



## Research Article–Editor's Choice

## Seed Production and Seedling Fitness Are Uncoupled from Maternal Plant Productivity in Three Aridland Bunchgrasses ☆☆☆☆

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## ABSTRACT

Maintaining self-sustaining populations of desired plants is fundamental to rangeland management, and understanding the relationships among plant growth, seed production, and seedling recruitment is critical to these efforts. Our objective was to evaluate how changes in maternal plant soil resource environment influences maternal plant biomass and seed production and seedling fitness in three widespread perennial bunchgrass species (*Elymus elymoides* [Raf.] Sezey, bottlebrush squirreltail; *Festuca idahoensis* Elmer, Idaho fescue; and *Pseudoroegneria spicata* [Pursh] A. Löve, bluebunch wheatgrass). We supplied water and nutrients to adult plants growing in the field and measured their productivity and fecundity. Then, in the laboratory, growth chamber, and field we assessed effects of the maternal water and nutrient additions on offspring performance. Across the three study species, vegetative traits were more plastic than reproductive traits, with resource addition measurably increasing plant growth but not seed production. Germination was high in both the laboratory and field across treatments, although seeds from irrigated maternal plants tended to have higher field germination. Seedling relative growth rate, leaf mass ratio, and relative root elongation rate (RRER) were highly variable, although RRER tended to be higher in seedlings derived from irrigated maternal plants. In the field, seedling survivorship was low across all species, but survivorship doubled in seedlings produced by *P. spicata* plants that received additional water through the growing season. Overall, our results suggest that biomass production and fecundity responses to nutrients are decoupled in the species and environment tested but maternal effects can have significant, although variable, impacts in some grassland species. As a result, biomass responses to natural and anthropogenic changes in resource availability may not be strong predictors of how altered resource supply may ultimately influence plant community dynamics in aridland systems.

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## Introduction

Drylands comprise about 40% of terrestrial environments, support over 2 billion people, and account for one-third of global biodiversity hot spots (Millennium Ecosystem Assessment, 2005). These systems

face multiple anthropogenic pressures including climate change, invasive species, and land degradation (Millennium Ecosystem Assessment, 2005; Reynolds et al., 2007). Given their low resource availability and subsequent limited productivity, drylands are slow to recover from disturbance (Allen, 1995), and ecosystem recovery often requires active intervention using practices such as seeding (James et al., 2013). However, dryland seeding efforts often fail (Abella and Newton, 2009; Pyke et al., 2013; Sheley et al., 2011), with success rates in the United States estimated to be < 5% (Sheley et al., 2011). Early life history stages, including seed germination and seedling emergence, are particularly problematic due to high mortality (Chambers, 2000; Grubb, 1977; Pyke, 1990). Understanding the factors influencing seed production and seedling establishment is essential to understanding ecosystem resilience as these life history stages are important drivers of population dynamics (James et al., 2011, 2012) and community structure (HilleRisLambers et al., 2009). Whereas much research has focused on

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seed and seedling ecology in arid systems, our ability to forecast the factors influencing recruitment dynamics remains limited (Hardegree et al., 2011).

Most work on how changes in soil resource availability influences dryland plant performance has focused on growth and biomass production, with less work on how soil resources influence seed production, seedling vigor, and establishment (Breen and Richards, 2008; Drenovsky and Richards, 2005). Some work with shrubs (Breen and Richards, 2008; Drenovsky and Richards, 2005; Fisher et al., 1988), perennial forbs (Shock et al., 2012), perennial grasses (Pol et al., 2010), and annuals (Gutierrez and Whitford, 1987) suggests seed production and individual seed mass may be positively related to increased soil resource availability, similar to biomass production. However, reproductive structures tend to be more “expensive” to produce than vegetative organs (Harper, 1977; Watson, 1984), due to lower net carbon gain and greater nutrient investment. Therefore, allocation between vegetative and reproductive growth may not always be positively correlated, as has been observed in the limited studies cited.

Resource availability may influence maternal seed production and seed provisioning, as well as alter performance of seeds and seedlings. These maternal effects can have genetic and environmental components and can be adaptive if they increase offspring reproductive success (Lacey, 1998). For example, greater maternal provisioning of seeds can increase seed nutrient content and mass, resulting in higher germination, faster germination times, greater seedling survivorship, and faster seedling growth rates (Aarssen and Burton, 1990; Tungate et al., 2006; Wulff and Bazzaz, 1992). These traits may enhance seedling survival. However, little is known about how fluctuations in the maternal resource environment impact seedling recruitment in arid systems, although pulsed and unpredictable resource availability is common in these environments (Chesson et al., 2004).

We asked how water and nutrient availability influences maternal plant growth and reproduction, as well as offspring traits (i.e., germination, relative growth rate, and survivorship) of three perennial bunchgrass species from the Intermountain West of the United States (*Elymus elymoides* [Raf.] Swezey, *Festuca idahoensis* Elmer, and *Pseudoroegneria spicata* [Pursh] A. Löve). We predicted that maternal plant tillering, biomass production, and fecundity would increase with resource addition (e.g., Pol et al., 2010). We also predicted fitness proxies would be highest among seedlings produced by plants raised under elevated resources (Breen and Richards, 2008).

Ecological and physiological differences among the study species also were expected to influence outcomes. Although similar in phenology and life history traits, the three species differ in their successional status and growth rates. *E. elymoides* is an early seral grass and typically one of the first deep-rooted perennial species to colonize disturbed sites (Jones, 1998). In contrast, *F. idahoensis* and *P. spicata* have traits typifying late seral species, such as slower growth rates (Khasanova et al., 2013; Mangla et al., 2011). *F. idahoensis* tends to be restricted to wetter sites, and of our three study species, it is generally the most difficult to establish (Sheley et al., 2006). On the basis of these trait descriptions, we predicted *E. elymoides* would respond most strongly to increased resource availability and would show the greatest reproductive investment. Because of its habitat preference for wetter sites, we hypothesized *F. idahoensis* would respond most positively to water additions.

## Methods

### Study Site and Species

The field experiment was conducted at the Northern Great Basin Experimental Range (NGBER) located in eastern Oregon (43°22'N, 118°22'W; 1300 m elevation) in a sage-steppe plant community. The vegetation is typical of Wyoming big sagebrush steppe, in which the dominant plants are sagebrush and perennial grasses such as *E. elymoides*, *F. idahoensis*, and *P. spicata*. These grass species are

common throughout the Intermountain West and are targets of restoration efforts. Soils are Xeric Haplargids that range from sandy loams to clay loams. Mean (70 years) hydrologic year (i.e., 1 October to 30 September) precipitation is 279 mm, and mean temperature is 7.6°C. During the study (2008–2012), hydrologic year precipitation was 162 mm, 243 mm, 257 mm, 274 mm, and 115 mm, and mean temperature was 7.5°C, 8.5°C, 6.7°C, 6.9°C, and 8.4°C.

### Experimental Design of Maternal Plant Resource Addition Experiment

Resource additions were assigned in a completely randomized design to naturally established adults of the three grass species. Plants selected were similar in size within species (average basal area at the beginning of the experiment  $\approx$  53.2 cm<sup>2</sup>, 61.6 cm<sup>2</sup>, and 113.0 cm<sup>2</sup> for *E. elymoides*, *F. idahoensis*, and *P. spicata*, respectively) and were spaced approximately 1 m from neighboring individuals. Nutrient additions were applied October 2007 and 2008 when plants were dormant, and water was applied once weekly through the growing season (March–May 2008 and 2009). Treatments were applied in a factorial design with eight replicates per combination of species and treatment ( $n = 144$  plants total). Water additions had two levels (control, irrigated), and nutrient amendments had three levels (control; nitrogen, phosphorus, and potassium [NPK]; and NPK + micronutrients). Plants did not detectably respond to micronutrient addition; therefore, these replicates were pooled with the other NPK replicates for statistical analysis. Water was supplied to individual plants via a drip irrigation system, with drippers placed 10 cm from the base of each plant. Each irrigated plant received approximately 200 L of water each year. Ammonium nitrate (57 g N per plant), triple super phosphate (28 g P per plant), and potassium sulfate (28 g K per plant) were supplied twice to the same plants (October 2007, 2008) by mixing them with field soil from the 5–15 cm layer and depositing them into two holes 10 cm from plants on opposite sides. Thus, nutrients had almost 5 months to mineralize and disperse before plants broke dormancy and initiated new leaf growth.

### Adult Leaf Nutrients, Growth, and Seed Production

Plants were assessed for leaf nutrients, growth, and seed production. A representative sample of green leaves from each maternal plant was collected for total N and P concentration in early May 2010, during peak vegetative growth. An increase in leaf nutrients without a concomitant increase in growth suggests nutrient storage, whereas reduced leaf nutrients in conjunction with increased growth in amended versus control plants suggests biomass dilution of nutrients. Equivalent concentrations among treatments may indicate sufficient soil nutrient availability. Leaves were dried at 60°C for 72 h and then finely ground with a ball mill. Leaf N concentration was measured by micro Dumas combustion on a CN analyzer (ECS 4010, Costech Analytical Technologies, Ventura, CA), and leaf P concentration was measured on dry-ashed and acidified samples via ICP-OES analysis (Plasma 400, PerkinElmer, Waltham, MA). In July 2009 and 2010, we determined tillers per plant, and at the end of the experiment (July 2010) all aboveground biomass was harvested. We measured seeds per plant in 2008, 2009, and 2010. Because seed dispersal occurs rapidly after ripening, we wrapped five reproductive culms per plant with fine mesh organza bags shortly after flowering. Seeds were collected when fully ripe (mid to late July of each year). Seeds were counted on five culms per plant, and seed production was estimated by multiplying average seed production per culm by reproductive culms per plant. Mean seed mass was estimated by dividing seed mass by number ( $\approx$  100–300 seeds).

### Seed and Seedling Measurements

We measured percent seed germination each year (2008–2010) for each plant. To do this, we placed 50 seeds per mother plant on

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