Competition for microsites during recruitment in semiarid annual plant communities

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Abstract. The concept of microsites for recruitment is central to plant ecology, but it is unclear whether these sites are abstract constructs or real entities. I hypothesize that, in generally microsite-limited communities, microsites comprise a limiting physical resource for which different species compete. I tested this hypothesis on winter-annual communities on biocrust in the semiarid Northern Negev of Israel, in which most species are microsite-limited, while the dominant grass (Stipa capensis) has overcome this limitation by efficient microsite acquisition and a lack of secondary seed dormancy. I tested whether the dominant suppresses the subordinate species, collectively, during recruitment, rather than during growth. To this end, I conducted a field experiment with three blocks of six plots (6 m × 6 m) with two treatments – mowing in spring 2006 (intershrub, intershrub + shrub patches, and none) and shrub-patch removal (0% or 50% of the patches). I collected data from four seed traps per plot before spring 2007 and from five plant samples per plot at the end of spring. Mowing significantly reduced both seed and plant density of the dominant species, reflecting seed-limited recruitment, and increased subordinate plant density by competitive release. Multiple regressions of per-plant and per-gram effects and responses showed that competition was a direct effect of the dominant’s density. Total and per-group biomass was proportional to density, implying density-independent per capita growth. Subordinate species number also increased with their density, due to the sample-size effect. These findings indicate that the seed-limited dominant diffusely suppresses the subordinates during recruitment, supporting the microsite competition hypothesis. The shift from growth resources to microsites extends the role of inter-specific competition along productivity and disturbance gradients, and highlights the asymmetric relationship between the two kinds of competition, as microsite competition is only observable if initial abundances are not overshadowed by density-dependent growth and mortality. The findings also demonstrate that (1) lacking secondary seed dormancy is an evolutionarily stable strategy in dryland annuals, alongside seed dormancy in microsite-limited species, and (2) biomass removal (e.g., by herbivory) increases small-scale biodiversity, enhancing the sustainability of dryland grazing, but without compensatory growth.

Key words: annual plants; biocrust; cascading effects; density-independent growth; diffuse competition; microsite acquisition; microsite limitation; secondary seed dormancy; semiarid shrubland; Stipa capensis.

INTRODUCTION

Recruitment sites – also known as safe sites or microsites – form a central concept in our understanding of the structure and dynamics of plant populations and communities (Harper et al. 1965, Ross and Harper 1972, Grubb 1977, Pickett et al. 1987, Eriksson and Ehrlén 1992) and meta-populations and -communities (Leibold et al. 2004, Myers and Harms 2009). This concept successfully captures the degree to which the requirements of species for seed germination and seedling establishment match or mismatch the environmental conditions in specific locations at the scale of the individual seed. As such, the concept of microsites – even if only implicitly used – enables researchers to focus on the spatio-temporal context of plant recruitment and immigration (Leibold et al. 2004, Myers and Harms 2009) and on the role of microsite availability as a potentially important limiting factor at scales from plant neighborhoods and patches (Pickett et al. 1987, Leibold et al. 2004) to regional species pools (Eriksson and Ehrlén 1992, Nathan and Muller-Landau 2000, Rees et al. 2001, Foster et al. 2004, Münzbergová and Herben 2005).

Surprisingly, the theoretical consequences of microsites as a limiting factor have not been adequately explored. According to theory, natural selection should – in some species – favor plant traits that overcome microsite limitation, namely, the ability to acquire and exploit potential microsites more efficiently. Solutions include lower seed germination requirements for water and lower dependence on high-quality microsites (Rees et al. 2001) and, consequently, higher germination rates and earlier emergence (Ross and Harper 1972, Inouye 1980, Dyer et al. 2000, Lortie and Turkington 2002, Tilborg and Prasse 2009). This results in dependence of recruitment on seed densities (seed-limited recruitment) and, often, in numerical dominance (Rees et al. 2001, Foster et al. 2004). However, such adaptations during recruitment are invariably considered as pre-emptive strategies, promoting advantages of seedlings during subsequent growth (Ross and Harper 1972, Grubb 1977, Rees et al. 2001), rather than as a selective advantage per se, irrespective of growth after recruitment, or perhaps even offsetting poor growth.
A second, related, theoretical prediction is that the traits that increase the ability of a species to acquire and exploit a limiting resource (microsite availability), may also make the species a superior intra-specific competitor for it. Since microsite availability is considered, both implicitly and explicitly, to be an important potentially limiting factor for plant immigration, recruitment, colonization, succession, and species diversity (Harper et al. 1965, Ross and Harper 1972, Grime 1977, Fowler 1986, Pickett et al. 1987, Eriksson and Ehrlé 1992, Rees et al. 2001, Foster et al. 2004, Leibold et al. 2004, Myers and Harms 2009), it is surprising that no attention has been given to the possibility that plants compete for microsites, as has been demonstrated for sessile and territorial animals (Connell 1978, Garcia 1983, Roughgarden 1986). Microsites are not treated as an essential resource and are still an ambiguous entity in plant ecology. Indeed, it is yet unclear whether microsites are mere abstract constructs that explain observed phenomena as ‘recruitment opportunities’ (Myers and Harms 2009), similar to Ross and Harper’s (1972) ‘biological space’ and Grubb’s (1977) ‘regeneration niche’. Alternatively, microsites may be real entities that form an essential limiting resource for successful germination and establishment, as appears to be implied with the term ‘safe site’ (Harper et al. 1965), that is, the location where the seed and the emerging seedling survive external threats such as granivory and disturbance, until establishment. According to this alternative, plants are expected to compete for microsites from seed dispersal, through microsite acquisition and germination, on to seeding establishment. This kind of competition contrasts with the current pre-emptive paradigm, which assumes that competition in plants is solely for growth resources after establishment, based on the close correlation typically assumed between the suitability of microsites for recruitment and the availability of growth-related resources (Rees et al. 2001, Leibold et al. 2004, Myers and Harms 2009), even if the interference occurs during dispersal (Howe and Smallwood 1982, Schupp et al. 2010) or germination (Inouye 1980, Bergelson and Perry 1989, Dyer et al. 2000, Lortie and Turkington 2002, Tiellööger and Prasse 2009). Indeed, in competitive communities, hindering the recruitment of neighboring plants gives the early (or only) recruits the competitive advantage of a head start in growth. Nevertheless, if the actual interference (and competitive suppression) is for successful recruitment, its outcome is advantageous to the better competitor, even if there is no significant resource competition after establishment. Selective advantages of microsite competition are expected in low-productivity herbaceous communities under frequent stress or disturbance (Grime 1977). Indeed, density-dependent (within-season) delay in germination (Inouye 1980, Bergelson and Perry 1989, Dyer et al. 2000, Lortie and Turkington 2002, Tiellööger and Prasse 2009) is almost exclusively reported in water-limited environments. Competition for microsites may also be important in directed seed dispersal (Howe and Smallwood 1982, Schupp et al. 2010), where it may take place before arrival. Nevertheless, microsites remain an elusive ecological entity, and our ability to discern their involvement in inter-specific competition is very limited.

Including the acquisition of microsites as a precondition for successful plant recruitment (Harper et al. 1965) is the only way to test whether plants compete for microsites and, ultimately, whether these competitive interactions have any impact on the community as a whole. Answering these questions experimentally requires that microsite acquisition is allowed to vary without imposing or removing limits, which is not possible in experiments with transplanted seeds (Inouye 1980, Bergelson and Perry 1989, Dyer et al. 2000, Turnbull et al. 2000, Lortie and Turkington 2002, Foster et al. 2004, Münzbergová and Herben 2005, Tiellööger and Prasse 2009). In addition, it requires manipulating the intensity of competition without significantly disturbing the vegetation or the substrate, which cannot be achieved by experimentally removing or clipping seedlings or adult plants (Kadmon 1995, McCain et al. 2010, Segre et al. 2014). In principle, these criteria can be met in herbaceous plant communities, as they are mostly dominated by annuals with seed-limited recruitment (Rees et al. 2001). In such communities, manipulating the seed production of the dominant species should alter its recruitment in the following growing season. However, a third and more critical criterion for experimentally testing whether plants physically compete for recruitment microsites is that microsite competition should be distinguishable from resource competition during growth after establishment. This condition can be met if plant abundance is mostly limited by the low availability of microsites, not by density-dependent growth (Weiner and Freckleton 2010). This seems to be the case in low-productivity, semiarid winter-annual communities on exposed, biocrust-covered soil, where the abundance and diversity of plants are primarily limited by low recruitment rates from seeds, due to the low probability of seeds penetrating through the biocrust (Boeken and Shachak 1994, 1998), and to highly selective requirements for subsequent germination from existing seed banks (Boeken and Shachak 1998, Guterman 2002).

Competition for microsites may also occur in more productive ‘competitive’ communities along with selection of microsite acquisition traits, if microsite limitation plays a role, as in the case of successional vegetation dynamics and disturbance (Pickett et al. 1987). However, in these cases, distinguishing competition for microsites from competition for growth resources after establishment may be much more difficult, because density-dependent per capita growth, especially when resulting in density-dependent mortality, is likely to overwhelm advantages during recruitment (Weiner and Freckleton 2010).

In the current study, I demonstrate that inter-specific competition in winter-annual plant communities of patchy semiarid shrubland occurs for microsites rather than for resources during growth. I present the results of a field experiment in a community wherein the dominant species, the annual grass Stipa capensis Thurnb., has a specialized soil-penetration mechanism (Boeken and Shachak 2006) and a short imbibition time associated with its lack of secondary seed dormancy (Boeken et al. 2004). Accordingly, the recruitment of S. capensis is expected to be seed-limited, as are most dominants of herbaceous communities (Rees et al. 2001), such that plant density after establishment can be experimentally manipulated by reducing seed production in the previous growing season by means of biomass removal. In addition, although intra- and inter-specific
competitive interactions involving growth resources may also occur in these communities, neither growth nor survival appear to be affected by water stress during the short and generally cool growing season, as has been widely reported in herbaceous plants of semiarid and arid regions (Went 1948, Inouye 1980, Fowler 1986). This seems to be due to small plant size, as the <40 cm tall adult S. capensis plants are very slender and have relatively narrow root systems and their wide spacing, growing several centimeters apart (Fig. 1).

The reported field experiment was designed to test four hypotheses: (1) in these water- and microsite-limited annual plant communities on biocrust, efficient microsite acquisition and exploitation mechanisms by the dominant species lead to high, seed-limited recruitment, but not in the other species collectively (the ‘subordinates’); (2) these traits mediate inter-specific competitive suppression of recruitment of the subordinate species (from seed arrival to seedling emergence), involving microsites; (3) growth after establishment and mortality are mostly density-independent, allowing microsite competition to occur and be observed; and (4) microsite competition is important for the density and biomass structure of the community and its species diversity. To test these hypotheses, I reduced the biomass of herbaceous intershrub communities of patchy semiarid shrubland by mowing, thereby triggering a series of cascading processes throughout the community. Specifically, I mowed in 1 yr and measured changes in the densities of seeds trapped during subsequent dispersal, as well as changes in plant density, biomass, and species richness during the following growing season. To control for possible augmentation of the intershrub communities by additional seeds due to source-sink functions (Boeken and Shachak 1998) or mass effects (Auerbach and Shmida 1987), which may offset the hypothesized processes, I included mowing of the herbaceous understory communities of shrub patches (Boeken and Orenstein 2001, Golodets and Boeken 2006) as a treatment level at the patch–interface scale, and added a partial patch removal treatment to address external augmentation effects at the larger plot scale.

The findings of this study should help elucidate the role of competition along resource or disturbance gradients (Grime 1977, Tilman 1982, Tielbörger and Kadmon 2000), the importance of seed- and microsite-limited recruitment for community assembly and diversity (Eriksson and Ehrlén 1992, Rees et al. 2001, Leibold et al. 2004, Myers and Harms 2009), and the evolution of evolutionarily stable strategies (ESSs) pertaining to recruitment, which, in water-limited systems, is related to secondary seed dormancy and to dormancy breaking (Venable and Lawlor 1980, Pake and Venable 1995, Dyer et al. 2000, Rees et al. 2001, Gutterman 2002). From an applied perspective, such information is highly relevant for sustainable rangeland management in semiarid ecosystems (Ludwig et al. 2004, Maron and Crone 2006).

**METHODS**

*The research site*

I conducted the experiment on a flat hilltop (elevation 160 m) in the semiarid Northern Negev desert of Israel (31°17’ N, 34°37’ E), in a 40-ha watershed of the Park Shaked LTER station (Appendix S1: Fig. S1). The plant communities in this watershed are free from artificial or natural biomass removal, as livestock has been excluded since 1987. In this region, the average daily minimum winter temperatures are 6–8°C and the average maximum summer temperatures are 32–34°C (Stern et al. 1986). Rainfall occurs between November and March, with a long-term annual average of 150 mm since 1992 (Hoffman et al. 2016, B. Boeken and E. Zaady, daily meteorological data from Park Shaked LTER station, 1999–2018). Vegetation data used in the current study (Appendix S4: Tables S1, S2) were collected in the 2007 growing season; the total amount of annual rainfall until data collection of that year was 150 mm.

The vegetation in the research station is representative of the open shrub- and grasslands of the semiarid and arid zones of North Africa to Central Asia (USDA-ARS 2015). It is a patchy shrub-steppe with scattered shrub patches dominated by the thorny dwarf-shrubs Atractylis serratuloides (Asteraceae) and Noaea mucronata (Chenopodiaceae; Feinbrun-Dothan and Danin 1991), with a soil mound beneath their canopy (Boeken and Shachak 1994). The soil surface in the intershrub space – which amounts to 80–100% of the area of hill slopes and plains – is covered with a dense flat biocrust of cyanobacteria (Microcoleus vaginatus) with bacteria, mosses, and lichens (Zaady and Shachak 1994, Zhang et al. 2016). During the growing season, herbaceous vegetation, of mostly annual plants, develops on the biocrust, numerically dominated by the annual C3 grass Stipa capensis. The underlying soil is at least 1 m thick and is composed of loess, with 14% clay, 27% silt, and 59% sand. The salt content of the 0–25 cm soil layer is low, with an electrical conductivity of 0.4 mS/m (Boeken and Shachak 1994).

*The study species*

Stipa capensis dominates the herbaceous communities inhabiting the biocrust-covered open spaces in shrub- and grasslands throughout the sub-humid to arid regions from Western North Africa to Central Asia (USDA-ARS 2015); at present, it is also found in Southern Europe (USDA-ARS 2015), California (Tu and Randall 2003), and South Africa

![Fig. 1. Close-up of an *S. capensis*-dominated winter-annual community on biocrust in spring (March). Notice the wide spacing between individuals (Photo: B. Boeken).](image-url)
(Milton 2004). Because it lacks secondary seed dormancy (Boeken et al. 2004), S. capensis forms only transient, as opposed to persistent, seed banks, while its low site selectivity ensures high microsite availability, which should cause recruitment to be seed- rather than microsite-limited.

Many of the ca. 50 subordinate species of annual grasses and forbs on biocrust-covered intershrub in the experiment (listed in Appendix S2: Table S1), including Erucaria (Reboudia) pinnata, Anagallis arvensis, Plantago coronopus, Senecio glaucus, and Ononis reclinata, have some form of secondary seed dormancy (Jain 1982, Zaady et al. 1997, Gutterman 2002) and are, therefore, expected to be microsite-limited. Some of the minor species in the intershrub are also found in the denser vegetation of resource-enriched sites-limited. Some of the minor species in the intershrub are also found in the denser vegetation of resource-enriched patches, such as shrub patches, depressions, gullies, washes, and streambeds (Boeken and Shachak 1994, Boeken and Orenstein 2001, Golodets and Boeken 2006), with several dominant species and S. capensis as one of the subordinate species.

The abundance of S. capensis on the biocrust is mediated by the highly efficient microsite acquisition mechanism of its ‘seeds’ – small elongated caryopses of 1 mm × 6 mm with a seta (awn) of 10–12 cm (Boeken and Shachak 2006). During late spring (April–May), after primary dispersal of tens of centimeters across the vegetation and secondary dispersal of up to several meters across soil surfaces with few obstacles (Kadmon 1995), its own positions the seed vertically and bores into tiny surface holes and cracks (Boeken and Shachak 2006). During summer, the seeds lose their awn and finish after-ripening (Boeken et al. 2004), and are ready to germinate after the first rains (November–January), depending on the temperature. Wetted seeds that do not germinate either have already died, or will die (Boeken et al. 2004), while seeds that did not penetrate the soil are removed by harvester ants (Messor ebennus and M. arenaria; Wilby and Shachak 2000). In a study on dormant seed banks along the geographical rainfall gradient in Israel, Siewert and Tielbörger (2010) found evidence of few residual dormant seeds of S. capensis further south from the Park Shaked LTER station, at <100 mm of rainfall per year – apparently only in locations that remained dry throughout the rainy season.

**EXPERIMENTAL PROCEDURES**

In January 2005, I established three adjacent blocks of 18 m × 18 m as random replicates of a 3 × 3 orthogonal Latin square design. I used six of the nine 6 m × 6 m plots per block (18 plots out of 27) for two orthogonal treatment factors: patch removal (two levels) and mowing (three levels) (Appendices S3 and S4). I manipulated patchiness by removing 50% of the shrub patches and their soil mounds within the designated nine plots, with no patch removal as the control in the remaining nine plots. After patch removal, I flattened and slightly compacted the soil to resemble the biocrust cover of the intershrub space.

In March and April 2006, I mowed the herbaceous vegetation with a hand-held rotating string trimmer down to approximately 1 cm above ground level, in the intershrub space of the plot (‘partial mowing’), or in both the intershrub space and the understory of all shrub patches of the plot (‘complete mowing’), with no mowing as the unmanipulated control (Appendix S1: Fig. S2). I removed the mowed biomass carefully with a soft rake to prevent damage to the soil surface crust. Mowing in the understories of the shrub patches within some of the plots and reducing shrub patch density by 50% (relative to intact controls) allowed for testing possible seed augmentation from adjacent communities (Auerbach and Shmida 1987, Boeken and Shachak 1998).

**Data collection**

In April 2006, to sample seed input during dispersal, I placed two pairs of seed traps in the intershrub space within the central 4 m × 4 m part of each plot (for a total of 62 traps). Each pair of traps comprised a sunken trap, which was buried flush with the ground surface, and a raised trap, which was placed on the surface. Both types of trap were round plastic containers (15 cm in diameter and 10 cm in depth) and were anchored in place, perforated for drainage, lined with cheese-cloth, and covered with a metal mesh (1 cm gap size) to prevent access to seed predators. The seed traps were collected in November 2006, at the beginning of the rainy season. As the traps were relatively small, the number of captured seeds was generally low. I, therefore, pooled seeds from the two sunken traps and from the two raised traps in each plot to obtain data on seed abundance of S. capensis and of all subordinate species collectively. I also recorded the number of plant species present in the traps as seeds, which were identified by using a local seed reference (DuMosch 1999, Appendix S2: Table S1 and Appendix S3: Tables S1, S2).

In March 2007, one year after mowing the herbaceous vegetation in March and April 2006, I collected five samples of the herbaceous intershrub vegetation per plot (90 samples in total) by harvesting all plants within 20 cm × 30 cm frames, scattered randomly in the intershrub space of the central part of each plot. In each harvested sample, I identified all species (Feinbrun-Dothan and Danin 1991) and counted their plant density, measured dry biomass of the dominant species (S. capensis) and of the subordinate species (pooled together), and recorded the total number of species per sample (Appendix S2: Table S2 and Appendix S4: Tables S1, S2).

**Data analysis**

To analyze the overall effect of the manipulations on seed density, plant density, and plant biomass for the dominant species and the subordinate species collectively, and the latter’s species richness, I used blocked factorial ANOVAs (Statistica, Statsoft Inc., Tulsa, Oklahoma, USA) with random blocks, mowing, and patch removal as fixed independent categorical variables (Appendix S3: Table S1 and Appendix S4: Table S1), using Tukey post hoc tests to determine the effects of mowing. All response variables used in the statistical analyses are transformed to log(10) for seed and plant densities and to the cubic root for biomass, to ensure homoscedasticity of the residual errors and to approximate a normal distribution. To test the effect of the manipulations on seed responses, I used seed-trap position (raised or sunken) as an additional, fixed, treatment factor. I
omitted the patch removal manipulation from the seed analysis because it resulted in over-parameterization of the ANOVA model and had no significant effect in full factorial ANOVAs for either sunken or raised traps.

I tested the four hypotheses (seed-limited recruitment of the dominant, suppression of subordinates during recruitment, density-independent per capita growth after recruitment, and the effect of microsite competition on species richness) in a series of multiple regressions with a priori models on the density and biomass of *S. capensis* and the density, biomass, and species richness of the collective subordinate species across all treatments (see Table 3). Because the experimental design was orthogonal, all sequences of variable entry (a priori models and F-based stepwise procedures) yielded identical results. I used the same transformed data as in the ANOVAs, except for the square root of *S. capensis* density in response to mowing, which had a residual distribution closer to normal. I included mowing in all multiple regressions as an ordinal variable to identify additional direct effects, separate from expected indirect effects on density and/or biomass of either *S. capensis* or the subordinates. Mowing was represented with levels 0, 1, and 2 for no, intershrub, and complete mowing, or with 0 and 1 for subordinate biomass and species number where only intershrub mowing had an effect. For *S. capensis* density, mowing was the only predictor. I used the resulting slope estimates and partial $R^2$ values to examine the possible causal relationships between the plant variables, differentiating between per-plant (density) or per-gram (biomass) effects and responses (Goldberg and Landa 1991). This distinction adds important information on whether the interactions involve seeds until seedling emergence or density-dependent growth after emergence, assuming that (self-)thinning would also lead to per-plant responses only at high levels of resource competition.

**RESULTS**

**Trapped seeds**

Overall, mowing the herbaceous intershrub communities in the intershrub significantly decreased the total number of trapped seeds (log scale; Table 1, Fig. 2a), while further mowing in the shrub patches did not have any additional effect (Tukey post hoc test for no mowing vs. intershrub mowing: $Q_{22} [0,1] = 3.507, P = 0.05$; for the intershrub vs. complete mowing contrast: $Q_{22} [1,2] = 1.003, P > 0.05$). The effect of mowing resulted from a reduction of >50% in the number of *S. capensis* seeds (Table 1, Fig. 2a; Tukey post hoc: $Q_{22} [0,1] = 5.165, P < 0.01$ and $Q_{22} [1,2] = 1.408, P > 0.05$) with no reduction in the number of subordinate seeds (Table 1, Fig. 2b; $F_{1,21} = 2.0375, P = 0.1553$). Trap position had a significant effect on the numbers of trapped *S. capensis* and subordinate seeds, which were higher in sunken traps than in raised traps ($F_{1,21} = 12.352, P < 0.0001$ and $F_{1,21} = 64.225, P < 0.0001$, respectively; Table 1, Fig. 2a, b). The number of species, as represented by seeds, was also higher in sunken traps than in raised traps ($F_{1,21} = 30.9216, P < 0.0001$; Table 1, Fig. 2c), as a direct result of higher subordinate seed density (Fig. 2d; $F_{2,21} = 61.6909, P < 0.0001$), but not of mowing ($F_{2,21} = 0.4689, P = 0.6301$).

**Plant responses**

Mowing in the preceding growing season (Table 2) significantly reduced mean total and *S. capensis* plant density per sample (Fig. 3a; the latter determining 54–84% of the former), as well as total and *S. capensis* biomass (Fig. 3b), while it had a significant positive effect on mean subordinate density, biomass, and species number (Fig. 3c). Mowing the shrub-patch understory vegetation, in addition to the intershrub communities, had a significant effect on total and *S. capensis* density (Tukey post hoc tests: no vs. intershrub mowing and intershrub vs. complete mowing $P < 0.01$), but its effect on biomass was too weak to differentiate (no vs. complete mowing was significant only for *S. capensis*). Shrub-patch mowing did not have an additional effect on species density per sample (no vs. intershrub mowing $P < 0.01$, intershrub vs. complete mowing $P > 0.05$). Patch removal had one, marginally significant, main effect, namely, on subordinate density ($P = 0.0959$), and interacted with the effect of mowing on *S. capensis* density ($P = 0.0074$). There were also spatial differences in total plant density between blocks ($P = 0.0057$, Table 2), but these were weak for *S. capensis* and the subordinates separately ($P = 0.0898$, and $P = 0.0814$, respectively).

| Table 1. Main effects and two-way interactions of blocks, position, and mowing on the number of seeds and the number of species of seeds in sunken and raised seed traps (two of each position, pooled for each plot) ($n = 36$ traps, error df = 22). |
|---|---|---|---|
| | df | Total | *S. capensis* | Subordinates | Number of species |
| Block | 1 | 0.7757 | 0.9980 | 0.3197 | 0.8411 |
| Position | 1 | <0.0001 | 0.0020 | <0.0001 | <0.0001 |
| Block × Position | 2 | 0.5765 | 0.7380 | 0.6371 | 0.9062 |
| Mowing | 2 | 0.0004 | <0.0001 | 0.1553 | 0.7029 |
| Block × Mowing | 4 | 0.2569 | 0.5272 | 0.0926 | 0.5194 |
| Position × Mowing | 2 | 0.0962 | 0.1951 | 0.9165 | 0.3587 |
| Model | 13 | <0.0001 | 0.0004 | <0.0001 | 0.0135 |
| $R^2$ | | 0.789 | 0.755 | 0.799 | 0.631 |

Notes: Patch removal was not included in the analysis. Values are significance levels ($P$-values, $P < 0.05$ in bold) of blocked factorial ANOVA tests.
Plant density

The regression of mowing on S. capensis density (Table 3) showed a strong quadratic effect across the other treatments and blocks, reflecting its initial effect on seed densities (by reducing random dispersal as a function of area). In the multiple regression (overall $R^2 = 0.170$, Table 3), subordinate density was only negatively affected by S. capensis density (Fig. 4a), but not by S. capensis biomass or by mowing.

Plant biomass

Similar to its effect on plant density, mowing significantly reduced S. capensis biomass by 33% and total biomass by 53%, as the former determined 69% of the latter (see Fig. 3b), but it had no significant overall net effect on subordinate biomass (Table 2). No significant effects for blocks, patch removal or interactions were observed (Table 2).

The multiple regression showed that S. capensis biomass depended mostly on its density (overall $R^2 = 0.601$, $R^2_p = 0.435$, Table 3, Fig. 4b), with no direct effect of mowing. However, there was also a weaker, positive correlation between S. capensis and subordinate biomass ($R^2_p = 0.016$), likely reflecting covariance of similar responses to spatial environmental variability.

The multiple regression of subordinate biomass (overall $R^2 = 0.610$, $P < 0.0001$; Table 3) showed that it was mostly determined by their density ($R^2_p = 0.407$, $P < 0.0001$; Table 2).
While this is, in the experiment, an indirect effect of *S. capensis* density, the latter also had a separate, much smaller, direct, negative effect on subordinate biomass ($R^2_P = 0.048, P = 0.0020$; Fig. 4d). Unlike subordinate density (see above), subordinate biomass also correlated positively with *S. capensis* biomass ($R^2_P = 0.017, P = 0.0620$; Table 3), representing the same covariance as in the reciprocal analysis. Moreover, also in contrast to their density, there was an additional direct, negative effect of intershrub mowing on subordinate biomass ($R^2_P = 0.027; P = 0.0185$; Table 3) that was not detected in the ANOVA.

**DISCUSSION**

The cascading effects of biomass removal

The reported field experiment provides strong evidence in favor of all four hypotheses (on seed-limited recruitment, density-independent growth, inter-specific microsite competition, and community effects). Biomass removal by mowing as the experimental driver highlights recruitment limitation, competitive interactions during microsite acquisition and exploitation until establishment, and stochasticity as controlling principles of the processes cascading through this low-productivity semiarid herbaceous plant community on well-developed biocrust (Fig. 6).

Setting the initial conditions for the experiment, mowing efficiently reduced seed densities of *S. capensis*. During the following growing season, the dominant’s plant density in mown plots was also reduced. Given that seed numbers, their viability, and dormancy in the soil of the vegetation samples before recruitment cannot be known, the coinciding effects of mowing on seed and plant densities in separate locations (seed traps and vegetation samples) provide strong, although indirect, evidence of seed-limited recruitment of the dominant species. In contrast, the experiment did not provide information about recruitment limitation of the subordinates, since mowing did not affect their seed rain. The conclusion that recruitment in *S. capensis* is seed limited requires that final abundance is also proportional to seed densities, with no overriding effect of density dependence due to thinning after recruitment (Weiner and Freckleton 2010), which is explicitly addressed as hypothesis 2 (see below). The evidence on the relationships between plant density and biomass of the dominant and subordinates and their inter-specific interactions, as simultaneously measured effects and responses in the same samples, is direct and
therefore more reliable and accurate than that for the seed-plant relationships.

The strong negative per-plant effect of the dominant’s density on that of the subordinates is evidence of interspecific competition before growth. However, negative effects might also be the result of strong resource competition during growth, if it leads to severe density-dependent mortality by thinning. Apart from the question whether this is plausible in these low-productivity communities, thinning should involve per-plant responses to per-gram effects, but the lack of a negative per-gram effect of *S. capensis* biomass on subordinate density is not consistent with this interpretation.

### TABLE 3. Multiple regression analyses of density and biomass of *S. capensis* and subordinates as response and effect variables, with species density only as a response and mowing as an effect (in intershrub for subordinates, and intershrub and complete mowing for *S. capensis*).

<table>
<thead>
<tr>
<th>Regression model</th>
<th>df</th>
<th>b estimate</th>
<th>$R^2$</th>
<th>F</th>
<th>P</th>
<th>P (Wilks)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. capensis</em> density (sqrt)</td>
<td>88</td>
<td>0.339</td>
<td>45.039</td>
<td>&lt;0.0001</td>
<td>0.6605</td>
<td></td>
</tr>
<tr>
<td>Mowing (0,1,2)</td>
<td>1</td>
<td>-1.847</td>
<td>0.339</td>
<td>45.039</td>
<td>&lt;0.0001</td>
<td>0.0002</td>
</tr>
<tr>
<td><em>S. capensis</em> biomass (cbrt)</td>
<td>83</td>
<td>0.601</td>
<td>31.257</td>
<td>&lt;0.0001</td>
<td>0.0211</td>
<td></td>
</tr>
<tr>
<td><em>S. capensis</em> density (log)</td>
<td>1</td>
<td>1.149</td>
<td>0.435</td>
<td>90.496</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td>Subordinate density (log)</td>
<td>1</td>
<td>-0.064</td>
<td>0.001</td>
<td>0.2456</td>
<td>0.6215</td>
<td></td>
</tr>
<tr>
<td>Subordinate biomass (cbrt)</td>
<td>1</td>
<td>0.219</td>
<td>0.016</td>
<td>3.2668</td>
<td>0.0743</td>
<td></td>
</tr>
<tr>
<td>Mowing (0,1,2)</td>
<td>1</td>
<td>0.047</td>
<td>0.004</td>
<td>0.8107</td>
<td>0.3705</td>
<td></td>
</tr>
<tr>
<td>Subordinate density (log)</td>
<td>84</td>
<td>0.170</td>
<td>5.7424</td>
<td>0.0013</td>
<td>0.2432</td>
<td></td>
</tr>
<tr>
<td><em>S. capensis</em> density (log)</td>
<td>1</td>
<td>-0.511</td>
<td>0.071</td>
<td>7.2099</td>
<td>0.0087</td>
<td></td>
</tr>
<tr>
<td><em>S. capensis</em> biomass (cbrt)</td>
<td>1</td>
<td>0.138</td>
<td>0.012</td>
<td>1.1835</td>
<td>0.2798</td>
<td></td>
</tr>
<tr>
<td>Mowing (0,1,2)</td>
<td>1</td>
<td>0.041</td>
<td>0.006</td>
<td>0.6134</td>
<td>0.4357</td>
<td></td>
</tr>
<tr>
<td>Subordinate biomass (cbrt)</td>
<td>83</td>
<td>0.610</td>
<td>32.4965</td>
<td>&lt;0.0001</td>
<td>0.4498</td>
<td></td>
</tr>
<tr>
<td>Subordinate density (log)</td>
<td>1</td>
<td>0.750</td>
<td>0.407</td>
<td>86.6339</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td><em>S. capensis</em> density (log)</td>
<td>1</td>
<td>-0.458</td>
<td>0.048</td>
<td>10.1598</td>
<td>0.0020</td>
<td></td>
</tr>
<tr>
<td><em>S. capensis</em> biomass (cbrt)</td>
<td>1</td>
<td>0.178</td>
<td>0.017</td>
<td>3.5794</td>
<td>0.0620</td>
<td></td>
</tr>
<tr>
<td>Mowing (0,1)</td>
<td>1</td>
<td>-0.188</td>
<td>0.027</td>
<td>5.7777</td>
<td>0.0185</td>
<td></td>
</tr>
<tr>
<td>Species density</td>
<td>84</td>
<td>0.482</td>
<td>51.4566</td>
<td>&lt;0.0001</td>
<td>0.4127</td>
<td></td>
</tr>
<tr>
<td>Subordinate density (log)</td>
<td>1</td>
<td>4.842</td>
<td>0.460</td>
<td>109.747</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td><em>S. capensis</em> density (log)</td>
<td>1</td>
<td>0.144</td>
<td>0.000</td>
<td>0.0621</td>
<td>0.8039</td>
<td></td>
</tr>
<tr>
<td>Mowing (0,1)</td>
<td>1</td>
<td>0.932</td>
<td>0.018</td>
<td>4.2699</td>
<td>0.0419</td>
<td></td>
</tr>
</tbody>
</table>

**Notes:** Values are $b$-estimates for each effect, their partial $R^2$, $F$-values and significance levels, and $P$-levels of Wilk’s normality tests for the model residuals ($P < 0.05$ in bold). All residuals were homoscedastic with $P = 1$.

**FIG. 4.** Relationships between log density and cubic root of biomass for *S. capensis* and the subordinate species, and the latter’s species richness, as plant response and effect variables during the 2007 growing season, across all experimental treatments (open markers - no mowing, grey markers - intershrub mowing, black markers - mowing in both intershrub and shrub patches). (a) Subordinate vs. *S. capensis* plant density; (b) *S. capensis* biomass vs. *S. capensis* density; (c) Subordinate biomass vs. subordinate density; (d) Adjusted subordinate biomass vs. *S. capensis* plant density; (e) Number of species vs. subordinate density.
Weaker resource competition without thinning, on the other hand, would not lead to per-plant responses, but should be detected as negative per-gram effects and responses. Moreover, the positive covariance between subordinate and *S. capensis* biomass is additional evidence that negative resource-driven interactions during growth are not responsible for the competitive suppression of subordinate density. The subordinates did experience some moderate competition.

**Fig. 5.** Path analysis diagram based on the multiple regression analyses (Table 3) of the relationships between *S. capensis* (sc) and subordinate (sub) density *N* and biomass *B* (transformed), with species number *S* and mowing added. The path values are the estimated regression coefficients (*b*, in bold if significant at *P* < 0.05 - * , < 0.01 – ** or 0.01 – ***), with SEM values (Onyx, Von Oertzen et al. 2014) in parentheses. The arrowheads represent the direction of the interaction, the grey lines denote non-significance, and the thick black lines represent significant positive (solid lines) or negative (dashed lines) relationships.

**Fig. 6.** Diagram of the cascading causal effects of herbaceous biomass removal at time *t*−1 on the dominant, *S. capensis* (left) and on all subordinate species together (right) at time *t*. Ellipses indicate main driving principles; rectangular boxes show the sequential plant variables (light coloring indicates quantities that were not directly measured in the current experiment); up and down arrows within boxes indicate increase and decrease, respectively; thick arrows between boxes are their transitions (including growth); thin arrows between boxes are controls of the transitions by the drivers, with signs for positive (+), negative (−), or no (0) effect.

*Stipa capensis*
- Seed production (*t*−1) ↓
- Seed rain (*t*) ↓
- Seed density (*t*) ↓
- Seed limitation ↑

*Herbaceous biomass removal (*t*−1)
- Seed rain (*t*) ↑
- Seed bank density (*t*)
- Microsite competition
- Microsite availability

**Subordinate species**
- Plant density (*t*) ↓
- Plant density (*t*) ↑
- Species density (*t*) ↑
- Biomass (*t*) ↓
- Spatial covariance
- Density-independent growth and survival

*S. capensis* biomass is additional evidence that negative resource-driven interactions during growth are not responsible for the competitive suppression of subordinate density.
affecting their growth – which was not sufficiently strong to lead to mortality – as their biomass responded negatively to *S. capensis* density but not to its biomass, implying size-independent interference effects by individuals. This could be the result of equal resource uptake by *S. capensis* recruits after establishment, which is highly improbable. The more likely explanation is that the presence of individual *S. capensis* seeds, germinants, or seedlings until establishment interferes with the early growth of subordinates, most likely by delaying it. This phenomenon would lead to moderate size inequalities (Ross and Harper 1972, Weiner and Freckleton 2010), which are, as part of the variation of biomass in the experiment, preserved until sampling.

The strong positive correlation between biomass production (cubic root) and plant density (log) for the dominant and subordinates also implies that per capita growth is mostly density-independent, with no competitive effect of *S. capensis* biomass on subordinate density or biomass. This lack of strong density-dependent growth or mortality is an essential part of the proposed switch from resources to independent growth, rather than a logical assumption necessary to draw conclusions about microsite competition, is – more fundamentally – an ecological *conditio sine qua non* for its observation and possibly its existence.

Beside the minor direct environmental effect of mowing (likely due to positive responses of some subordinate species to reduced litter), the release from competitive inhibition during recruitment increased both the density of the subordinates and, through the stochastic sample-size effect on microsites as the focus of competition. However, density-independent growth, rather than a logical assumption, more fundamentally an ecological *conditio sine qua non* for its observation and possibly its existence.

The experiment did not reveal any consistent spatial effects of adjacent high-productivity patches on the inter-shrub community, except for a small additional effect of patch understorey mowing and patch removal on *S. capensis* density. Some small degree of seed augmentation by small-scale source-sink interactions seems to occur, but this is less important than during colonization after disturbance (Boeken and Shachak 1998). Patch reduction, due to clear-cutting or heavy grazing (Golodets and Boeken 2006), may cause resource loss (Hoffman et al. 2016), but only at spatial scales larger than that in this experiment.

**Seed limitation**

Seed-limited recruitment of the dominant species is a common phenomenon in temperate herbaceous plant communities (Turnbull et al. 2000, Rees et al. 2001, Foster et al. 2004, Munzbergová and Herben 2005, Clark et al. 2007, Knappová et al. 2017), usually associated with large seed size, which reduces dependence on high-quality microsites (Rees et al. 2001). However, seed limitation has not been documented adequately in more arid, water-limited dryland and desert ecosystems with annual rainfall <300 mm/yr (Rees et al. 2001). In addition, to the best of my knowledge, manipulating seed input by biomass removal has not been used extensively in experiments, in contrast to seed addition (Turnbull et al. 2000, Foster et al. 2004, Clark et al. 2007, Myers and Harms 2009). In *S. capensis*, seed limitation is mediated by ample microsite availability due to the specialized acquisition mechanisms of its small seeds for penetrating biocrust-covered soil (Boeken and Shachak 2006) and their short imbibition time due to a lack of secondary seed dormancy (Boeken et al. 2004). These traits make *S. capensis* very successful as the dominant species – with low site-selectivity as a highly adaptive ESS in a generally site-limited community (Boeken and Shachak 1994). Therefore, large seed size in dominants of mesic communities is equivalent to no dormancy in dryland annuals, contrary to what Dyer et al. (2000) and Rees et al. (2001) concluded. It should be noted that the selective advantage of the strategy employed by *S. capensis* is, in principle, independent of the occurrence of inter-specific competition for microsites, which is addressed by a separate hypothesis in this study.

The lack of secondary seed dormancy involved in seed limitation of *S. capensis* (Boeken et al. 2004) is also found in the grasses *Avena barbata* (Paterson et al. 1976) and *Bromus* spp. (*B. fasciculatus*, *B. alopecuroides*, and *B. rubens*; Zaady et al. 2003). These species occur among the subordinates in the experiment, but their incidences (between 0.11 and 0.19) are too low to study them individually. In contrast, desert annuals in general are widely known for their strictly microsite-limited recruitment associated with predictive and delayed (or, rather, postponed) germination from persistent, dormant seed banks (Went 1948, Cohen 1966, Pake and Venable 1995, Zaady et al. 1997, Gutterman 2002), as in many of the subordinate species (mostly forbs) in the experiment. In these microsite-limited species, the resulting negative density-dependent *per capita* probability of establishment buffers populations against environmental fluctuations, such that immediate negative effects of biomass removal, reduced seed production, or limited dispersal on their abundance are unlikely (Maron and Crone 2006). Although no direct effect of mowing was found on the collective plant density of the subordinate species (Tables 2, 3), the experiment does not provide direct evidence of microsite limitation per se, because mowing did not significantly reduce subordinate seed rain densities (Table 1), irrespective of their considerable dispersal potential. Rather, the results show that the subordinates, collectively, are less efficient in acquiring and exploiting microsites than the dominant, whether they have short- or long-term secondary seed dormancy or none at all. On the other hand, the rapid positive response of the subordinates to the reduced density of the dominant does suggest that the storage effect of persistent dormant seed banks play a role in dominant–subordinate coexistence in these communities (Chesson 1990, Rees et al. 2001).

Incidentally, the advantage of low microsite selectivity in *S. capensis* also addresses the trade-off between seed dormancy (high microsite selectivity) and dispersal, as proposed by MacArthur (1972) and Pake and Venable (1995). In *S. capensis*, efficient microsite acquisition compensates for the lack of seed dormancy-dependent predictive germination. Thus, low microsite selectivity also represents an ESS, and its selection does not require a trade-off with dispersal into highly unlikely “alternative environments”, as suggested by MacArthur (1972).
Density independence of biomass production

The strong correlation between plant density and biomass, which was found in the current experiment for *S. capensis*, the subordinates, and combined (Fig. 4, Table 3), is evidence of mostly density independence of per capita biomass production, without competition between growing plants. The linear relationship between log density and the cubic root of biomass (for both *S. capensis* and the subordinates) reflects the geometry of density-independent growth as individuals grow in volume, while the residuals did not indicate a leveling-off of biomass at high density as in density-dependent growth.

The wide spacing between individual plants (Fig. 1), in conjunction with short growing seasons (2–3 months), limits competition for growth resources sufficiently to prevent growth from reaching a constant final yield, with no compensation after biomass reduction of the dominant (Rees et al. 2001, Weiner and Freckleton 2010). Widely spaced plant cover is very common in Mediterranean-type semi-arid shrub- and grasslands with mostly biocrust-covered soil, a low annual rainfall (50–250 mm/yr), and short growing seasons (Boeken and Shachak 1994). In the denser vegetation of shrub patches and depressions scattered within the biocrust-covered matrix (Boeken and Shachak 1994, Boeken and Orenstein 2001), the absence of biocrust reduces microsite limitation, such that crowding and competition among growing annual plants are likely to occur and may locally result in a maximum final yield. Even in this case, however, the role of density-dependent mortality by thinning after establishment may be insignificant, as has been observed in dryland plant communities in general (Went 1948, Inouye 1980), due to short growing seasons or intermittent pulses, low densities, and spatial heterogeneity (Fowler 1986).

Inter-specific competition for microsites

The two negative inter-specific interactions between the dominant and the subordinates found in the experiment (Table 3) were effects of *S. capensis* density, but not of its biomass (or size), on subordinate density and biomass. These interactions reflect per-plant competitive effects of *S. capensis* seeds or early seedlings on others’ recruitment by inhibition, as a per-plant response, and delay, as a per-gram response due to time lost (Ross and Harper 1972). This is an extension of the approach of Goldberg and Landa (1991) in more competitive grasslands, where negative per-plant effects and responses were identified as competition during early seedling growth, in addition to per-gram interactions between growing adults, and per-plant responses to per-gram effects if resource competition leads to thinning (Schmitt et al. 1987, Goldberg and Landa 1991). In the experiment conducted here, no per-gram competitive effects were found, but there was a positive correlation between the biomass of both the dominant and the subordinates, suggesting common per-gram responses to spatial variation per sample in resource availability as a net effect, masking any negative interactions that could involve resources.

The strong competitive suppression (but not exclusion) by inhibition and delay of the subordinates occurred prior to and during the recruitment of individuals, and, therefore, involves microsites as the spatial resource for competition. This can be seen as the result of the high probability of acquisition, occupation, and exploitation by *S. capensis* of a wide range of microsites, some of which are potentially suitable also for the subordinates under some conditions. However, the species-specific suitability of these microsites is severely reduced by the presence of *S. capensis*, suppressing or delaying their recruitment as newly arrived or resident seeds from a transient or persistent seed bank, from before microsite acquisition until seedling establishment. Elucidating the detailed mechanisms underlying microsite acquisition, exploitation and competition will require further research. The competitive effects, resulting from *S. capensis*’s microsite acquisition and use, may vary from blocking or hindering microsite acquisition by other species, to mechanical displacement, inhibition of water uptake, elevated soil CO₂ concentrations, leached exudates, or other physical and chemical changes in the environment (Inouye 1980, Lortie and Turkington 2002, Tielbörger and Prasse 2009). The responses of subordinate species to these changes in microsite quality are likely to vary from reduced probability to acquire microsites for fresh seeds, to inhibition or delay of recruitment from seeds already occupying suitable microsites (i.e., the germinable fractions of dormant seed banks). Because non-random seed dispersal may contribute significantly to microsite acquisition, the mechanisms and traits of seeds associated with vector- and target-specific ‘directed’ dispersal by animals, wind, or water (Howe and Smallwood 1982, Guttermann 2002, Schupp et al. 2010, Giladi 2006) should be included as important components of the recruitment process, with multiple opportunities for intra- and inter-specific interactions.

Inter- and intra-specific microsite competition by interference may also play a role in microsite-limited, subordinate species, in the negative density-dependent delay of recruitment from dormant seed banks at high seed densities (Dyer et al. 2000, Lortie and Turkington 2002, Tielbörger and Prasse 2009). At low seed densities, recruitment rates would only involve ‘probabilistic’ negative density-dependence due to the chance of arrival and survival in suitable microsites. To test these microsite-related hypotheses, detailed experiments are needed on recruitment from persistent seed banks (Osem et al. 2006), which are much more difficult than the current experiment targeting the seed-limited dominant.

Microsite and resource competition

In general, at the small neighborhood scale, local competitive suppression of subordinates by dominants – and release by their reduction – is a very common phenomenon in annual and perennial herbaceous plant communities from tropical and temperate to sub-humid and semi-arid regions in most continents (Tielbörger and Kadmon 2000, Rees et al. 2001, Collins et al. 2002, Tielbörger and Prasse 2009, McCain et al. 2010, Segre et al. 2014). In these studies, competition involved resources required for growth and survival after establishment. In contrast, competition on biocrust in the *S. capensis*-dominated communities occurs in microsites between seed arrival and seedling emergence. Since the suppression of subordinate recruitment was not followed by
per-gram effects of *S. capensis* biomass, it could be argued that the species is a relatively weak competitor for growth resources. This is offset by its competitive advantage in microsite acquisition and use, notwithstanding its slightly faster growth than the subordinates as a group (see the regression coefficients of density on biomass in Table 3).

By highlighting the role of microsite competition in semiarid annuals on biocrust, the reported experiment could contribute to the development of a comprehensive theory of microsite and resource competition with testable hypotheses addressing their occurrence along resource availability gradients (Grime 1977, Tilman 1982, Tiellbörger and Kadmon 2000, Foster et al. 2004) and the evolution of associated competitive traits. Because of their sequential occurrence, the relationship between microsite competition and resource competition growth is asymmetric, due to the latter’s associated negative density-dependence. Without resource competition, natural selection for more efficient traits for microsite acquisition may be strong. If, in contrast, resource competition causes severe (self)-thinning due to crowding and shading, density-dependent mortality eliminates most if no all observable traces of efficient and competitive microsite-related traits, which will offer few fitness benefits. Such traits may only evolve if they are preemptively coupled with competitive growth, as seems to be the case for the large-seeded dominant herbs in mesic communities (Ross and Harper 1972, Rees et al. 2001). Preemption should not be assumed in water-limited communities, as has been tried in explaining delayed recruitment of dryland annuals (Inouye 1980, Dyer et al. 2000, Tiellbörger and Kadmon 2000, Lortie and Turkington 2002).

**Species richness**

Mowing increased the number of subordinate species in the vegetation, primarily due to the sample-size effect (Peet 1974) as a direct result of their greater density (Fig. 6). This stochastic species selection effect was expected only for seed species diversity, which is unaffected by inter-specific interactions. Stochasticity was also involved in the diffuse microsite competition observed in the experiment and can be considered as a null-model of species assemblage. Stochasticity increases species density only at the small neighborhood scale, with low species turnover (β diversity) at larger scales, similar to the effects of diffuse resource competition in more mesic temperate to Mediterranean communities (Rees et al. 2001, Segre et al. 2014). The resulting species composition is, therefore, likely to depend on species frequencies in the seed bank (Pärtel et al. 1996), their degree of dormancy and germinability, and their species-specific germination rates.

Another, apparently minor, direct effect of mowing on species diversity (Fig. 5) is soil exposure due to sparse litter cover, which was not directly measured in this experiment. This increased the availability of suitable microsites for species that require light or high surface temperatures for germination, such as the annual forbs *Erucaaria (Rebudalia)* pinnata (Zaady et al. 1997; Gutterman 2002).

From an applied perspective, inter-specific microsite competition, as well as stochasticity and density-independent growth, are highly pertinent to sustainable rangeland management (Ludwig et al. 2004, Maron and Crone 2006). Despite the lack of compensation of biomass production and constant final yield (Weiner and Freckleton 2010) due to seed-limited plant density and density-independent *per capita* growth, the release from inter-specific competition for microsites by biomass removal enhances the sustainability of rangeland grazing by increasing small-scale species density, which may also increase the nutritional value of the vegetation for herbivores.

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**Literature Cited**


USDA-ARS. 2015. Germplasm Resources Information Network (GRIN). National Germplasm Resources Laboratory, Beltsville, Maryland, USA.


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