Irrigation and fertilization effects on seed number, size, germination and seedling growth: Implications for desert shrub establishment

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Irrigation and fertilization effects on seed number, size, germination and seedling growth: implications for desert shrub establishment

A. N. Breen · J. H. Richards

Abstract Plants with limited resources adjust partitioning among growth, survival, and reproduction. We tested the effects of water and nutrient amendments on seed production, size, and quality in *Sarcobatus vermiculatus* (greasewood) to assess the magnitude and importance of changes in reproductive partitioning. In addition, we assessed interactions among the environment of seed-producing plants (adult plant scale), seed size, and seedling microenvironment (seedling scale) on successful seedling establishment. Interactions of these factors determine the scale of resource heterogeneity that affects seedling establishment in deserts. Both total number of seeds produced per plant and seed quality (weight and germination) increased significantly in the enriched treatment in a 3-year field experiment. Seedling length 3 days after germination and seed N concentration, other measures of seed quality, were higher for seed from both irrigated and enriched plants than for seed from control plants. Field *S. vermiculatus* seed production and quality can be substantially increased with irrigation and nutrient enrichment at the adult plant scale and this allows management of seed availability for restoration. However, based on a greenhouse study, seedling environment, not the environment of the seed-producing plant or seed size, was the most important factor affecting seedling germination, survival, and growth. Thus it appears that production of more seed may be more important than improved seed quality, because higher quality seed did not compensate for a low-resource seedling environment. For both natural establishment and restoration this suggests that heterogeneity at the scale of seedling microsites, perhaps combined with fertilization of adult shrubs (or multi-plant patches), would produce the greatest benefit for establishing seedlings in the field.

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Introduction

Plants with limited resources must partition them among growth, survival, and reproduction (Harper 1977; Ungar 1978). Plants change reproductive partitioning by changing the number, size, or quality of seed they produce (Janzen 1977; Stanton 1984). Plants with more resources can produce a greater number of large, high-quality seeds (Hou and Romo 1998; Drenovsky and Richards 2005). Although variation in seed size in natural populations occurs among plants within populations (Janzen 1977), seed size also varies substantially within single plants (Baker 1972; Weiner et al. 1997; Sousa et al. 2003). Seedling establishment is affected by this plasticity in reproductive partitioning through effects of seed size, quality, or dispersal structures as well as by seed nutrient stores (Harper 1977; Dolan 1984; Cheplick and Sung 1998).

Seedlings from larger seeds have at least an initial advantage over smaller seeds, so should be better able to establish, especially under stressful conditions and/or when competing in microsites with seedlings from smaller seeds

(Dolan 1984; Stanton 1984). Many studies have documented effects of seed size on seedling survival and eventual plant productivity and fecundity (Schimpf 1977; Dolan 1984; Cheplick and Sung 1998). Evidence on the duration of this "head start" advantage is not consistent, possibly because seldom has this been tested in stressful or competitive environments, and results from greenhouse and field studies differ depending on the environment, timing of emergence, and nutrient availability (Stanton 1984; Yanful and Maun 1996; Sousa et al. 2003). Many studies have focused on agronomic or weedy species grown in fertile soils and have found that large seeds result in greater grain yield (Martincic et al. 1997; Stougaard and Xue 2004), changed protein composition (Triboi et al. 2003), better early performance (Kristensen 2003), higher rates of germination (Martincic et al. 1997), and greater adventitious root growth under water-logged conditions (Singh and Singh 2003).

Studies focusing on the effects of seed size variation in non-agricultural, ecological situations are limited, however. One example focused on variation in seed size in natural populations of *Impatiens capensis* (Waller 1982), but many studies have examined overall seed-size effects between species, not the effects of seed size variation within an individual species (Green and Juniper 2004). However, seed size has been found to be a good predictor of early seedling growth (Sousa et al. 2003) and competitive ability (Dolan 1984; Stanton 1984), but not final plant biomass (Dolan 1984) or long-term seedling survival (Moles and Westoby 2004). Evidence supporting direct effects of maternal environment on seedling success is patchy, but generally shows that maternal effects, related to precipitation and nutrient levels, can contribute substantially to the size and subsequent success of a seedling (Roach and Wulff 1987). So, seed size may be important only during the early stages of seedling establishment, not for final plant biomass, depending on the seedling environment that supports the germinating seed. But, if nutrient availability in the environment that the seed germinates in is low, seed size may prove to determine ultimate seedling success.

The effects of water and nutrient availability on seed production by adult shrubs and seedling growth and survival in microsites are particularly important in desert basin habitats like the saline, alkaline play a at Owens Lake, California where this study was conducted. Soils at the field site are very stressful for plant growth because of high salinity, low nutrient availability, poor water holding capacity, and B toxicity (Dahlgren et al. 1997; James et al. 2005). In addition, diversion of water from the Owens River early in the twentieth century resulted in a dry lake bed and generation of fine particulate dust from the dry playa has created a severe air pollution hazard that must be reduced significantly or eliminated for both health and aesthetic reasons

(Dickey et al. 2005). Although seedling establishment is currently very low (Donovan et al. 1997; Fort and Richards 1998; Drenovsky and Richards 2005), adult *Sarcobatus vermiculatus* (Hook.) Torrey (Chenopodiaceae, greasewood) shrubs are able to withstand dry, high-salinity environments, and, as some of the longest-lived growth forms on the playa, are critical to long-term vegetation stability. Elucidating factors at the adult plant scale affecting seed production and quality, as well as interactions with factors that affect subsequent seedling establishment at smaller spatial scales, is important for a better understanding of population and vegetation processes that affect desert ecosystem resilience to disturbance (Whitford et al. 1999). Understanding these scale-dependent factors and interactions will also be useful for management of restoration and dust mitigation projects.

We assessed effects that the resource environment has on the reproductive success of the native, salt-tolerant shrub, *S. vermiculatus*. Field experiments were conducted to document effects of adult plant resource environment on seed production and quality and a greenhouse study was conducted to test the effects of seed size and seedling microenvironment on seedling performance. We hypothesized that: (1) water and nutrient amendments would increase adult shrub seed production and seed size; (2) larger seeds would be of higher quality (germinate faster, grow faster, and have higher N content); (3) larger seeds would be more likely to produce surviving seedlings than smaller seeds; and (4) the effect of seed size on seedling growth and survival would be more pronounced under stressful, low-nutrient conditions. Together, the results document the interacting effects of maternal and seedling environments on seedling establishment in stressful environments.

Materials and methods

Field studies

Owens (dry) Lake, California, USA (36°30′N, 118°W; 1,083 m elevation) is located on the eastern side of the southern Sierra Nevada with mean annual precipitation of 113 mm. Playa soils are extremely alkaline (pH ~ 10), saline (4.4–7.7 S m^{-1}), and have high B concentrations (Dahlgren et al. 1997). *Sarcobatus vermiculatus* is abundant surrounding the Owens playa and withstands extreme salinity, B toxicity, low water and nutrient availability, high winds, heat, and other stresses (Donovan et al. 1997; Dodd and Donovan 1999; Donovan and Richards 2000). To measure seed production and quality responses to maternal environment in *S. vermiculatus*, we created three environments (treatments) for naturally established, seed-producing plants: control (native, unamended), irrigated, and an "enriched"

environment that was both irrigated and fertilized annually in early spring (2001–2003) with a macronutrient fertilizer including N, P, K, Ca, and Mg (60 g N, 13 g P, 174 g K, 235 g Ca and 162 g Mg added as slow-release KNO_3, triple super phosphate, $CaSO_4 \times 2H_2O$, and $MgSO_4 \times 7H_2O$; all per plant). Treatments were applied in a randomized complete block design with five blocks and one shrub per treatment per block.

In August 2001 and 2002, nylon mesh bags were placed over two, randomly selected, representative branches per shrub and tied at both ends. Because seed production was variable between branches within plants, we increased the number of sub-sample branches to four per plant in 2003. Sub-sample values within each replicate plant were averaged. In November each year, mature seeds were collected and air-dried for 3 months. In addition, 300 seeds per plant were collected from throughout the canopy to measure range in seed weight within each plant for each treatment.

We measured seed production (seed number/cm of branch) and length, width, weight, and viability of seeds. Each seed was hand-scarified on 100-grit sandpaper. All seeds from each sub-sample (one nylon mesh bag) were placed on moist filter paper in a sealed dish and germination was observed. Scarified *S. vermiculatus* seeds germinate rapidly (1 h–3 days) and were visually inspected for an embryo. We repeated this study in 3 years that ranged from wet to very dry [122, 38, and 254 mm precipitation for 2001, 2002, and 2003 "water years" (1 October–30 September), respectively].

Seed quality was assessed by germination percentage, by seedling length 3 days after imbibition, and by seed N concentration [determined on dried seeds using a C/N analyzer (Carlo Erba NA 1500; Carlo Erba, Milan)]. Seed size was also used as a measure of seed quality.

Greenhouse studies

Effects of seed size and seedling environment on seedling growth and survival were assessed in a greenhouse at the University of California, Davis campus in summer 2004. Thirty percent relative humidity and maximum temperatures of 40°C, similar to the field environment, characterized the greenhouse environment. Seeds from control and enriched field plants ($n = 5$ maternal plants/environment) were collected in November 2003 and air-dried. Each individual dry seed was weighed on a microbalance. Seeds were germinated in 0.8% agarose (gel) pellets in 96-well plates, which allowed monitoring of individually weighed seeds' germination without disturbance. After 3 days, the germinated seedlings were planted into two seedling environments [low-N (1.5 mmol l^{-1} N) and high-N (4 mmol l^{-1} N) seedling environments]. Three seedlings from each maternal environment plant (five replicates; two

treatments) were planted into one of the two seedling environments for a total of 30 seedlings per seedling environment (high and low N).

The seedling environments were produced in 7.6 cm $\times$ 35.6 cm Zipset^{TM} plant bands (Stuewe & Sons, Corvallis, Ore.) containing a mixture of 10:1 quartz sand and fritted clay. All nutrients except N were applied with a 1/4 strength Hoagland's solution. The low-N seedling environment was watered with nutrient solution containing 1.0 mmol l^{-1} NO_3^-, 0.5 mmol l^{-1} NH_4^+, 0.27 mmol l^{-1} K^+, and 0.5 mmol l^{-1} Ca^{2+}, while the high-N seedling environment was watered with solution containing 3.5 mmol l^{-1} NO_3^-, 0.5 mmol l^{-1} NH_4^+, 1.8 mmol l^{-1} K^+, and 1.0 mmol l^{-1} Ca^{2+}. NaCl (50 mmol l^{-1}) was added to both nutrient solutions to simulate field salinity conditions. The salinized nutrient solutions were applied to each block as 2.0 l of evenly distributed solution once prior to planting of seedlings and then throughout the experiment on the following days (3, 5, 9, 14, 21, 28 June and 5 July 2004).

Seedling height and survival were recorded once per week from 9 June to 8 July 2004. Seedlings were harvested on 15 July 2004. Roots were rinsed to remove rhizosphere prior to drying. Plant tissue was oven-dried at 65°C for 48 h and weighed.

Statistical analyses

Treatment effects on seed production variables were determined using weighted, repeated-measures ANOVA, using 1/variance as the weighting factor to address heterogeneity of variance among treatments (Neter et al. 1996; SAS 2001; Stanton and Thiede 2005). Using shrub size as a covariate did not affect results, so results of analysis of covariance (ANCOVA) are not reported. If sphericity assumptions were met in the repeated measures analyses, univariate results are presented. If sphericity assumptions were not met, multivariate ANOVA results are given. Univariate ANOVA was used to analyze within-treatment and within-plant seed size variation. We used the Ryan-Einot-Gabriel-Welsch (REGW) multiple range test for means comparisons.

Because effects of maternal (seed-production) and seedling environments on seedling growth were of primary interest, the greenhouse seedling growth study was set up as a factorial design and results were analyzed with ANCOVAs using initial individual seed weight as the covariate. "Mother plant" (maternal environment replicate) was nested within maternal environment. Individual seed weight was used as a covariate to remove any effect of seed size from effects of maternal environment, seedling environment, or untested factors.

We weighted the ANCOVA to correct for heterogeneity of variance between treatment means. Response variables

were seedling shoot biomass, root biomass, and height. Seedling height over time was analyzed using repeated-measures ANOVA for seedlings that survived until the termination of the experiment. We tested the assumption of homoscedasticity and used the Greenhouse-Geisser test to adjust probabilities for unequal correlations among pairs of repeated measures when the assumption for sphericity was rejected. Seedling survival was analyzed using the Lifetest procedure in SAS. We used the log-rank test of homogeneity because it is weighted more to longer survival times (Scheiner and Gurevitch 1993).

Results

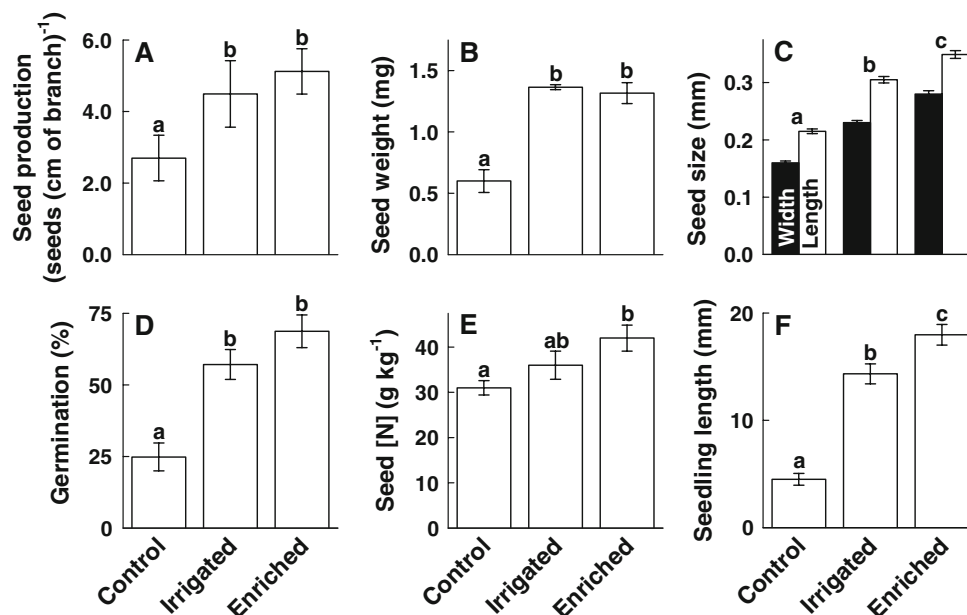### Seed production and quality in the field

There was a significant effect of year on seed production ($P = 0.004$). Seed number produced per branch in enriched treatments was nearly double that in control plants ($P = 0.05$), although irrigated and enriched plants did not produce significantly different amounts of seed (Fig. 1a). Over three growing seasons (2001, 2002, 2003) the total number of seeds produced per plant and seed weight increased significantly in the enriched treatment ($P = 0.007$).

There was a greater range in seed weight within plants in control (native) environments (20-fold) than in enriched environments (sevenfold, data not shown). Individual seeds from both irrigated and enriched treatments weighed slightly more than double the weight of seeds from control plants (Fig. 1b; $P = 0.06$ for both comparisons). Seed length and width were also greater in the irrigated treatment than in the control treatment, and greatest in the enriched treatment (Fig. 1c; $P = 0.03$ comparing irrigated and enriched treatments against the control treatment).

Percent germination increased 2.3- and 2.8-fold in seeds from irrigated and enriched treatments, respectively, compared with plants in the control treatment (Fig. 1d; $P = 0.004$). Three days after imbibition, seedlings from irrigated and enriched seed-producing (maternal) treatments were 3.2- to 3.9-fold larger than seedlings growing from control plant seeds (Fig. 1f). Seed N content was greatest in seeds from enriched environment plants (Fig. 1e; $P = 0.05$).

Effects of seed size and maternal environment on seedling growth in the greenhouse

There was a weak interaction between the environment of the seed-producing mother plant and seedling environment for seedling survival ($P = 0.06$), although there was no pattern of increased seedling survival with increased

Fig. 1a–f Seed production, seed size, germination, and other measures of seed quality of seed produced in the field in *Sarcobatus vermiculatus* for all 3 study years. a Average number of seeds produced per centimeter of branch length ±1 SE ($n = 5$ plants per treatment; within each plant, two to four subsample branches were averaged). b Average seed weight ±1 SE ($n = 5$ plants per treatment, two to four subsamples were averaged). c Average seed length and width ±1 SE ($n = 300$ per treatment). d Average germination percentage 3 days after imbibition ±1 SE ($n = 32$–38). e Average N concentration in whole seeds; sample run was of 20 seeds per treatment ±1 SE ($n = 3$ plants). f Average seedling length of germinated seed 3 days after imbibition ±1 SE ($n = 40$–91). *Different lowercase letters* signify different means at $P < 0.05$

N availability in the seedling environment ($P = 0.9$). Seed weight was a significant predictor of seedling survival to the termination of the experiment—seedlings from heavier seeds were more likely to survive ($P = 0.001$). Also, seedlings from heavier seed had greater biomass 3 days after germination ($P = 0.0001$) and had higher seedling N content 3 days after germination ($P = 0.01$).

After 6 weeks of growth, total root plus shoot biomass was significantly different between seedlings in the high- and low-N seedling environments ($P < 0.0001$), but not between the progeny produced in control versus enriched maternal environments (Fig. 2; $P = 0.3$). Root allocation was greater in enriched seedling environments (25 vs. 18%, $P = 0.02$). Seedling height growth rate was greatest in the enriched seedling environment ($P = 0.04$).

Seed weight, however, was not a significant predictor of seedling length 3 days after germination. Seedling stress, indicated by purple coloration of leaves, was highest in the low-N seedling environment ($P = 0.01$). Initial seed weight did not correlate with final seedling size after 6 weeks for either seedling environment or for any seed-producing plant environment (Fig. 3).

Discussion

To the extent that maternal investment in greater seed size or quality affects the ability of seeds to germinate and successfully establish, heterogeneity in resource availability at the adult plant scale could have implications for fitness variation among individuals. Further, irrigation or fertilization treatments at this scale could be of great importance to environmental mitigation that uses native plant seeding. Similar to our results that demonstrated some benefits of additional water (Fig. 1), and additional benefits of water

plus nutrients for seed production and some aspects of seed quality, others have found that precipitation is less important than other factors for seed production (Schimpf 1977; Moles and Westoby 2004; Valencia-Diaz and Montana 2005). Contrasting results, however, have also shown that shrub seeds show no tendency to change weight due to precipitation levels (Baker 1972), or that nutrient enrichment of the maternal environment caused no difference in seed production (Sills and Nienhuis 1995; Petersen and Ueckert 2005). Similar to our results, however, nutrient addition to *S. vermiculatus* in the Mono Basin, California, significantly enhanced seed production (Drenovsky and Richards 2005). Because some seed quality parameters were not different between irrigated and nutrient-enriched treatments, our results suggest that seed production by *S. vermiculatus* may be both water and nutrient limited at Owens Lake, similar to conclusions of Snyder et al. (2004) and James et al. (2005).

Our results demonstrated significant effects of enriched or irrigated maternal environments on seed production and also showed that several aspects of seed quality were improved concomitantly, i.e. germination, seed size and N content, and seedling size (Fig. 1). These field results suggest benefits for seedlings growing from seed produced in enriched or irrigated maternal environments. However, under the conditions of our greenhouse experiment, these improvements in seed quality were not large enough or persistent enough to influence the growth of seedlings over a 6-week simulated establishment period (Fig. 2). In the greenhouse experiment, seedling micro-environment was more important to seedling survival and growth than seed size or maternal environment (Fig. 3). Experiments that take into account seed size variation within mother plants, as in our greenhouse experiment, are needed to determine if differences in seed quality may be important when seedlings
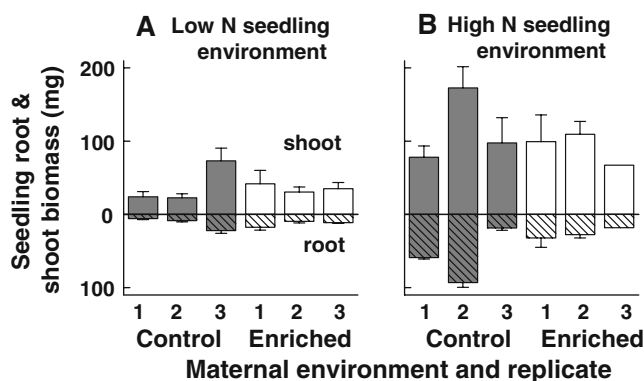
Fig. 2 Mean root and shoot biomass of seedlings grown in the greenhouse after 6 weeks' growth in low-N (**a**) and high-N (**b**) seedling environments (±1 SE, $n = 6$). *Dark bars* Seedlings grown from seed produced in the control seed-producing (maternal) field environment, *white bars* seedlings grown from seed produced in the enriched seed-producing (maternal) field environment. Each number on the abscissa is for a single replicate mother plant from each environment. Root biomass is indicated *below* (*hatched*) and shoot biomass *above* the zero line
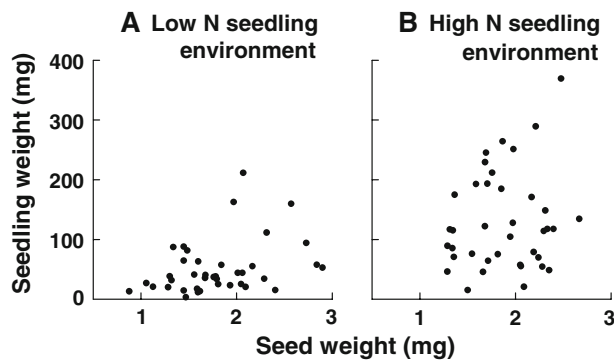
Fig. 3 Final seedling weight after 6 weeks' growth in the greenhouse plotted as a function of initial seed weight in the low-N seedling environment (**a**) and in the high-N seedling environment (**b**)

are establishing in the field, especially when competing among themselves in localized sites which trap many seeds. Although there was no competition in our greenhouse study, for systems such as the Owens Lake playa, where initial seedling density is often low, the greenhouse experiment with high temperatures, low water inputs, sodium additions, and low nutrient availability, may be a realistic model.

Despite the apparent unimportance of seed quality in overcoming stressful seedling environments, increased seed production by irrigated or enriched plants in the field should, by itself, increase seedling establishment because more potential seedling establishment sites will be saturated with seeds. Interactions of precipitation amount and seasonality, safe site availability, and soil nutrient availability, among other factors, appear to determine seedling establishment at this site. Given appropriate seasonal timing during years with above normal precipitation, plants can produce a greater number of successful seedlings than in normal years due both to increased seed production as well as increased seedling establishment (Breen and Richards, in review). These results suggest how water and nutrient limitations affect seed production and seedling establishment and will aid managers in determining the best approach to increase seedling growth and survival of shrubs at the saline, sandy Owens Lake playa. By understanding some of the factors that control seed production and early seedling establishment and survival, restoration projects in arid desert environments such as the Owens Lake playa can increase seedling recruitment and extend the longevity and success of such projects. In deserts, especially on open playa surfaces, successful seedling establishment will vary spatially and temporally as precipitation and nutrient availability, among other factors, affect seed production and seedling growth and survival. Increasing seed production with adult-scale treatments, combined with treatments to improve the quality of seedling micro-environments,

should increase seedling recruitment substantially with lower management intensity than transplanting or direct seeding.

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