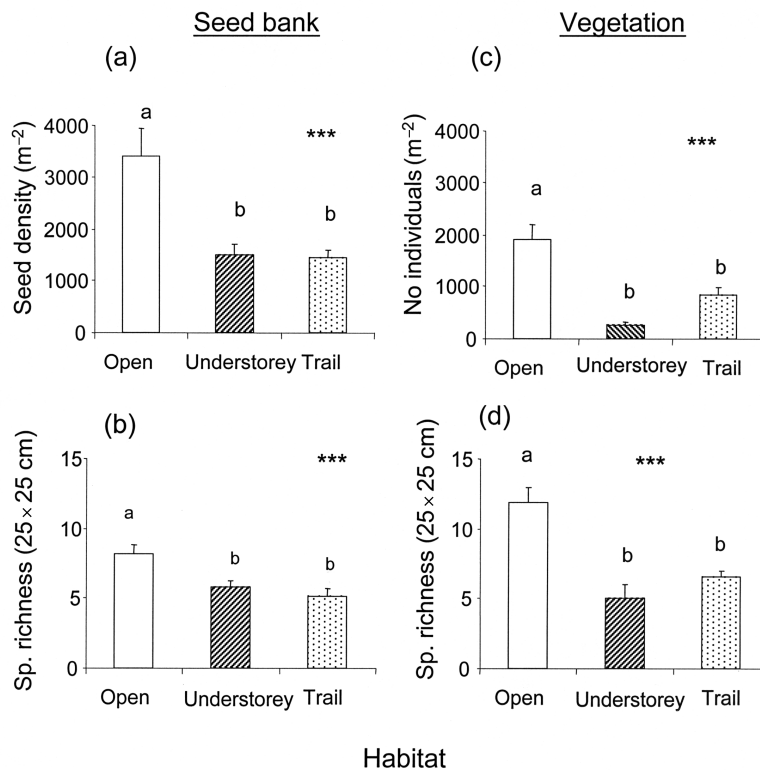


Fig. 1. The effects of microhabitat characteristics on soil seed bank and vegetation density and species richness. Significance: *** $p < 0.001$. Treatments bearing the same letter are not significantly different at $p < 0.05$.

gaps and shrub understorey had rather large persistent seed banks of 22.2% and 28.5%, respectively, while the lowest seed bank persistent values were noted in the trail microhabitat, with 6.1% (Fig. 2).

Soil seed bank density and germination fractions

varied among habitats and functional groups (Table 1). Annual grasses were significantly more abundant in the trails than in the shrub understorey ($F = 4.74, p < 0.0095$; Fig. 3a). Similarly, crucifers showed significantly lower seed densities in the shrub understorey

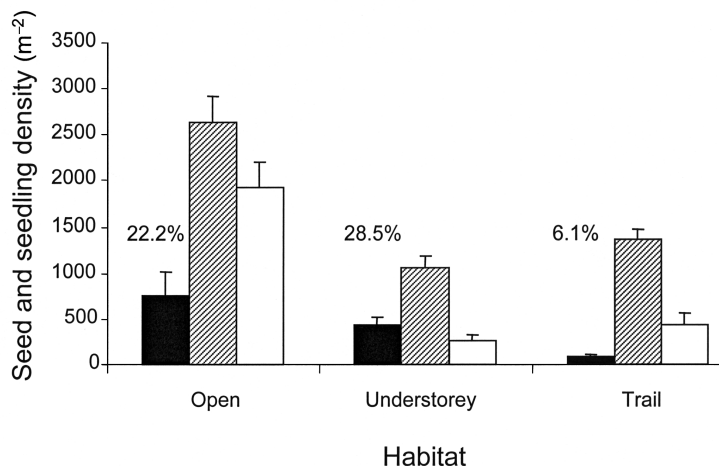


Fig. 2. Densities of non-germinated soil seed bank, seedlings, and established vegetation in the different microhabitats. Percentage (%) numbers refer to the proportion of non-germinated seeds from the total seed bank density.

Table 1

Soil seed bank composition by main functional groups in the different microhabitats. Data (mean \pm standard error) are the sum of germinated and non-germinated seeds. The relative proportion of each functional group and its mean germination percentage (%) within each microhabitat is presented

Plant func. groups	Open gaps			Shrub understory			Trail		
	Density (m ⁻²)	Prop. (%)	Germinat. (%)	Density (m ⁻²)	Prop. (%)	Germinat. (%)	Density (m ⁻²)	Prop. (%)	Germinat. (%)
Annual grasses	206.8 \pm 52	6	100	94.8 \pm 91	6	100	339.2 \pm 84	24	100
Crucifers	90.8 \pm 41	3	80	2.8 \pm 1.2	–	57	107.6 \pm 35	7	50
Composites	491.6 \pm 221	15	99	108.4 \pm 40	7	99	254 \pm 45	18	81
Legumes	1,377 \pm 266	41	53	402 \pm 49	27	29	121.6 \pm 36	8	74
Annual forbs	1,073 \pm 229	32	94	774 \pm 190	52	84	589 \pm 144	41	99
Perennial forbs	145.2 \pm 36	4	96	106.8 \pm 37	7	88	29.2 \pm 19	2	92
Total	3,385	100		1,493	100		1,440	100	

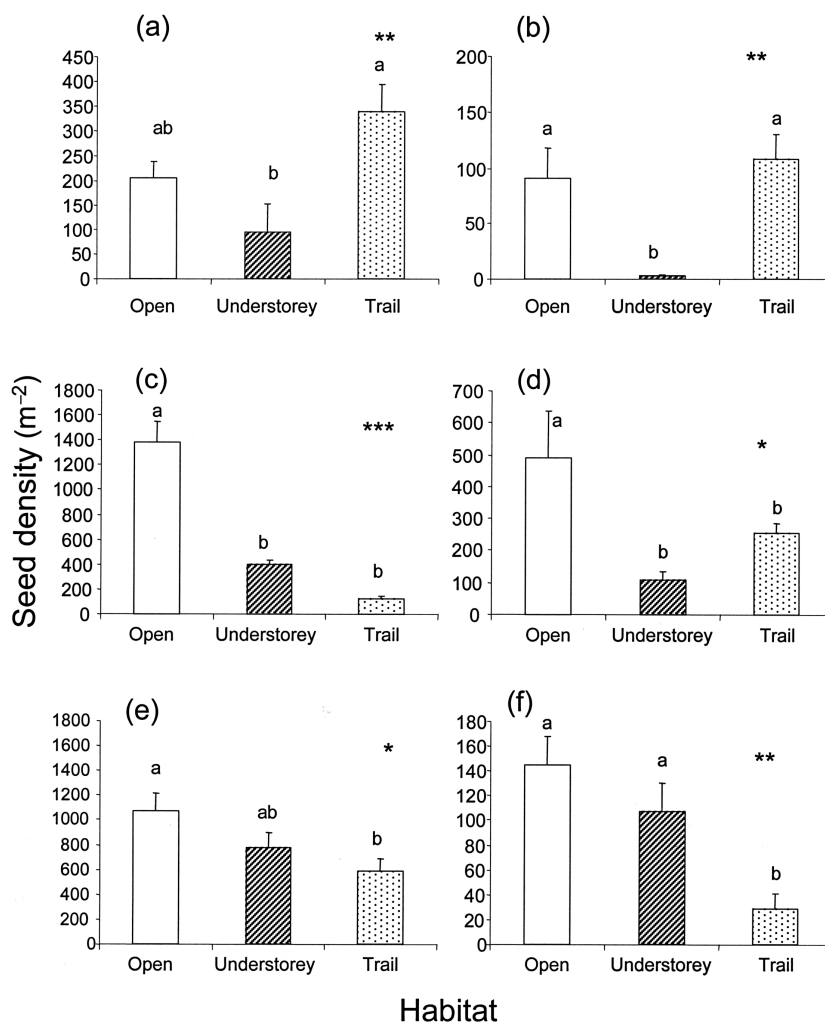


Fig. 3. The effects of microhabitat on seed density of functional groups. Annual grasses (a), crucifers (b), annual legume (c), composites (d), annual forbs (e), and perennial forbs (f). Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Treatments bearing the same letter are not significantly different at $p < 0.05$.

($F = 6.60$, $p < 0.0016$; Fig. 3b). Seed bank densities of annual legumes and composites were highest in the open gaps between the shrubs ($F = 12.0$, $p < 0.0001$; $F = 4.44$, $p < 0.013$; Fig. 3c and d, respectively). In contrast, annual and perennial forbs were significantly more abundant in the open gaps than in the trails ($F = 3.20$, $p < 0.042$; $F = 6.61$, $p < 0.0017$; Fig. 3e and f, respectively).

Vegetation characteristics

At the peak of the growing season the habitat distributions of annual plants were very similar to those observed for the soil seed bank. Significantly higher numbers of individuals were noted in the open gaps of the stabilized dune compared to densities at the shrub understorey and trails, ($F = 7.98$ $p = <0.001$; Fig. 1c). Similar patterns were also found for species richness. Significantly higher number of species ($F = 8.10$ $p = <0.001$) were found in the open gaps when contrasted to the shrub understorey and trails (Fig. 1d).

Seedlings vs. mature vegetation densities

Comparisons between seedling and adjacent mature vegetation densities indicated density-dependence pro-

cesses. Over all habitat types, densities from plots where seedlings were regularly removed after germination were 41% higher than densities of mature plants in adjacent plots. These effects varied among microhabitats. Beneath shrubs, 76% more seedlings germinated compared to 39%, and 27% more seedlings in the trails and open gaps, respectively.

Aboveground primary production and habitat heterogeneity

Aboveground biomass production of annual vegetation varied among the different microhabitats. Plant biomass was more than four times higher in the gaps between shrubs compared to shrub understorey and trails ($F = 7.10$ $p = <0.001$; Fig. 4a). No significant differences were found between shrub understorey and trails. Moreover, biomass production among the functional groups was similar across habitats, with more in open areas than other. Primary productivity of annual and perennial forbs and annual legumes was significantly greater in the open gaps (Fig. 4b–d). Remaining functional groups showed no significant differences among microhabitats.

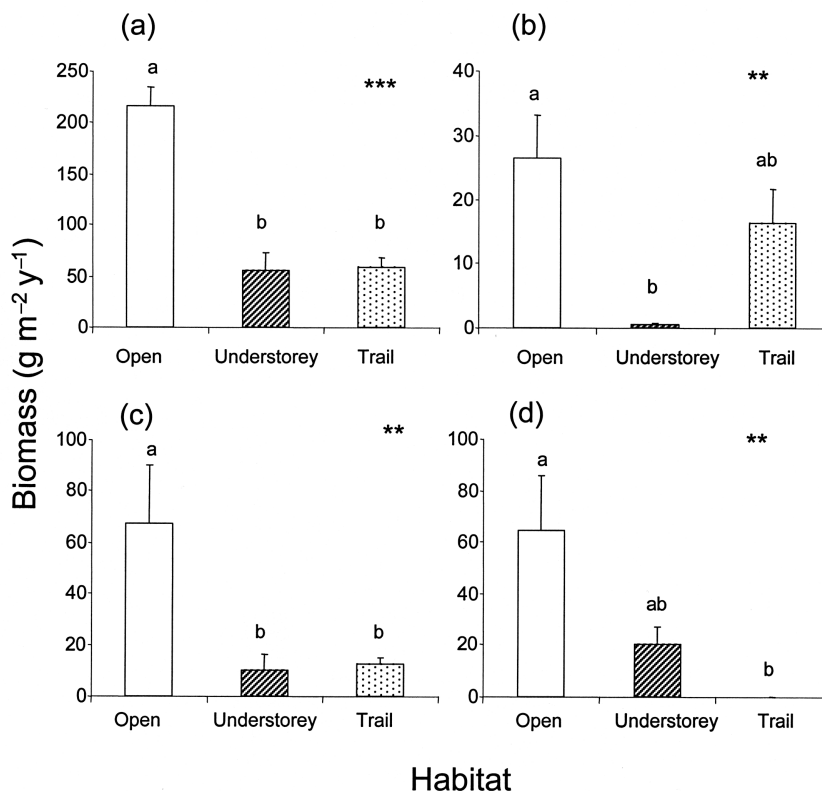


Fig. 4. Primary productivity of annual species in the different habitats by functional groups. Total biomass (all groups) (a), annual forbs (b), perennial forbs (c), and annual legumes (d). Significance keys as in Fig. 3.

DISCUSSION

Habitat heterogeneity and germination strategies

The results showed that seed bank density varied widely among microhabitats, with the fewest seeds in the trails. The reason for low densities in this microhabitat probably was the constant disturbance by public trampling. Despite closing trails to the public during the period of the study, the previous trampling on the sandy soil crust created an unstable environment where sand moved freely and with “risky” conditions for recruitment. Moreover, trampling effects in the past may have produced lower seed production of the established plants, affecting total seed numbers available at the microhabitat (Liddle and Greig-Smith, 1975a). The lack of the organic matter layer along the trails also may have affected seed production in the trails (Kutiel and Danin, 1987). The absence of this layer in the disturbed sandy soil crust enhanced sand movement, creating drier conditions for germination (lower soil water retention) and poorer nutrient availability for growth and development (Liddle and Greig-Smith, 1975b; Kutiel and Danin, 1987; Danin, 1991; Kutiel et al., 1999).

The highest plant and seed densities were in the stabilized open gaps between shrubs (52% of total seed bank density) where a developed organic matter layer was present.

The range of soil seed bank density found in this coastal sand dune (from 3,385 to 1,440 seeds m^{-2}) is relatively low compared to other studies on Mediterranean herbaceous communities, e.g., 11,600 seeds m^{-2} (Holzapfel et al., 1993), 110,000 seeds m^{-2} (Ortega et al., 1997), and 10,000–4,800 seeds m^{-2} (Sternberg et al., 2003). This wide variation in seed bank densities probably reflects differences in habitat and vegetation characteristics, soil properties, and climatic conditions.

Studies where only germinable seed banks were assessed may underestimate total seed abundance and provide biased estimates of composition due to seed dormancy and/or quiescence. We found that 20% of the overall seed bank remained dormant under natural conditions and that functional groups differ strongly in their germination rates (Sternberg et al., 2003). Nevertheless, we would have expected even lower germination rates of the overall seed bank, particularly in dry years, such as our study, where precipitation reached only 65% of the mean annual rainfall.

Open gaps showed the highest germination rates while shrub understorey, the lowest (Table 1). However, a wide spectrum of seed germinability levels was found in the different functional groups. Annual legumes showed in general intermediate and low germination fractions in open gaps and shrub understorey (53% and

29%, respectively). Similarly, crucifers in trails (particularly *Maresia pulchella*) showed relatively low germination fractions (45%). In contrast, grasses, forbs, and composites showed high germination fractions in all microhabitats (100%, 92%, and 93%, respectively, Table 1). These germinability trends indicated high and low potential for producing persistent seed banks in these functional groups. These results are consistent with other studies from the Mediterranean region that showed that legumes and crucifers formed persistent seed banks, while grasses have little seed carry-over between years (Russi et al., 1992; Peco et al., 1998; Sternberg et al., 2003). Taxonomic similarities in seed morphology (e.g., seed coat impermeability in legumes) or physiological mechanisms of germination control may explain the homogeneity in dormancy trends within each group. However, the relatively high germination rates in the remaining functional groups and habitats found in this study may have been affected by the density dependence processes that actually increased normal germination fractions when seedlings are not removed, as compared to the vegetation growing in the sampled plots.

Effects of shrubs on germination strategies

Facilitation processes between shrubs and annual vegetation defined as positive effects of the shrubs on the establishment, growth, and development of the annual vegetation growing in its understorey (Callaway, 1995; Holzapfel and Mahall, 1999; Kadmon and Tielboerger, 1999; Castro et al., 2002), have been recognized in several different sand dune ecosystems (Franks, 2003; Martinez, 2003). The importance of facilitation may even increase with increasing abiotic stress. However, our results showed no effects of facilitation of shrubs on the annual vegetation (Mack and Harper, 1977; Donovan and Richards, 2000). This was reflected by lower seed bank and vegetation densities and aboveground biomass production near shrubs. The rainfall conditions in the Mediterranean coastal sand dune imposed less soil moisture stress in annuals during the growing season, with light as probably the limiting factor for their development in the shrub understorey (Shumway, 2000; Tewksbury and Lloyd, 2001). Moreover, dense litter cover of *Retama raetam* in the understorey may have prevented the establishment of annual species that were not able to germinate under these conditions, resulting in low species richness.

The diversity of responses of the vegetation according to microhabitat characteristics reinforces the importance of conserving the spatial heterogeneity of the sand dune area and preventing the encroachment by natural successional processes that may lead to a loss in biodiversity (Kutiel et al., 2000; Briggs et al., 2002).

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