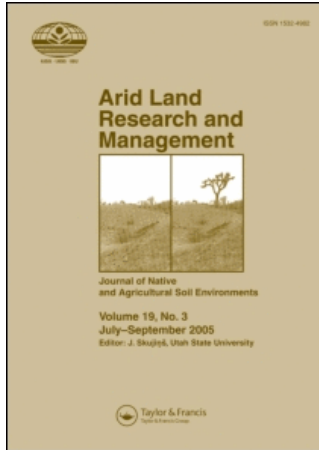


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Seed Size Effects on Seedling Emergence of Desert Psammophytes in China

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Seed Size Effects on Seedling Emergence of Desert Psammophytes in China

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To investigate the effects of seed size on the behavior of seeds and seedlings in sand, seedling emergence from sand was examined in Caragana korshinskii (Fabaceae; mean seed weight 65 mg) and Atraphaxis bracteata (Polygonaceae; mean seed weight 5.7 mg), two shrubs with nonphotoblastic seeds that grow on desert sand dunes in China. Seeds were sown at depths of 0 to 50 mm in sand-filled pots, and the pots were irrigated under different regimes. The results suggest that for both species, a high proportion of the seeds buried fairly deep germinate during the summer rainy season with or without producing emergent seedlings, whereas at shallow depths, where moisture is more likely to be lost by evaporation, some proportion of the seeds remain ungerminated and viable. Comparison of results in this study with those on several smaller-seeded species used in our previous studies shows that larger seeds did not always give rise to seedlings capable of emerging from deeper depths in sand. We suggested that for nonphotoblastic seeds, seed size is not a crucial determinant of the proportion of seeds that produce emergent seedlings in field conditions.

Keywords *Atraphaxis bracteata*, *Caragana korshinskii*, irrigation, sand dunes, seed burial depth, seed fate, seed weight, water availability

Seed size varies greatly among species within communities (Leishman et al., 2000). In the desert dunes of north central China, an annual *Eragrostis poaeoides* (mean seed weight 0.1 mg) and a shrub *C. korshinskii* (65 mg) have the smallest and largest seeds, respectively. In previous studies, we examined seed germination and seedling emergence of several species growing in desert sand dunes in China. Among them, four species with small seeds (*E. poaeoides* (unpublished results) and three *Artemisia* semi-shrubs [mean seed weight 0.27–0.76 mg; Tobe et al., 2006]) required light for germination. We suggested that the probability of seed germination of these species

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in the field is very limited because the light requirement restricts seed germination to shallow sand layers, where moisture is lost rapidly due to evaporation. On the other hand, species with medium-sized seeds (three annuals [*Agriophyllum squarrosum*, *Bassia dasyphylla*, and *Aristida adscensionis*; mean seed weight 1.8, 1.0, and 1.3 mg, respectively; Tobe et al., 2005b] and two Fabaceae herbs [*Astragalus adsurgens* and *Melilotus albus*; mean seed weight 1.7 and 2.8 mg, respectively; Tobe and Gao, 2007]) did not require light for germination and showed high percentages of seedling emergence, when the seeds were buried at appropriate sand depths. If seedling emergence from sand depends on seed size, the responses of larger-seeded species might differ from those of smaller-seeded species examined in our previous studies. To better understand the behavior of seeds and seedlings in desert sand dunes in China, we need to investigate how seed size affects the responses of seeds to water availability and burial depth.

Many studies (e.g., van der Valk, 1974; Buckley, 1982; Maun and Lapierre, 1986; Jurado and Westoby, 1992; Martínez et al., 1992; Bond et al., 1999) have indicated that larger nonphotoblastic seeds, which have more seed reserves than smaller ones, had the advantage of giving rise to taller seedlings that could emerge from deeper sand. Bond et al. (1999) reported that maximum seedling emergence depth is proportional to the cube root of seed weight. On the other hand, the effects of seed size on the response of seedling emergence to water availability have been less studied. Bansal et al. (1980) examined water absorption by seeds of 40 species growing in cultivated fields of an arid zone in India. They reported that seeds that absorbed less water during germination were more likely to be stimulated to germinate by lighter precipitation. Precipitation is usually the most crucial factor to seedling emergence in arid and semi-arid regions (Sala et al., 1992; Lauenroth et al., 1994), and water availability in sand depends on both precipitation and sand depth (Tobe and Gao, 2007). Thus, size-dependent responses of seeds to water availability can result in size-dependent differences in seedling emergence and seed bank behavior in desert sand dunes.

In the present study, we examined seedling emergence of *Caragana korshinskii* Kom. (Fabaceae) and *Atraphaxis bracteata* A. Los. (Polygonaceae), two deciduous shrubs that grow on desert sand dunes in China and produce nonphotoblastic seeds (unpublished data). *A. bracteata* is found on mobile sand dunes, whereas *C. korshinskii* is generally found on stable sand dunes. Seed weight of these species is considerably larger than that of species examined in our previous studies, and the mean seed weight of *C. korshinskii* (65 mg) is more than 11 times that of *A. bracteata* (5.7 mg). The amount of water absorbed by seeds before radicle protrusion begins is ca. 84 mg/seed for *C. korshinskii* and ca. 6.7 mg/seed for *A. bracteata* (estimated from data in Tobe et al. (2001)) versus ca. 0.75 mg/seed for *A. squarrosum* (unpublished data). Because seed germination of these two species, as well as that of the five species with non photoblastic medium-sized seeds examined in our previous studies (Tobe et al., 2005b; Tobe and Gao, 2007), does not depend greatly on temperature (Tobe et al., 2001), water availability and seed burial depth are crucial for emergence of their seedlings in the field.

Thus, the purpose of the present study was to understand how seed size affects seedling emergence and seed fates of species growing on desert sand dunes in China. We investigated seedling emergence of *C. korshinskii* and *A. bracteata* for seeds sown at different depths in sand and irrigated under different regimes. In addition, we tried to determine the fates of seeds that did not give rise to emergent seedlings

after irrigation. For *C. korshinskii*, we also investigated the effect of intraspecific differences in seed size on seedling emergence. The results were compared with those of several smaller-seeded species (especially with five species whose seeds are nonphotoblastic and medium-sized) used in our previous studies.

Materials and Methods

Seeds and Habitat Climate

Seeds of *C. korshinskii* were collected in June 2001 from a sand dune in Shapotou, China (37°26'N, 104°57'E, annual precipitation 188 mm, annual mean temperature 10.5°C), and seeds of *A. bracteata* were collected in August 2000 from a field botanical garden in Minqin, China (38°34'N, 102°58'E, annual precipitation 120 mm, annual mean temperature 7.8°C). Seeds were transported to Japan and stored at ca. 0°C in a refrigerator until used in experiments. Seed size of *C. korshinskii* varied more than that of *A. bracteata*; thus, we classified the *C. korshinskii* seeds as large (60–90 mg; ca. 67% of the total) or small (30–60 mg; ca. 33% of the total). The small *C. korshinskii* seeds were used only in one experiment. All experiments were carried out from May 2002 to March 2004. During the storage period in Japan, we found no indication of seed dormancy nor any reduction in seed germinability.

Mean winter temperature in Chinese deserts is below 0°C, and winter is an unfavorable season for seed germination and plant growth. In the eastern and central parts of deserts in China, where the two study species, as well as those used in our previous studies (Tobe et al., 2005b, 2006; Tobe and Gao, 2007), are distributed, precipitation occurs primarily in summer. For example, in Shapotou, which is a typical habitat for the two species investigated in this study, as well as for many of the other species investigated in our previous studies, daily precipitation during the summer rainy season often exceeds 16 mm, and it occurs at relatively short intervals. In contrast, daily precipitation in other seasons is usually less than 8 mm, and periods between precipitation events are usually separated by long dry periods (Tobe et al., 2005b).

Experimental Methods

All experiments were carried out in incubators maintained at 12-h 25°C/12-h 15°C, which is representative of temperatures in the habitats of these species in early summer, when seeds are expected to germinate. Seed germination and radicle growth in Petri dishes were examined in the dark following the method described in Tobe et al. (2005b).

To examine seedling emergence from sand, replicates of 10 or 16 seeds were sown on/in sand-filled cylindrical plastic pots (inside diameter 80 mm and sand surface area ca. 50 cm²) with a height of 50 mm (short pots) or 100 mm (tall pots). There was a circular drainage opening (diameter: 12 mm) at the bottom of each pot that was covered with cloth. Dry fine or coarse sand was used to fill the pots to a depth of 45 mm (short pots) or 90 mm (tall pots). In most experiments, we used fine sand (91% wt. was 63–250 µm), which had a particle-size distribution similar to that of sand dunes in China (Tobe et al., 2005b). However, in one experiment we used coarse sand (91% wt. was 250–600 µm) to examine the effects of particle size on seedling emergence. The pots were exposed to light in the 25°C part of the daily

thermoperiod. During the 12-h light period, the pots were illuminated with fluorescent lamps (photosynthetic photon flux density at the sand surface was 80–130 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Relative humidity in the incubator was generally 40–70% during the light period and 90–95% during the dark period. The pots were irrigated at the beginning of the light period by slowly and evenly dripping deionized water onto the sand with a pipette. They were observed daily, and emerging seedlings in each pot were counted. A seedling was considered to have emerged when its height above the sand surface exceeded 3 mm. For moisture condition in sand for each irrigation regime, refer to Tobe and Gao (2007).

Seedling Emergence from Seeds Sown on Surface of, or at a Depth of 10 mm in, Fine Sand and Irrigated Daily

Replicates of 16 seeds (large *C. korshinskii* seeds or *A. bracteata* seeds) were sown on the surface of, or at a depth of 10 mm in, fine sand in the short pots. The pots were initially irrigated with 16 mm P of water (where x mm P denotes irrigation equivalent to x mm precipitation) and were subsequently given 3 mm P of water at 1-d intervals (the [16 + 1/1] treatment) for 14 d. From pots in which seeds were sown on the sand surface, seeds were later transferred into Petri dishes, and germination was observed daily for an additional 10 d to determine whether seeds ungerminated after 14 d of irrigation were still viable.

Seedling Emergence from Seeds Buried at Different Depths in Fine or Coarse Sand and Irrigated under Different Regimes

Replicates of 10 seeds (large *C. korshinskii* seeds or *A. bracteata* seeds) were sown at depths of 10, 20, 30, 40, or 50 mm in fine or coarse sand in the tall pots. The pots were initially irrigated with 32 mm P of water and subsequently with 3 mm P of water at 1-d intervals (the [32 + 1/1] treatment) or at 4-d intervals (the [32 + 1/4] treatment) for 20 d (*C. korshinskii* seeds buried at 10–40 mm) or 30 d (all other seeds). To examine whether seeds that were buried deeply and that did not give rise to emerging seedlings had germinated, seeds buried at 50 mm were excavated from the sand after 30 d of irrigation in the pots and inspected for germination.

Seedling Emergence from Seeds Buried at a Depth of 10 mm in Fine Sand and Irrigated Once with Different Amounts of Water

To investigate the effect of a single irrigation on seedling emergence, replicates of 10 seeds (large *C. korshinskii* seeds or *A. bracteata* seeds) were sown at a depth of 10 mm in fine sand in tall pots, and the pots were initially irrigated with 8 or 16 mm P of water and subsequently were not irrigated at all for 14 d. For the treatment in which initial irrigation was 8 mm P, we determined whether seeds that did not give rise to emerging seedlings were viable by irrigating each pot with 8 mm P of water on day 14 after the initial irrigation and subsequently with 3 mm P of water at 2-d intervals (the [8 + 1/2] treatment) for an additional 12 d.

*Seedling Emergence from Small *C. korshinskii* Seeds Buried at a Depth of 10 or 30 mm in Fine Sand and Irrigated Once with Different Amounts of Water*

Replicates of 10 small *C. korshinskii* seeds were sown at a depth of 10 or 30 mm in fine sand in the tall pots. The pots were initially irrigated with 8, 12, 16, 24, or 32 mm P of water and subsequently were not irrigated at all for 16 d. For treatments in which the initial irrigation was 8 mm P, we determined whether seeds that did not

give rise to emerging seedlings were viable by irrigating the pots with 24 mm P of water on day 16 after the initial irrigation and observing seedling emergence for an additional 16 d.

Statistical Analysis

Student's *t*-test was used to test the significance of differences between two means. Two-way ANOVA or Tukey's test was used for comparison of multiple means. Percentage values were arcsine square-root transformed prior to statistical analysis.

Results

Seed Germination in Petri Dishes

Large *C. korshinskii* seeds moistened in Petri dishes in the dark germinated earlier than those of *A. bracteata* by ca. 1d (\times symbols in Figure 1). Germination percentages 10 d after moistening were $81 \pm 1.2\%$ (mean \pm standard error, $n = 4$) for *C. korshinskii* and $66 \pm 2.0\%$ for *A. bracteata*.

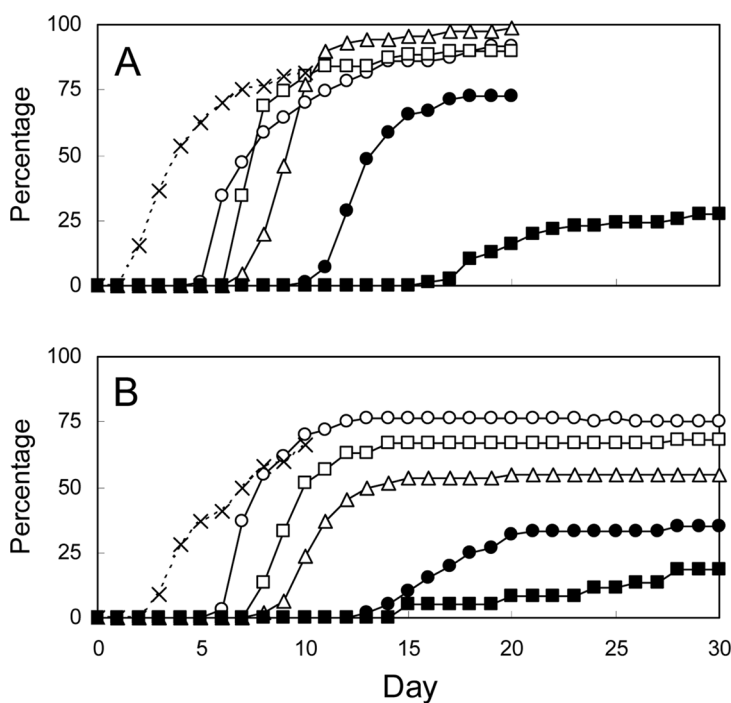


Figure 1. Changes over time in percentages of seedling emergence from seeds sown at different depths in fine sand in the [32 + 1/4] irrigation treatment. A: *C. korshinskii*, B: *A. bracteata*. Seed burial depth: ○: 10 mm, □: 20 mm, △: 30 mm, ●: 40 mm, ■: 50 mm. $n = 6$ for *A. bracteata* and $n = 7$ for *C. korshinskii*. The change over time in the percentage germination of seeds moistened in Petri dishes in the dark is also shown by \times symbols connected with a broken line ($n = 4$).

Seedling Emergence from Seeds Sown on Surface of, or at a Depth of 10 mm, in Fine Sand and Irrigated Daily

No seeds sown on the sand surface in the [16 + 1/1] treatment germinated in either species, but 10 d after they were transferred to Petri dishes, the total germination was $91 \pm 2.5\%$ for *C. korshinskii* and $61 \pm 5.0\%$ for *A. bracteata* (mean \pm standard error, $n = 5$). On the other hand, for seeds sown at a depth of 10 mm in the [16 + 1/1] treatment, seedlings of both species began to emerge 6 d after irrigation, and final percentages of seedling emergence were $86 \pm 14.6\%$ for *C. korshinskii* and $76 \pm 6.4\%$ for *A. bracteata* (mean \pm standard error, $n = 5$).

Seedling Emergence from Seeds Buried at Different Depths in Fine or Coarse Sand and Irrigated under Different Regimes

In both species and under both irrigation regimes, delay of seedling emergence increased with increase in seed burial depth (e.g., Figure 1). Generally, seedlings emerged 1–2 d earlier in *C. korshinskii* than in *A. bracteata*. Final percentages of seedling emergence decreased with increasing seed burial depth in both species, and they were generally higher in the [32 + 1/4] irrigation treatment than in the [32 + 1/1] irrigation treatment (Figure 2). There was no conspicuous difference between the two species in maximum seedling emergence depth (Figure 2). Two-way ANOVA (seed burial depth \times irrigation regime) indicated that in both species final seedling emergence percentage depended significantly ($P = 0.0005$) on both seed burial depth and irrigation regime. The percentage of seedling emergence of *C. korshinskii* seeds buried at 40 and 50 mm was higher in coarse sand than in fine sand in the [32 + 1/1] irrigation treatment (Figure 2).

Fairly high percentages of seeds of both species buried at 50 mm and excavated from the sand 30 d after irrigation had germinated, but few or none had reached the sand surface (Figure 2); lengths of seedlings that did not emerge were 20–150 mm (*C. korshinskii*) and 2–30 mm (*A. bracteata*). Since fairly high percentages of *A. bracteata* seeds buried at 50 mm did not germinate, the ungerminated seeds and germinated seeds with short radicles of *A. bracteata* were transferred to Petri dishes and moistened to examine their viability. No ungerminated seeds germinated, and there was no further growth of radicles that had emerged from seeds.

Seedling Emergence from Seeds Buried at a Depth of 10 or 30 mm in Fine Sand and Irrigated Once with Different Amounts of Water

For large *C. korshinskii* seeds and for *A. bracteata* seeds, a single irrigation of 8 mm P did not result in seedling emergence, whereas subsequent reirrigation with the [8 + 1/2] irrigation treatment resulted in a high percentage of seedling emergence (Table 1). A single irrigation of 16 mm P of water resulted in no seedling emergence from the large *C. korshinskii* seeds, whereas a fairly high percentage of seedlings emerged from small *C. korshinskii* seeds and *A. bracteata* seeds.

Percentage seedling emergence from small *C. korshinskii* seeds after a single irrigation was generally higher at a seed burial depth of 30 mm than at a depth of 10 mm (Table 2), but the difference was significant only for the 12 mm P treatment. Although a single 8 mm P irrigation did not result in seedling emergence from small *C. korshinskii* seeds, subsequent re-irrigation with 24 mm P of water 16 d after the

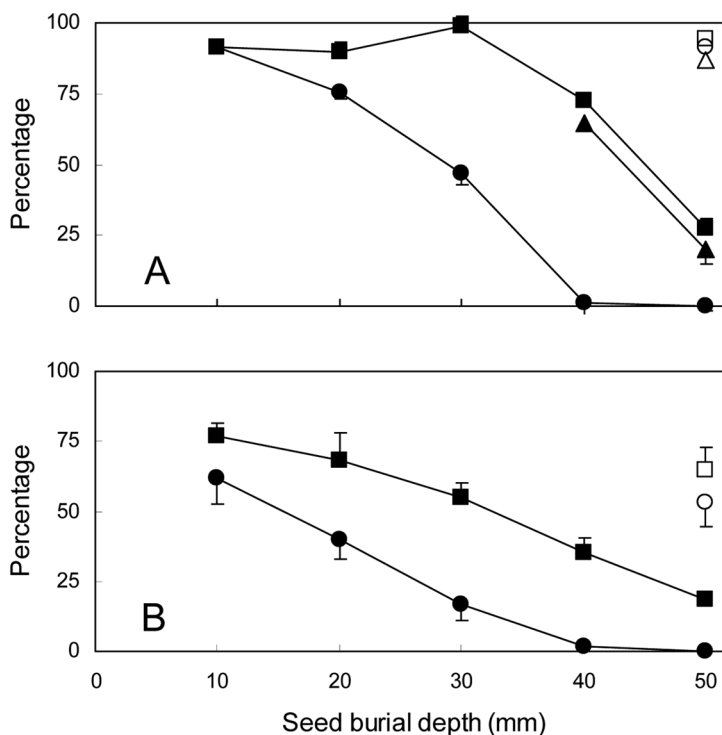


Figure 2. Final percentages of seedling emergence from seeds sown at different depths in fine or coarse sand and irrigated under different regimes (●: fine sand, [32 + 1/1], ■: fine sand, [32 + 1/4], ▲: coarse sand, [32 + 1/1]). A: *C. korshinskii*, B: *A. bracteata*. Final percentages of germinating seeds are also shown for seeds sown at 50 mm (○: fine sand, [32 + 1/1]; □: fine sand, [32 + 1/4]; △: coarse sand, [32 + 1/1]). Coarse sand treatment was carried out only for *C. korshinskii*. $n = 6$ for *A. bracteata* and $n = 7$ for *C. korshinskii*; bars indicate standard errors, which are shown only where they were larger than the symbol.

Table 1. Final percentages of seedling emergence of seeds buried at a depth of 10 mm in fine sand and treated with a single irrigation of 8 or 16 mm P of water. Since no seedlings emerged after a single 8 mm P irrigation, the pots were subsequently reirrigated with a single 24 mm P (small *C. korshinskii* seeds) or [8 + 1/2] (the other seeds)

Initial Irrigation	Final seedling emergence (%)		
	<i>C. korshinskii</i>		<i>A. bracteata</i>
	Large seeds	Small seeds	
8 mm P	0 (0)→68 (8.3)	0 (0)→30 (5.8)	0 (0)→74 (6.5)
16 mm P	0 (0)	47 (9.9)	59 (8.3)

Percentages of seedling emergence after reirrigation are shown at right of arrows. $n = 6$ for *A. bracteata* and $n = 7$ for *C. korshinskii*; standard errors are presented in parentheses.

Table 2. Final percentages of seedling emergence for small *C. korshinskii* seeds buried at a depth of 10 or 30 mm in fine sand and irrigated with different amounts of water. Since no seedlings emerged after a single 8-mm P irrigation, the pots were subsequently reirrigated with 24 mm P of water

Seed burial depth	Final seedling emergence (%)				
	8 mm P	12 mm P	16 mm P	24 mm P	32 mm P
10 mm	0 (0) c→30 (5.8)	6 (3.8) bc	47 (9.9) abc	57 (6.8) ab	56 (5.3) ab
30 mm	0 (0) c→4 (3.0)	63 (6.8) a	77 (6.4) a	67 (3.6) a	74 (3.0) a

Percentages of seedling emergence after the reirrigation are shown at right of arrows. Values with the same letter are not significantly different from each other ($P = 0.05$; Tukey's test). $n = 7$; standard errors are presented in parentheses.

8 mm P irrigation caused 30% and 4% of the seeds to produce emergent seedlings from the 10 and 30 mm depths, respectively. However, these percentages were considerably lower than those of seedling emergence after a single 24 mm P irrigation at the beginning of the study period (57% and 67%) (Table 2), indicating that the single 8 mm P irrigation reduced the number of viable seeds. For *C. korshinskii* seeds buried at 10 mm and reirrigated after the single 8 mm P irrigation, the percentage of seedling emergence (Table 1) was significantly higher ($P = 0.005$) from large seeds (68%) than from small seeds (30%), indicating that small seeds were more likely to lose viability by 8 mm P of irrigation. For small *C. korshinskii* seeds that were reirrigated after a single 8 mm P irrigation, percentage seedling emergence (Table 2) was significantly lower ($P = 0.005$) from seeds buried at 30 mm than from those buried at 10 mm (4% versus 30%).

Discussion

Dependence of Seedling Emergence on Seed Burial Depth

Comparison of maximum emergence depth among *C. korshinskii* (mean seed weight 65 mg), *A. bracteata* (5.7 mg), and the five species with medium-sized, nonphotosynthetic seeds in our previous studies (Tobe et al., 2005b; Tobe and Gao, 2007; mean seed weight 1.0–2.8 mg,) shows that larger seeds do not always improve seedling emergence. Despite the large difference in seed weight between *C. korshinskii* and *A. bracteata*, we found no conspicuous difference between the two species in the maximum seedling emergence depth. Moreover, seedling emergence from seeds buried at 40 mm was only 1% in *C. korshinskii* and 2% in *A. bracteata* in the [32 + 1/1] irrigation treatment (this study) versus 30% in *A. squarrosus* (mean seed weight 1.8 mg) in the [16 + 1/1] irrigation treatment (Tobe et al., 2005b). Many deeply buried seeds of both *C. korshinskii* and *A. bracteata* germinated, but seedling elongation was inhibited. Thus, ability of seedlings to emerge from deep burial in sand did not appear to be determined by seed size. The fairly large maximum seedling emergence depth in *A. squarrosus* seeds is because seedling elongation in this species was less inhibited than that of the other six species in moist sand (Tobe et al., 2005b).

The fact that seedling emergence was inhibited by the more frequent irrigation regime in *C. korshinskii* and *A. bracteata* (Figure 2) suggests that inhibition of

seedling growth in deep sand resulted from a higher moisture content deeper in the sand, where moisture persists due to the low evaporation rate (Bowers, 1982; Jalota and Prihar, 1986). A higher moisture content in the sand can result in an oxygen deficiency that inhibits normal seedling growth (Crawford, 1992). Furthermore, moisture can cause hardening of sand (Hornbaker et al., 1997; Halsey and Levine, 1998), which can impede seedling growth (Collis-George and Yoganathan, 1985a, 1985b; Tobe et al., 2005a, 2005b). Thus, it would be reasonable to interpret the suppression of seedling emergence of the two species in deep sand as the result of an oxygen deficiency and/or hardening of the sand caused by high moisture levels. Improved seedling emergence from coarse sand compared with emergence from fine sand could have resulted from a higher ratio of air to water and/or less hardening in coarse sand (Tobe et al., 2005a).

In the experiment in which seeds were buried deeply, the amount and frequency of irrigation ($[32 + 1/1]$ and $[32 + 1/4]$) were greater than the amount and frequency of precipitation that occurs naturally in the field. Thus, it might be argued that conditions for seedling emergence from deep sand may be more favorable in the field than under our experimental conditions, because the burial depth from which seedlings can reach the surface depends on the sand moisture conditions. However, field observations indicated that although *C. korshinskii* seeds are buried in sand up to a depth of 200 mm, seedlings emerged only from those buried at depths of less than 50 mm (Wen, 1992 cited in Zheng et al., 2004).

On the other hand, in shallow sand rapid evaporation can cause a moisture deficiency for seeds (Maun and Lapierre, 1986; Zhang and Maun, 1990b). Thus, in the present study suppression of germination of *C. korshinskii* and *A. bracteata* seeds sown on the sand surface may be due primarily to moisture deficiency. Similarly, the lower percentage seedling emergence from small *C. korshinskii* seeds buried at 10 mm than from those buried at 30 mm could have resulted from moisture deficiency. In the field, where evaporation from the sand surface is higher than that under our experimental conditions, seedling emergence from shallow depths in sand may be lower than under our experimental conditions. Suppression of seedling emergence of other species from shallow depths in sand has been observed in the field (Maun and Lapierre, 1986; Zhang and Maun, 1990a, 1990b; Yanful and Maun, 1995; Huang and Guterman, 1998). On the other hand, the fact that higher percentages of small *C. korshinskii* seeds appeared to have lost their viability after a single 8 mm P irrigation at a seed burial depth of 30 mm than at a depth of 10 mm indicates that seeds buried at shallow depths are more likely to remain viable after a precipitation event.

Dependence of Seedling Emergence on Irrigation

Larger *C. korshinskii* seeds evidently required a larger amount of water in a single irrigation for seedling emergence than did smaller seeds, suggesting that seed size can determine the fates of *C. korshinskii* seeds after a precipitation event. Also, when we compared the amount of a single irrigation required for seedling emergence from seeds buried at a depth of 10 mm among the two species in the present study and the five medium-seeded species in our previous studies, we found a general tendency for larger seeds to require more irrigation than for smaller seeds for seedling emergence. For example, although seeds of *C. korshinskii* and *A. bracteata* required a single irrigation of ≥ 16 mm P, seedlings of *B. dasyphylla* and *A. adscensionis* emerged

following a single, 8 mm P irrigation (Tobe et al., 2005b). An increase in the amount of irrigation results in a higher moisture content in sand and persistence of moisture for a longer period (Tobe and Gao, 2007). The requirement of a larger amount of water by larger rather than by smaller seeds for seedling emergence may have been due to a larger amount of water absorbed by larger seeds, which resulted in moisture deficiency in the sand adjacent to the seeds, thus preventing the seeds from imbibing enough water to germinate.

However, although seed size varied greatly among *C. korshinskii*, *A. bracteata*, and the five species with medium-sized seeds in our previous studies, there was no clear relationship among them between seed size and the amount of water required for seedling emergence. For example, although *A. squarrosus* seeds are much smaller than *A. bracteata* seeds and small *C. korshinskii* seeds, seeds in all three seed-size categories required a 16-mm P irrigation for seedling emergence. This suggests that interspecific differences in seed traits other than size influenced the responses of seeds to irrigation. In particular, rapid germination responses would favor germination in sand by allowing the seeds to absorb water before it was decreased by evaporation. The requirement of more water for seedling emergence in *A. squarrosus* than in the other four medium-seeded species (Tobe et al., 2005b; Tobe and Gao, 2007) may have been due primarily to slower germination in *A. squarrosus* than in the other four species. Also, more rapid germination in *C. korshinskii* seeds than in those of *A. bracteata* (Figure 1) may have counteracted the higher moisture requirement for germination of *C. korshinskii* seeds. The results suggest that the amount of water absorbed by seeds to germinate and rapidity of germination are crucial determinants of the amount of irrigation required for seedling emergence from sand.

Seedling Emergence Expected in the Field Conditions

Seeds of *C. korshinskii* and *A. bracteata* tested in the present study and those of the five species with medium-sized seeds in our previous studies germinated at temperatures that commonly occur between spring and autumn in many desert regions of China (Tobe et al., 2001, 2005b; Tobe and Gao, 2007). Moreover, seed dormancy did not appear to have crucial effects on germination. Therefore, it appears that germination of these species is determined primarily by water availability, which is determined by the amount and frequency of precipitation and depth of seed burial. Interspecific differences in the amount of water required for germination can result in differences in seedling emergence.

In Shapotou (see Materials and Methods) and many other parts of deserts in north-central China, precipitation occurs primarily in summer. Infrequent and small amounts of precipitation from autumn to spring will not result in seedling establishment of these seven species, although some proportion of seeds (especially, those of species with moisture-sensitive seeds) may germinate without resulting in surviving seedlings. Seedling establishment of these species would occur only during the summer rainy season.

The [8 + 1/2] and [16 + 1/1] irrigation treatments caused a high percentage of seedlings to emerge, even from the large *C. korshinskii* seeds (for [8 + 1/2], reirrigation in Table 1). Water content in sand in the summer rainy season in Shapotou occasionally becomes more favorable for seed germination than that in sand in the [16 + 1/1] treatment. Thus, for *C. korshinskii* and *A. bracteata*, as well as for the five medium-seeded species previously studied (Tobe et al., 2005b; Tobe and

Gao, 2007), high percentages of seeds buried at appropriate sand depths are expected to give rise to emergent seedlings. The large amounts of precipitation in the rainy season will moisten sand to relatively deep layers, and moisture deep in the sand persists for longer than that in shallow sand (Bowers, 1982; Jalota and Prihar, 1986). Thus, water availability in sand will not limit seed germination or seedling growth of these species except at shallow depths. When the nonphotoblastic seeds of these seven species are buried deeply, most seeds of five species, including *C. korshinskii* and *A. bracteata*, should germinate during this season without producing emergent seedlings and thus be lost from the seed bank (Tobe et al., 2005b; Tobe and Gao, 2007), whereas seeds of the other two species are expected to remain ungerminated and viable (Tobe et al., 2005b). On the other hand, at shallow depths, where water availability limits seed germination, some proportion of the seeds will remain ungerminated and viable, even during the rainy season and thus will germinate in the future if they become buried more deeply. The proportion of shallowly buried seeds that remain ungerminated depends on the amount of water they need to absorb to germinate and on the rapidity of their germination.

Although there were some differences among the seven species in responses of seeds and seedlings in sand, no clear seed size dependence is evident among these species in seedling emergence. For nonphotoblastic seeds, seed size does not appear to be a strong determinant of the proportion that produces emergent seedlings under the climatic conditions in Shapotou or in many other parts of deserts in north-central China. On the other hand, many photoblastic seeds, for which the light requirement for germination restricts their germination to dry shallow sand depths (Tobe et al., 2006), remain ungerminated and viable even after the rainy season. Thus, great differences in seedling emergence or seed bank behavior in desert dunes in China are expected between species with small photoblastic seeds and those with larger non-photoblastic seeds.

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