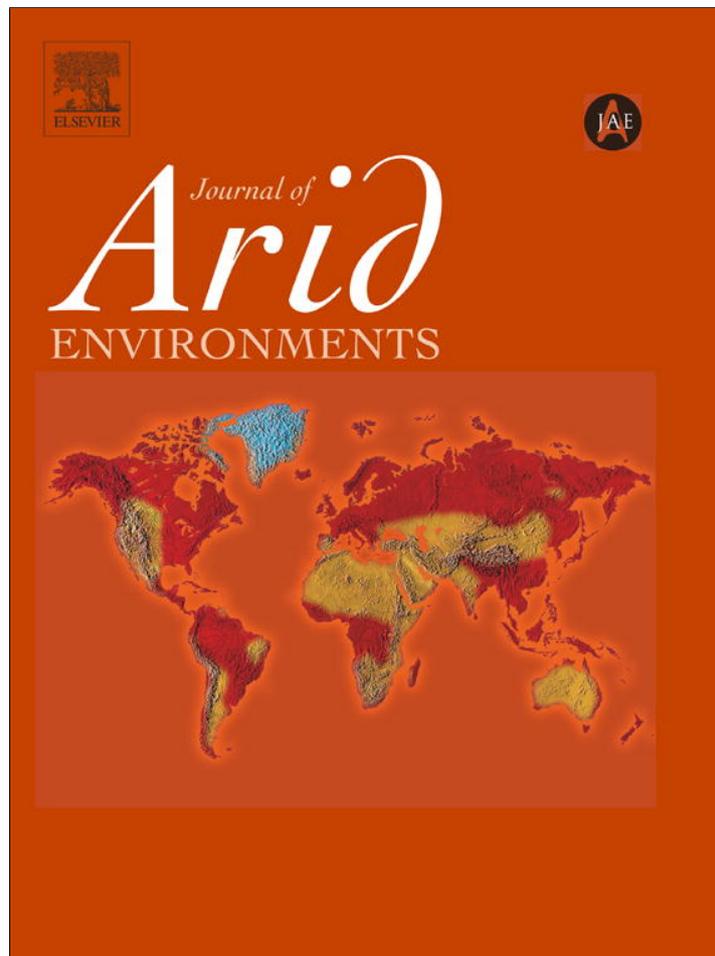


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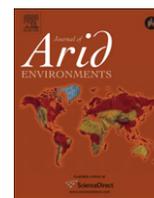
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Chronic wind and plant communities in dunes: Total biomass, inter-specific competition, and species abundance

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ABSTRACT

Chronic wind is an important ecological factor, but its direct roles in shaping plant communities remain poorly understood. We hypothesized that chronic wind can modulate community productivity, inter-specific competition, and species abundance in inland dunes. We conducted an experiment with three shrubs (*Artemisia ordosica*, *Caragana intermedia*, and *Hedysarum laeve*) common to semi-arid sandlands, set up seven kinds of plant communities (i.e. *Artemisia* monoculture, *Caragana* monoculture, *Hedysarum* monoculture, *Artemisia*–*Caragana* mixture, *Artemisia*–*Hedysarum* mixture, *Caragana*–*Hedysarum* mixture, and *Artemisia*–*Caragana*–*Hedysarum* mixture), and communities subjected to two levels of wind exposure: shielded (by means of fencing) or exposed (no fencing). We measured total biomass per plot, competitive effects, and relative species abundance. Wind exposure did not significantly affect the total biomass of monocultures but increased their root weight ratio. However, wind exposure enhanced the total biomass of three-species mixtures but not two-species mixtures, and had no effects on root weight ratio of all mixtures. Wind exposed condition increased the competitive ability and relative abundance of *Artemisia*, decreased the competitive ability of *Hedysarum* but had no effects on its abundance, and did not affect the competitive ability of *Caragana* but decreased its abundance. These results suggest that chronic wind, as an environmental filter, can directly modulate plant communities through altering competitive outcomes and thus affect community functioning.

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1. Introduction

Wind is a fundamental environmental factor in nature, and exhibits important ecological consequences for individual species and communities (Ennos, 1997; Grace, 1977; Mitchell, 2007; Xi and Peet, 2011). Understanding these effects is therefore of major interest in botany, ecology, agriculture and forestry, and many advances have been made in recent years (Anten et al., 2010; Coutts and Grace, 1995; de Langre, 2008; Mitchell, 2007; Ruck et al., 2003). For example, wind can affect physiological processes (Dixon and Grace, 1984; Grace and Russell, 1982), plant functional traits (Anten et al., 2010, 2005; Liu et al., 2007; Wang et al., 2008), and species composition and distribution (Grace, 1977; Mitchell, 2007; Ruck et al., 2003).

A central issue in plant ecology is how communities are assembled from species (Diamond, 1975; Weiher and Keddy, 1999). It is also well documented that wind impacts plant communities

through changing microclimate, water transport, energy transfer, and mechanical loading (Anten et al., 2010; Brüchert and Gardiner, 2006; Coutts and Grace, 1995; Grace, 1977; James et al., 2006; Liu et al., 2007; van Gardingen and Grace, 1991; Wang et al., 2008). But in spite of the ubiquitous nature of wind and its strong effect on plant growth, few studies have considered the roles of wind in shaping community structure, particularly in inland ecosystems. Studies that have done so have focused on catastrophic wind events (hurricane, tornados, and severe gales) on the forests in mountains or coastal areas (Coutts and Grace, 1995; de Langre, 2008; Grace, 1977; Mitchell, 2007; Ruck et al., 2003; Xi et al., 2008). Thus, the degree to which wind directly modulates the structure, species composition and functioning of plant communities remains poorly understood.

Inland sandy ecosystems (e.g. prevalent in large parts of China) are characterized by the shortages of soil water and nutrients, extreme climate, frequent disturbance (e.g., wind exposed) and low vegetation cover. The low surface roughness resulting from sparse and low vegetation cover facilitates high wind speeds and implies very limited wind shielding among individual plants (Ennos, 1997; Grace, 1977; Mitchell, 2007). These situations allow inland dunes

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to become an ideal stage for understanding the links between wind and community organization. Additionally, improved understanding of these links is beneficial to prevent soil erosion, stabilize dunes, and restore local vegetation in these areas (Temperton et al., 2004).

The objective of this study is to determine the extent to which chronic wind exposure directly modulates community productivity, inter-specific competition, and species abundance, which are critical in determining community structure and functioning (Cain et al., 2008). We answered the following questions: (1) Does strong wind exposure reduce net primary productivity of plant communities? (2) If wind exposed condition is a stressful factor, inter-specific competition may decrease with increasing wind. (3) Wind exposure may alter relative abundance of species in communities depending on species identity. We addressed these questions by an experiment with three dominant plant species, *Artemisia ordosica*, *Caragana intermedia*, and *Hedysarum laeve* in inland sandy areas.

2. Materials and methods

2.1. Study site and species

The Mu Us Sandland is located in the ecotone between arid areas and semiarid areas in northern China and characterized by low annual precipitation (i.e., mean precipitation of 360 mm), low vegetation cover, low species richness, poor soil nutrients, and frequent high wind (Zhang, 1994). Semi-mobile, semi-fixed, and fixed sand dunes are primary landscapes in this region. The Mu Us Sandland, where the local vegetation mainly consists of diverse artificial communities that were shaped through aerial seeding, has experienced severe desertification due to intensive human activities and is thus highly vulnerable (Zhang, 1994). Monocultures or mixtures, consisting of *Artemisia*, *Caragana*, or *Hedysarum*, are common in the Mu Us Sandland, and are among the most important components of the local artificial vegetation (Zhang, 1994). For our study, we used the following three shrub species. *A. ordosica* Kraschen. (Asteraceae) is a perennial shrub that can grow up to 1.5 m (Zhang, 1994). *C. intermedia* Kuang et H. C. Fu (Fabaceae) and *H. laeve* (Maxin.) H. C. Fu (Fabaceae) are N-fixing perennial shrubs that can grow up to 3.0 m (Wang et al., 2008; Zhang, 1994). These three dominant shrubs commonly occupy semi-mobile, semi-fixed, or fixed dunes, playing important roles in combating desertification. From here on all species are referred to with their genus names only (i.e., *Artemisia*, *Caragana*, and *Hedysarum*).

2.2. Experimental design

We selected two flat dunes (about 40 m × 40 m) near the Ordos Ecological Station (OES, 110°15' E, 39°34' N, 1,250 m) of the Institute of Botany, Chinese Academy of Sciences. These two dunes share the same aspect, precipitation, belowground water-table, height (i.e. ranging from 1150 to 1160 m in elevation) and soil texture (i.e., aeolian sandy soil); and they were 100 m apart from each other. Two wind treatments were implemented. In one plant communities were sheltered thus creating an environment with strongly reduced wind exposure while in other the communities were not sheltered and thus exposed to natural wind speeds. Each wind treatment was established on a separate dune. This experiment was conducted on dune ecosystems, as dunes represent the major landscape feature in the Mu Us Sandland.

Low wind environments were established using windbreaks. The high-wind dune was unfenced (hereafter denoted as “wind exposed”) and covered eight sub-dunes (6 m × 6 m) forming eight experimental replicates. The low-wind dune (hereafter “wind sheltered”) also covered eight sub-dunes (6 m × 6 m) forming eight

experimental replicates, each of which was fenced with plastic netting (100 cm in height) with 0.5 cm in diameter of mesh. More specifically, each dune was equally divided into three blocks horizontally, and then each block was equally divided into three sections vertically. Sub-dunes were randomly positioned in eight out of nine sections. The distance was over 8 m among sub-dunes. Windbreaks were set up after the establishment of a series of artificial plant assemblages (see below). In other words, we fenced each sub-dune with the plastic net described above. Microclimatic conditions (wind speed, temperature and humidity) were monitored throughout the experiment. Wind speeds were measured close to the top of the canopy of communities (about 0.5 m in height) at 2-min intervals using a Thermo Anemometer (AVM-01, Prova Instruments Inc., Taiwan) and air temperature and air relative humidity at 30-min intervals using a HOBO Data Logger (Onset Computer Corporation, USA) placed in each of the two wind regimes. The anemometers and dataloggers were calibrated prior to the experiment. Due to the partial loss of equipment, only one anemometer and one datalogger were available for each wind regime. Detailed information of these microclimatic conditions is presented in Fig. 1. The wind speed in the dune with windbreaks was approximately 5-fold lower than in the wind exposed condition

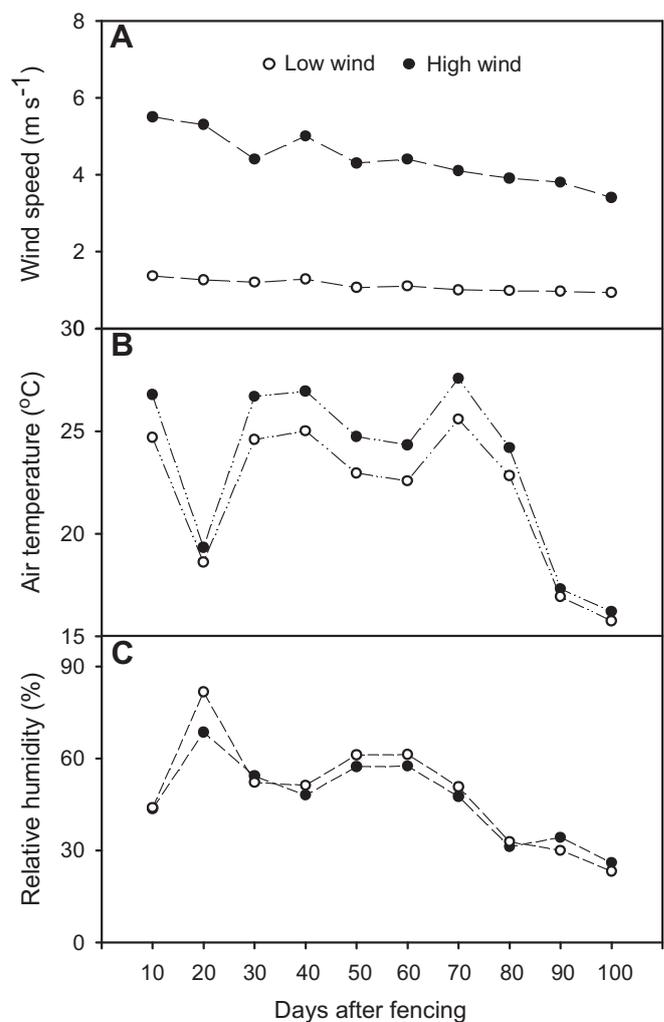


Fig. 1. Wind speed (A), atmospheric temperatures (B) and atmospheric relative humidity (C) in either the wind sheltered or the wind exposed condition. Each point represents means at 10-d intervals. The available data were from one anemometer and one datalogger. Wind speed was measured only during the day, and temperature and humidity were determined during the day and night.

(Fig. 1A), the mean air temperature was higher in the wind exposed condition (23.2 °C) than the wind sheltered (21.8 °C) (Fig. 1B), and the mean air relative humidity was lower in the high wind condition (46.1%) than the wind sheltered area (48.0%) (Fig. 1C).

We selected *Artemisia*, *Caragana* and *Hedysarum* to create plant communities. In early June 2007, we created seven plant assemblages (three kinds of monocultures and four kinds of mixture, including three two-species mixtures and one three-species mixture) (Appendix A). Each assemblage was crossed factorially with three densities and two wind regimes with each combination replicated eight times (7 assemblages \times 3 densities \times 2 wind regimes \times 8 replicates = 336 plots). Details regarding plant assemblages and densities were presented in Appendix A. To create experimental plant assemblages we planted seeds into 336 plots with 1 \times 1 m; 30, 60, and 120 seeds per plot were planted for the low-, medium-, and high-density, thereby shaping a density gradient. It is important to note that 30 and 60, 120 seed/plot plant assemblages roughly represent natural communities on semi-mobile, semi-fixed, and fixed sand dunes, respectively (personal observations).

All assemblages were weeded continuously to maintain predetermined levels of species richness and densities. Continuously weeding enabled us to remove the unwanted plants when they were very small, thereby minimizing disturbance (e.g., shaking target plants, destroying soil structure, and nutrient loss). All assemblages were watered if required and were supplied with 1 L 0.5% nutrient solution (g/g) (Peters Professional [20% N, 20% P₂O₅, 20% K₂O], Scotts Company, USA) once every three weeks to highlight the wind effect and to minimize the confounding effects of wind with soil water and nutrients. This experiment ran 100 days, from June 5 to September 15, roughly corresponding to one growing season in the field.

2.3. Plant harvest and calculation of indices

At the end of the experiment, all plants per plot were harvested by species. Roots were carefully dug out and washed, and each plant was then separated into shoot and roots. Dry weights of each part were determined after oven drying for 48 h at 85 °C. Here the total biomass per plot was equal to the sum of the total biomass of each species, and used to indicate the net primary productivity (NPP) of a plant community. Community-level root weight ratio (RWR) was calculated as the ratio of root dry biomass to total dry biomass. Community-level RWR can effectively indicate the biomass allocation strategies of plant communities to cope with contrasting environmental regimes.

There are many different indices for inter-specific interactions depending on specific research objectives. Here relative neighbor effect (RNE), as a measure for the competitive effect, was calculated as $(M - C)/\max(M, C)$, where M is the total biomass of plant with neighbors and C is the average total biomass of plants without neighbors and $\max(M, C)$ indicates the largest values of M and C (see the paper by Kikvidze et al. (2006) for more details). It is important to note that the two-species mixtures with 60 seeds and 120 seeds were chosen for determining RNE, and the other mixtures (i.e., two-species mixtures with 30 seeds and all three-species mixtures) were not used to quantify RNE because they had no corresponding controls (i.e., no monocultures with the same densities). The values of RNE are positive for facilitation among species and negative for competition among species. All the values of RNE were pooled across two densities before statistical analysis, thereby ruling out the density effect.

To examine the effects of wind on community structure, we calculated the relative species abundance (RSA), which is defined as the percent of the total biomass of a given species in a mixture to the total biomass per mixture. To our knowledge, we are the first to

propose this approach to quantify the wind effect on RSA. Specifically, we determined the RSA of each species in a mixture, and pooled all the values of RSA of each species across three densities before statistical analysis. This pooling practice rules out the density effect. Unlike the RNE, RSA covered all 12 mixtures rather than partial mixtures.

2.4. Data analyses

For total dry biomass and root weight ratio (RWR), three-way ANOVAs were used to test the effects of species combination, density, wind, and their interactions on both traits of monocultures and mixtures. For a given assemblage, two-way ANOVAs were used to test the effects of wind, density and their interactions on total dry biomass and RWR; one-way ANOVAs were also used to test the wind effects on total dry biomass and RWR when three densities per species were considered together. Total dry biomass was log-transformed and RWR was square-root transformed before analyzing.

For relative neighbor effect (RNE) and relative species abundance (RSA), two-way ANOVAs were used to detect the effects of species, wind, and their interactions on RNE of six two-species mixtures (i.e., assemblages with 60 and 120 seeds) and RSA of all 12 mixtures. We also ran an ANOVA with wind (low or high) as a fixed effect on RNE and RSA when mixtures were considered together or to test whether RNE and RSA differ for species in different mixtures. RSA was transformed via the square-root before analyzing.

All statistical analyses with significance at $P = 0.05$ level were conducted using SPSS 13.0 (SPSS Inc., Chicago, USA).

3. Results

3.1. Chronic wind and the growth of assemblages

For monocultures, there were significant interactions between wind and species combination on root weight ratio (RWR) but not total dry biomass. Such interactions were not detected between wind and density; in terms of effects of individual main factors, wind marginally affected RWR but had no effects on total dry biomass, species combination and density dramatically affected total dry biomass and RWR (Table 1). When three types of monocultures were considered separately, wind exposed and wind sheltered had no significant effects on their total biomass (all $P > 0.05$), but affected their RWR (all $P < 0.05$) (Fig. 2A–C). The wind-induced changes in RWR varied with species ($F = 6.80$, $P = 0.002$). For example, wind increased RWR in *Artemisia* ($F = 6.12$, $P = 0.018$) and *Caragana* ($F = 5.49$, $P = 0.024$), but decreased RWR in *Hedysarum* ($F = 5.50$, $P = 0.024$). Density did not affect total biomass and RWR of *Artemisia* monocultures (Fig. 2A; all $P > 0.05$),

Table 1

Analyses of variance of both total dry mass and root weight ratio of plant communities as affected by species combination, density, wind, and their interactions.

	Monoculture				Mixture			
	Total dry biomass		Root weight ratio		Total dry biomass		Root weight ratio	
	F	P	F	P	F	P	F	P
Combination (C)	2.51	0.085	520	<0.000	0.39	0.764	33.7	<0.000
Density (D)	12.9	<0.000	3.51	0.033	17.8	<0.000	1.13	0.327
Wind (W)	1.02	0.313	3.25	0.074	2.70	0.103	0.27	0.605
C \times D	0.10	0.983	0.67	0.615	0.18	0.981	0.13	0.993
C \times W	0.03	0.967	6.80	0.002	0.97	0.410	0.66	0.578
D \times W	0.19	0.828	0.11	0.894	0.06	0.946	0.12	0.890
C \times D \times W	0.01	0.999	0.29	0.882	0.15	0.989	0.10	0.996

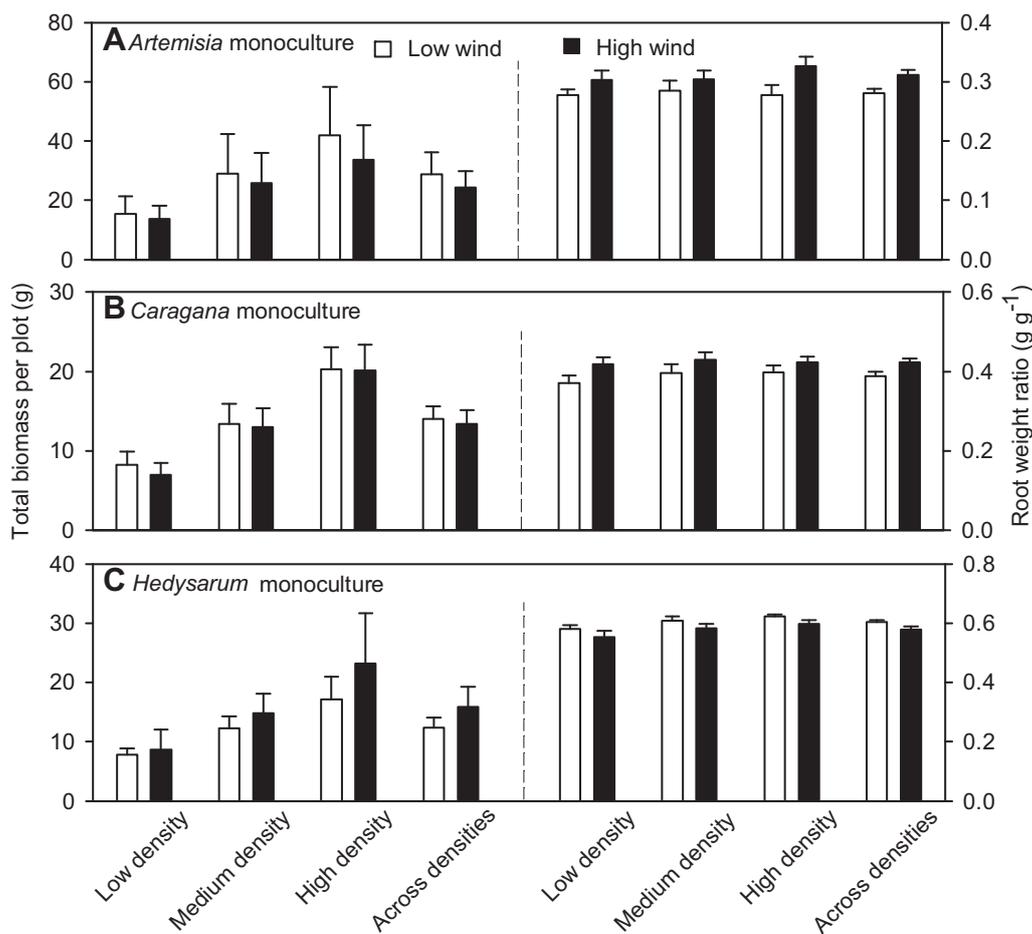


Fig. 2. Total dry biomass and root weight ratio (RWR) (means + 1 SE) in monocultures of *Artemisia* (A), *Caragana* (B), and *Hedysarum* (C) in different wind–density combinations.

increased biomass of *Caragana* monocultures (Fig. 2B; $F = 4.79$, $P = 0.042$), and increased both total biomass and RWR of *Hedysarum* monocultures (Fig. 2C; all $P < 0.05$).

For mixtures, wind had no effects on total dry mass and RWR, density affected total dry biomass and species combination did RWR; there were no interactions between wind and both species combination and density on total dry biomass and RWR (Table 1). When three types of mixtures were considered separately, wind exposed condition did not affect the total biomass of three two-species mixtures (Fig. 3A–C; all $P > 0.05$), but enhanced the total biomass of the *Artemisia*–*Caragana*–*Hedysarum* mixtures by 110% ($F = 4.86$, $P = 0.003$) (Fig. 3D). The total biomass of mixtures increased with density ($F = 6.88$, $P = 0.001$), but their RWR remained unchanged ($F = 1.13$, $P = 0.33$) (Fig. 3).

3.2. Chronic wind and inter-specific competition

Due to the lack of control monocultures, we only presented the values of relative neighbor effect (RNE) of six two-species mixtures. We did not consider density effect so that different densities were pooled. When three species were considered together, species, wind and their interaction had no significant effects on RNE (Table 2). When three species were considered separately, wind effect was significant for *Artemisia* and *Hedysarum*. Specifically, wind exposed condition increased the values of RNE of *Artemisia* ($F = 4.65$, $P = 0.042$) and decreased the values of RNE of *Hedysarum* ($F = 4.17$, $P = 0.046$) (Fig. 4A). However, wind exposed condition had no effects on RNE of *Caragana* ($F = 0.84$, $P = 0.385$) (Fig. 4A). RNE of each species did not vary significantly with mixtures (all $P > 0.05$).

3.3. Chronic wind and relative species abundance

The values of relative species abundance (RSA) were from all mixtures. Since we did not consider density effect, three densities were pooled. Unlike RNE, species identity and its interaction with wind dramatically impacted RSA; wind alone had no effects on RSA when three species were considered together (Table 2). When three species were considered separately, wind exposed condition increased RSA of *Artemisia* ($F = 5.95$, $P = 0.016$), decreased RSA of *Caragana* ($F = 5.17$, $P = 0.025$), and had no effect on RSA of *Hedysarum* ($F = 1.09$, $P = 0.299$) (Fig. 4B). In addition, RSA also varied with mixtures, regardless of *Artemisia*, *Caragana*, and *Hedysarum* (all $P < 0.05$).

4. Discussion

The current paper provides evidence – albeit preliminary – that chronic wind exposure can have important impacts on plant community structure and functioning in inland dunes. It thus provides an initial indication that chronic wind exposure can modulate plant assemblages through changing inter-specific competition and species abundance. According to the ecological assembly rules (Weiher and Keddy, 1999) and the twin-filter model of community assembly (Grime and Pierce, 2012), physical factors act as environmental filters through eliminating some species or individuals and promoting others, and finally determines the kinds of plant species and the numbers of individuals per species that will appear in plant communities. Thus, our findings suggest that chronic wind may play important roles in shaping local vegetation via filtering effects.

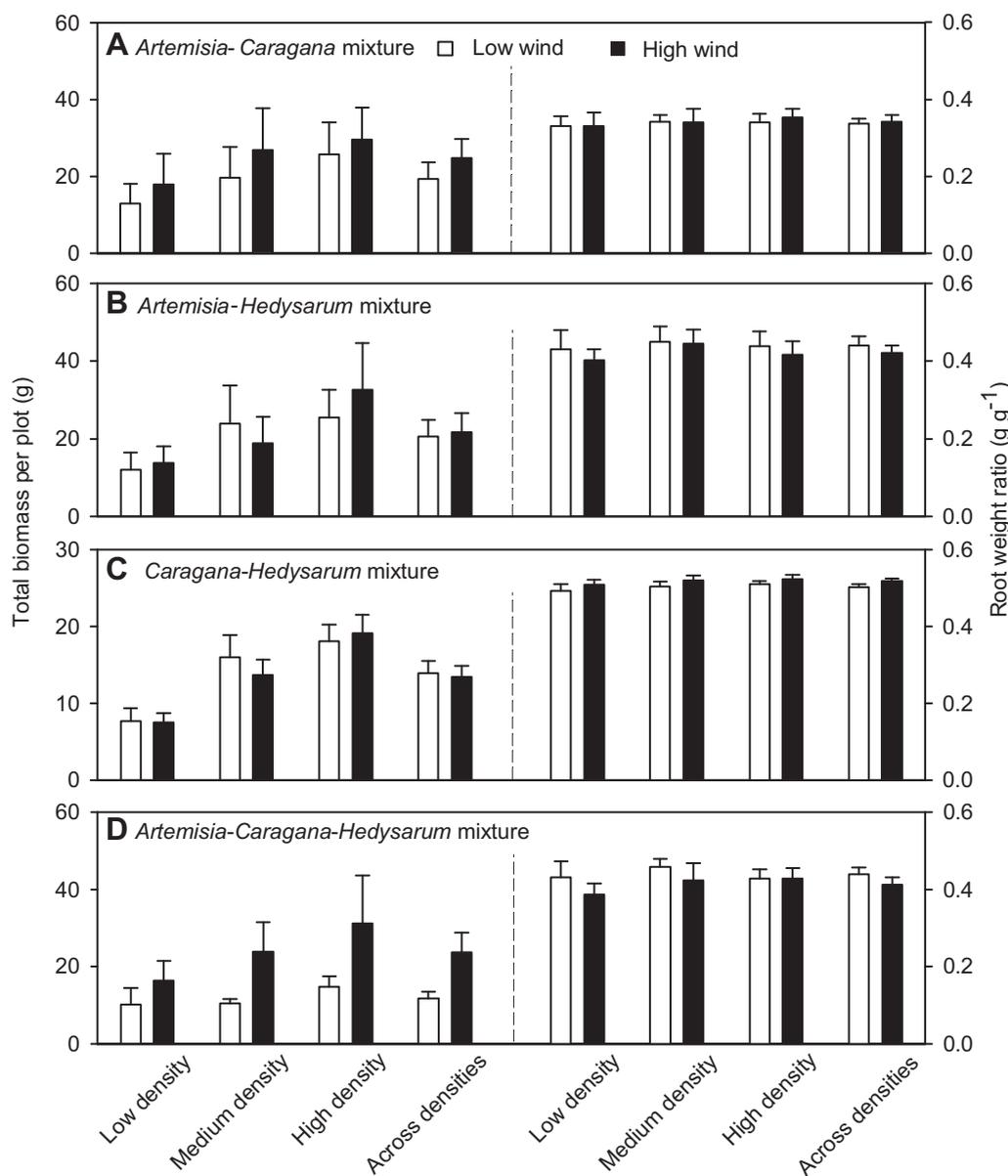


Fig. 3. Total dry biomass and root weight ratio (RWR) (means + 1 SE) in the mixtures of *Artemisia*–*Caragana* (A), *Artemisia*–*Hedysarum* (B), *Caragana*–*Hedysarum* (C), and *Artemisia*–*Caragana*–*Hedysarum* (D) in different wind–density combinations.

Heiligmann and Schneider (1975) found that wind barrier reduced solar radiation by 18%. In our study, the wind barrier reduced solar radiation by about 20% in early morning and late afternoon, such that daily total radiation was less than 10% lower in the wind sheltered than the high-wind. This difference might not yield a significant effect on plants, because photosynthetically active radiation in the study area reaches up to $2300 \text{ mol m}^{-2} \text{ s}^{-1}$

and the light saturation points of plant species used in our study are less than $1500 \text{ mol m}^{-2} \text{ s}^{-1}$ (Jiang and He, 1999).

Table 2

Analyses of variance of both relative neighbor effect and relative species abundance across community assembles with different densities as affected by species, wind, and their interactions.

	Relative neighbor effect		Relative species abundance	
	F	P	F	P
Species (S)	0.32	0.724	17.9	<0.000
Wind (W)	0.01	0.942	0.01	0.951
S × W	1.41	0.246	5.67	0.004

4.1. Chronic wind and community productivity

Net primary productivity (NPP), as measured by total dry biomass per plot, of plant communities was either unaffected by wind for two-species mixtures or was increased for three-species mixtures, which does not support our hypothesis that wind exposure reduces NPP of plant communities. These findings contradict the general findings from greenhouse pot experiments that wind exposure negatively affects growth of individual freestanding plants, including black walnut (Heiligmann and Schneider, 1975), *Festuca arundinacea* and *Lolium perenne* (Russell and Grace, 1978), *Sinapis alba* (Retuerto and Woodward, 1992) and *Plantago major* (Anten et al., 2010). The effects of wind on growth and its underlying processes (e.g. photosynthesis) can both be positive and negative. Wind can stimulate photosynthesis by reducing the

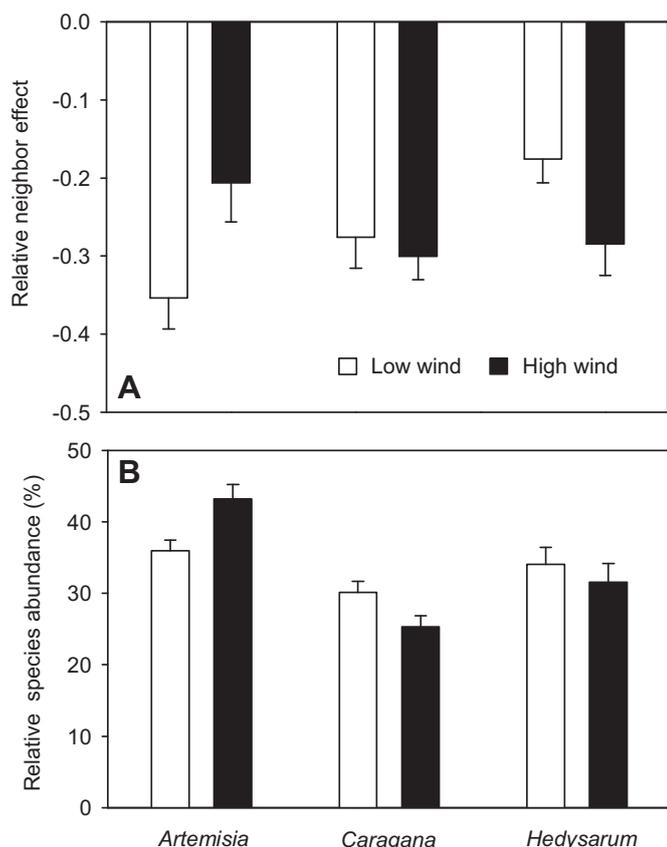


Fig. 4. Relative neighbor effect (A) and relative species abundance (B) (means + 1 SE) of *Artemisia*, *Caragana* and *Hedysarum* across plant communities subjected to either the wind sheltered or the wind exposed condition. See the text for more details about how to calculate relative neighbor effect and relative species abundance.

diffusive resistance to CO₂ (Grace, 1977), and by improving light penetration into plant canopies. However, wind can also reduce photosynthesis by inducing stomatal closure or by causing leaves to re-orientate thus reducing the light exposure of leaves. Additionally, wind may induce mechanical stress which may also negatively affect growth (Anten et al., 2010), though this effect is not always observed (e.g. Anten et al., 2005). Differences between previous findings for individual plants and ours for plant communities might be associated with experimental conditionality. Plants in vegetation stands can shield each other from wind, mitigating the both the mechanical impact and drying effect of wind (Anten et al., 2005; Liu et al., 2007; Wang et al., 2008). This notion is supported by the fact that in our study the positive effects of wind tended to increase with plant density, particularly for three-species mixtures. Overall, the production of all plants across two wind regimes tended to perform better along a density gradient.

4.2. Chronic wind and inter-specific competition

Interactions among species have long been recognized as drivers for shaping plant communities (Callaway, 2007; Grace and Tilman, 1990). Competition usually predominates in benign environments while facilitation commonly predominates in harsh environments (Callaway, 2007; Kikvidze et al., 2006). In our study, competition predominated in two wind regimes. We supplied additional water and nutrients to plants, alleviating to some extent soil resource shortages. This could partially explain why facilitation did not occur in our experiments. On the other hand, this addition of soil water and nutrient also minimize the confounding effects of

wind with soil water and nutrients. Competitive ability varied with wind and differed between species. For example, wind exposed condition increased the competitive ability of *Artemisia* but decreased the competitive ability of *Hedysarum*. Thus in the present study competitive outcomes depend on wind regimes and species identity, which partially support the hypothesis that inter-specific competition decreases with increasing wind. In the field conditions, wind-induced interactions among species may be modulated by the availability of other physical resources.

4.3. Chronic wind and species abundance

Wind dramatically shifted the relative abundance of three species, supporting the hypothesis that wind exposed condition can alter relative species abundance. For example, in general the relative abundance of *Artemisia* increased by 23% with wind whereas the relative abundance of *Caragana* decreased by 18% with wind. This shift could partly explain why *Artemisia* dominates over other species in the semi-arid Mu Us sandland. Interestingly, *Caragana* and *Hedysarum* exhibited contrasting sensitivity to wind. This difference may to some extent be linked to their life form. Specifically, *Caragana* is a non-clonal plant and anchors via its roots, and *Hedysarum* is a rhizomatous clonal plant and anchors through its rhizomes and roots simultaneously. Clonal integration within ramets can facilitate a greater drought tolerance in arid areas (Zhang et al., 2002). Since species abundance determines community structure (Cain et al., 2008), changes in relative abundance are important to modulate the structure of local vegetation. In addition, species abundance also varied with plant assemblages, showing the importance of community identity.

4.4. Potential implications

Wind is a ubiquitous factor, but research on its impact on plant communities has been limited to catastrophic wind events (Grace, 1977; Zimmerman et al., 1994). In our pilot study, only one pair of dunes were involved so that we can't extrapolate our findings broadly. However, our findings should provide a basis for further research to test wind effects in plant assemblages. If chronic wind can alter the competitive ability and relative abundance of species, it subsequently influences the succession of plant communities. Our findings may have implications for vegetation restoration in inland windy areas. For example, wind shielding may positively impact communities, especially at seedling stages. For *Artemisia*–*Caragana*–*Hedysarum* mixtures, chronic wind may enhance rather than decrease their net primary productivity, showing these plant communities are tolerant to wind stress. This study thus illustrates the potentially important impacts of wind, as an environmental filter, on community structure, functioning and species composition.

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Appendix A

Experimental scheme, showing seven types of plant assemblages and three levels of densities. The capital letters represent the corresponding species (i.e. A = *Artemisia*; C = *Caragana*; H = *Hedysarum*). The numbers following the capital letters indicate the number of seeds planted in a plot.

	Low density 30 seeds	Medium density 60 seeds	High density 120 seeds
<i>Artemisia</i> (A) alone	A30	A60	A120
<i>Caragana</i> (C) alone	C30	C60	C120
<i>Hedysarum</i> (H) alone	H30	H60	H120
A-C mixture	A15+C15	A30+C30	A60+C60
A-H mixture	A15+H15	A30+H30	A60+H60
C-H mixture	C15+H15	C30+H30	C60+H60
A-C-H mixture	A10+C10+H10	A20+C20+H20	A40+C40+H40

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