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Differential plant species responses to interactions of sand burial, precipitation enhancement and climatic variation promote co-existence in Chinese steppe vegetation

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Abstract

Aims: Sand burial and precipitation play important roles in vegetation of inland deserts and desertified areas, and both are under strong influence of climate and land-use change. Sand deposition and precipitation both vary greatly in space and time, and different plant species, with diverse adaptations, occupy different niches along spatial gradients in the combination of sand and water availability dynamics. We hypothesized that species specificity in spatial and temporal niche occupation along such gradients is a mechanism for their co-existence and, thereby, a driver and stabilizer of biodiversity in dry, sandy areas.

Location: Ordos Plateau, China.

Methods: We conducted a 2-yr field experiment with factorial treatments of precipitation (control, slight enhancement, strong enhancement) and sand addition (control, medium addition, large addition). Plant cover of the six dominant species was followed over different seasons, as we expected different species to benefit from different treatments in different seasons and years with different weather regimes.

Results: Sand burial alone significantly affected plant cover of all six dominant species, while precipitation enhancement had no significant effect. Effects of sand burial on plant cover changed overall during the two hydrologically contrasting years. Our key finding was that there were multiple significant two- and three-way interactions between species, sand burial and precipitation enhancement on plant cover, while there were also multiple two- and three-way interactions involving species, sand burial or precipitation treatment with year and/or season.

Conclusion: Our results supported our hypothesis, i.e. the co-existence of species in a semi-arid sand dune can be explained from the different niches they occupy in terms of seasonal and year-to-year variation in precipitation in combination with sand deposition regime. The interactions of these drivers on plant cover with experimental enhancement of precipitation, mimicking a realistic scenario for this region, suggest that shifts in species composition are to be expected this century. More generally, our findings advance our understanding of what drives species co-existence and thereby biodiversity, now and in the future.

Introduction

Sand burial is an important environmental factor in coastal and lake shoreline dunes, as well as in inland (semi-) deserts and desertified areas. It often increases moisture, nutrient availability, anaerobic microorganisms and the available soil volume for roots, but may decrease soil temperature and aeration, light intensity and competition (Maun & Lapierre 1984; Jayne & Daggy 2000; Teraminami et al. 2013). These factors have been shown to affect plant

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growth and community zonation (Wilson & Sykes 1999; Gilbert et al. 2008).

The responses of plants to sand burial are often species-specific (Owen et al. 2004; Zheng et al. 2005; Gilbert et al. 2008). For example, plants show variable responses to moderate burial, including tolerance (Bach 1998), growth impediment (Franks & Peterson 2003) or growth stimulation and biomass accumulation (Maun 1994; Yu et al. 2004). The effects of sand burial on plant species also depend on the degree of burial. Slight sand burial accelerated plant growth, while major sand burial reduced plant biomass and impaired survival in some studies (Yu et al. 2004; Liu et al. 2014). Thus, sand burial has different effects on different plant species and might thereby alter community composition. However, previous studies on the effects of sand burial on plants have focused principally on impacts on individual species, such as seed germination (Zhu et al. 2014), seedling growth and survival (Zheng et al. 2005), photosynthetic responses (Kent et al. 2005), plant individual growth (Gilbert et al. 2008; Teraminami et al. 2013; Xu et al. 2013; Liu et al. 2014), and have highlighted the importance of clonality as a successful strategy with respect to sand burial (Yu et al. 2004). Few studies have discussed the effects of sand burial on the patterns (Wang et al. 2013) and zonation (Maun & Perumal 1999; Wilson & Sykes 1999; Owen et al. 2004) of the plant community. To our knowledge, no experimental study has focused directly on the drivers of co-existence of plant species, as affected by sand burial as an environmental filter (*sensu* Keddy 1992; Diaz et al. 1998).

Unlike the coastal and lake shoreline dunes, in which nutrients are a limiting factor for plant growth (Maun 1994), precipitation regimes play a paramount role in inland (semi-)deserts and desertified areas. Precipitation is strongly correlated with species composition of plant communities (Knapp et al. 2008; Hallett et al. 2014). Climate models predict increasing inter- and intra-annual variability in precipitation patterns and increased frequency of extreme precipitation events in many regions (Allan & Soden 2008; Min et al. 2011; Durack et al. 2012). Such altered precipitation regimes will significantly alter the temporal supply of water and thus have important impacts on species co-existence in the plant community, especially in inland deserts and desertified areas, where precipitation is generally sparse and uneven.

Relationships between precipitation and species composition of plant communities are complex. In general, increased precipitation significantly alters plant community structure and composition at functional group level (Yang et al. 2011; Rollinson et al. 2012), as seen along spatial gradients of mean precipitation (Fraser et al. 2014). However, inter- and intra-annual variability in precipitation, and their interaction, also drive community composition. Perennial-dominated systems will be buffered against rising inter-annual variation in precipitation, while annual species will show the largest temporal variability in species composition (Cleland et al. 2013). Seasonal patterns of precipitation drive community productivity across ecosystems more than annual precipitation (Grime et al. 2000; Morecroft et al. 2004; Robinson et al. 2013). While previous studies hardly accounted for the interactive effects of changing precipitation amount and frequency, even less is known about how these drivers of community composition in turn interact with sand burial. Sand deposition and precipitation both vary greatly in space and time, and observations suggest that different plant species, with different adaptations, occupy different niches along spatial gradients in the combination of sand dynamics and water availability dynamics. Here we test the hypothesis that species specificity in spatial and temporal niche occupation along such gradients is a mechanism for their co-existence and, thereby, a stabilizing factor (Wilson 2011) for the maintenance of biodiversity in dry, sandy areas. There have been previous reports of complex interactions of community composition response to heterogeneity in soil properties and inter-annual climatic variability, e.g. in alpine grassland (Song et al. 2012) and humid-temperate grassland (Fridley et al. 2011). However, this is the first study to address species co-existence as driven by differential combined effects of substrate properties (sand deposition) and variability in precipitation (between and within years) on the performance of different species. We specifically address the following questions: (1) how do sand deposition depth, overall precipitation enhancement and inter-annual seasonal variation in precipitation affect plant cover dynamics of the main plant species in the community; and (2) could the responses of different species to interactive abiotic drivers over time be a mechanism for species co-existence and a stabilizing factor for maintaining biodiversity in a landscape with strong sand and water availability dynamics?

Methods

Study sites

The study was conducted in Ordos Sandland Ecological Station (OSES), Institute of Botany, Chinese Academy of Sciences (39°02′ N, 109°51′ E), in the northeast Mu Us sandy grassland, Ordos Plateau, China. The climate is continental, with extreme seasonal and diurnal temperature variation and low rainfall. Mean annual temperatures range from 5.0 to 8.5 °C, with an absolute temperate range from −28 to 40 °C (data from OSES weather station, 2004–2014). Mean annual precipitation is 350 mm, with large inter-annual fluctuations from 161 to 664 mm, and more than 80% of which is concentrated between June and September. The mean potential evaporation is 2300 mm.

Ordos Plateau occupies the southern part of Inner Mongolia in northern China (37.4–40.8° N, 106.3–112.2° E). The Mu Us sandy grassland comprises the main body of the plateau, and the Kubuqi sandy desert occupies the northern Ordos Plateau. Sand movements are frequent and large, due to the large area of sandy substrate, the perennial strong wind and surface erosion from overgrazing.

The typical steppe, which is the dominant ecosystem in the east of Ordos Plateau and is strongly impacted by strong sand dynamics, is dominated by perennial graminoids (herbaceous monocots) such as *Stipa bungeana* Trin. and/or *Stipa grandis* P. Smirn., *Leymus secalinus* (Georgi) Tzvel., *Pennisetum centrasiaticum* Tzvel. and *Cleistogenes squarrosa* (Trin.) Keng, with the perennial forbs *Allium mongolicum* (Regel), *Heteropappus altaicus* (Willd.) Novopokr., *Artemisia sacrirum* Ledeb. and *Ixeris chinensis* (Thunb.) Nakai, the annual forbs *Chenopodium aristatum* L., *Corispermum chinganicum* Iljin. and the herbaceous legumes *Astragalus melilotoides* Pall., *Lespedeza davurica* (Laxm.) Schindl. and *Oxytropis gracilima* Bunge as accompanying species (Chen 1964).

Experimental design

On 2 Sept 2010, a 100 m × 100 m area with a natural steppe plant community (*S. bungeana–Allium mongolicum*) was enclosed as the experimental site in OSES. Then 54 1 m × 1 m quadrats, with distances of at least 4 m between them, were chosen and randomly assigned to one of nine treatments in a factorial design of precipitation at three levels crossed with sand depth at three levels. Precipitation treatments were: P^{++}, strong precipitation enhancement; P^{+}, slight precipitation enhancement; P^{A}, ambient precipitation. Sand depth treatments were: S^{++}, heavy sand burial; S^{+}, medium sand burial; and S^{A}, ambient sand (i.e. no sand burial). There were six replications for each treatment. These treatments mimic realistic scenarios for this region of a slight overall increase in precipitation (Chen et al. 2012) and major sand dynamics due to intense land use leading to overgrazing and erosion (He et al. 2008).

Precipitation enhancement treatments were implemented through the transfer of a certain area of intercepted precipitation. Tin troughs collected precipitation just outside each quadrat (Fig. S1). The area of the trough was related to the amount of collected precipitation. Quadrats without a trough had no precipitation enhancement (P^{A}, around 350 mm of precipitation), one trough per quadrat (1/7 m^2, 50-cm long and 28.57-cm wide) added 1/7 of mean ambient precipitation (P^{+}, aiming for ca 400 mm), while two troughs per quadrat added 2/7 (P^{++}, aiming for ca 450 mm). The edge of each tin trough was 15 cm high. The trough was fixed at 50 cm from the ground, tilted at a 30° angle by two H-shaped steel supports. There was a 1-cm diameter hole in the bottom corner of the low end of the trough, so that the collected precipitation drained real-time into the quadrat, where it was distributed through a 1-cm diameter drip irrigation tube. The tube was 2-m long, with a small hole each 15 cm, coiled within the quadrat to distribute the collected precipitation as homogeneously as possible.

Quadrats were enclosed with a 0.5-cm thick and 20-cm high PVC fence (Fig. S1), and sifted sand collected from 100 m west of the experimental site was evenly sprinkled into the quadrats to simulate sand burial. For S^{+} treatment a 2-cm layer of sand was added; for S^{++} treatment, a 5-cm layer of sand was added; for S^{A} no sand was added.

Measurements

The experiment ran over two hydrologically contrasting years, until 6 Sept 2012. Meteorological data from OSES showed that total precipitation before the experiment (from Sept 2009 to Aug 2010) was 290.46 mm, rather similar to long-term mean precipitation (350 mm). However, the first year of experimental treatment (from Sept 2010 to Aug 2011) was a dry year at 191 mm (45% below long-term average) with 22 precipitation events (>2 mm). In contrast, the second treatment year (from Sep 2011 to Aug 2012) was wet at 596 mm (70% higher than long-term average) with 40 precipitation events (Fig. S2). Mean annual temperatures were similar: 6.5 °C in year 1 and 6.1 °C in year 2. Over the experimental period, average wind speed was 2.1 $m \cdot s^{-1}$ and its main direction was from SW to NW. Maximum wind speed was 26.6 $m \cdot s^{-1}$ and there were 124 episodes of wind at >17 $m \cdot s^{-1}$.

During the experiment, plants were monitored on 1 Sept 2010, 30 Apr 2011, 9 Jul 2011, 2 Sept 2011, 1 May 2012, 7 Jul 2012 and 6 Sept 2012. Six dominant plant species, together accounting for 82–86% of plant cover at ambient precipitation, were chosen for in-depth analysis: *S. bungeana*, *A. mongolicum*, *L. secalinus*, *P. centrasiaticum*, *L. davurica* and *C. chinganicum*. For each species, cover percentage (C; projected surface area of living plants as percentage of quadrat area), height and number of individuals (recognisable separate above-ground unit for clonal plants, such as clump for tillering clonal plants and single ramet for rhizomatous clonal plants; Cornelissen et al. 2003) were measured within each quadrat. For plant cover of the subordinate species see Fig. S3.

Statistical analysis

A five-way ANOVA with year (2011 vs 2012) and season (summer, autumn) as the two repeated measure factors, and species, experimental precipitation enhancement and sand burial as the three independent factors was carried out first, to examine the main effects and possible interactions of these factors on plant cover. Then a four-way ANOVA with season as a repeated measures factor, and species, experimental precipitation enhancement and sand burial as the three independent factors was carried out to examine the main effects and possible interactions of these factors on plant cover in 2011 and 2012.

For each of the six dominant plant species separately, three-way ANOVAs with one repeated measure factor (season) and two independent factors (precipitation enhancement and sand burial) were carried out to examine the effects of season, precipitation enhancement, sand burial and their possible interactions on plant cover in 2011 and 2012. Then two-way ANOVAs were used to examine the effects of precipitation enhancement and sand burial on plant cover in Sept 2011 and 2012 separately. Tukey HSD tests were used for multiple comparisons of effects of sand burial or precipitation enhancement treatments. All statistical analyses were performed using the SAS for Windows v 8 (SAS Institute, Cary, NC, US).

Results

The five-way repeated measure ANOVA results showed that species ($F = 16.16$, $P < 0.001$), year ($F = 217.59$, $P < 0.001$) and season ($F = 46.16$, $P < 0.001$) had significant single effects on plant cover for the six dominant species, but precipitation enhancement ($F = 0.49$, $P = 0.616$) and sand burial ($F = 1.19$, $P < 0.306$) did not. There were multiple significant two-way and three-way interactions between species, sand burial and precipitation enhancement on plant cover, while there were also multiple two-way and three-way interactions involving species, sand burial or precipitation treatment with year and/or season (Tables S1, S2).

Sand burial significantly decreased plant cover of *S. bungeana*, increased plant cover of *A. mongolicum*, *P. centrasiaticum* and *L. secalinus* in 2011; while it significantly decreased cover of *S. bungeana* and *C. chinganicum*, and increased cover of *A. mongolicum* and *P. centrasiaticum* in 2012 (Table 1, Fig. 1). Precipitation enhancement had no significant effects on plant cover of any dominant species neither in 2011 nor in 2012 (Table 1). Season affected cover of all six dominant species in 2011, but had no significant effects on cover of *S. bungeana* and *L. secalinus* in 2012 (Table 1).

Stipa bungeana had significantly higher cover than other plant species in all quadrats before experimental treatments. While it maintained the highest cover under P–S, P–S^{+}, P^{+}–S and P^{+}–S^{+} treatments in Sept 2011 (i.e. after 1 yr) and under P–S, P–S^{+}, P^{+}–S, P^{++}–S and P^{+}–S^{+} in Sept 2012 (after 2 yrs). *Allium mongolicum* had the highest cover under P–S^{++}, P^{+}–S^{++}, P^{++}–S and P^{++}–S^{+} in 2011 and under P–S^{++} in 2012, and *P. centrasiaticum* had the highest cover under P^{++}–S^{++} treatment in 2011 and under P^{+}–S^{++}, P^{++}–S^{+} and P^{++}–S^{++} in 2012 (Fig. 2).

Table 1. Results of repeated measures ANOVA with one repeated measure factor (season) and two independent factors (precipitation enhancement and sand burial) in 2011 and 2012.

Plant Species	df	*Lespedeza davurica*		*Stipa bungeana*		*Allium mongolicum*		*Pennisetum centrasiaticum*		*Leymus secalinus*		*Corispermum chinganicum*	
Source		F	Sig.	F	Sig.	F	Sig.	F	Sig.	F	Sig.	F	Sig.
In 2011													
Precipitation (P)	2	1.88	0.164	2.44	0.098	1.36	0.267	2.46	0.097	0.75	0.477	0.60	0.556
Sand burial (SB)	2	2.70	0.078	9.06	**<0.001**	3.57	**0.036**	5.04	**0.011**	7.49	**0.002**	1.63	0.208
P × SB	4	0.40	0.806	3.22	**0.021**	1.24	0.309	0.40	0.811	0.99	0.422	0.57	0.689
Season (SS)	1	19.05	**<0.001**	4.24	**0.045**	85.48	**<0.001**	18.83	**<0.001**	4.88	**0.032**	19.06	**<0.001**
SS × P	2	0.42	0.662	3.25	**0.048**	2.75	0.075	1.77	0.182	0.12	0.888	0.6	0.554
SS × SB	2	3.55	**0.037**	2.66	0.081	1.03	0.366	3.97	**0.026**	2.52	0.092	1.55	0.223
SS × P × SB	4	0.18	0.947	0.49	0.746	1.10	0.368	0.58	0.682	0.19	0.944	0.57	0.689
In 2012													
Precipitation (P)	2	1.19	0.315	1.54	0.225	0.35	0.707	1.55	0.224	0.48	0.624	0.61	0.546
Sand burial (SB)	2	3.68	**0.033**	5.56	**0.007**	3.43	**0.041**	5.34	**0.008**	2.28	0.114	54.03	**<0.001**
P × SB	4	0.10	0.983	1.71	0.164	1.01	0.415	0.27	0.894	0.57	0.683	0.44	0.776
Season (SS)	1	64.36	**<0.001**	1.08	0.305	48.77	**<0.001**	8.03	**0.007**	4.37	**0.042**	0.88	0.353
SS × P	2	0.03	0.970	1.68	0.198	0.75	0.478	0.12	0.890	0.87	0.425	1.27	0.292
SS × SB	2	9.04	**<0.001**	4.09	**0.023**	2.89	0.066	1.31	0.281	0.38	0.686	2.68	0.080
SS × P × SB	4	1.34	0.271	1.16	0.340	1.91	0.126	0.09	0.987	2.55	0.052	1.08	0.377

Values in bold indicate significance at $P < 0.05$.

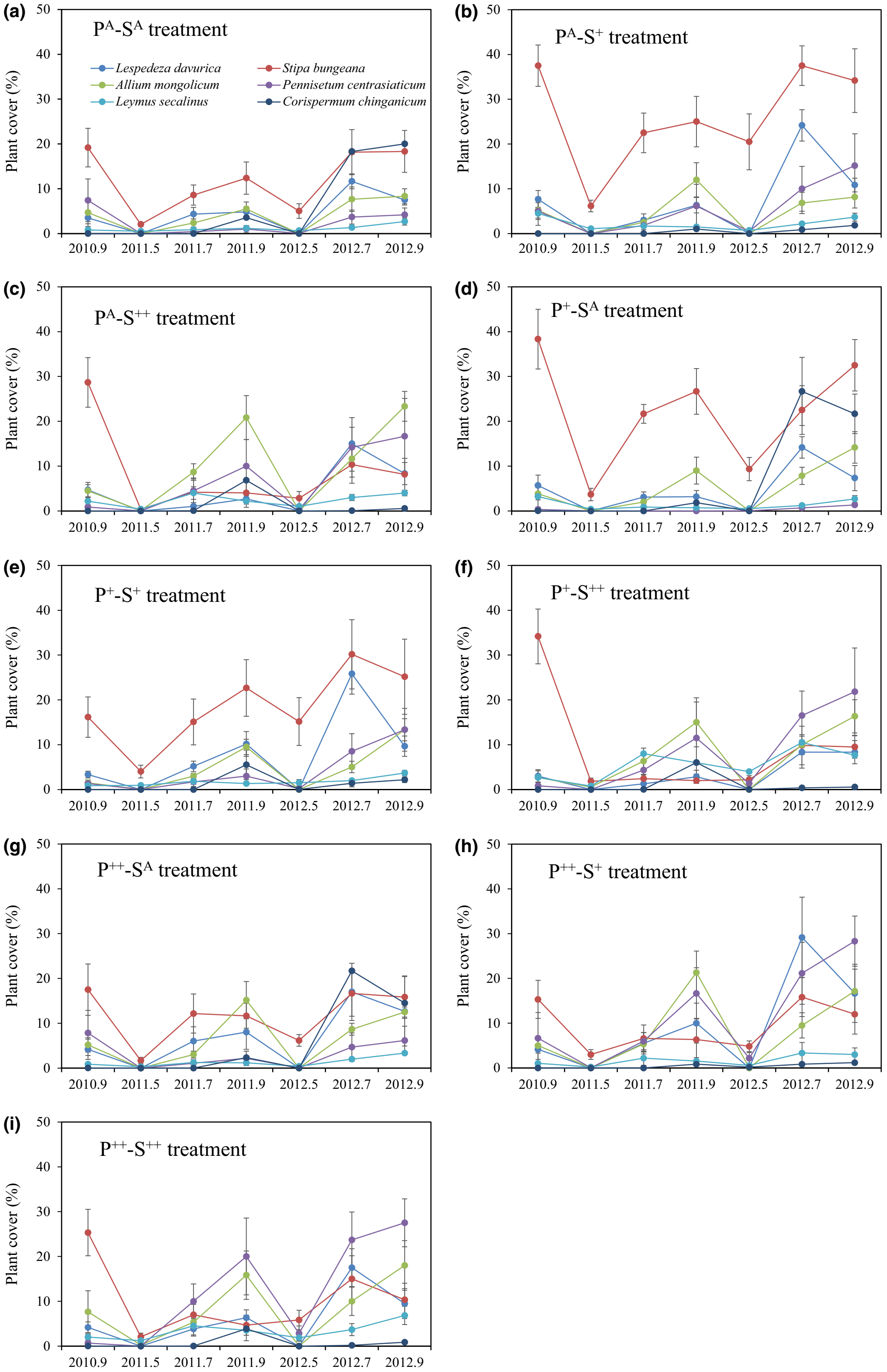

Fig. 1. Seasonal dynamics of plant cover of the six dominant species under different experimental treatments. P, P^+ and P^{++} represent, respectively, natural precipitation, adding 1/7 precipitation and adding 2/7 precipitation; S, S^+ and S^{++} represent no sand burial, 2 cm sand burial and 5 cm sand burial.

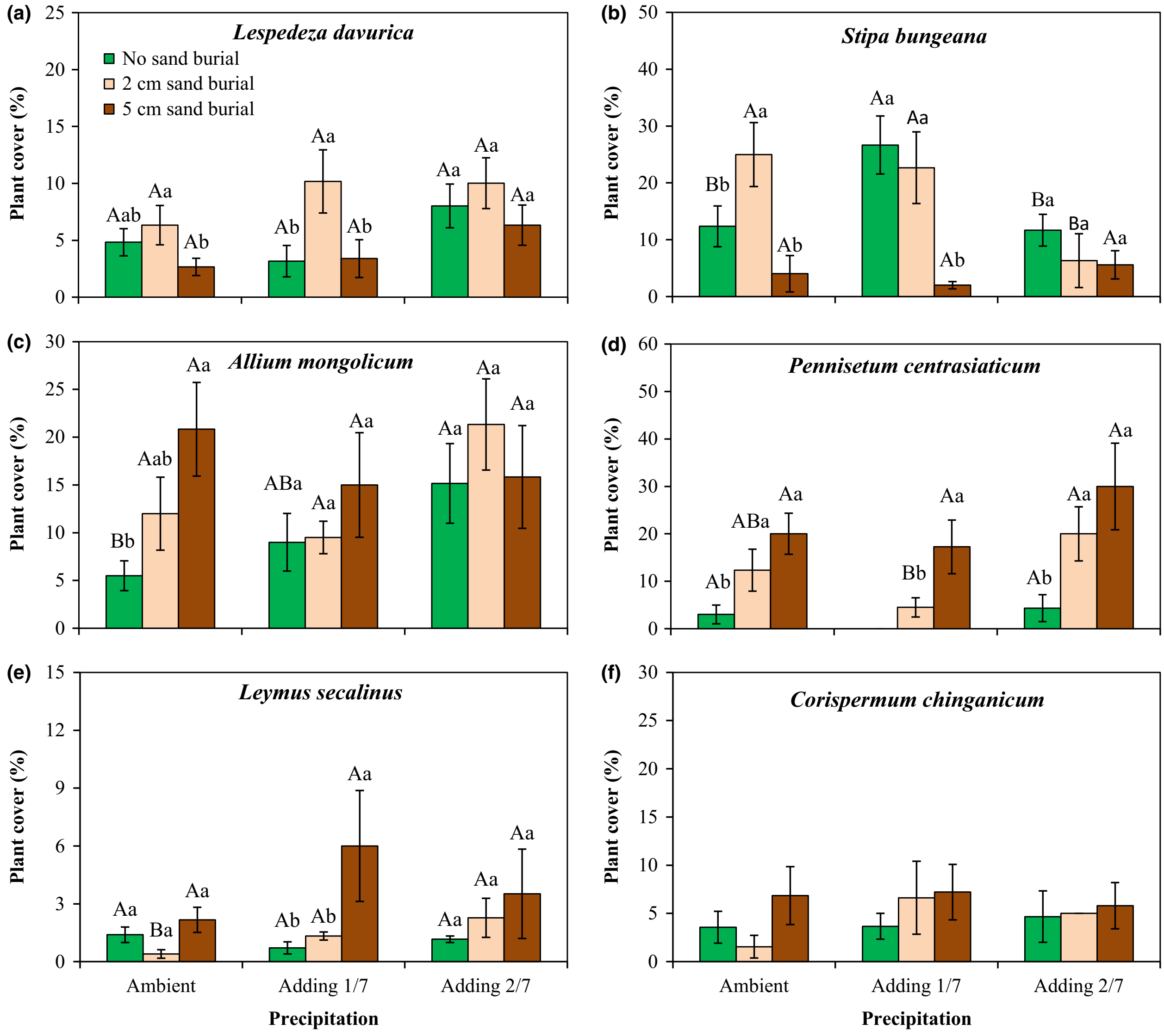

Fig. 2. Effects of precipitation enhancement and sand burial on cover of *Lespedeza davurica* (**a**), *Stipa bungeana* (**b**), *Allium mongolicum* (**c**), *Pennisetum centrasiaticum* (**d**), *Leymus secalinus* (**e**) and *Corispermum chinganicum* (**f**) in Sept 2011. Different capital letters represent significant differences among the three precipitation enhancement treatments, different lowercase letters represent significant differences among the three sand burial treatments, while no letters mean no significant differences between any treatment.

Sand burial and precipitation enhancement had different effects on plant cover in 2011, the dry year, and in 2012, the wet year. Sand burial significantly decreased cover of *L. davurica* and had no significant effects on *C. chinganicum* in Sept 2011, but decreased cover of *C. chinganicum* and had no significant effects on *L. davurica* in Sept 2012 under ambient and medium precipitation treatments (Figs 2, 3). Under the heavy precipitation enhancement treatment, sand burial only increased plant cover of *P. centrasiaticum*, and had no significant effect on cover of the other five species in Sept 2011; but increased cover of *P. centrasiaticum* and *L. secalinus* and decreased cover of *C. chinganicum* in Sept 2012 (Figs 2, 3). Precipitation enhancement increased cover of *P. centrasiaticum* and *L. secalinus* under medium sand burial treatment in Sept 2011, while it had no significant effect on cover of these two species under all three sand burial treatments (Figs 2, 3). Precipitation enhancement had no effect on cover of *A. mongolicum* under medium sand burial treatment in Sept 2011, but increased it in Sept 2012 (Figs 2c, 3c). Precipitation enhancement decreased cover of *S. bungeana* under medium sand burial treatment in Sept 2011, but had no effects on it in Sept 2012 (Figs 2b, 3b). Both in Sept 2011 and 2012, precipitation

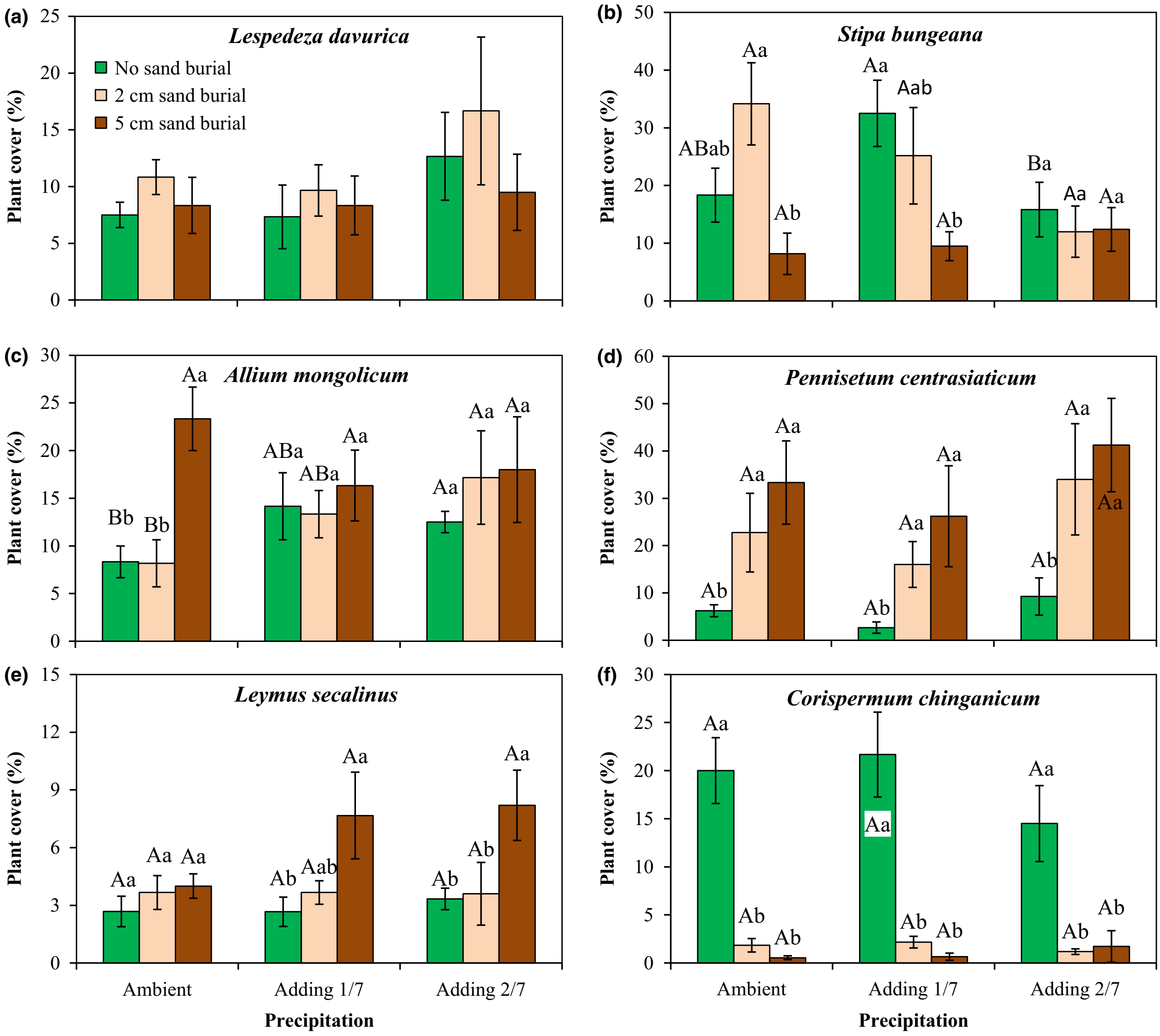

Fig. 3. Effects of precipitation enhancement and sand burial on plant cover of *Lespedeza davurica* (**a**), *Stipa bungeana* (**b**), *Allium mongolicum* (**c**), *Pennisetum centrasiaticum* (**d**), *Leymus secalinus* (**e**) and *Corispermum chinganicum* (**f**) in Sept 2012. Different capital letters represent significant differences among the three precipitation enhancement treatments, different lowercase letters represent significant differences among the three sand burial treatments, while no letters mean no significant differences between any treatment.

enhancement had no significant effects on cover of *L. davurica* and *C. chinganicum* (Figs 2, 3).

Discussion

Wilson (2011) comprehensively reviewed and ranked 12 mechanisms of species co-existence in plant communities. Among the likely realistic and important mechanisms, three may apply to our study: alpha niche (within-community) differentiation, environmental fluctuation and allogenic disturbance. Alpha niche differentiation and allogenic disturbance in combination are represented by the spatial environmental variation in abiotic conditions imposed by external sand blowing in. If, as Gause's (1930) principle states, all species should have their own niches (but see Leibold & McPeek 2006), plant co-existence may change due to the change in alpha niche differentiation caused by sand deposition interference in our study. At the temporal scale, variation in precipitation moisture and temperature related to seasonal and year-to-year variation in weather patterns reflects the possible maintenance of co-existence represented by environmental fluctuation *sensu* Wilson (2011). Moreover, experimental supplementation of ambient summer precipitation with

0%, 14% or 28% of additional rainfall represents realistic predictions of increased summer precipitation in northern China and the adjacent northern area (IPCC 2013). It may furthermore be relevant to local-scale spatial variation in soil moisture. Our findings, which have highlighted strong interactive effects of these (single or dual) drivers with plant species identity on their vegetative cover, provide novel and firm evidence in support of our hypothesis.

The differential effects of sand burial on the cover of different plant species in our experiment (Table 1, Figs 2, 3) must be tightly connected with their functional traits (Zheng et al. 2005; Gilbert et al. 2008; Lloret et al. 2016). Clonal plants, especially ‘guerilla’ clonal plants with vigorous lateral spread, have high tolerance of sand burial thanks to physiological connections with non-buried ramets through clonal integration (Yu et al. 2004). Sand burial increased the cover of two rhizomatous guerilla grasses, *L. secalinus* and *P. centrasiaticum*, both in 2011 and 2012; in contrast, sand burial decreased cover of the grasses *S. bungeana*, (Figs 2, 3) and *C. squarrosa* (Fig. S3), both of which feature a ‘phalanx’ (clumped) strategy with poor lateral spread. Life history may be important too with respect to sand burial response. Sand burial had a strong negative impact on the annual herb *C. chinganicum*, which showed explosive expansion in 2012 (Fig. 3), but virtually disappeared from both burial treatments. This response may be explained by its dependence on recruitment from seed on the surface. In contrast, sand burial had no significant effects on cover of the perennial forbs *H. altaicus* and *A. melilotoides* (Fig. S3), which do not depend on annual recruitment from seed and can regrow from below-ground buds to emerge above the sand every year. Three other perennial forbs, the dominant *A. mongolicum* and the subordinate *I. chinensis* and *O. gracilima*, all responded to burial as true psammophytes, presumably aided by annual remobilization of resources from bulb and taproot, respectively.

Altered precipitation regime, characterized by higher inter-annual variability and frequency of extreme events (Min et al. 2011; Durack et al. 2012), may differentially alter the performance of plant species and thereby add to their co-existence. Most previous field studies on increasing precipitation effects on plant communities could not distinguish between increasing precipitation amount and frequency (Yang et al. 2011; Rollinson et al. 2012). In our study precipitation enhancement without change in precipitation frequency had no significant overall effect on plant cover, even though there were still interactions of species x precipitation treatment and species x precipitation treatment by season (Table 1). In contrast, species varied significantly in their cover response to a dry vs wet year, as well as to the interaction of year and season (Table S1, Fig. 1). Thus, effects of precipitation on the co-existence of differentially adapted plant species may be due more to precipitation frequency than to the amount of precipitation per event. This may be because water from increased single precipitation events cannot be fully used by plants in this semi-arid region because of the high evaporation caused by a combination of strong sunlight, the sand matrix and wind.

Phenology and traits related to moisture and temperature preferences may be key to the changing hierarchies in the plant community in response to seasonal and year-to-year environmental fluctuations. Season and year, and their interaction, each interacted significantly with species in their effect on plant cover, leading to a changing species abundance hierarchy over the 2 yrs (Fig. 1). Moreover, effects of sand burial on plant cover also changed differentially over the seasons and years for different species (Table 1). Species had significantly different cover responses to interactions of season and sand burial, of year and sand burial, as well as of year, season and sand burial combined (Tables S1, S2). Our results therefore suggest that seasonal and/or annual environmental fluctuation intensify or moderate the effect of sand burial on plant cover differently depending on the species.

Thus, single effects and interactions of sand burial, precipitation enhancement treatments, as well as seasonal and year-to-year fluctuations in abiotic conditions, changed the cover (and height, number of plants: Table S3) of different species in different ways, leading to changes in rank among species through time. These dynamics, which can only be understood as the result of niche differentiation, may help to prevent a few species being continuously vigorous competitors that might otherwise dominate the community, thereby enabling subordinate species to co-exist (Figs 1, S3; Wilson 2011; Song et al. 2012).

Our 2-yr experimental period was not sufficient to directly confirm some species moving into or exiting from the plant community driven by sand burial and precipitation enhancement. Since most plant species in this community are perennials, long-term experiments are needed to confirm the effects of sand burial and precipitation enhancement on plant community composition, together with long-term monitoring to relate weather fluctuations and community dynamics. Combined experimental sand burial and sand removal would also be relevant to the effects of allogenic disturbance in sand dune landscapes, and would further help to elucidate the mechanisms of species co-existence.

Conclusions

Our study has demonstrated multiple two- and three-way interactions between species, sand burial and precipitation enhancement on plant cover, between species, sand burial or precipitation treatment and year or season. These results together indicate that species co-existence in a semi-arid inland desert can be explained from the different niches they occupy in terms of environmental fluctuations in combination with allogenic disturbance, such as sand deposition. These findings will help to understand how sand deposition, overall precipitation enhancement and inter-annual and seasonal variation in abiotic regime, including precipitation, affect species co-existence, and more generally, to understand what drives co-existence and thereby biodiversity, now and in the future.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Results of five-way repeated measures ANOVA.

Table S2. Results of four-way repeated measures ANOVA.

Table S3. Characteristics of the six dominant species in different years.

Fig. S1. Quadrat photos taken during the experimental period.

Fig. S2. Precipitation during the experimental period.

Fig. S3. Plant cover of the subordinate species.

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