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

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 ≈53.2 cm^2, 61.6 cm^2, and 113.0 cm^2 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 (≈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

moistened filter paper in petri dishes, sealed the plates with parafilm to retain moisture, and placed them on a laboratory bench top at ambient temperatures and light ($n = 4-16$ dishes per species for each treatment) and recorded which seeds germinated over a 21-d period. To assess relative growth rate, in 2009, individual germinated seedlings were transplanted into Cone-tainers (Steuwe & Sons, Tangent, OR) filled with a 2:1 mixture of sand and sieved (2 mm) field soil. There were eight replicates for each species by maternal plant treatment. Due to low seed production per plant in 2009, we did not have sufficient replication to compare RGR responses between maternal plants within treatments. Rather, responses represent seedling performance as averaged across the eight maternal plants per treatment. The growth chamber was maintained at 25°C with a 12-h photoperiod and a light intensity of 800 μmol m^{-2} s^{-1}. Soil moisture in the pots was maintained at field capacity. Following emergence of the first true leaves, eight replicates per species and treatment were harvested; a second harvest occurred 4 weeks later. For each harvest, biomass was separated into leaves, culms, and roots. Leaf area and root length were measured via image analysis using WinRhizo (Regents Instruments, Saint Foy, Canada). All biomass was oven dried at 60°C for 72 h and then weighed. To calculate seedling relative growth rate (RGR), leaf mass ratio (LMR), and relative root elongation rate (RRER), we followed Causton and Venus (1981) and used ungraded and unpaired harvests. Relative growth rate (RGR) is change in total seedling biomass per unit biomass over time, LMR is leaf biomass relative to total plant biomass, and RRER is change in root length per unit length over time.

Seed Germination and Survivorship in the Field

We assessed how maternal soil resource environment influenced seed germination and survivorship in the field. We collected seed from plants in summer 2010 that had received water, NPK, or water + NPK over two growing seasons, as well as from plants that received no supplemental soil resources (control); because micronutrients had no effect on treatment responses, seeds from maternal plants receiving this treatment were not included in further aspects of the study. To quantify emergence and survival, seeds collected from plants in the resource manipulation experiment were sown in the field in 0.5×2.0 m plots; plots were spaced 1.0 m apart and arranged in a 3×12 grid. One month before seeding (September 2010), plots were tilled and raked smooth. In October 2010, 290 viable seeds were hand-sown into each plot and covered with 1 cm of field soil. In general, each species by treatment combination was replicated three times in a completely randomized design. The exception was *F. idahoensis*, in which low seed production made no seeds available for the NPK maternal treatment and only two replicates available for the water + NPK maternal treatment. Emergence and survival were tracked monthly through the following growing season (2011).

To quantify germination in the field, we placed a nylon mesh germination bag filled with 50 seeds of the appropriate species and treatment mixed with sieved (2 mm) field soil adjacent to each plot in October 2010. In general, there were three replicate bags per species by treatment combination. Seed bags were harvested in early March 2011, following peak germination. All seeds with a radicle were scored as germinated. For 2 years, we quantified the portion of sown seeds that emerged and survived and also quantified the proportion of germinated seeds that emerged and survived. The differences between these two estimates allows us to determine if potential differences in seedling survival are due to greater mortality during germination or greater mortality of seedlings following germination.

Statistical Analysis

For adult plant measurements made at one point in time (vegetative biomass, leaf N and P concentrations), univariate analysis of variance (ANOVA) was used to compare differences among species and resource

addition treatments. Species, nutrient addition (control, NPK), and water addition (control, water addition) and their interactions were included in all ANOVA models. Normality and equal variance were tested using Shapiro Wilks and Levene's test, respectively. Vegetative biomass and leaf P concentration were log-transformed to meet model assumptions. For adult measurements made annually (seed number and mass, germination and tiller production), repeated measures ANOVA (RM-ANOVA) was used to test effects of species, nutrient addition, and water addition, as well as how these effects changed through time. Mauchly's criterion was used to test sphericity, and when this assumption was not met, we used the Huynh-Feldt *P* value correction. Because micronutrients had no detectable effect on maternal plant responses (means and standard errors not shown), the NPK + micronutrients treatment was pooled with the NPK treatment for response variables measured on maternal plants. Not all plants survived, nor did all plants produce seeds; therefore, most response variables had unequal replication among species and treatments. All figures indicate the level of replication for the response variables. Germination percentages were compared with ANOVA, and survivorship rates were compared with RM-ANOVA; these models were similar in structure to those used for adult measurements.

We calculated a trait plasticity index, PI$_v$, for aboveground biomass, tiller production, individual seed number, and seed mass. We calculated this index as the maximum response to a treatment-minimum response to a treatment/maximum response to a treatment (Valladares et al., 2006). A PI$_v$ was calculated for each species within each year the trait was measured, and then the value for each species was averaged across years. This index varies from zero (lack of plasticity) to one (maximal plasticity). Additionally, to assess potential for trade-offs between vegetative and reproductive traits, as well as within reproductive traits (i.e., individual seed number and individual seed mass), we used correlation analysis using Pearson's product moment correlations.

Results

Adult Growth and Seed Production

Compared with other treatments, *E. elymoides* and *P. spicata* tiller production was greater in the water + NPK treatment (water * nutrient interaction, $P = 0.05$; Fig. 1**A**–**C**). *P. spicata* tiller production was greater with NPK addition (species * nutrient interaction, $P = 0.009$), and the same was true for *E. elymoides* and *F. idahoensis* when water was added in addition to nutrients. With water and nutrient addition, there was a large increase in *P. spicata* vegetative biomass (species * nutrient interaction, $P = 0.01$; Fig. 2). Across all species, more vegetative biomass was produced when water and nutrients were supplied together (water * nutrient interaction, $P = 0.01$).

Control and water-amended plants had lower leaf N concentration than plants receiving only nutrient amendment, but the magnitude of these effects varied by species (water * nutrient * species interaction, $P = 0.03$; Fig. 3**A**). *F. idahoensis* tended to have the highest leaf P concentrations (species effect, $P = 0.004$; Fig. 3**B**). Across species, leaf P was slightly higher when only nutrients were supplied but was slightly lower when nutrients and water were supplied together (water * nutrient interaction, $P = 0.01$). Overall, differences in leaf P between species and treatments were quite small.

Seed and Seedling Traits

Seed production varied among years and species ($P = 0.01$; Fig. 4**A**) but did not differ in response to resource addition ($P > 0.05$ for all main and interactive effects including resource amendment). In general, all species produced few seeds in 2008 and seed production remained low across the 3 years of study for *F. idahoensis*. Seed production increased over the time period of the study in *E. elymoides*, and seed production was higher in this species than *F. idahoensis* and *P. spicata* in
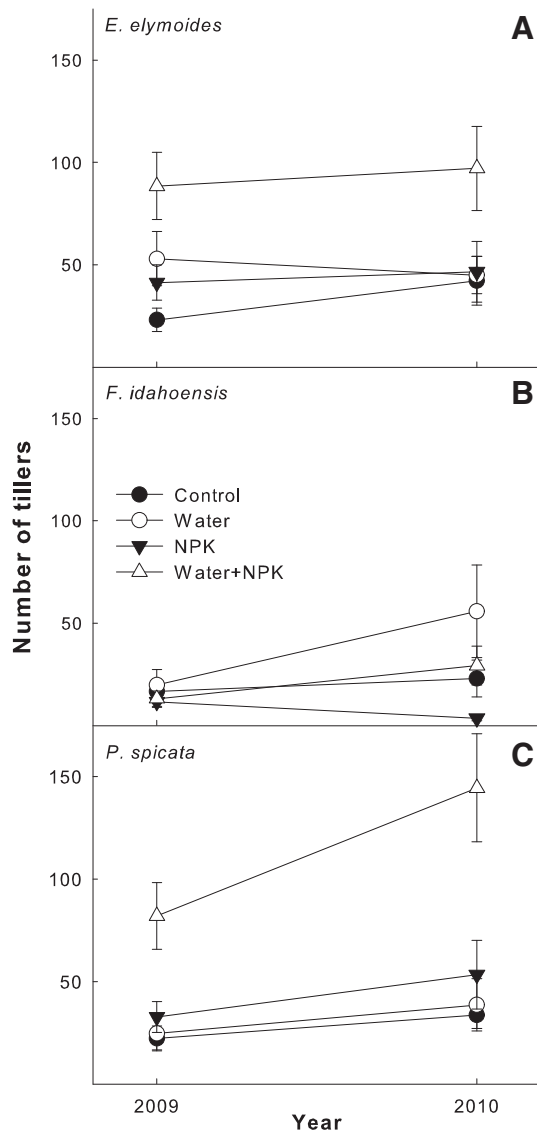
Figure 1. Tiller production per plant in maternal (**A**) *Elymus elymoides*, (**B**) *Festuca idahoensis*, and (**C**) *Pseudoroegneria spicata* in the second and third years following resource amendment. Data are means ± S.E. (*n* = 7–16).
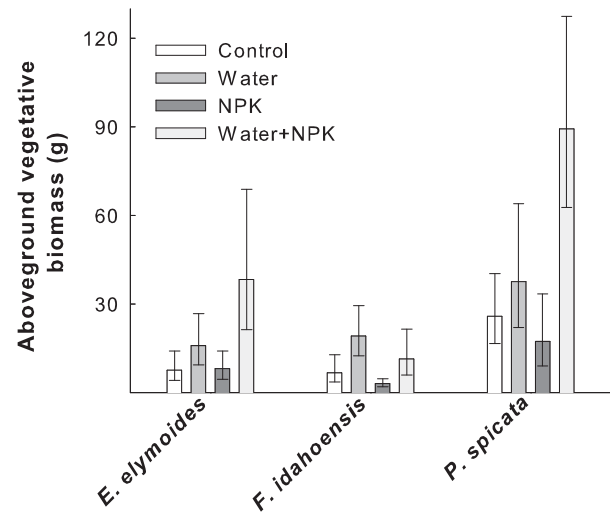

Figure 2. Total aboveground vegetative biomass per plant in maternal perennial bunchgrasses following resource amendment. Data are back-transformed means ± asymmetric 95% confidence intervals (*n* = 8–16).

their biomass to leaves (see Fig. 5B). Across species, RRER tended to be higher in seedlings from maternal plants receiving additional water, and across treatments, RRER tended to be highest in *P. spicata* and lowest in *E. elymoides* (see Fig. 5C).

Across species and treatments, germination was relatively high (>74%), but not all species responded equally to resource amendment (species * nutrient interaction, *P* = 0.0003; species * water interaction,

2009 and 2010. *P. spicata* produced a comparable number of seeds in 2008 and 2009 but more seeds in 2010. For the three species, average individual seed mass tended to be greater in one or more years with the addition of water (time * species * water interaction, *P* = 0.003; Fig. 4**B**). Overall, individual seed mass in *F. idahoensis* was lower than that of *E. elymoides* and *P. spicata*. Similarly, total seed mass (i.e., seed number * average individual seed mass) was highest in *E. elymoides*, particularly those plants supplemented with either nutrients or water, and lowest in *F. idahoensis* (species effect, *P* = 0.0009; nutrient effect, *P* = 0.03; water effect, *P* = 0.03; means not shown). Seed germination was high for all species and years (i.e., > ≈70%; Fig. 4**C**), and the highest germination percentages were observed for *E. elymoides* (species effect, *P* = 0.008). Germination tended to be lower in *F. idahoensis* and *P. spicata* in 2009, compared with 2008 and 2010 (time effect, *P* = 0.0001).

Seedling RGR and its components were highly variable among treatments (Fig. 5**A**–**C**). Although not significant, across all species, seedling RGR tended to be higher in seedlings from control plants, and across treatments, seedling RGR tended to be highest in *P. spicata* and lowest in *E. elymoides* (see Fig. 5A). Leaf mass ratio (LMR) was similar among species and treatments, with most seedlings allocating ≈30–40% of
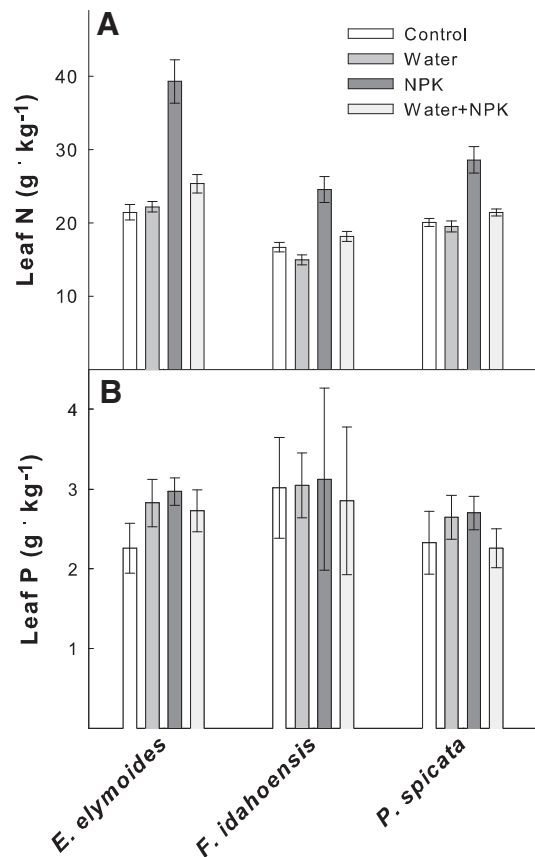

Figure 3. Leaf (**A**) N and (**B**) P concentration from maternal *Elymus elymoides*, *Festuca idahoensis*, and *Pseudoroegneria spicata* plants following 3 years of resource amendment. Data are means ± S.E. (**A**) and back-transformed means ± asymmetric 95% confidence intervals (**B**) (*n* = 7–16).
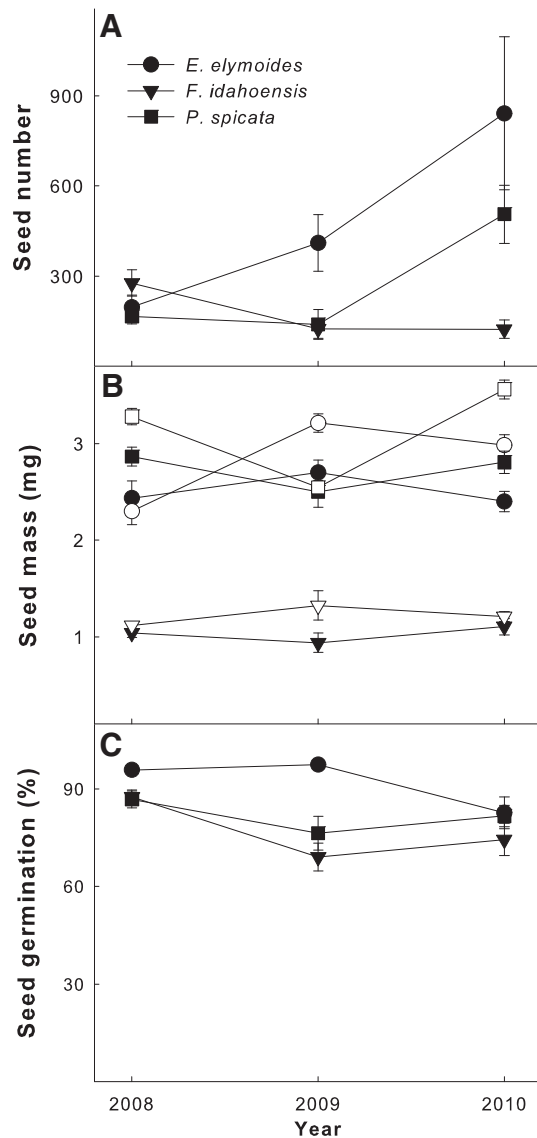
Figure 4. A, Total seed production per plant, **B**, mean individual seed mass, and **C**, laboratory germination percentages across the 3 years of study. For panels A and C, data are means ± S.E. ($n = 26$–48) averaged across resource amendment treatments, as responses depended solely on species and/or year, based on the RM-ANOVA model results. For panel **B**, data are means ± S.E. ($n = 11$–24). Black symbols reflect seed mass responses in which the maternal environment did not receive water amendment, and white symbols reflect seed mass responses in which the maternal environment received water amendments.

$P = 0.01$; Fig. 5**D**). *F. idahoensis* and *E. elymoides* seed germination varied little across treatments, whereas *P. spicata* tended to have higher germination in seeds from maternal plants that received additional water but lower germination in seeds from maternal plants receiving only additional nutrients.

Survivorship of planted seeds (calculated as the percentage of seedlings surviving based on the number of seeds sown) differed among years, species, and water availability (time * species * water interaction, $P = 0.03$; Fig. 6**A**–**C**). In general, survivorship of planted seeds was low across all treatments for *F. idahoensis* and differed little among years. Similarly, survivorship was similar between treatments in *E. elymoides*, although survivorship declined between 2011 and 2012. In contrast, survivorship tended to be higher in *P. spicata* seeds collected from maternal plants receiving additional water in 2011 and 2012, although there was a decrease in survivorship between years. Postgermination survivorship (calculated as the percentage of seedlings surviving

based on the number of seeds that germinated in the field) did not differ on the basis of maternal resource environment and was only influenced by a time * species interaction ($P < 0.0001$).

Trait Plasticity and Potential for Trade-offs Among Traits

Both vegetative traits were fairly plastic across all three species. Aboveground biomass per plant PI_vs ranged from 0.76 to 0.86, with *P. spicata* being the least plastic and *F. idahoensis* being the most plastic. Tiller production was slightly less plastic than biomass responses, with PI_vs ranging from 0.65 to 0.75, with *P. spicata* being the most plastic and *E. elymoides* being the least plastic. Average seed number per plant was more variable than average individual seed mass, with seed number PI_vs ranging from 0.70 to 0.81 and seed mass PI_vs ranging from 0.20 to 0.27. For both reproductive traits, *F. idahoensis* was most plastic and *E. elymoides* and *P. spicata* were similar in their plasticity.

Across all species and treatments, average seed number per plant was positively correlated with both tiller number (2009: $r = 0.34$, $P < 0.0001$; 2010: $r = 0.39$, $P < 0.0001$) and aboveground biomass per plant (2010: $r = 0.29$, $P = 0.0007$). Correlations among average seed number per plant and average individual seed mass varied from neutral to positive, depending on year (2008: n.s.; 2009: $r = 0.41$, $P < 0.0001$; 2010: $r = 0.19$, $P = 0.05$). Laboratory germination was positively correlated with average individual seed mass across all species (2008: $r = 0.21$, $P = 0.02$; 2009: $r = 0.30$, $P = 0.004$; 2010: $r = 0.34$, $P = 0.0003$).

Discussion

Overall, we predicted that resource addition would increase growth and fecundity of our suite of perennial bunchgrasses. However, species and individual plant traits differed in the strength of their responses to specific resource additions. As hypothesized, nutrient and water additions increased plant growth. This water and nutrient co-limitation was particularly evident in *E. elymoides* and *P. spicata*, while *F. idahoensis* showed stronger growth responses to water addition alone, as might be expected based on its preference for wetter sites. Contrary to our predictions, seed production and, in many ways, seed quality and seedling performance, were not strongly influenced by resource addition, even in the fast-growing *E. elymoides*, which was expected to be most plastic in response to resource addition. Seed production was highly variable among years and differed among species but was unresponsive to resource addition. Particularly in the second and third years of the study, *E. elymoides* had its highest seed production, as would be expected of this short-lived species, whereas the slow-growing *F. idahoensis* had the lowest seed production of the three species, producing few seeds across the 3 years of the study. These seed production data suggest that controls over plant productivity were decoupled from the drivers of seed production in our suite of perennial bunchgrasses.

The apparent lack of resource limitation to seed production was surprising, given the strong controls of water and nutrients on biomass productivity, below-average precipitation in the first year of the study (i.e., 2008), and previous observations of increased seed production in dryland plants following resource addition (Breen and Richards, 2008; Drenovsky and Richards, 2005; Fisher et al., 1988; Gutierrez and Whitford, 1987; Pol et al., 2010; Shock et al., 2012). However, other authors have observed minimal seed production responses to resource addition. For example, in a common garden study, N addition had little influence on seed production in 15 of the 18 herbaceous annual, biennial, and perennial Mediterranean plants studied (Fortunel et al., 2009). Similar results have been observed in the desert shrub, *Atriplex canescens* (Pursh) Nutt., in which ecotype was a stronger influence on seed production than nutrient or water amendments (Petersen and Ueckert, 2005). Our study suggests that factors beyond soil resource availability constrain seed production in our species; these factors likely include phenology, thermal regimes, or other environmental cues. Plant
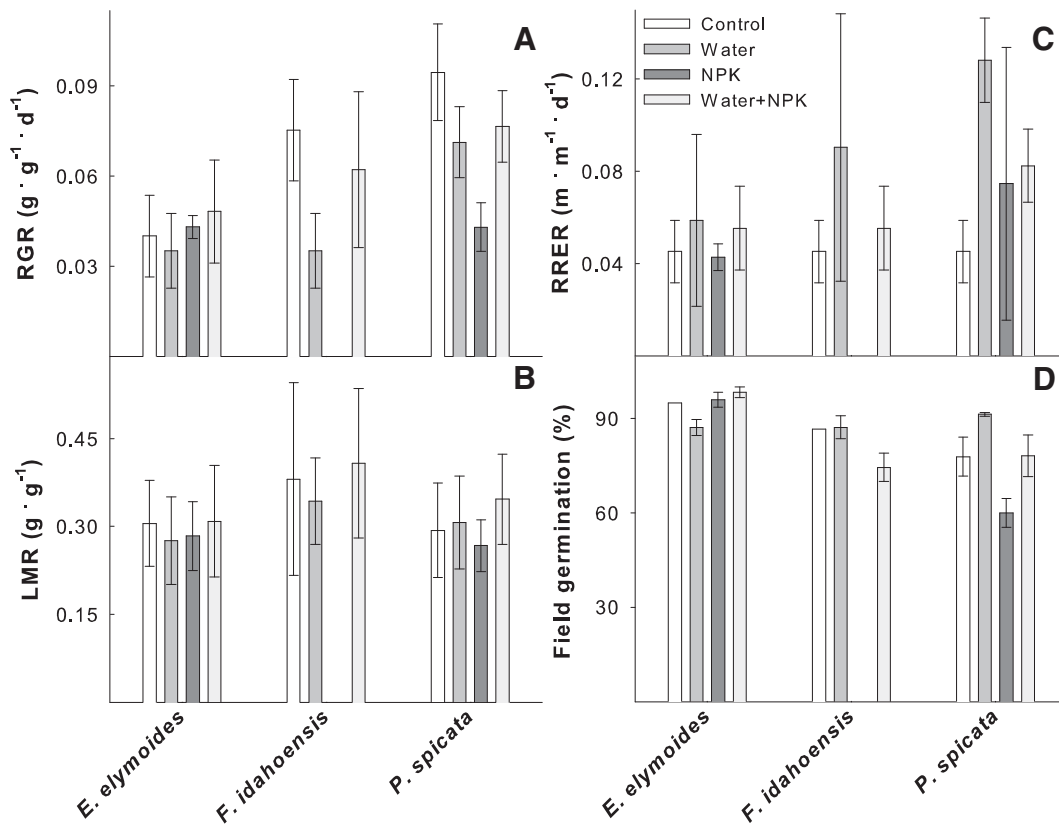
Figure 5. A, Seedling relative growth rate (RGR), **B**, leaf mass ratio (LMR), **C**, relative root elongation rate (RRER) for growth chamber-grown plants, and **D**, average seed germination under field conditions. Seedling "treatments" represent the maternal plant environment. Insufficient seed was produced by *Festuca idahoensis* maternal plants receiving NPK; therefore, this "treatment" was omitted from this portion of the experiment. Data are means ± S.E. (*n* = 1–3). No S.E. bars are included for *Elymus elymoides* from maternal control plants in (**D**) because all three replicates had equivalent field germination, and no S.E. bars are included for *F. idahoensis* from maternal control plants in (**D**) because there was only one replicate.

reproduction can be highly sensitive to temperature stress, impacting flower and gametophyte development, pollination, and fruit and seed set (Bykova et al., 2012). Furthermore, recent work with the masting tree *Nothofagus solandri* suggests that nutrient availability may interact with environmental factors such as rainfall and temperature to determine seed production (Smaill et al., 2011). Thus, the timing of environmental events (e.g., temperature extremes or resource pulses) in coordination with plant phenology may play a key role in the reproductive success of these bunchgrasses.

In contrast to seed production, seed mass (both individual and total per plant) was relatively more responsive to resource amendment, particularly in *E. elymoides* and *P. spicata*, although results were not consistent among years and in general, the degree of plasticity in individual seed mass was low across all three species. Greater seed mass has been linked to higher seedling survivorship (Moles and Westoby, 2004), particularly in heterogeneous environments (Coomes and Grubb, 2003). In our study, laboratory germination rates were positively correlated with seed mass across species and treatments. More importantly, field germination was slightly higher in *P. spicata* seeds that had been collected from irrigated maternal plants, and survivorship nearly doubled in *P. spicata* seedlings whose maternal plants had been irrigated, although the influence of maternal irrigation decreased over time. Given the low survivorship among the study species, any factor that doubles recruitment is significant. The increased survivorship observed in *P. spicata* seedlings from irrigated maternal plants is particularly impressive in the 2012 growing season, as precipitation was well below average (115 mm in 2012 compared with the 279-mm 70-year average). Although survivorship from seed to seedling stages increased for *P. spicata* with water addition in the maternal environment, postgermination survivorship of seedlings did not. This difference suggests higher survival rates of seeds collected from water-amended

maternal plants were due to higher germination rates and not higher RGR of seedlings. Thus, high rainfall years may increase seed size in *P. spicata*, improving its survivorship through higher germination. These gains could increase *P. spicata* abundance, as differences in plant performance among species at early life history stages can have large impacts on community structure (HilleRisLambers et al., 2009).

Although seed production per plant varied substantially across years, this variation was not related to cumulative treatment effects and individual seed mass was not very plastic across species or treatments. In contrast, vegetative production of adult plants was highly plastic in response to resource amendment. The high degree of biomass and tillering plasticity observed in the slow-growing *F. idahoensis* and *P. spicata* was surprising. Although a trade-off between vegetative and reproductive growth is often predicted, these trade-offs may not be realized if a minimum size is required for reproduction, if different resource pools support these functions, or if the two processes are developmentally correlated (Pulido et al., 2014).

Our experimental approach did not allow us to discern if phenotypic differences among offspring were due to changes in maternal provisioning or phenotypic plasticity (Bergum et al., 2012; Galloway, 2005). Regardless of the source, the overall lack of maternal effects for most seed and seedling traits was surprising, given the strong maternal plant growth responses to resource amendment. It is possible that the general lack of plasticity in seed and seedling traits could be the result of a lack of genetic variation among our maternal plants (Galloway, 2005). We used field-established maternal plants with unknown parentage, and, consequently, we do not know the degree of genetic variation among individuals in our population. However, self-pollination is one mechanism that can limit genetic variation by decreasing gene flow and reducing heterozygosity (Knapp and Rice, 1996). Although *P. spicata* is self-sterile (Jensen et al., 1990), both *E. elymoides* and
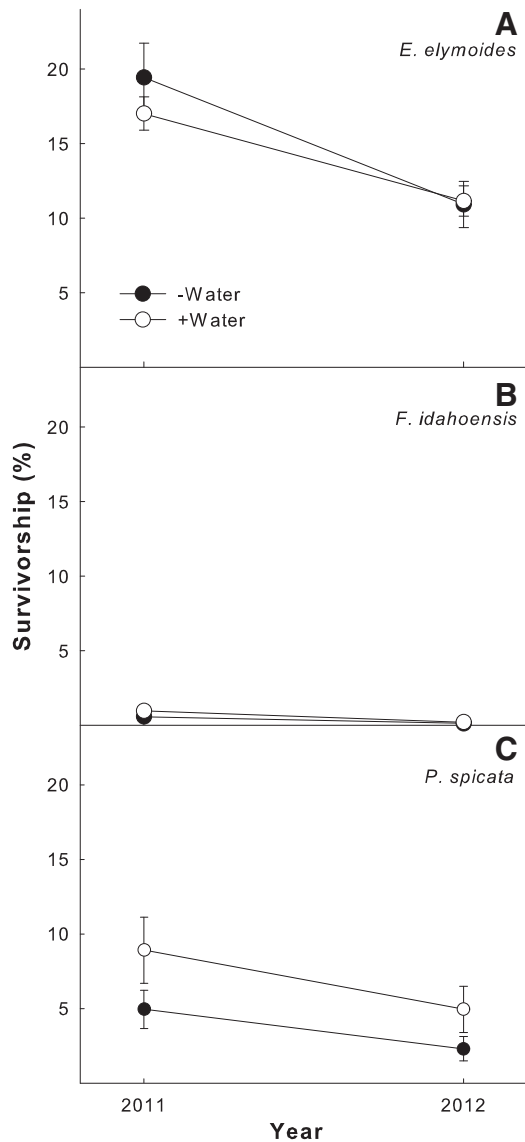
Figure 6. Average survivorship from seed to seedling stages under field conditions in 2011 and 2012 for (**A**) *Elymus elymoides*, (**B**) *Festuca idahoensis*, and (**C**) *Pseudoroegneria spicata*. Seed was planted in 2010, and seedling "treatments" represent the maternal plant environment. Replicates were averaged across nutrient treatments within a year as only species, water amendment, and year were significant in the RM-ANOVA model. Data are means ± S.E. (n = 3–6).

F. idahoensis can self-pollinate (Jones, 1998; Smith, 1944), which may limit genetic variation within populations of these species. If the measured seed and seedling traits are conserved within our populations, plasticity for these traits could be constrained. We did observe small (although variable) differences in seed mass in response to treatment. Additionally, our study and other studies in this system (Bates et al., 2009) found that seed production can vary more than twofold across years, suggesting strong plasticity in seed production. Changes in individual seed mass in response to resource amendment were particularly unexpected, as seminal work on maternal effects suggested that seed number is a much more plastic trait than seed size (Weiner et al., 1997). Although seed mass is considered one of the least plastic traits, seed mass may vary when seed number is restricted (Harper et al., 1970), as we observed in our study. In spatially or temporally heterogeneous environments, differences in seed size may be adaptive, as variation in seed provisioning may ensure that at least some seeds will have sufficient resources to survive poor conditions (Capinera, 1979).

Implications

Although much research has probed how environmental factors influence rangeland plant growth and biomass production, the corresponding impacts of this changed productivity on seed and seedling dynamics have received much less attention (Verheyen et al., 2009). This knowledge gap is critical to fill, given that changes in rangeland plant community composition, as a result of natural and anthropogenic environmental change, may occur primarily through impacts on seedling recruitment (Walck et al., 2011). In this study, we observed a strong decoupling of biomass and seed production in response to variation in soil resource availability. Namely, while increases in soil water and nutrient availability stimulated aboveground vegetative production, increases in soil nutrient availability did not significantly stimulate more seed production or improve seed vigor. The impact of maternal plant water addition on seed and seedling dynamics was limited primarily to *P. spicata*. These data indicate that although belowground resources limit the growth and survival of established plants in arid systems, fecundity and population growth responses to soil resources appear to be constrained by complex sets of aboveground environmental conditions and cues that vary substantially across years. A larger focus on the controls that may drive episodic periods of elevated seed production and recruitment independent from short term changes in soil resource availability will be fundamental if we are to be able to forecast patterns of natural seedling recruitment and native plant population maintenance in these systems.

Acknowledgments

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