



Adaptation of *Nitraria sphaerocarpa* to wind-blown sand environments at the edge of a desert oasis

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Abstract

This study addresses the adaptation of *Nitraria sphaerocarpa* to blown sand at the edge of a desert oasis with regard to the aspects of soil seed banks, seedlings, and population. Horizontally, the total number of seeds per unit area decreased from the shrub canopy center to intershrub areas, and most seeds were found under shrub canopies. Vertically, the highest proportion of seeds was found at depths of 5–10 cm. The emergence percentage, seedling mass, and seedling height, which were significantly affected by both burial depth and seed size, were highest at the optimal burial depth of 2 cm, and decreased with increasing burial depth in each seed size-class. Although seedling mass was usually greatest for large seeds and least for small seeds at each burial depth, little difference was observed in seedling height at shallow burial depths of 0–3 cm. The population shows a patchy and discontinuous distribution pattern. Population height increases with increasing sand depth. Also the density increases with increasing depth of sand in the desert; however, there is a steady decrease when the depth of sand is more than 100 cm. This result indicates that the depth of sand that is most suitable for the growth of *Nitraria sphaerocarpa* is 100 cm. The size of the population is significantly correlated with the sand depth, which increases with increasing depth in the desert.

Key words: *Nitraria sphaerocarpa*; soil seed bank; seedling growth; sand burial; adaptation

Introduction

In dune systems, sand accretion and deflation mediated by wind may be important selective forces in the evolution of plant species (Zhang *et al.*, 2002). Adaptation is the process of adjustment to environmental stress. In their seed and seedling stages, plants are particularly vulnerable to environmental conditions (Symonides, 1974). The processes occurring during these stages influence the structure of adult populations and communities (Guàrdia *et al.*, 2000).

Seed populations in soils play prominent ecological and evolutionary roles linking past, present, and future plant population and community structure and dynamics (Thompson and Grime, 1979). In arid ecosystems, seed banks are characterized by high spatial and temporal variability (Thompson, 1987), and are particularly affected by spatial patterns of vegetation (Guo *et al.*, 1998).

The germination of seeds is directly related to the depth at which seeds are buried (Zhang and Maun, 1994). Shallow burial particularly improves the germination of seeds and the subsequent emergence and survival of seedlings. However, deep burial may prevent seedlings

from emerging above the sand or otherwise affect their survival, because pre-emergence mortality results from the cessation of a seedling's growth before it reaches the soil surface and seeds may be unable to germinate due to lack of oxygen or light and temperature fluctuation (Maun and Riach, 1981; van Assche and Vanlerberghe, 1989; Zhang and Maun, 1990; Vleeshouwers, 1997). These traits suggest that there is an optimal range of burial depth to maximize seedling emergence and subsequent seedling growth. The optimal burial depth of seedling emergence could be strongly influenced by seed mass (Chen and Maun, 1999). Larger seeds are generally superior to smaller seeds in that they have a higher probability of emergence (Dolan, 1984; Stanton, 1984; Winn, 1988) and that they tend to develop into seedlings with better competitiveness (Stanton, 1984), higher survival (Simons and Johnston, 2000), and better performance in later life stages (Wulff, 1986; Vaughton and Ramsey, 2001). Sand burial can accelerate plant population growth, especially for shrubs. However, deep burial could reduce survival and biomass of plants and constrain plant growth.

In this study, we address the adaptation of *Nitraria sphaerocarpa* to blown sand at the edge of a desert oasis with regard to the aspects of soil seed banks, seedling, and population. The aim is to present the horizontal and

vertical distribution patterns of seed banks, to examine the effects of sand burial depth and seed size on seedling emergence and growth, and to test the influence of sand burial on population characteristics.

1 Methods

1.1 Study areas

The site chosen for this study is in northwest China (39°21'N, 100°07'E) and has an elevation of 1382 m. The mean annual temperature and rainfall are 7.6°C and 117.1 mm, respectively. The mean monthly temperature ranges from -27°C (January) to 39.1°C (July). The soil is dominated by blown sand with a coarse texture and loose structure. The vegetation is dominated by shrubs, including *Nitraria sphaerocarpa*, *Hedysarum scoparium*, *Nitraria tangutorum*, *Calligonum mongolicum*; subshrubs such as *Reaumuria soongorica*; and annuals such as *Suaeda glauca*, *Agriophyllum squarrosum*, *Bassia dasyphylla*, *Halogeton arachnoideus*.

1.2 Plant species

Nitraria sphaerocarpa is one of the major sand binding species in the sandlands of Northwest China. Seeds of *Nitraria sphaerocarpa* are dispersed by wind when they mature, and dispersed single seeds may be picked up again by wind and moved over long distances. Seeds and seedlings of the species may be buried in sand to various depths during their establishment. Burial in sand may be a critical episode for the successful establishment of the seedlings. After seedlings are established, *Nitraria sphaerocarpa* can populate the mobile dunes or semimobile dunes in a sandland habitat.

1.3 Soil seed banks

Soil samples were collected both horizontally and vertically. Horizontally, samples were collected at different distances from locations under the canopies of shrubs, as well as inter-shrub areas (between two shrubs). The sampling areas were measured by sampling distances from the center of a shrub canopy. Vertically, samples were collected from the soil profiles in four depth ranges, 0–2, 2–5, 5–10, and 10–20 cm, at each of the above sampling distances (samples of surface litter were included when it was present).

The soil samples were sieved through a set of 1, 0.5 and 0.2 mm meshes, and seeds were counted. No effort was made to test the viability or germinability of seeds at any site, for there was no satisfactory means of distinguishing death from dormancy. Therefore, the number of seeds counted may be an overestimate of the number of germinable seeds.

1.4 Emergence and seedling growth

Fruiting bodies were collected in the fall of 2004 from multiple individuals in the desert. Seeds were cleaned, dried at room temperature for 2 to 3 weeks, and then stored at 8°C under dry, dark conditions. The seeds were weighed

individually and sorted into three seed size-classes based on mass per seed (mean±S.E.): large (23.49±2.999 mg), medium (17.31±1.545 mg) and small (10.78±1.874 mg). For each group, counted seeds (20 each) were planted at 0, 1, 2, 3, 4, 5 and 6 cm depths in plastic pots (15.5 cm in diameter) filled with unsterilized sifted sand. The drainage outlets at the bottom of the pots were covered with strips of nylon mesh to prevent the loss of sand while allowing drainage of excess water. Sand was poured into each pot up to the lower mark and moistened. Seeds were then placed on the sand surface and the pots were filled up to the upper mark with additional sand. There were five pots per treatment. Pots were watered daily with tap water. The temperature in the greenhouse was maintained at 23°C during the day (16 h photoperiod) and 14°C at night.

Emerged seedlings were counted daily. Seedling emergence was defined as the first appearance of a seedling at the sand surface. After 8 weeks of seedling emergence and growth in the greenhouse, the experiment was terminated. All the seedlings were measured for their height above the sand surface, and then they were harvested. At harvest, the seedlings were dug out by hand and trowel, and care was taken to collect as many roots belonging to the seedlings as possible. The roots were cleaned with water, and the seedlings were separated into three parts: aboveground stems, belowground stems, and roots. After drying at 70°C for 48 h, each part was weighed.

1.5 Population characters

In the *Nitraria sphaerocarpa* population, a subsample of 0.5 m×0.5 m or 1.0 m×1.0 m in a population was selected according to its size from a plot of 100 m × 100 m. The depth of sand burial, population height, size, density and biomass were measured. The population size was considered as an ellipse through measuring its long axis and short axis. The population height was measured from the sand surface, and the population biomass was weighed after drying at 70°C for 48 h.

2 Results

2.1 Soil seed banks

In general, the total number of seeds per unit area (combining all depths) decreased from the shrub canopy center to intershrub areas (Fig.1). Most seeds were found under shrub canopies, and there were almost no seeds in the intershrub areas.

Most seeds were found at depths in the range of 5–10 cm (Fig.2). About 82.6% of the seeds were at depths of 5–10 cm, while only 3.5% of the seeds were at depths of 0–2 cm, 6.2% at 2–5 cm, and 7.7% at 10–20 cm.

2.2 Emergence and seedling growth

In the seven treatments, the emergence percentage was significantly affected by both burial depth ($F=98.134$, $df=6$, $P<0.0001$) and seed size ($F=18.668$, $df=2$, $P=0.0002$). Seedling emergence was the highest at

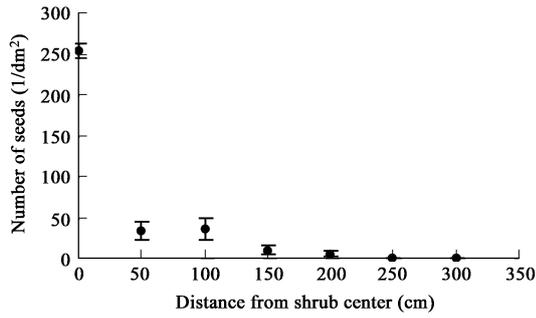


Fig. 1 Horizontal seed distribution from the center of shrub canopies to intershrub areas.

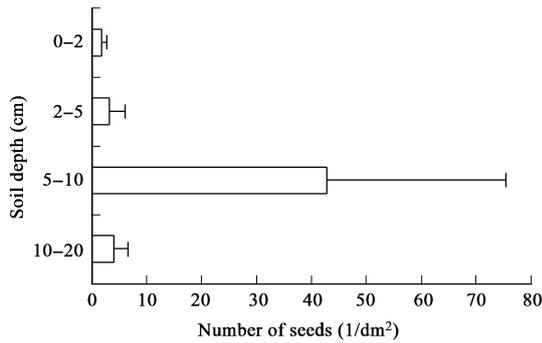


Fig. 2 Vertical seed distribution at the four soil depths.

2 cm burial depth, but decreased with increasing burial depth in each seed size class (Fig.3a). The emergence percentage was not significantly different between large and small sized seeds, although the emergence was usually highest for large seeds and lowest for small seeds at each sand burial depth. For the sand burial depth of 0 cm, the emergence was lower for the drought. There was a significant decline in emergence at 4 and 5 cm burial depths. No seedlings emerged from 6 cm depth for the small seeds.

Seedling size was measured in terms of mass and height. Seedling mass was significantly affected by both burial depth ($F=22.660$, $df=5$, $P<0.0001$) and seed size ($F=22.744$, $df=2$, $P<0.00019$), while seedling height was affected only by burial depth ($F=18.922$, $df=5$, $P<0.0001$) but not by seed size ($F=6.190$, $df=2$, $P=0.018$). Both seedling mass and seedling height were usually greatest at 2 cm burial depth, and decreased with an increase in burial depth for all seed size-classes (Figs.3b and 3c). Although seedling mass was usually greatest for large seeds and least for small seeds at each burial depth, little difference was observed in seedling height at shallow burial depths (0–3 cm).

2.3 Population characteristics

Population height increases with increasing sand depth (Fig.4a). The mean height of the *Nitraria sphaerocarpa* population was 30 cm. However, some could reach 80 cm in height. Also the density increases with increasing depth of sand in the desert. However, there is a steady decrease when the depth of sand is more than 100 cm (Fig.4b). This result indicates that the depth of sand that is most

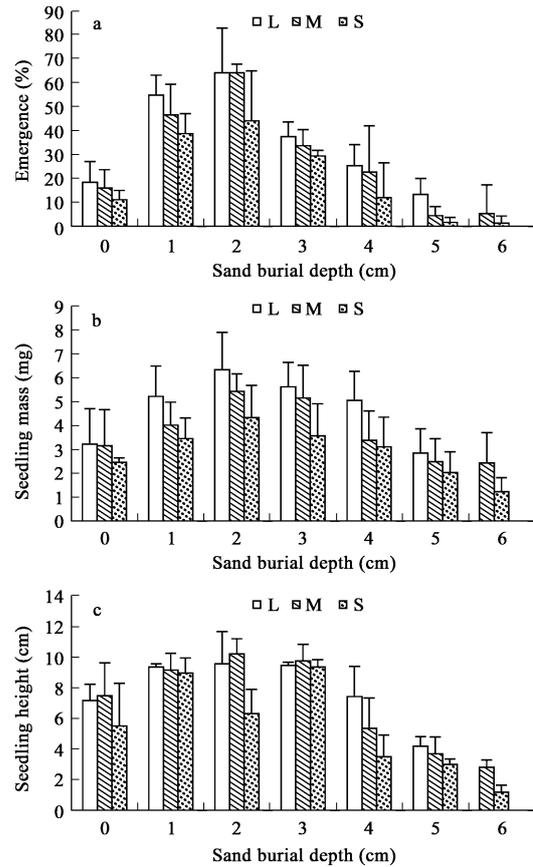


Fig. 3 Mean (\pm S.E.) emergence percentage of seedlings (a), seedling mass (b) and seedling height (c) at various sand burial depths for large (L), medium (M) and small (S) sized seeds of *Nitraria sphaerocarpa*.

suitable for the growth of *Nitraria sphaerocarpa* is 100 cm. The size of the population is significantly correlated with the sand depth, which increases with increasing depth in the desert, and the significant correlation coefficient was up to 0.814 (Fig.4c). Population biomass of *Nitraria sphaerocarpa* also increased with the increasing of sand burial with a correlation coefficient of 0.251 in the desert oasis (Fig.4d).

3 Discussion

3.1 Soil seed banks

Soil seed banks are important components of vegetation dynamics affecting both ecosystem resistance and resilience. In deserts, wind, sheet flooding, seed-eating animals, and soil surface microtopography are major factors affecting seed dispersal and distribution (Reichman, 1984). Most studies in desert ecosystems have shown that seed reserves are highly variable in both space and time. Seed abundance in any particular microhabitat depends on the input of seeds during both phase of movement of a seed from the parent to a surface and the phase of subsequent horizontal and vertical movements in the soil.

Patches under shrubs accumulate large seed banks (Aguiar and Sala, 1997) because of the high seed output of clumped vegetation, the trapping of wind-dispersed seeds, the protection from predators, and possibly deposition by

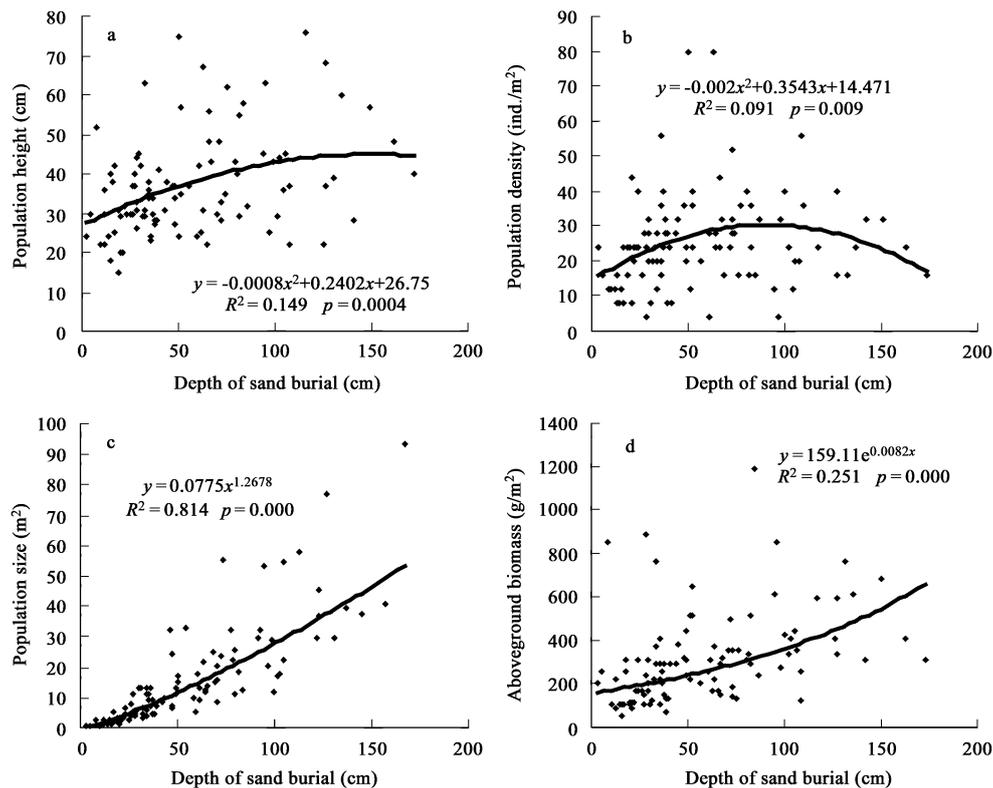


Fig. 4 Regression equations between the depth of sand burial and some parameters of *Nitraria sphaerocarpa* population.

birds using the shrubs as perches (Keeley, 1987; Mull and MacMahon, 1996). Seed accumulation is higher in the center of the patch and decreases towards the edges. Similar results also reported that the total number of seeds per unit area decreased under the shrub canopy to intershrub areas in North American deserts (Guo *et al.*, 1998).

For a given set of soil attributes, seeds of a particular size are likely to be found at a particular depth. Vertical movements and final distribution of seeds in the soil are determined mainly by seed morphology, soil structure and particle size, animal disturbances or other physical processes (Chambers *et al.*, 1991). In the desert, seed banks depend critically on the sampling techniques and timing of data collection. For this study, the soil seed bank was sampled in May, after several months of seeds dispersal. The seeds may have been buried by sand, so in our study, the highest proportion of seeds was at depths of 5–10 cm, not in the shallower depth of 0–5 cm. However, Guo *et al.* (1998) reported that in North American deserts, the total number of seeds declined as soil depth increased, and medium-large seeds tend to be distributed deeper in the soil and very small and very large seeds tend to stay in the upper layer of soil.

3.2 Emergence and seedling growth

Seed burial has both positive and negative consequences for seedling emergence. The most obvious negative consequence is burial so deep that seed germination is prevented. Germination sometimes occurs with deep burial but seed reserves may be exhausted before the seedling reaches

the soil surface, which leads to seedling death. As might be expected, deep burial is more detrimental to small seeded than to large seeded species (King and Oliver, 1994; Forcella *et al.*, 2000). The benefits of burial are reduced exposure to air. Soil overlying very young seedlings creates mulch that maintains high humidity and allows growth to proceed relatively rapidly. Moreover, soil burial also provides protection of seeds and seedlings from abnormally low and high air temperatures as well as predators that dwell on or near the soil surface.

Buried seeds may show one of four responses (Maun, 1994): (1) they may germinate and emerge as seedlings; (2) they may germinate but the seedlings are unable to emerge above the sand surface; (3) the seeds may acquire dormancy and become part of the soil seed bank; or (4) the seeds may succumb to various mortality factors. So of the total number of seeds produced by any plant, only a small fraction becomes seedlings (Cavers, 1983). Large losses occur between seed dispersal and seedling emergence because of various causes such as predators, emigration to unsuitable habitats and soil factors.

The burial experiment of *Nitraria sphaerocarpa* showed that deep burial reduced seedling emergence, but greater seedling emergence was observed for large seeds compared with small seeds, probably due to the greater food reserves that can produce longer shoots, thus facilitating their emergence above the surface soil. Seedling mass and height of the *Nitraria sphaerocarpa* were significantly affected by burial depth, mainly due to the following reasons. A greater fraction of seed reserves would be exhausted by the time of the seedling emergence, because seedlings

that emerged from deep burial showed smaller plant size initially. These seedlings would have less initial investment to future growth. Since seedlings from deeper burial depths usually emerge later than those from shallower burial depths, the period of growing season will be shorter and biomass gain and vertical growth will be lower than the seedlings from shallow buried seeds.

As mentioned above, seed burial has both positive and negative consequences for seedling emergence. This means that there is an optimal range of burial depth to maximize the seedling emergence and subsequent seedling growth. In this study, the shallow burial depth seems to be advantageous for seedling establishment of the *Nitraria sphaerocarpa*, because the greatest emergence, height and mass were observed at 2 cm burial depth in this experiment. If optimal caching depth for a propagule is considered as the probability of escaping predation by a forager times the probability that it will emerge, grow and survive in the absence of predation, is maximized (Li *et al.*, 2006; Vander Wall, 1993; Seiwa *et al.*, 2002), the optimal depth for a seed of *Nitraria sphaerocarpa* is in the range of a shallow burial depth—approximately 2 cm sand burial depth. At the optimal burial depth of 2 cm, there was little difference in the seedling emergence and the seedling height among seed size-classes, although seedling mass was dependent on seed size. Small differences in the seedling height among seed size-classes may reflect little difference in their competitive ability, which means the small-seeded seedlings are similar to the large-seeded seedlings in acquiring light, oxygen, nutrients and so on.

3.3 Population characteristics

Vegetation patches act as a sink for resources, either actively through root absorption of water and nutrients (Belsky, 1994), or passively accumulating wind-blown dust and litter (Barth and Klemmedson, 1982), in a feedback process that reinforces vegetation heterogeneity (Wilson and Agnew, 1992). *Nitraria sphaerocarpa* shows patchy and discontinuous distribution patterns. Sand burial makes the population a relatively independent shrub coppice dune, which can be formed in four ways: seedling reproduction, sprouting reproduction, habitat fragmentation, and combination of neighboring shrub coppice dunes.

Not only does sand burial constrain plants to grow by burying their stems and nutritive organs, but it is also beneficial for *Nitraria sphaerocarpa* by improving soil porosity and water content in soil, reducing soil bulk density breeds of other sandy plants. Which aspect acts as the main role depends on the degree of sand burial and durable competence of sandy plants. For *Nitraria sphaerocarpa*, moderate sand burial favored its growth and the moderate depths were 100 cm.

Water content determined coverage and density of plants; on the other hand, coverage and density of plants affected water content. Soil water content coming from rainfall or underground water was one of the most important constraining factors for the growth of *Nitraria sphaerocarpa*. The depth of the water table was 4.3–4.6 m in the sampling plots. Shallow underground water under

the shrub-coppice dunes was the main water source for the growth and development of *Nitraria sphaerocarpa*. High density makes plants die away early for shortage of water; low density affects the ability of plants for less coverage. It can be seen from the relationships of sand burial and population density that moderate sand burial could improve the growth of *Nitraria sphaerocarpa*. Deep sand burial, however, constrained the growth of *Nitraria sphaerocarpa* when sand was over 100 cm deep, for the insufficient water could not sustain oversize density of plant population.

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