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Intraspecific Variation in the Response of *Elymus Elymoides* to Competition from *Bromus Tectorum*

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INTRASPECIFIC VARIATION IN THE RESPONSE OF *ELYMUS ELYMOIDES* TO COMPETITION FROM *BROMUS TECTORUM*

by

Rebecca K. Mann

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Dr. Kari E. Veblen Major Professor	Dr. Thomas A. Monaco Committee Member
Dr. Eugene W. Schupp Committee Member	Dr. Mark R. McLellan Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
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ABSTRACT

Intraspecific Variation in the Response of *Elymus elymoides* to Competition from *Bromus tectorum*

by

Rebecca K. Mann, Master of Science

Utah State University, 2016

Major Professor: Dr. Kari E. Veblen
Program: Ecology

Native plant materials are often seeded to restore biodiversity and ecosystem function in areas overtaken by exotic weeds. Plant materials are evaluated on intraspecific differences in productivity and expression of traits advantageous to establishment (e.g., phenology, seed mass, and growth rate); some investigations also consider population-level adaptation to exotic species. However, there is a lack of studies that broadly evaluate response to competition from exotic species at multiple scales within a species.

In a greenhouse experiment, we used analysis of variance to assess the growth response of a perennial grass native to the Intermountain West, (*Elymus elymoides)*, to competition from a common invasive species, (*Bromus tectorum)*, at three levels of intraspecific differentiation: subspecies, lineage (wild vs. domestic germplasm), and population. We used regression analysis to assess whether *E. elymoides* populations from highly invaded areas were less affected by *B. tectorum* competition. Finally, we explored the relationship between growth traits and competitive response using random forest regression. We found significant differences among *E. elymoides* subspecies in their response to *B. tectorum* competition, no difference between wild and domestic lineages, and no population-level differentiation within subspecies. Field abundance of *B. tectorum* had a significant positive relationship with *E. elymoides* biomass, but not competitive response, suggesting that *E. elymoides* has not adapted to the invader. *Elymus elymoides* plants which were less affected by competition were smaller, allocated more biomass to leaves, and had fewer fine roots, suggesting that light interception and tissue retention were prioritized by seedlings in this competitive greenhouse environment.

(95 pages)

PUBLIC ABSTRACT

Intraspecific variation in the response of *Elymus elymoides* to competition from *Bromus tectorum*

Rebecca Mann

In the western United States, thousands of acres of degraded rangelands are dominated by aggressive invasive species such as cheatgrass (*Bromus tectorum*), and are seeded by managers with native plants in an attempt to restore species diversity, wildlife habitat, and ecosystem services. There are many options for obtaining seeds of native plants; for instance, they can be collected from the region where restoration is to occur, or they may be purchased through commercial producers. For a given plant species, managers may also select seeds from unique subspecies, cultivars, and populations. Genetic differentiation among these within-species groups can not only affect their growth form and trait expression, but also how well these groups are able to compete with invasive species.

I assessed how within-species groups of a commonly-seeded native bunchgrass, squirreltail (*Elymus elymoides*), differed in their response to competition from cheatgrass. I specifically looked at differences among representatives of: 1) three squirreltail subspecies, 2) wild-collected vs. commercially-available squirreltail seed, and 3) eighteen distinct squirreltail populations. I hypothesized that there would be variation among all representatives of these three within-species groups. I also hypothesized that squirreltail seeds collected from areas that are heavily invaded with cheatgrass will have higher tolerance of competition, resulting from their opportunity to locally adapt to the competitor. Finally, I assessed whether plant traits could predict the response of squirreltail to competition from cheatgrass; my hypothesis was that plants which partitioned a greater portion of their biomass to roots would better tolerate competition.

To test these hypotheses, I performed a greenhouse study in which I grew squirreltail plants both alone and with cheatgrass, and created an index of how much squirreltail biomass was lost due to competition. I found that there was variation in response to competition among subspecies, but no variation among populations, and no variation between wild and commercial seeds. Contrary to my hypotheses, populations from cheatgrass-invaded areas were no different in their response to competition than those from un-invaded areas, suggesting that local adaptation is not occurring. Finally, although several growth traits were good predictors of competitive response, the plants which were less affected by competition partitioned more biomass to leaves, not to roots as I had expected; this finding suggested that light was the primary limiting resource for seedlings in this competition experiment. By confirming variation among squirreltail subspecies in their ability to tolerate competition, and by linking growth traits to competitive tolerance, this work provides information to restoration practitioners who must choose among seed sources for revegetation of invaded rangelands, and to native plant breeders aiming to create improved native plant varieties by selecting for traits associated with higher establishment success in invasion-prone areas.

DEDICATION

In dedication to D. M. S.

“Learn as if you were to live forever.”

-Mahatma Gandhi

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Rebecca Mann

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INTRODUCTION

Rangelands of the Intermountain West are commonly affected by overuse, particularly prolonged, heavy livestock grazing and resource extraction, which often lead to a conversion of perennial-dominated plant communities to alternative stable states dominated by exotic annual grasses (Davies et al. 2011; Bestelmeyer et al. 2015). Degraded areas are associated with accelerated fire regimes, increased soil erosion and water loss, and altered nutrient cycling rates (D'Antonio and Vitousek 1992), which in turn severely constrain native plant species diversity, productivity, and habitat value (Eviner et al. 2010; Davies et al. 2011). Integral to the restoration of desirable ecological states and processes is the re-establishment of native perennial plant species (Eviner et al. 2009; Davies et al. 2011), which is widely attempted by broadcasting seeds to augment sites limited by propagule supplies (Turnbull et al. 2000), especially in areas where seeds banks are dense with exotic annual species (Humphrey and Schupp 2001).

Intraspecific variability of the seeded native species can be substantial, however; seed sources may differ in their ability to establish under given abiotic and biotic site constraints (Carroll et al. 2007). Propagules from different native populations may differ in their ability to co-exist and compete with the invasive species that restoration practitioners intend the natives to replace (e.g., Mealor and Hild 2006; Callaway et al. 2008; Ferrero-Serrano et al. 2011; Rowe and Leger 2011; Sebade et al. 2012). In the Intermountain West, testing and determining the competitive response of intraspecific subspecies, lineages (e.g. wild-collected varieties vs. domestic varieties produced in increase-fields), and populations to the widespread invasive species, *Bromus tectorum*, will further efforts to identify taxa that are successful in ecological restoration efforts.

In addition, clarifying the relationship between plant growth traits and tolerance to competitors can guide selection criteria for breeding plant materials with higher establishment (Leishman 1999; Burns and Straus 2012, Clark et al. 2012, Laughlin 2014), and greater resilience in areas affected by exotic plant invasions (Funk et al. 2008; Jones et al. 2010; Abella et al. 2011; Abella et al. 2012; Jones 2013b; Jones et al. 2015). For instance, seedling emergence from the soil is a critical phase in grass development (Larson et al. 2015), and is tied to greater seed mass and coleoptile tissue density (Larson et al. 2015). Seed mass (Leishman and Westoby 1994), specific leaf area (Craine et al. 2001), relative growth rate (Grace 1990), and resource partitioning (Roberts et al. 2010) may also be important to establishment. In arid rangelands that have been overtaken by exotic annual grasses, Jones et al. (2010a) suggest that beneficial plant traits will function to overcome three primary ecological obstacles: *priority effects, interference, and positive feedbacks*. The high reproductive output, early germination, and rapid growth rate of cheatgrass allows it to establish before most native species, and to take control of space and nutrient cycling processes. Traits of native plants that may overcome these *priority* advantages of cheatgrass include high seed output, greater seed mass, seed dispersal structures, and fast growth rate. Similarly, leaf nitrogen productivity, root growth, and ability to grow in early-season cold temperatures enable native plants to avoid or overcome *interference* from established cheatgrass seedlings; tissue quality and fire and drought tolerance enable native plants to persist despite the altered ecological processes driven by the *positive-feedback* mechanisms associated with cheatgrass (Jones et al. 2010a).

Domestication (selection and/or breeding) of native plant materials may result in heritable trait changes that affect establishment and growth of seeded plants (Allard 1988; Frary and Doganlar. 2003; Lambert et al. 2011; Schroder and Prasse 2013). Breeding programs tend to emphasize increased plant size, seed production, germinability, and seedling establishment (Leger and Baughman 2015), and domestic cultivars can have higher tolerance of invasive species and environmental stress (Burton and Burton 2002; Gustafson et al. 2004; Jones 2009). However, domestic plant materials do not always show greater performance compared to wild types (Humphrey and Schupp 2002), and domestication sometimes results in mal-adaptation to site conditions (Schroder and Prasse 2013). Regardless, domestic plant materials are widely available and commonly used in restoration efforts, and it is important to develop an understanding of how they compare to wild types in terms of competitive tolerance.

Elymus elymoides (bottlebrush squirreltail) is a common component of native seed mixes, and can be widely planted across the Great Basin due to its broad geographical native range (Wilson 1963). This perennial grass is valued for several reasons, including its ability to rapidly establish in disturbed sites (Mack and Pyke 1983; Jones 1998), tolerate moderate fires (Wright 1971; Blank et al. 1994), and self-fertilize, allowing it to set seed even at low population densities (Jensen et al. 1990). Moreover, *E. elymoides* can tolerate and persist in annual-grass invaded communities (Hironaka and Tisdale 1963; Booth et al. 2003). *E. elymoides* consists of four recognized subspecies (Wilson 1963), which express considerable morphological and genetic variation (Clary 1975; Jones et al. 2003; Larson et al. 2003; Parsons et al. 2011), which in turn may vary considerably in their relative competitive tolerance (Strauss et al. 2006; Leger and

Espeland 2010). Population-level variation in tolerance to invasive species has been observed for its congener, *E. multisetus* (Leger 2008; Goergen et al. 2001; Rowe and Leger 2011), as well as for other species (Callaway et al. 2005; Ferrero-Serrano et al. 2011; Lau 2006; Lankau 2012; Sebade et al. 2012). However, the competitive ability of *E. elymoides* sub-species and populations has not been evaluated.

Our research goals were to test whether there is intraspecific variation in *E. elymoides* response to *B. tectorum* competition, and to investigate whether *E. elymoides* growth traits and environmental factors, including *B. tectorum* abundance, are related to competitive response. Our specific research questions were: 1) Do subspecies, lineages (wild vs. domestic germplasm), or individual populations of *E. elymoides* differ in competitive response to *B. tectorum*? 2) Within a subspecies, is field abundance of *B. tectorum* at a collection site a better predictor of competitive response than other environmental parameters? *B. tectorum* and 3) Do taxa with higher tolerance of competition express a particular suite of growth traits? We hypothesized that there would be substantial variation at all three levels of intraspecific variation and that wild lineages would have greater tolerance of competition than domestic lineages. Secondly, we hypothesized that field abundance of *B. tectorum* would be the greatest predictor of competitive response, compared to other environmental variables. Finally, because of the competitive nature of *B. tectorum* for soil resources (Melgoza et al. 1990; Booth et al. 2003; Monaco et al. 2003; Adair et al. 2008), we predicted that competitive tolerance would be associated with higher allocation of biomass to roots, including high root to shoot ratio, high fine to coarse root ratio, and low average root diameter.

LITERATURE REVIEW

Bromus tectorum in the Intermountain West

The sagebrush (*Artemisia tridentata*) biome is a semi-arid region with relatively low vegetative cover (Winward and Tisdale 1977; Winward 1980; West 1983; Davies et al. 2011). It dominates most arid regions in western North America, providing habitat to a vast diversity of species, including the iconic Greater sage grouse (Davies et al. 2011). It is also rich with human activities, from energy extraction to cattle ranching and recreation. But the landscape on which wildlife and humans depend is a seriously threatened ecosystem (Davies et al. 2011), largely due to the pervasive impacts of a single diminutive plant: cheatgrass, *Bromus tectorum* L. (D'Antonio and Vitousek 1992). This annual grass was introduced in the late 1800s as a grain contaminant on European ships (Mack 1981), and it spread rapidly following heavy grazing from cattle and sheep in the Intermountain rangelands in the late 19th and early 20th century (Mack 1981). Cheatgrass dispersal and establishment continues today in sites experiencing vegetation removal, trampling, and other disturbances associated with land development and heavy livestock grazing (Chambers et al. 2007).

Cheatgrass commonly co-exists with several other annual, weedy species that can establish in arid rangelands, most of which are broad-leaved forbs, such as mustards (*Sisymbrium altissimum, Descurania sophia, D. pinnata, and Lepidium perfoliatum*), filaree (*Erodium cicutarium*), and Russian thistle (*Salsola kali*) (Piemeisel 1951; Allen and Knight 1984). Cheatgrass may exist as patches in these annual forb-dominated areas, and prevalence of these functional groups can cycle through time. Cheatgrass, however, is often becomes the prominent species following initial site disturbance (Stewart and

Hull 1949; Piemesel 1951; Evans and Young 1970; Mack 1981), its dominance driven by positive feedback mechanisms that facilitate its own persistence, including an alterations to germination microsites, fire cycles, and soil nutrient conditions.

Monocultures of cheatgrass can produce hundreds to thousands of seeds per square foot (Humphrey and Schupp 2001), and its growth in favorable years can result in near-continuous canopy cover across a site (Young et al. 1969; Mack and Pyke 1983). When the plants die in spring or early summer (D'Antonio and Vitousek 1992), dry cheatgrass litter (dead, procumbent leaves, stems, and inflorescences) remains and can accumulate over several generations (Evans and Young 1970; Knapp 1996). By moderating heat and moisture loss through shading, litter from prior generations of cheatgrass promotes germination and establishment of cheatgrass seeds in the soil (Evans and Young 1970; Bansal et al. 2014); its germination can be at least four times greater under litter compared to open interspaces (Evans and Young 1970).

The continuously-distributed litter of cheatgrass also acts as fine fuel that can readily catch fire (Whisenant 1990; Knapp 1996). Cheatgrass-enabled fires result in plant mortality, increased availability of soil nutrients (Young and Evans 1978; Blank et al. 1994; Davis et al. 2000; West and Yorks 2002; Evangelista et al. 2004) and open space for future cheatgrass establishment. Fire enables the establishment of cheatgrass, and cheatgrass promotes fire, creating a cycle of burning that can be as frequent as every 3-5 years (Whisenant 1990; D'Antonio and Vitousek 1992; Brooks et al. 2004; Balch et al. 2013; Weltz et al. 2014), dramatically higher than the historic regime of every 60-110 years in sagebrush communities (Whisenant 1990; Weltz et al. 2014). Native species are mal-adapted to this shorter interval (Brooks et al. 2004; Pellant et al. 2004; Davies and

Svejcar 2008), especially those that are unable to re-sprout, such as sagebrush (Stewart and Hull 1949; Britton and Ralphs 1979; Knapp 1996).

Once established, cheatgrass also drastically alters nutrient cycling processes and other properties of the soil environment. The rapid growth and fine root development of cheatgrass results in an overall decrease in soil water availability (Melgoza et al. 1990). Cheatgrass plant litter stimulates the activity of soil bacterial, which in turn accelerates nitrogen cycling rates (Stark and Norton 2015). Although concentrations of soil active nutrients increase during the growing season (Sperry et al. 2006; Stark and Norton 2015, Blank and Morgan 2016), the decrease in higher-quality, slow pools of soil organic matter, such as humus (Norton et al. 2004), plus accelerated erosion rates associated with the ephemeral annual roots of cheatgrass (Knapp 1996; Miller et al. 2011) results in overall nutrient loss from invaded soils (Norton et al. 2004; Sperry et al. 2006). Increased bacterial activity is also associated with a decrease in soil invertebrate and fungal species abundance, including mycorrhizae that form mutualisms with native species (Belnap and Phillips 2001); the result are barren substrates that are not conducive to native plant establishment (Mack 2011).

As described, cheatgrass-invaded areas are associated with processes that promote its own persistence: increased germination under thick leaf litter, an accelerated fire cycle, and accelerated nutrient cycling rates. These altered ecosystem processes in addition to ongoing site disturbances that led to the initial invasion (e.g. agriculture, heavy grazing, road development for energy extraction), lead to the continued loss of native species. Cheatgrass-affected ecosystems are at risk of (or have already undergone) a change in plant community assembly that is very difficult to reverse. In other words, invaded sites transition to an alternative stable state governed by strong, positive feedbacks which favor cheatgrass (Stringham et al. 2003; Chambers et al. 2014; Jones et al. 2015). Landscapes that have crossed this threshold are very challenging to restore to a native-plant dominated condition (Suding et al. 2004; Davies et al. 2011).

Today, there are many estimates of how much land has been converted to persistent annual grass communities. In the Great Basin alone, there are reports of between 20,000 km^2 to 127,000 km^2 of land converted to cheatgrass dominance (Menakis et al. 2002; Bradley and Mustard 2005), with estimates that 40-45% of other areas are at risk of invasion (Bradley and Mustard 2005; Suring et al. 2005). In the Intermountain West, potentially 280,000 km^2 are at risk of future invasion (Menakis et al. 2002; Meinke et al. 2009). Cheatgrass continues to invade areas affected by natural and human-related disturbances, but is further enabled by its ability to germinate in a wide range of conditions (Meyer et al. 1997) and to adapt to novel environmental conditions at the edge of its range (Novak 1992; Meyer and Leger 2010).

There are no clear answers for restoring vast landscapes that have transitioned to an annualized grass state (Pellant 1990; Davies et al. 2011; Mack 2011). On sites where invasion is not widespread, targeted grazing can be used to maintain low population levels (Vallentine and Stevens 1994). In heavily invaded sites, control has been attempted through early-season burning, mechanical, and biological control treatments, which may destroy plants before they set seed (Davies et al. 2011). However, grazing, burning, and mechanical treatments do not offer long-term solutions and can be detrimental to biological soil crusts (Belnap and Eldridge 2001; Mack 2011), which are imperative for soil retention and nitrogen fixation (Belnap and Eldridge 2001).

Herbicides, especially glyphosate (Whitson and Koch 1998) and imazapic (Ogg 1994; Kyser et al. 2007; Morris et al. 2009), are also widely employed to manage large-scale cheatgrass invasions, although successive treatments may be necessary and expensive (Currie et al. 1987). Biological control has promise for controlling cheatgrass population levels, but is not yet ready for wide-scale use (Knapp 1996). Regardless the reduction tactics, successful establishment of perennial plants is critical for preventing reinvasion of cheatgrass (Stevens 1999; Chambers et al. 2007; D'Antonio et al. 2009; Morris et al. 2009). Intact perennial plant communities can suppress annual grass growth and resist future invasion (Perry et al. 2009; McGlone et al. 2012). For instance, a greenhouse experiment showed that adult plants of two native grasses, bottlebrush squirreltail (*Elymus elymoides*) and western wheatgrass (*Pascopyrum smithii*), were highly competitive for nitrogen, phosphorus, and water, and the adult natives significantly reduced total cheatgrass biomass and seed production per pot (McGlone et al. 2012). In a field setting, density and cover of a similar invasive grass, medusahead (*Taeniatherum caput-medusae*), are also negatively correlated with established perennial grass density (Davies 2008).

Unfortunately, establishing desirable adult plants in previously invaded areas is another major challenge to restoration practitioners; seeding is often the only option for treating large landscapes (Young and Evans 1978; Aguirre and Johnson 1991, Arrendondo et al. 1998). Cheatgrass seeds are often in the topsoil (Pekas and Schupp 2013) and can remain viable for several years (Hulbert 1955; Hull and Hansen 1974). Because it can germinate in fall (Aguirre and Johnson 1991) and over-winter as a seedling, cheatgrass can take advantage of spring resources before seedlings of latergerminating native plants (Link et al. 1995; Arrendondo et al. 1998), including water (Harris and Wilson 1970, Melgoza et al. 1990; Booth et al. 2003) and nutrients (Lowe et al. 2002; Monaco et al. 2003; Adair et al. 2008). Dense leaf production and heavy accumulation of litter may also result in the limitation of light available to seedlings of desirable perennials (Facelli and Pickett 1991), albeit of less importance than water stress in arid environments (Holmgren et al. 1997). Due to the competitive environment and altered soil conditions, restoration efforts to re-establish native plants is rarely a success, often requiring several costly attempts (Young 1992; Vitousek et al. 1997; Rafferty and Young 2002; Monaco et al. 2005). One tactic currently being pursued is the selection and development of plant materials that are more successful in altered and invaded plant communities (Funk et al. 2008; Sandel et al. 2011; Jones et al. 2015; Leger and Baughman 2015), discussed in the following section.

Plant Materials for Restoration

Seeding plants into areas that have been disturbed can be key to creating a plant community resistant to future exotic species invasions (Allen-Diaz and Bartolome 1998; Chambers et al. 2007; Davies 2008; Eviner et al. 2009; James et al. 2012). Seeding is most often applied where vegetation has been removed by wildfire or by intentional removal of unwanted woody plants and weeds. Establishing plant communities from bare ground is a substantial challenge, and often fails due to unpredictable seasonal precipitation a lag in the germination of desirable native perennial plants compared to that of invasive plants (Young and Mangold 2008; Davies et al. 2011; Hardegree et al. 2011; Mangla et al. 2011, Ray-Mukherjee et al. 2011). To address this situation, substantial research on plant materials has been performed to identify germination and growth attributes (e.g., phenology, biomass allocation, height, growth rate) conferring establishment success for desirable species in harsh arid landscapes.

When selecting plant material for restoration, managers can choose from non-native or native species; local genotypes or commercially produced seed. Non-native species, such as crested wheatgrass (*Agropyron cristatum* and *A. desertorum*), intermediate wheatgrass (*Thinopyrum intermedium*), and Siberian wheatgrass (*Agropyron fragile)* are frequently used to seed western rangelands and provide many immediate benefits such as soil stabilization, forage production, and suppression of exotic species (D'Antonio and Meyerson 2002; Asay et al. 2003). The most commonly seeded non-native species are perennial grasses which grow quickly, and are easily and cheaply obtained from commercial suppliers (Pellant 1990; Asay et al. 2001; Epanchin-Niell et al. 2009). These species offer a quick and often effective solution for stabilizing sites at risk of major conversion to an eroded or annualized grass state (Asay et al. 2001; Davies et al. 2011). However, the concern about the use of non-native species is their potential for competitive exclusion of native plants (Hull and Klomp, 1967; Asay et al. 2001), which are critical for wildlife habitat (Trammell and Butler 1995; Fuhlendorf and Engle 2001, Pyke 2011), integral in maintaining species diversity (Asay et al. 2001), and critical for maintaining historical ecosystem processes (Jones and Johnson 1998; Anderson and Inouye 2001; Zavaleta et al. 2001; Monaco et al. 2012). Conversion of a non-native wheatgrass community to native vegetation is difficult (Hulet et al. 2010; Fansler and Mangold 2011); it is dependent on unpredictable climatic variables (Bakker et al. 2003; Hulet et al. 2010; Fansler and Mangold 2011), and requires the flexibility for adaptive management (Henderson and Naeth 2005; Davies et al. 2011). Ultimately, the decision of whether to use non-native or native species depends management goals, site history, and available resources (Jones and Johnson 1998).

When using seeds of native species for revegetation, it is recommended (Asay et al. 2003; Vogel et al. 2005; Jones and Monaco 2009) to source seeds from regions ("seed transfer zones") that broadly share the climatic and edaphic properties of the restoration site, in order to improve the likelihood of their establishment given abiotic site constraints (Jones and Monaco 2007). Level III or Level IV ecoregions can generally serve as a suitable region for seed transfer (Jones and Monaco 2007). Refinement of seed transfer zone boundaries can be achieved through a combination of experimental field tests (Johnson et al. 2010; Johnson et al. 2012; Johnson et al. 2013; Kramer et al. 2015) and statistical models, which can verify the association between trait diversity and climactically defined regions (Hamann et al. 2011; Bower et al. 2014).

Seed zones provide a good benchmark for sourcing seed material, but finer-scale collection regions are also recognized for their importance in maintaining genetic integrity of local populations (Kramer and Havens 2009) and ensuring plant adaptation to smale-scale climate regimes, soil conditions, and vegetation community composition (Linhart and Grant 1996; Joshi et al. 2001; Jones and Monaco 2007; Leimu and Fischer 2008; Johnson et al. 2010; Vander Mijnsbrugge et al. 2010). Federal agencies managing large tracts of public land in the western United States also recognize the importance of locally gathered seeds (Richards et al. 1998; Johnson et al. 2010).

When selecting plant material that is appropriate for particular restoration needs, it is also important to consider plant traits (Jones et al. 2010). Plant materials can be selected based on traits that confer higher probability of success in invaded areas that present novel abiotic and biotic stresses (Jones and Monaco 2009; Jones et al. 2010). Which traits are most beneficial will depend on what functions are most limiting to plant establishment in a particular environment (Jones and Monaco 2009). In the case of exotic species, rapid germination and fast growth rates can improve success of desirable plants (Gross 1984; Houssard and Escarre 1991; Jones and Monaco 2009). Rapid growth at an early stage can be especially important in nutrient-rich environments, where other fast-growing (ruderal) species are prevalent and create a highly competitive atmosphere (Grime and Hunt 1975; Poorter and Remkes 1990; van der Werf et al. 1993). Growth rate is tied to traits such as seed size (Winn 1988; Leishman and Westoby 1994, Mojonnier 1998) and measured via relative growth rate (RGR). Other traits have been shown to be highly correlated to RGR, such as leaf area ratio and specific leaf area (Poorter 1989; Poorter and Remkes 1990).

Adaptive selection for plant traits is driven by environmental conditions (Clausen et al. 1947; Loveless and Hamrick 1984; Linhart and Grant 1996; Kawecki and Ebert 2004). For instance, species that have evolved in infertile environments are often slow-growing and stress-tolerant, expressing low specific leaf area (Grime 1977). Conversely, early successional species have evolved to thrive in areas experiencing resource pulses; they typically have a high RGR, associated with high specific leaf area, leaf area ratio, and leaf mass ratio (Poorter and Remkes 1990; Lambers and Poorter 1992). Fast growing ruderal species have a competitive advantage at any site where nutrient levels are high, because of their accelerated rate of resource acquisition (Cook 1980).

Despite efforts to improve plant materials based on desirable plant traits, not all commercially-available germplasms do well in the field (Leger and Baughman 2015).

More research is needed to link plant growth traits to field performance, especially performance in invaded plant communities and other successful in altered ecosystems (Funk et al. 2008; Kardol and Wardle 2010; Cadotte et al. 2011; Drenovsky et al. 2012; Jones et al. 2015).

Elymus elymoides Overview and Use in Restoration

Bottlebrush squirreltail, *Elymus elymoides* (Raf.) Swezey, is a perennial grass native to the Intermountain West, and is a common component of native seed mixes used for restoration (Jones and Larson 2005). This species can be widely recognized by its namesake characteristic: long, spreading awns that resemble a squirrel's tail and which aid in seed dispersal as inflorescences disarticulate from the culm (Chambers 2000). It is a cool-season bunchgrass (i.e., C-3 photosynthetic pathway) with a range that extends from California to the Dakotas in the United States, and from British Columbia in Canada, south to central Mexico (Wilson 1963). Throughout its range, it is able to persist in multiple environments, from approximately sea level in Great Basin deserts to alpine meadows over 3,500 meters (Wilson 1963).

E. elymoides consists of four currently recognized subspecies (Barkworth et al. 1983), which are adapted to different regions within the species' broad distribution (Wilson 1963; Clary 1975). Subspecies *elymoides* is widespread, occurring in low to middle elevations in desert and steppe vegetation communities (Wilson 1963; Jones 1998). It is most closely related to ssp. *californicus* (Jones and Larson 2005), and the two subspecies can hybridize where their range overlaps. Subspecies *californicus* is typically found in mid- to high-elevation montane and alpine communities (Wilson 1963), concentrated on the eastern slope of the Sierra Nevada (Jones and Larson 2005).

A third subspecies, *hordeoides*, consists of short-statured plants that have a limited range in the northwestern United States and are restricted to dry, rocky, often shallow soils, typically in an *Artemisia rigida – Poa secunda* association (Wilson 1963). The final subspecies, *brevifolius*, shows the widest ecological range, occurring from 600 - 3,500 m elevation, located in regions between and including the Sonoran desert and subalpine mountain plant communities (Wilson 1963). This subspecies is also variable in size, containing the largest and most robust morphology within the species as a whole (Wilson 1963). The diversity of ssp. *brevifolius* is split among four genetically distinct races (Jones et al. 2003; Larson et al. 2003), one of which, “Race C” may be distinct enough to warrant its own recognition as a subspecies (Parsons et al. 2011).

Squirreltails (both *E elymoides* and its congener, *E. multisetus* – hereafter simply ‘squirreltail’) are short-lived plants (Jensen et al. 1990), which exist in both early seral and climax communities, although they are typically associated with the former (Harniss and West 1973; Jones 1998). Squirreltail increases following disturbances such as fire and the removal of more palatable grasses by grazing animals (Tueller and Blackburn 1974; Blank et al. 1994). Compared to other native species, squirreltail has higher emergence rates in the field (Wood et al. 1982; Chambers 2000) and exhibits faster growth (Hironaka and Sindelar 1973; Hironaka and Sindelar 1975), especially on soil where nitrogen levels are high (Redente et al. 1992; Young and Mangold 2008), as is often the case immediately following fire (Blank et al. 1994).

Despite its success in disturbed environments, squirreltail is not competitive with other native perennials (Barney and Frischknecht 1974; Marlette and Anderson 1986). It does not generally establish in native perennial plant communities or densely planted perennial range grasses (Tisdale et al. 1969; Marlette and Anderson 1986; Jones 1998), in part because plant available nitrogen is low in these late-seral, perennial plant communities (Jones 1998) Conversely, native species such as sagebrush can be established from seed in early-seral, squirreltail-dominated communities specifically because squirreltail does not deplete soil resources (Booth et al. 2003).

Although it typically falls out of dominance as other native perennial species re-establish on a site, squirreltail is valued for restoration (Jones 2003; Jones and Larson 2005). One reason is its ability to compete with annual exotic range grasses (Hironaka and Tisdale 1963; Booth et al. 2003; Rowe and Leger 2011). It is useful for "assisted succession" efforts, which transition invaded sites first to a rapidly growing perennial species, and then to slower-growing native species, which can be inter-planted among the transition species (Jones 1998; Cox and Anderson 2004). Squirreltail is an autogamous (self-pollinating) species (Jensen et al. 1990), facilitating its colonization of new sites by enabling seed set even if its initial density is low (Jones 1998; Young et al. 2003). The seeds of squirreltail do not express dormancy (Young and Evans 1977) and can germinate rapidly across a range of temperatures, with active root elongation even at low temperatures (Hironaka and Tisdale 1973; Jones 1998). Squirreltail is tolerant of drought (Humphrey and Schupp 1999), especially those populations from low-elevations (Clary 1979; Zhang et al. 2011). Finally, squirreltail can survive moderate fires (Wright and Klemmedson 1965; Wright 1971), and burning can even promotes its growth due to elevated soil nitrogen levels. Dramatic increases in squirreltail biomass (Blank et al. 1994) and population size (Young and Miller 1985) has been observed following fire, increasing its ability to compete with cheatgrass (Jones 1998).

There is much interest in the capacity of squirreltail to reduce the overall impacts of invasions (Hironaka and Tisdale 1963; Arrendondo et al. 1998; Booth et al. 2003; Humphrey and Schupp 2004; Young and Mangold 2008; McGlone et al. 2012). Although the growth of adult squirreltail plants can be suppressed by cheatgrass (Melgoza et al. 1990; Humphrey and Schupp 2004), they are able to resist displacement (McGlone et al. 2012). Seedlings however, do not compete as well with the invasive grass (Humphrey and Schupp 2004; Mazzola et al. 2011; McGlone et al. 2011). The fall germination (Aguirre and Johnson 1991; Arrendondo et al. 1998) and rapid spring growth of cheatgrass decrease nitrogen and water availability to a point that reduces survival of seedlings (Humphrey and Schupp 2004; MacKown et al. 2009; Leffler et al. 2011), limiting expansion of squirreltail populations (James et al. 2011).

It is not fully understood what mechanisms enable the survival or occasional encroachment of squirreltail plants into hospitable invaded areas (Arrendondo et al. 1998). Although it is not as aggressive as cheatgrass (Arrendondo et al. 1998), squirreltail does exhibit traits of colonizing species that other perennial grasses do not, enabling it to take advantage of resource pulses. These traits include rapid phenological development (Hironaka and Sindelar 1973; Hironaka and Sindelar 1975), efficient use of soil moisture (Booth et al. 2003), high specific leaf area (Arrendondo et al. 1998), ability to maintain root growth when temperatures are cool (Harris 1967; Harris and Wilson 1970), high specific root length, and the ability to store resources in roots (Hironaka and Sindelar 1975; Arrendondo et al. 1998). Furthermore, squirreltail exhibits a high degree of morphological (Jones 2003) and genetic (Larson et al. 2003; Parsons et al. 2011) diversity, and is more prone to ecotypic differentiation because it is autogamous (Karron

1991). This diversity allows squirreltail to become highly adapted to specific geographic areas (Clary 1975) and potentially to biotic interactions as well. Several studies have noted that a congener of *E. elymoides*, big squirreltail (*E. multisetus*), becomes locally adapted to cheatgrass invasion (Leger 2008; Rowe and Leger 2011) whereby plants from invaded areas are better able to survive with and reduce the biomass of cheatgrass. Similar studies are lacking for *E. elymoides*.

Adaptation of Native Plants to Invasive Species

Evolution and adaptation shape speciation, species interactions, and population dynamics (Carroll et al. 2007). Local adaptation to an array of environmental conditions is widespread among plants, and experiments have shown that populations generally perform better on their own site than on foreign sites (Turreson 1922; Clausen et al. 1947, Joshi et al. 2001; Leimu and Fischer 2008). Local adaptation to invasive species is also possible (Strauss et al. 2006; Carrol et al. 2007; Leger and Espeland 2010), and interest in this topic has risen in recent years (Caroll et al. 2007). This adaptation may be expressed either by increased tolerance of an invasive species, or may be expressed as an ability to suppress the growth of the invader (Leger and Espeland 2010).

However, it can be hard to predict how adaptation will occur or over what time scale, due to fluctuation in the selection pressure of competitive stress through time and frequent shifts in the direction of selection pressure on a given trait (Siepielski et al. 2009). Native plants that exists in invaded areas are not necessarily adapted to the invader, and could represent three potential scenarios: a) remnants of a population that declining towards extinction, b) individuals that establish and persist without adaptation in occasional but recurrent niche openings, or c) adaptive populations which are undergoing a change in gene frequency due to selective forces imposed by the invader (Leger and Espeland 2010). Some have proposed experimental designs for testing the presence of adaptation to invasive species (Strauss et al. 2006; Leger and Espeland 2010). Straus et al. (2006) suggest three integrated experimental strategies: 1) demonstrate that there is a genetically-based heritable shift in traits between populations from native vs. invaded areas, 2) perform tests in a common environment that is removed from the site where the invader occurs to demonstrate that the native species is adapting to the invasive species rather than site conditions preferred by the invasive species and 3) comparison of genetic phylogenies (Losos and Glor 2003). Regardless of the method, it can still be difficult to tease apart the specific cause of the genetic shift: the invasive species, other correlated environmental factors, or genetic drift (Strauss et al. 2006).

Although it is difficult to prove the cause of adaptation, there are a growing number of examples in which some populations of native plants are more tolerant of a particular invasive species; these studies have been conducted with both forbs (Lau 2006; Cipollini and Hurley 2008; Lankau 2012) and grasses (Nasri and Doescher 1995, Callaway et al. 2005; Leger 2008; Ferrero-Serrano et al. 2011; Goergen et al. 2001; Rowe and Leger 2011; Sebade et al. 2012). How plants develop adaptation to invasive species is manifested in a variety of ways. Many times, heritable growth traits allow the native species to better compete for vital resources such as light, water, and nutrients (Nasri and Doescher 1995; Mealor and Hild 2007; Goergen et al. 2001; Rowe and Leger 2011; Sebade et al. 2012). In other cases, adaptation is more indirect. For instance, populations of native forb species (*Pilea pumila,* and *Impatiens capensis*) from invaded areas have higher fitness when grown with strong competition from an invader, garlic mustard

(*Alliaria petiolata*), than populations from uninvaded sites (Cippollini and Hurley 2008; Lankau 2012; Lankau 2013). The adapted populations have higher tolerance of soil microbial communities which are altered from allelopathic chemicals of *Alliaria* (Lankau 2012; Lankau 2013). Direct resistance to an allelopathic chemical has been observed as well; populations of Montana native grasses from areas invaded by *Centaurea maculata* developed resistance to the allelopathens released by the exotic species (Callaway et al. 2005). Another native species, Alkali sacaton (*Sporobolus airoides*), has adapted to more than one invasive species: both Russian knapweed (*Rhaponticum repens*) and Canada thistle (*Cirsium arvense*) (Sebade et al. 2012). Three-species systems have also been studied. Reciprocal transplant experiments involving a native plant (*Lotus wrangelianus*), an exotic invasive plant (*Medicago polymorpha*), and an exotic herbivorous weevil (*Hypera brunnipennis*) revealed that the native plant could adapt to either the invasive plant or the invasive herbivore (Lau 2006; Lau 2008).

The specific growth traits that experience change over the course of natural selection will differ in each scenario, and will depend on the limiting resource in the competitive environment. Alkali sacaton that has adapted to Russian knapweed and Canada thistle expressed increased germination, faster growth rate, greater tiller production, and greater leaf growth. These shifts represented adaptations to intense shading from the competitors (Mealor and Hild 2006; Mealor and Hild 2007; Ferrero-Serrano et al. 2011; Bergum et al. 2012; Sebade et al. 2012). For big squirreltail (*Elymus multisetus*) however, decreased plant size appears to confer a competitive advantage, whereby smaller plants lose less biomass (relative to their potential size when grown alone) in response to competition than do larger plants (Leger 2008; Goergen et al. 2001;

Nasri and Doescher 1995; Rowe and Leger 2011). Big squirreltail populations from cheatgrass-invaded sites also show increased partitioning of plant resources to fine roots (Leger 2008; Goergen et al. 2001; Rowe and Leger 2011), potentially a mechanism of persisting with a fast-growing invader.

METHODS

We conducted a greenhouse competition experiment to assess response of *E. elymoides* seedlings to competition from *B. tectorum*. The experiment was performed using three levels of within-species variation of *E. elymoides*: subspecies, lineage (wild types vs domestic accessions), and population (unique accessions within subspecies-lineage groups) (Table 1). Eighteen populations of *E. elymoides* were used in the study, including fourteen from naturally occurring communities ("wild" lineages) and four accessions developed for commercial release ("domestic" lineages). Two subspecies, *brevifolius* and *elymoides*, were represented within wild lineages, and two subspecies, *elymoides* and *californicus*, were represented within domestic lineages.

Seed Collection

All wild populations were collected from the Central Basin and Range Ecoregion of Utah (Fig. 1). Seeds from seven populations of subspecies *elymoides* were collected in northwestern Utah, and seeds from seven populations of subspecies *brevifolius* were collected in central Utah. Collection sites were separated by at least 1 km and targeted to represent a range of *B. tectorum* abundance. Within a site, *B. tectorum* field cover was relatively homogeneous, but average cover across sites ranged from 0% cover to 62% (Table 1). One inflorescence from each of two hundred plants was gathered per population; seeds were pooled by population, cleaned from chaff, and then stored at 2 °C for 7 months before being used for planting. Vegetation composition and soil properties were described for each collection site; see Appendix 1 for details of seed collection and site characterization methods.

The domestic *E. elymoides* populations were supplied by the USDA-ARS Forest and Range Research Lab in Logan, UT. Rattlesnake (Jones 2010b) and Fish Creek (Jones et al. 2004a) germplasm (originally collected from Elmore Co. and Blaine Co., ID, respectively) represented ssp. *elymoides*, and Toe Jam Creek (Jones et al. 2004b) and T-1735, an unreleased accession (Jones 2013a), represented ssp. *californicus* (from Elko Co., NV and Gooding Co., ID, respectively). The domestic accessions are "natural-track," meaning that no intentional selection or breeding were performed on the plant materials (Jones 2009).

Greenhouse experiment

The competitive effect of *B. tectorum* on *E. elymoides* was assessed using a greenhouse experiment that was structured as a randomized complete block design. One plant from each of the eighteen *E. elymoides* populations was crossed with a competition treatment (presence vs. absence of six *B. tectorum* plants). These 36 combinations of *E. elymoides* and *B. tectorum* were seeded into pots, and combinations were replicated across twenty blocks (720 total pots). The experiment was performed at the USU Research Greenhouse in Logan, UT, USA from April to June 2014. Daily temperature averaged 20.7-29.8 °C. Ambient light was available throughout the growing period, reaching a maximum of 15.2 hours in June.

One *E. elymoides* plant was established from seed in the center of each pot, and in pots receiving the competition treatment, six *B. tectorum* plants were established around the *E. elymoides* plant to achieve 600 plants/m^2, which is within the range of plant densities in heavily invaded sites (Hulbert 1955; Klemmedson and Smith 1964; Humphrey and Schupp 2004) and a density which was shown to have measureable

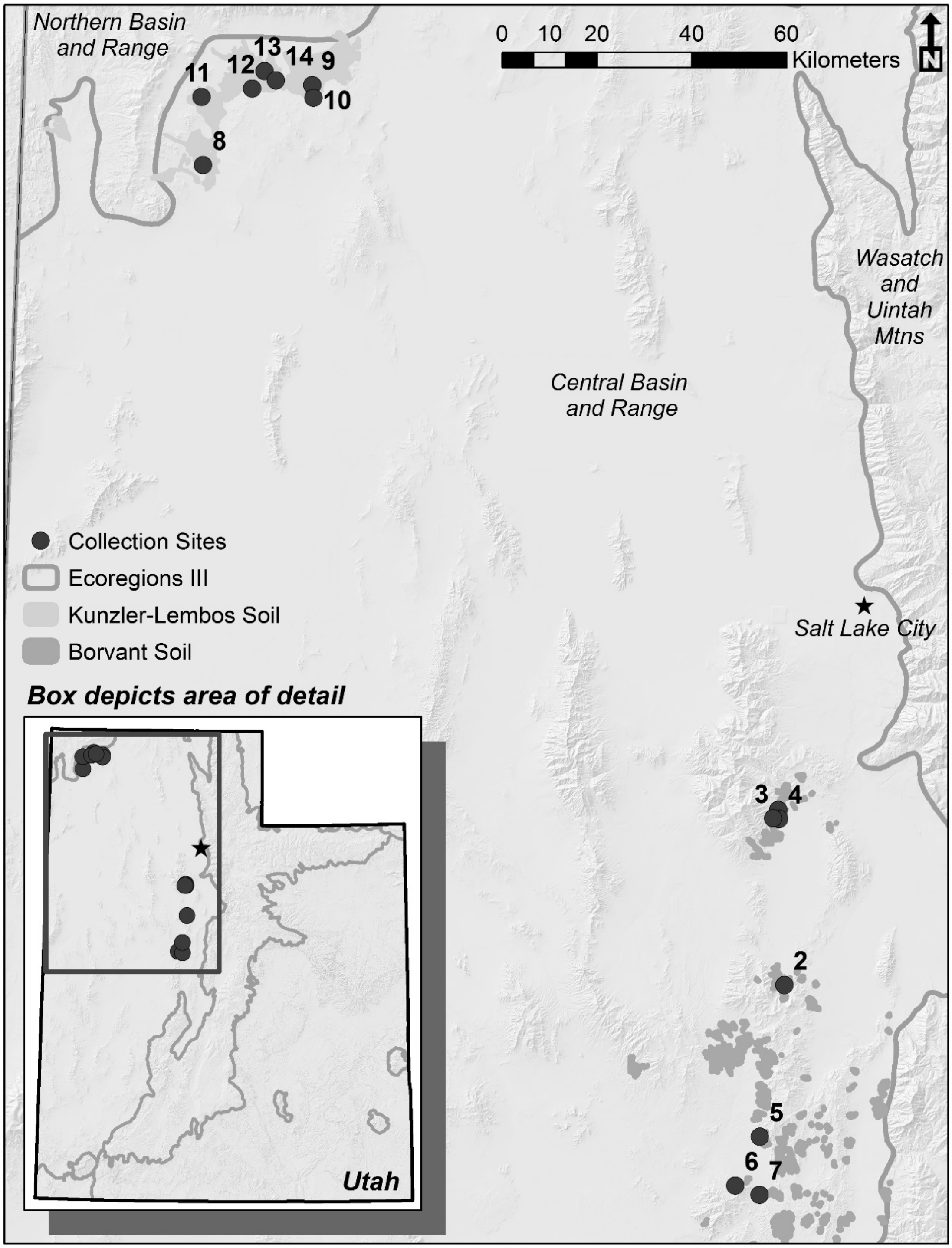

Figure 1. Seed collection locations for wild-lineage *E. elymoides* populations. Locations 1-7 occurred on Borvant series soil and were associated with *E. elymoides* ssp. *brevifolius*; 8-15 occurred on the Kunzler-Lembos soil association and were associated with *E. elymoides* ssp. *elymoides*.

Table 1. Collection site details for *E. elymoides* populations, grouped by lineage and subspecies. Soil map unit and *B. tectorum* relative field abundance were only available for wild lineage populations. Collection site county and state, annual precipitation, and elevation for domestic lineages were gathered from published germplasm release notices.

Pop. Num.	*Collection Site County, State*	*Annual Precip. (cm)*	*Elev. (m)*	*Soil Map Unit*	*Cover B. tectorum*
Wild subspecies *brevifolius*					
1	Utah Co, UT	43	1693	Borvant gravelly loam	20%
2	Utah Co, UT	38	1653		80%
3	Utah Co, UT	44	1709		1%
4	Utah Co, UT	38	1617		3%
5	Juab Co, UT	38	1755		11%
6	Juab Co, UT	37	1760		504%
7	Juab Co, UT	33	1611		6%
Wild subspecies *elymoides*					
8	Box Elder Co, UT	23	1471	Kunzler-Lembos association (loam)	1%
9	Box Elder Co, UT	27	1485		80%
10	Box Elder Co, UT	27	1469		39%
11	Box Elder Co, UT	24	1612		40%
12	Box Elder Co, UT	24	1539		0%
13	Box Elder Co, UT	27	1538		55%
14	Box Elder Co, UT	27	1514		4%
Domestic subspecies *elymoides*					
15	Blaine Co, ID	30	1448	*Fish Creek Germplasm*	
16	Elmore Co, ID	30	1169	*Rattlesnake Germplasm*	
Domestic subspecies *californicus*					
17	Gooding Co, ID	25	1190	*T-1735 Germplasm*	
18	Elko Co, NV	31	1829	*Toe Jam Creek Germplasm*	

effects on *E. elymoides* seedling growth in a pilot study (Mann and Veblen 2014). Seeds of both species were sown on the same day, 0.5 cm deep in soil, and planted at high initial rates: four *E. elymoides* per pot and ten *B. tectorum* per pot. *B. tectorum* was thinned to six plants one week after sowing, and *E. elymoides*, which took longer to emerge, was thinned to a single plant two weeks from the sowing date. Planting containers were 10 x 10 x 12 cm square pots filled with 800 ml of steam-sterilized Preston fine sand (Soil Survey Staff 1998) and treated once with 125 ml of a fertilizer solution (3.75 g of Peters' Excel Base B formulation per liter of water), on the day prior to planting. Pots were placed in solid trays and watered from the bottom with tap water every 2-3 days, which allowed soil to become dry before being wetted again to field capacity.

Data on seed weight, emergence, and growth characteristics were collected for all plants in the study. Prior to planting, we obtained average seed weights by weighing ten sets of 20 seeds per population. Total percent *E. elymoides* emergence (out of the four seeds sown) was recorded for all pots, and days to emergence, i.e., when the cotyledon breached the soil surface, was recorded for each emerged *E. elymoides* seedling. An emergence range was also calculated as days to emergence of last seedling minus days to emergence of first seedling plus one day. Measurements of plant height, number of tillers, and number of leaves (live and dead) were recorded for each *E. elymoides* plant weekly, including one day prior to harvest.

After eight weeks of growth, harvest of *E. elymoides* and *B. tectorum* plants occurred in random order across five consecutive days. Aboveground plant material was cut just below soil level and separated into leaf blades, culms, and crowns; roots were thoroughly washed from soil. All plant material was bagged and stored at 2°C until further processing. Roots and all in-tact, live leaf blades that could be laid flat by hand were scanned at 400 dpi on an LA 2400 flatbed scanner (Epson America Inc., Long Beach CA, USA), then analyzed using scanning software (WinRhizo Pro version 2005b, Régent Instruments Inc., Quebec, CAN; Arsenault et al. 1995) to determine final total root length (TRL), specific root length (SRL, m length/g tissue), fine to coarse root length ratio (F2C, fractions distinguished using a 0.5 mm diameter cutoff), average root diameter (Diam), and specific leaf area (SLA, cm^2 leaf area/g tissue). Plant tissue samples were then dried at 50 °C for 48 h, and weighed. Biomass values were used to calculate additional common growth indices: root to shoot mass ratio (RSR), above-ground mass to plant mass ratio (AMR), leaf mass to plant mass ratio (LMR), leaf area to plant mass ratio (LAR: SLA*LMR). Leaf mass ratio was approximated from the mass of all scanned leaves, rather than total leaves per plant; dead leaves and tightly rolled, young leaves were generally excluded from scanning and LMR calculation. Although stem weight was not recorded per plant, we did generate two indices to represent stem growth relative to plant size, which were plant height to plant mass ratio (HMR), and the ratio of tiller number to total plant mass (TMR).

We also assessed soil mineral N concentration after the 8-week grow-out period. Soil samples were taken from ten randomly selected pots from each of the 36 *E. elymoides* x *B. tectorum* treatment combinations (i.e. half of the total samples were included for soil nitrogen measurements). Each set of ten soil samples was homogenized before approximately 50 g was subsampled, weighed, stabilized in approximately 75g of 1-M KCl solution, and stored at 2 °C until processing (< 5 days). Soil-KCl solutions were agitated on a shaker table for 5 hours prior to gravity filtration, which removed solids > 11μm. Filtrates were used to determine concentration of soil nitrate and ammonium (Sparks et al. 1996) using a flow injection auto-analyzer (QuikChem 8500 Series 2 FIA System, Lachet Instruments, Hach Company, Loveland, CO, USA).

Data analyses

Intraspecific variation in response to competition

The effects of intraspecific *E. elymoides* variation and *B. tectorum* competition on final *E. elymoides* seedling biomass were assessed using analysis of variance (ANOVA). Fixed predictor variables included *B. tectorum* competition (presence vs. absence), group (1-4; see below), *E. elymoides* population (1-18) nested in group, *B. tectorum**group and *B. tectorum**population. Random factors in the model included block and block*group. The "group" factor represented the four unique subspecies-lineage combinations: 1) wild ssp. *elymoides*, 2) wild ssp. *brevifolius*, 3) domestic ssp. *elymoides*, and 4) domestic ssp. *californicus*. *E. elymoides* population was a fixed factor in the model because wild populations were targeted to represent a range of *B. tectorum* field abundance, rather than being randomly selected. The response variable, total plant dry biomass, was log transformed to meet model assumptions. To assess differences among biomass of lineages and subspecies within the competition treatments, we contrasted least squares means (lsmeans) of groups using a simulation to adjust for multiplicity.

We then assessed intraspecific variation in response to competition using a Relative Interaction Index, RII (Armas et al. 2004), as the ANOVA response variable. RII accounts for inherent intraspecific differences in plant size, and represents response to competition in proportion to potential size that can be achieved when seedlings are grown in the non-competitive environment (Armas et al. 2004). Dry plant biomass was used to calculate an RII value for each of the eighteen *E. elymoides* populations in each block according to:

Eq. 1

$$\text{RII} = \frac{(\text{Mass WITH } \textit{B. tectorum} \text{ competition} - \text{Mass WITHOUT } \textit{B. tectorum} \text{ competition})}{(\text{Mass WITH } \textit{B. tectorum} \text{ competition} + \text{Mass WITHOUT } \textit{B. tectorum} \text{ competition})}$$

RII values are bound between -1 and +1, where -1 indicates strong competition (biomass of a plant is less when grown with a neighbor) and +1 indicates strong facilitation, (biomass of a plant is greater when grown with a neighbor). An RII value of 0 indicates no effect of neighbor plant on the target plant.

Fixed predictors in the RII analysis were group and population nested in group; random factors were block and block*group interaction. To meet ANOVA model assumptions, RII was transformed by first adding 1 to RII values (thus creating a set of all positive values), then log-transforming the resulting sum. To assess differences among lineages (wild vs. domestic *elymoides*) and subspecies within lineages (wild *brevifolius* vs. wild *elymoides* and domestic *californicus* vs. domestic *elymoides*), we contrasted lsmeans of these groups, using a simulation option to adjust for multiplicity. Multiple lsmeans comparisons among all groups was also performed using the Tukey-Kramer method, and lsmeans of populations within groups were compared using a simulation method of adjustment. ANOVA tests of biomass and RII were performed using PROC GLIMMIX in SAS software Version 9.4 TS Level 1M2 (SAS Institute Inc., Cary, NC, USA). The LSMESTIMATE statement was used to contrast specific groups, and LSMEANS was used to perform multiple comparisons among groups and populations.

Bromus tectorum field abundance and the competitive response of *Elymus elymoides*

For wild lineage populations of *E. elymoides*, we hypothesized that cover of *B. tectorum* at *E. elymoides* collection sites would have a significant positive effect on response to competition (i.e. result in higher RII scores) and furthermore, that *B. tectorum* field abundance would have more influence on competitive response than other environmental attributes of the collection locations, which included precipitation, elevation, slope, heat load, soil texture attributes, cover of functional groups, and ground cover (Appendix 1).

We used an exploratory approach to test this hypothesis; each environmental variable was regressed on mean *E. elymoides* mass (with and without *B. tectorum*) and RII (transformed as in the preceding analysis) at the site level using a mixed model in which the predictors were subspecies (*elymoides* or *brevifolius*), the environmental factor, and the interaction between subspecies and the environmental factor. AIC scores were compared to determine the models with the best fit. Pearson's correlation tests (PROC CORR in SAS) were performed to assess the direction of the relationships between environmental factors and *E. elymoides* mass and RII. PROC GLIMMIX in SAS was used to create the model, using a Gaussian quadrature to approximate likelihood.

Relationship among trait values, biomass, and RII

To explore how *E. elymoides* expression of *E. elymoides* traits differed across intraspecific groups and was influenced by *B. tectorum* competition, we first performed multiple, separate ANOVA analyses treating each of the measured or calculated growth traits as the response variable. The trait-based ANOVA models used the same analytical structure and post-hoc tests as was used for the analyses of total biomass (described above). One trait, "percent emergence," was assessed using a binary distribution due to its interval response values, a result of the small number of seeds (4) sown per pot. Trait values were log-transformed when necessary to meet model assumptions, and one extreme outlier was removed to obtain homoscedasticity for analyses of AMR.

We then ran a variable selection model using random forests regression analysis ("RF", Brieman 2001) to determine the relative importance (metric described below) of specific plant traits in their ability to predict RII. Random forests analysis can be used with numerous variable formats (e.g., continuous, interval, discrete), is unaffected by correlated or nonlinear predictors, and does not require that data meet distributional assumptions (Jones and Linder 2015, Prasad et al. 2006, Cutler et al. 2007). By integrating multiple iterations of classification trees, RF analysis ultimately derives an importance value (z-score/SE) for each plant trait variable in the model, where z-score reflects the increase in prediction accuracy of RII when the variable is added to the model. We used the Boruta package (Kursa et al. 2010) available for R (Version 3.2.3, R Core Team 2015) for our analysis, which also allowed us to determine the significance of plant trait variables, in addition to their relative importance. Boruta performs multiple RFs, using the resulting distribution of z-scores to perform a two- sided t-test and determine if the input predictor variables perform significantly better than randomly generated variables (Appendix 2).

Data from all subspecies x lineage groups were initially combined for the Boruta trait analysis; subsequent models assessed trait importance within each group individually. To maintain consistency with prior ANOVA tests, we used the log-transformed RII as the response variable. All plant trait variables were included as predictors in the analysis except for measurements of plant size (height, total leaf number, total root length) and measurements of soil nitrogen. Plant size metrics were excluded from Boruta trait analysis because they were reflections of and highly correlated with ($p < 0.0001$) final plant biomass (Appendix 3), and thus confounded with RII scores. Soil nitrogen measurements (final ammonium and nitrate concentrations) were tested in a separate Boruta trait analysis model because those data were associated with only a subset (half) of the pairs in the study. For all analyses, the dataset included only *E. elymoides* pairs in which both the plant grown alone and the plant grown with *B. tectorum* were alive at the end of the study, and which also had no missing trait data. Two sets of trait values were associated with each RII value (traits of the *E. elymoides* plant grown alone and traits of the plant grown with *B. tectorum*); both sets were used in the Boruta trait analysis models..

Boruta was set to run for 200 iterations; when importance scores did not converge for a variable, we identified it as an non-significant predictor. The direction of the relationships (positive or negative) between significant trait variables and RII were determined using Pearson’s correlation coefficients. Percent of RII variance explained by the variables selected from Boruta analysis was calculated as an average using 10 RF models, using the randomForest package in R (Liaw and Wiener 2002).

RESULTS

Response of *Elymus elymoides* Biomass to *Bromus tectorum* Competition

At the end of the growing period, 334 pairs of *E. elymoides* plants (i.e., plants with vs. without *B. tectorum*) survived and were included in analyses. We found that *B. tectorum* competition had a strong main effect on growth of *E. elymoides* seedlings ($F=1512.6_{1,556}$, $p<0.0001$), reducing mass by an average of 82 % (without *B. tectorum* = 0.537 ± 0.016 g; with *B. tectorum* = 0.096 ± 0.004 g; Fig. 2). *Bromus tectorum* presence also significantly reduced percent emergence ($p=0.0009$) and all other measures of growth: leaf number, total root length, and height (Table 2, 3). The competitive impact of *B. tectorum* is also indicated by average RII values, which were negative for all groups (Table 3, Fig. 3) and populations (Appendix 4).

Among seedlings grown alone, wild lineage *brevifolius* seedlings had the greatest total biomass, followed by *elymoides* (domestic > wild lineages), then domestic lineage *californicus* (Table 3a); these size differences were significant among subspecies (lsmeans contrasts of *brevifolius*-wild vs. *elymoides*-wild: $t_{556} = 9.52$, $p<0.0001$; *californicus*-domestic vs. *elymoides* domestic: $t_{556} = 3.77$, $p = 0.0009$), and marginally significant between wild vs. domestic lineages of ssp. *elymoides* ($t_{556} = 2.55$, $p = 0.0593$). When seedlings were grown with *B. tectorum*, ssp. *californicus* became intermediate in size between *brevifolius* and *elymoides*, although the difference was only statistically significant between the wild-lineage subspecies (Table 3a).

Analysis of RII indicated that there was significant variation among groups in their response to *B. tectorum* competition (Table 2). Contrasts of least squares means indicated that this group-level variation was driven by differences between subspecies within the domestic lineage (RII of domestic *californicus* > domestic *elymoides*, $t_{57} = -3.25$, p = 0.005), rather than differences among wild subspecies ($t_{57} = -1.7$, p = 0.2305) or lineages within ssp. *elymoides* ($t_{57} = 0.56$, p = 0.8758). Tukey-Kramer groupings indicated that domestic ssp. *californicus* had significantly higher tolerance of competition than all other groups (Table 3a). Subspecies with larger biomass when grown alone consistently had lower (albeit not statistically) RII values, i.e., they were proportionately reduced more by *B. tectorum* than smaller subspecies. For example, within the wild lineage, *brevifolius* had greater mass than *elymoides* (Fig. 2), whether grown alone or with *B. tectorum*, and it experienced a greater relative reduction in mass, resulting in its lower RII value. Similarly, within the domestic lineage, *elymoides* had greater biomass than *californicus* when grown alone, and a lower RII value. The same pattern held for the comparison of wild vs. domestic lineages within *elymoides*.

Population-level variation in *E. elymoides* was limited. Population was a significant predictor of total plant biomass (Table 2), but not of RII, as indicated by an insignificant main effect ($F_{14,240}$=0.84, p=0.63) and no significant lsmeans differences. Contributing to this insignificant differentiation was the high variability in RII response values among replicates within populations (Appendix 4).

Bromus tectorum Field Abundance and Competitive Response of *Elymus elymoides*

Mass of *E. elymoides* plants grown alone (in a non-competitive environment), was best represented by the mixed model in which the predictor was cover of *B. tectorum* at field collection sites (Appendix 5), and there was a significant (p = 0.01) interaction between field cover of *B. tectorum* and *E. elymoides* subspecies, indicating that the growth of the two subspecies was differently affected by *B. tectorum* abundance.

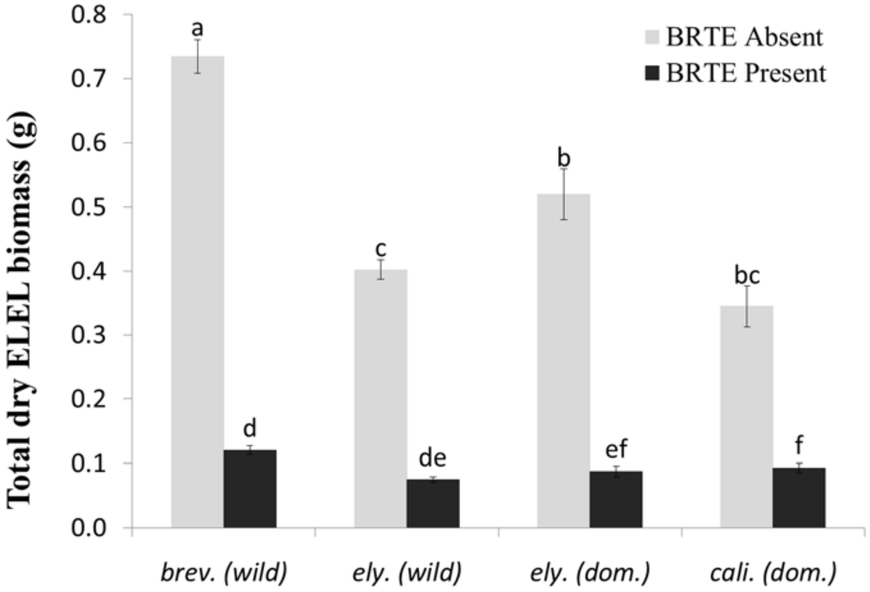

Figure 2. Average total dry biomass of *E. elymoides* subspecies x lineage groups**.** Mean ± 1 SE dry weight for the lineage x subspecies groups, grown with and without competition from *B. tectorum*. A shared letter above bars indicates that the groups are not significantly different at p=0.05 (Tukey-Kramer groupings).

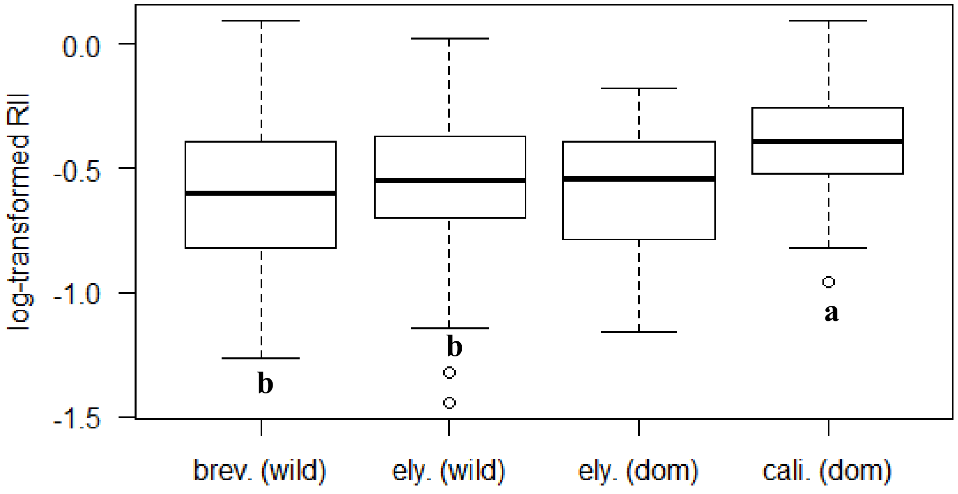

Figure 3. Boxplots summarizing RII for *E. elymoides* subspecies x lineage groups. The index, RII, was log-transformed. A shared letter below the plots indicates that the groups are not significantly different at p=0.05 (Tukey-Kramer groupings).

Table 2. Results of ANOVA on biomass and trait expression of *E. elymoides*. Predictor variables were *B. tectorum* (presence or absence), subspecies x lineage group, population, and interactions of *B. tectorum* with group and population. A "*" indicates data were log-transformed for analysis. Plant biomass indices are: RSR (root to shoot ratio), AMR (above-ground mass to total plant mass ratio), HMR (height to total plant mass ratio), LMR (leaf mass to total plant mass ratio), LAR (leaf area to total plant mass ratio), SLA (specific leaf area), SRL (specific root length), F2C (ratio of fine to coarse root length), and Diam (mean root diameter).

	B. tecorum			*group*			*population*			*B. tectorum x group*			*B. tectorum x population*		
	df	*F-val*	*pr >F*	*df*	*F-val*	*pr >F*	*df*	*F-val*	*pr >F*	*df*	*F-val*	*pr >F*	*df*	*F-val*	*pr >F*
Competitive Tolerance															
log(RII)				3,57	7.35	0.00	14, 240	0.8	0.63						
Plant Size Traits															
Total biomass*	1,556	1513.7	<.0001	3,57	48.92	<.0001	14,556	1.8	0.04	3,556	7.83	<.0001	14,556	0.9	0.55
Height	1,556	242.2	<.0001	3,57	49.89	<.0001	14,556	1.7	0.05	3,556	2.28	0.08	14,556	0.7	0.75
Total leaves*	1,556	1101.1	<.0001	3,57	37.23	<.0001	14,556	2.3	0.00	3,556	12.31	<.0001	14,556	0.8	0.63
Tot. root length*	1,556	2161.8	<.0001	3,57	73.89	<.0001	14,556	1.4	0.14	3,556	14.78	<.0001	14,556	1.0	0.42
Seed & Emergence Traits															
Seed Weight*				3,153	545.88	<.0001	14,153	32.5	<.0001						
Emerg. Days*	1,556	0.0	0.85	3,57	13.12	<.0001	14,556	2.9	0.00	3,556	0.47	0.71	14,556	1.4	0.17
Emerg. Range*	1,499	1.0	0.31	3,57	1.20	0.32	14,499	1.3	0.18	3,499	0.47	0.71	14,499	0.8	0.72
Emerg. Pct	1,556	11.4	0.00	3,57	6.96	0.00	14,555	3.0	0.00	3,555	0.53	0.66	14,555	1.3	0.19
Plant Biomass Indices															
RSR*	1,556	54.5	<.0001	3,57	33.80	<.0001	14,556	2.5	0.00	3,556	3.08	0.03	14,556	1.2	0.31
AMR	1,555	50.0	<.0001	3,57	37.83	<.0001	14,555	2.3	0.00	3,555	4.09	0.01	14,555	1.2	0.30
HMR*	1,556	1491.2	<.0001	3,57	35.50	<.0001	14,556	2.7	0.00	3,556	7.92	<.0001	14,556	0.8	0.65
TMR*	1,556	615.1	<.0001	3,57	41.58	<.0001	14,556	2.9	0.00	3,556	7.77	<.0001	14,556	1.5	0.10
LMR	1,556	112.7	<.0001	3,57	15.10	<.0001	14,556	2.7	0.00	3,556	4.88	0.00	14,556	1.0	0.46
LAR*	1,555	53.5	<.0001	3,57	4.29	0.01	14,555	2.2	0.01	3,555	3.90	0.01	14,555	1.2	0.25
SLA*	1,555	38.1	<.0001	3,57	11.24	<.0001	14,555	0.9	0.57	3,555	1.83	0.14	14,555	1.2	0.30
SRL*	1,556	146.1	<.0001	3,57	60.71	<.0001	14,556	3.6	<.0001	3,556	8.22	<.0001	14,556	1.1	0.36
F2C*	1,556	142.1	<.0001	3,57	32.69	<.0001	14,555	2.0	0.01	3,555	3.53	0.01	14,555	0.8	0.71
Diam*	1,555	22.9	<.0001	3,57	45.53	<.0001	14,554	2.5	0.00	3,554	7.35	<.0001	14,554	0.9	0.59
Soil Nitrogen															
Ammonium*	1,245	7.7	0.01	3,47	2.61	0.06	14,245	1.0	0.50	3,245	1.30	0.27	14,245	1.1	0.39
Nitrate*	1,247	21.4	<.0001	3,47	2.71	0.06	14,247	2.2	0.01	3,247	4.07	0.01	14,247	2.5	0.00

Table 3a. Mean RII and trait values (plant size, emergence, soil nitrogen) for the *E. elymoides* subspecies x lineage groups. Shared letters within a trait indicate no significant differences. 'N' or 'Y' in the BRTE column indicates whether plants were grown alone (N) or with (Y) *B. tectorum* competition. A "*" indicated the variable was log-transformed for analysis.

Trait (unit)	*BRTE*	*ssp. brev (wild)*	*ssp. ely (wild)*	*ssp. ely (domestic)*	*ssp. cali (domestic)*
Competitive Tolerance					
RII*	--	-0.693 ^{b}	-0.667 ^{b}	-0.686 ^{b}	-0.519 ^{a}
Plant Size Traits					
Total biomass*	N	0.74 ^{a}	0.40 ^{bc}	0.52 ^{b}	0.35 ^{c}
(grams)	Y	0.12 ^{d}	0.08 ^{f}	0.09 ^{ef}	0.09 ^{de}
Height	N	21.0 ^{a}	17.5 ^{bc}	19.0 ^{b}	19.1 ^{b}
(cm)	Y	16.3 ^{cd}	13.7 ^{e}	15.0 ^{de}	16.2 ^{cd}
Total leaves*	N	38.4 ^{a}	28.7 ^{b}	31.0 ^{b}	19.3 ^{c}
(number)	Y	11.5 ^{d}	9.5 ^{e}	10.8 ^{de}	9.5 ^{de}
Tot root length	N	29.6 ^{a}	13.6 ^{c}	19.8 ^{b}	10.9 ^{c}
(m)	Y	3.6 ^{d}	2.4 ^{e}	2.7 ^{e}	2.5 ^{e}
Seed & Emergence Traits					
Emerg. Days*	N	11.3 ^{a}	10.1 ^{abc}	8.8 ^{c}	10.2 ^{abc}
(days)	Y	11.1 ^{ab}	10.2 ^{abc}	9.3 ^{c}	9.7 ^{bc}
Emerg. Range*	N	6.80 ^{a}	5.90 ^{a}	5.62 ^{a}	5.56 ^{a}
(days)	Y	5.69 ^{a}	5.64 ^{a}	5.43 ^{a}	5.65 ^{a}
Emerg. Percent	N	78.5 ^{a}	83.2 ^{a}	86.5 ^{a}	81.1 ^{a}
(pct.)	Y	68.6 ^{b}	78.4 ^{a}	83.8 ^{a}	77.8 ^{ab}
Seeds *(g/100)* *	--	0.20 ^{c}	0.15 ^{d}	0.23 ^{b}	0.31 ^{a}
Soil Nitrogen Post Grow-out					
Ammonium	N	0.86 ^{a}	1.44 ^{a}	0.74 ^{ab}	0.73 ^{ab}
(ug/g)	Y	0.30 ^{b}	0.78 ^{ab}	1.03 ^{ab}	0.54 ^{ab}
Nitrate	N	1.90 ^{abc}	2.17 ^{ab}	2.54 ^{a}	2.40 ^{ab}
(ug/g)	Y	1.65 ^{bc}	1.45 ^{c}	2.05 ^{abc}	1.89 ^{c}

Table 3b. Mean trait values (plant biomass indices) for the *E. elymoides* subspecies x lineage groups. Shared letters within a trait indicate no significant differences. 'N' or 'Y' in the BRTE column indicates whether plants were grown alone (N) or with (Y) *B. tectorum* competition. Convert SRL to mm mg^{-1}. A "*" indicated the variable was log-transformed for analysis.

Trait (unit)	*BRTE*	*ssp. brev (wild)*	*ssp. ely (wild)*	*ssp. ely (domestic)*	*ssp. cali (domestic)*
Plant Biomass Indices					
RSR	N	0.23 ^{e}	0.30 ^{bc}	0.29 ^{bcd}	0.24 ^{de}
(g/g)	Y	0.30 ^{bc}	0.40 ^{a}	0.34 ^{ab}	0.24 ^{cde}
AMR	N	0.82 ^{a}	0.78 ^{cd}	0.78 ^{bcd}	0.81 ^{ab}
(g/g)	Y	0.78 ^{bcd}	0.72 ^{de}	0.75 ^{e}	0.81 ^{abc}
HMR	N	33.5 ^{e}	51.2 ^{d}	44.4 ^{de}	69.5 ^{c}
(cm/g)	Y	180.8 ^{b}	235.1 ^{a}	226.5 ^{ab}	197.7 ^{ab}
TMR	N	11.8	16.8	13.1	14.3
(#/g)	Y	26.7	33.4	29.7	22.6
LMR*	N	0.021 ^{a}	0.017 ^{bc}	0.020 ^{ab}	0.022 ^{a}
(g/g)	Y	0.015 ^{c}	0.014 ^{c}	0.014 ^{c}	0.017 ^{bc}
LAR*	N	2.53 ^{a}	2.13 ^{bcd}	2.29 ^{abc}	2.49 ^{ab}
*(LMR*SLA)*	Y	1.93 ^{de}	1.99 ^{cde}	1.83 ^{e}	2.08 ^{bcde}
SLA*	N	121 ^{c}	127 ^{bc}	117 ^{c}	114 ^{c}
(cm2/g)	Y	128 ^{bc}	143 ^{a}	137 ^{ab}	128 ^{abc}
SRL*	N	2.42 ^{a}	1.65 ^{b}	1.80 ^{b}	1.83 ^{b}
(m/g)	Y	1.64 ^{bc}	1.35 ^{d}	1.41 ^{cd}	1.57 ^{bc}
F2C*	N	8.34 ^{a}	5.13 ^{bc}	6.13 ^{b}	6.31 ^{bcd}
(m/m)	Y	5.49 ^{cd}	4.28 ^{e}	3.95 ^{ed}	4.23 ^{ed}
Root Diam.*	N	0.28 ^{d}	0.34 ^{ab}	0.33 ^{bc}	0.34 ^{abc}
(mm)	Y	0.32 ^{c}	0.36 ^{a}	0.34 ^{abc}	0.34 ^{abc}

Correlations (Appendix 6) indicated that as cover of *B. tectorum* increased, size of ssp. *brevifolius* plants increased (r = 0.81, p = 0.03); no significant relationship was revealed for ssp. *elymoides*.

However, contrary to our hypothesis, models in which *B. tectorum* was the environmental predictor were neither significant nor ranked among those best fit for predicting mass of *E. elymoides* when grown with *B. tectorum*, or for predicting *E. elymoides* RII (Appendix 5). Models representing soil surface features (specifically, % rock and % bare ground), were those which best predicted *E. elymoides*' RII (higher AIC scores) and these models exhibited significant interactions between subspecies and the environmental factor. However, main effects of these factors were insignificant and correlations between RII and %rock or %bare ground were also weak and insignificant, indicating that these variables also are poor predictors of RII.

Change in *Elymus elymoides* Trait Expression Due to *Bromus tectorum*

Values of nearly all *E. elymoides* growth traits were significantly changed due to *B. tectorum* competition (Table 2, 3). Relative to *E. elymoides* seedlings grown alone, seedlings grown with *B. tectorum* generally allocated more biomass to below-ground plant tissue, as shown by a significant increase in root: shoot mass ratio (RSR), and significant decreases in above ground mass to total plant mass ratio (AMR), leaf mass to total plant mass ratio (LMR), and leaf area to total plant mass ratio (LAR). Although *B. tectorum* reduced above-ground biomass of *E. elymoides*, it significantly increased height to mass ratio (HMR). Specific leaf area (SLA) also increased, indicating leaves became thinner or less dense due to *B. tectorum* competition. Finally, *E. elymoides* plants grown with competition exhibited a decrease in fine roots relative to coarse roots, associated with increased average root diameter (Diam) and decreased specific root length (SRL).

The Relationship Between Trait Expression and RII for *Elymus elymoides*

The Boruta random forest analysis of all combined subspecies identified 18 of the 33 assessed traits as significant predictors of RII values (Table 4), and these predictors explained 82% of total RII variance (or 51-82% within subspecies x lineage groups, Appendix 7). Trait values of plants grown with *B. tectorum* were often better predictors of RII (i.e. had higher importance scores) than trait values of plants grown alone; the notable exception being LMR. Height to mass ratio (HMR) was clearly the most relevant among the significant traits (importance scores > 29). Following HMR in importance were TMR, RSR, LMR, and AMR, then measures of root mass partitioning (F2C, SRL, SLA), and finally traits portraying leaf area (SLA, LAR). Correlation tests indicated that for these significant traits, higher RII scores were associated with plants that partitioned less biomass to height and tillers, more biomass to leaves, and less biomass to fine roots when grown with *B. tectorum*. Seed weight was significant when all groups were combined for analysis, but not important within any group (Appendix 7), indicating that it may be correlated with group differences, but not important to RII.

Although Boruta analysis did not identify soil nitrogen as significantly related to RII, we did observe patterns in soil nitrate that appeared to correspond to RII values. Among groups, those with high RII scores exhibited smaller differences in soil nitrate concentration between pots grown with *B. tectorum* compared to pots grown without *B. tecotrum*. For instance, *californicus* (highest RII among the groups) had the largest difference in soil nitrogen concentration between the competition / no competition treatments, and *brevifolius* (lowest RII) had the smallest difference. Furthermore, soil nitrate concentration weighted by total plant biomass (Fig. 4b) revealed that when grown alone, *californicus* consumed the least nitrate from the soil per gram of plant tissue, *brevifolius* the most, and *elymoides* (wild and domestic) an intermediate amount.

Table 4. Significance and relative importance of E. elymoides growth traits for predicting RII. Average z-scores from Boruta random forests analyses are reported for each trait variable; an "*" indicates that the variable was confirmed as significant to the response (RII). Mean percent variance in RII explained by significant traits in the model was 82%. Sign (-/+) of the Pearson correlation coefficient between RII scores and trait values is reported in the right-hand columns. Correlations were performed separately for *E. elymoides* plants grown alone and *E. elymoides* plants grown with *B. tectorum*.

	Trait importance and significance		*Relationship between E. elymoides trait and RII*	
Traits	*ELEL Alone*	*ELEL+ BRTE*	*ELEL Alone*	*ELEL+ BRTE*
Seed Weight	3.48 *		+	
Emerg. Days	0.79	0.59	none	none
Emerg. Range	0.78	0.18	none	none
Emerg. Pct	-0.19	-0.29	-	none
RSR	6.27 *	10.29 *	+	-
AMR	5.61 *	8.82 *	-	+
HMR	29.36 *	31.79 *	+	-
TMR	12.57 *	13.10 *	+	-
LMR	9.51 *	7.66 *	-	+
LAR	3.39 *	3.20 *	-	+
SLA	1.32	5.06 *	none	-
SRL	0.90	5.61 *	none	-
F2C	5.38 *	6.04 *	+	-
Diam	1.94	7.12 *	none	+
NO3	-0.48	0.49	none	none
NH4	-0.55	-0.81	none	none

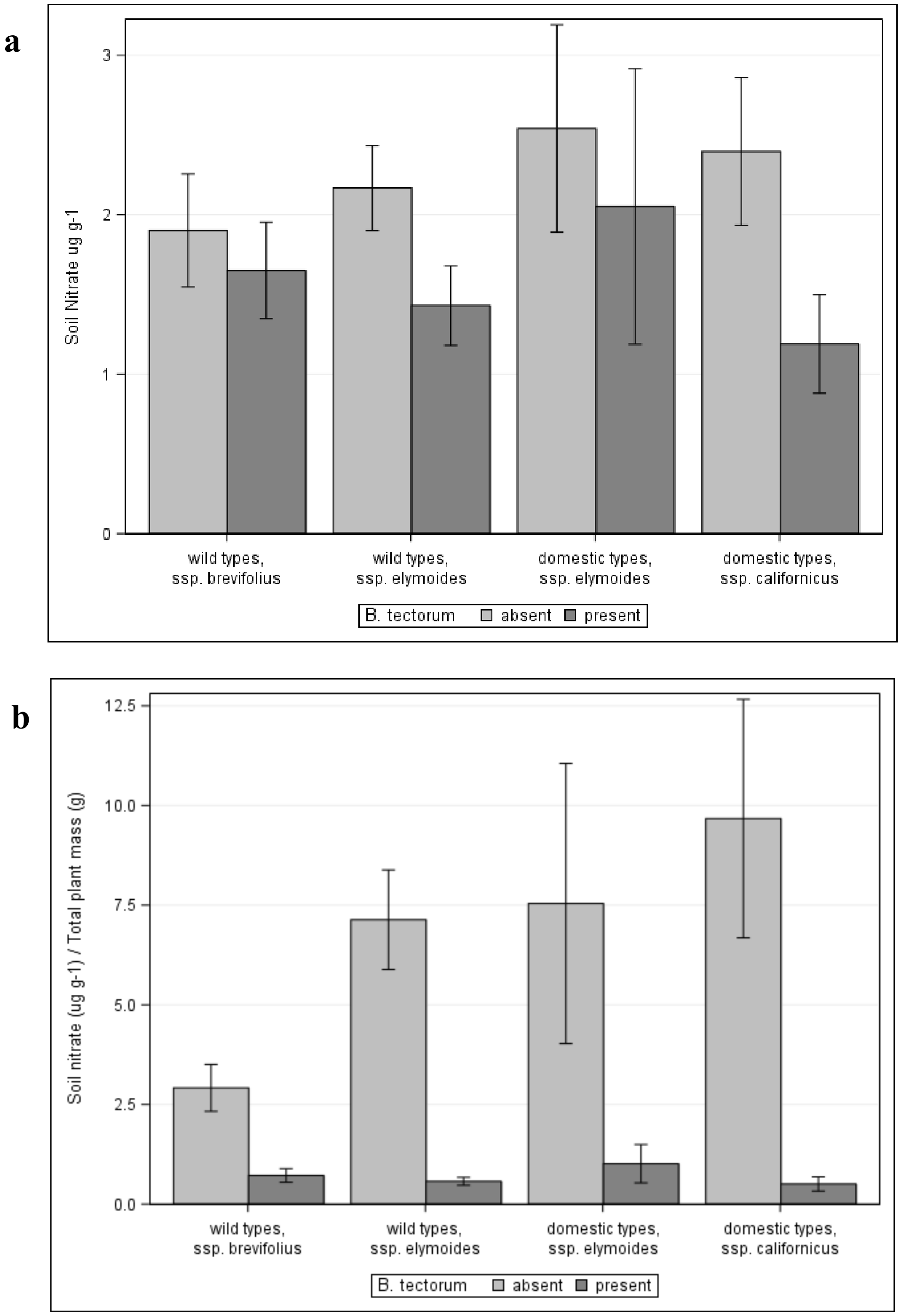

Figure 4. Nitrate concentration within pots at the end of the experiment, comparing pots planted with *Bromus tectorum* to those without. The top graph (a) shows mean concentration (µg/g) of nitrate in soil from pots containing *E. elymoides* alone or with *B. tectorum*. Soil was sampled at the end of the 8-week grow-out period. The lower graph (b) shows mean nitrate concentration remaining in soil at the end of the grow-out, divided by total plant biomass in pots. Error bars represent +/- 1 SE.

DISCUSSION

Bromus tectorum **Field Abundance and Competitive Response of** ***Elymus elymoides***

Our hypothesis that *E. elymoides* from areas invaded by *B. tectorum* would have higher tolerance of competition stemmed from results of studies which examined competitive relationships of a congener, *Elymus multisetus*. Although plants from populations of *E. multisetus* collected in areas with > 30% cover of *B. tectorum* were consistently smaller, they were found to have greater competitive ability, both as seedlings (Rowe and Leger 2011; Kulpa and Leger et al. 2012) and adults (Leger 2008; Goergen et al. 2011), greater reducing effect on *B. tectorum* growth. Although the model of biomass based on *B. tectorum* abundance was the best predictor of *E. elymoides* mass, we found a significant positive relationship between field abundance of *B. tectorum* and *E. elymoides* biomass for ssp. *brevifolius*. Furthermore, there was no relationship, for either subspecies, between field abundance of *B. tectorum* and competitive response (RII) of *E. elymoides*, nor do any other significant environmental predictors of RII exist.

There are a few potential explanations for these results, which contradict what has been found for *E. multisetus*. First, although several seed collections were made at heavily invaded sites, we did not ascertain the long-term invasion history of those areas. Although populations can potentially evolve rapidly under consistent biotic or abiotic stress (Carroll et al. 2007), our populations from invaded areas may not have increased expression of traits conferring higher RII if *B. tectorum* presence was not a consistent selective agent acting on *E. elymoides* fitness. Secondly, we may have observed a lack of relationship between competitive response and *B. tectorum* abundance if the field conditions to which plants were adapted were not well replicated in the greenhouse environment. Water and nitrogen limitation typically prevail in *B. tectorum*-dominated sites (Chambers et al. 2007), yet our pots in our experiment likely did not experience these limitations. Instead, we believe light limitation, due to densely arranged greenhouse pots, may have had a greater impact for our study, especially since the later emerging seedlings of *E. elymoides* were shaded by *B. tectorum* plants. Thus, traits conferring competitive tolerance in the field were possibly less important to plant growth in the greenhouse where light levels were lower. Finally, in our exploratory analysis, we found that several site factors (elevation, soil crust cover, shrub cover, and *B. tectorum* cover) were significantly related to size differentiation among *E. elymoides* populations; site resource availability at higher elevations may be driving growth rates of both the exotic and native grasses alike, without having an influence on the ability of *E. elymoides* to tolerate competition.

Influence of Competition on Growth Traits

We observed that, on average, *E. elymoides* plants competing with *B. tectorum* allocated proportionally more plant mass to below-ground tissues, compared to *E. elymoides* plants grown alone. We also observed a significant decrease in fine roots, suggesting that *E. elymoides* roots may have avoided overlap with prolific *B. tectorum* roots, which tend to cluster in the top layer of the soil (Melgoza et al. 1990). Perennial species are able to allocate resources to root elongation in order to seek out soil moisture at greater depths (Etherington 1987; D'Antonio and Mahall 1991; Wilkinson 2000). This root exploration is associated with the production of larger diameter roots (Jackson and Caldwell 1989) and may come at a cost of proliferation of fine lateral roots essential for uptake (Eissenstat 1992; Wilkinson 2000; Peek et al. 2005).

Above-ground biomass of *E. elymoides* was reduced in the presence of *B. tectorum,* and, on average, was allocated to greater stem growth (height and tiller production). As seedlings grew and total plant canopies increased, competition for light would have intensified, and height increase is a typical shade tolerance response (Kigel and Cosgrove 1991; Lambers et al. 2008). Specific leaf area also increased, which is a typical response to light-limited situations (Ryser and Eek 2000), whereby plants construct leaves with greater leaf surface area to improve the probability of encountering light. The increased allocation we observed to height and SLA, in addition to the overall reduction of above ground resources in general, was likely associated with the decline we observed in leaf area ratio and leaf mass ratio, a consequence of trade-offs inherent in resource partitioning (Lambers et al. 2008).

Relationship Between Growth Traits and Competitive Tolerance

Several mass partitioning indices were identified as significant predictors of RII, including height to mass ratio, leaf mass ratio, above plant mass ratio, and root to shoot ratio; indices related to root attributes (fine to coarse root ratio, average diameter, specific root length) were also identified but of less importance. Generally, traits associated with *E. elymoides* plants grown with competition were better predictors of RII than traits associated with plants grown alone, and some traits (SLA, SRL, and average root diameter) were only revealed as significant to competitive response when measured on plants grown with *B. tectorum*. This finding supports the idea that plant trials which evaluate performance of plant materials in a competitive environment will reveal more about their performance in real world environments than trials that assess plant materials in isolation (Leger and Baughman 2015).

From this study, we were unable to determine whether traits identified as significant predictors of RII were drivers of competitive response, or simply associated with the change in plant size that was impacted by the presence of *B. tectorum*. For instance, *B. tectorum* had a strong, significant reducing effect on *E. elymoides* biomass partitioning to above-ground tissues, resulting in higher RSR values (Table 3b). The fact that RSR was found to be a significant predictor or RII (per random forest analysis), could imply two different scenarios: a) plants which selectively partitioned to above-ground mass were more tolerant of *B. tectorum* competition; or b) in some pots, *B. tectorum* competition was less (for unidentified reasons), resulting in less impact on *E. elymoides* biomass and, if mass is inherently associated with biomass partitioning, also resulting in less of an increase in RSR values. Because traits may have been correlated with but not causative of high RII, a more robust test is needed to assess how biomass partitioning changes due to competition, while correcting for the inherent change that is directly a function of biomass (Burns and Strauss 2012). Regardless, the growth traits we identified may be important indicators of competitive response and warrant further investigation.

Intraspecific Differences in Competitive Response and Trait Expression

We investigated variation in response of *E. elymoides* to competition from *B. tectorum* at three intraspecific levels that are relevant to decision making for revegetation projects: subspecies, lineages (wild-collected seeds vs. commercially available accessions), and populations (e.g., seeds collected from different locations or different commercially-available domestic accessions). We were surprised to find limited variation among these groups. Subspecies *californicus* had significantly higher RII than all other subspecies, but there was not significant differentiation between *elymoides* and *brevifolius*. Furthermore, competitive response was not significantly different between lineages or among populations within subspecies x lineage groups.

Subspecies

The higher RII values of *californicus* may have been attributable to a more conservative growth strategy. This subspecies had less total biomass, fewer leaves, and lower total root production. Small stature and slow growth rate are qualities suggestive of a stress-tolerant growth strategy and may allow for the persistence of *californicus* in a resource-limited environment (Grime 1977). Work by others has also found a positive relationship between competitive ability and small plant size (Goergen et al. 2001; Rowe and Leger 2011). Emphasis on slower growth with higher resources capture may increase the probability of coexistence of *californicus* with *B. tectorum* (Grime 2001); it would be beneficial to further investigate the relationship between its growth strategy and seedling survival.

Subspecies *brevifolius*, by contrast, had the lowest (although not significantly so) RII value, but also the greatest biomass, height, leaf number, and total root length compared to all other subspecies (Table 3a), it also exhibited large changes in several growth indices due to competition, suggesting that this taxon has a high degree of plasticity (Table 4). The larger size of this taxon as a seedling and as an adult (Wilson 1963; Jones 2003), may make it desirable when high biomass production is a priority, and trait plasticity may also be an advantage in accommodating environments where resource availability is variable. However, the large proportional reduction of seedling biomass noted in this subspecies due to competitive stress may ultimately impair its establishment and survival (Aarssen and Keogh 2002). Furthermore, *Elymus* is in general much less plastic than *B. tectorum*, which is capable of faster resource exploitation during pulses (Arrendondo 1998; Leffler et al. 2011); without a longer term study under various growth conditions (e.g. controlled soil moisture and temperature regimes), it is not clear whether the apparent trend towards higher growth rate and plasticity of *brevifolius* would be an advantage or disadvantage when competing with a highly aggressive exotic annual grass.

Wild vs. domestic

We had hypothesized that domestic lineages would, on average, be larger than their wild counterparts because of the tendency of plant breeding programs to select for larger seed and plant size, greater vigor, and faster emergence; (Jones 2009; Schroder and Prasse 2013; Leger and Baughman 2015). We also expected that wild lineages would be smaller and have a greater competitive ability (RII) than domestic lineages, due to the influence of size (Goergen et al. 2001; Rowe and Leger 2011), and because this lineage was recently exposed to a competitive environment to which it may have adapted. We indeed found that within *elymoides*, domestic lineages tended to be larger than wild lineages in all measures of size, but this was only significant for total root length, and RII did not differ between the lineages. Although sample sizes were uneven (7 wild populations vs. 2 domestic accessions), and seeds were not collected from the same regions, the lack of significant differences between lineages nevertheless suggests that domestication did not result in an advantage under this high level of competition from *B. tectorum*. However, it should also be noted that biomass allocation did differ significantly between the lineages (Table 5); wild populations experienced significantly less reduction in leaf mass and leaf area due to competition.

Population-level

Within-population variation is common in autogamous species (Allard et al. 1968; Lande 1977; Allard 1999; Govindajaru 1989) and can be responsible for significant differences in trait expression within the *Elymus* genus (Erickson et al. 2004; Rowe and Leger 2011). We had expected to observe among-population differentiation in response to *B. tectorum* because differentiation has, in other studies, been observed in *E. elymoides* for morphological traits (Jones et al. 2003), and in the *Elymus* genus for traits conferring local adaptation (Erickson et al. 2004; Rowe and Leger 2011). However, populations did not differ for either biomass or RII. Lack of population differentiation may have been due to high variability among replicates, attributable to either greenhouse microclimate effects, or potentially due to genetically-driven intra-population variation, which can be high for members of this genus (Rowe and Leger 2011).

Cross-taxa patterns

Overall, we observed a pattern in which the smallest taxa (*elymoides* within wild lineages, *californicus* within domestic lineages) experienced the least relative reduction of biomass due to competition. Others have also observed that smaller statured plants have higher tolerance to competition for *E. multisetus* (Rowe and Leger 2011), and higher establishment success in high-stress restoration environments (Rowe and Leger 2011; Kulpa and Leger et al. 2012). For these studies, however, small stature was apparently an outcome of local adaptation from biotic and abiotic selection pressure, rather than due to existing genetic differences among recognized taxa as we have found here.

The significance of the relationship between small size and higher competitive tolerance is not yet fully understood and is contradictory to other theories that larger plants will have greater competitive ability (Gaudet and Keddy 1988; Keddy et al. 2002). It has been suggested that the association could be due to other advantageous mechanisms, such as allelopathic compounds or soil-organism mediated neighbor suppression (Mahall and Callaway 1992; Rowe and Leger 2011). An alternative possibility is that higher competitive tolerance of smaller *Elymus* plants may be attributable to a conservative growth strategy, in which resources are allocated to slower growing but longer lasting plant tissue. This growth strategy is hypothesized to be a characteristic of plants in low resource environments (Grime 1977) such as those that exist throughout the Great Basin (Noy-Meir 1973; West 1983; West and Young 2000; Chambers et al. 2007).

CONCLUSION

Our study verified intraspecific variation in response to competition with *Bromus tectorum* for *Elymus elymoides*, a species commonly used for rangeland seeding (Jones and Larson 2005). As anticipated, its biomass allocation patterns were also affected by the competitive environment (Schwinning and Weiner 1998; Curt et al. 2005) and differed according to the intraspecific groups we examined. Identifying the sub-species, lineages, populations, and growth traits which confer resistance to the competitive effects of a common exotic species such as *B. tectorum* can inform identification and breeding of germplasm that has greater fitness and overall success in a restoration context. Future studies into the success of various *E. elymoides* taxa in a competitive field environment will be the next step in verifying this potential utility. Field studies, however, should be conscious of plant materials that are appropriate to the targeted site. Planting seed material outside of its home range may have negative effects on the fitness of the established populations due to abiotic constraints, restrictions which may outweigh the benefits of higher tolerance of competition (Humphrey and Schupp 2004; McKay et al. 2005; Rice and Knapp 2008).

This study provides an example of how trait diversity can be an advantage to the long term persistence of populations. *B. tectorum* competes with native plants for a variety of resources (Chambers et al. 2007), which are often nutrients and water in field settings (e.g., Melgoza et al. 1990; Hirsch-Schantz et al. 2014), but which may also include light due to the fast above-ground growth (Bookman and Mack 1983) and associated heavy litter accumulation (Serpe et al. 2013) of *B. tectorum*. A genetically diverse population of *E. elymoides* will possess alleles that are suitable to this diversity of environmental constraints imposed by *B. tectorum*.

We focused on the impact of *B. tectorum* on *E. elymoides* seedling biomass, an important determinant of survival (Humphrey and Schupp 2004). Seedling size affects survival of plants in water-limited environments (Donovan et al. 1993; Gordon and Rice 2000), and small, young seedlings can be very vulnerable to mortality in the presence of competition (Humphrey and Schupp 2004; James et al. 2011). To fully understand the relative competitive tolerance of intraspecific taxa, further research should address how this relative loss of seedling biomass affects additional metrics of population success including survival through dry summer or cold winter seasons, seed production, and lifespan. Finally, more research into the mechanism of competitive tolerance should be performed. Isolating the mechanism though which growth rate and biomass allocation influences the competitive response can aid not only the identification of successful *E. elymoides* taxa, but may also assist the identification of other native species that are candidates for restoration of *B. tectorum*-invaded rangelands.

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APPENDICES

Appendix A. Details of seed collection from wild populations

We collected seeds of *Elymus elymoides* from wild populations located within the Basin and Range Ecoregion of Utah. Search efforts for *E. elymoides* seed sources were confined to two pre-selected NRCS soil units, the Kunzler-Lembos association in northwestern Utah near Park Valley (41°49′03″N, 113°19′45″W), and the Borvant soil series occurring in central Utah, roughly between Cedar Fort, UT (40°19′35″N 112°6′20″W) and Nephi, UT (39°42′33″N 111°49′53″W). The Kunzler and Lembos series are moderately- to very-deep alkaline soils on 0-8% slopes, associated with the Semidesert Alkali Loam (Black Greasewood) ecological site (Soil Survey Staff 2004, Soil Survey Staff 2011). The Borvant series is a gravelly loam, shallow to a petrocalcic horizon, on 2-60% slopes and support an Upland Shallow Hardpan (Pinyon-Utah Juniper) ecological site (Soil Survey Staff 2012). A different subspecies occurred on each of these soil units: *E. elymoides* ssp. *elymoides* on the Kunzler-Lembos association and ssp. *brevifolius* on the Borvant soil series. Locations of the Kunzler-Lembos association and Borvant soil series and were identified using the 2013 USDA-NRCS SSURGO database (Soil Survey Staff 2013).

We selected sites for seed collection based on the following *E. elymoides* and *B. tectorum* abundance criteria. First, *E. elymoides* density was required to be greater than five plants per 10m^2 and its total population greater than 300 individuals; these measures were estimated by counting *E. elymoides* plants within five randomly located 1m^2 quadrats, extrapolating the averaged abundance to the entire population. Secondly, collection sites were separated by a minimum of 1 km to increase the likelihood of their genetic isolation. Finally, we ensured that the collection area was not seeded during prior federal or state management efforts (Torgerson 2013, Chamberlain 2013, Jessop 2013, Whittaker 2013). Within the search area for each *E. elymoides* subspecies, collection sites were targeted to represent a wide range of *B. tectorum* invasion levels, ranging from < 1% to > 50% absolute cover. All patches of the Kunzler-Lembos association and Borvant series, on publicly accessible lands were searched for *E. elymoides* (approximately 99.5 km^2 and 79.6 km^2, respectively), resulting in the identification of seven populations for both subspecies *elymoides* and *brevifolius* that met aforementioned criteria. These seven populations served at seed sources for the study. Measurements were taken in summer of 2014 to document collection site conditions. Vegetation was described using the line-point method (Herrick et al. 2005). Plant species and ground intercepts were recorded every 0.5m along five, 50m-transects were set at 25m intervals to represent the area where seed collection occurred. Soil series was confirmed at each site by digging a soil pit and standard NRCS descriptive techniques (Schoeneberger et al 2012). Two composite soil samples were also created from 50 subsamples taken throughout the collection area, to represent the 0-5cm and 5-10cm depths. These were homogenized and used to determined average soil texture via the gravimetric method. For each field collection site, we also measured elevation (derived from global positioning system), slope, and aspect; the latter was used to calculate a heat load index (McCune and Keon 2002). Annual precipitation was derived from modelled precipitation values (PRISM Climate Group 2013, Daly et al 1997).

Seed was collected from June 23 - July 31, 2013, when inflorescences were starting to disarticulate from the culms. At each collection site, we set up a rectangular 100x50m grid from transects spaced 5m apart. One inflorescence was collected from the

E. elymoides plant closest to each of the 200 grid intersection points. In low-density areas, grids were expanded until a total of 200 plants were encountered. At sites where *B. tectorum* canopy cover exceeded an estimated 10%, we also collected approximately 10 seeds from *B. tectorum* plants near each grid intersection point. Inflorescences from *E. elymoides* and seeds *B. tectorum* were pooled by collection site. Seeds were rubbed on a leather-bound board to remove awns, cleaned using and a column separator, then sorted by hand to select only filled seeds. Seeds were counted and weighed, then stored at 2°C until used for planting.

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Appendix B. Description of random forests variable selection approach.

The random forests (RF) approach is a machine-learning technique, which evolved from the widely used classification tree method (Brieman 2001), and it has recently been recognized for its applicability to complex ecological data sets (Prasad et al. 2006, Cutler 2007). RF analysis can be used with numerous variable formats (e.g. continuous, interval, discrete), is unaffected by correlated and nonlinear predictors, and does not require that data meet distributional assumptions (Jones and Linder 2015). RF analysis integrates multiple iterations of classification trees, whereby each tree is built from a bootstrapped subsample of the original dataset. The variables selected in the fully-grown trees are used to predict values for the samples left out of the bootstrap set ('out-of-bag' observations), which can be used to calculate error rates for each tree. These error rates are compared to those attained when the out-of-bag observations are randomized for the variable in question. For each predictor variable, the change in error rate is averaged across all trees in the forest, and divided by the standard error to create an importance value (Z-score) for that predictor.

The Boruta package in R was used to perform random forest analysis, and is a wrapper algorithm built around the randomForest classification package (Liaw and Wiener 2002, Kursa et al. 2010). Although the Z-score generated from a random forest is a measure of variable importance, it cannot be tested for statistical significance because it cannot be compared to other Z-scores normally distributed around 0 (Kursa et al. 2010). The Boruta package addresses this by running multiple random forests with the inclusion of randomly generated "shadow" variables. Z-scores of predictor variables are compared to those of shadow variables, and a two-sided test of equality is performed to determine if the variable is significantly different from random. The Boruta algorithm was designed to detect all potentially significant predictors of the response variable, regardless of whether they are correlated among themselves or only weakly relevant. Aside from *iid* assumptions, this inclusive method of variable selection is a primary difference between the Boruta algorithm and other approaches such as regression-based model selection, and can be useful when exploring the potentially complicated relationships between biological responses (such as competitive tolerance) and their drivers (such as heritable plastic growth traits) (Kursa et al. 2010). A post-hoc visual evaluation of Z-scores may be used to compare relative importance of variables selected by the Boruta algorithm.

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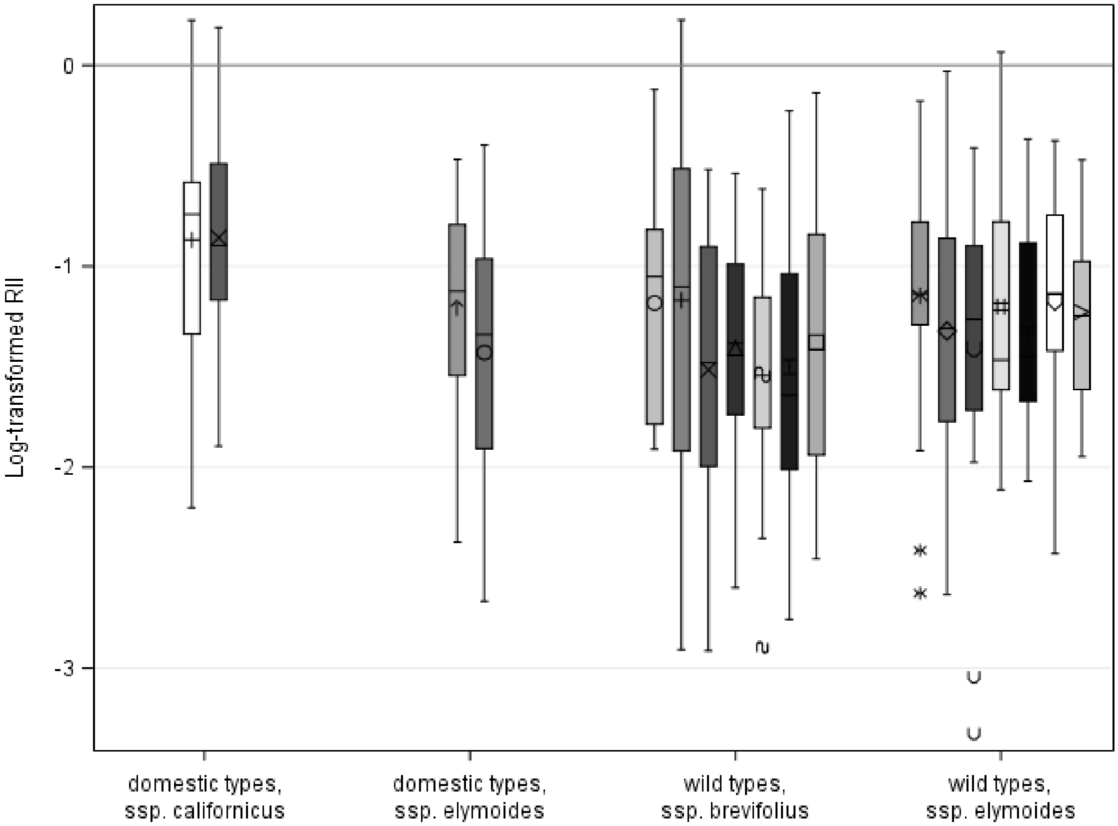
Appendix C. Correlation between growth trait values, biomass, and RII.

Traits of E. elymoides grown with B. tectorum	*Correlation with plant mass*		*Correlation with RII*	
	|r|	*p*	*|r|*	*p*
Seed Weight	0.05	0.39	0.18	0.00
Germ Percent	0.09	0.11	-0.12	0.03
Germ Days	0.05	0.41	0.09	0.10
Germ Range	0.29	<.0001	-0.05	0.39
RSR	-0.36	<.0001	0.16	0.00
SRL	0.31	<.0001	0.00	0.99
F2C	0.17	0.00	0.11	0.05
Diam.	-0.38	<.0001	0.06	0.26
AMR	0.36	<.0001	-0.14	0.01
HMR	-0.77	<.0001	0.58	<.0001
TMR	-0.64	<.0001	0.332	<.0001
LMR	0.54	<.0001	-0.23	<.0001
LAR	0.39	<.0001	-0.12	0.03
SLA	-0.02	0.65	0.09	0.12
NO3 in Soil	-0.03	0.70	0.00	0.98
NH4 in Soil	-0.08	0.32	-0.01	0.88
Final Height	0.50	<.0001	-0.25	<.0001
Final Leaf Number	0.80	<.0001	-0.40	<.0001
Total Root Length	0.83	<.0001	-0.49	<.0001
Mass Total			-0.51	<.0001

Traits of E. elymoides grown with B. tectorum	*Correlation with plant mass*		*Correlation with RII*	
	|r|	*p*	*|r|*	*p*
Seed Weight	0.16	0.00	0.18	0.00
Germ Percent	-0.11	0.05	-0.05	0.39
Germ Days	-0.01	0.85	-0.07	0.23
Germ Range	0.09	0.12	0.09	0.10
RSR	-0.48	<.0001	-0.32	<.0001
SRL	-0.18	0.00	-0.25	<.0001
F2C	-0.21	<.0001	-0.21	<.0001
Diam.	0.22	<.0001	0.31	<.0001
AMR	0.51	<.0001	0.34	<.0001
HMR	-0.72	<.0001	-0.55	<.0001
TMR	-0.51	<.0001	-0.40	<.0001
LMR	0.39	<.0001	0.32	<.0001
LAR	0.20	0.00	0.20	0.00
SLA	-0.29	<.0001	-0.20	0.00
NO3 in Soil	-0.11	0.16	-0.11	0.15
NH4 in Soil	-0.08	0.31	0.00	0.96
Final Height	0.60	<.0001	0.42	<.0001
Final Leaf Number	0.76	<.0001	0.45	<.0001
Total Root Length	0.80	<.0001	0.55	<.0001
Mass Total			0.67	<.0001

Appendix D. Boxplots of log-transformed RII for populations with the subspecies x lineage groups.



Appendix E. Linear regression of environmental variables on *E. elymoides* mass and RII.

The three models with the highest AIC scores are noted for each response variable.

Predictor	*Ssp.*		*Env. Factor*		*Interaction*		*Model Fit*	
(Environmental Factor)	*f*	*pr>f*	*f*	*pr>f*	*f*	*pr>f*	*AIC*	*Rank*
Response = Mass when grown alone								
Annual Precip.	2.5	0.14	0.1	0.73	0.3	0.58	-32.3	
Elevation	2.2	0.17	10.0	0.01	3.4	0.09	-41.6	3
Slope	34.5	0.00	0.1	0.72	0.0	0.86	-31.8	
Heat Load	78.8	<.0001	3.3	0.09	3.2	0.10	-35.5	
%Sand	3.8	0.08	0.2	0.70	0.3	0.60	-31.2	
%Silt,	4.6	0.06	0.3	0.59	0.5	0.52	-31.4	
%Clay	1.4	0.27	0.2	0.67	0.2	0.69	-31.2	
Surface: %Bare Ground	0.4	0.55	3.8	0.08	3.2	0.10	-37.8	
Surface: %Rock	26.4	0.00	0.1	0.72	0.1	0.80	-31.4	
Surface: %BSC	29.3	0.00	6.5	0.03	1.4	0.26	-42.1	2
Surface: %Litter	15.4	0.00	0.2	0.64	0.0	0.88	-31.2	
Per. Herb. %Cover	22.3	0.00	0.4	0.57	0.4	0.56	-32.1	
Shrub %Cover	72.4	<.0001	6.2	0.03	8.5	0.02	-40.7	
BRTE %Cover	148.7	<.0001	13.0	0.00	12.1	0.01	-43.4	1
Response = Mass when grown with Bromus tectorum								
Annual Precip.	0.1	0.78	1.1	0.33	0.6	0.46	-65.7	
Elevation	0.4	0.55	0.4	0.53	0.3	0.63	-65.3	
Slope	6.8	0.03	0.5	0.48	0.3	0.58	-65.2	
Heat Load	19.0	0.00	2.8	0.12	3.3	0.10	-68.9	3
%Sand	0.4	0.55	0.2	0.66	0.2	0.67	-64.9	
%Silt	1.3	0.28	0.4	0.57	0.3	0.60	-65.1	
%Clay	0.6	0.45	0.2	0.64	0.2	0.63	-65.1	
Surface: %Bare Ground	3.7	0.09	0.0	0.98	1.2	0.29	-66.0	
Surface: %Rock	12.6	0.01	0.1	0.72	1.4	0.26	-66.3	
Surface: %BSC	0.4	0.53	1.2	0.30	0.5	0.48	-65.9	
Surface: %Litter	0.1	0.74	3.0	0.12	3.1	0.11	-68.9	2
Per. Herb. %Cover	0.9	0.37	0.0	0.97	2.7	0.13	-67.6	
Shrub %Cover	21.3	0.00	3.0	0.11	6.7	0.03	-71.9	1
BRTE %Cover	12.1	0.32	1.1	0.32	1.1	0.32	-66.4	
Response = Relative Interaction Index*								
Annual Precip.	0.8	0.39	0.5	0.51	0.6	0.44	-33.2	
Elevation	2.6	0.14	0.3	0.61	2.7	0.13	-35.5	3
Slope	0.1	0.81	2.5	0.15	1.6	0.24	-34.8	
Heat Load	0.1	0.74	0.1	0.82	0.9	0.36	-33.7	
%Sand	0.7	0.44	0.1	0.73	0.2	0.71	-32.7	
%Silt	0.0	0.97	0.1	0.75	0.1	0.76	-32.6	
%Clay	0.2	0.65	0.1	0.74	0.4	0.54	-32.9	
Bare Ground %Cover	3.2	0.10	0.6	0.46	4.9	0.05	-37.9	1
Surface: %Rock	0.8	0.39	0.3	0.60	4.8	0.05	-37.4	2
Surface: %BSC	2.7	0.13	0.0	0.94	1.5	0.24	-34.8	
Surface: %Litter	4.9	0.05	0.7	0.42	2.4	0.15	-35.0	
Per. Herb. %Cover	3.8	0.08	0.1	0.77	0.8	0.40	-33.7	
Shrub %Cover	0.1	0.79	0.1	0.76	0.3	0.62	-32.9	
BRTE %Cover	1.9	0.20	0.3	0.58	0.2	0.71	-32.9	

Appendix F. Correlations between environmental variables, mass, and RII values. Tests were performed for the wild lineage *E. elymoides* subspecies combined (left columns), and for each wild lineage subspecies individually (right columns).

Predictor	*Combined ssp.*		*ssp. elymoides*		*ssp. brevifolius*	
(Environmental Factor)	*r*	*p* > |*r*|	*r*	*p* > |*r*|	*r*	*p* > |*r*|
Correlation of variable with E. elymoides mass (when grown alone)						
Annual Precip.	0.85	0.00	0.10	0.83	-0.32	0.49
Elevation	0.91	<.0001	0.52	0.23	0.75	0.05
Slope	0.45	0.10	-0.08	0.86	-0.26	0.57
Heat Load	-0.47	0.09	-0.05	0.91	-0.55	0.20
%Sand	-0.02	0.95	-0.21	0.65	0.14	0.77
%Silt	-0.30	0.30	0.17	0.71	-0.18	0.71
%Clay	0.81	0.00	0.45	0.31	0.01	0.99
Bare Ground %Cover	0.11	0.71	0.08	0.87	0.65	0.11
Surface: %Rock	0.73	0.00	0.06	0.91	0.20	0.67
Surface: %BSC	-0.65	0.01	-0.45	0.31	-0.77	0.05
Surface: %Litter	0.07	0.80	0.24	0.61	0.11	0.81
Per. Herb. %Cover	0.69	0.01	-0.01	0.99	0.30	0.52
Shrub %Cover	-0.28	0.33	0.19	0.68	-0.74	0.06
BRTE %Cover	0.13	0.67	0.06	0.89	0.81	0.03
Correlation of variable with E. elymoides mass (when grown with B. tectorum)						
Annual Precip.	0.69	0.01	-0.47	0.29	-0.10	0.83
Elevation	0.72	0.00	0.36	0.42	0.04	0.94
Slope	0.49	0.07	0.33	0.47	0.09	0.85
Heat Load	-0.47	0.09	0.05	0.92	-0.60	0.15
%Sand	0.02	0.96	0.01	0.98	0.15	0.75
%Silt	-0.29	0.32	-0.05	0.92	-0.18	0.69
%Clay	0.69	0.01	0.29	0.52	0.00	1.00
Bare Ground %Cover	-0.08	0.79	0.33	0.47	-0.27	0.56
Surface: %Rock	0.53	0.05	0.41	0.36	-0.28	0.54
Surface: %BSC	-0.49	0.08	-0.48	0.27	-0.12	0.80
Surface: %Litter	0.22	0.44	-0.01	0.99	0.61	0.15
Per. Herb. %Cover	0.61	0.02	-0.42	0.34	0.44	0.33
Shrub %Cover	-0.32	0.26	0.23	0.61	-0.74	0.06
BRTE %Cover	0.10	0.72	0.00	1.00	0.40	0.38
Correlation of variable with E. elymoides Relative Interaction Index						
Annual Precip.	-0.45	0.11	-0.40	0.38	0.04	0.92
Elevation	-0.49	0.08	0.32	0.48	-0.48	0.28
Slope	-0.08	0.80	0.68	0.09	0.17	0.72
Heat Load	0.29	0.31	0.48	0.28	-0.14	0.77
%Sand	0.02	0.94	-0.02	0.96	0.12	0.79
%Silt	0.12	0.68	-0.01	0.98	-0.10	0.83
%Clay	-0.37	0.19	0.30	0.52	-0.08	0.87
Bare Ground %Cover	-0.22	0.45	0.39	0.39	-0.62	0.14
Surface: %Rock	-0.48	0.08	0.64	0.12	-0.50	0.25
Surface: %BSC	0.41	0.14	-0.30	0.51	0.42	0.35
Surface: %Litter	0.09	0.75	-0.26	0.57	0.44	0.32
Per. Herb. %Cover	-0.19	0.52	-0.16	0.72	0.32	0.48
Shrub %Cover	0.00	0.99	0.07	0.87	-0.18	0.70
BRTE %Cover	-0.10	0.73	-0.07	0.88	-0.19	0.68

Appendix G. Boruta random forests analyses for E. elymoides groups. Each subspecies x lineage group was assessed separately. Average z-scores are reported for each trait variables; an "*" indicates that the variable was confirmed as significant to the response (RII). The percent variance in RII explained by significant traits is an average calculated from results of 10 random forest models.

ssp. brevifolius (wild)		*ssp. elymoides (wild)*		*ssp. elymoides (domestic)*		*ssp. californicus (domestic)*	
ELEL Alone	*ELEL+ BRTE*	*ELEL Alone*	*ELEL+ BRTE*	*ELEL Alone*	*ELEL+ BRTE*	*ELEL Alone*	*ELEL+ BRTE*
0.52		-0.94		0.12		-0.20	
-0.68	1.51	1.21	-0.76	-0.54	-0.90	-0.33	1.54
0.24	-0.47	-0.38	0.15	-0.27	0.54	-0.27	3.09 *
0.09	-0.19	-0.40	1.01	-0.57	-0.98	3.29 *	-0.76
1.50	8.11 *	4.19 *	4.59 *	3.79 *	4.77 *	0.36	2.69
1.44	7.46 *	3.46 *	3.70 *	3.22 *	3.73 *	0.67	1.98
18.87 *	25.81 *	14.98 *	20.25 *	6.93 *	15.42 *	12.56 *	1.22
8.52 *	10.52 *	9.20 *	5.23 *	-0.93	1.20	2.62	1.29
8.11 *	4.49 *	4.56 *	5.55 *	1.07 *	2.25	-0.09	-0.87
4.46 *	1.12	0.94	2.03	-0.24	0.65	-0.72	-0.09
-0.39	2.34 *	2.23	4.40 *	0.07	-0.29	-0.22	0.04
-0.78	3.47 *	-0.65	4.96 *	4.65 *	0.68	-0.47	3.12 *
-0.05	2.57 *	0.85	2.99 *	2.11	0.08	-1.00	3.73 *
-0.28	1.84	0.10	7.25 *	4.80 *	0.30	-0.43	4.52 *
-1.83	-1.56	-2.23	-0.77	-2.80	-0.61	-2.98	-2.14
-1.04	-0.46	-1.93	-2.23	-2.69	-2.60	-0.51	-1.24

Percent variance in RII explained by variables selected from Boruta random forest analysis

82%	68%	65%	51%