



Shrub cover regulates population dynamics of herbaceous plants at individual shrub scale on the Mongolian steppe

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Nomenclature

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Abstract

Questions: Do shrubs regulate herbaceous plant community by modifying seed and plant distributions at the individual shrub scale? Do the magnitude and extent of effects at this scale change with shrub cover?

Location: A desert steppe, Mandalgobi, Mongolia.

Methods: We compared soil properties, seed accumulation and the establishment of plants of three functional types (annual forb, perennial forb and perennial graminoid) between shrub microsites (on mounds vs mound interspace) at sites differing in shrub coverage (high and low).

Results: Shrub patches (a legume *Caragana microphylla*) promoted seed accumulation but inhibited plant establishment on mounds, relative to the mound interspace, for all functional types. However, the effects varied with shrub cover, particularly in the mound interspace, with responses specific to each functional type. The accumulation of soil and annual forb seeds increased with shrub cover at both microsites. Additionally, the density of annual forbs was positively related to shrub cover in the mound interspace. In contrast, the density of perennial forbs and graminoids decreased with increasing shrub cover at both microsites, possibly because of enhanced sand accumulation.

Conclusion: Shrubs shape herbaceous plant community by causing differences at the individual shrub scale in seed and plant distributions. Additionally, we showed that individual shrub effects are shrub cover-dependent: dense shrub stands enhanced the dominance of annual forbs in spite of the negative effect found at the individual shrub scale, whereas perennial forbs and graminoids were less abundant in denser shrub stands. Shrubs can play an important role in structuring plant communities via shrub cover-dependent variation at microsites.

Introduction

Woody plants that are widely distributed in drylands strongly influence the surrounding herbaceous communities. A single woody plant can facilitate the establishment of understorey herbaceous species (Bertness & Callaway 1994; Scholes & Archer 1997; Callaway 2007) by reducing abiotic stress or grazing damage (Facelli & Temby 2002; Weedon & Facelli 2008; Cushman et al. 2010). Such ecosystem engineers (Jones et al. 1994; Badano et al. 2006; Wright et al. 2006) also modify environments at the landscape level and thus influence community-level species richness (Badano et al. 2006; Báez & Collins 2008; Maestre

et al. 2009a). The landscape-level effects of ecosystem engineers vary with the plants' density or cover, and are often inconsistent with their individual-level effects (Badano et al. 2006; Riginos et al. 2009; Eldridge et al. 2011). That is, individual-level effects of ecosystem engineers do not scale up to landscape-level effects for two reasons. First, the landscape-wide coverage of ecosystem engineers, not cumulative effect of single individuals, drives the distribution and abundance of landscape-wide herbaceous species (Irving & Bertness 2009; Salazar et al. 2012; Eldridge et al. 2013). Second, the individual-level effects of ecosystem engineers are density- or cover-dependent (Breshears 2006; Soliveres & Eldridge 2014). However, most relevant

studies have poorly investigated the density- or cover-dependent variation in plant–plant interactions in the latter process; i.e. how and whether the effects of ecosystem engineers at the individual scale change with density or cover (Riginos et al. 2009; Soliveres & Eldridge 2014).

Shrubs are widely distributed across arid and semi-arid ecosystems and form soil mounds, offering protection from the wind to understorey plants, accumulating seeds and improving soil fertility under their canopies (Moro et al. 1997; Shumway 2000; El-Bana et al. 2002; Pugnaire et al. 2004). Microsites formed by individual shrubs determine the distribution and performance of herbaceous plants, whose response to shrub microsites can be either positive or negative within a single life stage (Armas & Pugnaire 2005; Schiffrers & Tielbörger 2006; Gómez-Aparicio 2009). Seedling emergence and subsequent plant establishment are regulated mainly by species-specific physiological responses to light, soil water and nutrients, which individual shrubs can alter (Hastwell & Facelli 2003; Liancourt et al. 2005; Gross et al. 2010; Soliveres et al. 2011). On the other hand, seed accumulation at shrub microsites is driven mainly by modifications to the physical environment (e.g. protection from wind and water erosion). The seed accumulation by individual shrubs is regarded as a principal positive interaction (Aguar & Sala 1997; Giladi et al. 2013). Thus, different determinants (physical seed trapping and species-specific biotic interactions) may regulate the net effect of individual shrubs on the surrounding herbaceous plants.

Denser shrubs would intensify the magnitude of environmental alteration beneath the shrubs (Wright et al. 2006; Irving & Bertness 2009; Salazar et al. 2012). The effects of individual shrubs may be overridden or enhanced by the influence of collected, overlapping neighbouring shrubs as cover increases (Breshears 2006; Soliveres & Eldridge 2014). This would homogenize the environment (e.g. light) at the landscape level and thereby alter community species richness (Breshears 2006; Riginos et al. 2009; Eldridge et al. 2013). As their cover increases, shrubs may also extend their influence to the spaces between them (Breshears et al. 2003; Maestre et al. 2009a). The density- or cover-dependent variation in the extent of shrub-induced effects would influence seed and plant distributions and the subsequent plant establishment. Here, we examined whether the magnitude and extent of plant interactions change according to the cover of mound-forming shrubs, focusing on individual-level effects.

On the Mongolian desert steppe, the leguminous shrub *Caragana microphylla* (Pall.) Lam. dominates, and develops mounds by accumulating sand under its canopy. The shrub stabilizes the soil and fixes nitrogen (Su & Zhao 2003; Yue et al. 2008; Cao et al. 2011). Denser *C. microphylla*

communities are likely to increase plant species richness at the landscape scale (Sasaki et al. 2010; Yoshihara et al. 2010). In this study, we examined the effects of *C. microphylla* on herbaceous plant communities; in particular, we studied how shrub cover influences seed and plant performance. We asked the following questions: (i) how do shrubs determine the population dynamics of herbaceous plants through their effects on seed accumulation and subsequent plant establishment at the individual shrub scale; and (ii) do the magnitude and extent of individual shrub scale effects vary with shrub cover?

Methods

Study site

The study was conducted in the desert steppe ecological zone at Mandalgobi, Dundgobi province, Mongolia (45°47' N, 106°12' E). This area has been historically used as rangeland for domestic livestock, mainly sheep. The annual precipitation is 120 mm (average from 2000 to 2010; National Climatic Data Center) and peak rainfall occurs in July. The average air temperature is 2.7 °C, ranging from –17 °C in January to 22 °C in July. The vegetation growing period is generally from late May to late September, and seed dispersal occurs until October. A nitrogen-fixing leguminous shrub, *C. microphylla*, predominates on gently wind-exposed slopes with sandy soils (Sasaki et al. 2010; Yoshihara et al. 2010).

We established 13 sites at least 1 km apart across an area of ~20 km². At each site, paired (20 m × 20 m) plots differing in *C. microphylla* shrub cover (low and high cover; Fig. 1a, b) were established (26 plots in total). To minimize the topographic and edaphic differences within each pair, we established each pair in the same slope direction and minimized the distance within them, which is 95 m (43–278 m) on average. The mean *C. microphylla* shrub cover ± SD ($n = 13$) was $2.4 \pm 0.8\%$ (1.1–3.5%) in the low-cover plots and $12.3 \pm 3.6\%$ (8.4–21.6%) in the high-cover plots. With reference to each shrub, we defined shrub microsites as 'on-mound' or 'mound interspace' (Fig. 1c). 'On-mound' microsites are often beneath the shrub canopy. 'Mound interspace' microsites lie outside of this region. We also set an 'edge-mound' zone, where the two microsites meet.

Soil analyses

In August 2011, we collected soil samples (20 cm² area × 5-cm depth), using a stainless steel core, in the on-mound and the mound interspace microsites of three randomly selected shrubs in each plot. The samples from each zone were bulked, air-dried, and analysed for pH in water (soil:solution = 1:2.5 w/v, using deionized water), electri-

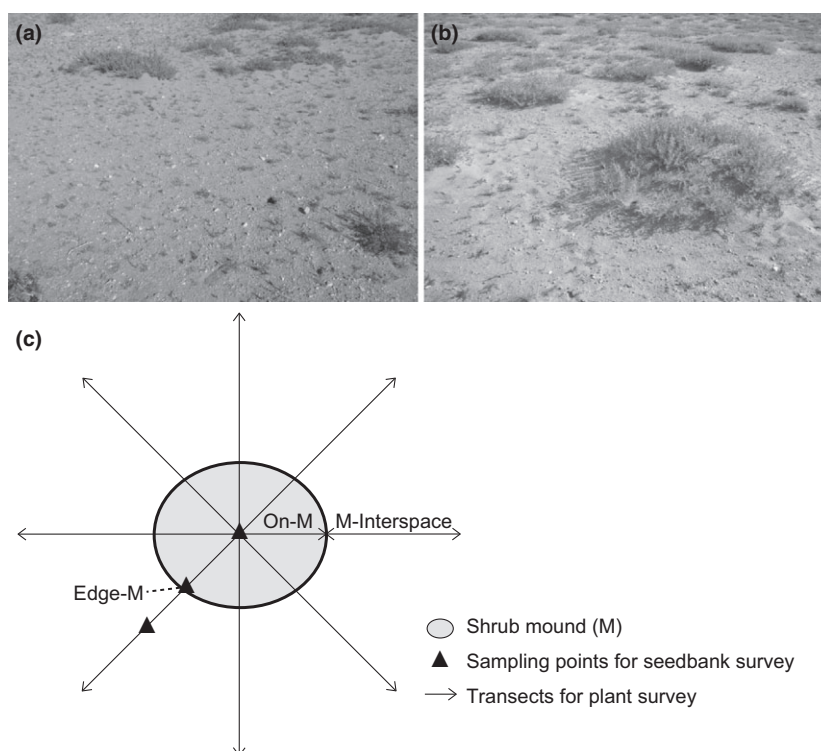


Fig. 1. (a, b) *Caragana microphylla* shrubs growing at (a) low and (b) high cover. (c) Survey transects and sampling sites in relation to a shrub mound (M).

cal conductivity (EC; Sparks 1996) and particle size distribution (coarse sand, fine sand, silt and clay) according to the International Society of Soil Science (ISSS) standard.

We measured the soil water content in the on-mound and the mound interspace microsites of one shrub in each plot using time-domain reflectometry (TDR) with 12-cm probes.

Seed bank survey

We selected five isolated shrubs in each plot and calculated the area of each shrub mound from the long and short diameters based on the assumption that the mounds were elliptical in cross-section. The mean area (\pm SD) was $1.4 \pm 0.9 \text{ m}^2$ ($N = 130$), and the mean mound height was $17 \pm 8 \text{ cm}$; the mean canopy height was $40 \pm 10 \text{ cm}$.

In October 2011, after seed dispersal, we established three sampling points in one of eight cardinal orientations, alternately selected, from each shrub and collected soil core samples (20 cm^2 area \times 5-cm depth) in the on-mound, mound interspace and edge-mound zones (390 samples in total; Fig. 1c). The mound interspace points were set 2.0–2.5 m from the centre of a mound. We then assessed the amount and species richness of germinable seeds by means of a germination experiment in incubators. Moistened soil samples were first cold-stratified for 8 wk at

4 °C in the dark incubator in plastic bags. The samples were then thinly spread (<1 -cm thick) on plastic trays filled with seed-free sand, and were held at 20/10 °C, 12/12 h light/dark in incubators. All soils were moistened and were stirred after 1 mo to enhance germination from the bottom soil layer. Germinated seedlings were counted every 2–7 d for 2 mo. To identify species, we grew seedlings in pots filled with garden soil under natural light.

Plant survey

Using the shrubs selected for the seed bank survey, we established eight 3-m transects from the centre of each mound to the mound interspace zone (1040 transects in total) along the eight cardinal orientations (Fig. 1c). Any transect that reached a point 80 cm, which is the average radius length of a shrub mound, from the edge of any other shrub mound, was cut off at that point. The total length of the transects was 1057 m in the mound interspace zone and 288 m on mounds at low-cover sites; and 745 m in the mound interspace zone and 435 m on mounds at high-cover sites. In early September 2011, all plants along the transects were recorded with their distance from the centre of the mound, microsite type, species and plant functional type (annual forb, perennial forb or perennial graminoid).

Statistical analysis

We examined the effects of shrub microsite, shrub cover and their interaction on soil properties, seed bank seeds and plants. All analyses were conducted using a generalized linear mixed effects model (GLMM), which can use appropriate probability distribution according to data type, with consideration of a nested design to recognize the differing shrub covers between paired sites. We analysed the soil properties using a hierarchical generalized linear model with a gamma error distribution and a log-link function, with pair site ID as a random intercept. We analysed the density of seed bank seeds (per core sample) of all species and of each functional type with a negative binomial error distribution using the glmmADMB program in the R software package (R Foundation for Statistical Computing, Vienna, AT), with pair site ID as a random intercept. This model is appropriate to analyse over-dispersed data including amount of zero counts. The number of species present as seeds and plant density were analysed by GLMM using a Poisson error distribution, with pair site ID as a random intercept. To account for plant density, the number of plants was calculated as the sum of the results of the eight transects from each shrub mound, and the difference in transect length was included as an offset variable in the model.

Further analysis was conducted to examine the shrub-induced effects on plant distribution on a smaller scale, focusing on the variation of plant distribution within each microsite type. We counted the number of plants of each functional type at 15-cm intervals along each transect, and analysed them using a zero-inflated negative binomial GLMM in glmmADMB for each shrub microsite separately. The explanatory variables were shrub cover, distance from the centre of the shrub and their interaction. The best model was selected on the basis of Akaike's information criterion (Burnham & Anderson 2002).

Results

Soil properties

Soil pH, EC and water content did not differ with shrub cover (Table 1), indicating that soil chemical and water conditions were homogeneous between paired sites. Soil EC and water content were significantly higher on mounds than in the mound interspace. Soil texture differed between microsites and between shrub covers: the content of coarse sand was higher on mounds than in the mound interspace, and was higher at high-cover sites (Table 1). The content of fine sand showed the converse pattern, and was lowest on mounds at high-cover sites.

Table 1. Soil chemical and physical properties (mean \pm SD) at two shrub microsites (mound interspace and on-mound) at sites with low and high shrub cover. Coefficients estimated using hierarchical generalized linear models are shown.

Soil Property	Low Cover		High Cover		Microsite (on-mound)		Shrub Cover (high cover)		On-mound \times High Cover	
	Mound Interspace	On-mound	Mound Interspace	On-mound	Coef.	t-Value	Coef.	t-Value	Coef.	t-Value
Chemical										
pH	6.4 \pm 0.4	6.5 \pm 0.4	6.3 \pm 0.2	6.3 \pm 0.4	0.01	0.63 ^{n.s.}	-0.02	-1.03 ^{n.s.}	-0.01	-0.45 ^{n.s.}
EC (dS·m ⁻¹)	0.11 \pm 0.05	0.15 \pm 0.05	0.09 \pm 0.02	0.18 \pm 0.10	0.32	2.22*	-0.22	-1.53 ^{n.s.}	0.38	1.87 ^{n.s.}
Soil Water Content (%)	9.9 \pm 0.6	11.0 \pm 0.6	9.7 \pm 0.7	10.9 \pm 0.7	0.11	7.30***	-0.02	-1.44 ^{n.s.}	0.01	0.44 ^{n.s.}
Particle Size										
Coarse Sand (%)	25.2 \pm 8.8	42.3 \pm 12.3	33.3 \pm 10.9	63.0 \pm 7.9	0.52	4.47***	0.28	2.43*	0.12	0.71 ^{n.s.}
Fine Sand (%)	54.3 \pm 9.2	40.4 \pm 12.1	45.8 \pm 11.9	20.1 \pm 5.6	-0.30	-2.72**	-0.17	-1.56 ^{n.s.}	-0.53	-3.42***
Silt (%)	11.4 \pm 2.7	10.1 \pm 2.5	12.2 \pm 3.6	9.5 \pm 2.8	-0.13	-1.23 ^{n.s.}	0.06	0.57 ^{n.s.}	-0.12	-0.80 ^{n.s.}
Clay (%)	8.9 \pm 1.9	7.5 \pm 1.5	9.0 \pm 2.2	7.4 \pm 1.6	-0.17	-2.04*	0.01	0.12 ^{n.s.}	-0.02	-0.20 ^{n.s.}

The coefficients for on-mound microsites and high shrub cover were calculated with respect to those for mound interspace microsites and low cover (both set to 0).

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s., not significant.

Table 2. Effects of shrub microsite, shrub cover and their interactions on seed density and species richness of three plant functional types. Results of GLMMs.

Variables	Annual Forb		Perennial Forb		Perennial Graminoid	
	Coef.	z-Value	Coef.	z-Value	Coef.	z-Value
Seed Density						
Intercept	−0.09	−0.43 ^{n.s.}	−1.37	−3.30***	−2.85	−5.21***
On-mound	1.23	5.32***	1.18	2.76**	1.76	2.96***
Edge-mound	0.74	3.13***	0.52	1.15 ^{n.s.}	0.67	1.02 ^{n.s.}
High Shrub Cover	0.66	2.74**	0.02	0.03 ^{n.s.}	0.41	0.59 ^{n.s.}
On-mound × High Cover	−0.19	−0.62 ^{n.s.}	0.57	0.95 ^{n.s.}	−1.45	−1.72 ^{n.s.}
Edge-mound × High Cover	−0.17	−0.52 ^{n.s.}	0.52	0.81 ^{n.s.}	−0.65	−0.71 ^{n.s.}
Seed Species Richness						
Intercept	−0.28	−1.85 ^{n.s.}	−1.74	−5.44**	−2.84	−5.52**
On-mound	0.75	4.38**	0.90	2.74**	1.39	2.48*
Edge-mound	0.25	1.31 ^{n.s.}	0.27	0.73 ^{n.s.}	0.41	0.63 ^{n.s.}
High Shrub Cover	0.16	0.85 ^{n.s.}	−0.06	−0.14 ^{n.s.}	0.42	0.65 ^{n.s.}
On-mound × High Cover	−0.08	−0.35 ^{n.s.}	0.28	0.60 ^{n.s.}	−1.25	−1.58 ^{n.s.}
Edge-mound × High Cover	0.02	0.09 ^{n.s.}	0.19	0.36 ^{n.s.}	−0.81	−0.89 ^{n.s.}

The coefficients for on-mound and edge-mound microsites and high shrub cover were calculated with respect to those for mound interspace microsites and low cover, respectively.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s., not significant.

Seed bank

The germinable seed bank comprised 1573 seeds of 23 species, of which 95% belonged to the three functional types: 1094 annual forbs, 337 perennial forbs and 56 perennial graminoids. The dominant species of annual forb were *Artemisia macrocephala* Jacquem., *Chenopodium* spp. and *Bassia dasyphylla* (Fisch. et Mey.) Ktze. The seed density and species richness of all functional types were significantly higher on mounds than in the mound interspace at both shrub covers (Table 2, Fig. 2). The seed density of annual forbs was also higher on the edge of mounds than in the mound interspace (Table 2). Shrub cover positively influenced the seed density (but not species richness) of annual forbs at all microsites, but not of perennial forbs or graminoids.

Plants

We recorded 8354 plants of 38 species, of which 99% belonged to the three functional types: 5816 annual forbs, 911 perennial forbs and 1538 perennial graminoids. The dominant annual forbs were *Salsola collina* Pall., *Chenopodium* spp. and *A. macrocephala*. Unlike the seed bank seeds,

the plant density of all functional types was significantly lower on mounds than in the mound interspace (Table 3, Fig. 3a–c). Additionally, shrub cover had different effects on plant density among the three functional types, depending on the microsite: it was positively related to the density of annual forbs in the mound interspace (Fig. 3a), but was negatively related to the density of perennial forbs and graminoids on both microsites (Fig. 3b, c).

Model selection showed that the plant density on mounds decreased with high shrub cover and increased with increasing distance from the shrub (Table 4, Fig. 4a–c). The density of annual forbs in the mound interspace increased with high shrub cover (Table 4, Fig. 4d), indicating a cover-dependent positive effect of shrubs in the mound interspace microsites. Additionally, the distance from the shrub was negatively related to the density of annual forbs in the mound interspace. Unlike annual forbs, the densities of perennial forbs and graminoids were negatively related to shrub cover at all microsites (Table 4, Fig. 4e, f). The density of perennial forbs increased with increasing distance from the shrub in the mound interspace and on mounds, while that of perennial graminoids did so only on mounds (Table 4, Fig. 4e, f).

Discussion

Effects at the individual shrub scale

Caragana microphylla strongly shaped herbaceous plant communities at the individual shrub scale. Shrubs enhanced seed accumulation on the mounds but inhibited subsequent plant emergence (Figs 2, 3). These effects result in different distributions between seeds and plants at a small scale. In most previous studies, evidence of facilitation by neighbouring plants has been seen in seed accumulation, without consideration of the following plant establishment stages (Aguilar & Sala 1997; Giladi et al. 2013), or in final survival, biomass and reproductive success without regard to the fate of immigrant seeds (Armas & Pugnaire 2005; Schiffers & Tielbörger 2006). In Mongolian grasslands, the accumulation of seeds by shrubs could contribute to herbaceous community structuring in wind-exposed regions. In contrast, our results suggest that shrubs negatively regulate herbaceous population dynamics through the different responses of seeds and the subsequent plants to microsite formation by individual shrubs.

Shrubs capture seeds and protect them from wind and water erosion (Ma & Liu 2008; DeFalco et al. 2009; Giladi et al. 2013). However, they have both positive and negative effects on the subsequent plant life-history stages (Weedon & Facelli 2008). Increasing the soil water content and fertilization, as *C. microphylla* does (Cao et al. 2011; Wang et al. 2011), should promote the survival, growth and reproduction of understorey plants (Shumway 2000;

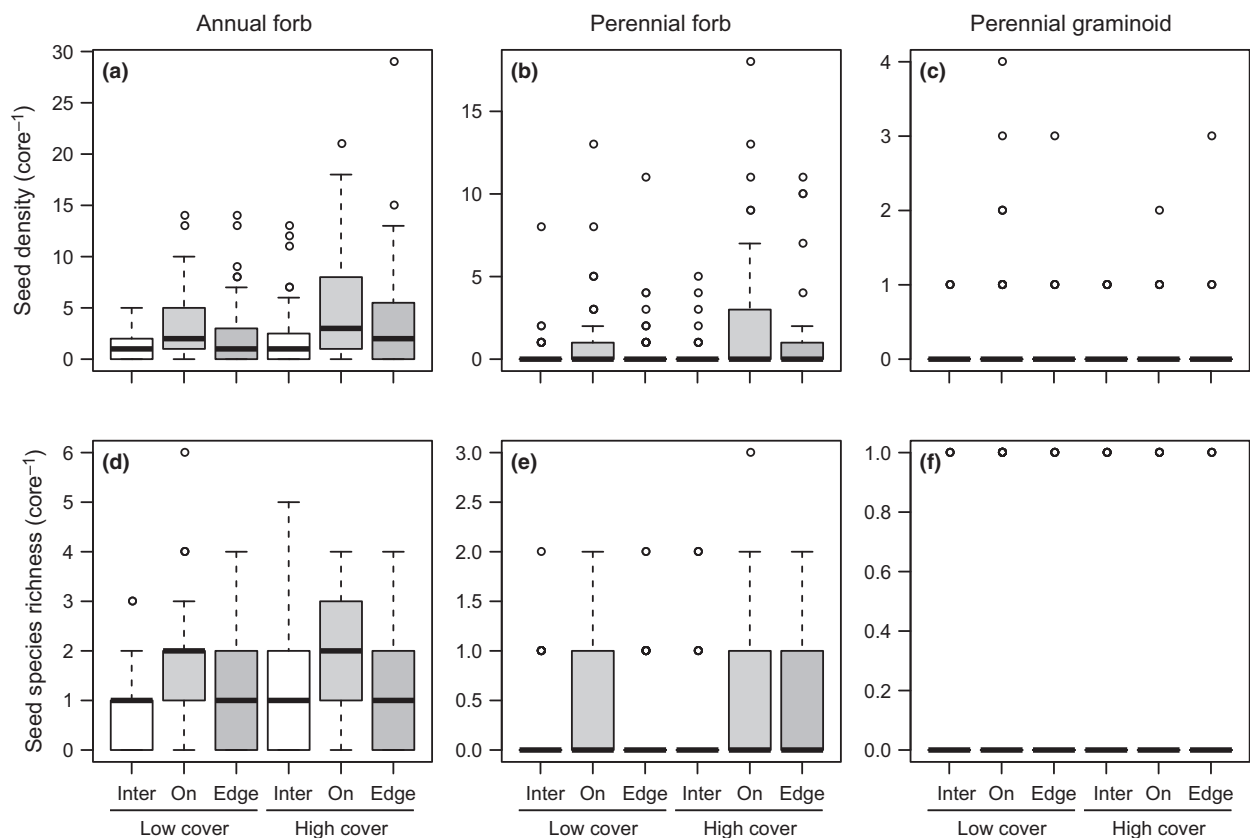


Fig. 2. (a–c) Seed bank seed density and (d–f) species richness of three plant functional types within a soil core (100 cm⁻³) at three shrub microsites (mound interspace, on-mound and edge-mound) at sites with low and high shrub cover. Boxes indicate 75th, 50th and 25th percentiles, and whiskers indicate 90th and 10th percentiles. Circles show outliers.

Pugnaire et al. 2004). However, competition for light, water and nutrients should decrease them (Facelli & Temby 2002; Weedon & Facelli 2008). Although we did not measure the survival and growth of herbaceous plants, the soil fertilization by *C. microphylla* (Cao et al. 2011; Kondo et al. 2012) would moderate its competitive effects on herbaceous plant density (Franco-Pizaña et al. 1996; Gómez-Aparicio et al. 2004). On the other hand, the accumulation of coarse sand, which retains less water and nutrients than fine soil (Ekwoanya & Ojanuga 2002), must inhibit plant emergence and growth on shrub mounds (Li et al. 2009). Therefore, modification of the physical environment (i.e. protecting soil and seeds from wind) by shrubs would lead to differences between seed and plant distributions at the individual shrub scale in this ecosystem.

Shrub cover-dependent variation in individual-level effects

Another important finding is the shrub cover dependency of individual-level effects of shrubs, particularly in the mound interspace. High shrub cover enhanced the

Table 3. Effects of shrub microsite, shrub cover and their interaction on plant density of three plant functional types. Results of GLMMs.

Variable	Annual Forb		Perennial Forb		Perennial Graminoid	
	Coef.	z-Value	Coef.	z-Value	Coef.	z-Value
Intercept	0.56	2.91***	-0.59	-4.13***	-0.23	-1.73 ^{n.s.}
On-mound	-0.18	-3.62***	-1.81	-9.53***	-1.79	-11.35***
High Shrub Cover	0.40	13.65***	-0.99	-11.64***	-0.28	-5.10***
On-mound × High Cover	-0.42	-6.52***	0.40	1.40 ^{n.s.}	-0.29	-1.25 ^{n.s.}

The coefficients for on-mound microsite and high shrub cover were calculated with respect to those for mound interspace microsites and low cover, respectively.

*** $P < 0.001$, n.s., not significant.

accumulation of sand and seeds both on mounds and the mound interspace (Table 1, Fig. 2) and changed plant distribution, especially in the mound interspace (Figs 3, 4). In semi-arid Australian woodland, shrubs enhanced several ecosystem functions (e.g. soil stability and nutrient

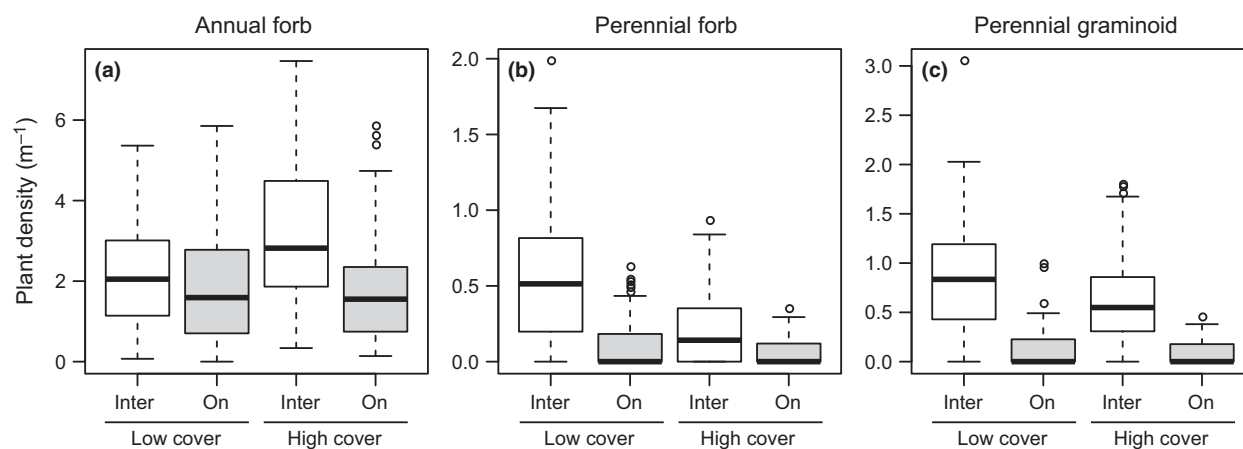


Fig. 3. (a–c) Plant density at two shrub microsites (mound interspace and on-mound) at sites with low and high shrub cover.

Table 4. Effects of shrub cover, distance from centre of a mound and their interactions on plant density of three plant functional types in each shrub microsite. Results of model selection are shown.

Variable	Annual Forb		Perennial Forb		Perennial Graminoid	
	Coef.	z-Value	Coef.	z-Value	Coef.	z-Value
On-mound						
Intercept	−1.98	−7.15***	−8.75	−9.24***	−7.97	−10.73***
High Shrub Cover	−1.34	−4.92***	−1.15	−3.90***	−1.05	−4.42***
Distance	0.14	2.50*	1.26	5.32***	1.17	6.20***
High Cover × Distance	0.34	4.52***				
Inter-mound						
Intercept	−0.75	−3.04**	−3.76	−8.69***	−2.34	−6.71***
High Shrub Cover	0.39	13.18***	−2.92	−2.44*	−1.52	−2.25*
Distance	−0.12	−3.79***	0.24	3.01**	0.04	0.596 ^{n.s.}
High Cover × Distance			0.35	1.54 ^{n.s.}	0.24	1.811 ^{n.s.}

The coefficients for high shrub cover was calculated with respect to those for low cover.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s., not significant.

cycling) under their canopies as their cover increased (Soliveres & Eldridge 2014). In contrast, we found cover-dependent variation in individual shrub effects also in the mound interspace, which can be considered to contain unmodified microsites (Badano et al. 2006). This result suggests that the shrubs modify microsites beyond their mounds. As shrub cover increases, soil and seed accumulation would be enhanced not only on shrub mounds, but also in the narrowed space between mounds, probably because of decreasing wind speed (Breshears et al. 2003; Breshears 2006; Maestre et al. 2009b). Our study shows the possibility of density- or cover-dependent variations in

plant–plant interactions, and that the magnitude and extent of individual-scale plant interactions depend on the density or cover of neighbouring plants.

The response of herbaceous plants to cover-dependent effects of individual shrubs was specific to each functional type (Riginos et al. 2009). Annual and perennial species showed markedly different responses of distribution to shrub cover (Figs 3, 4). Shrub cover had a positive effect only for annual forbs in the mound interspace. This response by annual species but not perennial species may be due to differential sensitivity of plant emergence to sand accumulation: sand accumulation often alleviates seed dormancy and thus increases the germination of annual species, but inhibits the germination of perennial species (Huang et al. 2004a,b; Holzapfel et al. 2006; Liu et al. 2013). Additionally, sand dune-specific annual forbs with short roots (e.g. *S. collina*, *Chenopodium* spp., *B. dasyphylla*) can grow in wind-exposed habitats (Bonser & Ladd 2011), resulting in wide geographic distribution within the study area. Therefore, increasing sand and seed accumulation would favour the establishment of annual forbs in the mound interspace at high shrub cover, but would inhibit the establishment of perennial species by burying them.

Additionally, the occurrence of perennial forbs increased with distance from shrubs regardless of microsite, while that of perennial graminoids increased with distance only on the mounds (Table 4, Fig. 4). The difference between perennial forbs and graminoids may result from morphological traits: rosette-forming species of perennial forbs (e.g. *Heteropappus* spp., *Convolvulus ammannii* Desr. and *Potentilla bifurca* L.) can tolerate wind-eroded and rocky habitats because of their short stature, but are more susceptible to burial in sand than erect perennial graminoids. Therefore, sympatric cover-dependent variation in the effects of individual *C. microphylla* shrubs and the species-specific responses of herbaceous species would change

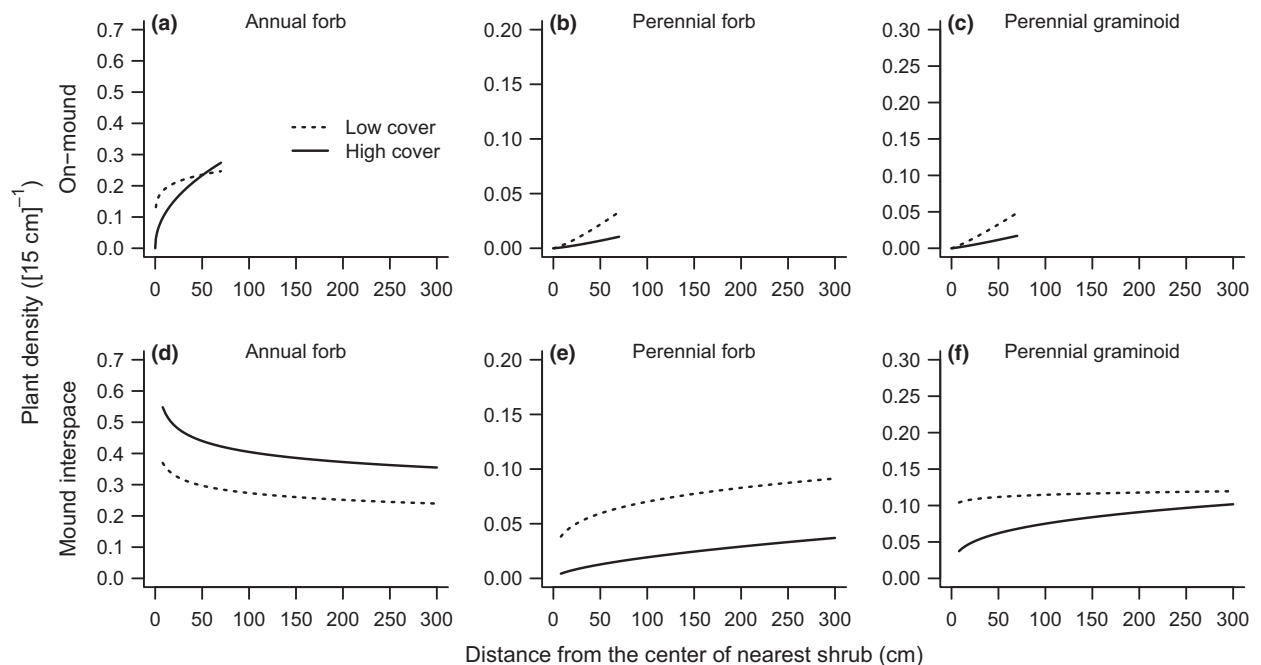


Fig. 4. Estimated plant density of three plant functional types with distance from the centre of a shrub at sites with low and high shrub cover for two shrub microsites (on-mound and mound interspace), respectively. The regression lines span the minimum to mean transect lengths for on-mound microsites and the minimum to maximum for mound interspace. For the regression equations, refer to Table 4.

herbaceous community composition and thus species richness.

Density- or cover-dependent facilitation of community species richness could be solely responsible for the consequences of increasing shrub density with constant positive effects on plant density (Soliveres & Eldridge 2014). In addition to this process, our results suggest that density- or cover-dependent variation in the magnitude and extent by which a single shrub modifies a microsite can contribute to community diversity. On the other hand, external factors driving shrub cover could also cause the differences in herbaceous species composition between high- and low-shrub covers (Sankaran et al. 2004). Nevertheless, our paired site comparison and the small differences in soil properties (pH, EC, soil water content) between high- and low-shrub cover plots support the minor influence of external effects on our results. Thus, at the landscape level, the shrub community consists of shrubs growing at various densities at smaller scales, which form a diversity of microsites dependent on cover.

Implications for management and restoration

Land degradation in drylands is a serious global problem (Reynolds et al. 2007). In Mongolian rangelands, heavy grazing changes plant species composition from one dominated by palatable perennial graminoids to one dominated

by unpalatable forbs and annual weeds (Fernandez-Gimenez & Allen-Diaz 2001; Sasaki et al. 2008). Shrubs can trap seeds of various functional types, increasing species diversity and ecological functioning in drylands (Sasaki et al. 2010; Yoshihara et al. 2010). However, from the rangeland management perspective, our results suggest that maintaining a range of shrub cover in the landscape can create habitats suitable for a wider range of species and life forms than maintaining a more homogeneous shrub cover. The maintenance of shrub cover that is desirable for rangeland management is essential to maintaining both small-scale and larger-scale ecological processes.

Woody ecosystem engineering species have been planted to restore vegetation cover (Padilla & Pugnaire 2006; Gómez-Aparicio et al. 2009). *C. microphylla* is commonly planted on sand dune systems in Inner Mongolia, where it exceeds 1 m in height, stabilizing shifting sand (Su & Zhao 2003; Zhao et al. 2007; Cao et al. 2011). Planted *C. microphylla* tends to enhance soil fertilization and the establishment of herbaceous species, dominated by annual plants, in the interspace of shrubs over time (Su & Zhao 2003). Our results show that the density or cover of woody species planted to restore rangelands must allow for a range of plant interspaces. In conclusion, shrubs determine population dynamics and the composition of herbaceous species through density- or cover-dependent variation in the effects of microsites.

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