

University of Nevada, Reno

**Will Local or Commercial Native Plants Succeed Where Exotic Invaders Fail?
Cheatgrass Die-offs as an Opportunity for Restoration in the Great Basin, USA**

A Thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science in Natural Resources and Environmental Science

by

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May, 2014



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We recommend that the thesis
prepared under our supervision by

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entitled

**Will Local Or Commercial Native Plants Succeed Where Exotic Invaders Fail?
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be accepted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

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ABSTRACT

The exotic annual *Bromus tectorum* (cheatgrass) commonly occurs in dense, near-monocultures in the Great Basin, U.S.A. after diverse native plant communities have been mostly extirpated. Efforts to reestablish native species via direct seeding, typically with commercially produced, non-local seeds, are often unsuccessful. In addition to abiotic factors that often limit establishment, *B. tectorum* competition can impede native establishment in highly invaded communities, and commercially produced seeds may differ from local genotypes in their responses to these limitations. The phenomenon of complete *B. tectorum* stand failure, or ‘die-off’, can leave areas within near-monocultures devoid of growth for one or more years. Such areas may represent restoration opportunities if native seeds can establish within them. In October 2012, local and nonlocal (commercial) sources of *Poa secunda* (Sandberg bluegrass) and *Elymus elymoides* (bottlebrush squirreltail) were precision-planted in a recent die-off and adjacent near-monoculture (control) in northern Nevada under six treatments: litter removal, fungicide application, and no treatment; each with and without added simulated precipitation. I addressed the following questions: 1) Can native species be successfully restored in recent *B. tectorum* die-offs, and is establishment related to seedbed treatments and competition with *B. tectorum*? 2) Do local and nonlocal materials differ in their performance as restoration material, and if so, are these differences consistent across seedbed treatments and in and out of a recent die-off? Seeded plots were monitored nine times throughout two growing seasons for emergence and seedling activity, and seedling

growth was measured in May of the first season. Emergence of native seeds was significantly lower in die-off plots, but there were significantly more actively growing seedlings of both species in die-off plots than in adjacent control plots by the end of the first growing season, and seedlings in the die-off exhibited more leaves, increase late season vigor, and, for *E. elymoides*, increased height. Second year survival patterns also suggested greater establishment in die-off plots. Local *P. secunda* demonstrated improved performance over nonlocal material ('Mt. Home' germplasm) in both seasons, whereas nonlocal *E. elymoides* ('Toe Jam Creek' germplasm) demonstrated aspects of higher performance than the local collection in the first year but not the second. Litter removal had a positive influence on seedling activity for both species, but only affected the survival of *P. secunda*. Late autumn (early growing season) water addition affected emergence timing for both species and resulted in more *E. elymoides* seedlings, but this affect was equal across controls and die-offs. Although these results are representative of conditions at only one site, they suggest that *B. tectorum* die-off may support increased establishment of native species regardless of seedbed treatment, and may therefore represent valuable opportunities for restoration. Also, they indicate that local and nonlocal seeds differ in performance in important but idiosyncratic ways, which supports the belief that seed source should be considered as a factor affecting restoration success but contradicts the idea of generalizable local vs. nonlocal performance patterns.

ACKNOWLEDGMENTS

This work was funded in part by the Bureau of Land Management under the Integrated Cheatgrass Die-off Project, as well as by the Nevada Department of Wildlife and the Great Basin Landscape Conservation Cooperative. Thank you.

The completion of this study was a product of the efforts of many individuals. My advisor, Dr. Elizabeth Leger, has been an incredible facet to my education and professional experiences, and I was fortunate to have a scientist and mentor of such a high caliber as my advisor. Drs. Lee Turner and Matthew Forister were supportive and pleasant committee members who, along with Dr. Leger, allowed me a level of autonomy that greatly enriched my research experiences. For logistical support and collaboration, I thank Drs. Susan Meyer of the Rocky Mountain Research Station Shrub Science Laboratory, Dr. Zachary Aanderud and Josh Nicholson of Brigham Young University, Rob Burton and Dr. Calvin Jennings of the Winnemucca District of the Bureau of Land Management, and Steve Foree and Dr. Lee Turner of the Nevada Department of Wildlife. I am also grateful to field assistants and volunteers for helping conduct over 700 hours of often tedious field work, including Lyndsey Boyer, Bryce Wehan, Meghan Whitman, Molly Bechtel, Brian McMillan, Jacob Brannam, Curt Baughman, Dr. Kevin Badik, Dr. Lauren Porensky, Dash Hibbard, Dr. Dan Atwater, Michelle Hochrein, Dr. Wendy Trowbridge, Erica Burnett, Wailea Johnston, Brittany Trimble, Riley Anderson, Jaron Audette, Dr. Wu Nan, and Stephanie Braden. I also thank my family, who supports me by rarely doubting the direction of my endeavors, whatever they may be. Finally, I thank L&H Seeds, Inc. for donating commercial material for this study.

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INTRODUCTION

The introduction and spread of exotic invasive species is a primary cause of ecological degradation and biodiversity reduction worldwide. The exotic annual grass *Bromus tectorum* (cheatgrass) is an aggressive invasive that was introduced from Europe into western North America more than a century ago and has come to colonize tens of millions of acres of cold desert shrublands (Mack 1981, Knapp 1996). Its dominance dramatically shortens fire return intervals (D'Antonio & Vitousek 1992, Skipper et al. 1996, Brooks et al. 2004)), alters the distribution and quantity of ecosystem carbon and nitrogen (Norton et al. 2004, Hooker & Stark 2008, Adair & Burke 2010), and facilitates pathogen spillover (Beckstead et al. 2010, Mordecai 2013), a phenomenon in which an abundant host modifies the prevalence of pathogens as well as their effects on co-occurring species (Mordecai 2011). Many native plant species become sparse or locally extirpated as a result of these complex disturbances (Stewart & Hull 1949), and *B. tectorum*'s competitive abilities (Nasri & Doescher 1995, Rafferty & Young 2002) can reduce native species' ability to recolonize infested systems (Humphrey & Schupp 2004). Together, the vegetation community changes associated with *B. tectorum* invasion have far-reaching ecological and socio-economic consequences (D'Antonio & Vitousek 1992, Brunson & Tanaka 2011).

Currently, *B. tectorum* invasions create a management predicament with few options for effective control. In addition to the large geographic scale of this invasion, restoring more functional plant communities to *B. tectorum* invaded lands is even more

challenging because of incomplete knowledge currently guiding management practices in important areas (Davies et al. 2011), such as the relative effectiveness of different seeding methods (Knutson et al. 2009, James & Svejcar 2010), the factors most important for seedling establishment in the Great Basin (Davies et al. 2011, Mangla et al. 2011, Ray-Mukherjee et al. 2011, Hardegree et al. 2012), and the importance of seed source for optimal performance (Hardegree et al. 2011). Because the seeded material and its performance is generally the foundation of restoration efforts, understanding the importance of seed source and how it relates to establishment is a particularly pressing issue.

It is well understood that phenotypic traits in plants are often correlated with or predicted by environmental or ecological conditions that vary geographically (Clausen et al. 1947, Loveless & Hamrick 1984, Linhart & Grant 1996, Kawecki & Ebert 2004). When traits confer higher fitness for local than for foreign genotypes when evaluated in local conditions, this is considered local adaptation. Though many studies and reviews agree that local adaptation in plants is common, the incidence, magnitude, and causes of local adaptation are influenced by population demographics, species life histories and interactions, climate, and other factors (Linhart & Grant 1996, Joshi et al. 2001, Leimu & Fischer 2008, Hereford 2009, Johnson et al. 2010a). The Great Basin is heterogeneous with respect to such factors (Comstock & Ehleringer 1992), thus it is likely that intraspecific variation in this region is widespread and its patterns of local adaptation are complex.

Although the current literature includes experiments on only a fraction of important Great Basin species, differences in morphology and phenology have been found to correspond with specific climatic variables (Meyer et al. 1989, Meyer et al. 1995, Erickson et al. 2004, Johnson et al. 2010b, Parsons et al. 2011, Johnson et al. 2012, Johnson et al. 2013b, St Clair et al. 2013), interspecific competition (Nasri & Doescher 1995, Leger 2008, Rice & Knapp 2008, Goergen et al. 2011, Rowe & Leger 2011, Phillips 2012), and more generally to geographic location (Kramer et al. 2011, Rowe & Leger 2012, Johnson et al. 2013a). The few studies that have directly tested for local adaptation in species in this region have found clear (Rice & Davis 2009, Rice & Knapp 2008, Rowe & Leger 2012) and marginal (Humphrey & Schupp 2002) support for it. Additionally, no empirical evidence has demonstrated local maladaptation in the Great Basin, where local material is poorly adapted to its home site, despite claims that the widespread loss of native species associated with exotic invasions and the associated changes in ecosystem dynamics indicates maladaptation in those lost species (Jones & Monaco 2009).

Our understanding of the importance of seed source in the Great Basin is far from complete, and this knowledge gap is of concern to restoration practitioners (Johnson et al. 2010a). Furthermore, demand for restoration material in this region is typically enormous and unpredictable, making it infeasible to meet that demand with local material (Johnson et al. 2010a). Currently, the great majority of seeded native material is commercially produced and derived from programs aiming to create widely-adapted, multi-purpose genotypes (Asay et al. 2003, Jones & Monaco 2009). Unfortunately, the portions of the

Great Basin most at risk of degradation are poorly represented by these commercial materials (Jensen and Stettler, unpublished data), though recent efforts have demonstrated methodologies for understanding and developing species-specific seed transfer zones to aid in rectifying this situation (Johnson et al. 2012, Johnson et al. 2013b, St Clair et al. 2013). Therefore, restoration material is generally a nonlocal genotype and is likely to lack any locally adapted traits. Given this reality, it is vital that more research address the existence and importance of local adaptation in Great Basin species, especially in highly invaded and potentially modified systems, such as those containing *B. tectorum* near-monocultures.

Bromus tectorum die-off is a common but poorly understood phenomenon occurring in near-monocultures in which an abundant *B. tectorum* seed bank fails to produce a stand of living plants for one or more years, despite receiving precipitation that is sufficient for establishment. Several recent studies have advanced our knowledge of the recovery and effects of die-offs. While some areas experiencing die-off continue to show stand failure for several years and may lose soil to erosion, many areas recover to considerable *B. tectorum* densities the following year (Table 1). Recovery is possible because the phenomenon does not appear to directly affect the persistent (carry over, dormant) seed bank of *B. tectorum*, and sites therefore retain a pool of viable *B. tectorum* seeds (Blank et al. 2011, Baughman & Meyer 2013). A greenhouse experiment in which ‘bait’ *B. tectorum* seeds were planted into sterilized and unsterilized field soils collected from inside and outside of two die-offs showed increased growth in die-off soils after 21 days, regardless of sterilization (Meyer et al. *in press*), while a similar experiment using

one of the same die-offs found no differences in growth of bait seeds after 40 days (Blank et al. 2011). Both studies observed a many-fold increase in multiple forms of soil nitrogen (N) in die-off soils when compared to immediately adjacent soils not exhibiting die-off. This excess N following prevention of *B. tectorum* growth for a single season has been observed elsewhere (Eckert et al. 1970), and has been posited to cause increased seedling growth (Eckert & Evans 1967) similar to what was found by Meyer et al. (*in press*).

The factors directly responsible for *B. tectorum* die-off have yet to be determined, and recent experimental studies have sought evidence of pathogenic, fungal culprits. Baughman and Meyer (2013) found no evidence that the ubiquitous seed pathogen *Pyrenophora semeniperda* (known as the ‘black fingers of death’) was directly involved, and Meyer et al (*in press*) obtained isolates of *Fusarium*, a genus of common grass pathogens, from bait *B. tectorum* seeds and demonstrated high pathogenicity in the laboratory under specific water stress regimes. These findings corroborate anecdotal observations that very particular microenvironmental conditions are important for die-off manifestation. Pre-germination seedbed moisture is undoubtedly mediated by litter (Facelli & Pickett 1991), which is often relatively dense where die-offs occur. Thus, manipulating soil moisture directly and/or through litter modification could affect the expression of the die-off phenomenon.

Regardless of the cause, *B. tectorum* die-offs represent a sudden but temporary decrease of an undesirable exotic. Such a decrease could be an opportunity for restoration if native species will establish in these altered conditions. For example, excess soil

nitrogen and a lack of competition with *B. tectorum* in die-offs could aid in native establishment, or alternately, the causal agents of the die-off may cause mortality of native species seeded into die-offs. In order to examine whether die-offs are possible restoration opportunities, this study employed a two-year, *in situ* seed establishment experiment using two native grass species, *Poa secunda* and *Elymus elymoides*, under several seedbed treatments at a naturally occurring die-off in north-central Nevada to address the question: 1) Can native species be successfully restored in recent *B. tectorum* die-offs, and is establishment related to seedbed treatments and competition with *B. tectorum*? Additionally, seeds of both local and nonlocal (commercial) origin were included in the experiment to address the question: 2) Do local and nonlocal materials differ in their performance as restoration material, and if so, are these differences consistent across seedbed treatments and in and out of a recent die-off? Seedbed treatments included early season water addition, litter removal, and fungicide application. These treatments were selected in order to provide a range of microenvironmental conditions experienced by seeds and to potentially affect the occurrence of the die-off phenomenon.

METHODS

Site selection and description

Extensive portions of north-central Nevada were searched in spring 2012 for recent die-offs. Surveys were guided by knowledge of previous die-off areas as well as by preliminary recommendations generated through a remote sensing effort aimed at

detecting die-offs (Weisberg pers. com.), and a single die-off site was found near Dun Glen in northern Buena Vista Valley (Figure 1). The site is a scarcely sloped, 1384m elevation steppe of well drained, relatively deep fine sandy loams with a 30-year average annual precipitation of 180mm (PRISM Climate Group 2012, NRCS Soil Survey Staff 2014). The die-off existed in a former *Artemisia tridentata* var. *wyomingensis* dominated community that has been affected by several wildfires, the last occurring in 1999. At the time of the study, it was occupied primarily by *B. tectorum* and low densities of *Sisymbrium altissimum* (tall tumble mustard), *Salsola tragus* (Russian thistle), and *Lepidium perfoliatum* (clasping pepperweed), *Elymus elymoides* (bottlebrush squirreltail) and *Microsteris gracilis* (slender phlox). *Bromus tectorum* die-offs were first observed and investigated in the area in 2008 (Baughman & Meyer 2013). One area (70m x 50m) that contained a representative sample of the recent die-off and unaffected areas was selected as the experimental area and fenced with barbed wire to exclude livestock and wildlife. The affected die-off area supported virtually no *B. tectorum* growth during the growing season prior to installation of the experiment (2012), and the adjacent ‘control’ areas supported dense stands of small-statured (<20cm) *B. tectorum*. September 2012 seed bank samples showed no significant differences between die-off and control conditions in viable (6200 ± 1500 SE in control, 10200 ± 4500 SE in die-off), nonviable (12300 ± 2000 SE in control, 10300 ± 2200 SE in die-off), or total (18500 ± 2800 SE in control, 20400 ± 5900 SE in die-off) *B. tectorum* seeds per square meter. Site precipitation was estimated to be about 115mm for the 2012 growing season (65% of 1981-2010 average), and 128mm for the 2013 growing season (71% of 1981-2010 average, PRISM Climate Group 2014).

Species Selection, Seed Acquisition and Processing

I surveyed the Dun Glen die-off site and immediately surrounding areas (within a 3 mile radius) for native species, selecting the perennial grasses *Poa secunda* (Sandburg bluegrass) and *Elymus elymoides* (bottlebrush squirreltail) as experimental species. *Poa secunda* is a widely distributed and genetically diverse complex of perennial bunchgrasses that often grows and matures earlier in the growing season than most other native perennial grasses (Majerus et al. 2009). It is considered a pioneer species and is relatively tolerant of fire and other disturbances. *Elymus elymoides* is also a widely distributed perennial bunchgrass, and is fire-adapted and relatively tolerant of *B. tectorum* invasion (Humphrey & Schupp 2004, Tilley et al. 2006). It generally matures and shows active growth later in the season than *P. secunda*. These species were selected based upon site availability and because they are commonly used in restoration in the region. Additionally, both species have been found to demonstrate abilities to compete with *B. tectorum* (Booth et al. 2003, Goergen et al. 2011, Stevens et al. 2014).

Mature seeds were hand-collected throughout June and early July from as many individuals (>50) and as close to the die-off site as possible. Seeds were stored at room temperature in paper envelopes for up to 6 months. Commercially produced, nonlocal seed for these species was obtained from L&H Seeds, a private seed grower in eastern Washington. For *P. secunda*, I selected the Mt. Home germplasm (Lambert et al. 2011) because its origin in southern Idaho is geographically closer and more environmentally similar to the Dun Glen site than any other commonly available germplasm. For *E. elymoides*, I selected the Toe Jam Creek germplasm (Jones et al. 2004), originating from

northern Nevada, for similar reasons. Both local and nonlocal seed lots were hand sorted on a light table, and only seeds with well-developed endosperms were selected. The viability of each hand sorted lot was assessed through a 30-day, room temperature germination trial of 25 seeds in each of 8 petri dishes per seed lot.

Precision Seeding

Using Titebond 5062 Original wood glue, seeds were attached by their lemmas, with embryo down, to 15cm long bamboo skewers at 5cm from skewer tip and inserted so that seeds were 0.6-1.2cm below the soil surface. Target seedlings grow up along the skewer and can be differentiated from resident seedlings, allowing for very high seedling detectability as well as confirmation of seedling identity during monitoring.

Field Design

Six treatments in both die-off and adjacent non die-off (henceforth, 'control') conditions were established with the dual purpose of varying the conditions under which native establishment would occur as well as attempting to trigger the die-off phenomenon at the plot level. These treatments were: seeding into unaltered plots, seeding with litter removal ('raked'), and seeding with fungicide application, each with and without simulated precipitation addition ('watered'). Litter was removed by gentle hand-raking, removing as much of the coarse organic litter as possible while minimizing soil disturbance. Captan fungicide powder (N-trichloromethylthio-cyclohexene-1,2-dicarboximide) was mixed into a 50/50 slurry (by weight) with deionized water, and skewers were dipped into this slurry to just above the seed and left to dry for at least 48 hours before planting.

Ten blocks were established in the experiment, each composed of two arrays, with one array in the die-off condition paired with one in the adjacent control condition (Figure 1). Blocks were arranged in two rows of five in each condition. Within each array, 24 unique plots (experimental unit) representing the six treatments, two species, and local/nonlocal origin design were randomly arranged in two rows of 12 with 15cm spacing. Each plot contained a four by five matrix of seeds on skewers, all from the same seed lot, planted 5-6.5cm from one another. This ten block design contained a total of 480 plots and 9,800 seeds.

All plots were planted during the last week of October, 2012. Plots assigned to the simulated precipitation treatment were watered with 2.3 liters at both one and three weeks post-planting using a Ziploc bag perforated with 5 small holes suspended above the litter layer on hardware cloth and a wooden frame. This achieved 2.5cm of simulated precipitation for the 0.1m² plot, and care was taken to avoid runoff. After mid-November, only natural precipitation supplied moisture to the plots.

Data collection

All skewers were examined down to the soil level for emergence the last week of November 2012, and all unemerged seeds were examined for emergence every month thereafter until plants began to senesce in late May 2013. Skewers were examined again in November 2013 and February 2014 for second season activity. Green cotyledons above the soil surface were marked with a paperclip. The litter layer was gently parted to examine down to the soil surface when necessary, then tucked back into place. First season data are reported in terms of actively growing seedlings rather than living

seedlings because it was not possible to nondestructively differentiate seedling mortality from senescence (dormancy). The general phenology of *P. secunda* and *E. elymoides* suggest that senescence as early as March is almost certainly mortality, whereas senescence in subsequent months is likely a mix of early dormancy and mortality. Therefore, March senescence was assumed to be synonymous with mortality.

All plants exhibiting active growth in early May were measured in late May for two growth variables, leaf number and longest leaf length (height), and given a greenness integer rating from 0 (0% green) to 3 (75-100% green). *Bromus tectorum* density was recorded in each plot in early May 2013, and aboveground *B. tectorum* biomass was harvested from within plots in August 2013 after most seeds had shattered. Biomass was dried in an oven at 40°C for at least two days and weighed.

Soil samples were taken in October, 2012 and June 2013 from within each array in 6cm diameter x 8cm deep cores. October samples were stored in paper bags and frozen for 10 months while June samples were stored at room temperature in paper bags for several weeks. All samples were analyzed for pH, organic matter, nitrate, phosphorus, potassium, calcium, and magnesium (A&L Analytical Laboratories, Memphis, TN).

Data Analysis

Emergence and seedling activity were calculated as percentages of the total seed planted on a per-plot basis. These percentages were adjusted by the viability of each seed lot (*P. secunda*: 70% for nonlocal and 77.5% for local; *E. elymoides*: 96.3% for nonlocal, 98.8% for local) to normalize responses as percentages of the total viable seed planted.

This resulted in occasional values slightly exceeding 100%, when plot emergence or seedling activity was higher than the lot's average viability.

Response variables were measured by plot and included proportion of viable seeds that emerged in the first season, proportion of viable seeds actively growing at each of eight sampling dates, proportion of emerged seedlings showing mortality in March, mean plot leaf length and leaf number in May, and late season vigor. Plot responses were analyzed separately for each species, using a mixed model ANOVA with condition (CND: control, die-off), soil treatment (TRT: none, raked, fungicide), water treatment (WTR: unwatered, watered), and origin (ORGN: local, nonlocal) as fixed factors, with all possible interactions, and block as a random factor (JMP v10.0, SAS Institute Inc.). Tukey's HSD tests were used to determine pairwise differences of significant ANOVA interactions. Because interactions with resident *B. tectorum* may have influenced the response of seeded native species, May *B. tectorum* plot density and midsummer biomass of *B. tectorum* were individually added as a covariate into the main model in two separate analyses, and results were screened for changes in significance. These two measures of *B. tectorum* were not strongly correlated ($R=0.32$). The resulting models are referred to as the density-covariate and biomass-covariate models. These models did not include data from November through February because interspecific interactions were assumed to be minimal that early in the season. Response variables were transformed where necessary to improve residual normality and homogeneity of variance.

A fungicide treatment was included in the experiment in order to investigate the effect of fungal mortality. Fungicide treated plots supported equal or, more often, significantly less active seedlings than plots with other treatments (not shown), providing

no evidence of fungal mortality and indicating that the fungicide treatment itself potentially the cause of mortality. For these reasons, fungicide treatment plots (160) were removed from the analyses presented here. Additionally, unwatered plots were removed from analyses of March mortality for both species because few seeds in these plots had emerged prior to this time.

RESULTS

In both October 2012 and June 2013, die-off soils had significantly higher acidity, phosphorous (P), and nitrate-nitrogen (N) than adjacent control soils (Table 2). During the first growing season, die-off plots supported lower densities (22.2 plants/plot ± 1.4 SE in control, 14.4 ± 1.7 SE in die-off) but generally higher biomass ($4.3\text{g} \pm 0.2$ SE in control, $7.2\text{g} \pm 0.4$ SE in die-off) of *B. tectorum* than control plots.

Experimental combinations from the first growing season (November, 2012 to May, 2013) supported emergence of viable *P. secunda* ranging from 37 to 79% ($59.4\% \pm 1.9\%$ SE), with 0 to 31% ($10.2\% \pm 1.1\%$ SE) showing active growth in late May 2013. Overall, *P. secunda* seedlings ranged from 2 to 4 cm tall (3.3 ± 0.1 SE) and had 2 to 6 leaves ($4.3 \pm .2$ SE). For *E. elymoides*, emergence of viable seed ranged 56 to 89% ($72.5\% \pm 1.3\%$ SE), with 20 to 71% ($41.2\% \pm 1.7\%$ SE) showing active growth in late May 2013. Overall, *E. elymoides* seedlings ranged from 4 to 9 cm tall (6.6 ± 0.2 SE) and had 3 to 11 leaves (5.6 ± 0.3 SE). By February 2014, experimental combinations showed

establishment rates of 6 to 21% ($13.1\% \pm 0.9\%$ SE) in *P. secunda* plots and 0 to 15% ($5.3\% \pm 0.7\%$ SE) in *E. elymoides* plots.

Seeds of both species that received simulated precipitation showed emergence through November and December 2012, with the majority of emergence completed by February 2013 for *P. secunda* and March - April 2013 for *E. elymoides* (Figure 2). Seeds in unwatered treatments remained mostly ungerminated until March 2013, when natural precipitation triggered the majority of seeds to germinate and emerge.

Effects of die-off on *P. secunda*

From November 2012 through April 2013, between-condition differences in number of active *P. secunda* seedlings were consistently significant, but often dependent upon watering and litter treatment (Table 3). Die-off plots supported significantly fewer seedlings than control plots in the watered treatment from November 2012 to February 2013 (CND*WTR interactions), as well as across water and litter treatments in March 2013 (Figure 3). Unwatered plots showed no significant condition effects from November 2012 to February 2013. Unraked plots had fewer seedlings in die-off than in control plots in November 2012 and April 2013 (unraked control: $18\% \pm 3\%$ SE in Nov., $61\% \pm 3\%$ SE in Apr.; unraked die-off: $8\% \pm 2\%$ SE in Nov., $43\% \pm 3\%$ SE in Apr.), with raked plots showing no condition differences in active seedlings for these months (CND*TRT interactions). However, die-off plots supported significantly more active seedlings than control plots regardless of other factors in early and late May 2013 (control: $15\% \pm 2\%$ SE in early May, $5\% \pm 1\%$ SE in late May; die-off: $25\% \pm 2\%$ SE in early May, $15\% \pm 2\%$ SE in late May). In the second growing season, there were no significant differences

in number of established *P. secunda* between control and die-off plots, regardless of other factors (November: 15% \pm 1.3% SE in control, 17.4% \pm 1.7% SE in die-off; February: 12.2% \pm 1.2% SE in control, 14.1% \pm 1.4% SE in die-off).

First season cumulative emergence for *P. secunda* was significantly higher in control than die-off plots (Figure 4.I). A strong pattern in most seedling growth variables of *P. secunda* was observed when comparing plots in die-offs to those in controls (Table 4). Seedlings in die-off plots were significantly more leafy and had greater late season vigor than those in control plots regardless of other factors (Figure 4.II, 4.III). For seedling height, unwatered die-off plots supported significantly taller seedlings than unwatered control plots (CND*WTR interaction), though this trend was driven mostly by nonlocal seedlings in die-off plots that were significantly taller than local and nonlocal seedlings in control plots (CND*ORGN interaction) (Figure 4.IV).

Effects of die-off on *E. elymoides*

Die-off plots had more active *E. elymoides* seedlings than control plots (Figure 5) late in the first season as well as in the second season, however early season results showed numerous interactions (Table 5). Die-off plots supported significantly fewer active seedlings than control plots in watered treatments in November and December 2012, and February and April 2013 (CND*WTR interactions, Figure 5), though in November this difference was due to a strong germination response of nonlocal seeds in watered control plots (CND*WTR*ORGN interaction, watered control: 51.7% \pm 6.5% SE for nonlocal, 44.3% \pm 5.8% SE for local; watered die-off: 26.8% \pm 4.1% SE for nonlocal, 37.3% \pm 4.2% SE for local; unwatered: < 2%). In March 2013, die-off plots

exhibited fewer seedlings than control plots regardless of other factors ($71.8\% \pm 2.1\%$ SE in control, $53.4\% \pm 2.5\%$ SE in die-off). Unwatered plots exhibited mixed trends, with no significant between-condition differences in November 2012 and April 2013, and significantly more active seedlings in die-off than control plots in December 2012 and February 2013 (Figure 2). In December, this difference was driven by a strong germination response of nonlocal seeds in unwatered die-off plots (CND*WTR*ORGN interaction; unwatered die-off: $5.5\% \pm 1.4\%$ SE for nonlocal, $3.8\% \pm 1.5\%$ SE for local; unwatered control: $.3\% \pm .3\%$ SE for nonlocal, $2\% \pm 1.3\%$ SE for local). In early May 2013, control and die-off plots did not differ in number of active seedlings, and in late May, die-off plots supported significantly more active seedlings than control plots regardless of other factors ($38.2\% \pm 2.6\%$ SE in control, $44.3 \pm 2.3\%$ SE in die-off). In the second growing season, die-off plots supported significantly more established *E. elymoides* than control plots regardless of other factors (November 2013: $0.7\% \pm 0.3\%$ SE in control, $7.8\% \pm 1.1\%$ SE in die-off; February 2014: $1.1\% \pm 0.2\%$ SE in control, $9.5\% \pm 1.2\%$ SE in die-off), with nonlocal material showing higher activity than local in the control ($1.2-1.8\% \pm 0.5\%$ SE for nonlocal, $0.3-0.5 \pm 0.2\%$ SE for local) but less than local in the die-off ($5.9-7.6\% \pm 1.3\%$ SE for nonlocal, $9.7-11.3\% \pm 1.8\%$ SE for local) for both months (CNDxORGN interactions).

Between-condition differences in cumulative first season *E. elymoides* emergence were also mediated by watering treatment, with significantly higher total emergence in control than die-off plots when watered, and no such difference when unwatered (CND*WTR interaction, Figure 6.I). Strong differences in seedling growth variables of

E. elymoides was observed when comparing plots in die-offs to those in controls (Table 6). Seedlings in die-off plots were more leafy, taller, and had more late season vigor than those in control plots regardless of other factors (Figure 6.II-IV). The magnitude of this die-off over control difference was significantly greater for unraked than for raked plots for late season seedling vigor (CND*TRT interaction, Figure 6.II), as well as for local than for nonlocal plots for seedling height (CND*ORGN interaction, Figure 6.IV).

Effects of seed origin on *P. secunda*

Plots of locally collected *P. secunda* seeds produced more active seedlings throughout the first season than plots of nonlocal seeds (Figure 7), though this result was dependent upon watering treatment in the early growing season (Figure 8, Table 3). November 2012 through February 2013 seedling numbers were significantly higher for local than nonlocal plots in watered plots, while unwatered plots showed similarly low numbers of seedlings regardless of origin (WTR*ORGN interaction). From March through late May 2013, as well as in February 2014, there were more active seedlings in plots of local than nonlocal seeds regardless of other factors. Early in the second growing season (November 2013), there were no significant effects of origin on number of established *P. secunda* seedlings.

Cumulative emergence for the first growing season was significantly higher for local than nonlocal *P. secunda* material (Figure 4). Seedlings from local seeds showed significantly greater late season vigor than those from nonlocal seeds, but there were no differences in leafiness associated with seed origin (Table 4). Nonlocal seedlings were

significantly taller than local seedlings in the die-off, as well as taller than seedlings in control plots, where height did not differ by origin (CND*ORGN interaction).

Effects of seed origin on *E. elymoides*

Early season differences in proportion of active seedlings between nonlocal and local *E. elymoides* seedlings were dependent upon condition and watering treatment, but nonlocal plots were clearly exhibiting more seedlings than local plots in the later part of the season (Figure 7). Despite a series of complex CND*WTR*ORGN interactions (not shown) from November 2012 through February 2013, the presence of active seedlings in control and die-offs did not differ dramatically by origin. In March 2013 there were no differences in active seedling numbers associated with seed origin. From April through late May 2013, plots seeded with nonlocal material exhibited significantly more active seedlings than those with local material. Plots of local seeds supported more established plants than plots of nonlocal seed in die-off plots in November 2013 ($5.9\% \pm 1.3\%$ SE for nonlocal, $9.7\% \pm 1.8\%$ SE for local), whereas control plots showed no origin effects ($1.2\% \pm 0.6\%$ SE for nonlocal, $0.3\% \pm 0.1\%$ SE for local). In February 2014, local plots supported more plants than nonlocal in unraked ($3.6\% \pm 0.9\%$ SE for nonlocal, $7\% \pm 1.5\%$ SE for local) but not raked plots ($5.8\% \pm 1.3\%$ SE for nonlocal, $4.8\% \pm 1.6\%$ SE for local, TRTxORGN interaction).

Cumulative first season emergence of *E. elymoides* did not differ significantly between plots of nonlocal and local material (Figure 6). Nonlocal seedlings were significantly more leafy, taller, and had more late season vigor than local seedlings. For

seedling height, this difference was significantly smaller in die-off plots than control plots (CND*ORGN interaction).

Effects of watering treatment on *P. secunda*

From November 2012 through February 2013, watered plots supported more active seedlings than unwatered plots overall (Figure 2), though this difference was significantly smaller in die-off than in control plots (CND*WTR interaction, Figure 3, Table 3) and for nonlocal vs. local plots (WRT*ORGN interaction, Figure 8). For the rest of the first growing season as well as early in the second (March - November 2013), watering treatment had no effect on the number of active seedlings. In February 2014, watered plots supported more established plants than unwatered in unraked ($12.5\% \pm 1.6\%$ SE in watered, $7.8\% \pm 1.2\%$ SE in unwatered) but not raked plots ($15.9\% \pm 2.4\%$ SE in watered, $16.3\% \pm 1.7\%$ SE in unwatered, TRT*WTR interaction).

First season cumulative emergence of *P. secunda* was not affected by watering treatment (Figure 4). *Poa secunda* seedlings from watered plots had significantly more leaves but did not differ in late season vigor from those in unwatered plots. Seedlings from watered plots were taller than those from unwatered plots in the die-off, whereas control plots showed no effects of watering.

Effects of watering treatment on *E. elymoides*

Watered plots supported significantly more active seedlings than unwatered plots from November 2012 through April 2013 (Table 5, Figure 5). This effect was significantly less in die-off than control plots and raked than unraked plots in November

(CND*WTR and TRT*WTR interaction, Figures 5 and 9). In both early and late May 2013, watered plots supported more active seedlings in raked plots, while unraked plots showed no effects of watering treatment (TRT*WTR interaction).

End of season, cumulative emergence was significantly higher in watered than unwatered plots regardless of other factors (Table 6). In the second growing season, there were no effects of watering treatment on number of established *E. elymoides* (Figure 5). Seedlings showed no differences in late season vigor, leaf number or height associated with watering treatment.

Effects of litter removal on *P. secunda*

Fewer active seedlings were observed in raked and unraked plots in control plots in November 2012 and April 2013, while die-off plots showed no effects of litter treatment at these times (CND*TRT interaction, Table 3). No effects of litter treatment on number of active seedlings were observed from December 2012 through March 2013. Raked plots supported significantly more active seedlings than unraked plots in both early and late May 2013, with this difference significantly larger for plots of local ($19.1\% \pm 2.3\%$ SE in unraked, $33.4\% \pm 3.3\%$ SE in raked) than nonlocal ($9.2\% \pm 2\%$ SE in unraked, $19.3\% \pm 2.6\%$ in raked) material in late May (TRT*ORGN interaction). Litter removal was associated with more established *P. secunda* in November 2013 regardless of other factors ($13.3\% \pm 1.3\%$ SE in unraked, $19.1\% \pm 1.7\%$ SE in raked), but this trend was apparent in February 2014 only in unwatered plots (unwatered: $7.8\% \pm 1.2\%$ SE in unraked, $16.3\% \pm 1.6\%$ SE in raked; watered: $12.5\% \pm 1.6\%$ SE in unraked, $15.6\% \pm 2.4\%$ SE in raked; TRTxWTR interaction).

First season cumulative emergence for *P. secunda* was not affected by litter treatment (Figure 4, Table 4). *Poa secunda* seedlings from raked plots had significantly greater late season vigor and were leafier than those from unraked plots, though seedling height showed no differences associated with litter treatment.

Effects of litter removal on *E. elymoides*

In November 2012, significantly fewer active seedlings existed in raked than unraked plots in control plots that were watered, while unwatered control plots and die-off plots of either watering treatment did not exhibit effects of raking (CND*TRT*WTR interaction, data shown, Table 5). Fewer seedlings existed in raked than unraked plots in December 2012 regardless of other factors ($34.5\% \pm 3.8\%$ SE in unraked, $29\% \pm 3.7\%$ SE in raked), as well as in February 2013 in unwatered (but not watered) plots (TRT*WTR interaction, Figure 9). There were no effects of litter treatment on number of active seedlings in March or April 2013. Raked plots supported more seedlings than unraked plots under the watering treatment in early May 2013, while unwatered plots showed no significant effects of litter treatment (TRT*WTR interaction). In late May, raked plots supported significantly more seedlings than unraked plots regardless of other factors, though this difference was greatest in watered plots (TRT*WTR int). Litter removal showed no effects on *E. elymoides* survival in November 2013, but in February 2014 was associated with fewer established plants in plots of local ($7\% \pm 1.5\%$ SE in unraked, $4.8\% \pm 1.6\%$ SE in raked) but not nonlocal material ($3.6\% \pm 0.9\%$ SE in unraked, $5.8\% \pm 1.3\%$ SE in raked; TRTxORGN interaction).

End of season, cumulative emergence of *E. elymoides* was not affected by litter treatment (Figure 6). Seedlings in raked plots had significantly more late season vigor, especially in the control (CND*TRT interaction), and had more leaves than those in unraked plots. Also, raked plots produced significantly shorter seedlings than unraked plots.

Effects of experimental design on *B. tectorum* dynamics

Density of *B. tectorum* in May 2013 was significantly lower in die-off plots than control plots, raked than unraked plots, and unwatered than watered plots (Figure 10.I). Neither the species planted nor their origin had significant effects upon *B. tectorum* density.

June 2013 biomass of within-plot *B. tectorum* was significantly higher in die-offs than controls in all groups except unwatered plots in the raked treatments, where there were no between-condition differences (TRT*WTR*CND interaction, Figure 10.II). Similarly, raked plots showed significantly less *B. tectorum* biomass than unraked plots except in unwatered die-off plots, where no treatment differences were observed. Higher biomass was exhibited in watered than in unwatered plots in unraked control plots and raked die-off plots, while there was no effect of watering on biomass in raked control plots and unraked die-off plots (WTR*TRT*ORGN interaction, Figure 10.III). Additionally, higher biomass in watered than unwatered plots was exhibited in all TRT*ORGN groups except unraked plots of nonlocal seeds. The species of native seed in a plot did not have any effects upon *B. tectorum* biomass ($5.9\text{g} \pm 0.3$ SE for *P. secunda*, $5.7\text{g} \pm 0.3$ SE for *E. elymoides*).

Covariate models: effects of *B. tectorum* dynamics on native species

When *B. tectorum* density was included as a covariate in the *P. secunda* model, there was no longer a significantly greater number of active seedlings in control than die-off plots in April 2013, but there were significantly more seedlings in die-off than control plots for both November 2013 and February 2014 (data not shown). For *P. secunda* growth data, there was no longer a significant between-condition difference in cumulative first season emergence, a significant effect of litter removal on late season vigor, or a significant interaction between condition and watering treatment seedling height. Additionally, there was a significant three-way interaction regarding *P. secunda* leaf number in the density-covariate model. In this interaction, seedlings in die-off plots had more leaves than control plots except in unraked plots of local material, where there were no condition differences (CND*TRT*ORGN interaction, data not shown). In the *E. elymoides* model, the COND*ORGN interaction for actively growing plants in February 2014 was no longer significant, but it did not modify any other effects on active *E. elymoides* seedlings.

When midsummer *B. tectorum* biomass was included as a covariate in the *P. secunda* model, the significant condition effect on number of active seedlings in April 2013 (more in control than die-off) as well as the significant TRT*ORGN interaction in late May 2013 were no longer significant. In the *E. elymoides* model, the significant effects on number of active *E. elymoides* seedlings from origin in April 2013 (more nonlocal than local), and from condition in late May 2013 (more in die-off than control) were no longer significant. Additionally, under this biomass-covariate model, neither the

significant TRT*WTR interaction on active *P. secunda* individuals in February 2014 nor the significant CND*ORGN interaction on active *E. elymoides* individuals in November 2013 were significant. When included for growth variables, neither the CND*WTR interaction regarding *P. secunda* seedling height nor the CND*ORGN interaction regarding *E. elymoides* seedling height were significant. However, under the biomass-covariate model, there was a significant two-way interaction regarding the number of active *P. secunda* seedlings in March 2013. In this interaction, unraked plots supported more seedlings than raked plots in the die-off but not control, though control plots still supported more seedlings than die-offs regardless of litter treatment (CND*TRT interaction, data not shown).

DISCUSSION

The dramatic alteration of ecological structure (Stewart & Hull 1949, Mack 1981) and biogeochemical processes (Brooks et al. 2004, Adair & Burke 2010) associated with *B. tectorum* invasion in the Great Basin greatly reduces native species abundance and makes restoration of these species challenging (Davies et al. 2011). The existence of the phenomenon of complete *B. tectorum* stand failure, or die-off, may improve the restoration potential of these highly invaded systems if native species can benefit in the wake of the phenomenon.

Native species establish in recent die-offs

The recent *Bromus tectorum* die-off was found to be associated with increased first year growth and vigor of the native perennial bunchgrasses *P. secunda* and *E.*

elymoides. Although emergence for both native species was generally lower in the die-off than the adjacent and continuously infested area, individuals that did emerge in the die-off exhibited longer active growing periods and increased leaf numbers and height during the first season relative to seedlings in the adjacent, continuously infested area. While previous work has found heightened *B. tectorum* growth in die-off soils (Meyer et al. *in press*), this study is the first to demonstrate the effects of die-off on native species establishment. Furthermore, there was evidence that this first-year ‘die-off advantage’ was meaningful for longer term establishment, with increased second year survival in die-off vs. control plots for *E. elymoides*. Although this trend was not observed for *P. secunda*, this does not rule out other second year benefits, such as improved second year growth or reproductive output, both of which are yet unmeasured. Nonetheless, these findings are a case study in support of the notion that *B. tectorum* die-offs represent an opportunity for increasing the success of native material in restoration. Results from the soil analyses revealed higher N and P in die-off soil, suggesting nutrient availability plays a role in this opportunity. This corroborates N pulses observed in previous studies on *B. tectorum* die-offs (Blank et al. 2011, Baughman & Meyer 2013), as well as other studies in which *B. tectorum* stands were fallowed for a growing season (Eckert & Evans 1967, Eckert et al. 1970). Future studies which aim to determine the mechanistic causes of this restoration potential should more extensively examine soil nutrients and properties.

Despite the low precipitation during this study (~72% of 30 year average), my results somewhat exceed other experimental restoration establishment results for *E. elymoides* and the closely related *E. multisetus* in the first season, which have reported active growth from less than 2% (Clausnitzer et al. 1999, Bernstein et al. 2014) up to 10-

30% (Humphrey & Schupp 2004, Rowe & Leger 2012), and are similar to reported second season survival rates, which vary from 0% to 5% (Humphrey & Schupp 2004, Boyd & Davies 2012, Rowe & Leger 2012). Regarding the lesser studied *P. secunda*, first year survival from below 1% (Bernstein et al. 2014) to 20%-31% (Leger, unpublished data) have been encountered, though these two measures likely represent below- and above-average responses. It must be considered that the results in the current study may be artificially high due to the seeding method employed in this study, which certainly did not simulate the seeding methods commonly utilized in restoration in the region. Seeding methods play a large role in determining the patterns of success when restoring resource-limited, semiarid sites (James & Svejcar 2010, Bernstein et al. 2014) because they determine the conditions that germinating seeds will experience, which are perhaps the conditions of most concern for improving restoration success (Boyd & Davies 2012). The hand-sorting and precision-seeding method of planting in this study attempted to maximize viability and germination, and this likely improved the observed seedling activity and survival rates. Therefore, identifying the effects of recent *B. tectorum* die-offs on native establishment using more realistic restoration methods should be the goal of future studies, but this experiment has nonetheless highlighted the potential for increased native success in die-off areas.

Seed origin affected native performance

The Great Basin is heterogeneous with respect to many factors relevant to plant distribution (Comstock & Ehleringer 1992), and for species with large ranges such as *P. secunda* and *E. elymoides*, such factors are expected to have generated intraspecific genetic variation through differential selection pressures (Loveless & Hamrick 1984,

Linhart & Grant 1996). In this study, clear differences in growth and establishment were observed between locally collected and commercially produced, nonlocal seeds, and these differences varied by species. First season-effects showed both local (*P. secunda*) and nonlocal (*E. elymoides*) performance advantages, but only local advantages were seen to persist into the second year. Neither species provided evidence that strategies involving high first season growth were more successful. However, these findings represent only one site and two growing seasons, so general claims regarding particular performance patterns in the origin of plant materials used should not be over generalized.

Locally collected *P. secunda* material had significantly higher cumulative emergence and supported more active seedlings in the first season than nonlocal material (Mt. Home). This local advantage was not apparent early in the second growing season, but by February 2014, local material continued to show greater establishment. This two-season trend of more active local than nonlocal seedlings averaged across all other experimental factors indicates that local material was more adapted to the site given the growing conditions during the study. Local seedlings showed increased late season vigor but in some instances were shorter than nonlocal seedlings and did not differ in leaf number in the first season, indicating that second season establishment was related to a longer active period and perhaps a more conservative growth strategy in the first season rather than increased aboveground growth. This finding substantiates other evidence from the Great Basin that large above-ground body size in herbaceous plants is unnecessary, especially in competitive environments, for increased survival (Rowe & Leger 2012) and

reproduction (Kulpa & Leger 2013), as well as similar findings in other systems (Chambers & Aarssen 2009).

Plots of nonlocal *E. elymoides* (Toe Jam Creek) supported significantly more seedlings than plots of local seeds in the later part of the first season, and nonlocal seedlings were leafier, taller, and had greater late season vigor than local seedlings. There was evidence in some early season condition and treatment combinations that nonlocal *E. elymoides* material may have been somewhat more immediately germinal than local material under the given seedbed conditions, and because early germination has been found to improve first season growth (Verdú & Traveset 2005), this may be one mechanism by which between-origin differences in growth arose in this species. Increased seedling growth and vigor have been highly prioritized traits in material development in the region (Leger & Baughman, *in press*), and this is true for Toe Jam Creek (USDA, ARS 2013). However, there is evidence that increased first year growth is independent of some fitness components, such as survival (Verdú & Traveset 2005) and fecundity (Chambers & Aarssen 2009), and one example from *Elymus* demonstrated higher survival of smaller genotypes in invaded systems (Rowe & Leger 2012). With second year establishment as a proxy for survival, my results support this notion, as the clear advantage observed in first season performance for nonlocal material did not lead to an advantage in second season establishment. However, very low second season establishment for both origins suggests that the given conditions experienced by seeds during the study (e.g. lower than average precipitation) were not conducive to *E. elymoides* recruitment regardless of seed source. Indeed, patterns of environmental variation may often have more influence on fitness than heritable traits (Sultan 1987),

especially in resource-limited environments and in the seed- and seedling-stage (Kindell et al. 1996, Gordon & Rice 1998). Therefore, the observed results for the early life stages of *E. elymoides* do not rule out longer-term differences in seed sources. Furthermore, others have posited that more conservative strategies (Humphrey & Schupp 2002), and/or beneficial and novel traits (Leger & Espeland 2010, Lankau 2012) of local genotypes can lead to a delayed manifestation of local adaptation (Rice & Knapp 2008). Regardless of how performance plays out in the long-term, the differences in season-to-season performance observed here strongly advocates against assessing the quality of restoration material after only one growing season.

Native establishment in die-off was not dependent upon seedbed treatment

There were significant effects of both water addition and litter removal treatments on emergence, first season seedling activity, and growth that varied through time and differed by species. Densities of *B. tectorum* across the study indicate that the treatment combinations applied here did not appear to succeed in triggering complete stand failure or die-off off at the plot level as hoped. Previous studies on the phenomenon have also failed to produce high seed/seedling mortality (Blank et al. 2011), likely because die-offs are triggered by fairly specific seedbed conditions (Meyer et al. *in press*) which are yet unknown. Also, because the complex effects of the treatments in this study were generally consistent between the die-off and control condition, they provide no evidence supporting the notion that any of the seedbed treatments used in this study facilitated or hindered the establishment of native species differently in a recent die-off than in the adjacent, continuously infested area. Nonetheless, some seedbed treatment effects

demonstrate several meaningful differences and consistencies in how *E. elymoides* and *P. secunda* respond to their environment, and are therefore briefly discussed.

Poa secunda and *E. elymoides* showed different demographic and physiological responses to early watering that appeared to have consequences for both first and second-season success. Plots receiving early water supported more active *E. elymoides* seedlings for the entire first growing season but produced only early season differences in *P. secunda* seedling activity (Figure 2). With regard to seedling growth, early watering promoted more leafy and, in the die-off, taller *P. secunda* seedlings but had no significant effects on the growth of *E. elymoides*. Therefore, *P. secunda* responded to early season water with increased growth but not increased emergence, while *E. elymoides* responded with increased emergence but not increased growth. The response of *P. secunda* matches recent findings using similar species in the northern Great Basin, in which modest water additions in fall (Boyd & James 2013) and spring (James & Svejcar 2010) affected germination timing but not overall germination percentage or seedling density. The modest increase in germination percentage seen in *E. elymoides* are also not unparalleled in semi-arid literature (Bernstein et al. 2014). The limited effects of modest water additions in the current and above cited studies likely resemble responses of native seeds and seedlings to realistic, above average ‘wet years’. Water additions in great excess of average precipitation are found to have larger effects on establishment and growth of similar perennial grasses (Porensky et al. 2014). In addition to the evidence that responses to water addition varied by species in the current study, the importance of such responses is their longer-term effect on survival. To that end, neither species in the current study continued to show convincing benefits of the watering treatment in the

second season. However, one should interpret this cautiously, as most aspects of second year fitness were not measured, and the benefits of increased water availability and early emergence may have yet to play out, as others have noted (Boyd & James 2013).

Although no studies were found that modified litter in ways comparable to this study, the presence of surface organic matter and/or mulches is generally viewed as having positive effects on establishment of desirable species in an arid land restoration context (Whisenant 1999). However, in low litter, arid systems, native species may not be suited to benefit from the effects of litter (Woods et al. 2012), and the effects of litter in this study support that notion. The removal of *B. tectorum* litter in the current study generally had positive effects on native species, was never associated with reduced native emergence or survival, and varied by species and through time. Cumulative emergence was not affected by litter removal for either species. Litter removal was associated with fewer early season active *E. elymoides* but more active late season seedlings of both *E. elymoides* and *P. secunda*. Additionally, active seedlings of both species were significantly more leafy and had more late season vigor in raked than unraked plots. These positive effects of litter removal remained significant for survival in the second season for *P. secunda*, but not *E. elymoides*. The mechanisms behind the effects of litter removal are not well addressed by the current data. One potential factor is that litter removal may have altered competitive effects by removing resident *B. tectorum* seeds, but results from the covariate models were not suggestive that the observed native responses to litter removal were related to differences in *B. tectorum* competition (those results are discussed in more detail below). Whatever the cause, these results are a case study suggesting that removing *B. tectorum* litter from near-monocultures may improve

native establishment. Of course, manual litter removal at the large scales common to Great Basin restoration is unfeasible. However, because die-offs often occur at the scale of a few acres, litter removal could be feasible if there was substantiated evidence that doing so was beneficial for restoration. Future studies regarding die-offs restoration would be wise to further investigate this topic.

Little evidence for *B. tectorum* competition affecting native establishment

Because competition with resident *B. tectorum* may have affected the responses of native species to die-off conditions, I quantified the between-condition and between-treatment differences in resident *B. tectorum* dynamics (density and biomass), then looked for evidence that these dynamics played a role in main-model patterns of native growth. *Bromus tectorum* densities were higher in control vs. die-off, watered vs. unwatered, and in unraked vs. raked plots. Biomass was generally higher in die-off vs. control, and had minor responses to water addition (positive) and litter removal (negative). Though not a primary focus of this study, these differences in *B. tectorum* dynamics across the experimental design were important to consider because of their potential to exert differential competition. *Bromus tectorum* can have strong competitive effects on native perennial grasses in the semi-arid Great Basin (Melgoza et al. 1990, Humphrey & Schupp 2004), and these effects are generally stronger when natives are in the seedling stage (Humphrey & Schupp 2004, Ferguson 2012). However, these competitive effects are not ubiquitous, and have been found to be absent and/or much less influential of native perennial grass establishment than other factors (James & Svejcar 2010, Elseroad & Rudd 2011, Mangla et al. 2011). Although the current study only addressed competition indirectly using *B. tectorum* density and biomass as covariates, the

scattered results were mostly inconsistent with patterns that would indicate competition affecting survival and performance. In fact, higher density and biomass production of *B. tectorum* was, in some instances, associated with heightened native seedling activity, but the reasons for this are unclear. For example, there were four instances in which accounting for *B. tectorum* densities (which were higher in control than die-off plots) significantly reduced response values from control plots relative to die-off plots and/or significantly increased die-off response values relative to control values. Such patterns are more consistent with facilitation than competition, or may be the results of neutral interactions between species but parallel responses to increased soil resources. The few instances that were consistent with competition included increased mid-season activity (in unraked die-off plots) and late season vigor (in unraked plots) values for *P. secunda* where *B. tectorum* density and biomass were high (in unraked plots) after covariate inclusion. Because *B. tectorum* density was not manipulated, these effects are inadequate to meaningfully demonstrate the importance of competition between *B. tectorum* and the study species, but the lack of large and clear competitive effects from these correlative results suggests that such effects were minimal in this study.

Native species show unexplained lack of emergence in die-off

Complete *B. tectorum* stand failure was not observed in this study, and die-offs were not associated with epidemic levels of native mortality. However, emergence was lower in die-off than control plots for *P. secunda* and, in the watered treatment, *E. elymoides* as well, and it is possible that such a trend could be due to die-off causal factors affecting native seeds. Few lines of evidence from this study assist in interpreting these results. This trend did not appear to be dependent upon early season water addition,

and differences in soil (slightly lower pH, and greatly higher P and N in die-off than control) do not logically support a role for soil nutrient conditions to cause lower emergence in die-off. Litter removal appeared inconsequential to this trend for *E. elymoides*, but because the density-covariate model no longer supported less emergence in die-off plots than control plots of *P. secunda* in which litter were removed, an intact litter layer may have been associated with reduced emergence in die-off plots for this species.

CONCLUSIONS

In the face of one of the more significant biological invasions of the western United States, there is much to be gained by attempting to reduce and reverse ecological degradation through native plant restoration. This case study demonstrated source-related and species-dependent differences in performance of native perennial grasses seeded into an invaded site, which contributes to a better understanding of the importance of seed selection in restoration for the region. Additionally, it answered the call from previous studies to investigate the potential for restoring areas experiencing *B. tectorum* die-off, or complete stand failure. To that end, the results from this northern Nevada site observed some negative but mostly positive effects of these areas on native grass growth and establishment. These findings demonstrate that further investigations of this restoration potential of these areas are warranted. However, it must be considered that the single site in this study may represent only one way in which the die-off phenomenon is expected to

affect native establishment, and the specific environmental conditions during the limited duration of the study were likely important determinants of the observed effects. Though it may be difficult, future efforts should examine multiple die-off sites, or at least supply enough information about individual sites to enable informed comparison of sites and results, such as soil types and analyses, local climates, and previous and existing vegetation.

FIGURES

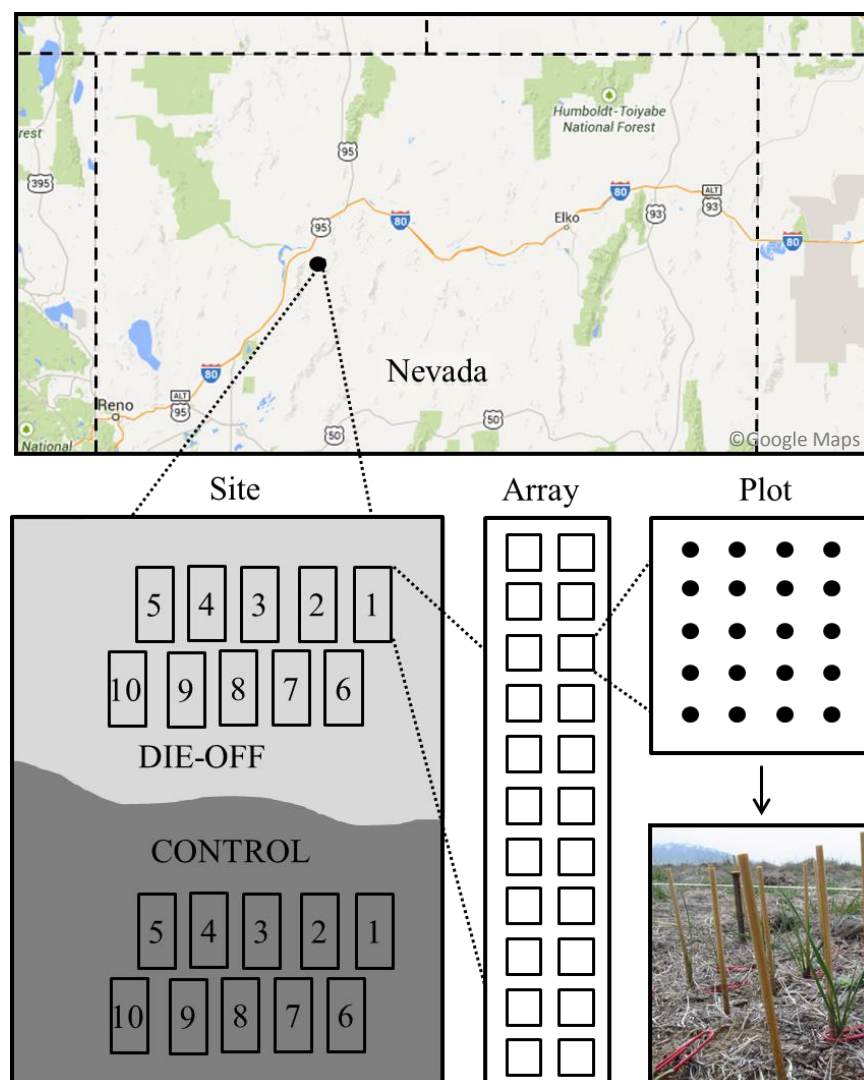


Figure 1. The Dun Glen die-off is located in Northern Nevada, and is composed of one fenced site that includes portions of a larger recent die-off (light gray) as well as adjacent, apparently unaffected control conditions (dark gray). Each of 10 blocks (numbered) contained two arrays, one in each condition. Each array was composed of 24 randomly organized, unique plots representing the 24 combination of experimental factors. Each plot contained 20 seeds from the same seed lot glued to skewers.

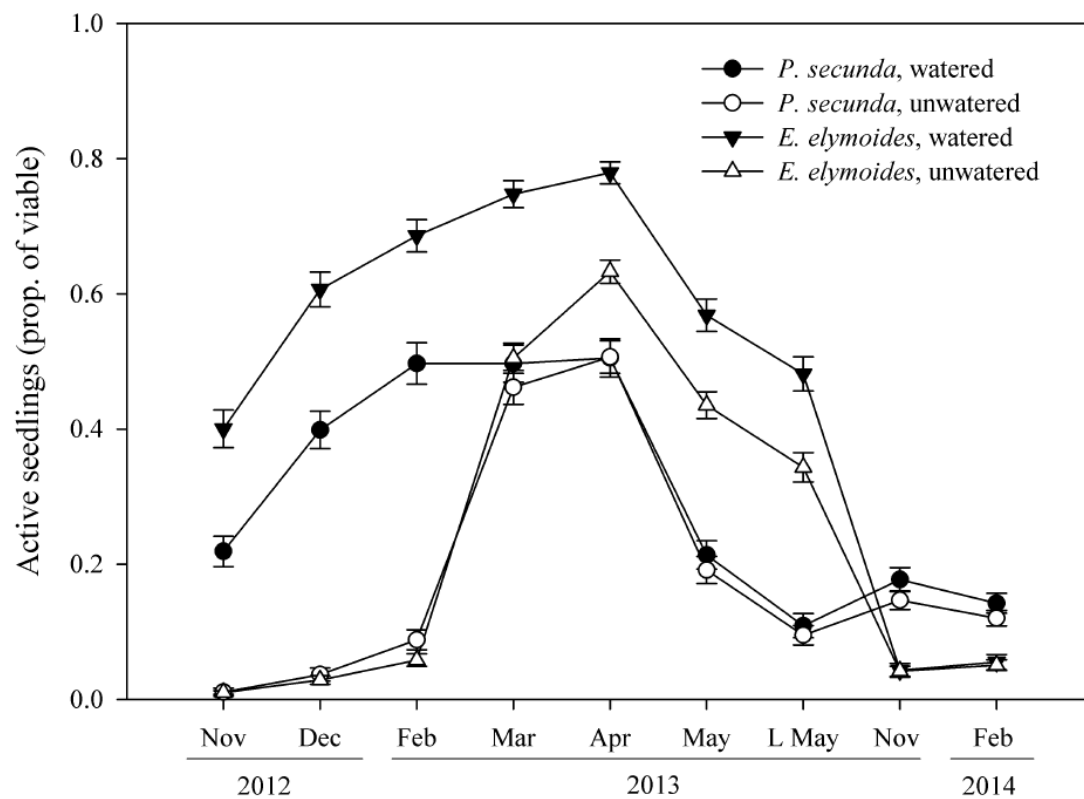


Figure 2. Mean proportion of viable seeds showing active growth through time for *E. elymoides* (circles) and *P. secunda* (triangles) for early season watered (filled) and unwatered (empty) plots. Means and standard errors are from untransformed data.

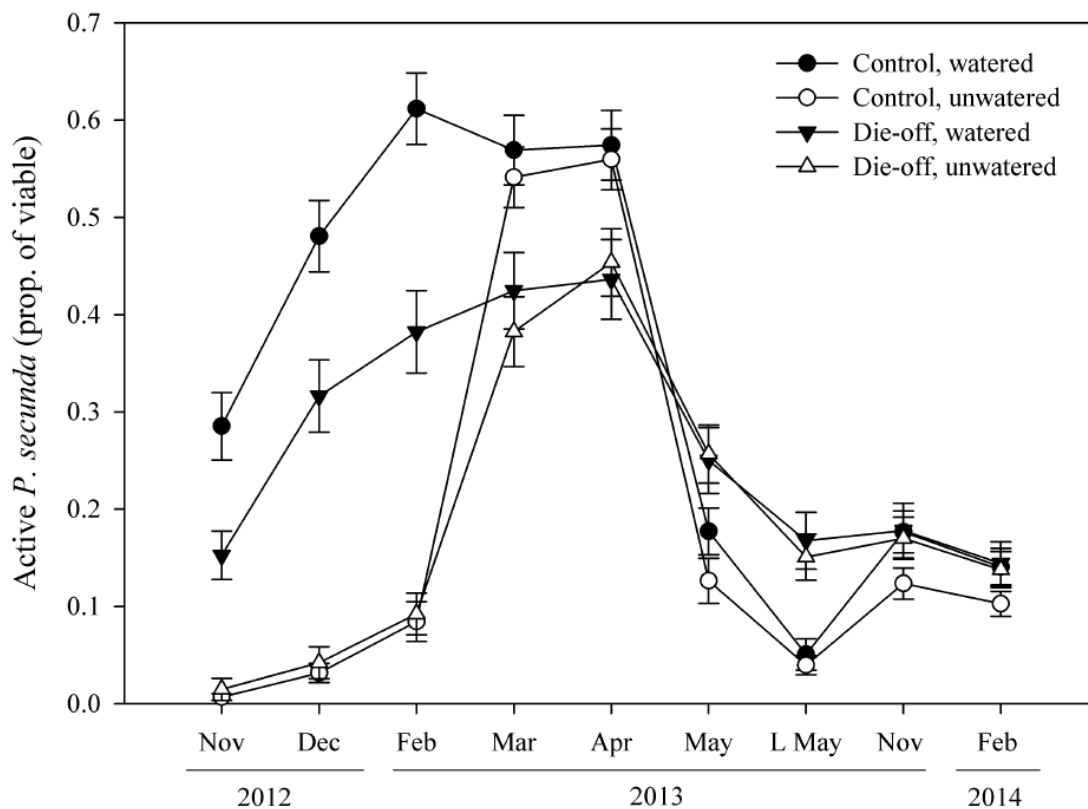


Figure 3. Mean proportion of viable *P. secunda* seeds showing active growth through time in the control (circles) and die-off (triangles) condition for early season watered (filled) and unwatered (empty) plots. Means and standard errors are from untransformed data.

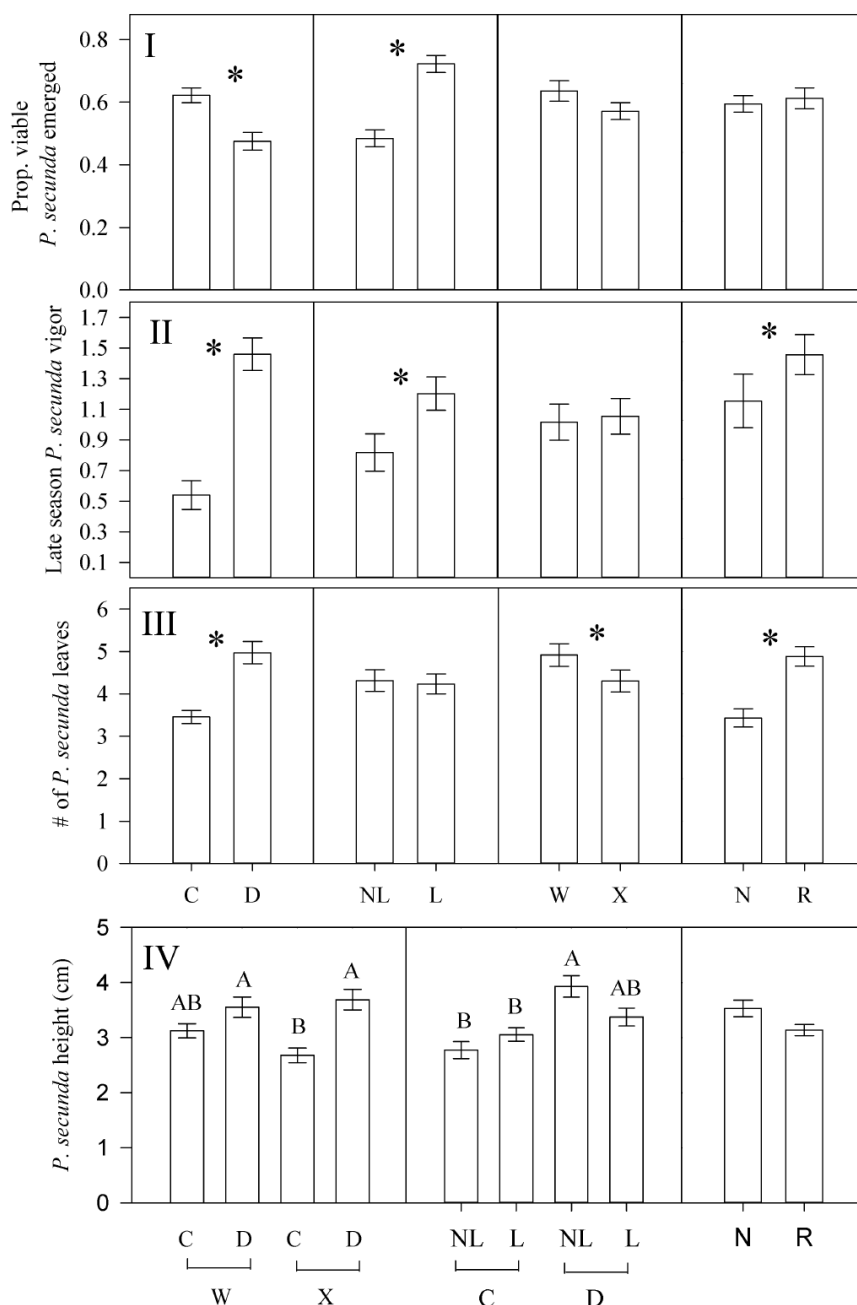


Figure 4. Mean first season emergence, late season vigor, number of leaves, and seedling height for *P. secunda* by main experimental factors; control (C) and die-off (D) condition, early season watering treatment (W) and unwatered (X), raked (R) and unraked (N) litter, and nonlocal (NL) and local (L) material. Asterisks indicate significant main effects ($P < 0.05$). Significant interactions between factors are indicated by combined, 4-bar graphs. Letters above bars indicate significant differences based on Tukey's comparisons ($P < 0.05$). Means and standard errors are from untransformed data.

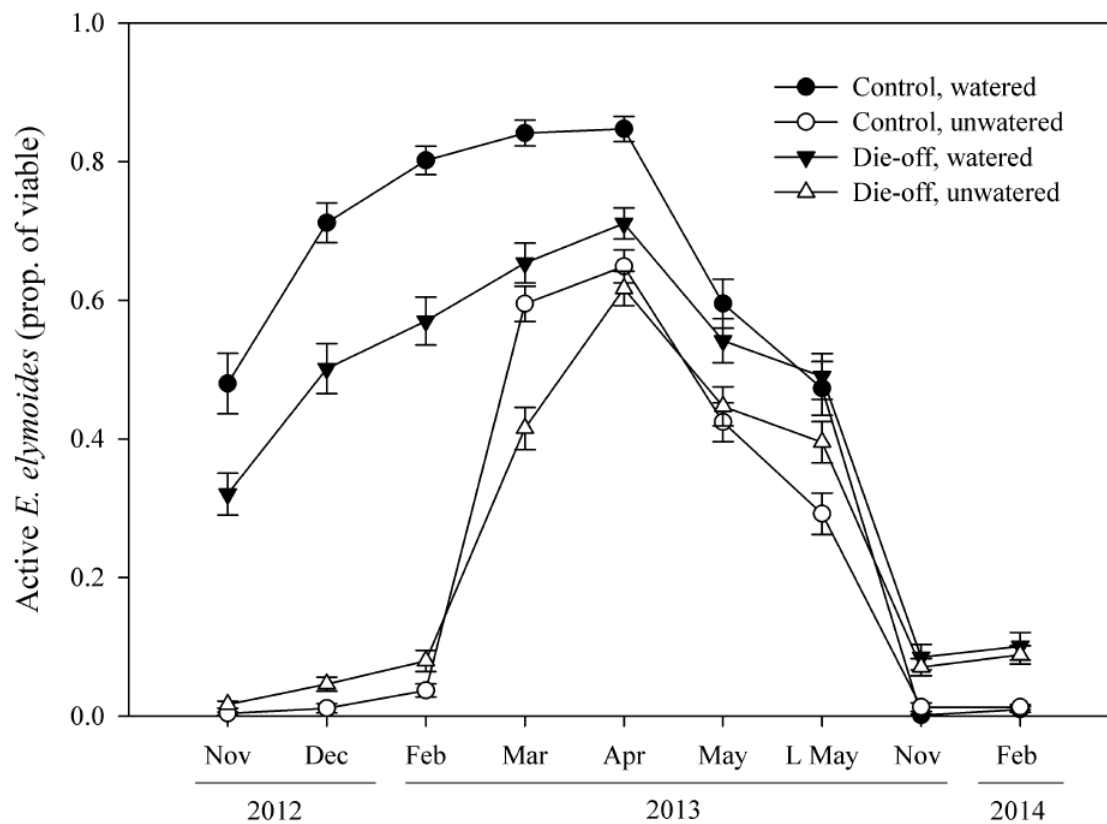


Figure 5. Mean proportion of viable *E. elymoides* seeds showing active growth through time in control (circles) and die-off (triangles) for early season watered (filled) and unwatered (empty) plots. Means and standard errors are from untransformed data.

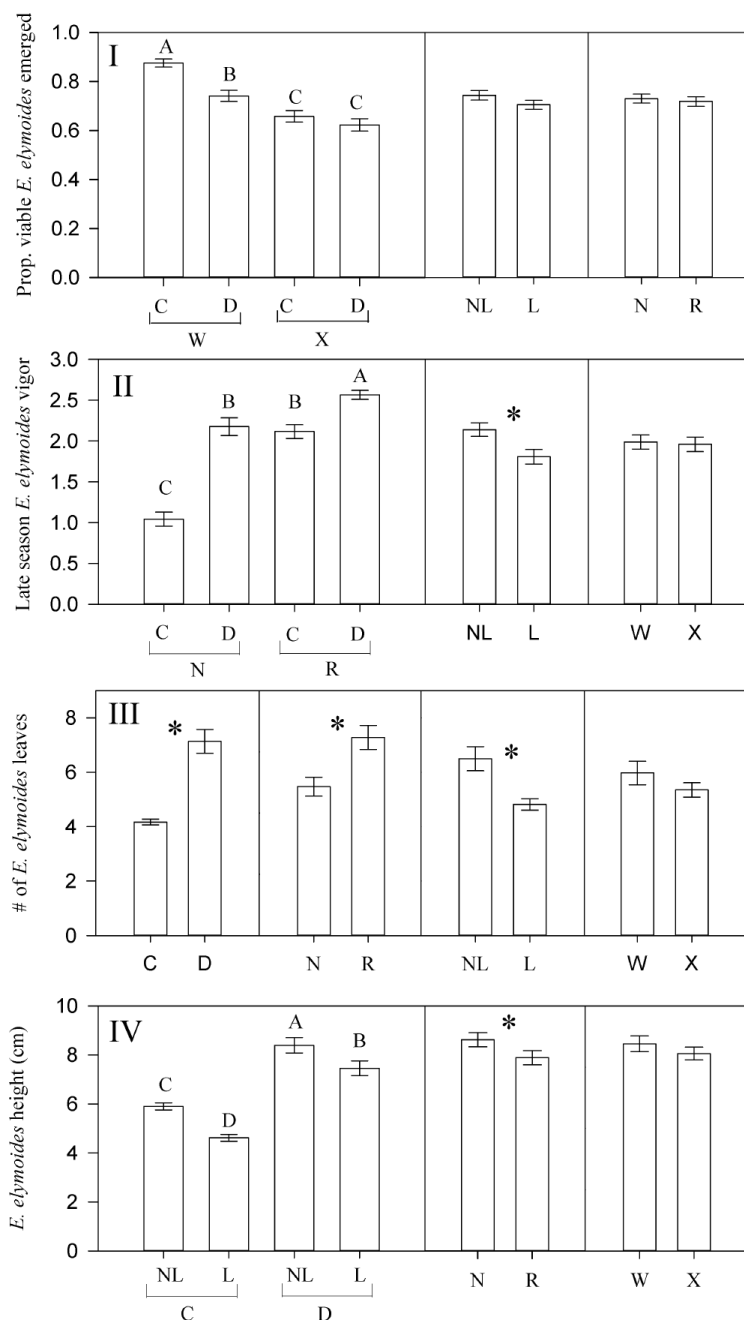


Figure 6. Mean first season emergence, late season vigor, number of leaves, and seedling height for *E. elymoides* by main experimental factors; control (C) and die-off (D) condition, early season watered (W) and unwatered (X) plots, raked (R) and unraked (N) litter, and nonlocal (NL) and local (L) material. Asterisks indicate significant main effects ($P < 0.05$). Significant interactions between factors are indicated by combined, 4-bar graphs. Letters above bars indicate significant differences based on Tukey's comparisons ($P < 0.05$). Means and standard errors are from untransformed data.

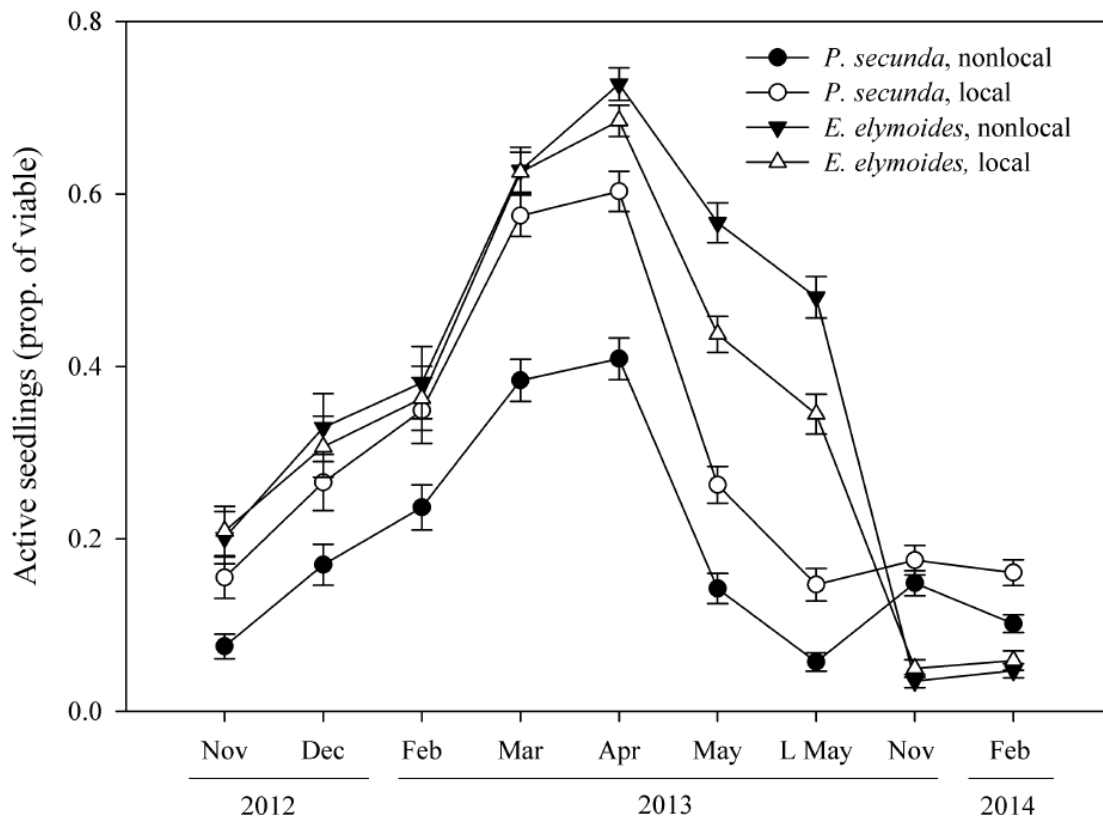


Figure 7. Mean proportion of nonlocal (filled) and local (empty) viable *P. secunda* seeds showing active growth through time. Means and standard errors are from untransformed data.

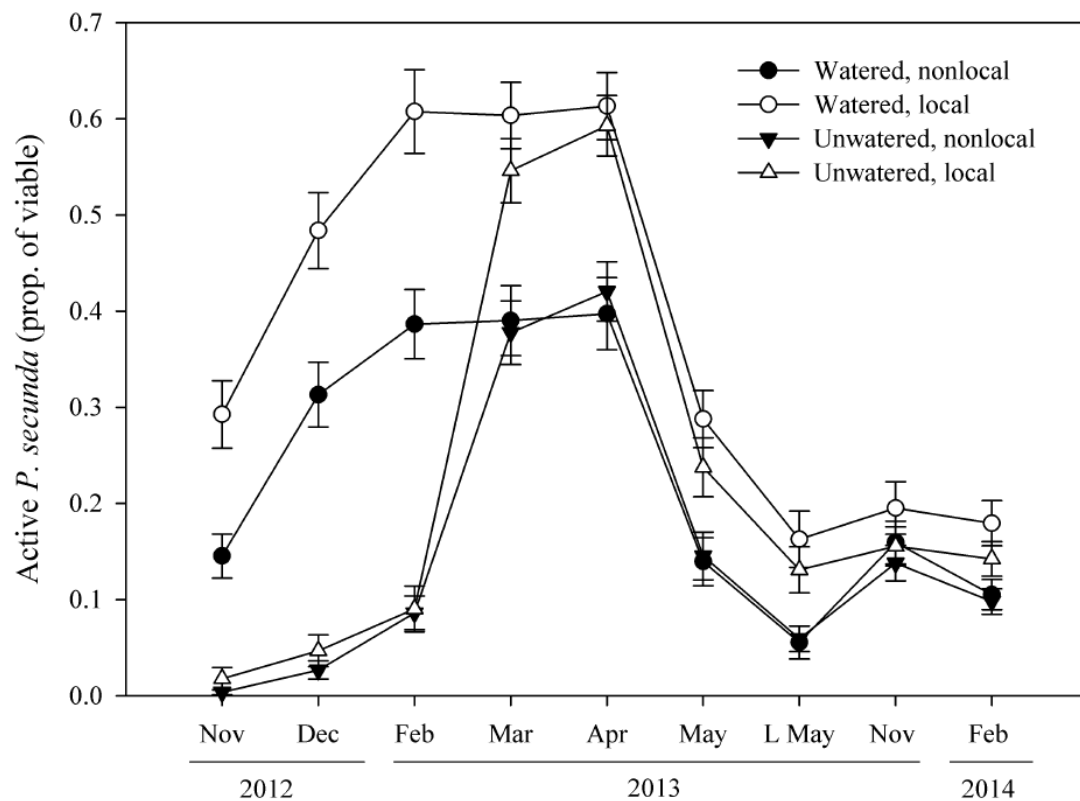


Figure 8. Mean proportion of viable *P. secunda* seeds showing active growth through time in early season watered (circles) and unwatered (triangles) plots, for nonlocal (filled) and local (empty) material. Means and standard errors are from untransformed data.

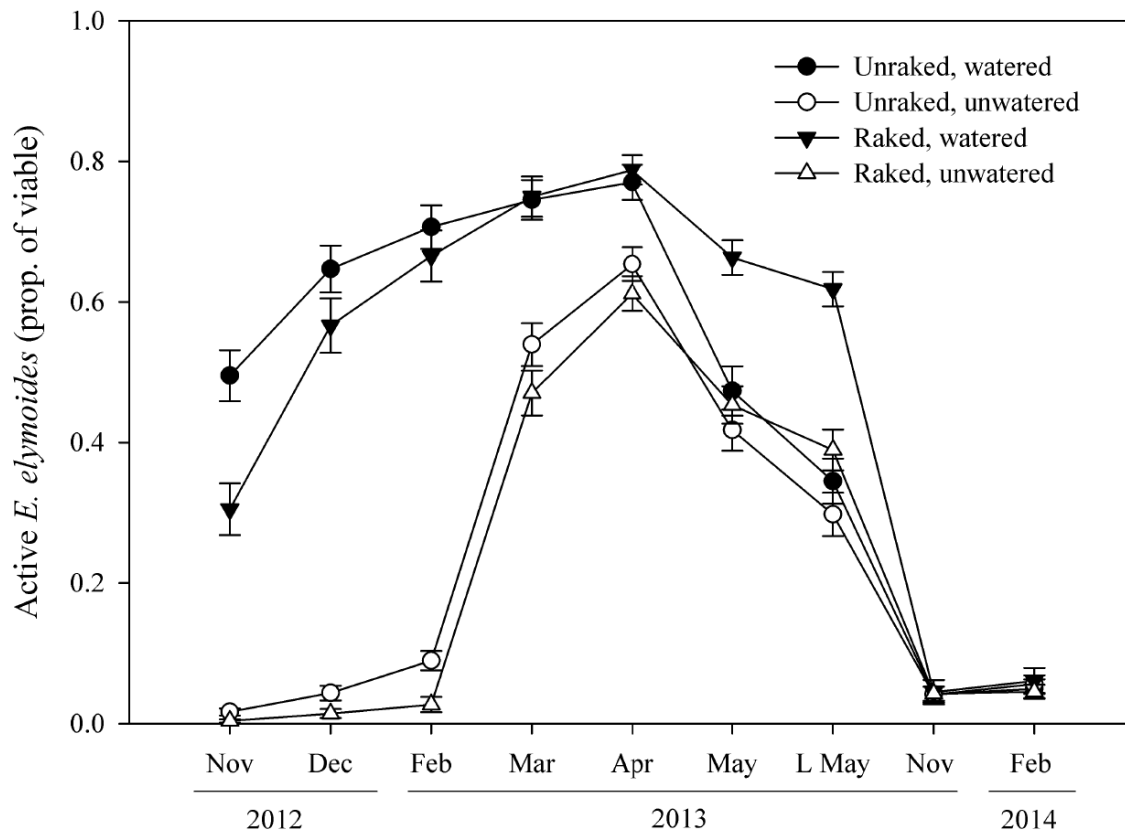


Figure 9. Mean proportion of viable *E. elymoides* seeds showing active growth through time in unranked (circles) and raked (triangles) plots, for early season watered (filled) and unwatered (empty) treatments. Means and standard errors are from untransformed data.

TABLES

Table 1. Locations and determined age of die-off during the year of study for ten previously studied die-off sites, with status of *B. tectorum* in both the control and die-off one year later.

Site	Location	Study year Die-off age	Following year	
			Die-off	Control
<i>Sites described in Meyer et al, in press</i>				
Eden Valley	Northern Nevada	Recent	+	0
Lost Dog	Western Utah	Recent	+	↑
<i>Sites described in Baughman and Meyer 2013</i>				
Dry Creek	Northern Nevada	Older	=	0
Stewart Gap	Northern Nevada	Older	=	0
Curlew	Northern Nevada	Older	+	↓
Pronghorn	Western Utah	Older	=	↑
Pronghorn South	Western Utah	Older	+	↑
White Rocks	Western Utah	Recent	=	↓
Wagner	Eastern Washington	Recent	=	0
Lost Dog	Western Utah	Recent	=, +	↑

Sites were revisited the year following their discovery to determine if *B. tectorum* had recovered to die-off areas. Sites from Meyer et al (*in press*) were qualitatively assessed at the site level for *B. tectorum* recovery while those from Baughman et al. (2013) were photographed at the plot level the year of study as well as one year later, and ocular estimates of *B. tectorum* density were derived from photographs. Presented data are the most common difference (less, equal, or more) of second vs. first year *B. tectorum* density for each site. To help determine if between-year differences in die-offs were associated with non-die-off related factors (such as below average precipitation), this resurvey was carried out on control plots as well.

+ - recovery of *B. tectorum* to the site

= - persistent stand failure (die-off); no recovery

0 - adjacent control maintained similar *B. tectorum* density

↑ - adjacent control increased *B. tectorum* density

↓ - adjacent control decreased *B. tectorum* density

Table 2. Between-condition ANOVA results for soil nutrients (ppm) and organic matter (%) analysis. Bolded effects are significant ($P < 0.05$).

	Fall 2012				Summer 2013			
	Control	Die-off	F	P	Control	Die-off	F	P
pH	6.9 ± 0.05	6.52 ± 0.05	42.47	0.003	7.45 ± 0.06	6.84 ± 0.12	26.81	0.001
P	72.4 ± 3.78	91.8 ± 4.55	47.88	0.002	68 ± 7.62	116 ± 5.55	26.67	<0.001
K	473 ± 16.0	536 ± 48.1	1.09	0.356	627 ± 43.1	778 ± 38.9	7.47	0.023
Ca	1242 ± 28.2	1119 ± 88.9	1.64	0.270	1426 ± 38.8	1271 ± 48.5	4.01	0.076
Mg	243 ± 6.22	210 ± 18.4	2.66	0.178	330.1 ± 12.4	275 ± 10.4	7.34	0.024
OM	2.52 ± 0.15	3.08 ± 0.12	5.44	0.080	1.66 ± 0.06	1.7 ± 0.13	0.06	0.819
NO3N	7.8 ± 0.49	18.8 ± 1.24	80.67	0.001	3 ± 0.39	11.2 ± 2.98	13.92	0.005

Table 3. Full factorial ANOVA results for mean proportion of viable *P. secunda* seedlings showing active growth through time (F, P). Bolded effects are significant (P<0.05).

Factor**	2012				2013				2014									
	Nov ^L	Dec ^A	Feb ^B	Mar	Apr	May ^A	L. May ^L	Nov ^B	Nov ^B	Feb ^B								
CND	7.2	0.008	9.3	0.003	12.1	0.001	25.1	< 0.001	15.6 †‡	0.000	15.1	0.000	52.3	< 0.001	0.4†	0.508	0.8†	0.367
TRT	3.6	0.061	0.3	0.604	1.2	0.282	1.4	0.239	0.6	0.424	27.4	< 0.001	39.3	< 0.001	6.7	0.010	12.1	0.001
WTR	206	< 0.001	269	< 0.001	231	< 0.001	1.3	0.250	0.0	0.964	1.7	0.201	0.1	0.755	1.4	0.247	1.3	0.259
ORGN	9.9	0.002	12.9	0.001	8.4	0.004	39.7	< 0.001	39.4	< 0.001	25.9	< 0.001	34.1	< 0.001	1.3	0.251	12.0	0.001
CND*TRT	4.7	0.033	2.4	0.121	1.2	0.276	3.4‡	0.067	4.2	0.043	1.9	0.168	0.3	0.579	0.0	0.854	0.1	0.726
CND*WTR	7.5	0.007	12.9	0.001	14.9	0.000	0.1	0.813	0.3	0.607	2.9	0.091	0.1	0.756	1.8	0.177	1.0	0.313
TRT*WTR	3.9	0.051	0.0	0.983	0.0	0.884	0.2	0.685	0.1	0.753	0.5	0.466	0.8	0.364	2.1	0.151	4.0 ‡	0.048
CND*TRT*WTR	1.0	0.312	0.1	0.806	0.2	0.630	1.2	0.271	1.3	0.250	0.3	0.610	2.0	0.163	0.0	0.931	0.0	0.881
CND*ORGN	0.3	0.610	0.8	0.373	0.1	0.726	0.1	0.715	0.1	0.746	0.0	0.873	0.4	0.535	0.0	1.000	0.9	0.358
TRT*ORGN	0.3	0.602	0.6	0.444	0.2	0.674	1.4	0.242	1.3	0.248	0.0	0.872	5.2 ‡	0.025	1.2	0.273	2.0	0.157
COND*TRT*ORGN	0.2	0.626	0.0	0.851	0.1	0.749	0.3	0.580	0.2	0.677	0.4	0.512	2.7	0.103	0.5	0.489	0.7	0.413
WTR*ORGN	4.1	0.044	5.5	0.020	9.5	0.003	0.5	0.461	0.5	0.484	1.8	0.186	2.9	0.089	0.2	0.695	0.7	0.407
COND*WTR*ORGN	0.4	0.532	0.0	0.989	0.2	0.674	0.0	0.893	0.0	0.966	1.4	0.240	0.9	0.349	0.5	0.483	0.0	0.902
TRT*WTR*ORGN	0.4	0.515	0.0	0.997	0.1	0.771	0.7	0.416	0.7	0.407	0.1	0.791	1.0	0.327	0.2	0.680	0.0	0.826
CND*TRT*WTR*ORGN	0.5	0.475	0.0	0.833	0.4	0.540	0.8	0.376	1.1	0.292	0.7	0.405	0.1	0.781	0.0	0.853	0.3	0.579

* CND - condition (control, die-off), TRT - treatment (raked, unraked), WTR - water addition (watered, unwatered), ORGN - origin (local, nonlocal)

L - ln(y+0.025) transformation

A - arcsin(√y) transformation

B - best Box-Cox Y transformation

† - significance changed under density-covariate model

‡ - significance changed under biomass-covariate model

Table 4. Full factorial ANOVA results for mean March mortality (watered only), first season emergence, late season vigor, number of leaves, and seedling height for *P. secunda* (F, P). Bolded effects are significant (P<0.05).

Factor*	March Mortality ^L	Emergence	Late season vigor ^B	No. of leaves ^B	Seedling height ^B
CND	1.6 0.215	21.7 † <.001	42.9 <.001	43.9 <.001	15.4 <.001
TRT	4.4 0.039	0.3 0.608	6.9 † 0.010	46.1 <.001	3.2 0.076
WTR	.	3.5 0.064	0.0 0.841	13.1 0.001	2.9 0.094
ORGN	0.3 0.563	47.0 <.001	7.8 0.006	0.4 0.548	1.2 0.267
CND*TRT	4.5 0.039	2.1 0.153	0.1 0.788	0.5 0.490	0.2 0.651
CND*WTR	.	1.1 0.299	1.3 0.262	2.2 0.144	4.4 ‡ 0.039
TRT*WTR	.	0.2 0.641	0.1 0.810	2.2 0.138	2.3 0.131
CND*TRT*WTR	.	0.3 0.590	0.4 0.529	0.2 0.665	2.5 0.115
CND*ORGN	0.1 0.737	0.3 0.570	1.2 0.284	2.6 0.111	4.0 † 0.047
TRT*ORGN	0.3 0.610	2.8 0.095	1.3 0.255	0.0 0.879	1.5 0.229
COND*TRT*ORGN	0.0 0.839	0.3 0.572	0.0 0.862	3.3† 0.074	0.2 0.686
WTR*ORGN	.	1.2 0.277	0.1 0.745	2.3 0.130	0.0 0.825
COND*WTR*ORGN	.	0.0 0.825	0.0 0.903	1.6 0.203	0.3 0.605
TRT*WTR*ORGN	.	0.1 0.763	0.1 0.722	2.6 0.111	0.2 0.621
CND*TRT*WTR*ORGN	.	1.1 0.297	0.1 0.760	0.0 0.912	0.1 0.782

* CND - condition (control, die-off), TRT - treatment (raked, unraked), WTR - water addition (watered, unwatered), ORGN - origin (local, nonlocal)

^L - ln(y+0.025) transformation

^B - best Box-Cox Y transformation

† - significance changed under density-covariate model

‡ - significance changed under biomass-covariate model

Table 5. Full factorial ANOVA results for mean proportion of viable *E. elymoides* seedlings showing active growth through time (F, P). Bolded effects are significant (P<0.05).

	2012				2013				2014									
	Nov ^A	Dec ^A	Feb ^A	Mar	Apr	May	L. May	Nov ^L	Nov ^L	Feb ^L								
CND	4.7	0.032	5.9	0.017	9.3	0.003	52.2	< 0.001	16.3	< 0.001	0.3	0.575	5.3 ‡	0.023	62.5	< 0.001	64.1	< 0.001
TRT	25.2	< 0.001	11.0	0.001	13.3	< 0.001	1.6	0.208	0.3	0.563	17.3	< 0.001	48.9	< 0.001	0.0	0.914	0.2	0.689
WTR	421	< 0.001	814	< 0.001	782	< 0.001	90.9	< 0.001	49.1	< 0.001	24.1	< 0.001	28.0	< 0.001	0.8	0.380	0.8	0.368
ORGN	0.0	0.899	1.1	0.291	1.4	0.233	0.0	0.936	4.1 ‡	0.044	22.8	< 0.001	26.9	< 0.001	0.9	0.344	0.0	0.931
CND*TRT	5.8	0.017	0.1	0.704	0.1	0.747	0.6	0.460	1.8	0.185	0.3	0.576	1.2	0.285	1.6	0.210	0.4	0.523
CND*WTR	14.0	< 0.001	39.5	< 0.001	38.1	< 0.001	0.0	0.884	6.3	0.014	2.0	0.161	2.7	0.103	0.6	0.436	0.0	0.948
TRT*WTR	11.8	0.001	0.0	0.906	4.9	0.029	2.1	0.151	2.0	0.156	8.1	0.005	12.1	0.001	1.0	0.328	0.1	0.743
CND*TRT*WTR	8.1	0.005	1.1	0.295	0.0	0.883	1.3	0.252	1.7	0.201	0.9	0.341	0.9	0.342	0.5	0.493	0.3	0.571
CND*ORGN	2.3	0.129	1.8	0.187	2.0	0.161	3.0	0.083	0.6	0.428	0.5	0.460	0.8	0.385	4.4 ‡	0.037	6.1	0.015
TRT*ORGN	0.0	0.910	0.5	0.497	1.0	0.322	0.0	0.860	0.0	0.950	0.5	0.480	0.2	0.695	2.2	0.137	5.9	0.016
COND*TRT*ORGN	0.5	0.487	2.0	0.161	0.2	0.658	1.1	0.293	0.9	0.334	0.0	0.892	0.0	0.830	0.1	0.730	1.5	0.218
WTR*ORGN	0.1	0.800	1.0	0.322	1.6	0.202	0.8	0.380	0.2	0.689	0.1	0.714	0.0	0.870	2.0	0.155	0.5	0.482
COND*WTR*ORGN	4.1	0.045	9.7	0.002	4.7	0.032	0.0	0.888	1.5	0.230	0.3	0.574	1.0	0.319	0.6	0.431	0.5	0.491
TRT*WTR*ORGN	0.0	0.882	0.7	0.399	1.0	0.320	1.3	0.252	2.5	0.119	0.0	0.900	0.1	0.719	0.0	0.924	1.3	0.252
CND*TRT*WTR*ORGN	0.4	0.555	1.5	0.226	1.3	0.259	0.5	0.464	1.0	0.308	0.0	0.867	0.2	0.695	2.5	0.118	1.9	0.167

* CND - condition (control, die-off), TRT - treatment (raked, unraked), WTR - water addition (watered, unwatered), ORGN - origin (local, nonlocal)

† - significance changed under density-covariate model

‡ - significance changed under biomass-covariate model

A - arcsin(\sqrt{y}) transformation

L - ln(y+0.025) transformation

Table 6. Full factorial ANOVA results for mean March mortality (watered only), first season emergence, late season vigor, number of leaves, and seedling height for *E. elymoides* (F, P). Bolded effects are significant (P<0.05).

Factor**	March Mortality ^L	Emergence	Late season vigor	No. of leaves ^B	Seedling height
CND	0.3 0.598	16.4 < 0.001	118 < 0.001	124 < 0.001	177 < 0.001
TRT	0.0 0.847	0.3 0.569	91.2 < 0.001	56.3 < 0.001	10.1 0.002
WTR	.	65.3 < 0.001	0.1 0.725	1.2 0.273	1.8 0.182
ORGN	2.3 0.138	3.4 0.068	20.9 < 0.001	30.9 < 0.001	37.0 < 0.001
CND*TRT	1.8 0.184	1.0 0.310	16.4 < 0.001	0.4 0.532	0.1 0.707
CND*WTR	.	5.7 0.019	0.1 0.724	0.3 0.577	0.4 0.534
TRT*WTR	.	2.0 0.155	3.1† 0.079	0.7 0.421	0.2 0.683
CND*TRT*WTR	.	2.2 0.136	0.4 0.516	0.0 0.913	0.9 0.349
CND*ORGN	1.2 0.270	0.7 0.403	1.6 0.211	0.0 0.967	5.4‡ 0.022
TRT*ORGN	0.8 0.386	0.0 0.917	1.0 0.322	0.9 0.356	0.2 0.691
COND*TRT*ORGN	8.8 0.004	2.2 0.138	0.0 0.998	0.9 0.354	1.7 0.195
WTR*ORGN	.	0.3 0.615	0.7 0.417	0.6 0.430	0.1 0.782
COND*WTR*ORGN	.	2.3 0.133	0.1 0.725	0.1 0.800	0.1 0.772
TRT*WTR*ORGN	.	1.3 0.254	1.2 0.266	0.2 0.645	0.4 0.514
CND*TRT*WTR*ORGN	.	0.1 0.782	0.1 0.774	0.1 0.700	0.2 0.688

* CND - condition (control, die-off), TRT - treatment (raked, unraked), WTR - water addition (watered, unwatered), ORGN - origin (local, nonlocal)

^L - ln(y+0.025) transformation

^B - best Box-Cox Y transformation

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