Trees (2010) 24:515–521
DOI 10.1007/s00468-010-0422-0

ORIGINAL PAPER

Seedlings of the semi-shrub *Artemisia ordosica* are resistant to moderate wind denudation and sand burial in Mu Us sandland, China

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Received: 20 May 2009 / Revised: 20 January 2010 / Accepted: 30 January 2010 / Published online: 17 February 2010

Abstract Sand movement is a common stress for plants in dune ecosystems. Seedlings in such an environment often experience various degrees of denudation or burial. A field experiment was conducted with *Artemisia ordosica*, a dominant semi-shrub species in Mu Us sandland, China, to test seedling survival and growth under different degrees of denudation and burial. Seedlings from two cohorts with height of 5.0 ± 0.02 cm (*S1*) and 9.3 ± 0.09 cm (*S2*) were selected and randomly subjected to three denudation treatments (2.5, 5, and 10 cm), five burial treatments (2.5, 5, 7.5, 10, and 15 cm), or a control. *S2* seedlings had a higher survivorship than *S1* seedlings, especially under severe denudation (10 cm) and complete burial (5 cm in *S1*; 10 cm in *S2*). Seedling survivorship was unaffected by moderate burial (<5 cm in *S1*; <10 cm in *S2*) or denudation (<10 cm), but it was significantly reduced under complete burial or severe denudation. Seedling growth in leaf area, height, and biomass only declined in severe denudation or complete burial. Seedling burial led to higher biomass investment in shoots, while the reverse was the case in denudation. The results indicate *A. ordosica* is highly tolerant to moderate burial and denudation, showing adaptive responses that likely increase survival. Differences in responses between seedling cohorts suggest that large seedling size is beneficial for successful establishment in sandy environments and measures to prevent severe denudation and burial of recently germinated seedlings are necessary in attempts to restore steppe vegetations.

Keywords *Artemisia ordosica* · Dunes · Sand burial · Sand denudation · Seedling size · Shrub

Communicated by B. Engelbrecht.

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Introduction

Sand movement by wind is a common event in coastal and inland dune ecosystems (Moreno-Casasola 1986; Maun 1994; Danin 1996; Brown 1997; Yu et al. 2002, 2004, 2008). As a result, plants growing on the windward slopes of dunes may experience various degrees of denudation and those on the leeward slopes often suffer from partial or complete burial, while on the crest both denudation and burial may occur (Maun 1998; Yu et al. 2004, 2008). Small seedlings are most vulnerable to burial and denudation, as a few centimetres of removed or added sand may result in full exposure of the root system or complete coverage of the aboveground plant parts. Thus, the ability of seedlings to withstand denudation and burial is crucial for successful establishment and population maintenance of dune species.

The most important stresses caused by wind denudation include water loss and elevated temperature in the root system after exposure (Fryrear et al. 1973; Maun 1998; Yu et al. 2008). Long-term deep burial may strongly suppress seedling growth as it creates a physical barrier for vertical growth, reduces the photosynthetic area, and limits oxygen availability to roots (Harris and Davy 1988; Maun 1994). When burial is short-term and relatively shallow, it may promote plant growth in terms of vertical elongation (Disraeli 1984; Shi et al. 2004; Dech and Maun 2006; Zhao et al. 2007), number of leaves (Shi et al. 2004), and biomass (Brown 1997; Shi et al. 2004; Dech and Maun 2006; Zhao et al. 2007; Liu et al. 2008).

Tolerance of seedlings to various degrees of burial has been widely studied in herbaceous (Maun and Lapierre 1984; Zhang 1996) and woody species (Brown 1997; Shi et al. 2004; Dech and Maun 2006), but denudation responses are less clear (Fryrear et al. 1973; Yu et al. 2008). Moreover, no study has tested the effects of both denudation and burial on the same plant species. Such comparative studies are relevant as adaptation to these opposing stresses may involve completely different strategies.

Here we report effects of both burial and denudation on seedlings of the desert woody species *Artemisia ordosica*, a semi-shrub that is thriving in inland dune harsh conditions of strong sand denudation and burial. *A. ordosica* is a dominant species in the Mu Us sandland, a semi-arid area with highly mobile sand located in the Ordos Plateau, Inner Mongolia, China (Zhang 1994; Kobayashi et al. 1995). Vegetation restoration is currently a major issue in Mu Us sandland with *A. ordosica* being one of the main plants used (Zhang 1994; Kobayashi et al. 1995; Huang and Gutterman 2000). *A. ordosica* is distributed in fixed, semi-fixed as well as semi-mobile sand dunes (Zhang 1994; Kobayashi et al. 1995; Huang and Gutterman 2000). The wind-dispersed seeds of *A. ordosica* reach both windward and leeward sites of dunes and germinate continuously during the main growing season (from May to September). Thus, at every moment there are seedlings belonging to various cohorts that differ in size (Huang and Gutterman 2000; Zhu et al. 2004; Zheng et al. 2006). These cohorts likely vary in survival rates and in response to denudation and burial. Here we investigate the tolerance of different-sized seedlings of *A. ordosica* to denudation and burial in terms of survivorship, growth, and biomass allocation in a field experiment.

Materials and methods

Study site

This study was conducted at Ordos Sandland Ecological Station (OSES, 39°29′37.6″ N, 110°11′29.4″ E) of the Institute of Botany of the Chinese Academy of Sciences, located in the southeastern Ordos Plateau in Inner Mongolia, China. This is a semi-arid area, with the mean annual temperature of 7.5–9.0°C, maximum of 20–24°C in July and minimum of −12 to −8°C in January. The mean annual precipitation is 260–450 mm, which is concentrated in summer, following a prolonged spring drought (Zhang 1994). Formerly, highly productive grassland was present in the region (Zhang 1994). However, due to serious desertification caused by overgrazing, mining, and inappropriate agricultural management practices, it has been degraded to a steppe or desert vegetation dominated by shrubs and herbs, in which sand movements are frequent (Zhang 1994; Ohte et al. 2003; Yu et al. 2004, 2008).

The mean annual wind speed in 2007 was 2.06 ± 0.13 m s^{-1} (mean ± SE), with strong wind (≥17 m s^{-1}) for 23 days and mainly occurring in spring and early summer (recorded at the Weather Station at OSES). An ongoing study on natural sand movement at OSES showed that sand removal caused denudation of 2.63 ± 0.36 cm within 15 days with the maximum of 4.98 cm, while sand addition led to 3.3 ± 0.63 cm burials within 15 days with the maximum of 10.47 cm (16 intervals of 15 days; 57 measurement sticks; OSES, unpublished data).

Study species

Artemisia ordosica Krasch (Asteraceae) is a shrub of approximately 0.5–1.0 m tall consisting of short-lived shoots which bear plumose, linearly lobate leaves. It is endemic to the Ordos-Alashan region, but overwhelmingly dominant in the Mu Us sand district on semi-fixed or fixed dunes, and sometimes occurs on active sand dunes. Shrubland dominated by *A. ordosica* covers 31% of the whole Mu Us district (Kobayashi et al. 1995). *A. ordosica* plays an important role in combating desertification and rehabilitating desertified dunes. Natural regeneration is generally realized by seeds, although plants may occasionally split into clonal fragments. Small seedlings often experience various depths of denudation or burial (Kobayashi et al. 1995; Yu et al. 2002; Zhang et al. 2002; Li et al. 2005).

Experimental design

The experiment was carried out in an area of about 1,000 m^2 close to the OSES station, in flat terrain with vegetation dominated by *A. ordosica* (70% of cover), and presence of *Hedysarum laeve, Bassia dasyphylla* and *Incarvillea sinensis* (summed cover < 5%). On 16 May, 2007, 423 naturally regenerated seedlings from two cohorts were selected at this lowland area, with 270 small seedlings of 5.0 ± 0.02 cm high (*S1*), and 153 large seedlings of

9.3 ± 0.09 cm high (*S2*). All seedlings were at least 1 m away from adult *A. ordosica* shrubs and 30 cm away from each other. An additional number of 20 seedlings per cohort (*S1* and *S2*) were excavated and harvested at the onset of the study to obtain starting values of biomass. The roots of small seedlings and large seedlings penetrated 19.5 ± 0.75 cm and 22.5 ± 0.72 cm into the soil, respectively.

Experimental seedlings were randomly assigned to 1 of the following 9 treatments: denudation by removal of 2.5, 5 or 10 cm, sand burial by 2.5, 5, 7.5, 10 or 15 cm, or control (no burial or denudation). To sustain new soil levels in the treatments and limit influx and efflux of sand, we placed white plastic drainage tubes (13.3 cm in diameter) around all seedlings (including the control treatment). Seedlings were kept vertical while being buried or kept vertical by sticks after denudation. After applying the treatment, we marked the new soil level on the tubes for later reference. Changes in the actual soil level were monitored on a weekly basis, and sand was added or removed whenever actual soil level was lower or higher than the treatment level. Each of the nine treatments comprised 30 replicates in *S1* and 17 replicates in *S2*. The study was carried out within a fenced area without grazing. The experiment terminated after 126 days, on 19 September 2007. It was conducted entirely within the growing season.

Measurements

At the end of the experiment, seedling survival was recorded. For all surviving seedlings height relative to the original soil level was measured, as well as diameter at that level. Then, all plants were carefully excavated, and each plant was separated into leaf, stem, and root. Leaf images were obtained by a scanner and leaf area was then measured by analyzing the leaf images (ImageJ, National Institute of Health, USA). Leaf, stem, and root biomass of these seedlings, as well as those initially harvested were determined after drying at 80°C for 48 h. Relative growth rates of height and total biomass during the experimental period were calculated using data obtained during initial and end harvests (Padilla et al. 2007). To calculate relative height growth, we used the initial height measurements of all individuals at the onset of the experiment. To calculate relative biomass growth rate, we used average values obtained from destructive harvests of 20 individuals per size class (*S1* and *S2*) at the start of the experiment.

Statistical analysis

Binary logistic regression was used to test the effects of treatments and cohort on seedling survival. When the test showed significant differences, multiple comparisons among treatments within each cohort were carried out through simple binary logistic regression, with each P value corrected according to Bonferroni criteria, by multiplying the original P value with the numbers of pairwise comparisons made between treatments.

The effects of treatment and cohort on final seedling height, stem diameter, leaf area, biomass, relative growth rates, and root to shoot ratio were analyzed using two-way ANOVA. If ANOVA showed significant differences, multiple comparisons among treatments within each cohort were conducted using Scheffe tests. Heteroscedastic variables were log-transformed to meet ANOVA assumptions. The burial treatments deeper than 5 cm in *S1* and 10 cm in *S2* were not included in these analyses, as no seedlings survived these treatments. All analyses were conducted with SPSS ver.15.0 (SPSS Inc. Chicago, IL, USA) and differences were considered significant at $P < 0.05$. Data are presented as means ± 1 SE.

Results

Survivorship

Survivorship of *A. ordosica* was significantly affected by both treatment (Wald statistic = 53.46, $df = 1$, $P < 0.001$) and cohort (Wald statistic = 29.04, $df = 1$, $P < 0.001$). *S2* generally showed higher survival rate than *S1* (Fig. 1). In *S1*, seedling survival was not significantly affected by partial burial or by denuding the plants up to 5 cm, and survivorship in these treatments was 50% or more. However, the survival rate was significantly reduced to 27% when the denudation depth was increased to 10 cm, and it declined sharply to 20% in complete burial. No seedlings survived complete burial, i.e. burial depth >5 cm for *S1* and >10 cm for *S2* (Fig. 1). Almost complete burial (5 cm for *S1* and 10 cm for *S2*) significantly decreased survival, but moderate burial did not lead to increased mortality (Fig. 1).

Plant size and biomass allocation

Burial/denudation treatment and cohort significantly influenced final height, stem diameter, leaf area, and biomass (Table 1). Final size generally was larger for *S2* compared to *S1*. In small seedlings (*S1*), final height, stem diameter, leaf area, and biomass were not significantly affected by any of the denudation or burial treatments (all multiple comparisons $P > 0.05$, Fig. 2a, c, e, g). Similarly, we found no effect of treatments on final height or leaf area in large seedlings (*S2*, Fig. 2b, f). Only final stem diameter and biomass in *S2* were significantly reduced in 10 cm denudation and/or 10 cm burial treatments (Fig. 2d, h).

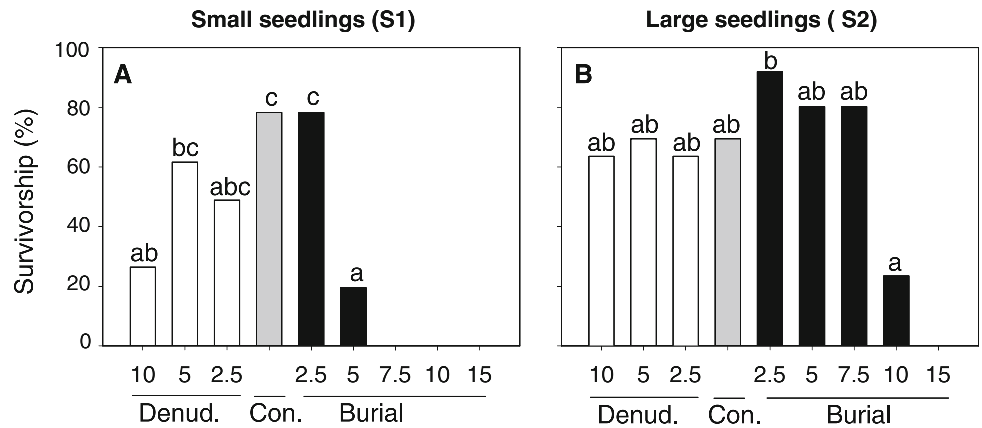


Fig. 1 Survival rates of small (*S1*, **a**) and large seedlings (*S2*, **b**) of *Artemisia ordosica* under control (Con., *grey bar*) or various denudation (Denud., *white bars*) or burial treatments (*black bars*). Numbers along *x*-axis are centimetres burial or denudation

Table 1 ANOVA results on effects of cohort and burial/denudation treatments on height, stem diameter, total biomass, root to shoot ratio and relative growth rates (RGRs of height and biomass) of *Artemisia ordosica* seedlings in Mu Us sandland

Trait	Size		Treatment		Size × treatment	
	$F_{1,176}$	*P*	$F_{7,176}$	*P*	$F_{5,176}$	*P*
Height[a]	14.23	<0.001	4.26	<0.001	1.75	0.126
Stem diameter[a]	47.43	<0.001	6.80	<0.001	1.59	0.165
Leaf area[a]	14.81	<0.001	2.54	0.017	0.74	0.596
Biomass[a]	38.18	<0.001	3.72	0.001	0.88	0.497
Leaf area ratio	3.71	0.056	1.38	0.216	0.81	0.544
Root to shoot ratio	0.39	0.536	12.23	<0.001	4.27	0.001
RGR of height	65.57	<0.001	4.08	<0.001	2.89	0.016
RGR of biomass	5.00	0.027	3.73	0.001	0.88	0.497

[a] log-transformed data

Leaf area ratio remained similar to control in all treatments and both cohorts (Table 1). Root to shoot ratio was significantly affected by the treatment of denudation and burial, but not by size (Table 1). In *S1*, root to shoot ratio was higher for denudation treatments and lower for burial treatments (Fig. 2i). In *S2*, it was also increased in 10 cm denudation treatments (Fig. 2j).

Relative growth rates

Relative growth rates (RGRs) of height and biomass were significantly affected by both cohort and depths of denudation and burial (Table 1), with higher values for *S1*. In *S1*, RGR of height or biomass was not significantly affected by any of the burial and denudation treatments (Fig. 3a, c). In *S2*, there was no effect of denudation or burial on RGR of height, but RGR of biomass was significantly reduced in the 10 cm burial treatment with respect to the control (Fig. 3b, d).

Discussion

Effects on seedling survival

In our experiment, larger seedlings showed generally higher survival rates than smaller ones and the deep burial and denudation were more detrimental to smaller seedlings. This may help to explain the considerably lower abundance of larger seedlings (>10 cm height) compared to smaller ones, which was also observed in a demographic census in the study area (S.-L. Li unpublished data). This result indicates that gaining sufficient size before substantial sand denudation or accumulation happens is beneficial for seedlings to increase chances for survival and successful establishment in moving dune environments.

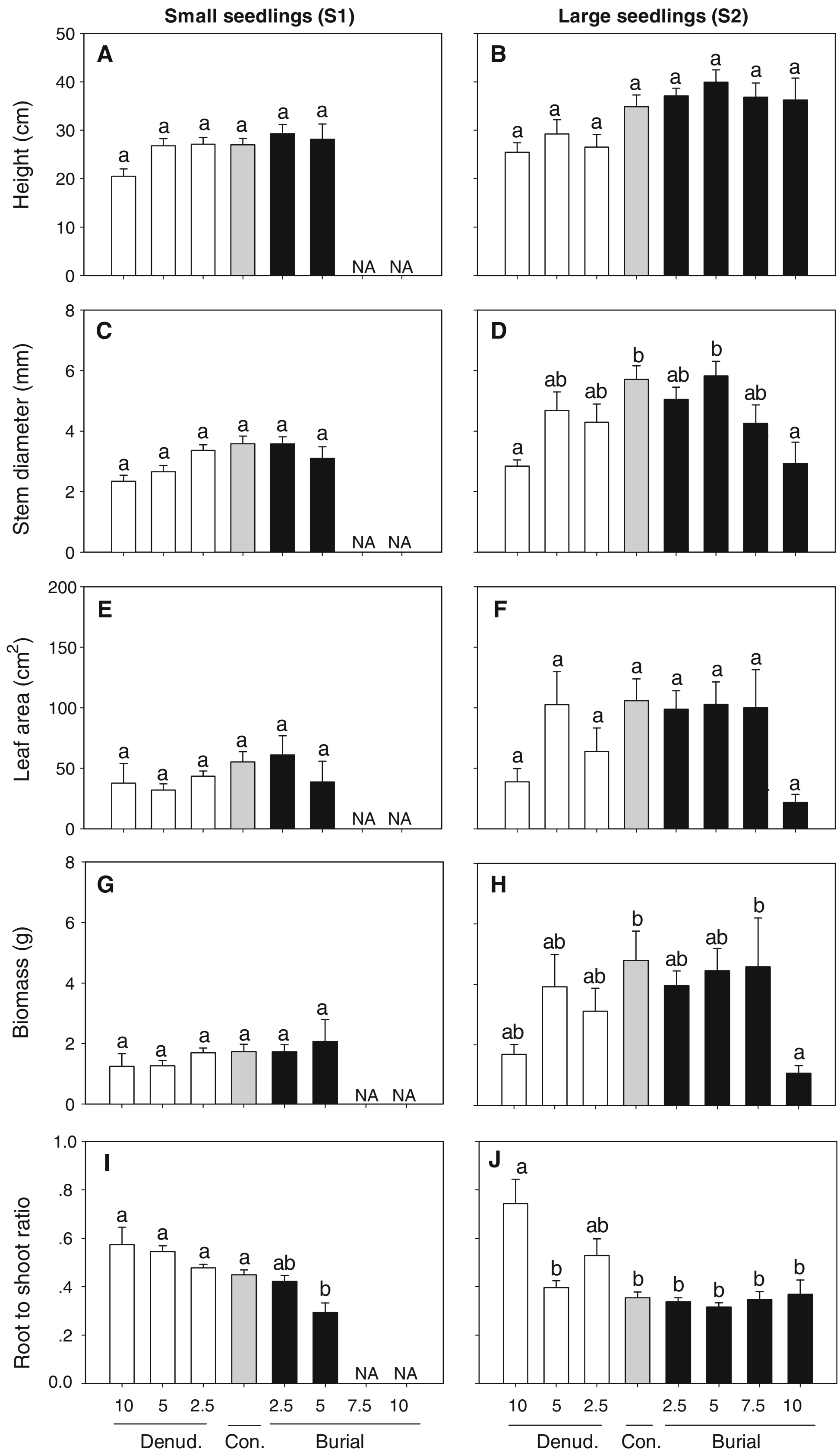
We found high mortality after complete burial of *A. ordosica* seedlings. Similar results were reported for various coastal and riverine dune species (Zhang and Maun 1990; Maun 1996). Our results contrast those for some Inner Mongolia species, e.g. *Hedysarum laeve* and *Ulmus pumila* of which seedlings succeeded to emerge from complete burial, although with strongly reduced vigour and incapable of surviving renewed burial (Zhang et al. 2002; Shi et al. 2004).

Moderate denudation did not affect seedling survivorship of *A. ordosica* in our experiment. This species has deeper roots and this trait may help the seedlings to survive water stress as a result of denudation, which is usually a main cause of death of many other dune species (Maun 1998).

Effects on seedling growth and biomass allocation

Small *A. ordosica* seedlings realized higher relative growth rates in terms of height and biomass compared to large seedlings. In spite of their higher growth rates, the young-seedling cohort was still smaller than the older cohort at the end of experiment. Thus, early size differences due to

Fig. 2 Final height (**a**, **b**), stem diameter (**c**, **d**), leaf area (**e**, **f**), biomass (**g**, **h**) and root to shoot ratio (**i**, **j**) (±1 SE) of small (*S1*, **a**, **c**, **e**, **g**, **i**) and large seedlings (*S2*, **b**, **d**, **f**, **h**, **j**) of *Artemisia ordosica* under control (Con., *grey bar*) or various denudation (Denud., *white bars*) or burial treatments (*black bars*). Numbers along *x*-axis are centimetres burial or denudation



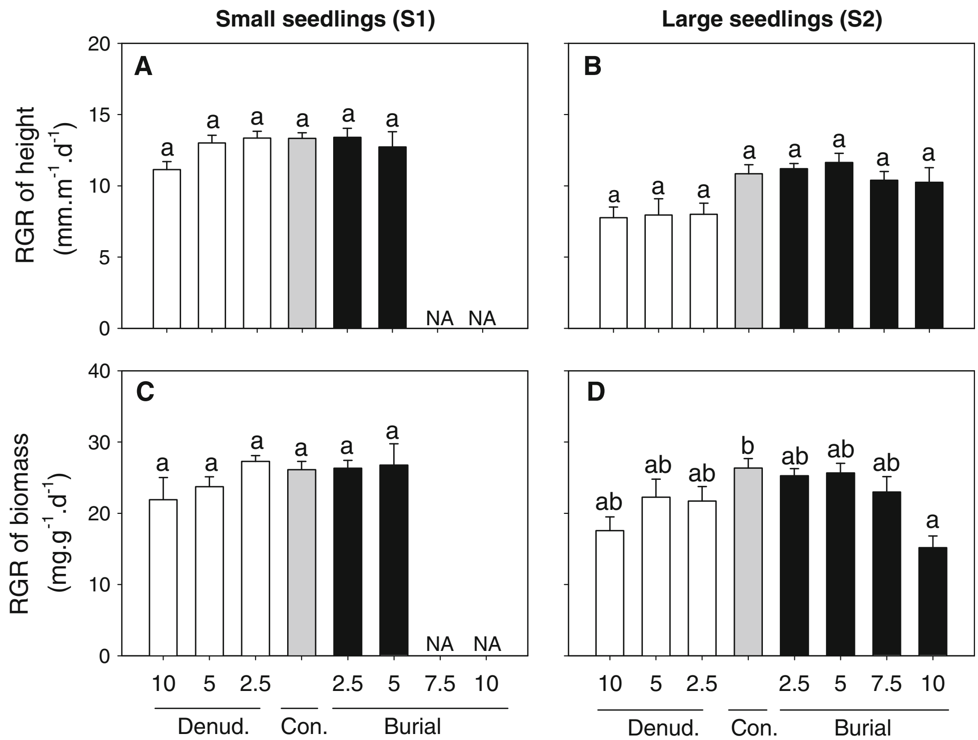


Fig. 3 Relative growth rates (RGRs) of height (**a**, **b**) and biomass (**c**, **d**) (±1 SE) of small (*S1*, **a**, **c**) and large seedlings (*S2*, **b**, **d**) of *Artemisia ordosica* under control (Con., *grey bar*) or various denudation (Denud., *white bars*) or burial treatments (*black bars*). Numbers along *x*-axis are centimetres burial or denudation

variation in seedling emergence likely will have a long-term effect on seedling performance.

The growth of the *A. ordosica* seedlings that had survived burial was not affected, as long as their burial was not complete. Similar results were reported in some other dune species (McLeod and Murphy 1983; Brown 1997; Maun 1998). The continued growth after moderate burial was probably possible as seedlings were able to rapidly recover lost leaf area. Maintenance of photosynthetic tissue was considered to be an adaptive trait to burial (Wagner 1964; Shi et al. 2004; Perumal and Maun 2006).

Only severe denudation treatments reduced the growth of the large *A. ordosica* seedlings, probably because of root exposure to the air and reduced capacity to take up water and nutrients (Fryrear et al. 1973; Eldred and Maun 1982; Yu et al. 2002, 2008). However, as long as denudation did not exceed 10 cm, seedling growth remained remarkably constant. The deeper root of *A. ordosica* seedling is likely an important trait that allowed resisting denudation.

Seedlings of *A. ordosica* showed different biomass allocation patterns in response to burial and denudation. Proportionally more biomass was allocated to shoots in burial treatments and to roots in denudation treatments. More investment in shoots after burial was also reported for many other specialized dune species (McLeod and Murphy 1983; Maun and Lapierre 1984; Brown 1997, Liu et al. 2008). Shifting resources from roots to aboveground components supports the vertical elongation of stems, facilitates emergence from a deep location and compensates the loss of photosynthetic tissues buried in sand and thus restore the photosynthetic capacity of the plants (Harris and Davy 1988; Zhang and Maun 1992; Brown 1997; Dech and Maun 2006). However, contrasting results have also been reported in several other species such *as Hedysarum laeve*, and another two *Artemisia* species of *A. wudanica* and *A. halodendron*, which showed unchanged biomass allocation under burial (Zhang et al. 2002; Liu et al. 2008). Allocation changes after denudation were also adaptive, as *A. ordosica* increased biomass allocation to roots, thus restoring the capacity for uptake of water and nutrients (Callaway et al. 1994; Wang 2005; Zheng et al. 2006).

Conclusions

We showed that *A. ordosica* seedlings resisted moderate levels of sand denudation and burial. The rates of survival and growth under denudation and burial showed remarkably similar to control as long as the plants were not extremely denudated or completely buried. *A. ordosica* seedlings are able to change biomass allocation under denudation and burial, indicating high adaptation to the moving dune environment. Differences in survival responses between seedlings of different cohorts show that gaining sufficient size before substantial sand denudation or accumulation happens is beneficial for successful seedling establishment in sandy environments. This also suggests that artificial sand binding measures are necessary in steppe restoration projects to prevent that extreme denudation and sand addition lead to large-scale mortality of recently germinated seedlings.

Acknowledgments We thank Paul Westers and Heinjo During for help with statistical analysis and Chang-Yuan Li, Jian-Jiang Qiao, Guo-Fang Liu, Bin Jiang and Jun-Qing Yang for assistance with field work. This research was supported by NSFC (30770357), the National Key Basic Research Program of China (2007CB106802) and a CAS-KNAW joint PhD Training Program.

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