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Cheatgrass die-offs as an opportunity for restoration in the Great Basin, USA: Will local or commercial native plants succeed where exotic invaders fail?

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ABSTRACT

Bromus tectorum (cheatgrass) has widely invaded the Great Basin, U.S.A. The sporadic natural phenomenon of complete stand failure ('die-off') of this invader may present opportunities to restore native plants. A recent die-off in Nevada was precision-planted with seeds of the native grasses *Poa secunda* (Sandberg bluegrass) and *Elymus elymoides* (bottlebrush squirreltail), of both local and nonlocal origin, to ask: 1) Can native species be restored in recent *B. tectorum* die-offs? And 2) Do local and nonlocal seeds differ in performance? Additionally, we asked how litter removal and water addition affected responses. Although emergence and growth of native seeds was lower in die-off than control plots early in year one, in year two, seedlings in die-offs had increased vigor and growth, at equal or higher densities, than control plots. Local seeds consistently outperformed nonlocal seeds for *P. secunda*, whereas for *E. elymoides*, nonlocal showed an advantage in the first season, but in the second season, there were more local seeds present under die-off and unraked conditions. Seedbed treatments affected performance, but did not notably improve establishment or modify other results. Our results warrant further investigation into die-off restoration as well as recognition of the importance of seed source selection in restoration.

1. Introduction

The introduction and spread of invasive exotic species is an ongoing global issue with broad and negative impacts on biodiversity, ecosystem integrity, and essential ecosystem services on which human well-being depends (Pyšek and Richardson, 2010). Within the United States, exotic species invasion is second only to habitat loss and degradation as a leading cause of biodiversity reduction (Wilcove et al., 1998). One such species, the annual grass *Bromus tectorum* L. (cheatgrass), has come to colonize tens of millions of acres of cold desert shrublands since introduction more than a century ago (Mack, 1981; Knapp, 1996). Because of its effects on ecosystem processes (Brooks et al., 2004; Adair and Burke, 2010; Beckstead et al., 2010) and strong competitive effects on native species (Nasri and Doescher 1995; Rafferty and Young 2002). *B. tectorum* invasion can dramatically limit land management options and make restoring more desirable species challenging (Davies et al., 2011).

Bromus tectorum die-off is a common but poorly understood phenomenon in which an abundant *B. tectorum* seed bank fails to produce a stand of living plants, despite receiving precipitation that is sufficient for establishment. While some areas experiencing die-off continue to show stand failure for several years, many areas recover to considerable *B. tectorum* densities the following year (Baughman, 2014). The factors directly responsible for *B. tectorum* die-off have yet to be determined, though recent studies have implicated several fungal pathogens that demonstrated high pathogenicity in the laboratory under specific conditions (Meyer et al., 2014; Meyer pers. com.). Such naturally occurring and complete stand failures of dominant annual species in arid or semi-arid wildlands are unprecedented in the literature. However, similar die-off processes do occur in agricultural settings, including take-all fungus of wheat (Bithell et al., 2011), sudden

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death syndrome of soybeans (Hartman et al., 2015), and maize streak virus of corn (Shepherd et al., 2010). The existence of these examples of pathogens causing stand failure in agricultural systems suggests that this mechanism is possible in other high density, low diversity, annual systems, such as *B. tectorum* near-monocultures.

Because these *B. tectorum* die-offs represent a sudden but temporary decrease of a highly competitive exotic, they could be an opportunity for restoration if native species can establish in these altered conditions. Following die-off, soils show a many-fold increase in soil mineral nitrogen (N) relative to immediately adjacent soils not exhibiting die-off (Blank et al., 2011; Meyer et al., 2014). This abundant soil nitrogen and reduced 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. This approach of investigating windows of restoration opportunity may be of use in other situations where large disturbances have temporarily removed undesirable and/or invasive species, such as wildfire, herbicide applications, recent agricultural abandonment or fallowing, or successful biocontrol efforts.

Restoring native plant communities to *B. tectorum*-invaded lands is made challenging not only by the presence of the invader, but also due to incomplete knowledge currently guiding management practices in several important areas (Davies et al., 2011). One such area is the importance of seed source in restoration (Hardegree et al., 2011). Local adaptation, or higher fitness of local than non-local genotypes when evaluated in local conditions, is common in many plant communities (Clausen et al., 1947; Loveless and Hamrick, 1984; Linhart and Grant, 1996; Kawecki and Ebert, 2004), including the Great Basin (e.g. Meyer et al., 1995; Rice and Davis, 2009; Rowe and Leger, 2012; Johnson et al., 2013). Despite this, seed demand in the Great Basin is typically met with commercially-produced native seed derived from programs aiming to create widely-adapted, "workhorse" genotypes (United States Department of Agriculture, 2013). Unfortunately, the portions of the Great Basin most at risk of degradation are poorly represented by the collection locations of many of these commercial seed lots (Jensen and Stettler, 2012), and thus for much of the Great Basin, seeds used in restoration are likely to lack traits that are adapted to local biotic or abiotic conditions, including the die-off phenomenon. It is vital that more research compare the success of local and nonlocal native plants in the Great Basin, especially in highly invaded and potentially modified systems, such as those containing *B. tectorum* near-monocultures.

To examine whether die-offs are potential restoration opportunities, this study employed a two-year, *in situ* seed establishment experiment within a naturally occurring die-off in north–central Nevada using two common grass species native to the Great Basin, *Poa secunda* J. Presl. (Sandberg bluegrass) and *Elymus elymoides* (Raf.) Swezey (bottlebrush squirreltail). We address the following question: 1) Can native species be successfully restored in a recent *B. tectorum* die-off? Additionally, seeds of both local and nonlocal (commercial) origin were included in the experiment to address the question: 2) Do native plants of local and nonlocal origins differ in performance, and if so, are these differences consistent in and out of a recent die-off? Further, we included early-season water addition and litter removal treatments to determine if such ameliorations are necessary for establishing native plants in die-off areas. We also documented soil fertility, soil moisture, soil temperature, and the abundance of *B. tectorum* in die-off and infested areas to determine if these factors were associated with any differences in native plant establishment.

2. Methods

2.1. Site selection and description

Extensive surveys in Northern Nevada, 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.), revealed only a single die-off site in spring 2012 in northern Buena Vista Valley, north–central Nevada (Fig. 1). The study site is located at 1384 m elevation, and the 30-year mean annual precipitation is 222 mm, and mean annual temperature is 9.8 °C (PRISM Climate Group, 2014). Formerly dominated by *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (Wyoming big sagebrush), the site was last affected by wildfire in 1999. It is shallowly sloping and has well-drained, relatively deep fine sandy loam soils (Natural Resources Conservation Service Soil Survey Staff, 2014). At the time of the study, the general area was occupied primarily by *B. tectorum*, with low densities of *Sisymbrium altissimum* L. (tall tumble mustard), *Salsola tragus* L. (Russian thistle), *Lepidium perfoliatum* L. (clasping pepperweed), *E. elymoides* and *Microsteris gracilis* (Hook.) Greene (slender phlox). *B. tectorum* die-offs were first observed and investigated in the area in 2008 (Baughman and Meyer, 2013). An area (70 m × 50 m) that contained a representative sample of the recent die-off as well as an adjacent, unaffected area with an intact *B. tectorum* stand (control) was selected for the experiment and was fenced to exclude grazing. The die-off area supported virtually no *B. tectorum* growth during the growing season prior to installation of the experiment (2012), while the adjacent 'control' area supported a stand of *B. tectorum*. September 2012 seed bank samples showed no significant ($P > 0.05$) differences between die-off and control conditions in *B. tectorum* seeds per square meter, for viable (6200 ± 1500 SE in control, 10,200 ± 4500 SE in die-off) or nonviable seeds (12,300 ± 2000 SE in control, 10,300 ± 2200 SE in die-off), indicating that it was in fact a recent, first year die-off (Baughman and Meyer, 2013). Site precipitation was estimated to be 56% of average in the 2012 water year (October 1 2011–September 30 2012) during which the die-off occurred, as well as 69% and 92% in the 2013 and 2014 water years, respectively, during which the experiment took place.

2.2. Species selection, seed acquisition and processing

The cool-season, perennial grasses selected for this study were *P. secunda* (Sandberg bluegrass) and *E. elymoides* (bottlebrush squirreltail), which were found growing in natural populations within 2 km of the site. *P. secunda* is a widely distributed bunchgrass that generally grows and matures earlier in the growing season than most other native perennial grasses. It is considered a pioneer species and is relatively tolerant of fire and other disturbances. *E. elymoides* is also a widely distributed bunchgrass, and matures slightly later than *P. secunda*. These species were selected because they commonly grow in similar habitats and are frequently used in restoration in the region. Additionally, both species have demonstrated abilities to compete with or tolerate *B. tectorum* (Booth et al., 2003; Goergen et al., 2011; Stevens et al., 2014).

Mature seeds of local collections were hand-harvested throughout June and early July, 2012 from as many individuals (>50) and as close to the study site (<6 km) as possible. Seeds were stored at room temperature in paper envelopes for 6 months. Commercially produced, nonlocal seeds were obtained from L&H Seeds, a private seed grower in eastern Washington. Mt. Home germplasm *P. secunda* (Lambert et al., 2011) was chosen because its origin in southern Idaho was geographically closer and more environmentally similar to the study site than any other commonly

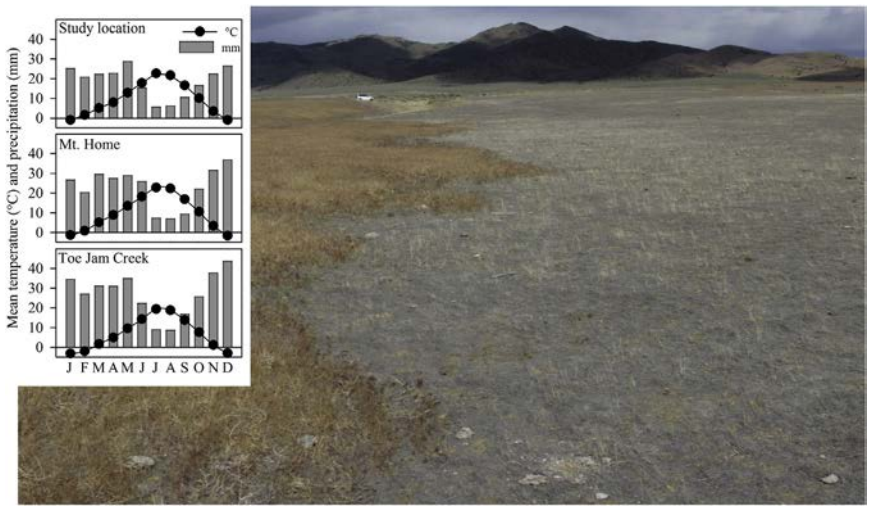

Fig. 1. An example of a *Bromus tectorum* die-off in Pershing County, NV in 2014. *Bromus tectorum* grew in a near-monoculture on the land in both sides of this image in 2013, but experienced stand failure on the right during the 2014 growing season. The gray litter layer on the right is typical of *B. tectorum* die-offs, and is in contrast to the standing, healthy stand of *B. tectorum* on the left. The stark edge between these two conditions is not delineated by obvious topographical, edaphic, or climatic boundaries. Inset climate graphs for the study location/local germplasm origin (40.6882°N, 117.9582°W) and nonlocal germplasm origins for Mt. Home *P secunda* (42.3127°N, 115.5821°W) and Toe Jam Creek *E. elymoides* (41.3127°N, 116.4738°W) are based on 30-year averages (PRISM Climate Group, 2014).

available germplasm at the time. Toe Jam Creek germplasm *E. elymoides* (Jones et al., 2004), originating from northern Nevada, was selected for similar reasons. The origins of the Mt. Home and Toe Jam Creek germplasms experience an average of 273 mm and 322 mm annually, respectively, compared to 222 mm at the planting site where local germplasms were collected (Fig. 1, PRISM Climate Group, 2014), but conditions at the commercial growing site are unknown. Both local and nonlocal seed lots were hand-sorted on a light table, and only seeds with well-developed endosperm were selected. This sorting was required as seed set at the local site was low, presumably due to water limitations during the 2011–2012 growing season. 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 type.

2.3. Field design

Seeds were directly planted into both die-off and adjacent non die-off (henceforth, 'control') conditions. Four seedbed treatments were implemented, varying the micro-environments under which native establishment could occur. These treatments were designed to determine if native seed establishment was dependent on amelioration of any site factors, such as excessive litter or dry conditions. Treatments were: seeding into unaltered plot and seeding with litter removed ('raked'), each with and without artificial precipitation addition ('watered'). Litter was removed by gentle hand-raking, and water was added using a plastic bag perforated with 5 small holes suspended above the plot on hardware cloth and a wooden frame.

Ten blocks were established in the experiment. Each block was composed of two arrays, with one in the die-off condition and the other in the control condition, each beginning a minimum of 5 and a maximum of 12 m from the die-off edge. Within each array, 16 square 0.1 m^2 plots representing factorial combinations of the four treatments, two species, and two seed origins were randomly arranged in two rows of 8, with 15 cm spacing between plots and block edges (see Baughman, 2014). Using Titebond 5062 Original wood glue, seeds were attached by their lemmas, with embryo down, to 15 cm long bamboo skewers at 5 cm from skewer tip and inserted so that seeds were 0.6–1.2 cm below the soil surface. This method allowed for confident differentiation of target seedlings from resident seedlings, and very high seedling detectability through time. Each plot contained a four by five matrix of seeds on skewers (20 seeds total), all from one of the four seed lots, planted 5–6.5 cm from one another. This design of ten planting blocks contained a total of 320 plots covering 32 m^2 planted with 6400 seeds. Soil moisture and temperature measurements were taken in all treatment combinations in each of three additional blocks, interspersed between planting blocks. These soil monitoring plots received the same seedbed manipulations and seeding density as seeded plots, but were not monitored for seedling activity.

Seeds were planted during the last week of October, 2012. Seeded plots and soil monitoring plots assigned to the artificial precipitation treatment were watered with ~2.5 cm at one and three weeks post-planting. After mid-November, moisture to all plots was dependent upon natural precipitation.

2.4. Data collection

Seeds were carefully examined for emergence in November, December, and monthly from February–May of the first growing season (2012–2013) and newly-emerged seedlings were marked with colored paper clips. All seedlings that had at any point shown active growth in the first season were monitored in November, December, February, April and May of the second growing season (2013–2014). In both seasons, plants were showing senescence (dormancy) by the end of May. Data are reported in terms of actively growing seedlings rather than living seedlings because it was not possible to differentiate seedling mortality from senescence.

All plants exhibiting active growth in early May were measured in late May (even if senesced) for leaf number and longest leaf length (hereafter, height), and given a greenness integer rating (hereafter, late-season vigor) from 0 (0% green) to 3 (75–100% green). In the second year, the number of plants in each plot producing flowering structures was recorded. *B. 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 samples were dried in an oven at 40 °C for at least two days and weighed.

To determine the effects of experimental factors on soil conditions, real-time soil moisture (cm^3 H_2O cm^{-3} soil) and temperature (°C) were measured with ECH_2O-TM sensors and Decagon data loggers (Decagon Devices, Pullman WA, USA). Sensors were placed at 2 cm below soil surface in all treatment combinations in each of three blocks (for a total of 24 sensors). All values were expressed on a daily time-step to remove diel variability. Moisture and temperature data were separated into three time periods: winter (1st Nov – 28th February), early spring (1st March – 30th April), and late spring (1st May – 31st May), with these divisions based on the timing of spring-thaw (end of February) or stable warm soil temperatures (>15 °C beginning of May) in the first growing season (Gornish et al., 2014).

Soil samples were taken before the growing season, in October 2012, and after the growing season in June 2013 in 6 cm diameter × 8 cm deep cores. October samples were a composite of 5 randomly-located cores per planting array from five blocks, stored in paper bags and frozen for 10 months, while June samples were a composite of 2 random cores per array from all ten blocks, and stored at room temperature in paper bags for several weeks. One composite sample from each array and sample date was analyzed for pH, organic matter, nitrate, phosphorus, potassium, calcium, and magnesium (A&L Analytical Laboratories, Memphis, TN).

2.5. Data analysis

Cumulative emergence, seedling number, and number of plants producing flowering structures were calculated as percentages of the total seed planted on a per-plot basis. These percentages were then adjusted for the viability of each hand-sorted 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 proportions of the total viable seed planted. Response variables included cumulative emergence (sum of seedlings per plot that emerged at any point during the experiment), proportion of viable seeds actively growing at each of eleven sampling dates, mean plot plant height, leaf number, and late-season vigor in May of both seasons, mean plot number of flowering plants in the second season, and first season *B. tectorum* plot density and biomass. Data were analyzed separately for each species, using a mixed model ANOVA with condition (CND: control, die-off), seedbed treatment (TRT: none, raked), 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.). Initially, data were analyzed as a repeated measures (RM) ANOVA, with TIME (11 sampling dates) included as a fixed and fully crossed factor in the above model for the active growth response, but all factors had highly significant interactions with TIME for both species (analysis not shown). Therefore, the above model was run separately for each sampling date. Late-season vigor, height, leaf number, and second season flowering were analyzed with nonparametric Wilcoxon signed rank tests without BLOCK for only the factors CND and ORGN due to small sample sizes and unequal variance that precluded analysis of these responses with the ANOVA model described above. The effects of the treatments on soil moisture and temperature for the first season time periods winter, early spring, and late spring were evaluated with RM ANOVA with CND, TRT, WTR, and TIME as fixed factors and BLOCK as a random factor in the R Statistical Environment (R Development Core Team, 2013). Soil data were also analyzed with ANOVA, with a model containing CND as a fixed factor and BLOCK as a random factor. Response variables were transformed where necessary to improve residual normality and homogeneity of variance, and Tukey's HSD tests were used to determine differences for significant ANOVA interactions.

To test whether differences in *B. tectorum* dynamics may have contributed to differences in seedling performance between die-off and control sites, we conducted additional analyses that included plot-level *B. tectorum* biomass and density individually as covariates in the main model described above. Both *B. tectorum* measures were used because they were not strongly correlated ($R^2 = 0.10$). We report both the significance of the relationship between *B. tectorum* dynamics and response variables, as well as changes in significance of CND effects and CND interactions, focusing on first season emergence and April and May active seedling number in the first year as responses for this test. Changes in significance of effects were interpreted as follows: if, for example, there was a significant CND effect in the main model, but including *B. tectorum* density as a covariate eliminated this effect, this is consistent with the hypothesis that differences in *B. tectorum* density between conditions may have been responsible for any observed differences in plants grown in die-off vs. control conditions. Note, however, that we did not manipulate *B. tectorum* densities as part of this experiment, and these analyses present only correlative patterns, and the results could indicate plant responses to factors other than competition.

Unless otherwise noted, data are presented as plot means ± SE, and significance of results is interpreted as P values < 0.05.

3. Results

3.1. Soil resources, moisture, and temperature

Both before and after the first growing season, die-off soils had significantly lower pH, greater P, and greater NO_3 than adjacent control soils, and after the growing season, die-off soils had significantly lower Mg (Table A.1). Soil in the die-off was continually wetter in winter and early spring, as well as cooler in winter, early, and late spring (Table A.2, Figure A.1). Litter removal and water addition affected soil moisture and temperature, with some differences in these effects in the die-off vs. control (Table A.2, Appendix 1).

3.2. Bromus tectorum dynamics

Density (plants/0.1 m^2) of *B. tectorum* in May 2013 was significantly lower in die-off than control (die-off: 14.4 ± 1.7 SE, control: 22.2 ± 1.4 SE; $F = 20.6_{(1,9)}$, $P = 0.001$), in raked than in unraked treatment (raked: 12.7 ± 1.0, unraked: 24.1 ± 1.8 SE; $F = 50.9_{(1,9)}$, $P < 0.001$), and in unwatered than watered treatment (unwatered: 14.1 ± 1.1 SE, watered: 22.8 ± 1.8 SE; $F = 9.1_{(1,9)}$, $P = 0.01$). Though densities were lower, biomass (g/0.1 m^2) of *B. tectorum* in August 2013 was significantly higher in the die-off than the control across most treatments (die-off: 6.6–9.7 ± 0.6–0.9 SE, control: 4.0–5.4 ± 0.3 SE; $F = 13.3_{(1,9)}$, $P = 0.005$), with the exception of unwatered plots in the raked treatment, where there were no between-condition differences (TRT×WTR×CND interaction; $F = 12.6_{(1,230)}$, $P < 0.001$). Watering generally increased *B. tectorum* biomass and raking generally decreased biomass, with some exceptions in some treatments (data not shown, see Baughman, 2014). Neither the native species planted nor their origin had significant effects upon *B. tectorum* density or biomass.

3.3. Emergence timing and cumulative emergence

Seeds of both species that received additional water emerged earlier than unwatered seeds, showing more active growth from November 2012 through Feb 2013 (Tables 1 and 2, Fig. 2), with some different responses to water based on site condition, seedbed

Table 1
Full factorial ANOVA results for *P. secunda*, for first season (Nov. 2012–May 2013) cumulative emergence (CE) and first and second season (Nov. 2013–May 2014) mean proportion of viable seedlings showing active growth. Values are F statistics (numerator, denominator degrees of freedom 1, 9 for main factors, 1, 98–99 for interactions), and bolded effects are significant ($P < 0.05$), and bold italics indicates $P < 0.06$. Factors include condition (CND, control vs. die-off), seedbed treatment (TRT, raked vs. unraked), water treatment (WTR, watered vs. unwatered) and seed origin (ORGN, local vs. nonlocal).

	CE	2012		2013					2014		
		Nov[a]	Dec[b]	Feb[c]	Mar	Apr	May[a]	Nov[c]	Feb[c]	Apr[b]	May[a]
CND	**10.9****	**12.3****	**7.6***	**5.3***	**12.0****	**9.1***	**49.5*****	0.2	0.3	0.0	***4.8***$^{\#}$
TRT	0.1	2.9	0.2	1.2	0.8	0.3	**69.7*****	**8.5***	**16.8****	**16.1****	**37.6*****
WTR	**8.7***	**79.3*****	**96.7*****	**129*****	3.0	0.0	0.1	2.5	2.3	4.5	1.1
ORGN	**141.5*****	**5.6***	**8.0***	**7.9***	**101*****	**79.2*****	**28.6*****	2.2	**9.0****	**10.1***	**45.8*****
CND×TRT	2.2	**5.8***	3.3	1.4	3.6	**4.5***	0.3	0.0	0.1	0.0	0.3
CND×WTR	1.2	**9.3****	**17.3*****	**18.4*****	0.1	0.3	0.1	1.9	1.2	2.8	2.0
TRT×WTR	0.2	**4.8***	0.0	0.0	0.2	0.1	0.8	2.2	**4.7***	0.2	**6.1***
CND×TRT×WTR	0.3	1.2	0.1	0.3	1.2	1.4	2.0	0.0	0.1	0.0	0.9
CND×ORGN	0.3	0.3	1.1	0.2	0.1	0.1	0.4	0.0	0.9	0.0	0.1
TRT×ORGN	3.0	0.3	0.8	0.2	1.4	1.4	**5.2***	1.3	1.8	1.6	0.5
COND×TRT×ORGN	0.3	0.3	0.0	0.1	0.3	0.2	2.7	0.5	0.7	0.9	0.4
WTR×ORGN	1.3	**5.1***	**7.3****	**11.7*****	0.6	0.5	3.0	0.2	0.7	0.9	**7.6****
COND×WTR×ORGN	0.1	0.5	0.0	0.2	0.0	0.0	0.9	0.5	0.1	1.1	0.1
TRT×WTR×ORGN	0.1	0.5	0.0	0.1	0.7	0.7	1.0	0.2	0.1	0.0	0.5
CND×TRT×WTR×ORGN	1.2	0.6	0.1	0.5	0.8	1.2	0.1	0.0	0.4	0.1	0.2

$^{\#}$P (0.055), *P (0.05–0.01), **P (0.009–0.001), ***P (<0.001).
[a] $\ln(y + 0.025)$ transformation.
[b] Arcsin($\sqrt{y}$) transformation.
[c] Best Box–Cox Y transformation.

treatments, and origin of seeds; these interactions are discussed below. Seeds in unwatered treatments remained mostly ungerminated until March 2013; the majority of emergence was completed by March 2013 for *P. secunda* and April 2013 for *E. elymoides* (Fig. 2).

First season cumulative emergence was significantly higher in control than die-off for *P. secunda* (Table 1, Fig. 3a). Cumulative emergence was significantly higher in watered *E. elymoides* control than in watered die-off, but when unwatered, there was no difference between conditions (Table 2 CND×WTR interaction, Fig. 3b). Cumulative emergence was significantly higher for local than nonlocal *P. secunda*, and significantly higher for nonlocal than local *E. elymoides* (Tables 1 and 2, Fig. 3a and b). Water addition was associated with significantly higher cumulative emergence of both species, and litter removal did not significantly affect cumulative emergence of either native species (Tables 1 and 2).

3.4. Effects of die-off and treatments on *P. secunda* active growth

The die-off supported significantly fewer *P. secunda* seedlings than the control in the watered treatment, but not in the unwatered treatment, from November 2012 to February 2013 (Table 1 CND×WTR interactions, Fig. 2a), and regardless of other factors in March 2013. The unraked treatment had fewer seedlings in the die-off than in the control in November 2012 and April 2013 (November: 18% ± 3% SE in control, 8% ± 2% SE in die-off; April: 61% ± 3% SE in control, 43% ± 3% SE in die-off), with the raked treatment showing no condition differences in active seedlings for these months (Table 1 CND×TRT interactions). Water addition had

Table 2
Full factorial ANOVA results for *E. elymoides*, for first season (Nov. 2012–May 2013) cumulative emergence (CE) and first and second season (Nov. 2013–May 2014) mean proportion of viable seedlings showing active growth. Values are F statistics (numerator, denominator degrees of freedom 1, 9 for main factors, 1,99 for interactions), and bolded effects are significant ($P < 0.05$). Factors include condition (CND, control vs. die-off), seedbed treatment (TRT, raked vs. unraked), water treatment (WTR, watered vs. unwatered) and seed origin (ORGN, local vs. nonlocal).

	CE	2012		2013					2014		
		Nov[a]	Dec[a]	Feb[a]	Mar	Apr	May	Nov[b]	Feb[b]	Apr[b]	May[b]
CND	**10.3***	3.1	**5.7***	**6.5****	**19.7****	**8.5***	3.2	**20.2****	**14.7****	**17.4****	**17.0*****
TRT	0.2	**23.0****	**9.6***	**12.6****	1.2	0.2	**37.7*****	0.0	0.2	1.6	0.9
WTR	**87.4*****	**154*****	**417*****	**648*****	**186*****	**86.4*****	**47.4*****	2.3	2.2	0.8	0.9
ORGN	**7.13***	0.0	0.7	1.1	0.0	**8.7***	**40.1*****	0.6	0.0	0.8	2.1
CND×TRT	1.1	**8.0****	0.2	0.1	0.6	1.8	1.2	1.9	0.6	0.5	2.1
CND×WTR	**5.8***	**19.5*****	**47.4*****	**41.9*****	0.0	**6.7***	2.8	0.7	0.0	0.0	0.1
TRT×WTR	2.1	**16.3*****	0.0	**5.4***	2.3	2.2	**12.3*****	1.1	0.1	0.5	0.6
CND×TRT×WTR	2.3	**11.2****	1.3	0.0	1.5	1.8	0.9	0.6	0.4	1.4	0.2
CND×ORGN	0.7	3.2	2.1	2.2	3.4	0.7	0.8	**5.2***	**8.0****	2.8	**4.3***
TRT×ORGN	0.0	0.0	0.6	1.1	0.0	0.0	0.2	2.6	**8.0****	**7.3****	**4.4***
COND×TRT×ORGN	2.3	0.7	2.4	0.2	1.2	1.0	0.0	0.1	2.0	**4.3***	3.2
WTR×ORGN	0.3	0.1	1.2	1.8	0.9	0.2	0.0	2.4	0.7	0.3	1.5
COND×WTR×ORGN	2.3	**5.7***	**11.6*****	**5.2***	0.0	1.5	1.0	0.7	0.6	1.0	2.3
TRT×WTR×ORGN	1.3	0.0	0.9	1.1	1.5	2.6	0.1	0.0	1.8	2.4	1.3
CND×TRT×WTR×ORGN	0.1	0.5	1.8	1.4	0.6	1.1	0.2	2.9	2.6	0.8	0.7

*P (0.05–0.01), **P (0.009–0.001), ***P (<0.001).
[a] Arcsin($\sqrt{y}$) transformation.
[b] $\ln(y+0.025)$ transformation.

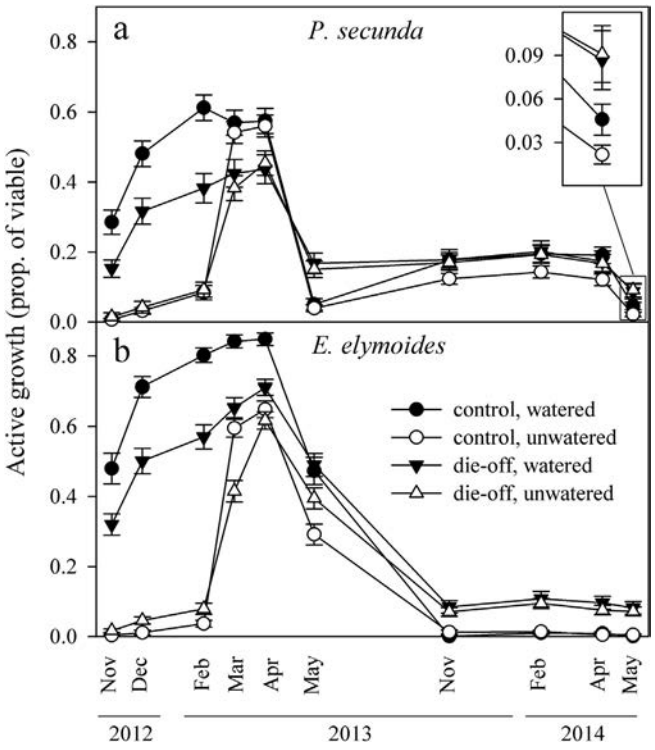

Fig. 2. Proportion of viable seed showing active growth through two growing seasons for *P. secunda* (a) and *E. elymoides* (b), showing differences between control (circles) and die-off (triangles) as well as watered (black) and unwatered (white). Means and standard errors are from untransformed data, and the inset figure magnifies end-of-season *P. secunda* results that are difficult to see at larger scale.

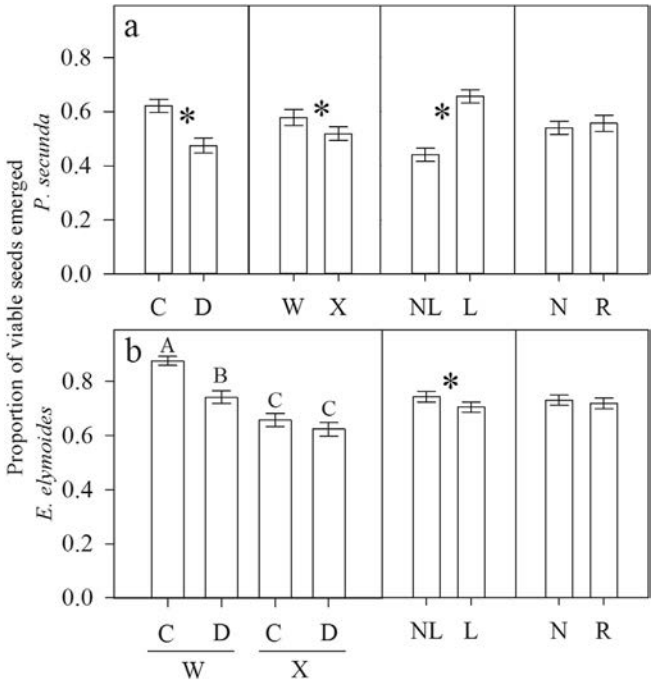

Fig. 3. Proportion of viable seeds that emerged in the first growing season for *P. secunda* (a) and *E. elymoides* (b) by experimental factors: control (C) and die-off (D) condition, early-season watering treatment (W) and unwatered (X), raked (R) and unraked (N) litter, and nonlocal (NL) and local (L) seed origin. Main effects are shown when no interactions are present; * = P < 0.05, and significant interactions are indicated by the 4-bar graph. Letters above bars indicate significant differences based on Tukey's HSD (P < 0.05). Means and standard errors are untransformed data.

no effect after March 2013 (Table 1). The pattern of reduced active growth in die-off reversed in May 2013, when the die-off supported significantly more active seedlings than the control regardless of other factors (Fig. 2). In the second growing season, there were no significant differences in number of active *P. secunda* between control and die-off condition, regardless of other factors, but in May 2014 differences were nearly significant (Table 1, P = 0.0552), with more active *P. secunda* growing in the die-off (8.9% ± 1.4% SE) than control (3.3% ± 0.6% SE, Fig. 2a).

Litter removal was associated with significantly more *P. secunda* active growth in May 2013 (raked: 15.2% ± 1.9% SE, unraked: 5.2% ± 1% SE) as well as throughout the second season, although this was only true in the unwatered treatment in February and May 2014 (Table 1 TRT×WTR interactions, not shown).

3.5. Effects of die-off and treatments on E. elymoides active growth

Similar to *P. secunda*, there were initially fewer *E. elymoides* seedlings in the die-off, reversing to more active *E. elymoides* late in the first season as well as throughout the entire second season (Table 2, Fig. 2b). The die-off supported significantly fewer active seedlings than the control when water was added only in November and December 2012 and February and April 2013 (Table 2 CND×WTR interactions, Fig. 3). In November and December, these effects were due to a strong germination response of nonlocal seeds in the watered control and unwatered die-off, respectively (Table 2 CND×WTR×ORGN interactions, data not shown). There were no significant between-condition differences in the unwatered treatment in November 2012 and April 2013, and significantly more active seedlings in unwatered die-off than control in December 2012 and February 2013 (Table 2 CND×WTR interactions). Water had no continuing effects after May 2013. Litter removal had mixed effects on *E. elymoides* seedlings, with some interactive effects with water addition and seed origin (Appendix 2).

3.6. Effects of seed origin on P. secunda active growth

Cumulative emergence was significantly higher for local *P. secunda* seeds (Fig. 3a), and there were more actively growing locally-collected seeds than nonlocal seeds for all but one of the survey dates (November 2014, Table 1, Fig. 4), though this result was only evident in the water addition treatments at some survey

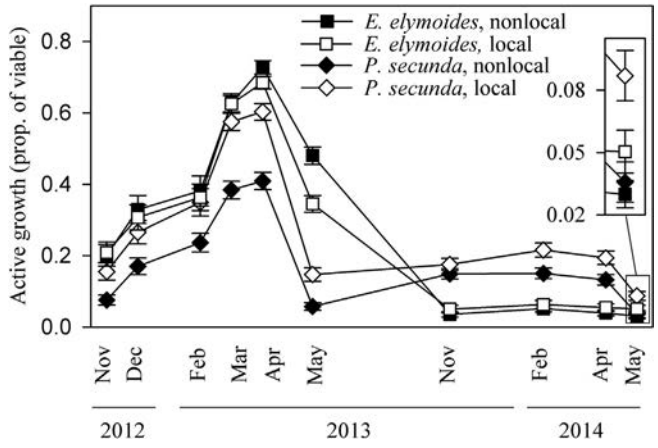

Fig. 4. Proportion of viable seed showing active growth through two growing seasons from nonlocal (black) and local (white) seeds of *P. secunda* (diamonds) and *E. elymoides* (squares). Means and standard errors are untransformed data, and the figure inset magnifies end-of-season results that are difficult to see at larger scale.

periods, including early in the first season (Nov 2012–Feb 2013) and in May 2014 (Table 1 WTR×ORGN interactions, data not shown). In May 2013, the difference in seedling activity between raked and unraked treatments was three times larger for local than nonlocal seeds, with higher activity in raked than unraked plots (Table 1 TRT×ORGN, data not shown).

3.7. Effects of seed origin on E. elymoides active growth

Effects of seed origin on active growth were less consistent for *E. elymoides* than for *P. secunda*, with more interactions with other factors (Table 2). Cumulative emergence was significantly higher for nonlocal than local *E. elymoides* seeds (Table 2). Despite a series of complex CND×WTR×ORGN interactions (data not shown) from November 2012 through February 2013, the presence of active seedlings in control and die-off did not differ dramatically by origin until April and May 2013, when nonlocal plants exhibited significantly more active seedlings than local plants (Fig. 4). In November 2013 and February 2014, there were more nonlocal seedlings in the control (nonlocal: 1.2–1.8% ± 0.5% SE, local: 0.3–0.5 ± 0.2% SE) but fewer than local in the die-off (nonlocal: 5.9–7.6% ± 1.3% SE, local: 9.7–11.3% ± 1.8% SE; Table 2 CND×ORGN interactions). Additionally, in February 2014, there were more local than nonlocal plants in unraked (nonlocal: 2.8% ± 1% SE, local: 5.5% ± 1.3% SE) but not raked plots, and this pattern was also apparent in April 2014, but only in die-off plots (unraked die-off nonlocal: 5.5% ± 1.7% SE, unraked die-off local: 13.1% ± 2.4% SE; Table 2 TRT×ORGN and CND×TRT×ORGN interactions, data not shown for three-way interaction). In May 2014, there were significantly more local than nonlocal plants in die-off but not control plots (die-off nonlocal: 5.6% ± 1.2% SE, die-off local: 9.8% ± 1.8% SE; Table 2 CND×ORGN interaction, Fig. 4) and in unraked but not raked plots (unraked nonlocal: 2.6% ± 0.8% SE, unraked local 6.2% ± 1.4% SE; TRT×ORGN interaction, data not shown).

3.8. Effects of experimental factors on late-season vigor and growth

Seedlings of both *P. secunda* and *E. elymoides* in die-off plots exhibited significantly greater late-season vigor, more leaves, and greater height than in control plots for both seasons, and more individuals flowered in die-off plots in the second season (Table 3, Figs. 5 and 6). Local *P. secunda* exhibited significantly greater late-season vigor than nonlocal plants in both growing seasons, though there were no differences in leaf number or plant height for either season (Table 3, Fig. 5). Nonlocal *E. elymoides* plants exhibited greater late-season vigor, more leaves, and greater height than local in the first season but not the second, where there were no significant effects of origin on any of these responses (Table 3, Fig. 6).

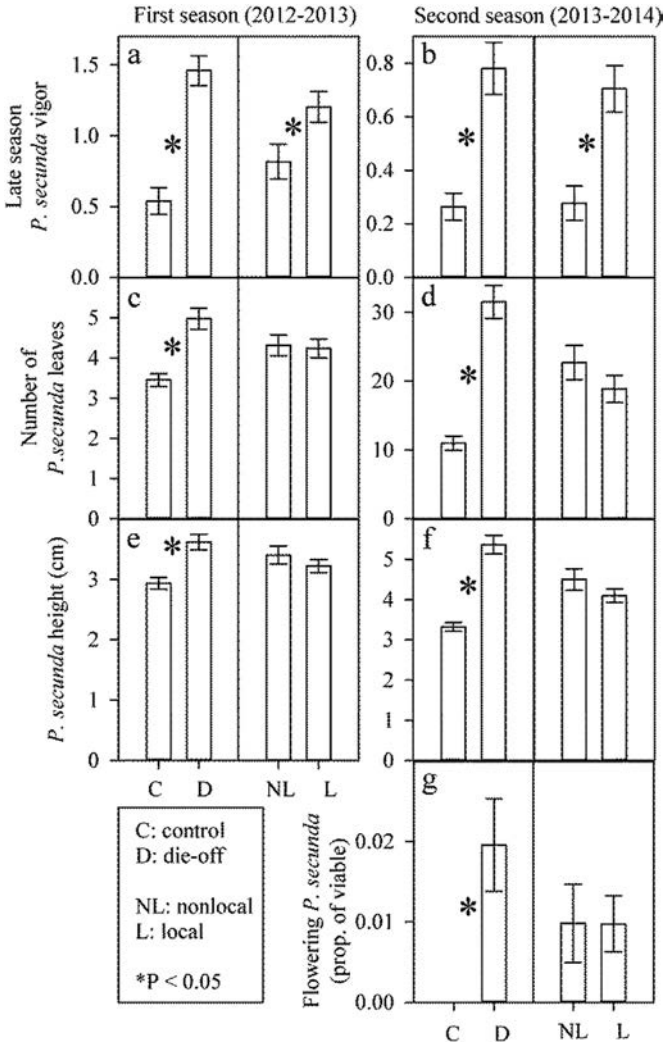

Fig. 5. For *P. secunda*, late-season vigor (a, b) as measured by greenness index (0 = 0% green, 1 = 1–25%, 2 = 26–75%, 3 = 76–100%), total number of leaves (c, d), plant height as measured by longest leaf in centimeters (e, f), and proportion of viable seeds that produced plants with flowering structures (g) during the first (left panels) and second (right panels) growing seasons, by condition (control vs. die-off) and seed origin (nonlocal vs. local). Asterisks indicate significance based on Wilcoxon signed rank tests (P < 0.05). Values are plot means and standard errors.

3.9. Effects of B. tectorum dynamics on native emergence and growth

When *B. tectorum* density was included as a model covariate for *P. secunda*, it showed a significant positive relationship with

Table 3
Results of nonparametric Wilcoxon signed rank tests for late-season vigor, number of leaves, seedling height, and number of plants with flowering structures for *P. secunda* and *E. elymoides* in both growing seasons. Values are χ^2, and bolded effects are significant (P < 0.05). Due to small sample size, factors include only condition (CND, control vs. die-off) and seed origin (ORGN, local vs. nonlocal), with no block effects or interactions included.

	First season (2012–2013)			Second season (2013–2014)			
	Late-season vigor	No. of leaves	Seedling height	Late-season vigor	No. of leaves	Seedling height	No. flowering
P. secunda							
CND	**30.4*****	**19.3*****	**14.2*****	**19.4*****	**50.2*****	**54.0*****	**17.6*****
ORGN	**6.14***	0.17	0.78	**16.8*****	0.78	0.83	0.19
E. elymoides							
CND	**43.8*****	**53.9*****	**77.8*****	**7.30****	**13.6*****	**8.87****	**20.2*****
ORGN	**7.96****	**10.0****	**13.5*****	1.65	1.66	1.23	2.92

*P (0.05–0.01), **P (0.009–0.001), ***P (<0.001).

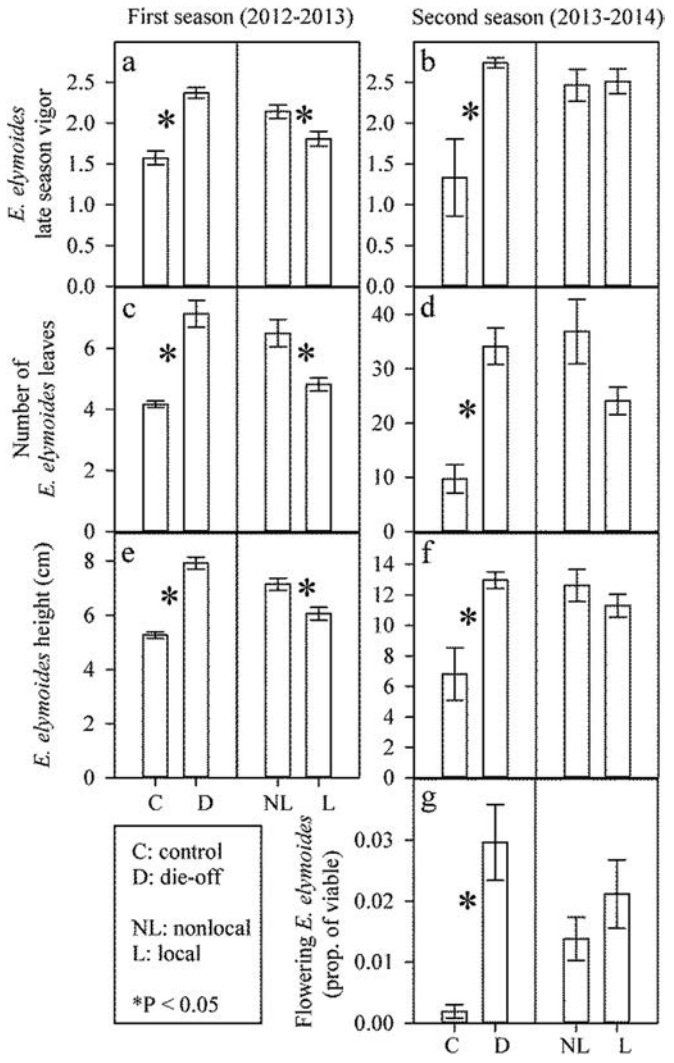

Fig. 6. For *E. elymoides*, late-season vigor (a, b) as measured by greenness index (0 = 0% green, 1 = 1–25%, 2 = 26–75%, 3 = 76–100%), total number of leaves (c, d), plant height as measured by longest leaf in centimeters (e, f), and proportion of viable seeds planted that produced plants with flowering structures (g) during the first (left panels) and second (right panels) growing seasons, by condition (control vs. die-off) and seed origin (nonlocal vs. local). Asterisks indicate significance based on Wilcoxon signed rank test ($P < 0.05$). Values are plot means and standard errors.

emergence ($F = 6.6_{(1,70)}$, $P = 0.0121$) and April active seedling number ($F = 7.3_{(1,94)}$, $P = 0.0082$), and a significant negative correlation with May active seedling number ($F = 4.3_{(1,104)}$, $P = 0.040$). The main effects of condition on April *P. secunda* active seedling number (Table 1) were reduced when *B. tectorum* density was included as a covariate ($F = 2.7_{(1,12)}$, $P = 0.125$), though the CND×TRT interaction for April activity remained significant ($F = 4.2_{(1,9)}$, $P = 0.043$). No such correlations or results modifications were observed for *E. elymoides* plots in response to *B. tectorum* density as a covariate. When first season *B. tectorum* biomass was included in the model as a covariate, it showed a significant positive relationship with May active seedling number for *E. elymoides* ($F = 5.9_{(1,95)}$, $P = 0.0174$), but main model results were not significantly modified.

4. Discussion

Restoration of highly-invaded arid systems can be extremely challenging, especially when invaders exert strong effects on community structure, disturbance regimes, and biogeochemical processes (Brooks et al., 2004; Adair and Burke, 2010). Temporary reductions in invasive species presence, through either management actions or, in our case, the naturally-occurring phenomenon of complete *B. tectorum* stand failure, or die-off, may improve the restoration potential of these highly invaded systems if native species can establish during these windows of opportunity. We found lower cumulative emergence of two native perennial grasses seeding into a die-off site than in the adjacent control, but seedlings that did emerge in the die-off exhibited significantly greater vigor, growth, and more individuals flowered. Survival was also improved in the die-off site: there were more actively growing plants in the die-off at the end of both growing seasons for *P. secunda* and throughout the whole second season for *E. elymoides*. While previous work has examined the effect of die-off on *B. tectorum* growth (Meyer et al., 2014; Nicholson, 2014), this study is the first to demonstrate the positive effects of die-off on native species establishment. *B. tectorum* die-offs may represent an opportunity for increasing the success of native seeds in highly invaded systems.

We found higher N and P in die-off soil than in adjacent control, which corroborates similar increases in N observed in previous studies on *B. tectorum* die-offs (Blank et al., 2011; Meyer et al., 2014), and removal experiments (Eckert and Evans, 1967; Eckert et al., 1970). Additionally, we found die-off soil to be significantly wetter than adjacent control soil in winter and early spring, especially when litter layers were left intact, and die-off soils were also significantly cooler than adjacent controls throughout the first growing season. These differences in soil conditions likely played a role in the enhanced vigor, growth, and establishment observed.

We also observed differences in growth and establishment between locally collected and commercially produced, nonlocal seeds, with differences varying by species and through time. Local (*P. secunda*) had greater cumulative emergence, higher numbers of active seedlings, and increased late-season vigor through both growing seasons, consistent with trends of local adaptation in many other plant species (Joshi et al., 2001; Leimu and Fischer, 2008). In contrast, nonlocal *E. elymoides* (Toe Jam Creek) seedlings had higher cumulative emergence, were more abundant, vigorous, leafier, and taller than local seedlings in the later part of the first season, but this clear advantage of nonlocal plants disappeared in the second season. In fact, by the end of the second season, only local advantages were apparent, under specific conditions: there was greater survival of local *E. elymoides* plants in die-off, but not control areas, and in unraked but not raked plots. Increased seedling growth and vigor have been highly prioritized traits in plant material development in the region (Leger and Baughman, 2015), and this is true for Toe Jam Creek (United States Department of Agriculture, 2013). In our study, however, increased performance was not associated with greater plant size, for either *P. secunda* or *E. elymoides*. There is evidence that increased first year growth is independent of some fitness components, such as survival (Verdú and Traveset, 2005) and fecundity (Chambers and Aarssen, 2009), and our findings substantiate other studies from the Great Basin which have similarly shown that large above-ground size in herbaceous plants is not necessarily related to increased survival (Kulpa and Leger, 2013), especially in competitive environments (Rowe and Leger, 2011).

We added early-season water and removed litter to see if these treatments aided in the establishment of native seeds, in general, or in sites that had experienced the die-off phenomenon. Although cumulative emergence of both species was boosted by pre-

germination water addition and unaffected by pre-planting litter removal, these treatments had mixed effects on seedling performance, but effects were mostly consistent between the die-off and control. Water addition was generally unrelated to patterns of *P. secunda* activity in either season, and litter removal was associated with higher *P. secunda* activity in the second but not the first season. For *E. elymoides*, water addition was associated with higher activity in the first but not the second season, and litter removal had few but mixed effects throughout both growing seasons. In short, native species did not show lasting benefits of water addition in the fall of the first season, and removing litter appeared to enhance survival of *P. secunda*. Given these findings, litter reduction may lead to improvements of some native species, in or out of a recent die-off.

Competitive effects of *B. tectorum* on native Great Basin perennial grasses can be substantial (Humphrey and Schupp, 2004; Melgoza et al., 1990), though some studies have found such competition to be absent and/or much less important for native performance than other factors (James and Svejcar, 2010; Elseroad and Rudd, 2011; Mangla et al., 2011). In our study, *B. tectorum* densities were higher in control, watered, and unraked plots, while biomass was generally higher in the die-off, and showed positive responses to water addition and litter removal. Both measures of *B. tectorum* had positive, significant correlations with native active seedling growth in the first growing season, suggesting either facilitation or parallel responses to favorable plot conditions. Only one correlation, between *B. tectorum* density and *P. secunda* active seedling number in May, was negative and suggestive of competitive effects, and including *B. tectorum* dynamics in the model did not eliminate the significant effect of condition on native seed performance. Thus, our correlations failed to suggest that differences in interactions with *B. tectorum* were the main factors responsible for increased native seedling performance in die-offs. Collective *B. tectorum* density and biomass in both conditions during the study were far below maximum possible values (Eckert and Evans, 1967; Knapp, 1996), perhaps due to below-average precipitation or in response to die-off conditions, and this could account in part for a lack of clear competitive effects.

Though *B. tectorum* stand failure was not observed in this study, emergence and early-season active growth of native species was generally lower in die-off than control plots for both species. This pattern was not clearly affected by early-season water addition or litter removal treatments, and the observed differences in soil (slightly lower pH, and higher P and N in die-off than control) would not be expected to directly affect emergence in this way. The cooler and wetter conditions in die-off soils may have somehow reduced emergence, either directly or through their effects on soil pathogen activity, though this is only speculation. This study did not directly investigate the causes of native seed mortality in the former die-off area, and this should be a topic of future research, especially given the otherwise positive effects of recent die-off sites for the studied native species.

Finally, we note that the hand-sorting, precision-seeding, and intensive monitoring methods employed in this study are not those employed in large-scale restorations, and thus our establishment rates are not directly comparable to studies reporting survival or success of native perennial grasses in wildland settings. Seeding methods play a large role in determining the patterns of success when restoring resource-limited, semiarid sites (James and Svejcar, 2010; Bernstein et al., 2014) by determining the conditions that germinating seeds will experience, which are perhaps the conditions of most concern for improving restoration success in this region (Boyd and Davies, 2012). Our future efforts will identify the effects of recent *B. tectorum* die-offs on native establishment using realistic, larger-scale restoration seeding methods.

5. 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. Results from this northern Nevada die-off site indicated some initial negative but overall positive effects of seeding in a die-off area on the growth and establishment of two native grasses. Additionally, this case study demonstrated source-related and species-dependent differences in performance of native perennial grasses seeded into an invaded site, highlighting the importance of seed selection in restoration for the region. Our findings demonstrate that further investigations of the restoration potential of die-offs in other areas are warranted, as results may differ as environmental conditions vary between sites, or between years at the same site. To maximize our understanding of the effects of die-offs on native seed establishment, we recommend that future efforts examine multiple die-off sites, manipulate *B. tectorum* densities and soil resources, and test whether establishment benefits are observed on larger scales and when traditional restoration methods are used.

Acknowledgments

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Appendices

Table A.1
Means ± standard errors of untransformed data, and ANOVA results for soil nutrients (ppm) and organic matter (%) analysis in control and die-off soils. Asterisks indicate significant differences ($P < 0.05$), and greater values are bolded when there are significant between-condition differences.

	Fall 2012			Summer 2013		
	Control	Die-off	$F_{(1,4)}$	Control	Die-off	$F_{(1,9)}$
pH	**6.9 ± 0.05**	6.52 ± 0.05	42.4**	**7.45 ± 0.1**	6.84 ± 0.12	26.8***
P	72.4 ± 3.78	**91.8 ± 4.55**	47.9**	68 ± 7.62	**116 ± 5.55**	25.2***
K	473 ± 16	536 ± 48.1	1.09	627 ± 43.1	778 ± 38.9	7.5*
Ca	1242 ± 28.2	1119 ± 88.9	1.64	1426 ± 38.8	1271 ± 48.5	4.01
Mg	243 ± 6.22	210 ± 18.4	2.66	**330 ± 12**	275 ± 10.4	7.3*
OM	2.52 ± 0.15	3.08 ± 0.12	5.44	1.66 ± 0.06	1.7 ± 0.13	0.06
NO_3	7.8 ± 0.49	**18.8 ± 1.24**	80.7***	3 ± 0.39	**11 ± 2.98**	8.8*

*P (0.05–0.01), **P (0.009–0.001), ***P (<0.001).

Table A.2
Repeated measures ANOVA results for soil moisture and temperature during the winter (1st Nov – 28th February), early spring (1st March – 30th April), and late spring (1st May – 31st May) in the first season. Values are F statistics, *df* (treatment, error, presented in parentheses for moisture and are the same for temperature), and bolded effects are significant ($P < 0.05$). Factors include condition (CND, control vs. die-off), seedbed treatment (TRT, raked vs. unraked), and water treatment (WTR, watered vs. unwatered), and time.

	Soil Moisture			Soil temperature		
	Winter	Early spring	Late spring	Winter	Early spring	Late spring
CND	**240$^{***}_{(1,106)}$**	**180$^{***}_{(1,59)}$**	2.25 $_{(1,29)}$	**7.74****	**2236*****	**1792*****
TRT	**190$^{***}_{(1,106)}$**	**186$^{***}_{(1,59)}$**	**70.6$^{***}_{(1,29)}$**	3.70	**345*****	**40.7*****
WTR	**47.4$^{***}_{(1,106)}$**	**41.0$^{***}_{(1,59)}$**	0.09 $_{(1,29)}$	**96.6*****	**30.7*****	**70.7*****
Time	**64.5$^{***}_{(1,106)}$**	**29.0$^{***}_{(1,59)}$**	**55.3$^{***}_{(1,29)}$**	**1870*****	**127*****	**392*****
CND×TRT	1.97 $_{(1,106)}$	**4.55$^{*}_{(1,59)}$**	**5.25$^{*}_{(1,29)}$**	**103*****	**63.6*****	**12.5*****
CND×WTR	**34.0$^{***}_{(1,106)}$**	3.21 $_{(1,59)}$	**23.4$^{***}_{(1,29)}$**	2.93	**9.97****	**32.4*****
CND×Time	0.99 $_{(1,106)}$	0.81 $_{(1,59)}$	0.36 $_{(1,29)}$	**23.8*****	**6.69*****	**5.84*****
TRT×WTR	**63.1$^{***}_{(1,106)}$**	**223$^{***}_{(1,59)}$**	**81.0$^{***}_{(1,29)}$**	**19.5*****	**52.8*****	**72.5*****
TRT×Time	**1.34$^{*}_{(1,106)}$**	0.54 $_{(1,59)}$	0.75 $_{(1,29)}$	**5.42*****	**5.87*****	**7.63*****
WTR×Time	1.02 $_{(1,106)}$	0.13 $_{(1,59)}$	0.08 $_{(1,29)}$	0.33	0.32	0.76
CND×TRT×WTR	0.77 $_{(2,212)}$	**5.62$^{*}_{(2,118)}$**	**9.47$^{**}_{(2,58)}$**	**5.00***	**4.12***	4.89*
CND×TRT×Time	0.20 $_{(2,212)}$	0.11 $_{(2,118)}$	0.09$_{(2,58)}$	0.58	0.38	0.44
CND×WTR×Time	0.67 $_{(2,212)}$	0.17 $_{(2,118)}$	0.32$_{(2,58)}$	0.26	0.18	0.87
TRT×WTR×Time	0.19 $_{(2,212)}$	0.29 $_{(2,118)}$	0.12$_{(2,58)}$	0.22	1.05	0.32
CND×TRT×WTR×Time	0.28 $_{(3,318)}$	0.001 $_{(3,177)}$	0.18 $_{(3,97)}$	0.14	0.19	0.11

$^{*}P$ (0.05–0.01), $^{**}P$ (0.009–0.001), $^{***}P$ (<0.001).

Appendix 1. Effects of die-off, litter removal and watering on soil moisture and temperature

Litter removal and watering altered the effects of the die-off on moisture in the winter, early spring, and late spring (CND×WTR, TRT×WTR and CND×TRT×WTR interactions, Table A.2). Soil moisture was slightly higher (0.002 cm^3 H_2O cm^{-3} soil ± 0.001) in winter and substantially higher (0.02 cm^3 H_2O cm^{-3} soil ± 0.001) in early spring in die-off than control soils when unraked. Litter removal created relatively dry soils through the season, especially in early spring following spring-thaw when soils dried down more quickly. For example, by March, soil moisture was at least 32% lower in control than die-off treatments when raked and watered. Although watering reduced the differences between control and die-off conditions, from early spring on, the driest soils were watered control and die-off plots that were raked. Soil moisture in these two treatments was at least 25% lower than any other treatment combination. In the winter, all treatment soils experienced a series of freeze–thaw cycles that caused soil moisture to freeze leading to a decrease in available soil water. In early and late spring, soils experienced six drying–rewetting cycles due to rainfall events beginning in early March.

Soil temperatures were influenced by condition, litter removal, and water addition during the entire first season (Table A.1). Litter removal and water altered the effects of the die-off on temperature in early spring and late spring (Table A.2 CND×TRT×WTR interactions). In winter, temperatures were 0.78 °C ± 0.06 ($n = 21$) cooler in die-off than control soil but only during freeze–thaw cycles with the absence of litter further depressing soil temperatures. Also, in early spring and spring, temperatures in die-off soil were 1.93 °C ± 0.09 ($n = 90$) cooler, and these differences were accentuated when litter was intact. Generally, winter pulses of water slightly decreased soil temperatures over the season regardless of other factors.

Appendix 2. Effects of litter removal and water addition treatments on E. elymoides active growth

In November 2012, significantly fewer active *E. elymoides* seedlings existed in raked than unraked treatment in the control that was watered, while the unwatered control and die-off of either watering treatment did not exhibit effects of raking (Table 2 CND×TRT×WTR interaction).

Fewer seedlings existed in the raked than unraked treatment in December 2012 regardless of other factors (unraked: 34.5% ± 3.8% SE, raked: 29% ± 3.7% SE), as well as in February 2013 in the unwatered but not watered treatment (TRT×WTR interaction, data not shown). By May 2013, this pattern had reversed, with the raked treatment showing higher activity (unraked: 32.1% ± 2.2% SE, raked: 50.4% ± 2.3% SE). There were no effects of litter treatment on number of active seedlings in March or April 2013.

Water addition increased *E. elymoides* seedling activity regardless of other factors from November 2012 through April 2013, with the effect larger in unraked than raked treatments early in the season (Table 2 TRT×WTR interactions, data not shown). In May 2013, the watered treatment supported more active seedlings than unwatered only when raked (watered: 61.8% ± 2.4% SE, unwatered: 38.9% ± 2.9% SE), with no difference when unraked (Table 2 TRT×WTR interaction, data not shown).

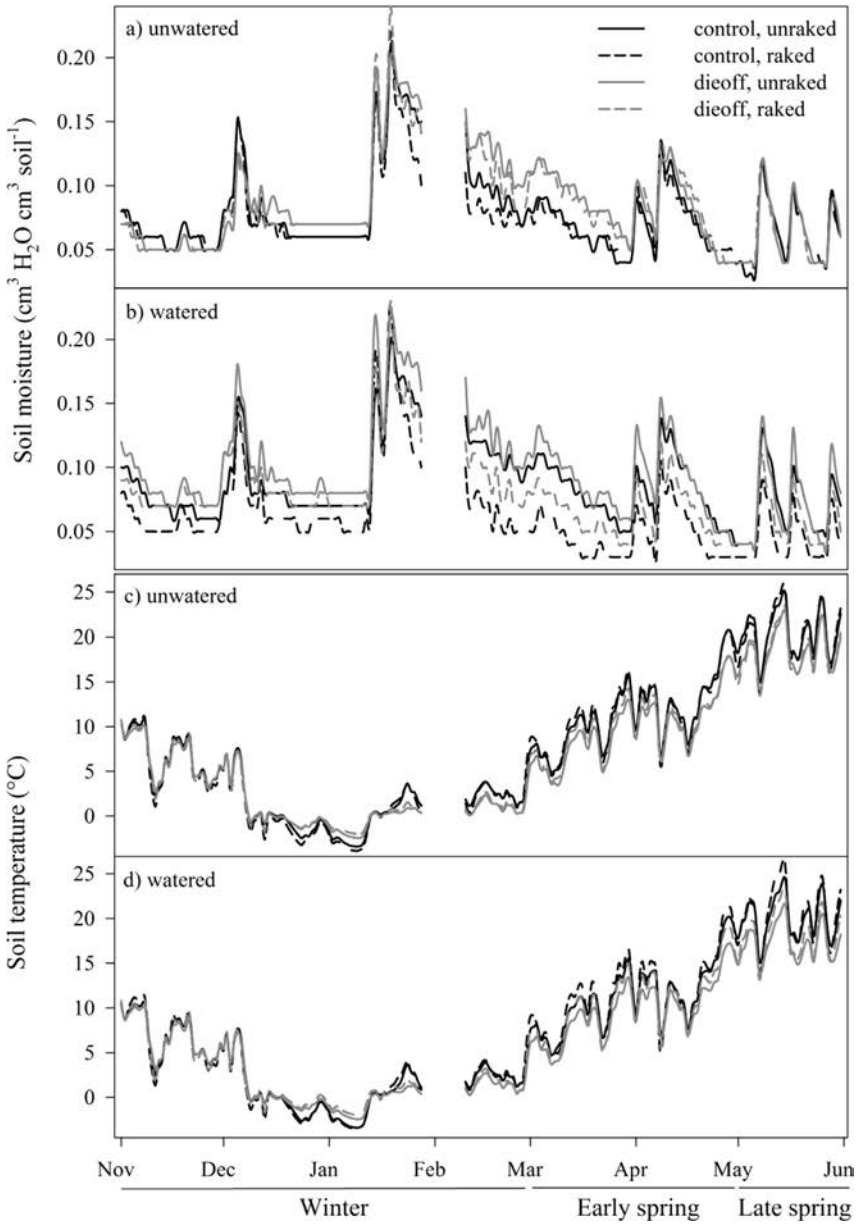

Fig. A.1. The effects of the die-off condition and litter removal by early season watering treatment on soil moisture (a & b) and temperature (c & d). Values ($n = 6$) are real-time sensor data expressed on a daily time step from a soil depth of 2 cm. The gap in the data from January 28th to February 10th was due to an electrical storm resetting the data loggers. Soil in the die-off was continually wetter in winter (die-off: 0.095 cm^3 H2O cm-3 soil ± 0.002 SE, control: 0.083 ± 0.002 SE) and early spring (die-off: 0.081 ± 0.002 SE, control: 0.066 ± 0.002 SE), as well as cooler in winter (die-off: 2.29 °C ± 0.17 SE, control: 2.35 ± 0.19 SE), early spring (die-off: 10.00 ± 0.22 SE, control: 11.43 ± 0.25 SE), and late spring (die-off: 18.06 ± 0.21 SE, control: 20.28 ± 0.25 SE).

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