

Effects of foliage litter of a pioneer shrub (*Artemisia halodendron*) on germination from the soil seedbank in a semi-arid sandy grassland in China

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Abstract Vegetation recovery during succession is an important process for ecological restoration of the soil, especially in degraded sandy land. However, the driving mechanisms, such as how a pioneer species competes with other species, is uncertain. In China's Horqin Sandy Land, *Artemisia halodendron* is an important shrub that is common on semi-fixed dunes, where it replaces *Agriophyllum squarrosum* during succession, and is an important indicator species of the second stage of dune stabilization. However, how it outcompetes other species is still unclear. In this study, we conducted a seed bank germination experiment using soil from the native habitats of *A. halodendron* on semi-fixed dunes. We covered the soil with foliage litter of *A. halodendron* at a range of concentrations. Seed germination and seedling growth were strongly affected by the foliage litter. Seed germination and seedling growth were not harmed by a low concentration ($\leq 50 \text{ g m}^{-2}$) of the foliage litter but severely inhibited by high concentrations ($\geq 100 \text{ g m}^{-2}$). Strong allelopathy, indicated by decreased germination, increased seedling loss, and decreased plant biomass, appeared during the later stages of germination (after about 20 days of incubation). Our results suggest that as a pioneer shrub during the vegetation succession

that occurs during dune stabilization, *A. halodendron* out-competed other species through the allelopathic effect of its foliage litter. This helps to explain the patchy distribution and heterogeneity of vegetation communities in the Horqin Sandy Land.

Keywords Allelopathy · *Artemisia halodendron* · Degraded sandy grassland · Seed bank · Seedling growth · Vegetation recovery

Introduction

Much of the world's sandy land occurs in arid to semi-arid areas, where it has been subject to considerable degradation of the vegetation communities (Zhao et al. 2013; Zuo et al. 2012). As a result, it has high potential for carbon sequestration if the vegetation can recover. The ecosystems in sandy land cover large areas, and therefore have multiple effects in terrestrial ecosystem, such as livestock production from grazing (Zhao et al. 2003), sandstorm prevention (Li et al. 2004) and carbon sequestration (Li et al. 2012b). Large amounts of C are potentially stored in the soil of these ecosystems; soil storage may account for more than 80% of the C and N storage in some habitats of a degraded grassland ecosystem (Zuo et al. 2015). The resulting C and N storage ranges from 35.05 to 388.13 g m^{-2} and 1.09 to 16.06 g m^{-2} , respectively, to a depth of 60 cm in a desertified grassland (Li et al. 2006). Moreover, plants are the major source of C for soil, and the most important organisms for transforming C between organic and inorganic forms. Carbon dioxide captured by plants via photosynthesis is released by physiological activities including respiration, litterfall, root turnover, and release of root exudates. The net accumulation or emission of C by plants in sandy

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land varies greatly in response to human activities and natural climate conditions. For example, beneficial human actions such as afforestation (Li et al. 2013), shrub planting (Miao et al. 2015), and grazing exclusion (Li et al. 2012b; Miao et al. 2015) can greatly enhance C and N accumulation, whereas harmful activities such as overgrazing and inappropriate reclamation of land for agriculture (Zhao et al. 2011) can cause serious degradation of the vegetation community, thereby reducing C and N accumulation.

Vegetation succession is a common phenomenon during ecosystem development, particularly in ecosystems that are recovering from disturbance. In sandy land, and especially in arid to semi-arid regions, climate variations and soil heterogeneity lead to a patchy distribution of plants, but when environmental conditions are suitable for vegetation, succession to more abundant and complex communities can occur rapidly (Zuo et al. 2008a, 2010). For example, after 26 years of grazing exclusion that allowed succession to occur without human disturbance in the Horqin Sandy Land of northeastern China, species that grow on mobile dunes were replaced by species that grow on fixed dunes (Li et al. 2012a). The plant community structure, dominant species, vegetation cover, total plant density, and species richness all changed greatly (Li et al. 2012a).

Artemisia halodendron Turcz., a member of the Compositae, is a common sub-shrub in the Horqin Sandy Land and the Hulun Buir grassland of eastern Inner Mongolia, China. It is well adapted to mobile and semi-mobile sand dunes due to its high tolerance of drought, wind erosion, and burial by sand (Huang et al. 2011; Liu et al. 2007). It also has a strong ability to capture water deep in the soil (Ma et al. 2010). In addition, it can propagate by both sexual and vegetative propagation. These characteristics help it to survive burial by sand, which is a common stress on mobile and semi-mobile dunes (Zhao et al. 2013). Thus, it is commonly used in sand-stabilization projects (Li et al. 2005), particularly in the Horqin region (Su et al. 2005; Zhang et al. 2004, 2005). Once the shrub is established, it grows and propagates rapidly due to its low nutrient requirements and its capacity for vegetative propagation, and it increases stocks of organic matter both through its aboveground and belowground growth and through its ability to trap wind-transported dust and litter (Li et al. 2005).

Foliage is important because of its ability to capture carbon by photosynthesis, through the high concentration of essential elements it stores to support metabolism, and via the rapid decomposition of its tissues when it enters the soil. Foliage also has strong effects on other organisms such as soil microorganisms and nearby species by means of allelopathy (Tesio et al. 2012). For example, *Eucalyptus urophylla* has a significant allelopathic effect on seed germination and seedling growth of three sympatric species (*Acmena acuminatissima*, *Cryptocarya concinna*, and

Pterospermum lanceaefolium), and the allelopathy that results from decomposition of its foliage is stronger than the allelopathy that results from root exudates and volatilization of allelochemicals (Chu et al. 2014).

Allelopathy is a common mechanism that plants use to outcompete other species (Zhang et al. 2016). *Artemisia* species commonly exhibit allelopathic effects on other vegetation (Zuo et al. 2011). Under natural conditions, species richness in communities dominated by *A. halodendron* is low (Li et al. 2012a; Zuo et al. 2009). Given the high accumulation of foliage litter under the canopy of *A. halodendron*, growth of new seedlings and other species is rare. On this basis, we hypothesized that allelopathy could explain how *A. halodendron* can outcompete other species during vegetation recovery through succession. To test this hypothesis, we examined whether foliage litter from this species could restrict germination and seedling growth of other species. To achieve this goal, we conducted a seed bank experiment in which we investigated seed germination and biomass allocation along a gradient of foliage litter addition.

Materials and methods

Study site

This study was conducted at the Naiman Desertification Research Station of the Chinese Academy of Sciences (42°58'N, 120°43'E; elevation 360 m a.s.l.), in the eastern part of China's Inner Mongolia Autonomous Region. The region belongs to the cold temperate zone, with a semi-arid continental monsoon climate. Annual mean precipitation from 1971 to 2015 averaged 335 mm, with high variability (CV = 28.0%), and 86.1% of the total precipitation falls from May to August. The annual mean temperature is about 6.7 °C, with a minimum monthly mean temperature of −12.6 °C in January and a maximum of 24.3 °C in July. The annual frost-free period ranges from 120 to 150 days. The average annual wind speed ranges from 3.4 to 4.5 m s^{−1}, but the mean wind speed during the season (spring) with the most severe wind erosion ranges from 5.0 to 6.0 m s^{−1} (Zhao et al. 2003). The landscape is characterized by sand dunes alternating with gently undulating lowlands between the dunes (Li et al. 2010). The soil is classified as a sandy chestnut soil, and is highly vulnerable to wind erosion (Li et al. 2010).

Experimental design

In mid-September 2015, we collected foliage litter of *A. halodendron* from the soil surface below the shrub canopy on three semi-fixed dunes. We mixed the litter

together to provide a single composite sample, washed it with distilled water to remove the attaching soil or dust, and then stored it in a refrigerator to air-dry at 4 °C until the experiment began.

At the beginning of the following growing season (20 April 2016), we selected five semi-fixed dunes dominated by *A. halodendron* as study plots. In each plot, we established 20 randomly distributed quadrats (20 cm × 20 cm) in which we measured the litter mass. All litter in each quadrat was collected and taken to the laboratory. We then collected the foliage litter of *A. halodendron* (which was easy to identify) and washed it with distilled water to remove the attaching soil or dust. We then oven-dried the samples for 48 h at 65 °C to determine the dry mass of foliage litter in each quadrat. We used this data to understand the range of leaf litter mass that accumulated under natural conditions.

At the same time when we collected the litter samples, we collected the soil seed bank to a depth of 5 cm from five semi-fixed dunes dominated by *A. halodendron*, with sampling of 5–10 plots on each dune. All samples were sieved to pass through a 2 mm mesh to remove gravel and larger litter. We then mixed the samples thoroughly to produce a single composite sample, and placed the resulting seed bank soil in 30 plastic pots (20 cm in length, 30 cm in width, and 7 cm in depth) to a depth of 5 cm. We then divided the pots into five groups of six pots and added the dried foliage litter uniformly to the surface of the seed bank soil at one of five rates that covered the range of values we observed in our field samples on the semi-fixed dunes: 0 (the control), 25, 50, 100, and 200 g m⁻². Hereafter, we refer to these treatments as T0, T25, T50, T100, and T200, respectively. All pots were then labeled and placed in a greenhouse. The light transmittance of the glass of the greenhouse was high, thus, the light was fully supplied by natural sunlight. Temperature in the greenhouse ranged from 20 to 30 °C. Water was then added to each pot to field capacity; three holes were drilled at the bottom of each pot to prevent excess water. Then pots were then incubated for 50 days. Because of that, all soil seed bank samples collected from wild field in spring (20 April 2016), seed dormancy condition was not considered. The number of seedlings were counted in each pot daily. During the incubation, each pot was weighed daily, and enough water was added to replace the water that was lost to evaporation during the previous day. At the end of the incubation, all above-ground plant biomass was harvested and the litter was removed. The belowground biomass was then collected by gently washing away the soil with tap water. The above- and belowground biomasses were then oven-dried for 48 h at 65 °C and weighed to determine the dry mass.

Experimental parameters

We defined a germination index (*GI*) as follows (Omezzine and Haouala 2013):

$$GI = \sum G_t/t,$$

where G_t is the total number of germinated seeds on day t .

We calculated the number of seedlings that died as the difference between the total number of germinated seeds and the final number of seedlings at the end of the 50 days.

We defined an allelopathic index (*AI*) as follows (Omezzine and Haouala 2013):

$$AI = (T_x - T_0)/T_0 \times 100,$$

where T_x is the maximum (or final) number of seedlings in treatment x , and T_0 is the maximum (or final) number of seedlings in treatment T0.

Statistical analysis

Statistical analysis was conducted using version 20.0 of the SPSS software (<http://www.ibm.com/software/analytics/spss/>). We analyzed differences in the maximum and final number of seedlings, *GI*, seedling loss, and the total biomass among the treatments by means of one-way ANOVA, with treatment as the factor. We performed multiple comparisons using the LSD test whenever the ANOVA indicated a significant difference ($P < 0.05$).

Results

Foliage litter distribution

On the semi-fixed dunes, the foliage litter mass of *A. halodendron* at the soil surface ranged from 0 to 211.09 g m⁻², and averaged 89.12 g m⁻²; these values were approximately normally distributed (skewness < 0.5, kurtosis ≤ 1.0). In all five plots, foliage masses had a high variance, with a coefficient of variation greater than 50% (Table 1).

Germination

Germination of the seed bank revealed three stages (Fig. 1). In the first stage, which lasted about 20 days, seeds in all treatments germinated and produced the maximum number of seedlings. At the end of this stage, the number of seedlings in T200 was significantly less than in the other treatments but for T100 (which was

Table 1 Descriptive statistics for the *Artemisia halodendron* foliage litter mass distribution on semi-fixed sand dunes

	<i>N</i>	Range (g m ⁻²)	Min. (g m ⁻²)	Max. (g m ⁻²)	Average (g m ⁻²)	Standard deviation (g m ⁻²)	Skewness	Kurtosis
Plot 1	20	198.97	0.00	198.97	87.82	49.86	0.49	0.12
Plot 2	20	160.59	0.00	160.59	79.99	47.82	-0.10	-0.93
Plot 3	20	182.81	0.00	182.81	92.31	56.17	0.13	-1.01
Plot 4	20	198.97	0.00	198.97	92.57	53.99	0.30	-0.37
Plot 5	20	205.43	5.66	211.09	92.90	56.57	0.48	-0.54

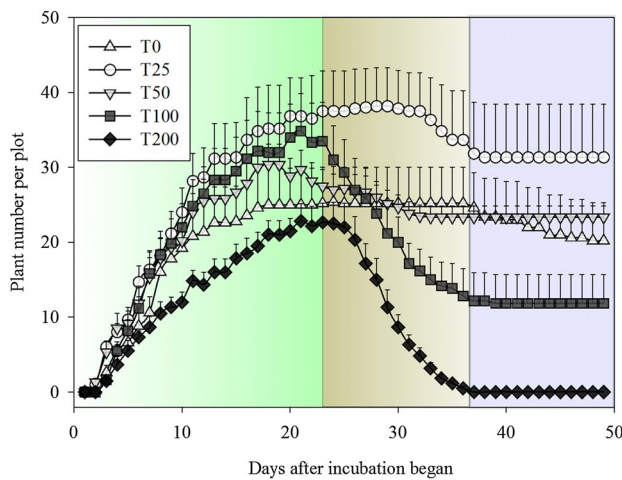


Fig. 1 Seed bank germination dynamics. Values represent means \pm SE ($n=6$). Treatments T0, T25, T50, T100, and T200 represent additions of 0 (the control), 25, 50, 100, and 200 g m⁻² of *Artemisia halodendron* foliage litter, respectively, to the soil surface. Shaded areas represent (from left to right) periods of increasing germination, seedling death, and stabilization of seedling numbers

insignificant). The second stage was about 15 days long, and lasted from day 20 to day 35. During this stage, increasing numbers of the germinated seedlings died with increasing incubation duration. Seedling loss differed among the treatments, with the greatest a significantly greater seedling loss in the in T100 and T200 treatments. T25 showed the least loss of seedlings. The third stage was from about day 35 to the end of the incubation. During this stage, the number of seedlings remained stable in all treatments except T0, which showed fluctuations and a slow decrease.

Germination index (*GI*) differed slightly but significantly among the treatments, with T25 and T50 having significantly higher values than T200 (Fig. 2a). The maximum number of seedlings during the incubation period did not differ significantly among the treatments, even though T25 and T100 had higher numbers than the other treatments (Fig. 2b). The final number of germinated seedlings differed significantly among treatments, with significantly higher numbers of surviving seedlings in T0, T25, and T50

than in T200 (Fig. 2c). Thus, seed germination and survival were not harmed at lower foliage litter concentrations, but were inhibited at higher concentrations. Seedling loss in T100 and T200 was significantly higher than in T0, T25, and T50 (Fig. 2d).

AI was positive for T25 and T50 based on both the maximum and the final germination, and the value was higher in T25 than in T50 (Fig. 3). In T100, *AI* based on the maximum number of seedlings was positive, but it was negative based on the final number of seedlings. In T200, *AI* was negative based on both the maximum and the final number of seedlings, and reached the maximum value (-100%) based on the final number.

Seedling growth

Plant biomass differed significantly among the treatments (Fig. 4). The aboveground biomass is significantly lower in T100 and T200 than in T0, T25, and T50. That is, plant growth and mass accumulation for both aboveground and belowground tissues were not harmed by low concentrations of foliage litter, but were severely inhibited by high concentrations. Furthermore, the inhibitory effect was greater for belowground biomass than for aboveground biomass, and the magnitude of the inhibition increased with increasing litter concentration. This affected the ratio of belowground biomass to aboveground biomass, which was significantly lower in T100 and T200 than in T0, T25, and T50.

Discussion

Allelopathy is a common phenomenon when two species compete for the same habitat. The inhibition of other species by allelopathy, especially for weeds, is commonly used to provide biological weed control (Fiorentino et al. 2009; Rawat et al. 2013; Tesio et al. 2011). For example, shoot extracts of Jerusalem artichoke (*Helianthus tuberosus*) have been reported to strongly inhibit the germination and seedling growth of lettuce, particularly for the diethyl ether extract (Tesio et al. 2011). Both the fresh and the

Fig. 2 The germination index (GI), maximum number of germinated seeds, final number of germinated seeds, and seedling loss (maximum number minus final number) in the different treatments. Values represent means \pm SE ($n=6$). Bars labeled with different letters differed significantly among the treatments ($P<0.05$). Treatments T0, T25, T50, T100, and T200 represent additions of 0 (the control), 25, 50, 100, and 200 g m^{-2} of *Artemisia halodendron* foliage litter, respectively, to the soil surface

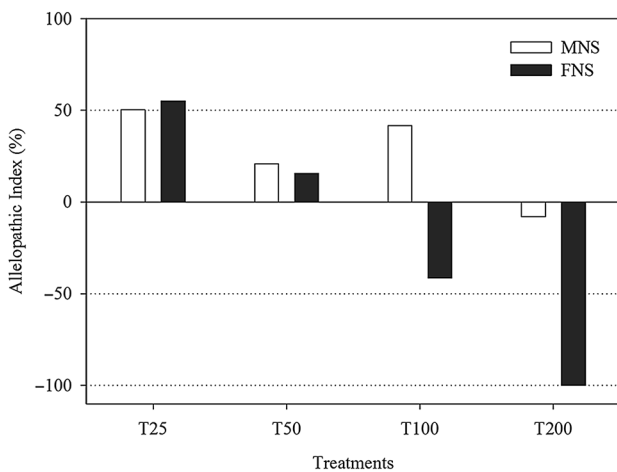
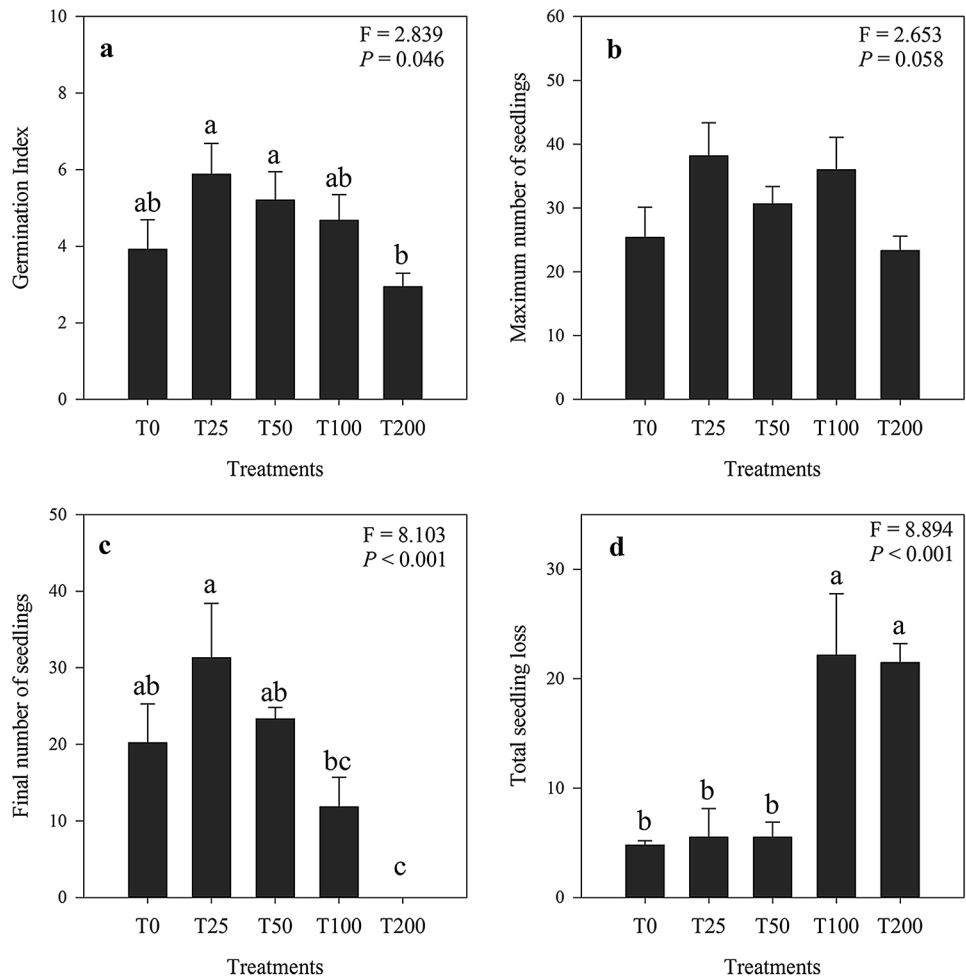
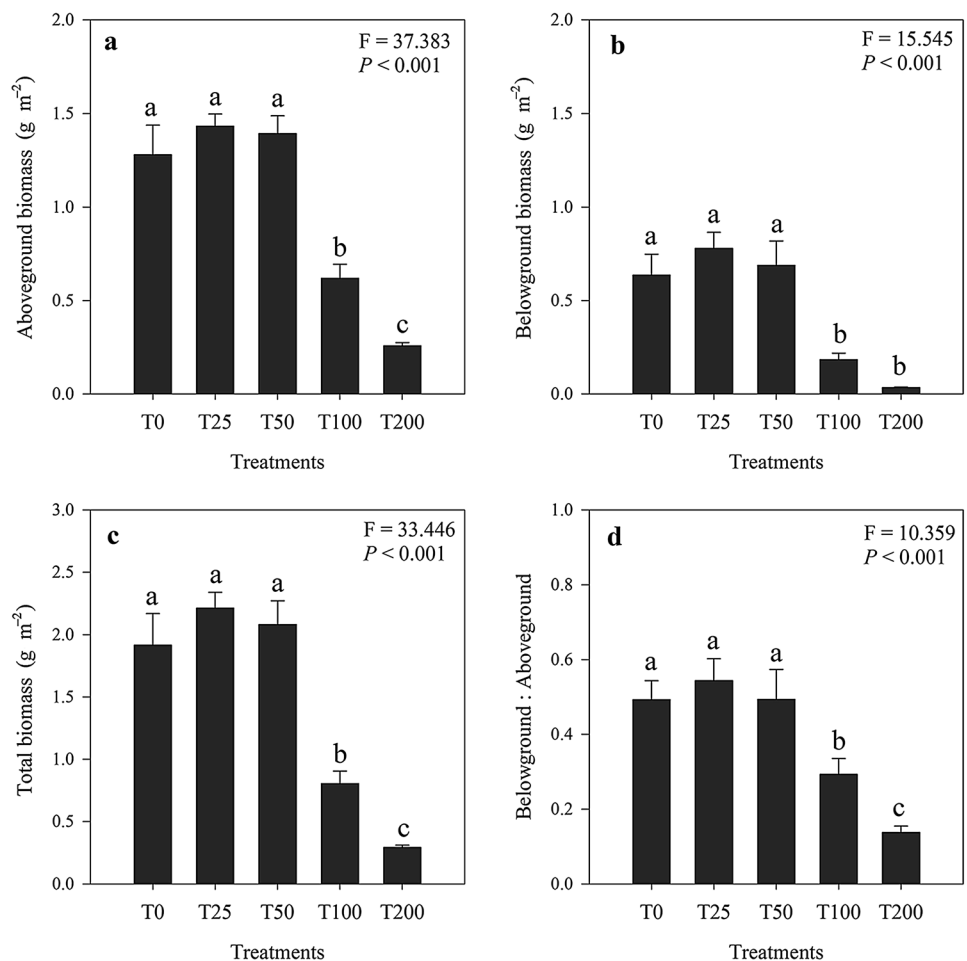


Fig. 3 Allelopathic index (AI) for foliage litter of *Artemisia halodendron* based on the effects on seed bank germination for the maximum number of seedlings (MNS) and the final number of seedlings (FNS). Treatments T25, T50, T100, and T200 represent additions of 0 (the control), 25, 50, 100, and 200 g m^{-2} of foliage litter, respectively, to the soil surface

dry peels of the coffee (*Coffea arabica*) fruit significantly inhibit seed germination and seedling growth of Malaysian cabbage [*Brassica chinensis* var. *Parachinensis* (Sinskaja)] (Silva et al. 2013). Furthermore, secondary metabolites from the root exudates of mangrove plants greatly inhibited the growth of the alga *Cyclotella caspia* (Liu et al. 2013), thus allelopathy could potentially be used to control eutrophication (Cheng et al. 2008; Fernández-Herrera et al. 2016; Pakdel et al. 2013).

Under natural condition, many plant species exhibited allelopathy, and this can offer them an important advantage in their competition with other species. In a forest ecosystem in south of China, the allelopathic effects of eucalyptus appeared to be the major factor that limited the establishment of other native species in eucalyptus forests by suppressing seed germination and seedling growth (Chu et al. 2014; Zhang and Fu 2009). Furthermore, allelopathy was considered to be an important strategy to control invasive plants (del Fabbro and Prati 2015; Vidotto et al. 2013). However, in sandy land such as that of our study area, the plant community changed rapidly in response to variation of the biotic and abiotic environments (Zuo et al. 2009,

Fig. 4 Differences in **a** above-ground biomass, **b** belowground biomass, **c** total biomass, and **d** the ratio of belowground to aboveground biomass among the treatments. Values represent means \pm SE ($n=6$). Bars labeled with different letters differed significantly among the treatments ($P<0.05$). Treatments T0, T25, T50, T100, and T200 represent additions of 0 (the control), 25, 50, 100, and 200 g m^{-2} of *Artemisia halodendron* foliage litter, respectively, to the soil surface



2010). Apart from the present study, we are unaware of any studies that focused on the allelopathy phenomenon in sandy areas such as the Horqin Sandy Land. In this typical degraded sandy grassland, vegetation succession occurred along the gradient of sand dune stabilization from mobile dunes to the fixed dunes and fully restored grassland. During the processes of succession, the *A. squarrosus* was transferred from a pioneer species into a dominant species, with a few accompanying species. It was gradually replaced by *A. halodendron*, which became the dominant species on semi-fixed dunes. Then, species richness increased and *A. halodendron* was replaced by other species, including *A. frigida*, *Cleistogenes squarrosa*, *Corispermum macrocarpum* and *Salsola collina* (Li et al. 2012a; Zhang et al. 2005; Zuo et al. 2008b, 2009, 2011).

Zhao et al. (2003) proposed that the mechanism for plant succession along the gradient of dune stabilization depended on both the environment (wind strength and its ability to transport sand) and the resource availability (water and nutrients). However, Zhao et al. (2003) noticed an interesting phenomenon when semi-mobile dunes began to stabilize: under the canopy of *A. halodendron*,

some seedlings germinated initially, but few became successfully established and mature plants were rare. In contrast, in areas farther from *A. halodendron*, many other species developed successfully. This was unlikely a result of shading, since *A. halodendron* produces a relatively small amount of needle-shaped leaves. In these adjacent habitats, resource availability and environmental condition would be similar. Thus, we hypothesized that there was a strong allelopathic effect that inhibited seed germination or subsequent seedling growth. Seedling growth will be affected by abiotic factors after full root growth has been achieved; this suggested that under stress, seeds in the seed bank germinated successfully, but were injured or died later (Sohrabi et al. 2016; Wang et al. 2016). The present results also supported this hypothesis. The germination dynamics showed that the inhibitory effect of the foliage litter on seed bank germination was slight during the initial stage, but that allelopathy occurred during later stages (Fig. 1). The extent of the allelopathy was related to the concentration of the litter, with much greater seedling loss in T100 and T200 than at lower concentrations (Fig. 2d).

The present result also demonstrated that the allelopathic effect of the foliage litter of *A. halodendron* depended on the concentration. Soil seed bank germination was not harmed at the low levels of concentration, even in T25 and T50; and allelopathic indexes were both positive (Fig. 3). It indicated a slight promotion for germination of soil seed bank. However, in high levels of concentration of T100 and T200, allelopathic index for final number of seedlings were negative (Fig. 3), it means that soil seed bank germination were inhibited by high concentration of the foliage litter of *A. halodendron*. A previous study of the stabilization gradient from mobile to fixed sand dunes found that the species dominance value of *A. halodendron* on semi-fixed dunes was 51.66, but decreased to 0.00 on fixed dunes (Zuo et al. 2012), with species richness values of 6.53 and 10.53, respectively, on semi-fixed and fixed dunes. Moreover, a morphological study of *A. halodendron* showed that the canopy area, ramet number, and root/shoot ratio were all significantly lower on fixed dunes than on mobile dunes (Huang et al. 2012). These findings suggested that foliage litter production by *A. halodendron* decreased markedly as dune stabilization progressed, leading to a lower concentration of foliage litter that was no longer able to inhibit seed germination or seedling establishment of other species (Fig. 2). This may partially explained why restoration of the plant community is initially slow, but then accelerated during later stages of dune stabilization. And this explanation was also demonstrated by the result of biomass differences among treatments (Fig. 4). In low concentration treatments of T25 and T50, the aboveground, belowground, and total biomass were all similar with control (differed insignificantly). However, in high concentration treatments of T100 and T200, plant biomass was significantly lower than control (Fig. 4a–c). This phenomenon can be evidenced in field investigation (Li et al. 2006; Zhao et al. 2003; Zuo et al. 2012): dominance value of *A. halodendron* was lower while plant biomass was high in habitats of semi-fixed and fixed dune, and opposite vegetation feature occurred in mobile dune (dominated by *A. halodendron* and vegetation biomass is low). Furthermore, result of plant biomass also demonstrated that, the allelopathy mainly produced at the belowground (Del Fabbro and Prati 2015; Rawat et al. 2013). In high concentration treatments of T100 and T200, the ratio of belowground: aboveground were both significantly lower than the control (Fig. 4d). It indicated that, the foliage litter of *A. halodendron* inhibited plant root accumulation more than the shoot.

In Horqin Sandy Land, our previous research found that strong winds occurred from mid-September to the following April (Yang et al. 2016). In winter, most of the plant foliage litter is produced by natural litterfall and by snow deposition and freezing-thawing cycles. In the

following spring, the surface litter is then redistributed by the region's strong winds, leading to considerable heterogeneity in the litter distribution. The present results agree with this previous research (Table 1).

In addition, soil properties and plant distribution in Horqin Sandy Land exhibited high spatial heterogeneity (Zuo et al. 2008a, b, 2010). This suggested that redistribution of foliage litter of *A. halodendron* by the wind may partially explained the heterogeneous distribution in Horqin Sandy Land.

Conclusions

During plant succession in Horqin Sandy Land, high concentrations of the foliage litter of *A. halodendron* can strongly inhibit seed germination and seedling establishment of other species. Seedling establishment was significantly inhibited after germination, with rapid seedling loss beginning around 3 weeks after incubation began. For seedlings that survived, both the aboveground biomass and the belowground biomass were decreased at high foliage litter concentrations. However, at low concentrations, the foliage litter did not significantly inhibit seed germination and seedling establishment of other species. This allelopathic effect on the growth of other species may be an important mechanism that affects plant succession along a successional gradient during restoration of sandy land. At the semi-fixed dune stage, the dominance of *A. halodendron* and its relatively high concentration of foliage litter gives this species an advantage during competition with other species; subsequently, at the fixed dune stage, low concentrations of the foliage litter are insufficient to control the establishment of other species. In future research and implications for restoration practice and management, it will be necessary to perform chemical extraction of the foliage litter to confirm that allelochemicals (and not other factors such as the difficulty of shoot penetration of the thicker litter layer in the T100 and T200 treatments) are responsible for the observed results and to determine whether there is a clear dose–response relationship for the extracted chemicals.

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References

- Cheng W, Chang XX, Dong HJ, Li DF, Liu JY (2008) Allelopathic inhibitory effect of *Myriophyllum aquaticum* (Vell.) Verdc. on *Microcystis aeruginosa* and its physiological mechanism. *Acta Ecol Sin* 28:2595–2603
- Chu C, Mortimer PE, Wang H, Wang Y, Liu X, Yu S (2014) Allelopathic effects of Eucalyptus on native and introduced tree species. *Forest Ecol Manag* 323:79–84
- Del Fabbro C, Prati D (2015) The relative importance of immediate allelopathy and allelopathic legacy in invasive plant species. *Basic Appl Ecol* 16:28–35
- Fernández-Herrera LJ, Band-Schmidt CJ, López-Cortés DJ, Hernández-Guerrero CJ, Bustillos-Guzmán JJ, Núñez-Vázquez E (2016) Allelopathic effect of *Chattonella marina* var. *marina* (Raphidophyceae) on *Gymnodinium catenatum* (Dinophyceae). *Harm Algae* 51:1–9
- Fiorentino A, D'Ambrosia B, Esposito A, Izzo A, Pascarella MT, D'Angelo G, Monaco P (2009) Potential allelopathic effect of neo-clerodane diterpenes from *Teucrium chamaedrys* (L.) on stenomediterranean and weed cosmopolitan species. *Biochem Syst Ecol* 37:349–353
- Huang WD, Zhao XY, Zhao X, Zhao HL, Wang SK, Lian J (2011) A combined approach using ISSR and ITS analysis for the characterization of *Artemisia halodendron* from Horqin sandy land, northern China. *Biochem Syst Ecol* 39:346–351
- Huang G, Zhao XY, Padilla FM, Zhao HL (2012) Fine root dynamics and longevity of *Artemisia halodendron* reflect plant growth strategy in two contrasting habitats. *J Arid Environ* 79:1–7
- Li FR, Zhao LY, Zhang H, Zhang TH, Shirato Y (2004) Wind erosion and airborne dust deposition in farmland during spring in the Horqin Sandy Land of eastern Inner Mongolia, China. *Soil Till Res* 75:121–130
- Li FR, Zhang AS, Duan SS, Kang LF (2005) Patterns of reproductive allocation in *Artemisia halodendron* inhabiting two contrasting habitats. *Acta Oecol* 28:57–64
- Li YQ, Zhao HL, Zhao XY, Zhang TH, Chen YP (2006) Biomass energy, carbon and nitrogen stores in different habitats along a desertification gradient in the semiarid Horqin Sandy Land. *Arid Land Res Manag* 20:43–60
- Li YQ, Zhao HL, Zhao XY, Zhang TH, Li YL, Cui JY (2010) Effects of grazing and livestock exclusion on soil physical and chemical properties in desertified sandy grassland, Inner Mongolia, northern China. *Environ Earth Sci* 63:771–783
- Li YQ, Zhao XY, Chen YP, Luo YQ, Wang SK (2012a) Effects of grazing exclusion on carbon sequestration and the associated vegetation and soil characteristics at a semi-arid desertified sandy site in Inner Mongolia, northern China. *Can J Soil Sci* 92:807–819
- Li YQ, Zhou XH, Brandle JR, Zhang TH, Chen YP, Han JJ (2012b) Temporal progress in improving carbon and nitrogen storage by grazing enclosure practice in a degraded land area of China's Horqin Sandy Grassland. *Agric Ecosyst Environ* 159:55–61
- Li YQ, Brandle JR, Awada T, Chen YP, Han JJ, Zhang FX, Luo YQ (2013) Accumulation of carbon and nitrogen in the plant–soil system after afforestation of active sand dunes in China's Horqin Sandy Land. *Agric Ecosyst Environ* 177:75–84
- Liu B, Liu ZM, Guan DX (2007) Seedling growth variation in response to sand burial in four *Artemisia* species from different habitats in the semi-arid dune field. *Trees* 22:41–47
- Liu Y, Li F, Huang QX (2013) Allelopathic effects of gallic acid from *Aegiceras corniculatum* on *Cyclotella caspia*. *J Environ Sci China* 25:776–784
- Ma JL, Liu ZM, Zeng DH, Liu B (2010) Aerial seed bank in *Artemisia* species: how it responds to sand mobility. *Trees* 24(3):435–441
- Miao RH, Jiang DM, Musa A, Zhou QL, Guo MX, Wang YC (2015) Effectiveness of shrub planting and grazing exclusion on degraded sandy grassland restoration in Horqin sandy land in Inner Mongolia. *Ecol Eng* 74:164–173
- Omezzine F, Haouala R (2013) Effect of *Trigonella foenum-graecum* L. development stages on some phytochemicals content and allelopathic potential. *Sci Hortic Amst* 160:335–344
- Pakdel FM, Sim L, Beardall J, Davis J (2013) Allelopathic inhibition of microalgae by the freshwater stonewort, *Chara australis*, and a submerged angiosperm, *Potamogeton crispus*. *Aquat Bot* 110:24–30
- Rawat LS, Maikhuri RK, Negi VS (2013) Inhibitory effect of leachate from *Helianthus annuus* on germination and growth of *Kharif* crops and weeds. *Acta Ecol Sin* 33:245–252
- Silva RMG, Brigatti JGF, Santos VHM, Mecina GF, Silva LP (2013) Allelopathic effect of the peel of coffee fruit. *Sci Hortic Amst* 158:39–44
- Sohrabi S, Ghanbari A, Mohassel MHR, Gherekhloo J, Vidal RA (2016) Effects of environmental factors on *Cucumis melo* L. subsp. *agrestis* var. *agrestis* (Naudin) Pangalo seed germination and seedling emergence. *S Afr J Bot* 105:1–8
- Su YZ, Zhang TH, Li YL, Wang F (2005) Changes in soil properties after establishment of *Artemisia halodendron* and *Caragana microphylla* on shifting sand dunes in semiarid Horqin Sandy Land, northern China. *Environ Manag* 36:272–281
- Tesio F, Weston LA, Ferrero A (2011) Allelochemicals identified from Jerusalem artichoke (*Helianthus tuberosus* L.) residues and their potential inhibitory activity in the field and laboratory. *Sci Hortic Amst* 129:361–368
- Tesio F, Vidotto F, Ferrero A (2012) Allelopathic persistence of *Helianthus tuberosus* L. residues in the soil. *Sci Hortic Amst* 135:98–105
- Vidotto F, Tesio F, Ferrero A (2013) Allelopathic effects of *Ambrosia artemisiifolia* L. in the invasive process. *Crop Prot* 54:161–167
- Wang PC, Mo BT, Long ZF, Fan SQ, Wang HH, Wang LB (2016) Factors affecting seed germination and emergence of *Sophora davidii*. *Ind Crop Prod* 87:261–265
- Yang L, Han G, Luo YQ, Wang Y, Zhu MN (2016) The intensity of sand drift activities in spring in the downstream of the Laoha River, China. *J Arid Land Resour Environ* 30:174–179
- Zhang CL, Fu SL (2009) Allelopathic effects of eucalyptus and the establishment of mixed stands of eucalyptus and native species. *For Ecol Manag* 258:1391–1396
- Zhang TH, Zhao HL, Li SG, Li FR, Shirato Y, Ohkuro T, Taniyama I (2004) A comparison of different measures for stabilizing moving sand dunes in the Horqin Sandy Land of Inner Mongolia, China. *J Arid Environ* 58:203–214
- Zhang JY, Zhao HL, Zhang TH, Zhao XY, Drake S (2005) Community succession along a chronosequence of vegetation restoration on sand dunes in Horqin Sandy Land. *J Arid Environ* 62:555–566
- Zhang CL, Li XW, Chen YQ, Zhao J, Wan SZ, Lin YB, Fu SL (2016) Effects of *Eucalyptus* litter and roots on the establishment of native tree species in *Eucalyptus* plantations in South China. *For Ecol Manag* 375:76–83
- Zhao HL, Zhao XY, Zhang TH, Wu W (2003) Desertification processes and its restoration mechanisms in the Horqin Sand Land. China Ocean Press, Beijing
- Zhao HL, Okuro T, Zhou RL, Li YL, Zuo XA (2011) Effects of grazing and climate change on sandy grassland ecosystems in Inner Mongolia. *Sci Cold Arid Reg* 3:223–232
- Zhao HL, Qu H, Zhou RL, Li J, Pan CC, Wang J (2013) Effects of sand burial on growth in two psammophyte seedlings and

- differences in their physiological responses. *Chin J Plant Ecol* 37:830–838
- Zuo XA, Zhao HL, Zhao XY, Zhang TH, Guo YR, Wang SK, Drake S (2008a) Spatial pattern and heterogeneity of soil properties in sand dunes under grazing and restoration in Horqin Sandy Land, Northern China. *Soil Till Res* 99:202–212
- Zuo XA, Zhao XY, Zhao HL, Zhang TH, Guo YR, Li YQ, Huang YX (2008b) Spatial heterogeneity of soil properties and vegetation–soil relationships following vegetation restoration of mobile dunes in Horqin Sandy Land, Northern China. *Plant Soil* 318:153–167
- Zuo XA, Zhao HL, Zhao XY, Guo YR, Yun JY, Wang SK, Miyasaka T (2009) Vegetation pattern variation, soil degradation and their relationship along a grassland desertification gradient in Horqin Sandy Land, northern China. *Environ Geol* 58:1227–1237
- Zuo XA, Zhao XY, Zhao HL, Guo YR, Zhang TH, Cui JY (2010) Spatial pattern and heterogeneity of soil organic carbon and nitrogen in sand dunes related to vegetation change and geomorphic position in Horqin Sandy Land, Northern China. *Environ Monit Assess* 164:29–42
- Zuo ZJ, Zhang RM, Gao PJ, Wen GS, Hou P, Gao Y (2011) Allelopathic effects of *Artemisia frigida* Willd. on growth of pasture grasses in Inner Mongolia, China. *Biochem Syst Ecol* 39:377–383
- Zuo XA, Zhao XY, Wang SK, Li YQ, Lian J, Zhou X (2012) Influence of dune stabilization on relationship between plant diversity and productivity in Horqin Sand Land, Northern China. *Environ Earth Sci* 67:1547–1556
- Zuo XA, Zhang J, Zhou X, Zhao XY, Wang SK, Lian J, Lv P, Knops J (2015) Changes in carbon and nitrogen storage along a restoration gradient in a semiarid sandy grassland. *Acta Oecol* 69:1–8