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Effects of sand burial on the survival and growth of two shrubs dominant in different habitats of northern China

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Abstract Plants that grow in dune ecosystems always suffer from sand burial. Shrubs play implications on the healthy functioning of dune ecosystems due to control blowing sand. However, the survival and growth responses of shrubs to sand burial remain poorly understood. The survival rate and seedling height of two shrubs (*Artemisia halodendron* and *Lespedeza davurica*) along with the soil properties under different burial depths were examined in order to reveal the causing ecophysiological attributes of sand burial on shrubs in the desertified region. It was found that *A. halodendron* can survive a burial depth of 6 cm greater than its seedling height, which is a dominant shrub in mobile dunes with intense burial, whereas a burial depth equivalent to three fourths of its seedling height is detrimental to *L. davurica*, which is dominant in fixed dunes with less burial. The reasons for the shrub death under sand burial were associated with the physical barrier to vertical growth and the reduction in photosynthetic area. In conclusion, *A. halodendron* can facilitate the stabilization of mobile dunes because of their high tolerance to the frequent and intensive sand burial, while *L. davurica* can be beneficial for the recovery process because of their higher survival rates under shallow burial following restoration of mobile dunes.

Keywords Sand burial · Horqin Sandy Land · Survival rate · Seedling height · Dune shrubs

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Introduction

Sand burial, a commonly recurring natural hazard in dune ecosystems, influences the different growth stages of plants (e.g., seeds, seedlings, and adult plants) in both coastal and inland dunes (Maun 1994, 1996; Brown 1997; Szczucinski 2012). Sand burial is not considered a primary stress but is a complex process that causes soil conditions to change (e.g., temperature, moisture, pH value, oxygen levels, bulk density and nutrient status), which in turn affects the survival and growth of dune plants included both vascular plants and cryptogams like lichen and moss (Poulson 1999; Jia et al. 2012, 2014). There are a large number of literatures focusing on seed germination and seedling emergence after sand burial (Maun 1996; Wang et al. 1998; Chen and Maun 1999; Benvenuti et al. 2001; Li et al. 2006). Gilbert et al. (2011) and Wang et al. (2016a) reported that the survival, growth, and reproduction of plants were positive to the shallow sand burial. It was reported that the moderate burial caused the leaf area to increase to compensate for the reduced photosynthetic rate (Martinez and Moreno–Casasola 1996; Gilbert et al. 2008) and the shoot, stem, and leaf petioles to elongate to promote

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vertical growth (Maun et al. 1996; Zhao et al. 2007a; Jia et al. 2008), which increased or maintained the production of flowers and seeds per plant to benefit reproduction (Maun 1994; Li et al. 2010) and produced adventitious roots for nutrient uptake (Dech and Maun 2006). However, plant burial beyond the tolerance limit is fatal because vertical growth is inhibited by the physical barrier presented by deep burial, as well as by the reduction in photosynthetic area and limited oxygen availability to the roots (Harris and Davy 1988; Maun 1994; Li et al. 2010). In addition, the tolerance limit of plants under sand burial depth varies depending on species (Maun et al. 1996; Qu et al. 2011), and Liu et al. (2008) and Zardi et al. (2008) found that species from habitats with intense burial exhibit better survival than those from habitats with less burial under the same burial stress.

In all, previous studies were mainly focused on crops and annual plants (Qu et al. 2011, 2012; Li et al. 2015). However, it was largely unknown about whether shrubs (i.e., survival and growth attributes) living in different habitats of dune ecosystems respond differently to sand burial intensity. Shrubs are integral to the healthy functioning of sand dune ecosystems and are the basis for controlling blowing sand, an issue that contributes to desertification globally and affects nearly 10,000 ha of land in China alone. Furthermore, seedlings are more susceptible to environmental stress than adult plants (Salo and Pedersen 2014), and the growing condition of shrub seedlings and their ecophysiological attributes are of primary concern in the process of stabilization of degraded ecosystems (Zhao et al. 2006; Luo et al. 2010).

In summary, to learn more about the response of shrubs to sand burial, seedlings of two dominant shrub species (*Artemisia halodendron* and *Lespedeza davurica*) were selected for study in Horqin Sandy Land, one of the most severely desertified regions in northern China. The burial of plants in sand is a common phenomenon in Horqin Sandy Land (Liu et al. 1992; Zhao et al. 2007b), making it an ideal model to assess the effects of sand burial on the survival and growth of seedlings. *A. halodendron* is a pioneer shrub for sand fixing and is dominant in mobile dunes and semi-fixed dunes, and its main way of population spread is asexual reproduction under sand burial. *L. davurica* is mainly growing in fixed dunes in Horqin Sandy Land and also a forage with drought resistance adapted to the barren soil (Li et al. 2002; Zhang et al. 2004; Zhang et al. 2005; Zhao et al. 2008; Qu et al. 2009; Wang et al. 2016b). And whether the different distribution patterns of the two shrubs is caused by sand burial is what we want to answer in this study, so the present objectives were as follows: (1) to compare the tolerance limit and growth of *A. halodendron* and *L. davurica* to sand burial on the basis of their survival rate and seedling height, respectively; (2) to reveal the underlying mechanism for shrub death under sand burial; and (3) to provide suggestions on how to protect plants against sand burial and promote the rehabilitation of dune vegetation. Two hypotheses were generated as follows: (1) *A. halodendron*, which is dominant in mobile dunes and semi-fixed dunes with intense sand burial, has a higher survival rate than L. *davurica*; and (2) the seedling height of a shrub can be promoted by moderate burial.

Materials and methods

Experimental site

The experiment site is located in Naiman County (42° 55′ N, 120° 42′ E; altitude approximately 360 m) in the southwestern part of Horqin Sandy Land, Inner Mongolia, China. This area is one of the most severely desertified regions in China because of the stress caused by grazing, cultivation, and the collection of fuelwood. The distribution pattern of the natural vegetation in this region is characterized by a mosaic of lowland grasslands, fixed dunes, semi-fixed dunes, and mobile dunes. The dunes are covered with native plants to varying extents and are generally dominated by grasses (e.g., *Setaria viridis* L., *Cleistogenes squarrosa* L.), forbs (e.g., *Salsola collina* L., *Agriophyllum squarrosum* L., *Corispermum macrocarpum* L.), and shrubs (e.g., *Caragana microphylla* L., *L. davurica* L., *A. halodendron* L.). And for the two shrubs we selected in this study, *A. halodendron* and *L. davurica* are dominant in local mobile dunes and fixed dunes, respectively.

The climate is temperate, semi-arid continental, and monsoonal. The mean annual temperature is 6.4 °C, and the region receives 360 mm of annual precipitation, with 1935 mm annual pan evaporation. The mean annual wind velocity is 3.5 m/s, and the average wind speed in spring and the threshold wind velocity of sand in mobile dunes are both 4.3 m/s. Flying sand occurs between 20 and 30 days/year. The average migration speed of mobile dunes is 10.53 m/year, and the total transport rate from 0 to 40 cm height of mobile dunes is 132.04 g/(cm/h). The maximum depth of local plants buried by sand was 30.2 cm, which was observed in a mobile dune. Taken together, these results are true for nearly 10,000 ha of grassland engulfed by mobile sand dunes annually (Zhao et al. 2006; Luo et al. 2010; Zhao et al. 2013).

Experimental design

The experiment was conducted from April 2010 to September 2011. The burial experiment was performed throughout the entire growing period of *L. davurica* and *A. halodendron* in 2011 (April to September). In early April 2010, seeds of *L. davurica* and *A. halodendron* were separately sown in 2 m × 2 m × 2 m cement plots that were filled with sand from their native habitats. The first thinning was performed after the seedlings emerged to avoid death caused by competition. A total of 100 seedlings with similar growth were kept in each plot. No additional water or fertilizer was added, during the experiment to keep the soil condition as close as possible to natural conditions. The second thinning was conducted in April 2011, after which a total of 50 seedlings with similar growth were left and marked in each plot.

The sand burial treatments were conducted approximately 20 days after the second thinning. The seedlings were kept in a vertical position when buried and marked for easier identification. The sampling shrubs were similar and their difference in height was not significant ($P > 0.05$). The average heights of the *L. davurica* and *A. halodendron* seedlings were 7.6 ± 0.2 and 7.8 ± 0.6 cm, respectively. The seedling emergence days of *L. davurica* and *A. halodendron* when the sand burial treatments were conducted were 339 and 332 days, respectively. The unmarked seedlings that emerged after the sand burial treatment were removed. Based on the actual depth of sand burial in the natural conditions investigated previously (Zhao et al. 2013), we divided the sand burial treatments into 10 groups: one control (no burial, CK) and nine buried treatment groups. The seedlings in the nine treatments were buried at one fourth (A), one half (B), three fourths (C), and 100% (D) of their height and at 2 cm (E), 4 cm (F), 6 cm (G), 8 cm (H), and 10 cm (I) above their height. We used a completely randomized design for this experiment. Each treatment comprised four replicates (four plots) for a total of 80 plots. The thickness of the sand was regularly verified to ensure consistency throughout the duration of the experiment.

During the experimental period, soil properties, such as the pH, temperature (T), volumetric soil water content (W), hardness (H), organic carbon, and total nitrogen content, were observed at burial depths of 0, 10, and 20 cm with an interval period of 10 days. The illumination intensity (I) of dry and wet sand (0 to 20 cm, with 2 cm intervals) was recorded using an illuminometer. The dates when leaves first showed signs of wilting and when they were completely dead were recorded. In cases of burial depth equal to or above seedling height, sand was uncovered carefully and seedlings were recovered after observation. The survival rate (the ratio of the number of living seedlings at the end of experiment relative to the number before sand burial) and seedling height (measured using a ruler) were measured in mid-September, and for seedlings that died after treatment, the final seedling height when they died was recorded.

Data collection

The soil pH was determined with a pH tester (Multiline F/SET-3, Germany) in 1:1 soil-water slurry. The soil hardness was measured with a soil penetrometer (TYD-1, China). The soil temperature and volumetric soil water content were determined using geothermometers (HH82, Exphil Calibration Labs, Bohemia, NY, USA) and hygrometers (TRIME-FM, IMKO, GmbH, Ettlingen, Germany), respectively. The soil total carbon content (C) and total nitrogen content (N) were measured by using an elemental analyzer (vario Macro cube, Elementar, Germany). The illumination intensity under different sand burial depths (including dry sand and wet sand with a saturated water content of 15%) was recorded using an illuminometer (Testo 545, Germany).

Resistance index

In order to compare the resistance ability of the two shrub species to sand burial in quantity, the resistance index (RI) was adopted (Orwin and Wardle 2004; Jia et al., 2012).

$$\mathrm{Ri} = 1 - 2|D0| \Big/ \left(C0 + |D0|\right)$$

where $D0$ was the difference in the mean survival rate and seedling height between the control ($C0$) and the treated plants over the whole experimental period. The higher the value, the greater the resistance ability is.

Statistical analysis

SPSS version 13.0 (SPSS Inc., Chicago, IL, USA) was used to perform analysis of variance (ANOVA). All statistical tests were conducted at a 5% significance level. The Bonferroni correction for multiple testing was applied ($P = 0.05/n$). We tested for the effects of soil properties after sand burial on the survival rate and seedling height of shrubs using generalized linear mixed models [GLMM; lme4 library] obtained from the R package (R Core Team 2015), where plots are random effects.

Results

Soil properties and precipitation

After 1 year, there were no differences in soil properties between the plots that were planted with the two different shrub species ($P > 0.0125$, after the Bonferroni correction for multiple testing, $n = 4$). There was no significant difference in the soil pH (8.30 to 8.45) at different burial depths. The maximum values of the soil temperature (26.85 °C) occurred at 0 cm of depth, significantly higher than other layers. Soil hardness significantly increased with burial depth ($P < 0.0125$, after Bonferroni correction for multiple testing, $n = 4$). There was no significant difference in the soil organic carbon contents among different layers ($P > 0.0125$, after Bonferroni correction for multiple testing, $n = 4$), and the highest content of 0.73 g/kg was observed in the 10 cm layer and no significant difference in soil total nitrogen among different layers ($P > 0.0125$, after Bonferroni correction for multiple testing, $n = 4$); the highest content was also found at 10 cm burial depth (Table 1). With increasing burial depth, the illumination intensity through both dry and wet sands was sharply decreased because no light could penetrate to the 10 cm burial depth (Table 2). During the burial experiment, the maximum precipitation occurred in July (90.8 mm) and the minimum occurred in April (1.6 mm) (Fig. 1). The soil water content increased with the burial depth; the maximum values of 0 cm (9%) and 5 cm (11.9%) layers appeared in August, while the maximum values of 10 cm (24.6%) and 20 cm (28.3%) layers appeared in September (Fig. 1).

Leaf performance

No seedlings of *A. halodendron* and *L. davurica* were found dead or wilted under CK, treatment A, and treatment B throughout the burial experiment. However, at the burial depths of treatments D and E, *A. halodendron* seedlings were found to wilt by the 12th day of sand burial. Meanwhile, the situation of the *L. davurica* seedlings was even worse, exhibiting signs of wilting after 3 days of burial and even death after 6 days. The wilting date of *A. halodendron* seedlings appeared earlier with increasing burial depth: at the eighth day under treatment G, third day under treatment H, and completely dead under treatment I after being buried for 5 days. Similar to *A. halodendron*, the wilting and death date of *L. davurica* seedlings also came earlier with increasing burial depth: when burial depth reached the levels of treatments H and I, wilting occurred after being buried for 2 days, and the seedlings were completely dead after the seedlings had been buried for 4 days (Online Resource 1).

Survival rate

The survival rate of *A. halodendron* seedlings decreased with increasing burial depth. However, the difference with CK was not significant until the burial depth reached the level of treatment D ($P < 0.0125$, after Bonferroni correction for multiple testing, $n = 4$). The survival rate sharply decreased with increasing burial depth: only 6.35% of the *A. halodendron* seedlings survived under treatment E, and no seedlings survived under treatment I. For *L. davurica*, a slight increase in the survival rate was observed under treatment A compared with that observed under CK, but this difference was not significant ($P > 0.0125$, after Bonferroni correction for multiple testing, $n = 4$). When the burial depth increased to the level of treatment C, only 12.5% of *L. davurica* seedlings remained alive, and no seedling survived a burial depth equal to or beyond the seedling height. The difference in survival rate between two species was not significant under CK ($P > 0.0125$, after Bonferroni correction for multiple testing, $n = 4$). When the burial depth was shallow (treatments A and B), *L. davurica* seedlings had a higher survival rate than *A. halodendron* seedlings, but the situation was reversed

Table 1 Soil properties at different sand burial depths during experimental period

Depth (cm)	pH value	Temperature (°C)	Hardness (kg/cm^2)	C (g/kg)	N (g/kg)
0	8.45 ± 0.27a	26.85 ± 1.3a	0.121 ± 0.005c	0.68 ± 0.03a	0.088 ± 0.002a
10	8.30 ± 0.34a	16.91 ± 1.1b	0.159 ± 0.008b	0.73 ± 0.06a	0.102 ± 0.004a
20	8.34 ± 0.36a	17.27 ± 0.9b	0.187 ± 0.004a	0.65 ± 0.07a	0.098 ± 0.002a

The data were means of multiple measurements observed with an interval period of 10 days during the experimental period. Values were assigned as mean ± SE. Mean values with different lowercase letters in the same column are significantly different among the different burial depths ($P < 0.0125$, after Bonferroni correction for multiple testing, $n = 4$). Measurements were made every 10 days during the experimental period

C soil total carbon content, *N* soil total nitrogen content

when the burial depth increased to the level of treatment C because of the high mortality of *L. davurica* seedlings (Fig. 2).

Seedling height

Shallow burial did not inhibit the seedling height of *A. halodendron*; the differences among treatments A, B, C, D, and E were not significant ($P > 0.0125$, after Bonferroni correction for multiple testing, $n = 4$). However, the height growth of *A. halodendron* seedlings was inhibited by the deep burial depth. The average seedling height of this species decreased significantly when the burial depth was beyond treatment F, significantly shorter than the 18.8 cm average height recorded in CK ($P < 0.0125$, after Bonferroni correction for multiple testing, $n = 4$). Under treatment I, the *A. halodendron* seedlings completely died and stopped growing at the height of 7.9 cm (Fig. 3a). Shallow burial (treatments A and B) did not inhibit the seedling height of *L. davurica*, but when the burial depth increased to the level of treatment C, the average seedling height of *L. davurica* was only 7.9 cm, significantly shorter than that in CK (12.9 cm) as well as that in treatments A (12.1 cm) and B (12.8 cm) ($P < 0.0125$, after Bonferroni correction for multiple testing, $n = 4$). When the burial depth beyond treatment D, the *L. davurica* seedlings completely died and stopped growing at the height of 7.6 to 7.8 cm (Fig. 3b).

Table 2 Illumination intensity in different sand burial depth

Depth (cm)	Illumination intensity of dry sand (LUX)	Illumination intensity of wet sand (LUX)
0	67,900 ± 1103a	67,900 ± 1103a
2	1230 ± 137b	1145 ± 123b
4	850 ± 11b	798 ± 39b
6	410 ± 16c	408 ± 19c
8	148 ± 9d	139 ± 13d
10	80 ± 6d	76 ± 4d
12	0e	0e
14	0e	0e
16	0e	0e
18	0e	0e
20	0e	0e

Values were assigned as mean ± SE. Mean values with different lowercase letters in the same column are significantly different among the different burial depths ($P < 0.017$, after Bonferroni correction for multiple testing, $n = 3$)

Resistance ability

Generally, the RIs of the survival rate and seedling height measured for the two shrubs decreased monotonically as the sand burial depth increased. Under the shallow burial (treatments A and B), the RI of survival rate of *L. davurica* was significant higher than *A. halodendron*, while when burial depth beyond treatment C, *A. halodendron* exhibited markedly higher RI for the survival rate than *L. davurica* ($P < 0.0125$, after Bonferroni correction for multiple testing, $n = 4$). For

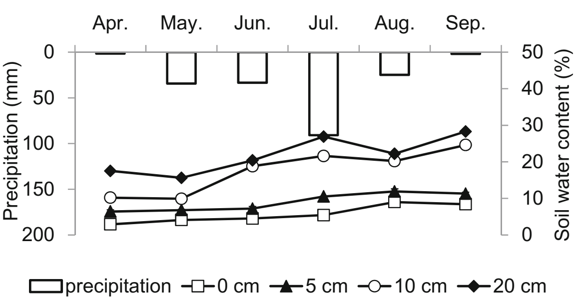

Fig. 1 Precipitation and soil water content during the experimental period

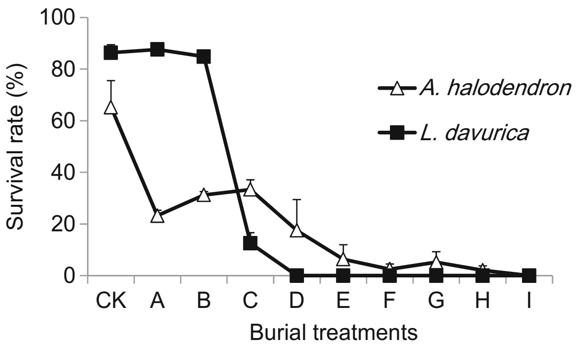

Fig. 2 Survival rate of two shrub seedlings under different sand burial depths. *AH Artemisia halodendron*, *LD Lespedeza davurica*, *CK* control treatment, no burial, *A* buried to one fourth of seedling height, *B* buried to one half of seedling height, *C* buried to three fourth of seedling height, *D* buried to 100% of seedling height, *E* buried to 2 cm above seedling height, *F* buried to 4 cm above seedling height, *G* buried to 6 cm above seedling height, *H* buried to 8 cm above seedling height, *I* buried to 10 cm above seedling height

the RI of seedling height, the difference between the two species was not significant ($P > 0.0125$, after Bonferroni correction for multiple testing, $n = 4$) (Table 3).

Effects of sand burial on different soil properties in relation to the survival of two shrub seedlings

We tested for the effects of soil properties (T: soil temperature; W: soil water content; H: soil hardness; I: soil illumination intensity) after sand burial on the survival rate and seedling height of shrubs in a generalized linear mixed model (GLMM) (Huang et al. 2014), where plots are random effects. The conditional R^2 was calculated using both fixed and random effects, and the marginal R^2 was calculated using only the fixed effects (Nakagawa and Schielzeth 2013). Akaike's information criterion (AIC) and Bayesian information criterion (BIC) were used to assess model performance; models with lower AIC and BIC are considered to perform better (Aho et al. 2014). The results showed that the full model was the best model. The fixed effects alone explained the majority of the total variability in the survival rate and seedling height of shrubs due to the higher marginal R^2, while the random effects accounted for only a minor amount of variation. The full model also demonstrated that survival was significantly affected by the soil water content ($P < 0.01$), soil hardness ($P < 0.05$), illumination intensity ($P < 0.05$), and the T × W ($P < 0.05$) and H × I ($P < 0.05$) interactions. The seedling height was significantly affected by the soil water content ($P < 0.05$), soil hardness ($P < 0.05$), illumination intensity ($P < 0.01$), and the W × H interaction ($P < 0.05$) (Online Resource 2).

Discussion

Sand activity is a frequent phenomenon that occurs in inland and coastal dune ecosystems (Maun 1994; Brown 1997). As a consequence, plants growing in dune ecosystems often suffer from varying degrees of sand burial (Maun 1998), and the seedling stage is the growth stage when plant is the most vulnerable to adverse environmental factors (Zhao et al. 2008). Sand burial is a complex process that alters many aspects of soil conditions that may influence the survival and growth of dune plants (Poulson 1999; Jia 2012, 2014).

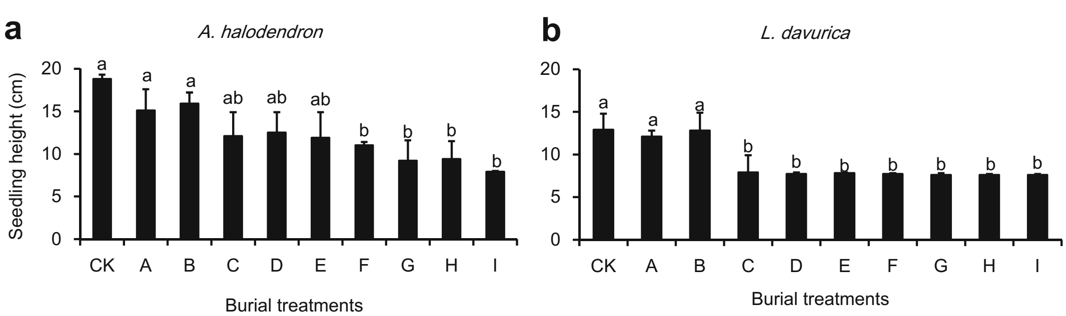

Fig. 3 Seedling height of two shrubs under different sand burial depths. **a** *A. halodendron;* **b** *L. davurica*; *CK* control treatment, no burial, *A* buried to one fourth of seedling height, *B* buried to one half of seedling height, *C* buried to three fourth of seedling height, *D* buried to 100% of seedling height, *E* buried to 2 cm above seedling height, *F* buried to 4 cm above seedling height, *G* buried to 6 cm above seedling height, *H* buried to 8 cm above seedling height, *I* buried to 10 cm above seedling height. Mean values with different lowercase letters are significantly different among the different burial depths. For seedlings that died after treatment (treatment *I* for *A. halodendron* and treatment *D* to *I* for *L. davurica*), the seedling height was recorded when they died

Table 3 Resistance indices of survival rate and seedling height of two shrub species in response to different sand burial depths

Burial treatments	Survival rate		Seedling height	
	Artemisia halodendron	*Lespedeza davurica*	*A. halodendron*	*L. davurica*
A	0.22 ± 0.02aA	0.97 ± 0.02aB	0.67 ± 0.01aA	0.88 ± 0.05aA
B	0.32 ± 0.03bA	0.97 ± 0.03aB	0.73 ± 0.02aA	0.98 ± 0.03aA
C	0.34 ± 0.01bA	0.08 ± 0.01bB	0.49 ± 0.00bA	0.44 ± 0.01bA
D	0.16 ± 0.03aA	0.00 ± 0.00cB	0.50 ± 0.02bA	0.43 ± 0.02bA
E	0.05 ± 0.02cA	0.00 ± 0.00cB	0.46 ± 0.01bA	0.43 ± 0.01bA
F	0.02 ± 0.04cA	0.00 ± 0.00cB	0.41 ± 0.02bA	0.43 ± 0.04bA
G	0.04 ± 0.01cA	0.00 ± 0.00cB	0.32 ± 0.03cA	0.42 ± 0.03bA
H	0.02 ± 0.01cA	0.00 ± 0.00cB	0.33 ± 0.04cA	0.42 ± 0.05bA
I	0.00 ± 0.00cA	0.00 ± 0.00cA	0.27 ± 0.02cA	0.42 ± 0.06bA

Values were assigned as mean ± SE. Mean values with different lowercase letters in the same column are significantly different among the different burial depths of same species. Mean values with different capital letters in the same row are significantly different among the different species under same depths ($P < 0.0125$, after Bonferroni correction for multiple testing, $n = 4$)

A buried to one fourth of seedling height, *B* buried to one half of seedling height, *C* buried to three fourth of seedling height, *D* buried to 100% of seedling height, *E* buried to 2 cm above seedling height, *F* buried to 4 cm above seedling height, *G* buried to 6 cm above seedling height, *H* buried to 8 cm above seedling height, *I* buried to 10 cm above seedling height

In our study, the soil pH value was unaffected by sand burial, and soils were alkaline at all depths. As burial depth increased, light transmittance decreased because of limited incident light. Soil hardness, an indicator of soil compaction, increased with increasing burial depth, possibly because of the common effects of overlying sand and the bonding material caused by plant roots in deeper soil (Li et al. 2007). The increased soil water content and decreased soil temperature with increased burial depth may be attributed to the precipitation infiltration process and intensive solar radiation and evapotranspiration on the soil surface observed under similar sand dune conditions (Li et al. 2007). The decomposition of dead roots through microbial activity may explain why the soil organic carbon and total nitrogen content were the highest in the 10 to 20 cm burial depth layer (Qu et al. 2010). Statistical analyses showed that some of the changes in soil properties with depth also influenced the survival and growth of the two shrub seedlings. The survival rates and seedling height of both shrubs were significantly affected by illumination intensity, soil hardness, and soil water content, respectively. These findings were consistent with those of previous studies indicates that the major factors causing seedling death under sand burial were associated with the physical barrier to vertical growth and the reduction in photosynthetic area (Harris and Davy 1988; Maun 1994), and water has a positive effect on the recovery of plants after sand burial by stimulating the photosynthesis and shoot elongations (Jia et al. 2008, 2014). On the other hand, our finding also confirms the previous studies that shoot elongation is an important strategy which enables plants to withstand and recover caused by sand burial (Shi et al. 2004; Jia et al. 2008), because it is fatal for those seedlings that cannot penetrate above the buried sand when burial depth is above their height.

The tolerance limit of plants under sand burial depth varies with species. For example, all *Cirsium pitcheri* seedlings died in the complete (100%) burial treatment, whereas 20% died in the 75% burial treatments (Maun et al. 1996). By contrast, *A. squarrosum* seedlings can further tolerate stress along the sand burial gradient, with 9% of *A. squarrosum* seedlings surviving even when the burial depth reached 10 cm higher than seedling height (Qu et al. 2011). The intensity of burial is also a factor; a lower survival rate was generally observed in species from habitats with less intense burial than in those from habitats with intense burial (Liu et al. 2008; Zardi et al. 2008). In accordance with previous research (Maun et al. 1996; Chen and Maun 1999; Liu et al. 2008), we also found that tolerance to sand burial varied with species. In our study, no *L. davurica* seedlings survived under a burial depth equal to or above their height, whereas *A. halodendron* seedlings withstood the stress much further along the sand burial gradient, not reaching their upper threshold limit until the burial depth reached 8 cm higher than the seedling height. The wilting and death of *A. halodendron* leaves occurred later relative to those of *L. davurica* under the same burial depth. This point may be explained by that species grown in habitats with intensive burial had stronger resistance to sand burial (Liu et al. 2008; Zardi et al. 2008). Liu et al. (2008) concluded that species from habitats with intensive sand burial exhibited higher survival rates and stem elongation speeds than species found in habitats with less intensive sand burial in a study of four dominant *Artemisia* species in different habitats. Zardi et al. (2008) obtained similar results in their study on the effects of sand burial on invasive species and indigenous species. They found that indigenous species could withstand sand burial stress better than invasive species.

Our results also suggest that tolerance to burial is a requisite for survival. As a pioneer species of mobile dunes in Horqin Sandy Land, *A. halodendron* experiences sand burial stress more intensively than *L. davurica* and has thus developed effective mechanisms to adapt to or withstand sand burial (Zhang et al. 2005). Generally, for plant species in Horqin Sandy Land, the sand burial depth less than 50% of their plant height was regarded as shallow burial or moderate burial and deep burial was that burial depth exceeds their height (Zhao et al. 2013). However, contrary to our initial expectations, the survival rate and seedling height of *A. halodendron* decreased continuously with increasing burial depth, and its resistance index of survival rate is lower than *L. davurica*. This finding suggests that *L. davurica* seedlings has greater resistance ability to shallow burial than *A. halodendron*, and unlike most sand dune species that require moderate burial in sand to maintain high vigor and promote growth (Van Der Putten et al. 1993), shallow burial also has negative effects on the survival and growth of *A. halodendron*, despite its capability to withstand intensive burial. The survival rate and seedling height of *L. davurica* did not show a significant decrease until the burial depth reached three fourths of its seedling height. This finding indicates that shallow burial should not be regarded as stress to *L. davurica*, given that the increase in soil moisture and the decrease in soil temperature in the root zone corresponding to the increased soil depth may be beneficial to its growth (Shi et al. 2004). This condition may be attributed to the fact that dry soil conditions and high temperatures are major factors limiting plant growth in arid regions (Niu et al. 2003).

Conclusion

The first hypothesis was partially supported by our results; the survival rate of *A. halodendron* was higher than that of *L. davurica* only after the burial depth reached three fourths of the seedling height. The second hypothesis was not supported by our results. Notably, neither the seedling height nor the survival rate of *A. halodendron* was promoted by moderate burial, and even shallow burial will have a negative impact on the survival and growth of *A. halodendron*, although this species can withstand even when the burial depth reached 6 cm higher than seedling height. Moderate burial seems to have no negative effect on *L. davurica*, but deep burial was fatal to this species. Our results revealed that the deaths of both species after sand burial were caused by the physical barrier to vertical growth and the reduction of the photosynthetic area, and thus shoot elongation stimulated by soil water content is the strategy for *A. halodendron* to penetrate above the buried sand and maintain photosynthesis to survive in the intensive burial.

It was found that the different distribution pattern of the two shrubs is caused by sand burial due to their different withstand ability to sand burial. We suggest that *A. halodendron* can be helpful as a sand dune stabilization species for areas with frequent and intensive sand burial (e.g., mobile dunes) because of its high tolerance. When mobile dunes have been restored to a semi-mobile state, *L. davurica* should be introduced because of its high survival under shallow burial.

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