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Seedling emergence on Sonoran Desert dunes

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Seedling emergence of psammophiles (plants restricted to active dunes) was examined with germination experiments and with field observations at the Algodones Dunes, California, U.S.A., and the Sierra del Rosario Dunes, Sonora, Mexico. In the field, perennial psammophiles germinated in response to smaller rainfall triggers (≥ 10 mm) than other woody desert plants (≥ 16 mm). In germination experiments, seedlings of three perennial psammophiles, *Astragalus magdalenae* var. *peirsonii, Helianthus niveus* subsp. *tephrodes*, and *Palafoxia arida* var. *gigantea*, emerged in larger numbers from greater soil depths than those of three nonpsammophiles, *Cercidium microphyllum, Fouquieria splendens*, and *Palafoxia arida* var. *arida*. Seed size for these six species did not correlate in any consistent fashion with emergence depth, suggesting that food reserves are not the only variable that ensures emergence of deeply buried psammophile seeds.

Keywords: dunes; seed size; seedling emergence; Sonoran Desert

Introduction

In the Sonoran Desert of the south-western United States and north-western Mexico, mass germination and emergence of the dominant perennials may be an infrequent occurrence that depends on unusual climatic events (Bowers, 1994). For example, *Agave deserti* Engelm., which germinated in only one of 17 years in the north-western Sonoran Desert, requires above-normal rains from winter–spring frontal storms (Jordan & Nobel, 1979, 1981), and *Fouquieria splendens* Engelm., which germinated in three of 8 years in the northern Sonoran Desert, needs heavy and unusually early summer rains (Bowers, 1994). Recently emerged seedlings of most woody desert plants suffer high mortality as a result of seasonal drought and predation, and recruitment is rare (Shreve, 1911, 1917; Sherbrooke, 1977, 1989; Goldberg & Turner, 1986; McAuliffe 1986, 1990).

On active sand dunes in the Sonoran Desert, perennial seedling establishment is subject to these constraints and also to certain substrate-specific hazards. Accumulating sand may bury seeds so deeply that newly germinated seedlings exhaust their energy reserves before they can emerge. A common adaptation among psammophiles, or plants restricted to active dunes, is large seeds containing abundant food reserves. Psammophile seedlings can emerge from depths as great as 14 cm (Van der Valk,

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1974), although depths of 4–8 cm (Maun & Riach, 1981; Zedler *et al.*, 1983) may be more typical. After emergence, the seedlings are extremely vulnerable to burial and excavation. For example, during a 42-day period on the Algodones Dunes, sand accumulation ranged from 1 cm to > 15 cm, and only 29% of 94 perennial seedlings survived 6 weeks. Where sand accumulation exceeded 15 cm, no seedlings survived. The highest survival was where sand accumulation was 1·3 cm and 7·6 cm (Bowers, unpublished data). Seedlings of woody desert plants on rocky substrates can show much higher early survivorship: in one study, 63% of newly emerged *Cercidium microphyllum* (Torr.) Rose & Johnst. seedlings lived at least 6 weeks (Shreve, 1911); in another, 79% of newly emerged *Simmondsia chinensis* (Link) Schneid. seedlings lived at least 8 weeks (Sherbrooke, 1977).

The favorable moisture status of dune sand counters these constraints. Soil water is more readily available to plants in sand than in clay (Chadwick & Dalke, 1965), which might facilitate seed imbibition and germination. Moreover, even during drought, dune sand retains moisture at depths > 30 cm (Shreve, 1938; Chadwick & Dalke, 1965; Sharp, 1966; Prill, 1968; Bowers, 1982), which suggests that seedlings capable of rapid root elongation might readily survive seasonal drought.

This paper compares perennial seedling emergence on and off Sonoran Desert sand dunes using laboratory experiments and field observations. In the laboratory, seedling emergence of several Sonoran Desert psammophiles was determined and compared with similar data from nonpsammophiles growing nearby. In the field, seedling emergence of several psammophiles was monitored, and the conditions necessary for germination and emergence were determined. The field work was conducted on two of the largest dune fields in the western Sonoran Desert, the Algodones Dunes, Imperial County, California, and the Sierra del Rosario Dunes, Sonora, Mexico. The initial hypotheses were: (1) seeds of psammophiles should be larger (heavier or longer) than those of closely related nonpsammophiles; (2) larger seeds should emerge in higher numbers from greater depths than smaller seeds; (3) seeds of psammophiles should emerge in higher numbers from greater depths than those of nonpsammophiles; and (4) in a season of average rainfall, more seedlings should emerge on dunes than on nondune substrates nearby.

Materials and methods

Study area

The Algodones Dunes of south-eastern California (Fig. 1) lie at 90 m a.s.l. within the Lower Colorado Valley subdivision of the Sonoran Desert (Shreve, 1951). Active transverse dunes 60–90 m high dominate the dune field, forming an unsystematic mass of peaks and valleys (Norris & Norris, 1961). Low, stable dunes around the perimeter confine the field within an area 64 km long and 5–10 km wide.

At the nearest weather station, Yuma Valley, Arizona, about 30 km east of the dune field, the climate is warm and arid. Annual rainfall averages 65 mm, and the average January and July temperatures are 11·4°C and 32·7°C (Sellers & Hill, 1974).

Dominant plants in the central, active portion of the dune field include the psammophiles *Helianthus niveus* (Benth.) Brandg. subsp. *tephrodes* (Gray) Heiser, *Eriogonum deserticola* Wats., *Panicum urvilleanum* Kunth., *Croton wigginsii* Wheeler, *Palafoxia arida* Turner & Morris var. *gigantea* (Jones) Turner & Morris, and *Astragalus magdalenae* Greene var. *peirsonii* (Munz & McBurney) Barneby. On stable marginal dunes, dominance is shared by *Ephedra trifurca* Torr., *Ambrosia dumosa* (Gray) Payne, *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., *Psorothamnus emoryi* (Gray) Rydb., and *Croton wigginsii*. On rocky or gravelly substrates near the dune field, dominants include *Cercidium floridum* (Benth.) ex Gray, *Fouquieria splendens* and *Larrea tridentata*.

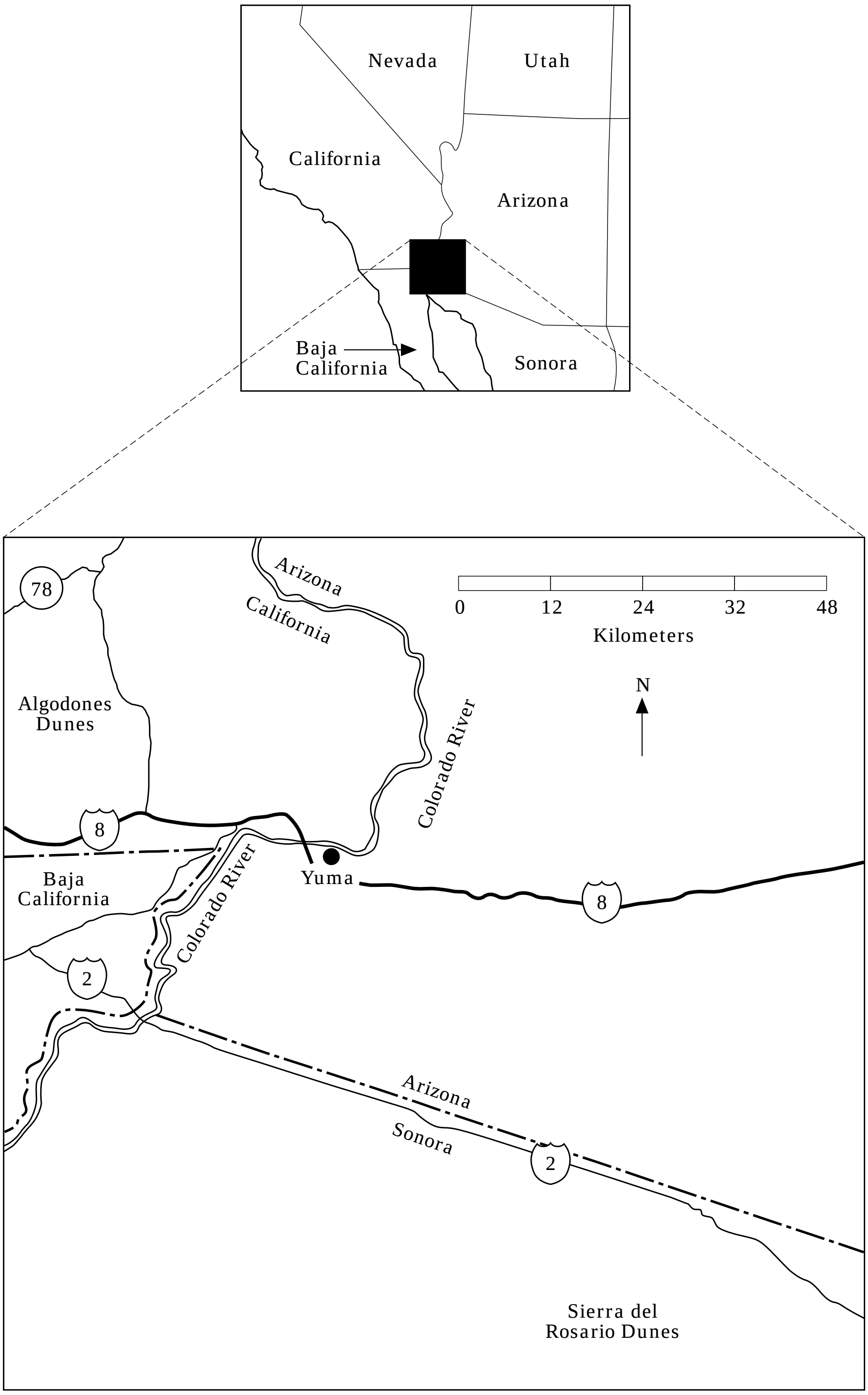

Figure 1. Map of study area showing locations mentioned in text.

The Sierra del Rosario dunes (Fig. 1) in north-western Sonora, Mexico, comprise a vast field of active dunes and stable sand sheets covering about 4500 km^2 (Felger, 1980). The northern end of the dunes field lies at about 125 m a.s.l. This area also lies within Shreve's (1951) Lower Colorado Valley subdivision.

There is no long-term weather station at or near the dunes. Short-term weather data from the site show that temperatures may drop below freezing in winter and often exceed 38°C between April and October (Felger, 1980). Annual rainfall is less than 100 mm; some years are without measurable rain (Felger, 1980).

Perrenial dominants on the dunes include *Eriogonum deserticola*, *Ambrosia dumosa*, *Ephedra trifurca*, *Hilaria rigida* (Thurb.) Benth. ex Scribn. and *Psorothamnus emoryi*. *Helianthus niveus* subsp. *tephrodes* and *Palafoxia arida* var. *arida* are also present (Felger, 1980). On rocky or gravelly substrates near the dune field, dominants include *Larrea tridentata*, *Fouquieria splendens*, *Ambrosia dumosa* and *Cercidium floridum*.

Field observations

The Algodones Dunes were visited on 14 March 1981, 19 May 1983, and 27 February 1984 to assess perennial seedling emergence. Recently emerged seedlings of the obligate psammophiles *Helianthus niveus* subsp. *tephrodes*, *Astragalus magdalenae* var. *peirsonii* and *Palafoxia arida* var. *gigantea* were observed on each occasion. In 1981 and 1983, the seedlings most likely emerged several weeks or more before the observation date. Weather records from Yuma Valley were used to determine the likely rainfall triggers for each emergence event. A triggering rain is the smallest single rain capable of stimulating emergence (Bowers, 1994). In the cool season, emergence might not occur until several weeks after the trigger (Bowers, 1994). For this study, cool-season rains were rare enough that in each year a single large storm stood out as the most likely trigger. If there was some doubt, such as two large rains close to the time of emergence, the first of the two was chosen. At Yuma Valley, likely triggering rains occurred on 12 January 1981 (13 mm), 9 December 1982 (24 mm), and 1 December 1983 (13 mm) (Table 1).

Table 1. *Cool-season storms ≥5 mm) at Yuma Valley, Arizona, U.S.A., 1980–1984*

Season	Date	Rain (mm)
Nov. 1980–April 1981	12 Jan. 1981	13·0
	9 Feb. 1981	5·0
	2 March 1981	10·0
	5 March 1981	13·0
	6 March 1981	13·0
Nov. 1981–April 1982	22 Jan. 1981	8·0
	25 Feb. 1981	5·0
	15 March 1981	22·0
Nov. 1982–April 1983	9 Dec. 1982	24·0
	10 Dec. 1982	19·0
	28 Jan. 1983	9·0
	3 Feb. 1983	9·0
Nov. 1983–April 1984	1 Dec. 1983	13·0
	25 Dec. 1983	10·0
	10 April 1984	10·0

On 19 March 1982, emergence of dominant perennials at the north end of the Sierra del Rosario was measured using eight 15 m line transects, five on active dunes and three on gravelly flats nearby. Sixty-eight subplots, each 20 cm^2, were systematically alternated on either side of the line. The density (number m^2) of all seedlings, whether annual or perennial, in each subplot was determined. Total area sampled along each line was 2·72 m^2. Seedling emergence on and off the dunes was compared by calculating average density in each transect. Examination of Yuma Valley precipitation records suggested that triggering rains of 8–10 mm might have occurred on or about 21 January 1982.

Germination experiments

On the Algodones Dunes, seeds of three psammophiles, *Helianthus niveus* subsp. *tephrodes*, *Astragalus magdalenae* var. *peirsonii*, and *Palafoxia arida* var. *gigantea*, were collected in May 1983. Also in May 1983, seeds of two nonpsammophiles, *P. arida* var. *arida* and *H. niveus* subsp. *canescens*, were collected on unnamed dunes about 32 km south of Sonoyta, Sonora, Mexico. To provide a larger range of non-psammophile seed sizes, seeds of two widespread Sonoran Desert woody plants, *Cercidium microphyllum* and *Fouquieria splendens*, were collected on Tumamoc Hill, Tucson, Arizona, in June 1993. For each species, average seed length (n = 50) and weight (for *Cercidium*, n = 60; for all others, n = 150) were determined.

In the laboratory, germination of equal numbers of scarified and untreated seed were tested on moist filter paper at room temperature (*c*. 25°C). Seeds were scarified by cutting the seed coat with a razor blade. Seeds of *Helianthus niveus* subsp. *tephrodes*, *Astragalus magdalenae* var. *peirsonii* and *Cercidium microphyllum* required scarification. Those of *Palafoxia arida* var. *gigantea*, *P. arida* var. *arida* and *Fouquieria splendens* needed no pretreatment. *Helianthus niveus* subsp. *canescens* did not germinate. Seeds of each species (with the exception of *H. niveus* subsp. *canescens*) were planted in dune sand in waxed cardboard cartons 7 cm square and 19 cm deep. For each species, 10 seeds were planted at each of five depths (1, 3, 5, 8 and 12 cm below the surface). All seeds in a given carton were planted at the same depth. The sand was kept moist. Small holes in the bottom of each carton provided drainage. There were two replicates of the entire experiment. The number of seedlings that emerged from each depth was recorded daily. Emergence was considered complete when no new seedlings appeared for 12 days. Due to resource limitations, the species were tested sequentially, *Cercidium* and *Fouquieria* in 1994, the remainder in 1984. In the laboratory, average ambient air temperatures (day/night) during the experiment were as follows: for *Astragalus*, 29°C/20°C over 28 days; for *Helianthus*, 34°C/25°C over 16 days; for *Palafoxia*, 34°C/24°C over 23 days; for *Cercidium*, 24°C/19°C over 27 days; for *Fouquieria*, 25°C/19°C over 26 days. These temperatures are similar to those that would be experienced during germination in the wild.

A two-way analysis of variance was performed in which seedling emergence was the dependent variable and species and depth were the independent variables. Average emergence at different depths of three psammophiles (*Astragalus magdalenae* var. *peirsonii*, *Palafoxia arida* var. *gigantea*, *Helianthus niveus* subsp. *tephrodes*) and of three nonpsammophiles (*Fouquieria splendens*, *Cercidium microphyllum*, *P. arida* var. *arida*) was calculated, then another two-way analysis of variance was performed using seedling emergence as the dependent variable and habitat and depth as the independent variables. The same analyses were repeated with the omission of *Cercidium*, which had much heavier seeds than the other species. Because it has been suggested that heavier seeds emerge from greater depths, seed weight and maximum depth of emergence were compared using Pearson rank order correlation, first with *Cercidium*, then without.

Results

Field observations

On the Sierra del Rosario Dunes, seven plant species (four annuals and three perennials) were recorded in the five transects (Table 2). Perennial seedling density on the dunes averaged 4·26 m^{-2}. For annual seedlings, average density was 3·90 m^{-2}. Five species of annuals were recorded in the desert pavement transects (Table 2), where the density of annual seedlings was 76·35 m^{-2}. There were no perennial seedlings in the desert pavement transects, nor did a thorough reconnaissance of the area suggest that any perennial seedlings had emerged off the dunes that spring.

Germination and emergence experiments

As expected, seeds of two of the obligate psammophiles (*Helianthus niveus* subsp. *tephrodes* and *Palafoxia arida* var. *gigantea*) were about twice as heavy and half again as long as those of their nondune counterparts (*H. niveus* subsp. *canescens* and *P. arida* var. *arida*) (Table 3).

The first analysis of variance showed a highly significant interaction between emergence of the six different species and the depths at which they were planted (species × depth interaction, $F = 4·45$, $p < 0·001$). A *post hoc* *F*-test showed that there were significant differences among the six species in the number of seedlings that emerged (species, $F = 13·55$, $p < 0·001$). In the second analysis of variance, the interaction between depth of planting and habitat (psammophile *vs.* nonpsammophile) was highly significant (depth × habitat interaction, $F = 16·01$, $p < 0·001$). A *post hoc* *F*-test showed that there were also significant differences between emergence of

Table 2. *Density (seedlings m^{-2}) of annuals and perennials on dunes and gravelly flats at the Sierra del Rosario, Sonora, Mexico, March 1982**

Species	Dunes	Gravelly flats
ANNUALS		
Camissonia claviformis Torr & Frem.	–	0·25 (0·12)
Chamaesyce platysperma (Engelm.) Shinners	0·29 (0·21)	–
Chaenactis carphoclinia Gray	–	1·47 (1·47)
Dicoria canescens Gray	2·87 (0·66)	–
Mentzelia multiflora (Nutt.) Gray	0·37 (0·17)	–
Monoptilon bellioides (Gray) Hall	–	4·66 (4·66)
Oenothera deltoides Torr. & Frem.	0·37 (0·28)	–
Phacelia ambigua Jones	–	0·12 (0·12)
Plantago insularis Eastwood	–	69·85 (24·89)
All annuals	3·90 (0·85)	76·35 (18·34)
PERENNIALS		
Croton wigginsii	1·47 (0·66)	–
Eriogonum deserticola	1·54 (0·50)	–
Helianthus niveus	1·25 (0·83)	–
All perennials	4·26 (1·08)	–

*For each species, density was calculated as the mean of five (dunes) or three (gravelly flats) transects. For all annuals and all perennials density was calculated as the mean of means. SE is given in parentheses.

Table 3. *Seed weights and lengths of seven perennials from the western Sonoran Desert*

Species	Weight (mg)	Length (mm)*
PSAMMOPHILES		
Astragalus magdalenae	15·0	4·7 (0·07)
Helianthus niveus subsp. *tephrodes*	7·0	6·8 (0·09)
Palafoxia arida var. *gigantea*	6·0	15·7 (0·38)
NONPSAMMOPHILES		
Cercidium microphyllum	148·3	9·0 (0·11)
Fouquieria splendens	6·7	10·3 (0·17)
Helianthus niveus subsp. *canescens*	3·0	4·2 (0·07)
Palafoxia arida var. *arida*	3·0	10·9 (0·15)

*SE in parentheses.

psammophiles and nonpsammophiles (habitat, $F = 10{\cdot}98$, $p < 0{\cdot}01$). Omitting *Cercidium* from the analysis altered the results only slightly. The species × depth interaction was still significant ($F = 5{\cdot}13$, $p < 0{\cdot}001$), as was the habitat × depth interaction ($F = 7{\cdot}64$, $p < 0{\cdot}01$).

All species emerged in high numbers from the shallowest depth (1 cm) (Fig. 2(a)). *Fouquieria splendens* failed to emerge from 5 cm or below (Fig. 2a). The deepest level of emergence was 8 cm (*Palafoxia arida* var. *gigantea* and *Cercidium microphyllum*). Many seeds germinated at 12 cm but none emerged. Emergence of *Helianthus niveus* subsp. *tephrodes* was uniformly poor at all depths, perhaps due to low seed viability. The difference between psammophiles and nonpsammophiles was greatest at the 3 and 5 cm depths, with psammophiles emerging in larger numbers than non-psammophiles (Fig. 2(b)). At the shallowest depth, nonpsammophiles emerged in greater numbers than psammophiles. The difference between psammophile and

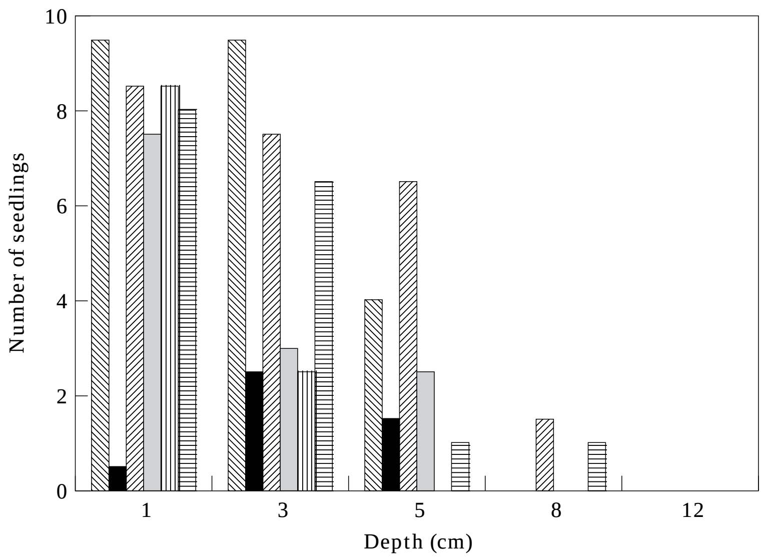

Figure 2(a). Total seedling emergence of six species at five depths. Values represent average of two replicates. Obligate psammophiles: (▧) = *A. magdalenae*; (■) = *H. niveus tephrodes*; (▨) = *P. arida gigantea*. Nonpsammophiles: (□) = *P. arida arida*; (▥) = *F. splendens*; (▤) = *C. microphyllum*.

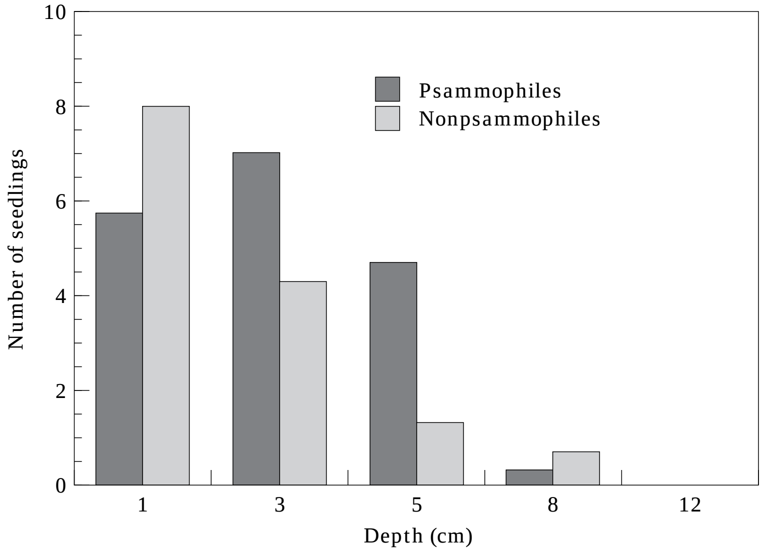

Figure 2(b). Average total seedling emergence of three psammophiles (*Astragalus magdalenae* var. *peirsonii, Palafoxia arida* var. *gigantea, Helianthus niveus* ssp. *tephrodes* ■) and three nonpsammophiles (*Palafoxia arida* var. *arida, Fouquieria splendens, Cercidium microphyllum* □) (at five depths. Values represent average of two replicates.

nonpsammophiles at the 8 cm depth was not statistically significant. There were no statistically significant relations between seed weight and maximum depth of emergence.

Discussion

As expected, psammophiles generally emerged in greater numbers at deeper levels than nonpsammophiles. This trend was particularly marked at depths of 3 and 5 cm. Within a given genus, large seeds are apparently better adapted to active dunes than small ones, perhaps because their larger food reserves enable them to emerge even when deeply buried. Seeds of the obligate psammophile *Astragalus magdalenae* var. *peirsonii*, for example, are the largest of any North American *Astragalus* (Barneby, 1964). Harper *et al*. (1970) noted that there is a trade-off between seed size and seed numbers such that large-seeded plants typically produce fewer seeds. On sand dunes, increasingly larger seeds would almost certainly be able to emerge from increasingly greater depths; however, seed number might eventually fall below the level at which populations could sustain themselves.

Unexpectedly, seed size for the six species studied did not appear to correlate in any consistent fashion with emergence depth. In clay soils, the heavy seeds of *Cercidium microphyllum* emerge readily from depths of 4–5 cm, where they have been buried by rodents (McAuliffe, 1990; Bowers, 1994). Their relatively large size, perhaps an adaptation to rodent burial, evidently does not facilitate emergence from depth on sand dunes. The poor correlation between seed size and depth of emergence seen in this study suggests that food reserves are not the only variable that ensures emergence of deeply buried psammophile seeds. Morphological traits may also play a role; for example, the epicotyls of psammophiles may extend to greater lengths than those of nonpsammophiles.

At the Sierra del Rosario, perennial seedling emergence differed markedly between dune and desert pavement. Seedlings of *Eriogonum deserticola*, *Croton wigginsii*, and

Helianthus niveus, all psammophiles, were frequent on the dunes (Table 2). They apparently germinated and emerged in response to a moderate storm of 8–10 mm in January 1982. On rocky flats nearby, where *Encelia farinosa* Gray ex Torr., *Larrea tridentata*, and *Ambrosia dumosa* were the dominants, no perennial seedlings were found (Table 2). Germination triggers reported in the literature are warm-season rains of 16–25 mm for *L. tridentata* (Went & Westergaard, 1949; Ackerman, 1979), cool-season rains of at least 19 mm for *E. farinosa* (Bowers, 1994), and warm- or cool-season rains of at least 25 mm for *A. dumosa* (Ackerman, 1979). These and other woody perennials in the Sonoran Desert apparently maximize their chances for survival by germinating only in response to substantial storms (Bowers, 1994). Given the rainfall pattern of November 1981–February 1982, no seedlings of *Ambrosia* or *Encelia* were to be expected in March 1982, and none were found. Seedlings of sand dune perennials apparently need less rain for germination and emergence than those of nondune desert plants, perhaps because sand particles hold water at much less negative matrix potentials than clay or silt particles (Chadwick & Dalke, 1965), thus making moisture more available for seed imbibition and germination.

Only a few woody plants in the Sonoran Desert are known to have persistent seed banks, that is, seeds that last in the soil 1 year or longer (Kemp, 1989; Bowers, 1994). Hard-coated leguminous seeds, e.g. *Cercidium* spp., *Acacia* spp. and *Prosopis velutina* Woot., however, can survive in the soil for at least 2 years (McAuliffe, 1990; Bowers, 1994). Persistent seeds banks are often found in early successional communities or in communities subject to natural disturbance, such as fire (Thompson, 1992). At various Great Lakes dunes in Ontario, Canada, buried seeds of several psammophiles remained viable in the soil for more than 1 year (Zhang & Maun, 1994); in this case, sand movement could be considered the disturbance for which a persistent seed bank is adaptive. It is virtually certain that the hard-seeded *Astragalus magdalenae* var. *peirsonii* has a persistent seed bank, and it seems likely that other perennial psammophiles in the Sonoran Desert also do.

Because of the abundance of *Plantago insularis* Eastwood, annual seedlings at the Sierra del Rosario were far more numerous on desert pavement than on dunes (Table 2). Of the many desert annuals that depend upon seed banks for long-term survival, a few risk germination after relatively light rains. In the Mojave Desert, scattered germination of annuals occurs with triggers as small as 15 mm (Beatley, 1974). Annuals that germinate after light rains typically risk only a small proportion of their total seed bank; the rest remain dormant (Philippi, 1993). Obligate perennial psammophiles behave more like risk-taking annuals than they do like risk-avoiding perennials.

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