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Effects of irrigation on seedling emergence and seedling survival of a desert shrub *Haloxylon ammodendron* (Chenopodiaceae)

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Abstract. *Haloxylon ammodendron* (C.A. Mey) Bunge (Chenopodiaceae) is a shrub occurring on desert sand dunes in China. Seedling emergence and seedling survival were investigated by sowing seeds at different depths (0, 2.5, 5.0 or 10 mm) in fine or coarse sand in pots irrigated under different regimes. Seed burial in sand was required for seedling establishment of this species. Seedling emergence depended greatly on seed burial depth, sand type, and irrigation regime; this appeared to be due to (1) seeds or seedlings suffering from oxygen or moisture deficiency depending on the air : moisture ratio in sand, and/or (2) higher moisture content in sand resulting in hardening of the sand and obstruction of seedling growth. Increased irrigation resulted in longer survival of emerging seedlings because sand was moistened more deeply, and moisture in deeper sand persisted longer. The results suggest that the infrequent and light precipitation common in desert environments is likely to cause germination of many of the buried seeds, but is insufficient for emerging seedlings to survive. It is suggested that water from melting snow in early spring is crucial in enabling seedling establishment of this species in the deserts of China.

Introduction

Haloxylon ammodendron is a shrub that occurs in the western deserts of China (Walter and Box 1983; Fu and Jin 1992). This species is commonly found on stable sand dunes, although it also occurs on salinised areas (Tobe *et al*. 2000*a*). Seeds of this species have no endosperm and have only a fully differentiated spiral embryo enclosed by pericarp. The germination process of this type of seed consists simply of water absorption by the dry spiral embryo and subsequent elongation (Wallace *et al*. 1968; Sharma and Sen 1989).

In a previous paper (Tobe *et al*. 2000*a*), we reported that for *H. ammodendron* seeds (1) germination after irrigation was very rapid; (2) germination showed low or no dependence on seed dormancy, temperature, light, or the water potential of the substrate; and (3) seeds were short-lived and were expected to lose viability in the field within one year of maturation. In the present study, we investigated the characteristics of seedling emergence from sand and seedling survival in this species.

Moisture content in sand depends not only on the frequency and amount of water supplied, but also on sand depth (Tobe *et al*. 2005). While moisture in sand near the surface evaporates quickly, moisture in deeper sand persists longer because of a lower evaporation rate. By contrast, an increase in the volume of moisture in sand causes a decrease in the volume of air, and this may result in oxygen deficiency for germinating seeds or growing seedlings. Because a reduction in oxygen availability inhibits seed germination and/or seedling growth (Gill and Miller 1956; VanderZee and Kennedy 1981; Crawford 1992), the air : moisture ratio in sand, as well as the moisture content itself, may be factors that affect seedling emergence. In addition, moisture in sand causes hardening of sand (Krumbein 1959; Hornbaker *et al*. 1997) and may cause mechanical resistance to seedling growth (Tobe *et al*. 2005). Therefore, because seeds located at different depths in sand are exposed to different moisture and oxygen conditions and sand hardness after water is supplied, seed germination and seedling emergence are expected to be affected by both the depth of seed burial in sand and the amount of water supplied.

This study was undertaken to investigate the effects of seed burial depth in sand and irrigation on seedling establishment of *H. ammodendron*. We examined the emergence and

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survival of seedlings when seeds were sown at different depths in sand and irrigated under different regimes. For the experiments, we used fine sand, the particle-size distribution of which was similar to that of sand dunes in China, but in some experiments, coarse sand was used to examine the effect of well draining sand with high air : moisture ratio on seedling emergence.

Materials and methods

Seeds

Seeds of *Haloxylon ammodendron* (mean seed weight: 3.48 mg) were collected soon after maturation in November 2001 from plants growing in the Tulufan Botanical Garden of the Xinjiang Institute of Pedology, Biology and Desert Research, Tulufan, China (42°56′N, 89°12′E). The collected seeds were initially stored at room temperature until transported to Japan in January 2002. In Japan, the seeds were stored at *c.* −18°C to avoid germination loss, and germination experiments were carried out within 12 months of the maturation of the seeds.

Petri dish experiments

Replicates of 25 seeds were sown on three layers of filter paper (Toyo, No. 1) in 90-mm plastic Petri dishes. About 15 mL of deionised water was added to each dish so that about half the volume of each seed was immersed. The Petri dishes were covered with lids and held at 12 h 25°C/12 h 15°C in the dark in an incubator. Seeds were observed daily through a magnifying glass with a scale and about two-thirds of the volume of water in each Petri dish was replaced daily.

Examination of germination of seeds submerged in water

Thirty-five seeds were placed in a glass bottle (130 mL), and 120 mL of deionised water was poured into the bottle (water depth: *c.* 60 mm); the 10–20% of seeds that floated were discarded. The bottle was covered with a lid and held at 12 h 25°C/12 h 15°C in the dark in an incubator. After being submerged for 2, 3 or 5 days, seeds were removed from the bottle, transferred to a Petri dish as described above, and seed germination and seedling emergence observed as described above for another 6 days. Each treatment was replicated four times.

Examination of seedling emergence from sand

Replicates of 16 seeds were sown on the surface or at different depths (2.5, 5.0 and 10 mm) in sand-filled cylindrical plastic pots (inner diameter: 80 mm, sand surface area: *ca* 50 cm^2) either 50 mm (short pots) or 100 mm (long pots) tall. There was a circular drainage opening (diameter: 12 mm) covered with cloth at the bottom of each pot. The pots were filled to a depth of 45 mm (short pots) or 90 mm (long pots) with air-dried sand (fine or coarse). Fine sand was collected from a beach in Japan and washed repeatedly to remove salt and mud. The particle-size distribution of the fine sand (91% by weight was 63–250 µm) was similar to that of sand dunes in China (Nanking Institute of Soil Science 1983). Coarse sand (91% by weight was 250–600 µm) was collected from a river bed in Japan, repeatedly washed to remove mud, and sieved to remove small particles.

The pots were placed in an incubator and held at 12 h 25°C (light)/12 h 15°C (dark). In the light period, the pots were illuminated with fluorescent lamps (photon flux density at wavelengths of 400–700 nm at the surface of the sand: 80–130 $\mu mol\ m^{-2}\ s^{-1}$). Relative humidity in the incubator was usually 40–70% during the 25°C (light) and 90–95% during the 15°C (dark) periods. Pots were irrigated at the beginning of light periods by slowly and evenly dripping water on the sand with a pipette. The pots were observed daily and the number of emerging and surviving seedlings in each pot was counted. A seedling was regarded as having emerged when its height exceeded 3 mm, and a seedling was regarded as having died when it fell over or most of the seedling turned yellow or brown.

Seedling emergence from seeds buried at different depths in different types of sand and irrigated under different regimes

Seeds were sown on the surface or at a depth of 2.5, 5.0 or 10 mm in fine or coarse sand in the short pots. The pots were initially irrigated with deionised water of 16 mmP (*x* mmP denotes irrigation equivalent to *x* mm precipitation) and subsequently with water of 3 mmP at 1-day intervals ([16 + 1/1] treatment) for 14 days, or initially irrigated with water of 8 mmP and subsequently with water of 3 mmP at 2-day ([8 + 1/2] treatment) or 4-day ([8 + 1/4] treatment) intervals for 14 days. Each treatment was replicated five times. For pots in which seeds were sown on the sand surface and irrigated for 14 days, seeds were transferred to Petri dishes described above and held in an incubator (12 h 25°C/12 h 15°C in the dark), and seed germination and seedling growth were observed daily as described above for another 10 days.

Seedling emergence and survival when seeds were buried at a depth of 10 mm in fine sand and irrigated with different amounts of water

To investigate the effect of the amount of irrigation on seedling emergence and seedling survival, seeds were sown at a depth of 10 mm in fine sand in the long pots and initially irrigated with deionised water at 4, 6, 8, 12, 16, 20, 24 or 32 mmP and subsequently was not irrigated at all for 20 days (4–16 mmP irrigation) or 40 days (20–32 mmP irrigation). For treatments in which initial irrigation was 4–16 mmP, each pot was irrigated with 8-mmP on day 20 after the initial irrigation and subsequently with 3 mmP at 2-day intervals for another 20 days to determine whether pots that did not produce emerging seedlings contained viable seeds. Each treatment was replicated seven times.

Statistical analysis

Tukey's test was used for comparison of multiple means. Percentage values were arcsine transformed before statistical analysis. Statistical tests were conducted at $P < 0.05$.

Results

Seed germination and seedling growth in water and in Petri dishes

After submergence of seeds for 2, 3 or 5 days, radicles (2–7 mm long) emerged from 10–50% of the seeds and many of the longer radicles appeared abnormal (coiled). After seeds were transferred to Petri dishes, some emerging radicles continued to elongate and some seeds germinated. The proportions of seeds that had been submerged for 2, 3 and 5 days that generated seedlings longer than 20 mm in the dishes were 48 ± 10%, 28 ± 5.4%, and 7 ± 2.2% (mean ± s.e.; $n = 4$), respectively.

By contrast, 99 ± 0.2% (mean ± s.e.; $n = 5$) of seeds that had not been submerged in water but were irrigated in Petri dishes generated seedlings longer than 20 mm on Day 4 after irrigation (Fig. 1). The length of these seedlings on Day 6 after irrigation was 82 ± 22 mm (mean ± s.d., $n = 76$), and most of these seedlings appeared normal.

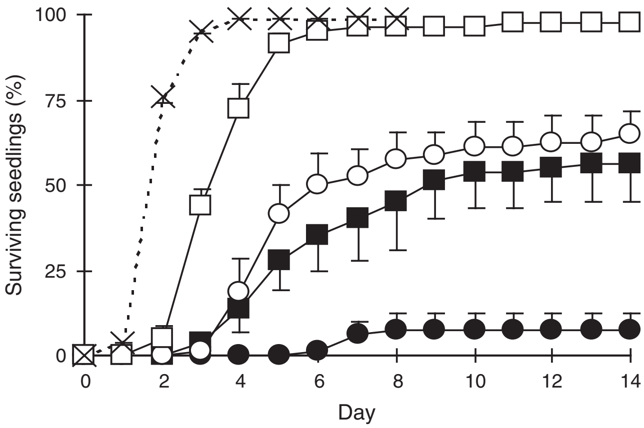

Fig. 1. Changes over time in seedling emergence (%) from seeds sown at 10 mm in coarse (○, □) or fine (●, ■) sand and irrigated with [16 + 1/1] (○, ●) or [8 + 1/2] (□, ■) treatments (refer to the caption of Table 1 for each treatment). The change over time in the percentage of seeds that generated seedlings longer than 20 mm when seeds were moistened in Petri dishes is also shown (··· × ···). Each point represents the mean of five replications; error bars indicate s.e. where it is larger than the symbol.

These results showed that contact of seeds with air was required for normal seedling growth and that submergence of seeds caused a gradual loss of germinability.

Seedling emergence from seeds buried at different depths in fine or coarse sand and irrigated under different regimes

Seedling emergence from sand depended on seed burial depth, irrigation regime, and sand type (Fig. 1; Table 1). For example, burial at 10 mm (Fig. 1) resulted in more rapid seedling emergence and higher final seedling emergence in coarse sand than in fine sand treatments, and in [8 + 1/2] than in [16 + 1/1] treatments. For the [16 + 1/1] treatment, the seedling emergence percentage from fine sand was highest at a seed burial depth of 2.5 mm and markedly decreased with increasing seed burial depth. Many of the seedlings that emerged from a depth of 2.5 mm in the [16 + 1/1] treatment trailed over the sand surface, whereas in the other irrigation treatments many seedlings elongated straight upward at the sand surface. By comparison, for the [8 + 1/2] and [8 + 1/4] treatments, seedling emergence percentage from fine sand was very low for seeds buried at 2.5 mm and fairly high for greater burial depths (Table 1). The final percentage of seeds that produced seedlings longer than 20 mm in Petri dishes (Fig. 1) was considerably higher than the final seedling emergence percentages from sand (Table 1), except for seeds buried at 10 mm in coarse sand and irrigated under the [8 + 1/2] treatment. Except for 39% of seedlings that emerged from coarse sand irrigated at [8 + 1/4] that died by the end of the experiment, all other emerging seedlings survived until the end of the experiment. When seeds that were buried at 10 mm in fine sand and irrigated with [16 + 1/1] for 14 days were excavated from the sand, 81% of seeds were found to have germinated (mean length of unemerged seedlings: 43 mm), but the radicles did not elongate downwards, and the seedlings tended to elongate laterally without emerging from the sand surface.

Table 1. Final seedling emergence percentages from seeds sown at different depths in fine or coarse sand in pots and irrigated under different regimes

Pots were initially irrigated with 16 mmP and subsequently with 3 mmP at 1-day intervals ([16 + 1/1]) for 14 days, or initially irrigated with 8 mmP and subsequently with 3 mmP at 2-day ([8 + 1/2]) or 4-day ([8 + 1/4]) intervals for 14 days. Data are the mean of five replications. Values with the same superscript letter are not significantly different from each other ($P < 0.05$; Tukey's test)

Irrigation	Sand type and seed burial depth				
	Fine sand				Coarse sand
	0 mm	2.5 mm	5.0 mm	10 mm	10 mm
[16 + 1/1]	0^{e}	55^{bc}	45^{c}	7^{de}	65^{bc}
[8 + 1/2]	0^{e}	5^{e}	66^{bc}	56^{bc}	97^{a}
[8 + 1/4]	not examined	1^{e}	37^{cd}	60^{bc}	84^{ab}

When seeds were sown on the surface of fine sand and irrigated under the [16 + 1/1] or [8 + 1/2] regimes, no established seedlings were produced (Table 1). For the [16 + 1/1] treatment, although emergence of radicles (lengths: 1–10 mm) was found in 60–100% of seeds, the radicles did not elongate further, and longer radicles elongated laterally without penetrating into the sand. When seeds were transferred to Petri dishes after 14 days of [16 + 1/1] irrigation on the sand surface, the final percentage of seeds that generated seedlings longer than 20 mm was 66 ± 11.3% (mean ± s.e.; $n = 5$). For many seeds that had generated fairly long radicles on the sand surface, the seedling length remained less than 20 mm in the Petri dishes, and the radicle tips were missing and/or the seedlings were coiled. For the [8 + 1/2] treatment, radicle emergence was found in *c.* 4% of seeds sown on the sand surface (radicle lengths: 1–2 mm). When seeds sown on the sand surface and irrigated with [8 + 1/2] were transferred to Petri dishes, the final percentage of seeds that generated seedlings longer than 20 mm in the dishes was 93 ± 2.7%, and all these seedlings appeared normal.

Seedling emergence and seedling survival when seeds were buried at a depth of 10 mm in fine sand and irrigated with different amounts of water

Initial irrigation of 8–20 mmP resulted in high seedling emergence percentages, but initial irrigation exceeding 20 mm tended to result in lower seedling emergence percentages (Fig. 2; Table 2). The seedling emergence percentage was very low or zero for the initial irrigation of 4 mmP or 6 mmP. Rewatering after the initial 4 mmP

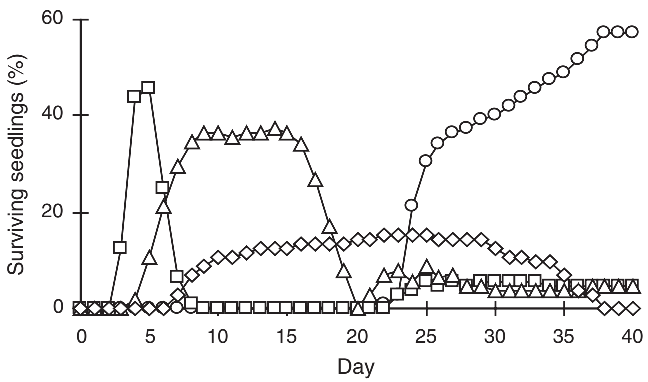

Fig. 2. Changes over time in seedling survival (%) from seeds buried at 10 mm in fine sand in pots and irrigated under different regimes. Pots were irrigated initially with 4 mmP (○), 8 mmP (□) or 16 mmP (△) and subsequently not irrigated for 20 days (day 0–20), and on day 20, the pots were rewatered with 8 mmP and subsequently with 3 mmP at 2-day intervals (days 20–40). ◇: Pots were irrigated initially with 32 mmP and subsequently not irrigated for 40 days. Each point represents the mean of seven replications.

treatment caused seedlings to emerge from 58% of seeds (Days 20–40), which was similar to the seedling emergence percentage when seeds buried at 10 mm were irrigated with [8 + 1/2] without pre-irrigation treatment (56%; Table 1). The seedling emergence percentage after rewatering decreased markedly as the amount of initial irrigation increased and was zero for the initial 16 mmP treatment (Table 2). For the initial 16 mmP treatment, although seedlings did not newly emerge after the rewatering, 9% of seedlings that had fallen over on Day 20 recovered (Fig. 2); for other irrigation treatments, recovery of seedlings was not observed after rewatering. As the amount of initial irrigation increased, emerging seedlings survived for longer periods (Fig. 2; Table 2). Seedling emergence was retarded with increasing amount of initial irrigation (Fig. 2; Table 2).

Discussion

The contrasting initial growth responses between submerged seeds and seeds irrigated in Petri dishes indicated that *H. ammodendron* requires contact with air for favourable seedling growth. Poor germination of submerged seeds has been reported for many species and has been attributed to reduced oxygen availability (Morinaga 1926; Hegarty 1978). Oxygen availability affects seed germination and seedling growth in many species (Heichel and Day 1972; Crawford 1977, 1992; VanderZee and Kennedy 1981; Al-Ani *et al*. 1985).

Emergence of seedlings of *H. ammodendron* from sand depends on seed burial depth, irrigation regime, and sand particle size, primarily because of the air : moisture ratio in sand. Excessive irrigation reduced seedling emergence presumably because the higher moisture content lowered the air content in the sand, resulting in oxygen deficiency for seeds and seedlings. Higher seedling emergence from coarse sand than from fine sand was probably due to air in the sand being purged by irrigation to a greater degree in finer sand. Nevertheless, fine sand appeared to favour survival of seedlings by retaining moisture because seedling death in the [8 + 1/4] treatment occurred only in the coarse sand treatment. Because the particle size of desert sand from dunes in China is relatively small (Nanking Institute of Soil Science 1983), these results suggest that only a small fraction of *H. ammodendron* seeds buried in sand develops into established seedlings. A similar response of seed germination

Table 2. Effects of amount of irrigation on seedling emergence and seedling survival

Seeds were sown at a depth of 10 mm in fine sand in pots, and the pots were initially irrigated with different amounts of water and subsequently not irrigated at all for 20 days (4–16 mmP) or 40 days (20–32 mmP). For treatments in which initial irrigation was 4–16 mmP, each pot was rewatered with 8-mmP on Day 20 after the initial irrigation and subsequently with 3 mmP at 2-day intervals for another 20 days. Data are the means of seven replications. In each column, the values with the same superscript letter are not significantly different from each other ($P < 0.05$; Tukey's test). Dashes denote that the values were not calculated because the final seedling emergence percentage of one or more of replications was zero

Irrigation (mmP)	Number of days after irrigation when seedling emerged initially	Emergence (%)	Number of days after irrigation when all seedlings died	New seedling emergence after rewatering (%)
4	–	0^{d}	–	58^{a}
6	–	5^{cd}	–	15^{b}
8	3.3^{a}	48^{a}	7.7^{a}	5^{bc}
12	4.4^{a}	36^{a}	13.1^{ab}	1^{c}
16	4.7^{b}	41^{a}	19.3^{b}	0^{c}
20	5.4^{b}	36^{a}	27.0^{b}	not examined
24	7.9^{b}	27^{ab}	34.3^{c}	not examined
32	–	15^{bc}	–	not examined

was reported for the shrub *Calligonum comosum* L'Her. in deserts in Israel (Koller 1956); seed germinability of this species was lost by washing the seeds with water, and because of the inhibitory effect of excessive water, its habitats are confined to areas covered with coarse sand and having low rainfall (Koller 1956).

The very low seedling emergence from seeds buried at 2.5 mm in fine sand in the [8 + 1/2] and [8 + 1/4] treatments may be attributed to moisture deficiency in shallower sand layers (Batanouny and Zieogler 1971; Maun and Lapierre 1986) where moisture is rapidly lost by evaporation.

Another factor affecting the emergence of seedlings of *H. ammodendron* from sand may be the obstruction of seedling growth by mechanical resistance of moist sand. Mechanical resistance of soil can impede shoot or root growth of seedlings (Gill and Miller 1956; Sedgley and Barley 1963; Barley and Greacen 1967; Taylor and Gardner 1963). When sand contains water, sand particles coagulate and the sand becomes harder (Hornbaker *et al*. 1997) and exerts stronger resistance to seedling elongation. In the [16 + 1/1] treatment, seedling emergence from fine sand was inhibited at depths of 5.0 mm or more, primarily because seedlings elongated laterally. Higher moisture content in deeper sand in the more frequent irrigation treatment can cause greater hardening of the deeper sand. This hardening of deeper sand appeared to have inhibited downward elongation of radicles and forced the seedlings to elongate laterally. The higher seedling emergence percentages from a depth of 2.5 mm in the [16 + 1/1] treatment may be because seeds were located closer to the sand surface, and the seedlings, although elongating laterally, were better able to emerge at the surface. Better seedling emergence from coarse sand in the [16 + 1/1] treatment may be because moist coarse sand is less hard than moist fine sand (Krumbein 1959).

Seeds sown on the sand surface did not give rise to established seedlings. This may be because moisture deficiency at the surface did not allow seed germination or seedling growth. In addition, radicles emerging at the sand surface were not able to penetrate into the sand. A similar response of radicles has been reported in other species (Maun and Riach 1981; Maun and Lapierre 1986; Tobe *et al*. 2005). These results indicated that seed burial in sand is a requirement for the establishment of *H. ammodendron* seedlings. For the short-lived seeds of *H. ammodendron*, many seeds may lose viability before becoming buried in sand.

Different amounts of irrigation produced different effects on the seedling emergence percentages, the number of days needed for seedlings to emerge after irrigation, percentages of viable seeds after irrigation, and the period of survival of emerging seedlings. These effects may have been because different amounts of initial irrigation caused different changes over time in the air : moisture ratio and hardness of the sand. As the amount of irrigation is increased, the moisture content in the sand increases and persists for longer periods (Tobe *et al*. 2005). Retardation and suppression of seedling emergence with greater irrigation may have resulted because oxygen deficiency (and perhaps sand hardening) caused by higher moisture content and longer persistence of moisture in sand hindered seed germination and/or seedling growth.

Increases in the period of survival of emerging seedlings with increased amounts of irrigation may be because a larger amount of irrigation moistened sand more deeply and moisture persisting in deeper sand supported the survival of seedlings for longer periods (Tobe *et al*. 2005). This indicates that after a light rainfall, successive rainfalls are needed within shorter periods for the emerging seedlings to survive. For *H. ammodendron*, the threshold amount of irrigation that was needed to cause seedling emergence was small compared to that for other species distributed in deserts (Went 1948; Tevis 1958; Ackerman 1979; Loria and Noy-Meir 1980; Gutterman and Evenari 1994; Tobe *et al*. 2005). This may be related to rapid germination after irrigation and seed germinability at extremely low water potentials in this species (Tobe *et al*. 2000*a*). However, emerging seedlings did not survive for longer periods in moisture-deficient conditions compared to those of other species distributed in deserts (Tobe *et al*. 2005). Our results suggested that infrequent supply of a fairly small amount of water causes germination of *H. ammodendron* seeds, eliminates a considerable fraction of buried viable seeds from the seed bank and results in the death of most emerging seedlings. Supplying a larger amount of water is more likely to result in successful seedling establishment, although it results in seedling emergence from only a small fraction of the seeds.

In deserts in China, where winter temperatures fall below 0°C, seedlings of *H. ammodendron* are likely to emerge from spring to autumn, and subsequently, ungerminated seeds lose viability. In a typical habitat of *H. ammodendron* in China, Fukang (44°18′N, 87°55′E; annual precipitation: 172 mm, annual mean temperature: 6.1°C), monthly precipitation from April to October is highest in June (28 mm) and lowest in August (11 mm) (means from 1958 to 1980), suggesting that rainfall in this region is less frequent or the amount of each rainfall is less than the frequency or amount of irrigation needed to support the survival of *H. ammodendron* seedlings in our experiments. Thus, in such habitats, rainfall may be more likely to cause the loss of viable seeds without resulting in established seedlings. However, in Fukang and other western parts of deserts of China, where *H. ammodendron* is distributed, some snowfall occurs in winter, and this snow melts in the early spring, thereby supplying fairly large amounts of water (Tobe *et al*. 2000*b*). For example, in Fukang, precipitation from November to March is 36 mm (mean from 1958 to 1980), and usually falls as snow. In these regions, *H. ammodendron* seeds, maturing in November, will remain ungerminated in the winter cold and be stimulated to germinate by the water supplied by melting snow. Some of the seeds will give rise to established seedlings, and most of buried viable seeds will be lost from the seed bank. After this season, seeds that had been located on the sand surface may remain ungerminated and viable, but for the short-lived seeds of this species, the opportunities for these seeds to generate established seedlings may be limited. Mature plants of this species disperse a large number of seeds every year, but a very small fraction of the seeds are expected to give rise to established seedlings in the field.

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