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REGULAR ARTICLE

Sand burial compensates for the negative effects of erosion on the dune-building shrub *Artemisia wudanica*

Bo Liu · Zhimin Liu · Xiaotao Lü · Fernando T. Maestre · Lixin Wang

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Abstract
Aims Plant species response to erosion or burial has been extensively studied, but few studies have examined the combined effects of erosion and subsequent burial on plants. In active sand dunes of northern China, *Artemisia wudanica* falls to the ground following wind erosion, accumulating sand among fallen stems in a process that may facilitate its further growth and development. Therefore, we hypothesize that subsequent sand burial might compensate for the negative effects of erosion in the growth of *A. wudanica*.
Methods A common garden experiment was conducted using *A. wudanica* seedlings to evaluate their growth in response to different degrees of burial and erosion as observed at the field. Seedlings were selected and randomly assigned to six erosion treatments, two burial treatments, twelve erosion and subsequent burial treatments, and control. Each treatment was replicated six times.
Results Compared with the control treatment, total biomass and the relative growth rate of shoots were stimulated in the erosion and subsequent burial treatments (significantly under the 10 cm burial), hampered in erosion only treatments, and were not affected in the burial only treatments. Adventitious roots and ramets were only observed under burial only and erosion and subsequent burial treatments.
Conclusions Our results indicate that subsequent sand burial following erosion compensate for the negative effects of erosion on the growth of *A. wudanica* seedlings, and greatly contributed to their tolerance to wind erosion.

Keywords Drylands · Intra-specific facilitation · Multiple disturbances · Sand dune · Vegetative reproduction

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Introduction

Wind erosion and sand burial are common environmental stressors in sand dune areas throughout the world (Maun 1998; Pimentel and Kounang 1998; Dong et al. 2000). These processes change the environmental conditions of soils (e.g., temperature, moisture, nutrient and oxygen availability), as well as the exposure to light of buried parts of the plants (Hagen 1991; Zhao et al. 2006; Liu et al. 2011). Therefore, these stressors may create selective pressures on physiological and morphological plant traits, affecting their survival and growth, and subsequently controlling the distribution and composition of vegetation in dune ecosystems (Hesp 1991; Dech and Maun 2006; Acosta et al. 2007; Levin et al. 2008). Thus, evaluating the tolerance of seedlings to wind erosion and sand burial are of major importance for understanding the establishment and dynamics of dune vegetation (Herman et al. 2001; Rozé and Lemauviel 2004).

An important feature of active sand dune habitats is the alternation between wind erosion and sand burial (Petru and Menges 2004; Liu et al. 2006; Ma and Liu 2008a). Some parabolic dunes are created under constant wind direction (Ardon et al. 2009), but wind direction in many other regions is not constant and often varies by seasons. The exposed roots or rhizomes may be partly or entirely re-buried (Liu et al. 2006; Ma and Liu 2008a), and buried roots or rhizomes could be exposed by erosion during the next wind event (Petru and Menges 2004). Seedling tolerance to various degrees of sand burial or wind erosion has been widely studied (Zhang and Maun 1990; Danin 1996, 1997; Gilbert and Ripley 2008; Li et al. 2010a, b; Burylo et al. 2011). Most previous studies have focused on either wind erosion only or sand burial only, rather than on the interaction between both processes (Brown 1997; Cabaço and Santos 2007; Samsone et al. 2009; Qu et al. 2012). Therefore, to fully understand how wind erosion and sand burial jointly affect plant performance in sand dunes it is important to study the effects of these stressors together, rather than on isolation from each other.

In the active sand dune ecosystems of northern China, the process of erosion and subsequent burial is very common. The erosion and subsequent burial process tends to bury the plants in the horizontal positions, in that erosion causes plants to fall to the ground in horizontal positions, and then plants are buried (Liu et al. 2006; Ma and Liu 2008a). Previous studies have demonstrated that wind erosion has negative effects on plant survivorship, growth and reproduction in many dune plants (Marbà and Duarte 1994; Petru and Menges 2004; Yu et al. 2008; Li et al. 2010a). Sand burial can stimulate plant physiological activity and growth (Shi et al. 2004; Perumal and Maun 2006), shifts in biomass allocation patterns (Burylo et al. 2011), and the production of adventitious roots (Dech and Maun 2006; Liu et al. 2008). Erosion causes plants to fall to the ground where they often become entirely or partly buried (e.g., when they are located at leeward slope and crest of the sand dune), stimulating further deposition of sand and burial on the fallen shoots. However, to our knowledge, the combined effects of erosion and subsequent burial on the performance of plants inhabiting sand dunes have not been investigated yet.

Artemisia wudanica (Liou & W. Wang) is a major pioneering sand dune species in sand dune ecosystems of northern China. Previous observations have shown that *A. wudanica* bends over by wind erosion and then accumulates blown sand among its fallen stems, forming a sand-protecting barrier (Jin and Ye 1989). The deposition of sand will enable the formation of adventitious roots from stems' nodes, contributing to the colonization and clonal expansion of this species (Li et al. 2005; Liu et al. 2008; Samsone et al. 2009; Sun et al. 2010). The formation of these roots will favor the acquisition of more nutrients from the sediment, stimulating aboveground growth (Liu et al. 2008). New ramets will need to grow through the overlying sediment to reach the surface (Maun 1996; Li et al. 2005). Because these ramets are able to branch, continued deposition of sediments at the surface increases complexity of the belowground system, and the density of stems above ground. Therefore, the process of erosion and subsequent burial, to some extent, facilitates plant growth, and we hypothesize that subsequent sand burial may compensate for the negative effects of erosion in *A. wudanica*. To test this hypothesis, seedlings of *A. wudanica* were grown under controlled conditions in a common garden experiment. Total biomass, adventitious roots biomass, number of ramets and relative growth rate of shoots biomass were examined under erosion only, burial only, erosion and subsequent burial treatments.

Materials and methods

Study site

The study area was located in Wulanaodu village (119°39′E, 43°00′N, 480 m a.s.l.) in the western part of the Horqin Sand Land, Inner Mongolia, China. This village is an experimental and demonstration site of the Wulanaodu Experimental Station of Desertification of the Chinese Academy of Sciences. The climate of the site is semi-arid continental. Mean annual temperature is 6.3 °C; the lowest and highest monthly mean occurs in January (−14 °C) and July (23 °C), respectively (Jiang et al.

2005). Mean annual precipitation is 340 mm, 70 % of which concentrated between June and August. The dominant winds have northwest directions from March to May and southwest directions from June to September. The northwest direction wind from March to May is the prevailing wind direction. The wind speed from 2003 to 2008 is 3.57 m s^{-1} and 1.58 m s^{-1} for the periods of March to May and June to September, respectively. In this region, overgrazing has led to a desertification of over 90 % of the land, and consequently, active sand dunes, advancing at a rate of 5–7 m·$year^{-1}$, are widely distributed (Liu et al. 2006; Ma and Liu 2008a). The active sand dune vegetation coverage is less than 5 % and the plants are found at all parts of the active sand dune, i. e., windward slope, leeward slope and crest of the active sand dunes. Spatial distribution of the plants is random (Jiang et al. 2013). The soils are classified as cambic arenosols (Cao et al. 2011), sandy in texture, light yellow in color, and low in organic matter content (1 to 2.5 %) (Zhang et al. 2009). Field capacity was between 9.5 % and 13.5 %% (Liu et al. 2005). Soil moisture contents were generally low in this region. It was 3.17 %, 3.41 %, 3.73 %, 3.23 % in depths of 0–20 cm, 20–40 cm, 40–60 cm 60–100 cm during the rainy season, respectively. Soil moisture content was 3.33 %, 2.73 %, 2.69 %, 2.84 % in depths of 0–20 cm, 20–40 cm, 40–60 cm 60–100 cm during the dry season, respectively (Cao 1984). Due to these characteristics, the soil is particularly susceptible to wind erosion. The vegetation of active sand dunes comprises only pioneering plant species such as *Agriophyllum squarrosum* Moq. and *A. wudanica*, with a coverage less than 5 %. Sand dune movement, wind erosion, and sand burial are frequent in this ecosystem (Yan et al. 2005; Ma and Liu 2008a).

Study species

Artemisia wudanica, a perennial psammophyte (i.e., plants that thrive on shifting sands (Jin and Ye 1989; Ma and Liu 2008b)), is typically found in active sand dunes, where erosion and sand burial are severe and frequent. There are many perennial buds on the rhizomes that sprout to form aboveground shoots. This species can reproduce through either seedling recruitment (sexual reproduction) or vegetative propagation. Population recruitment takes place generally by vegetative reproduction. The clonal growth of this species plays an important role in trapping and holding sand in place, contributing to protection of the active sand dune from wind erosion (Jin and Ye 1989; Liu et al. 2008). Seedlings of *A. wudanica* often experience various depths of erosion or burial in the field (Jin and Ye 1989; Liu et al. 2008).

Field experiment

Wind erosion and sand burial were monitored using iron sticks (2 mm diameter, 150 cm height; Yan et al. 2007). In active sand dunes, 120 isolated one-year old (the seedling age was determined by the emergence time with our continuous monitoring) individual of *A. wudanica* seedlings were randomly selected with iron sticks inserted close by. The selected plants were at least 15 m apart from each other, to ensure that shoots from one plant were not connected to any other selected plant. Seedling monitoring took place from 1st March to 30th May 2006 (wind season). The aboveground height of the sticks was measured and recorded at 10-day intervals. The height of the iron sticks was adjusted occasionally to prevent their complete burial or exposure. At the end of the experiment, we measured: 1) the erosion or burial depth of the 120 iron sticks; 2) the survival rate of the 120 selected seedlings; 3) the frequency of alive seedlings under five different scenarios: erosion only, burial only, erosion and subsequent burial, burial and subsequent erosion, and alternating sand burial and erosion.

Common garden experiment

Freshly matured seeds of *A. wudanica* were collected from multiple individuals in the fall of 2005. The seeds were allowed to dry naturally, and then were stored dry in paper bags until March 2006 (Ma and Liu 2008b). At this date, sand was poured into 30 plastic pots (50 cm in diameter, 15 cm in height) and moistened, then the seeds (n=50 per pot) were put and covered with sand at a burial depth of 0.5 cm. The drainage outlet at the bottom of the pots was covered with strips of nylon mesh to prevent the loss of sand while allowing drainage of excess water. During the experiment, the pots were watered regularly with tap water. After germination, one-week-old seedlings, similar in size and shape, were selected and transplanted into 200 pots made with PVC pipe (20 cm in diameter and 150 cm in deep) in April 2006 (one seedling per pot). The pots were filled with sand obtained from the same location where seeds were collected. The seedlings were then placed in a common garden with a randomized block design. All pots were exposed to the outdoor with adding water every 5 days to keep them moist. After one year, in April 2007, 136 one-year-old plants of similar size (~40 cm in height) were selected. Of the 136 seedlings, ten were randomly selected and harvested at the onset of study to determine the initial dry mass of different plant parts for growth analysis. Starting values of biomass were determined after drying them at 80 °C for 48 h. The remaining 126 plants were randomly assigned to one of the following 21 treatment combinations: (1) a control treatment (no burial and erosion); (2) two burial depths (B hereafter) treatments, created by adding a layer of sand of either 10 cm or 20 cm; (3) six erosion depths (E hereafter) treatments, generated by removing the top 10 cm, 20 cm, 30 cm, 40 cm, 50 cm or 60 cm of sand; and (4) twelve erosion and subsequent burial (EB hereafter) treatments, resulting from the combination of the six erosion and two burial treatments described above (Fig. 1a–d). The treatment of burial and subsequent erosion was not included in the design because their occurrence under field conditions is very low (<5 % of plants are affected by it; e.g., based on the stick observations from the "Field experiment" section, see "Results" below). Six replicates per treatment were used in the experiment. The average depth of wind erosion in the active dunes examined in this study ranged approximately from 1.5 cm to 86.5 cm, and seedlings *A. wudanica* would die when subjected to wind erosion exceeded 60 cm (based on the stick observations from the "Field experiment" section, see "Results" below). So, we designed the erosion regime from 10 cm to 60 cm. The average length of the branches located at notes of stem was 22 ±4.62 cm. Based on previous research (Liu et al. 2008), *A. wudanica* branch length significantly increased when partially buried and decreased when completely buried. We designed two burial regimes as 10 cm and 20 cm. The 10 and 20 cm depth burial treatments led to roughly half and complete burial. These burial and erosion depth values have a similar order of magnitude as the sand deposit heights and erosion depths observed in the field (e.g., based on the stick observations from the "Field experiment" section, see "Results" below). The study was carried out within a fenced garden without grazing.

For B treatments, PVC pipes (20 cm in diameter) were placed on top of each plant, and then filled with sand to the desired depth (Fig. 1a). The E treatments (Fig. 1c) were imposed by a fan running over the container; this experimental device did not impose any mechanical damage to the seedlings. The blowing part lasted short period of time (e.g., a couple of hours), so the negative effect on the plants (e.g., water stress) was kept to a minimum. For EB treatments, the seedlings were buried in a horizontal position after the application of the erosion treatments (Fig. 1d). For these burials, PVC frames (200 cm in length and 100 cm in width) were placed on the fallen shoots of each individual seedling, and were then filled with sand to the desired depth (Fig. 1d). This experiment was conducted from 1 April to 23 May 2007, a period corresponding with the time of year that plants are frequently buried or eroded by sand in Horqin Sandy Land (Liu et al. 2008). Thus, the duration of the experiment was enough to allow *A. wudanica* seedlings to replace the total shoot leaf area lost due to burial treatments.

To evaluate the responses of *A. wudanica* seedlings to the different experimental treatments, their survival was recorded every week throughout the experiment. At the end of the experiment, and for all the surviving seedlings, the number of new ramets was counted. At this date, PVC pipes and frames were gently removed and the entire seedling was excavated. Seedlings were carefully cleaned off the remaining soil particles and separated into shoots, roots, and adventitious roots for biomass measurements. Plant parts were dried at 80 °C for 48 h and weighed, and then their root to shoot ratio was calculated (Liu et al. 2008).

The relative growth rates of shoot biomass (RGR, g g^{-1} day^{-1}) during the experimental period were calculated using data obtained during the initial and the end harvests (Padilla et al. 2007). Initial mass was determined from the shoot biomass of ten individuals at the start of the experiment. The following equation was used to calculate the RGR (Padilla et al. 2007):

$$RGR = \frac{lnW_1 - lnW_2}{T_2 - T_1}$$

where W_1 and W_2 are the dry mass of shoots at the initial and the end of the experiment, respectively, and T is the time in days.

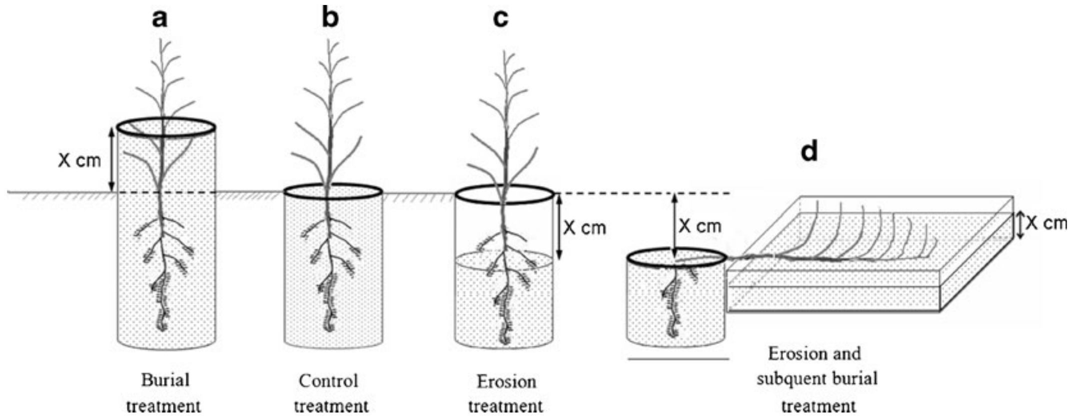

Fig. 1 Schematic representation of the experimental design used to examine the responses of plants to burial only, erosion only as well as erosion and subsequent burial treatments

Statistical analysis

Data were analyzed and summarized using SPSS ver. 16.0 for windows (SPSS Inc., Chicago, IL, USA). Values were presented as means ± SE. The effects of the different treatments (B, E and EB) on total biomass, RGR, adventitious root biomass and number of ramets were evaluated using one-way analysis of variance (ANOVA). If ANOVA showed significant differences, LSD's multiple comparison test was used to compare the treatment values with the control. The assumption of normal distribution of the data was checked before their analysis.

Results

In the field, the average erosion depth was 34.7 ±2.27 cm, ranging from 1.5 cm to 86.5 cm. The average burial depth was 26.1±1.84 cm, ranging from 0.5 cm to 56.0 cm. No seedlings of *A. wudanica* survived when subjected to wind erosion exceeding 60 cm and sand burial exceeding 50 cm. The survival rate was 34.2 % (41 out of 120 individuals survived). The frequency of survivors under erosion only, burial only, erosion and subsequent burial, burial and subsequent erosion, and alternating burial and erosion was 20.5 %, 27.9 %, 41.5 %, 4.7 % and 5.4 %, respectively.

In the common garden experiment, *A. wudanica* showed a high survival rate. Only one seedling in the treatment of 60 cm erosion and 20 cm burial died. There were no significant differences in survival rates among treatments.

Compared with the control treatment, total biomass was lower for E treatments, but higher for B and EB treatments, except for the treatments of 50 and 60 cm erosion and subsequent 20 cm burial (Table 1; Fig. 2a, b). Compared with B treatments, total biomass was higher for the treatments of 10, 20, 30, 40, 50 cm erosion and subsequent 10 cm burial, and for the treatment of 10 cm erosion and subsequent 20 cm burial. Total biomass declined with increasing erosion depths under E and EB treatments (Table 1; Fig. 2a). In the EB, the total biomass under the 10 cm burial was higher than that of those under the 20 cm burial (Fig. 2a).

Compared with the control treatment, RGR was lower for E treatments, but higher for B and EB treatments, except for the treatment of 60 cm erosion and subsequent 20 cm burial (Table 1; Fig. 2b). Compared with B treatments, RGR was higher for the treatments of 10, 20, 30, 40 cm erosion and subsequent 10 cm burial and for the treatments of 10, 20, 30 cm erosion and subsequent 20 cm burial. RGR declined with increasing erosion depths under E and EB treatments (Table 1; Fig. 2b). In EB treatments, the total biomass under the 10 cm burial was higher than that of those under the 20 cm burial (Fig. 2b).

No plants produced ramets and adventitious roots under the control and E treatments (Table 1; Fig. 2c, d). Compared with B treatments, the number of ramets was higher for EB treatments, except for the treatments of 50 and 60 cm erosion and subsequent 20 cm burial (Fig. 2c). Compared with the 10 cm B treatment, the biomass of adventitious roots was higher for the treatments of 10, 20, 30, 40, 50 cm erosion and subsequent 10 cm burial, and for the treatments of 10, 20 cm erosion and subsequent

Table 1 Mean values and results of one-way analysis of total biomass, relative growth rate (*RGR*), biomass of adventitious roots, number of ramets and root to shoot ratio of *A. wudanica* under control, burial only (*B*), erosion only (*E*) and erosion and subsequent burial (*EB*) treatments

Trait	Control	B	E	EB	$F_{(3,124)}$
Total biomass(g)	102.9±7.29a	122.9±7.42b	72.7±5.16c	118.9±6.99b	7.71^{***}
RGR (g g^{-1} d^{-1})	0.085±0.002c	0.098±0.002bd	0.061±0.004a	0.104±0.002d	37.73^{***}
Adventitious roots biomass (g)	0a	9.8±1.36b	0a	11.9±1.05b	26.4^{***}
Ramets number	0a	6.83±0.52b	0a	11.43±0.57c	81.9^{***}
Root to shoot ratio	2.12±0.13a	1.64±0.07a	3.54±0.23b	0.86±0.05c	91.83^{***}

Different letters in each row represent significant differences at $P<0.05$. Values are expressed by mean ± SE ($n=6$). Significance levels: *** $P<0.001$, ** $P<0.01$, * $P<0.05$

20 cm burial (Fig. 2d). Compared with the 20 cm burial only treatment, the biomass of adventitious roots was higher for the treatments of 10, 20, 30, 40, 50 cm erosion and subsequent 10 cm burial, and for the 10 cm erosion and subsequent 20 cm burial.

The number of emergent ramets and the biomass of adventitious roots declined with increasing erosion depths in the EB treatments (Table 1; Fig. 2c, d). In these treatments, the number of emergent ramets and the biomass of adventitious roots under the 10 cm burial

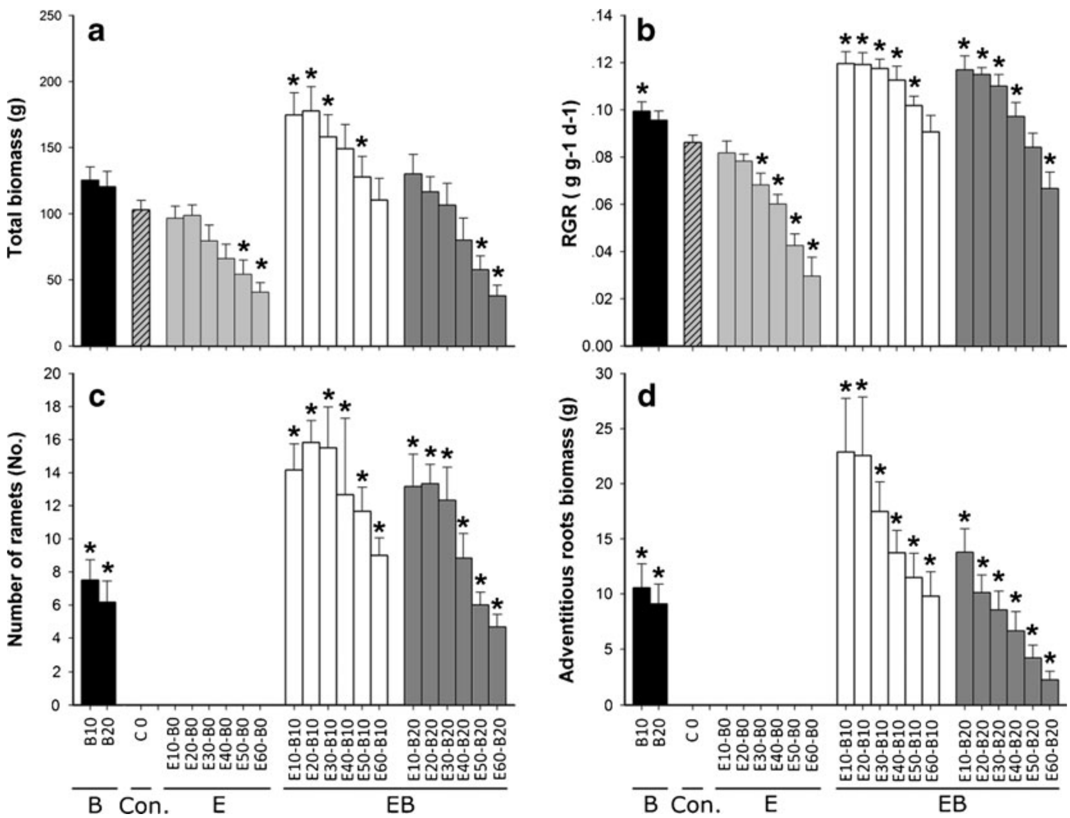

Fig. 2 Total biomass (**a**), relative growth rate (*RGR*) (**b**), adventitious roots biomass (**c**) and ramets number (**d**) of *Artemisia wudanica* in the control (*Con.*), burial (*B*), erosion (*E*), and erosion and subsequent burial (*EB*) treatments. The error bars are standard errors ($n=6$). "*B*" and "*E*" along the x-axis represent burial and erosion, respectively. Treatments with an asterisk are significantly different from the control at $P<0.05$ (LSD test)

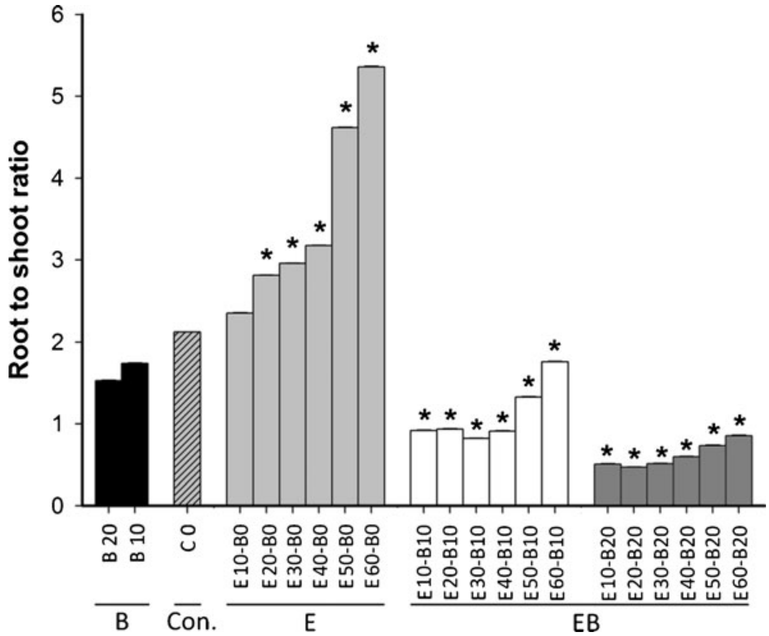

Fig. 3 Root to shoot ratio of *Artemisia wudanica* in the control (*Con.*), burial (*B*), erosion (*E*), and erosion and subsequent burial (*EB*) treatments. The error bars are standard errors (n=6). "*B*" and "*E*" along the x-axis represent burial and erosion, respectively. Treatments with an asterisk are significantly different from the control at P<0.05 (LSD test)

were higher than that of those under the 20 cm burial (Fig. 2c, d).

Compared with the control treatment, the root to shoot ratio was higher for E treatments, lower for EB, and similar to B treatments (Table 1; Fig. 3).

Discussion

The response of sand dune species to disturbances is typically classified into three categories (Maun 1998): positive, neutral and negative. In the present study, *A. wudanica* showed a neutral response to burial, a positive response to erosion and subsequent burial, and a negative response to erosion (Fig. 2a, b). Furthermore, our results showed that the process of erosion and subsequent burial increased the depth threshold of plant erosion survival, and stimulated the production of adventitious roots and emergent ramets. Therefore, our hypothesis that subsequent sand burial following erosion compensates for the negative effects of erosion in *A. wudanica* was supported. The compensation effect has been seen in other type of systems in stressful environments. For example, Duval and Whitford (2008) showed that stem girdling by the girdler beetle on *Prosopis glandulosa* Torr. individuals increase the production of stems in this species, and therefore enhance its ability to capture sand, leading to further enhancement of stem growth (Appendix Fig. 4).

Total biomass and RGR declined with increasing erosion depths in the E and EB treatments (Fig. 2a, b). These results indicate that erosion may suppress seedling growth due to root exposure to the air, reducing the capacity of *A. wudanica* seedlings to uptake water and nutrients (Yu et al. 2008; Li et al. 2010a, b).

An interesting phenomenon observed in our experiment is that the stimulation response to burial treatments alone was less than what occurred when burial happened after erosion. For example, compared with B treatments, both biomass and RGR were higher in the EB treatments (Fig. 2), which indicates the importance of the horizontal placement of stems induced by erosion. We propose three major reasons for the enhanced vigour in *A. wudanica* seedlings observed in the EB treatments: (1) horizontally-positioned plants would accumulate more sand around stems than vertically-positioned plants; (2) the production of adventitious roots was higher in horizontally-positioned plants (EB) than in vertically-positioned plants (B) (Fig. 2d); and (3) the production of ramets in horizontally-positioned plants was higher than such production in vertically-positioned plants.

The formation of adventitious roots for *A. wudanica* seedlings took place only when their shoots were partially or entirely buried (Fig. 2d). In this study, a significant increase in total biomass and RGR of *A. wudanica* seedlings were observed in EB treatments as compared with the control treatment, probably because of an increase in the growth of adventitious roots. These roots provide more nutrients and moderate growth conditions, and thus increase the growth of ramets (Perumal and Maun 2006). Similarly, studies conducted with other dune species have shown that the growth stimulation of partially buried seedlings were caused primarily by an increase in the production of adventitious roots (Dech and Maun 2006; Liu et al. 2008; Sun et al. 2010). The reasons for producing adventitious roots when buried are not well understood. Sand burial (including the relative large particle size of the sandy soil) substantially alters soil conditions, reducing temperature in the root zone, increasing soil compaction and lowering the concentration of oxygen surrounding the roots, which can result in root asphyxiation. Plants typically respond to anaerobic conditions by forming adventitious roots (Maun 1998; Dech and Maun 2006). In our study, this response may be related to the anaerobic conditions caused by sand burial since the formation of adventitious roots helps to improve the aeration status (Liu et al. 2008).

As found with the formation of adventitious roots, new ramets were produced only when the shoots of *A. wudanica* were partly or entirely buried. It is well known that new ramets are formed from vegetative buds located at nodes of buried stems, and that they exhibit intensive elongation above the sand surface under favorable moisture conditions (Deng et al. 2008; Liu et al. 2008). These young ramets become increasingly independent as they grow, and finally add new individuals to the population. Our results indicate that severe burial hampers the production of new ramets (Fig. 2c). One probable explanation would be that the energy stored by vegetative buds was not sufficient to make them sprout under severe burial (Dong et al. 2011).

The allocation and utilization of resources is a fundamental and vital activity of plants (Wang et al. 2006; Zhao et al. 2007). Seedlings of *A. wudanica* showed different biomass allocation patterns under control, B, E and EB treatments. In our experiment, proportionally more biomass was allocated to roots in E treatments. Such a response may help *A. wudanica* to maintain its capacity to uptake water and nutrients after erosion. More investment in roots after erosion processes has been also reported for the dune species *Artemisia ordosica* (Li et al. 2010a, b). In the EB treatments, plants shifted resources from roots to aboveground components that support the vertical elongation of stems, facilitating seedling emergence from an underground location and compensating the loss of buried photosynthetic tissues. In terms of burial response, specialized dune species typically increase the biomass investment in aboveground structure after burial (Harris and Davy 1988; Brown 1997; Dech and Maun 2006). However, some species clearly increase allocation to belowground structure in response to sand burial (Sykes and Wilson 1990). In the present study, seedlings of *A. wudanica* did not change allocation patterns in response to B treatments, compared with control treatment. Such contrasting results may be due to variations in the growth rates of the different sand dune species (Liu et al. 2008).

Because the experiment reported here was conducted under controlled conditions, the direct extrapolation of our results to the field conditions is restrictive. For instance, the complex environment and frequent disturbances that occur in the field may affect the threshold beyond which the plants are unable to survive burial and erosion episodes. Therefore, further studies should investigate the behavior of different species in the field. Disturbances such as the abrasion of plant tissues by sand grains and mechanical disturbances promoted by, to name a few, can also affect the physiology and growth of dune plants (Baker 2007; Baker et al. 2009). However, no study has tested these factors on growth and physiological properties of dune plants. More work is also needed to understand the physiological mechanisms that underlie the interactive effect of erosion and burial. Nevertheless, the present study provides strong evidence that subsequent sand burial dramatically reduces the negative effects of wind erosion on *A. wudanica*, and greatly contributes to its ability to tolerate erosion on inland dunes. The results also indicate that erosion and subsequent burial processes allow psammophytes to withstand erosion of active sand dunes by stimulating their growth.

Conclusions

Artemisia wudanica individuals under erosion and subsequent burial treatments have the largest total biomass, RGR, adventitious root biomass and number of emergent ramets. Therefore *A. wudanica* is stimulated by the process of erosion and subsequent burial, a response that is associated with the production of adventitious roots and emergent ramets. In addition, *A. wudanica* is able to modify biomass patterns allocation aboveground and belowground in response to erosion and erosion and subsequent burial. These responses indicated that sand burial following wind erosion could compensate for the negative effects of erosion in psammophytes on active sand dunes. We suggest the following processes and mechanisms are responsible for such compensation. First, erosion cause plants fall to the ground, leading to an increase in surface roughness, and resulting more burial on the fallen shoots. Second, buried fallen shoots can form adventitious roots from their nodes under favorable moisture conditions, stimulating the production of new ramets. Finally, the increased vegetative propagation would be advantageous to quickly replenish resources necessary for further growth and development. The mechanism described here can be very important to maintain the populations of psammophyte species, and thus the overall functioning of sand dune ecosystems.

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Appendix

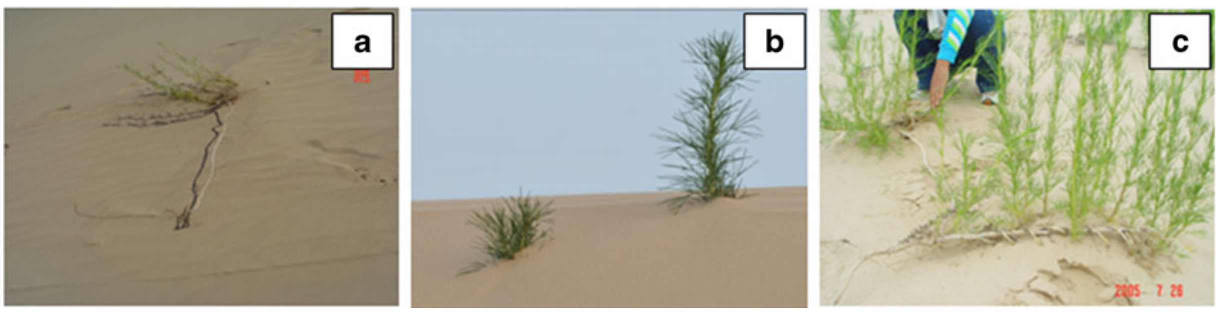

Fig. 4 *Artemisia wudanica* eroded by wind (**a**), buried by sand (**b**), eroded first and then buried (**c**)

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