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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.
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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

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