

THESIS

INTERACTIONS BETWEEN *BROMUS TECTORUM*, GRASSHOPPERS,
AND NATIVE PLANTS IN SAGEBRUSH STEPPE COMMUNITIES

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ABSTRACT

INTERACTIONS BETWEEN *BROMUS TECTORUM*, GRASSHOPPERS, AND NATIVE PLANTS IN SAGEBRUSH STEPPE COMMUNITIES

Invasion by the exotic grass *Bromus tectorum* L. (cheatgrass) has produced widespread, persistent changes in the Intermountain West. As a result of this and other disturbances, sagebrush shrubland is among North America's most imperiled ecosystems. Restoration of *B. tectorum*-infested areas has often been unsuccessful, and there is a need to understand the factors limiting revegetation success. There is evidence that *B. tectorum* is a superior competitor for space and resources. But it's also possible that *B. tectorum* dominance is enhanced by native herbivores through the mechanism of apparent competition: species competing indirectly through shared natural enemies. If an invasive exotic is a less preferred food source for herbivores than native plants, per capita feeding impacts may increase on natives, thus facilitating exotic proliferation.

In sagebrush shrubland, grasshoppers are often the dominant herbivores. Their feeding patterns have been shown to limit and structure plant distributions. The objective of this study was to elucidate whether grasshoppers may be promoting *B. tectorum* spread through herbivore-mediated apparent competition. Using native plants commonly seeded in sagebrush restoration projects and the native generalist grasshopper *Melanoplus bivittatus* in laboratory trials and greenhouse experiments, I tested how grasshopper herbivory affects native plants in comparison to *B. tectorum*. Grasshoppers significantly increased mortality rates for most native plants but had minimal impact on *B. tectorum* mortality. Certain native species were much more highly

preferred and / or impacted by herbivory, including the keystone shrub *Artemisia tridentata* (big sagebrush). However, several native species were either less preferred or more tolerant of herbivory than *B. tectorum*, and could therefore be good restoration candidates where grasshoppers are common. In addition, my results suggest *B. tectorum* could promote population increase in certain grasshopper species, particularly agricultural and rangeland pests. Study results could provide guidance regarding seed mixes and possible control of insect herbivores to improve restoration success in *B. tectorum*-invaded areas.

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Chapter 1. Introduction

The sagebrush steppe ecosystem

History

The sagebrush steppe ecosystem (*sensu* West 1983) once extended over 45 million hectares in Western North America (West 1983). This semiarid ecosystem, historically dominated by perennial bunchgrasses and sagebrush (*Artemisia* spp.), has been transformed by 150 years of human activity. More than 90% of sagebrush steppe has been degraded by livestock grazing (effects include shifts in plant species composition, soil compaction and soil erosion) (Noss et al. 1995). In addition, it has been fragmented by roads and cropland and invaded by exotic plants (Davies et al. 2011). Sagebrush steppe is now one of the most imperiled ecosystems in the United States (Noss et al. 1995). It currently occupies less than 60% of its historic range, and what remains is highly altered (Schroeder et al. 2004).

Hundreds of species are dependent on sagebrush steppe for all or part of their existence, and some sagebrush-obligate species are in steep decline (Knick et al. 2003). At least 350 sagebrush-associated plants and animals have been identified as species of conservation concern (Wisdom et al. 2005). Ongoing loss and degradation of sagebrush steppe is leading to increased risk of extirpation for sagebrush-dependent species (Davies et al. 2011). Preventing or reversing declines of sagebrush-associated wildlife has been identified as a conservation priority by ecologists and governmental agencies, and will require preservation of less-degraded areas as well as restoration of native plant communities.

Sagebrush steppe restoration

The greater sage grouse (*Centrocercus urophasianus*) is one example of a sagebrush-obligate species. Large-scale vegetation changes have negatively impacted sage grouse; the species has declined in abundance and productivity and is now absent from many parts of its historic range (Connelly et al. 2004). Sage grouse are considered an indicator of what could happen to other species in sagebrush steppe ecosystems if habitat loss and degradation continues.

A key cause of decline in sage grouse has been changes in the species' food supply. Loss of sagebrush fosters the spread of non-native plants and concurrent decline of native species. One study found native forb (herbaceous dicot) density decreased by more than 50% when sagebrush was removed (Prevey et al. 2010). Sage grouse fecundity is limited by the availability of certain preferred food plants: highly nutritious forb species that are disappearing from sagebrush steppe ecosystems. These native forbs are important during spring and summer for maintaining optimal nutritional status in hens, and promoting the growth and survival of chicks (Klebenow & Gray 1968).

Communities with a long history of disturbance are among the most difficult and costly to restore, due to changes in soil properties and depletion of native seed banks (Goergen et al. 2011; West 2000). In sagebrush steppe ecosystems, the principal plant community changes over the past century were encroachment by conifers and invasion by exotic annual grasses. Restoration efforts are most limited by annual grass invasion (due to the difficulty, expense, and extent of the problem); consequently, management recommendations for addressing the annual grass issue have been identified as most relevant (Davies et al. 2011).

Bromus tectorum

Among the many plants introduced to sagebrush steppe ecosystems, the most successful has been the Eurasian annual grass *Bromus tectorum* (cheatgrass), which was introduced many times during the past 150 years. Genetic tests of *B. tectorum* in the Central U.S. indicate that at least five independent seed introductions contributed to diversity of current populations, with source populations likely coming from Hungary, Slovakia, Germany and the Czech Republic. Hybridizing of these allopatric genotypes produced a new, unique U.S. genotype, with greater genetic diversity than founder populations (Huttanus et al. 2011). Hybrid vigor may have contributed to the species' spread and success in its new host range. By 1981 *B. tectorum* was common — and in many areas dominant — over an estimated 400,000 km² of sagebrush steppe (Mack 1981). *Bromus tectorum* has had profound impacts on sagebrush ecosystem function, chiefly through altering fire regime, modifying soil nutrients, and displacing native plant species (Knapp 1996; Whisenant 1990).

Consequences of *Bromus tectorum* invasion

1. Fire

Resource limitations in sagebrush biomes produced stands of shrubs and bunchgrasses with wide, relatively uniform spacing. *Bromus tectorum* colonizes gaps between plants, providing a dense, continuous fuel source that allows fire to cross interspaces. Although fire is a natural feature of sagebrush shrublands, *B. tectorum* infestation prolongs the fire season and increases fire frequency. Fire return intervals in *B. tectorum*-invaded areas decrease from decades to less than five years (Whisenant 1990). Sagebrush species are relatively intolerant of frequent fire, and

a shorter fire return interval eventually eliminates sagebrush. Repeated fires are acknowledged as the primary factor maintaining *B. tectorum* dominance (Knapp 1996).

2. Alterations to soil biota and nutrient balance

Researchers have demonstrated the importance of arbuscular mycorrhizal (AM) fungi in the ecology of grassland natives, and raised the possibility that successful restoration of native species could hinge on promoting beneficial soil biota (Jordan et al. 2011). Big sagebrush (*A. tridentata*), for example, is obligately mycotropic (Allen & Allen 1990). *Bromus tectorum* alters the soil AM community to the possible detriment of native plant species. Following *B. tectorum* invasion, AM richness decreases and AM community composition shifts toward non-mycorrhizal species (Belnap et al. 2005; Hawkes et al. 2006).

It has been demonstrated that where *B. tectorum* becomes dominant, soil biogeochemistry and plant nutrient cycling can undergo dramatic changes over relatively short time periods. This can occur through increased litter biomass accumulation, changes in litter chemistry, alterations in soil biotic communities and nitrogen mineralization rates, altered distribution of organic carbon in the soil profile, and reductions in organic nitrogen (via volatilization) as a result of decreasing fire return intervals (Blank 2008; Evans et al. 2001; Hawkes et al. 2006; Rau et al. 2011; Schaeffer et al. 2012). All of these disturbances can have synergistic interactions producing complex outcomes.

3. Displacement of native plant species

Bromus tectorum density is negatively correlated with native plant abundance (Davies et al. 2011; Knapp 1996). Numerous mechanisms appear to have contributed to this vegetation shift, beginning over 150 years ago with soil disturbances and a preference for herbaceous forage in grazing livestock (West 2000). Once established, *B. tectorum* successfully competes with natives

that survive fire, including mature plants able to access deep soil moisture (Melgoza et al. 1990). Native plant disappearance sets up positive feedbacks favoring *B. tectorum* spread: Where native grasses have been removed from *B. tectorum* patches, *B. tectorum* biomass and density significantly increased (Beckstead & Augspurger 2004).

Factors promoting *B. tectorum* dominance

1. Competitive ability

In the Intermountain West, *B. tectorum* occupies a region previously known as the *Agropyron spicatum* province (bluebunch wheatgrass, *Pseudoroegneria spicata*) (Daubenmire 1940). Experimental tests of interactions between *B. tectorum* and bluebunch wheatgrass found numerous indications of superior competitive ability in the invasive. *Bromus tectorum* competition reduced wheatgrass root growth, shoot growth, and water content; *B. tectorum* roots grew 50% faster and depleted soil moisture ahead of the developing roots of wheatgrass; *B. tectorum* roots were smaller in diameter, more finely branched, and reached similar depths as wheatgrass but reached those depths earlier (Harris 1967). Other native plants are similarly affected. Needle-and-thread grass (*Stipa comata*) and rabbitbrush (*Chrysothamnus viscidiflorus*) growing among *B. tectorum* has significantly lower water content and aboveground biomass (Melgoza et al. 1990). Unlike many annual grasses, *B. tectorum* is not shallow-rooted (Hulbert 1955). The species produces biomass very efficiently, with maximum growth rates when air temperatures and evapotranspiration rates are low.

Bromus tectorum gains another competitive edge through its germination and growth phenology. As a facultative winter annual, the species is actively growing when most native plants are dormant. Preemptive appropriation of space and resources is a key factor in competition. The

first seedlings to emerge generally become dominant (Ross & Harper 1972). Early germination may also provide protection from herbivory. Many insect herbivores hatch in spring. Fall- and winter-germinated *B. tectorum* has time to produce biomass before insect activity peaks. This headstart may allow *B. tectorum* to withstand herbivory until it reaches flowering stage, when the species possesses another competitive advantage: prodigious seed production. *Bromus tectorum* seeds have long viability (>10 years), with the capacity to germinate at practically any time of year when conditions are favorable (Hulbert 1955). Seeds have an unusually prompt and complete germination rate, with no evidence of a dormancy requirement (Stewart & Hull 1949). Initial germination in late summer is followed by major emergence throughout fall, which continues in winter provided there is little snow cover (Mack & Pyke 1983). Roots and leaves grow steadily even in cold temperatures (Mack & Pyke 1983). Recruitment continues in spring with new seedling germination, as well as tiller production on fall- and winter-emergent plants. Seeds from the previous year may germinate as late as mid-May and plants can produce seed within 30 days, allowing two or more generations to coexist annually (Mack & Pyke 1983).

2. Disturbance

Unrestricted grazing is widely acknowledged as the chief factor in degrading sagebrush steppe ecosystems and initiating *B. tectorum* spread (West 2000). Livestock trails and railroad lines provided routes of entry into undisturbed lands. Cattle hooves break the cryptogamic soil crust between sage plants, creating germination sites for *B. tectorum* seeds, which lodge and travel very effectively in the animals' hair (Mack 1981). Agriculture, roads, natural resource extraction, soil erosion and fire continue to provide conditions for *B. tectorum* dispersal and establishment. In fact, nearly any disturbance of sagebrush steppe promotes *B. tectorum* spread, even disturbances involved in *B. tectorum* removal efforts (Chambers et al. 2007).

3. Climate change

Increased atmospheric CO₂ concentration is predicted to have particularly dramatic effects on vegetation in semi-arid, northern latitude regions because elevated CO₂ improves water-use efficiency and alleviates water limitation on productivity. Invasive plant species may particularly benefit from CO₂ increase. Increased CO₂ produces greater growth stimulation in C₃ plants than C₄ plants, and increases growth more in fast-growing than slow-growing species (Poorter 1993). As a fast-growing C₃ annual, *B. tectorum* can be expected to show increased growth in response to rising CO₂ levels. In one test of the effects of CO₂ enrichment, *B. tectorum* and three other grass species were grown under low vs. high CO₂ conditions. All benefited in some way(s) from CO₂ enrichment, but *B. tectorum* showed the most consistently positive response (Smith et al. 1987).

Other researchers have noted the implications of elevated CO₂ on the *B. tectorum*-driven fire regime. Increased *B. tectorum* production increases the rate of fuel accumulation, which means less time needed to reach a minimum fuel threshold, longer time spent above that threshold, increase in fuel load leading to faster rate of spread, increased fire intensity, and increased likelihood of damage to native seedbanks and vegetation (Sage & Have 1996). Following fire, conditions favor *B. tectorum* establishment, since light and nutrients levels are increased and competition for water and nutrients is decreased (Blank et al. 1994). Finally, elevated CO₂ increases the C:N ratio of *B. tectorum*, potentially slowing the rate of bacterial decomposition and contributing to fuel load accumulation (Lambers 1993). Higher levels of atmospheric CO₂ over the last 20 years may in fact already have contributed to *B. tectorum* dominance (Ziska et al. 2005).

4. Herbivory

In addition to direct competition for space and resources, population dynamics of *B. tectorum* and native plants might be structured indirectly, through differential impacts of herbivory. Herbivory can produce changes in plant biochemistry; changes in biomass, diversity and distribution of plant functional groups via altered competitive balance; and changes in soil microbial biomass (Wardle & Barker 1997).

In the rangelands of Western North America, grasshoppers are often the dominant herbivores, and the collective impact of high-density grasshopper herbivory can equal or exceed that of mammalian consumers (Belovsky & Slade 2000; Branson et al. 2006). Grasshopper herbivory is occasionally the primary cause of loss of grazing forage, both directly and through forcing overgrazing by livestock (Chu & Knutson 1970). Grasshoppers may also reduce seed production by killing seedlings and severing immature seed heads. Though their impacts on agricultural crops are well documented (Branson & Redlin 2004; Pfadt 1994a), the effects of invertebrate herbivores on non-agricultural plant distributions have not been thoroughly investigated. The effects of grasshopper herbivory may be very different from those of vertebrates because they are present throughout the growing season, feed more selectively than vertebrates, and may remain in a relatively small area for much of their life cycle (Branson & Sword 2009; Chapman & Sword 1994; Narisu et al. 1999). Although grasshopper herbivory can have measurable impacts on plant community structure (Crawley 1989), their role in *B. tectorum* invasion is unknown.

Grasshoppers

Potential impacts of grasshopper herbivory

1. Alterations to soil biota and nutrient balance

There are multiple mechanisms through which grasshopper herbivory could affect the outcome of competitive interactions between native plants and *B. tectorum*. First, their herbivory contributes high-quality litter to the soil because grasshoppers are inefficient consumers. Much of the vegetation destroyed by their feeding activity is not actually ingested. Up to 75% of the foliage detached by one common, generalist species (*Melanoplus bivittatus*) ends up on the ground as “greenfall” (Bailey & Mukerji 1977). Since grasshoppers tend to choose the most nutritious plant parts, this results in an influx of nutrient-rich plant material to the detrital pool. In fact almost all (94%) of the potential energy of vegetation removed by *M. bivittatus* ends up recycled in the ecosystem, whether transferred to decomposers as greenfall, voided in frass (which decomposes faster than vertebrate feces), or as insect biomass (Bailey & Mukerji 1977). Consequently, grasshopper herbivory generally offsets the removal of photosynthetic material, accelerates nutrient cycling, and increases plant productivity (Belovsky & Slade 2000). Finally, grasshopper herbivory can impact soil nutrients via effects on soil biota. Grasshoppers act as dispersal vectors of mycorrhizal fungal spores via their droppings (Ponder 1980), and their herbivory can significantly increase mycorrhizal colonization of plant roots (Kula et al. 2005). Improved availability of nutrients and facilitation of nutrient cycling may promote competitive dominance of *B. tectorum*.

2. Alterations to plant community composition

Researchers have obtained varying results regarding invertebrate herbivory as a driver of plant community composition, relative to the impacts of vertebrates. One meta-analysis of 63 studies of the effects of herbivores on plant invasions concluded that “invertebrates have relatively modest impacts on plant survival;” the impact of vertebrate grazers was three to five times greater than that of invertebrates (Parker et al. 2006). However, other studies have found insect

herbivory to be a strong selective force in structuring plant populations, with influences on plant performance, successional dynamics, and the outcome of invasions (Brown & Gange 1992; Crawley 1989; Han et al. 2008). In some systems, insect herbivores may remove more plant biomass than any other consumer guild (Weisser & Siemann 2007). But even if insects only consume a small portion of annual plant production, their feeding may have community-level consequences, especially in a context of exotic species invasion. As noted in one study, “Insect herbivores need not consume a large amount of plant material to have a large effect on plant community composition; they need only reverse the outcome of competition” (Han et al. 2008).

The effect of grasshopper herbivory on structuring plant communities has not been widely studied compared to that of other insect herbivores. However, there is evidence that their impacts can be substantial. Parker & Salzman (1985) found survivorship and growth in the shrub *Gutierrezia microcephala* more than doubled when grasshoppers were prevented from feeding on plants (Parker & Salzman 1985). Elsewhere, Parker found plants attacked by grasshoppers had significantly lower nitrogen content, shoot water content, and biomass per stem than protected plants (Parker 1984). In a third study, Parker & Root (1981) observed seedlings of a native aster (*Machaeranthera canescens*) growing among other plants, but all were destroyed by grasshoppers before flowering. Protected transplants flowered at rates approximately equal to plants in areas lacking grasshoppers. Seedlings transplanted into areas where grasshoppers were prevalent were completely defoliated within a week, resulting in significantly higher mortality (Parker & Root 1981).

Impacts of food plants on grasshoppers

As *B. tectorum* invasion progresses and the proportion of native plants in sagebrush ecosystems is reduced, both vertebrate and invertebrate consumers will be affected by alterations in their

food supply. Not all plants support herbivore growth equally. Grasshoppers are more likely to complete their development on their preferred food plants, and may not survive to reproduce on less-preferred plants (Bailey & Mukerji 1976; Chapman & Sword 1994; MacFarlane & Thorsteinson 1979; Otte 1975). Studies of grasshopper growth and development show a linear relationship between food consumption and growth rate, and host plant quality affects fecundity at both the individual and the population scale (Awmack & Leather 2002; Bailey & Mukerji 1977; Belovsky & Slade 2000; Branson 2003; Branson et al. 2006).

Food selection by grasshoppers is influenced by plant nutrient composition. Grasshoppers' preferred food plants are highly correlated with plants producing the best growth, survival and reproductive outcomes (Mulkern 1967). If native plants provide high-quality food sources, an abundance of *B. tectorum* will not necessarily make up for an absence of native plants in their diet. Insects do not generally compensate for poor food quality by feeding at higher rates (Crawley 1989). Grasshoppers exhibit preferences not only for specific plants, but for particular parts of preferred plant species, and these preferences vary with developmental stage (Jonas & Joern 2008; Mulkern 1967). Nutrients such as nitrogen, for example, factor in food choice. But which foods are selected depends on the current nutritional status of the insect, the balance of nitrogen in a given food relative to other compounds present, and the plant's overall nutritional composition compared to other available host plants. In other words, grasshoppers do not select exclusively for high nitrogen content but rather for a particular balance of nutrients from their foods (House 1969). If *B. tectorum* is high in nitrogen (at least until bolt stage) but lacks other required nutrients provided by native plants, large-scale conversion of native plant communities to *B. tectorum* monocultures could eventually reshape grasshopper populations.

Bromus tectorum and grasshoppers

Bromus tectorum is a relatively recent introduction to North American grasslands. However, there is evidence – especially for insects colonizing exotic plant hosts – that herbivores may quickly adapt to utilize new food plants (Strauss et al. 2006). Researchers have noted that *B. tectorum* is eaten by native grasshoppers, though not necessarily in proportion to its availability. Rogers and Uresk (1974) reported that *B. tectorum* appeared with 100% frequency in survey areas but only 11% frequency in grasshopper crop contents (Rogers & Uresk 1974). In another study, the authors observed grasshoppers feeding on *B. tectorum* but “much less voraciously than on young perennial grasses” (Stewart & Hull 1949). Elsewhere, grasshoppers were observed consuming *B. tectorum* early in the spring, then switching to native forbs as *B. tectorum* senesced (Fielding & Brusven 1992). Similarly, Rogers and Uresk noted that plants that remained partially green late into the season (mostly perennial natives) were consumed more frequently than *B. tectorum* (Rogers & Uresk 1974).

In contrast, Beckstead, et al. (2008) characterized *B. tectorum* as “a highly utilized food source” by grasshoppers in their study system. They recorded significantly higher grasshopper densities in high- vs. low-density *B. tectorum* patches (Beckstead et al. 2008). However, the authors proposed that *B. tectorum* infestation ultimately increases feeding pressure on native plants: Grasshopper herbivory on squirreltail (*Elymus elymoides*) was significantly greater, and squirreltail produced 11x fewer reproductive structures, in high- vs. low-density *B. tectorum*. Again, the native species remained a viable food source after *B. tectorum* dried. In a related study, grasshopper herbivory on all plants was significantly lower where *B. tectorum* density was low (Beckstead & Augspurger 2004).

There has been some examination of the relative nutritional content of native plants vs. *B. tectorum*. One study compared protein content and digestibility in green *B. tectorum* and a common N₂-fixing native shrub, antelope bitterbrush (*Purshia tridentata*). Young *B. tectorum* was found to be much higher in both measures (Bishop et al. 2001). This result suggests *B. tectorum* may be a viable food source for native herbivores. However, concentrations of nutrients (N, P, K) in *B. tectorum* decline as the growing season progresses (Hart et al. 1932). Nutrients decline over the season in native forbs also, but overall, forb shoots have higher concentrations of nutrients than *B. tectorum* shoots (Rickard 1985). In another comparison, *B. tectorum* contained significantly higher levels of nitrogen than five native species (mostly perennial bunchgrasses) until seed-ripening stage, at which point the nitrogen content in *B. tectorum* dropped sharply (Beckstead et al. 2008). After seed-ripening, *B. tectorum* nitrogen levels were significantly lower compared to the natives. Natives with the highest nitrogen content were preferred by grasshoppers. Other researchers have also noted that plants consumed most frequently by grasshoppers were species that remained green later in the season, implying that even if some grasshoppers do consume young *B. tectorum*, they may switch to other plants as *B. tectorum* dries (Rogers & Uresk 1974). If so, this would increase herbivore pressure on native plants at precisely the point in the season when abiotic conditions become most stressful.

If actively growing *B. tectorum* is readily accepted as a food source by native grasshoppers, there is the potential for grasshopper herbivory to limit *B. tectorum* invasion or at least influence its direction. A study on the spread of another exotic (the forb *Crepis tectorum*) found grasshopper herbivory significantly reduced biomass, number of blooms, and number of seedlings of the invasive (Fielding & Conn 2011). The authors put forth two possible explanations: The invasive species was suppressed by herbivory either because the plant is preferred (perhaps because

native plants have evolved anti-herbivore defenses), or because it is less tolerant of herbivory. However, even in cases where an introduced plant is preferred by native insects, not all species will utilize it equally. Instead, a new plant can be expected to benefit species disproportionately. An invasive that obtains widespread dominance thus has the potential to alter insect community composition. There is some evidence this may be the case with *B. tectorum*. Fielding & Brusven (1992) studied grasshopper distributions on Idaho rangeland and found sites dominated by exotic annual grasses had the highest grasshopper densities but lowest species diversity, with more generalist and pest species. Sites with greater plant species richness were associated with greater grasshopper species richness (Fielding & Brusven 1992).

It's also possible for *B. tectorum* to influence insect community composition other than as a food source. Frequent fires, for example, may affect grasshopper assemblages in sagebrush steppe as in tallgrass prairie, where richness and abundance of grasshopper species is positively correlated with length of the fire return interval (Evans 1988). In addition, *B. tectorum* fills in the historically open structure formed by shrubs and native bunchgrasses in sagebrush ecosystems, which could impact grasshopper physiology. One study found increased height and density of vegetation in grasslands delays grasshopper egg and nymph maturation, possibly preventing slowly developing species from completing their life cycle (van Wingerden et al. 1992).

Native plants and grasshoppers

Perhaps owing to a shared evolutionary history, native insects may preferentially consume native plants rather than exotics. Investigations in tallgrass prairie have shown that native species tend to incur more insect feeding damage compared to their exotic congeners (Han et al. 2008).

Branson & Sword (2009) measured the effects of grasshopper herbivory in sites dominated by exotic grass (crested wheat, *Agropyron cristatum*) and showed that grasshoppers significantly reduced native forb abundance and suppressed establishment and persistence of native plants. Notably, natives did not disappear from study plots protected from grasshoppers, nor did they appear in plots where herbivory was allowed (Branson & Sword 2009).

Restoration of annual grass-invaded areas of sagebrush-steppe has often failed (Davies et al. 2011), possibly because restoration plantings contain grasshopper-preferred native food plants and experience high levels of herbivory. Shrubs in sagebrush steppe, mostly big sagebrush and rabbitbrush (*Chrysothamnus viscidiflorus*) can access and retain soil moisture until late in the growing season and are major food and water sources for herbivores (Sheldon & Rogers 1978). Grasshoppers may particularly curtail regeneration of sagebrush, which is a preferred food plant for some species (Shiojiri & Karban 2008). In Washington shrub-steppe, big sagebrush was the most frequently selected food plant for eight grasshoppers species, consumed at twice the proportion of any other plant; at the same time, *B. tectorum* averaged 20% cover but less than 1% of grasshopper crop contents (Sheldon & Rogers 1978). Takahashi & Huntly (2010) reported that grasshoppers voraciously consumed all parts of big sagebrush, especially in late summer and early fall. Insecticide-treated plants lost 1% of flower heads; control plants lost 46%. Almost all (99%) flower buds that were undamaged by herbivory became mature open flowers, while only 35% of damaged buds became open flowers. Mean number of undamaged flower heads and seed production were significantly greater in protected plants (Takahashi & Huntly 2010). Researchers in Southern Idaho concluded that big sagebrush was probably the single most influential factor structuring the grasshopper community (Fielding & Brusven 1992).

In the context of sagebrush ecosystem restoration, the most important effect of insect herbivory may be its impact on plants at the seedling stage. Mature plants may be able to recover from damage, but seedlings are more vulnerable. Seedling resistance to herbivory is a good predictor of a plant species' eventual relative abundance (Burt-Smith et al. 2003). One study found survival of seedling natives in *B. tectorum*-invaded sites was low, suggesting that competitive interactions when plants are young may be critical in native species reintroductions (Mazzola et al. 2011). Native perennial grasses have been found to be fairly good competitors to exotic annual grasses (Seabloom et al. 2003), and should therefore have a chance of survival, but a preference for natives by insect herbivores may limit their establishment. In another study, the number of native plant species doubled where grasshoppers were excluded, indicating that protection from herbivory may promote native seedling establishment (Branson & Sword 2009).

Ecological theories of invasion

A frequently cited explanation for why exotic plants become invasive in novel environments is the enemy release hypothesis: Escape from the specialist consumers and competitors with which they evolved permits exotics to flourish in a new locale (Darwin 1859). However, in a new setting an exotic species will also encounter new enemies against which it has not developed defenses. An alternative concept, the biotic resistance hypothesis, predicts that novel enemies in the exotic's new range will limit the invasive potential of newly introduced species (*i.e.*, new introductions to the plant community should be "fair game" for native consumers) (Elton 1958). Studies of insect interactions with plant invasions in North American provide some support for each of these hypotheses. In sagebrush steppe, there is evidence that grasshoppers prefer native plant species, in particular big sagebrush, and either avoid *B. tectorum* entirely or do not

consume it in proportion to its availability (Branson & Sword 2009; Fielding & Brusven 1992; Lambley et al. 1972; Sheldon & Rogers 1978; Shiojiri & Karban 2008; Stewart & Hull 1949; Takahashi & Huntly 2010). There is also indirect evidence suggesting some grasshoppers depend on particular native plants for survival. Mixed-feeding species in particular show greatest preference for forbs, which typically have higher protein content than grasses (Behmer & Joern 2008; Fielding & Brusven 1992; Kula et al. 2005). Where natives are preferred, the impact of grasshopper herbivory can be expected to favor *B. tectorum* dominance, especially if competitive suppression and fire effects of *B. tectorum* have already instigated native decline.

In support of the biotic resistance hypothesis, some researchers have identified *B. tectorum* as a good food source for insects (Bishop et al. 2001), one which is “highly utilized” by grasshoppers (Beckstead et al. 2008). Elsewhere, a meta-analysis of 63 manipulative field studies found native, generalist herbivores suppress exotics and impede invasions (Parker et al. 2006). However, even if *B. tectorum* does provide a food source, most grasshoppers would still require other plants to obtain an optimal balance of nutrients, so the simplification of plant communities related to *B. tectorum* spread could ultimately lead to decreased grasshopper diversity. Mixed-feeders and generalist species would be selected for, since they are more likely than specialists to utilize *B. tectorum* as a food source.

A final, unexplored mechanism potentially promoting *B. tectorum* dominance is apparent competition, mediated by herbivores (Holt 1977). Apparent competition occurs when the presence of exotics changes native consumers’ feeding behavior. In other words, exotic plants appear to outcompete natives, but in fact the suppressive effect of herbivory is facilitating exotic proliferation. Excluding native consumers from invaded areas can promote native plant

recruitment (Orrock & Witter 2010). For example, at sites dominated by the exotic grass *Agropyron cristatum*, protection from grasshoppers increased native plant abundance (Branson & Sword 2009). Grasshopper feeding appeared to weaken competitive ability in the exotic, but these effects were outweighed by negative impacts on native plants. Elsewhere, native plants experienced greater levels of grasshopper herbivory and produced fewer reproductive structures where *B. tectorum* density was heaviest (Beckstead & Augspurger 2004). It's possible that apparent competition in sagebrush ecosystems is acting along with direct competition to reduce the population viability of native species and promote *B. tectorum* invasion.

Research relevance

There has been a great deal of investigation into the impacts of *B. tectorum* invasion on plant communities, but little is known about the consequences of these impacts for non-domesticated herbivores, especially invertebrates. A Web of Science search using the keywords “insect” and “*Bromus tectorum*” returned 10 results; of these, only two were studies evaluating interactions with the potential to influence plant or insect abundance and distribution. Given that *B. tectorum* is often cited as a notorious invasive plant (Henderson et al. 2006; Sharma et al. 2005), this lack of investigation into the outcomes of *B. tectorum* spread at higher trophic levels leaves a considerable gap in our understanding of invasion dynamics.

The objective of these studies was to investigate whether native generalist grasshoppers' interactions with native plants and *B. tectorum* are most consistent with the enemy release hypothesis, the biotic resistance hypothesis, or are an example of herbivore-mediated apparent competition. Research questions include: Does *B. tectorum* indirectly increase grasshopper feeding pressure on native plants, because native grasshoppers preferentially consume those

plants? Or do grasshoppers view *B. tectorum* as just another food, one with minimal defenses against their attack? Grasshopper herbivory would exert the greatest influence if grasshoppers showed a strong preference either for or against *B. tectorum*. If they prefer *B. tectorum* to native plants, grasshoppers may inhibit *B. tectorum* spread; if they prefer natives they may promote it. I expected generalist grasshoppers would preferentially consume native plants vs. *B. tectorum* and that per capita impacts of herbivory on native plants would increase where *B. tectorum* is present.

The insect herbivore species I tested was the two-stripe grasshopper *Melanoplus bivittatus*, a widespread, generalist consumer. Testing a generalist allowed for the possibility of making inference regarding effects of herbivory by the grasshopper community as a whole. Forbs are preferred food plants and constitute a large portion of the species' natural diet (Behmer & Joern 2008). In addition, *M. bivittatus* also readily consumes certain C3 grasses (Lambley et al. 1972). *Melanoplus bivittatus* is a good candidate for illustrating the potential consequences for grasshoppers if sagebrush steppe communities undergo large-scale conversion to *B. tectorum* monoculture. Mortality in the species is high (> 50%) when given a single plant diet (Behmer & Joern 2008; MacFarlane & Thorsteinson 1979).

The USDA Agricultural Research Service identifies *M. bivittatus* as a major crop and rangeland pest species (Pfadt 1994b). The species has high reproductive potential: Each female can produce up to 350 eggs over a period of 32 days (Smith 1966). Because of the extra nutritional demand of egg production, female grasshoppers may be especially likely to consume high-nitrogen (green) *B. tectorum*. Where the timing of fall *B. tectorum* germination aligns with the *M. bivittatus* adult stage, *B. tectorum* could boost reproductive success in the species.

These studies tested 15 native species, five each of grasses, forbs, and shrubs. Native plants chosen were either (or both), 1) Species commonly utilized in sagebrush-steppe restoration projects, or, 2) Species that have shown potential, in experimental trials, to compete well with *B. tectorum*. For example, bottlebrush squirreltail (*Elymus elymoides*) has been identified as a potential restoration plant due to heavy seed production, good seed dispersal ability and capacity for seedlings to establish in competition with *B. tectorum* (Hironaka & Tisdale 1963). Sandburg bluegrass (*Poa secunda*) has also shown suppressive effect on *B. tectorum* growth, reducing biomass and seed production by more than 50% (Goergen et al. 2011). Because prior research has shown indigestibility of C₄ bundle sheath cells by grasshoppers (including some *Melanoplus* species), C₄ grasses such as Blue grama (*Bouteloua gracilis*) were not tested, though they may otherwise be good candidates for restoration (Caswell & Reed 1976).

I assumed life history traits of the plants chosen for these studies would play a key role in grasshopper food choices and fecundity outcomes. Most plants were expected to produce a “preference gradient.” As facultative winter annuals, *B. tectorum* plants are already at seedling stage in early spring, and thus are a potential source of high-nitrogen, tender plant material at the same time as two-stripe grasshopper nymphs hatch (May–June) (Smith 1966). Meanwhile, most native restoration plants will have barely developed their first true leaves. I predicted native seedlings would be preferred equally or more than *B. tectorum*. However, I expected grasshopper herbivory would have differential impacts, depending on plant growth form. For example, native forb species may be more affected by herbivory than grasses (including *B. tectorum*) because forb meristems are more exposed. At the middle life stage for all study organisms, I expected *B. tectorum* would be preferred equally or more than natives only until bolt stage, at which point

I predicted grasshoppers would switch their feeding preference to natives, which remain green after *B. tectorum* bolts. Finally, I expected a return to *B. tectorum* preference in early fall, when natives are either senescing or chemically / structurally defended and fresh *B. tectorum* seedlings germinate. Since *B. tectorum*' short life span means the period when it is tender and in high nitrogen is relatively brief, I hypothesized that grasshoppers would ultimately remove greater amounts of native vs. *B. tectorum* plant biomass over the growing season.

Results of this research may be used to inform efforts to restore native plant communities in areas with high local densities of grasshoppers and potential for *B. tectorum* infestation. Native species that are less preferred by grasshoppers or more tolerant of herbivory would likely be better performers where grasshoppers are prevalent. Study results could provide information regarding seed mixes and the possible need to control insect herbivores for improved restoration success in *B. tectorum*-invaded areas.

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Chapter 2. Interactions between *Bromus tectorum*, grasshoppers and sagebrush steppe restoration plants: greenhouse and field studies

Introduction

The sagebrush steppe ecosystem (SSE) of western North America has been degraded by overgrazing, roads, agriculture and invasion by exotic plants (Noss et al. 1995). It now occupies less than 60% of its historic range (Schroeder et al. 2004). Ongoing loss and degradation of sagebrush steppe is leading to increased risk of extirpation for sagebrush-dependent species (Davies et al. 2011). For example, large-scale vegetation changes have negatively impacted greater sage grouse (*Centrocercus urophasianus*); the species has declined in abundance and productivity and is now absent from many parts of its historic range (Knick et al. 2003). Hundreds of other SSE-dependent species are also in decline (Connelly et al. 2004). Preventing or reversing these declines will require active restoration.

The principal vegetation change in SSE is the spread of introduced grasses, notably the Eurasian annual *Bromus tectorum* L. (cheatgrass). *Bromus tectorum* density is negatively correlated with native plant abundance in SSE (Davies et al. 2011; Knapp 1996). The species outcompetes many SSE natives, growing more quickly and efficiently and producing self-facilitating alterations to fire regime and soil conditions (Knapp 1996; Whisenant 1990).

These direct interactions influence *B. tectorum* and native plant population dynamics, but an additional, indirect influence may be provided by herbivores. Herbivory affects plant biomass, diversity and distributions and can have synergistic effects with stressors such as drought (Wardle & Barker 1997). In SSE, grasshoppers are often the dominant herbivores, with impacts equaling or exceeding that of mammalian consumers (Belovsky & Slade 2000; Branson et al.

2006). Grasshopper herbivory is occasionally the cause of lost grazing forage, either directly or through forcing overgrazing by livestock (Chu & Knutson 1970). Even where grasshoppers only consume a small portion of primary production, their herbivory may have ecosystem-level consequences by influencing competitive outcomes between plants (Han et al. 2008). For example, some native perennial grasses are good competitors with exotic annual grasses and should be able to compete successfully (Seabloom et al. 2003), but a preference for natives by grasshoppers would limit this potential.

Feeding impacts of grasshoppers on agricultural crops are well documented (Branson et al. 2006; Bullen 1966; Hewitt & Onsager 1983), but their effect on wild plant distributions and role in the spread of exotics is largely unknown. However, there is evidence that where grasshoppers are the dominant herbivores, their influence on plant community composition can be substantial. Survivorship and growth of preferred plants can greatly increase when grasshoppers are excluded (Parker & Salzman 1985). In one study, seedlings of the forb *Machaeranthera canescens* (hoary tansyaster) were entirely consumed by grasshoppers before flowering, while protected plants flowered similarly to plants in areas lacking grasshoppers (Parker & Root 1981). Elsewhere, grasshopper herbivory indirectly benefited the exotic grass *Agropyron cristatum* (crested wheatgrass) by significantly reducing native plant abundance (Branson & Sword 2009). Native plants neither appeared in plots where grasshoppers were allowed nor disappeared from protected plots (Branson & Sword 2009).

Restoration of degraded SSE has been identified as a management priority but has often been unsuccessful (Davies et al. 2011). Grasshoppers could be a factor curtailing sagebrush regeneration, especially though impacts on *Artemisia tridentata* (big sagebrush), a preferred food plant (Shiojiri & Karban 2008). One study found *A. tridentata* was the most frequently consumed

plant for eight grasshopper species, with a proportion in grasshopper crops more than twice that of any other plant (Sheldon & Rogers 1978). Others noted severe impacts of grasshopper herbivory on sagebrush leaves, flower buds and flowers (Takahashi & Huntly 2010).

Bromus tectorum is also consumed by grasshoppers, though not necessarily in proportion to its availability. Rogers & Uresk (1974) found 100% occurrence of *B. tectorum* in survey areas but only 11% occurrence in grasshopper crops (Rogers & Uresk 1974). Elsewhere, grasshoppers were observed feeding on *B. tectorum* in the spring, then switching to native forbs as *B. tectorum* senesced (Fielding & Brusven 1992). Phenological asynchrony between *B. tectorum* and native plants allows the potential for *B. tectorum* to ultimately increase feeding pressure on natives even where it is “highly utilized” as a grasshopper food source (Beckstead et al. 2008).

A frequently cited explanation for why exotic plants may become invasive in novel environments is the enemy release hypothesis: Escape from the consumers with which they evolved permits exotics to flourish in a new locale (Darwin 1859). However, in a new setting an exotic species will also encounter enemies against which it has not developed defenses. The biotic resistance hypothesis predicts novel enemies will limit the exotic’s invasive potential (Elton 1958). A third possibility is herbivore-mediated apparent competition (a corollary of the enemy release hypothesis): Exotic plants alter native consumers’ feeding behavior such that the exotic appears to outcompete native plants, but in fact the suppressive effect of herbivory is facilitating exotic proliferation (Holt 1977).

The goal of this study was to investigate whether native generalist grasshoppers’ interactions with native SSE plants and *B. tectorum* support the enemy release hypothesis, the biotic resistance hypothesis, or are an example of herbivore-mediated apparent competition. Greater preference for natives would support the enemy release hypothesis; preference for the exotic

would support the biotic release hypothesis. I hypothesized that grasshoppers would generally prefer to consume native plants instead of *B. tectorum* and per capita impacts of herbivory on natives would increase when *B. tectorum* was present. If so, this would provide evidence that apparent competition could be acting along with direct competition in sagebrush ecosystems to reduce native species population viability and promote *B. tectorum* invasion.

I conducted two studies to test this hypothesis. In a greenhouse setting, I established artificial plant communities containing native SSE plant species, *B. tectorum*, and native generalist grasshoppers to determine whether grasshoppers removed greater amounts of native plant biomass compared to *B. tectorum* biomass. I also measured plant mortality outcomes, to determine whether survival in native plants and *B. tectorum* is affected by herbivory. Later, I established field mesocosms using the same plant and grasshopper species, to assess whether results from the greenhouse setting were applicable to a “real world” SSE restoration setting.

Materials and methods

Greenhouse Mesocosms

(i) Objectives. Determine whether native, generalist grasshoppers consume greater amounts of native plant biomass compared to *B. tectorum* biomass. Determine whether *B. tectorum* presence affects the amount of native plant biomass consumed by grasshoppers. Determine whether grasshopper herbivory affects mortality in native plants and *B. tectorum*.

(ii) Experimental insects. Insects tested were *Melanoplus bivittatus* (two-stripe grasshoppers) (Orthoptera: Acrididae: Melanoplinae), a widespread, mixed-feeding generalist. I collected adult *M. bivittatus* weekly from mid-September through late October 2011 at Colorado State University’s Environmental Learning Center (13T 498232 4489414) and brought

them to the CSU Restoration Ecology Laboratory (Fort Collins, Colorado, USA). Grasshoppers were caged in Precision[®]-818 illuminated incubators at 35/30 °C with a 14-h photoperiod. Grasshopper food preferences can change depending on prior experience (Otte 1975) and nutritional status of plants and insects (Simpson & Raubenheimer 2000). To maintain uniform influence on food choice, all insects were given romaine lettuce, wheatgrass held in a water-filled beaker, brewers yeast, and wheat bran. This diet is a common and effective preparation for successful laboratory rearing of *M. bivittatus* (Jonas & Joern 2013).

An egg-laying substrate (700-ml plastic container filled with moist sterilized sand) was provided in each cage. Egg containers were removed from cages after 7–10 days, maintained at room temperature for six weeks to allow pre-diapause egg development, then held at diapause temperature (4 °C) (Fisher 1994) from November 2011 until May 2012. Hatchlings from these eggs were used for greenhouse mesocosms.

(iii) Mesocosms. Testing took place at the CSU Plant Growth Facility. I created experimental plant communities containing *B. tectorum* and 15 native plant species commonly used in SSE restoration (often selected for this purpose largely because they are easily attainable through commercial sources) (Table 1). I established half the *B. tectorum* plants in winter (December 2011–January 2012), and native restoration plants plus remaining *B. tectorum* plants in spring (February 2012–April 2012) to mimic natural relative growth stages of plants when grasshoppers hatch (May–June). Plants were grown in well-draining media (potting soil:sand, 2:1 v/v) with no fertilization and no more than adequate water. Winter *B. tectorum* plants were moved outdoors approximately two weeks after germination. All other plants were grown indoors at the CSU Plant Growth Facility with a 16-h day/8-h night photoperiod and average day/night temperatures of 25.9/20.2 °C.

Table 1. Native plant species grown with *Bromus tectorum* in a greenhouse mesocosm study to test effects of grasshopper herbivory on plant community composition. These species were selected because they are commonly used in sagebrush steppe restoration. Duration indicates annual (A), biennial (B) or perennial (P) lifespan (USDA 2013).

Scientific Name	Common Name	Life Form	Duration
<i>Amsinckia menziesii</i>	Menzies' fiddleneck	forb	A
<i>Coreopsis tinctoria</i>	golden tickseed	forb	A/B/P
<i>Helianthus annuus</i>	common sunflower	forb	A
<i>Machaeranthera tanacetifolia</i>	tanseyleaf tansyaster	forb	A/B
<i>Oenothera pallida</i>	pale evening primrose	forb	B/P
<i>Elymus elymoides</i>	squirreltail	grass	P
<i>Leymus cinereus</i>	basin wild rye	grass	P
<i>Pascopyrum smithii</i>	western wheatgrass	grass	P
<i>Poa secunda</i>	Sandburg bluegrass	grass	P
<i>Pseudoroegneria spicata</i>	bluebunch wheatgrass	grass	P
<i>Artemisia frigida</i>	prairie sagewort	shrub	P
<i>Artemisia tridentata</i>	big sagebrush	shrub	P
<i>Chrysothamnus viscidiflorus</i>	yellow rabbitbrush	shrub	P
<i>Krascheninnikovia lanata</i>	winterfat	subshrub, shrub	P
<i>Purshia tridentata</i>	antelope bitterbrush	shrub	P

Mesocosms were constructed using SC-10 cone-tainer™ growing tubes (3.8 × 21 cm, 164-ml; Stuewe & Sons, Medford, OR) in 60- × 30-cm trays, which hold up to 98 tubes. Each mesocosm included an egg-laying substrate as described above. The egg container rested on the corner of the tray, leaving space for 90 plants (tubes). Each tube contained a single live plant at the start of the trial. Plant species were randomly positioned within each mesocosm. Mesocosms were placed in cages (0.65 m L × 0.35 m W × 1 m H) made of aluminum screening covering a PVC frame and placed on greenhouse benches in a randomized arrangement, with approximately 0.25-m space between adjacent mesocosms. Plants were watered weekly. The trial ran for six weeks (May 11–June 22).

I used a 2 × 2 factorial treatment design and tested ten replicates of each of four treatments:

1. All-native mesocosms without grasshoppers, consisting of six cone-tainers each of 15 native species for a total of 90 plants.
2. Native-plus-*B. tectorum* mesocosms without grasshoppers, consisting of three cone-tainers each of 15 native species (45 native plants in all), plus 44 *B. tectorum* plants for a total of 89 plants.
3. Same plants as treatment 1, plus grasshoppers.
4. Same plants as treatment 2, plus grasshoppers.

Early-instar grasshoppers experience high rates of mortality (Hewitt & Onsager 1983), so I expected some natural attrition in the number of grasshoppers per mesocosm and attempted to reduce density uniformly over the duration of the trial. Mesocosms were initially stocked with eight first-instar insects, then adjusted to five insects at week two and finally to two insects at week four. Replacement grasshoppers were reared on the same diet as grasshoppers in mesocosms (replacement grasshoppers for all-native treatments were allowed to self-select from native plants; replacements for native-plus-*B. tectorum* treatments were allowed to choose from *B. tectorum* and natives).

Stocking rate in the mesocosms of 25–40 grasshoppers m^{-2} was based on studies reporting natural grasshopper densities of 20–50 grasshoppers m^{-2} in SSE rangeland (Beckstead et al. 2008; Hewitt & Onsager 1983; Rogers & Uresk 1974). This is comparable to an outbreak-level infestation (Pfadt 1994). Densities of three to five grasshoppers m^{-2} are more commonly observed in this and other species (Branson et al. 2006; Hewitt & Onsager 1983). However, plant density in mesocosms was also high (about 450 plants m^{-2}), and herbivores other than the study insects were excluded by the screening (no other insects were observed in greenhouse mesocosms during the trial).

(iv) Data collection. After six weeks I harvested aboveground biomass remaining in cone-tainers by clipping plants at the soil surface. Material from each cone-tainer was bagged individually. Plants with no visible aboveground biomass remaining were recorded as mortalities. Biomass was oven dried at 65 °C to constant mass. Samples were weighed to obtain residual dry biomass of each plant from each mesocosm. Plants with dry biomass <0.0001 g were recorded as mortalities; this arbitrary (but conservative) cutoff value reflects the accuracy of the scale used to weigh samples.

(v) Statistical Analysis. Treatment effects were analyzed using SAS 9.3 (SAS Institute, Cary, NC, USA). To examine the effect of herbivory and plant community on whole-mesocosm biomass and individual species mortality, I used a two-way analysis of variance (SAS GLIMMIX procedure) with a Tukey-Kramer adjustment for multiple comparisons (mortality data were arcsine square root transformed prior to analysis). To compare treatment effects on individual species biomass, I used the non-parametric Kruskal-Wallis test (SAS NPAR1WAY procedure), since data violated the distribution assumptions of parametric tests. Where a significant difference in biomass was found, the simulation adjustment for least-squares means in the GLIMMIX procedure was used to distinguish which treatment effect(s) (herbivory, community, or interaction of herbivory and community) were significant at $\alpha = 0.05$.

Field Mesocosms

(i) Objective. Determine whether native, generalist grasshoppers remove greater amounts of native plant biomass compared to *B. tectorum* biomass. Determine whether *B. tectorum* presence affects the amount of native plant biomass removed by grasshoppers.

(ii) Experimental insects. I collected adult *Melanoplus bivittatus* weekly from mid-September through late October of 2012 at the ELC and brought them to the REL where they were raised using the same procedures as the Greenhouse Mesocosm study described above. An egg-laying substrate (700-ml plastic container filled with moist sterilized sand) was provided in each cage. Egg containers were removed from cages after 7–10 days and held at diapause temperature (4 °C) (Fisher 1994) from November 2012 until June 2013. Hatchlings from these eggs were used for field mesocosms.

(iii) Site Description. This experiment was conducted at a 130-hectare grassland site north of Fort Collins, Colorado (13T 0491505 4506630), which is owned by CSU. Elevation is approximately 1,525 m; topography is relatively flat (1–3% slopes). Soil type is Stoneham loam derived from mixed alluvium parent material (NRCS 2013). Dominant plants at the site are *Agropyron cristatum* L. Gaertn. (crested wheatgrass) and *Ericameria nauseosus* (rubber rabbitbrush). Winds are generally from the northwest at 4–5 m² average windspeed (US-DOE 2013). Average monthly precipitation and maximum daily temperatures during the growing season are approximately 3.75 cm and 19.7 °C (1994 to 2012; (HPRCC 2013). It rained 10.67 mm over the course of the experiment (June 22–August 19). Average daily temperature ranged from 16.72 to 23.55 °C during this period (recorded on a Campbell[®] Scientific CR1000 Weather Data Logger installed on site).

(iv) Site Preparation. In February 2013, existing vegetation was removed from the site using a tractor-mounted mower followed by a box scraper. The site was rototilled several times, lengthwise and crosswise, to 10-cm depth. Root wads and large rocks were removed. Rabbits were excluded from the site with poultry fencing around the perimeter (2.5-cm mesh approximately 1 m high, buried 10–15 cm below the soil surface).

(v) Mesocosms. I established field mesocosms using *B. tectorum* and eight native plant species. Native plant seeds were obtained in 2013 from Granite Seed Company. *Bromus tectorum* seed was collected in August 2011 from a site in Fort Collins, CO. I established forty plots (1.25×2 m) with 1-m rows between plots and a 2-m buffer around the entire plot layout. Plots were seeded in late February 2013 with one of two seed mixes (Table 2). Half the plots received a native-only mix with species seeded in equal proportions for a total of 3,000 pure live seeds (PLS) m^{-2} . The other half received a native-plus-*B. tectorum* mix using the same native seeding rate as native-only plots, plus *B. tectorum* at 1,000 PLS m^{-2} for a total of 4,000 PLS m^{-2} . Per-species seeding rates were adjusted to offset variable species germination rates and accomplish approximately equal cover of each native species in all plots, as well as 50% *B. tectorum* cover in native-plus-*B. tectorum* plots.

Table 2. Plant species and seeding rates used in a study testing effects of grasshopper herbivory in a context of *Bromus tectorum* invasion. Seed mix used in all-native plots included eight species commonly used in sagebrush steppe ecosystem restoration. Seed mix used in native-plus-*B. tectorum* plots included the same species and seeding rates as all-native plots, plus *Bromus tectorum*. Duration indicates annual (A), biennial (B) or perennial (P) lifespan (USDA 2013).

Scientific name	Common name	Life form	Duration	PLS m^{-2}
Species and seeding rates used in all-native plots:				
<i>Artemisia frigida</i>	Fringed sagebrush	shrub	P	420
<i>Artemisia tridentata</i>	Big sagebrush	shrub	P	600
<i>Chrysothamnus viscidiflorus</i>	Low rabbitbrush	shrub	P	300
<i>Coreopsis tinctoria</i>	Plains coreopsis	forb	A/B/P	375
<i>Helianthus annuus</i>	Common sunflower	forb	A	345
<i>Krascheninnikovia lanata</i>	Winterfat	shrub, subshrub	P	375
<i>Machaeranthera tenacetifolia</i>	Tanseyleaf tansyaster	forb	A/B	375
<i>Poa secunda</i>	Sandberg bluegrass	grass	P	210
Species and seeding rates used in native-plus- <i>B. tectorum</i> plots included the above plus:				
<i>Bromus tectorum</i>	cheatgrass	grass	A	1000

Immediately after seeding, plots were harrowed (using a 2-m length of 1.5-m chain link fencing attached to two support poles) to increase seed-soil contact, rolled with a water-filled roller to firm the seedbed, watered to 2.5-cm depth and covered with a 1-cm layer of wood straw. Plants were watered twice per month (if necessary) to approximate average precipitation conditions (1994 to 2012) (HPRCC 2013).

Grasshopper cages were constructed using Lumite[®] insect screening attached to a PVC frame (0.5 m L × 0.5 m W × 1 m H). Cages were installed in plots in one of six randomly chosen positions following seedling emergence in early June. Vinyl flaps along the bottom edge of the cage were partially buried and weighted with sandbags to prevent insect escape and entry. Two first-instar grasshoppers were placed in half of the mesocosms on June 22, 2013. Herbivores other than the study insects were excluded by the screening. Other insects (bees, moths, flies) and spiders were occasionally found in mesocosms during the trial period and were removed.

I used a 2 × 2 factorial treatment design and tested ten replicates of each of four treatments:

1. All-native plant community without grasshoppers, seeded with a native-only mix using eight species in equal proportions for a total of 3,000 PLS m⁻².
2. Native-plus-*B. tectorum* plant community without grasshoppers, seeded with the same native species and seeding rates as native-only plots, plus *B. tectorum* at 1,000 PLS m⁻² for a total of 4,000 PLS m⁻².
3. Same seed mix as treatment 1, plus two grasshoppers.
4. Same seed mix as treatment 2, plus two grasshoppers.

Grasshopper densities were increased to five first instar nymphs per cage (20 insects m⁻²) on June 26, 2013. As in the greenhouse mesocosm study, grasshopper stocking-rates were based on literature reports. Grasshoppers were censused twice per month and maintained at uniform

densities for the duration of the trial. Replacement grasshoppers were reared in additional cages in separate plots sown with the same seed combinations used in treatment cages.

(v) Data collection. After eight weeks the trial was ended (August 19, 2013). Grasshoppers were removed and plant biomass was harvested from cages. Plants were clipped at the soil surface, separated by species and bagged separately. Biomass was oven dried at 65 °C to constant mass prior to weighing. All species were weighed to the nearest 0.0001 g, except high-biomass species (*Helianthus annuus* and *B. tectorum*), which were weighed to the nearest 0.01 g.

(vi) Statistical Analysis. Where transformations were sufficient to achieve normality, I used two-way analysis of variance (SAS GLIMMIX procedure) with a Tukey-Kramer adjustment to assess the effects of community and herbivory on biomass. Where assumptions of normality were violated, I used the non-parametric Kruskal-Wallis test (SAS NPAR1WAY procedure) with a Monte Carlo simulation to estimate variance. Where a significant difference in biomass was found, the simulation adjustment for least-squares means in the GLIMMIX procedure was used to distinguish which treatment effect(s) (herbivory, community, or interaction of herbivory and community) were significant at $\alpha = 0.05$.

Results

Greenhouse Mesocosms: biomass

Grasshoppers significantly reduced native plant biomass as a group (all species pooled) ($p < 0.0001$). Presence of *B. tectorum* did not influence effects grasshoppers (Figure 1).

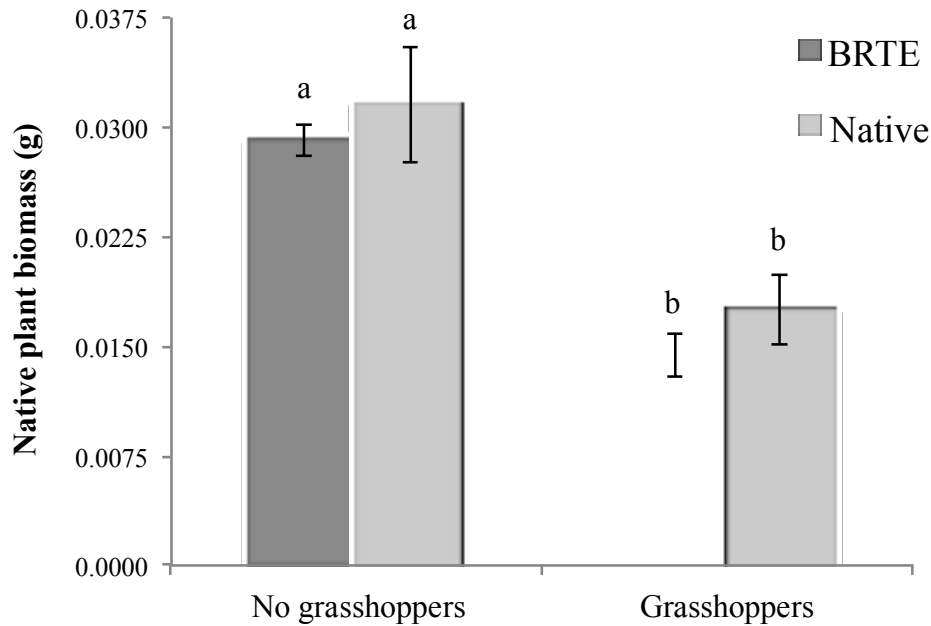


Figure 1. Total native plant biomass in greenhouse mesocosms, in a study testing effects of grasshopper herbivory in a context of *Bromus tectorum* invasion. All-native mesocosms (“Native”) contained 15 native plant species commonly used in sagebrush steppe ecosystem restoration. Native-plus-*B. tectorum* mesocosms (“BRTE”) contained the same native species as all-native mesocosms, plus *Bromus tectorum*. Means with the same letter are not significantly different at $\alpha = 0.05$.

Analysis of individual species responses showed grasshoppers significantly reduced biomass in all native species (Appendix, Table 7) except the following:

There was no effect of grasshoppers on biomass remaining in *Leymus cinereus* (basin wildrye), *Oenothera pallida* (pale evening primrose), and *Pascopyrum smithii* (Western wheatgrass). Grasshoppers significantly reduced *B. tectorum* biomass ($p < 0.0001$). Presence of *B. tectorum* increased *Elymus elymoides* and *Machaeranthera tenacetifolia* biomass in mesocosms lacking grasshoppers (both species; $p < 0.0001$).

Greenhouse mesocosms: mortality

Grasshoppers significantly increased mortality in native plants as a group ($p < 0.0001$) (Figure 2), as well as in *B. tectorum* ($p = 0.01$). Presence of *B. tectorum* had no effect on mortality in native plants as a group.

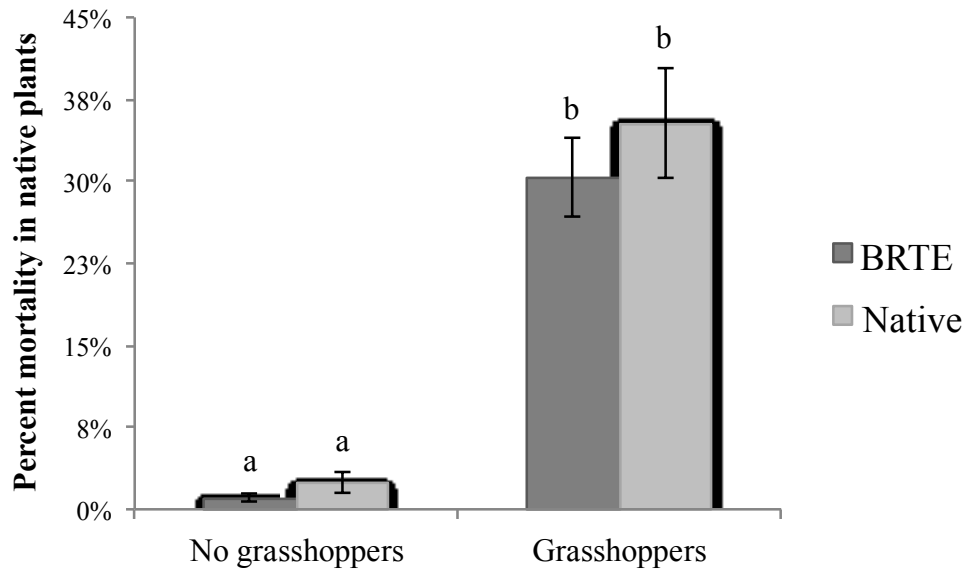


Figure 2. Mortality in native plants, in a study testing effects of grasshopper herbivory in a context of *Bromus tectorum* invasion. All-native mesocosms (“Native”) contained 15 native plant species commonly used in sagebrush steppe ecosystem restoration. Native-plus-*B. tectorum* mesocosms (“BRTE”) contained the same native species as all-native mesocosms, plus *Bromus tectorum*. Plants with dry biomass <0.0001 g were recorded as mortalities. Means with the same letter are not significantly different at $\alpha = 0.05$.

Analysis of individual species responses showed grasshoppers significantly increased mortality in all native plants except the following:

There was no effect of grasshoppers on mortality in *Elymus elymoides*, *Leymus cinereus*, *Pascopyrum smithii*, *Oenothera pallida*, and *Purshia tridentata* (antelope bitterbrush). Grasshopper herbivory increased mortality in *Pseudoroegneria spicata* (bluebunch wheatgrass) in all-native mesocosms, but not in mesocosms containing *B. tectorum*. Mortality in *Poa secunda* (Sandburg bluegrass) decreased in mesocosms with grasshoppers when *B. tectorum* was present ($p = 0.01$) (Figure 3).

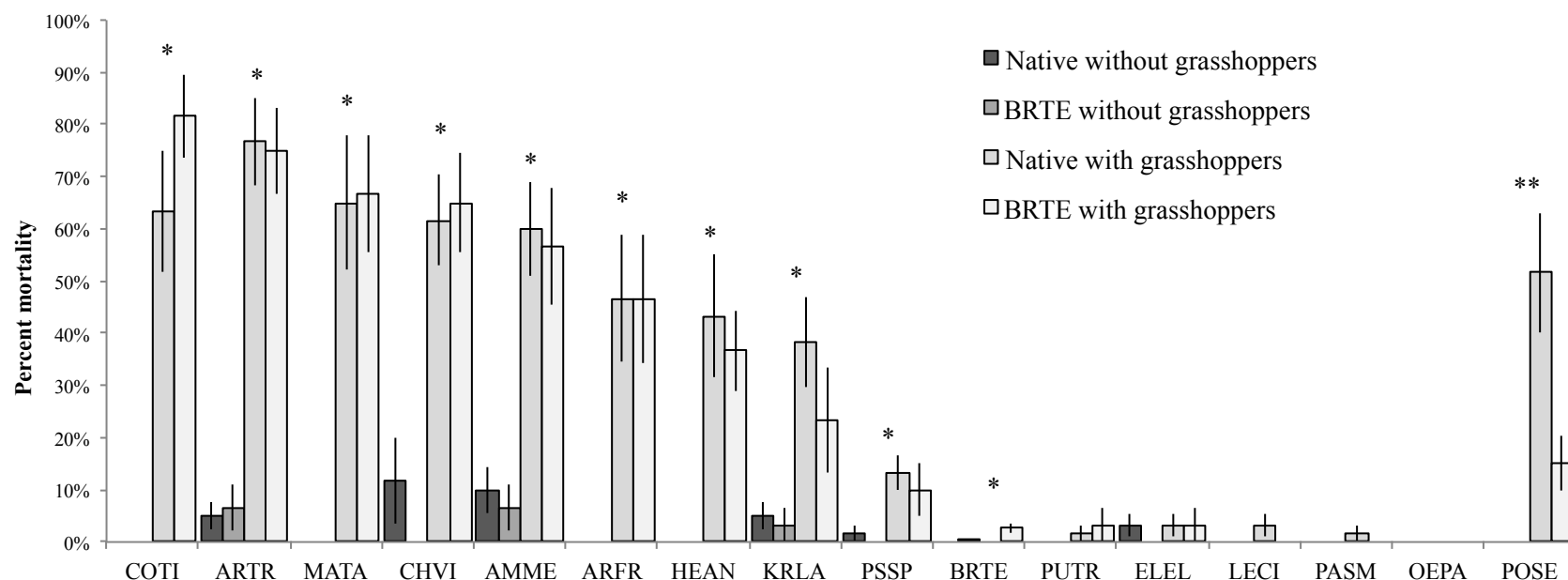


Figure 3. Mortality in native plants, in a study testing effects of grasshopper herbivory in a context of *Bromus tectorum* invasion. Plant biomass was collected from all-native (“Native”) vs. native-plus-*B. tectorum* (“BRTE”) greenhouse mesocosms with and without grasshoppers. Plants with dry biomass <0.0001 g were recorded as mortalities.

No asterisk indicates no significant difference in mortality between treatments.

* Significant increase in mortality resulting from grasshopper herbivory at $\alpha = 0.05$.

** Significant decrease in mortality resulting from *B. tectorum* at $\alpha = 0.05$

Species Codes

AMME	<i>Amsinckia menziesii</i>	KRLA	<i>Krascheninnikovia lanata</i>
ARFR	<i>Artemisia frigida</i>	LECI	<i>Leymus cinereus</i>
ARTR	<i>Artemisia tridentata</i>	MATA	<i>Machaeranthera tanacetifolia</i>
BRTE	<i>Bromus tectorum</i>	OEPA	<i>Oenothera pallida</i>
CHVI	<i>Chrysothamnus viscidiflorus</i>	PASM	<i>Pascopyrum smithii</i>
COTI	<i>Coreopsis tinctoria</i>	POSE	<i>Poa secunda</i>
ELEL	<i>Elymus elymoides</i>	PSSP	<i>Pseudoroegneria spicata</i>
HEAN	<i>Helianthus annuus</i>	PUTR	<i>Purshia tridentata</i>

Field Mesocosms

Helianthus annuus was the dominant species in field mesocosm plots both in terms of physical stature and density. I excluded it from the pooled analysis of native plants because 1) only one *Helianthus* sample (out of 38) had lower biomass than the highest-biomass native (out of 131 samples) and, 2) total *Helianthus* biomass was about 30 times the biomass of all seven other native plants combined (Figure 4)

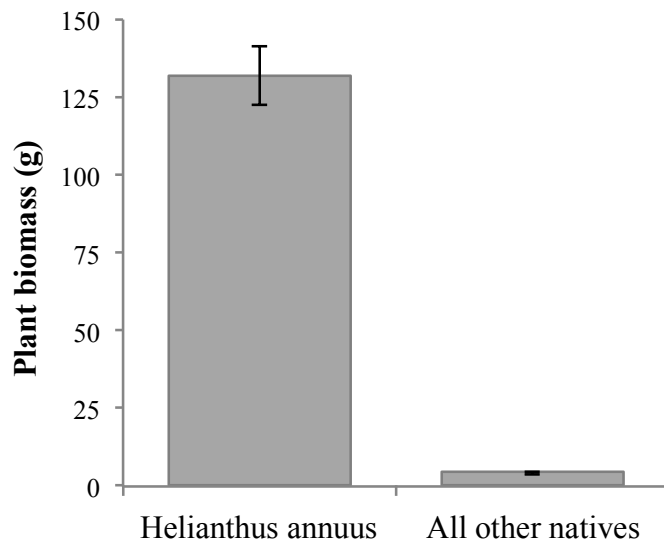


Figure 4. Biomass of *Helianthus annuus* biomass compared to native plant biomass (averaged across all treatments) in a study testing effects of grasshopper herbivory in a context of *Bromus tectorum* invasion. Plant biomass was collected from field mesocosms with and without grasshoppers. Means with the same letter are not significantly different at $\alpha = 0.05$.

Presence of either *B. tectorum* alone or grasshoppers alone did not affect *Helianthus annuus* biomass. However, the combined presence of *B. tectorum* and grasshoppers significantly reduced *H. annuus* biomass ($p = 0.02$) (Figure 5).

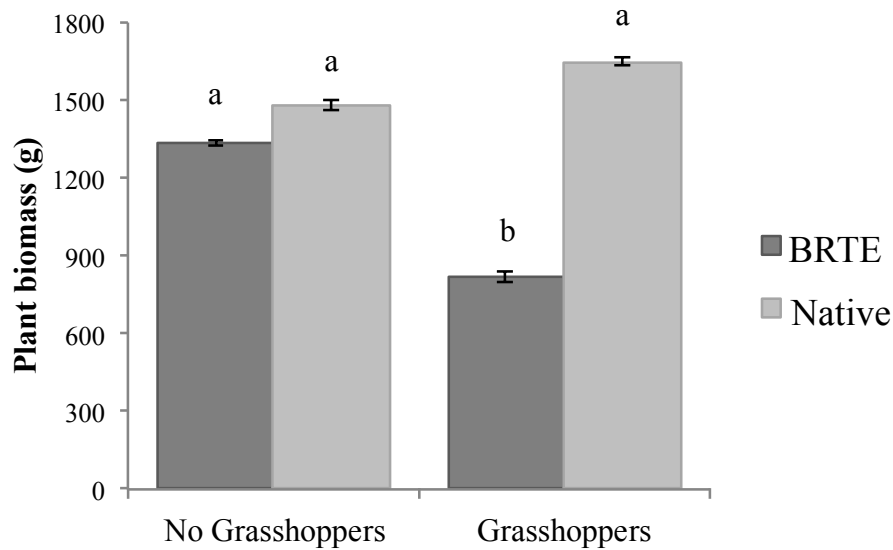


Figure 5. *Helianthus annuus* biomass from all-native field mesocosms (“Native”) compared to biomass in native-plus-*B. tectorum* mesocosms (“BRTE”) with and without grasshoppers. Means with the same letter are not significantly different at $\alpha = 0.05$.

For native plants as a group (all species pooled, except *Helianthus annuus*), grasshoppers had a significant effect on biomass ($p = 0.02$) (Figure 6). There was no effect of *B. tectorum*. Grasshoppers had no effect on *B. tectorum* biomass (data not shown).

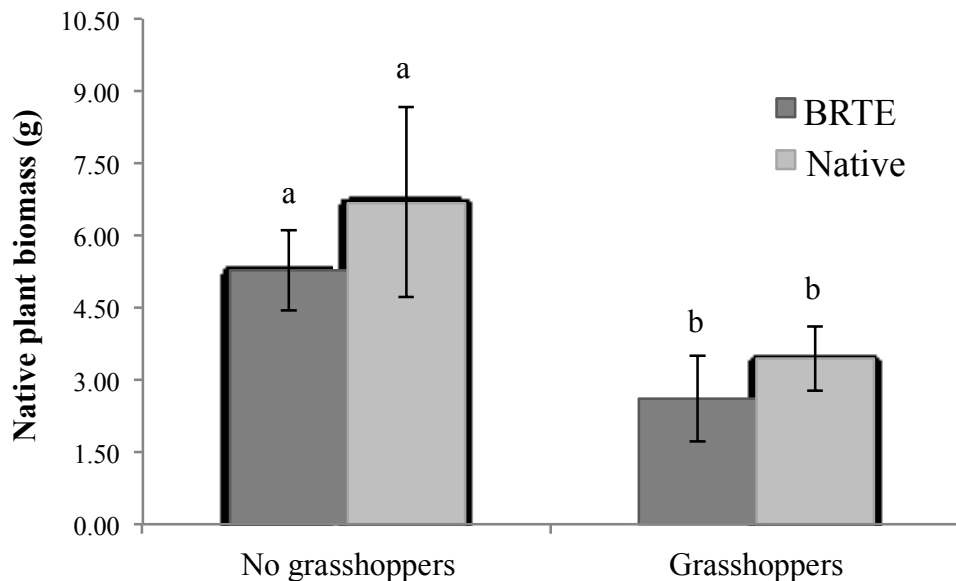


Figure 6. Biomass in native plants, in a study testing effects of grasshopper herbivory in a context of *Bromus tectorum* invasion. Plant biomass was collected from all-native (“Native”) vs. native-plus-*B. tectorum* (“BRTE”) field mesocosms with and without grasshoppers. Means with the same letter are not significantly different at $\alpha = 0.05$.

Analysis of individual native species biomass (Appendix, Table 8) indicated grasshoppers had no effect on biomass of individual native species for all but the following:

Grasshoppers reduced *Chrysothamnus viscidiflorus* (rubber rabbitbrush) biomass; the species appeared only in plots without grasshoppers ($p < 0.0001$). Grasshoppers reduced *Coreopsis tinctoria* (plains coreopsis) biomass ($p < 0.0001$); the species appeared in only one of 20 plots with grasshoppers (vs. 19 of 20 plots without grasshoppers). Either grasshoppers or *B. tectorum* significantly reduced *A. tridentata* biomass ($p < 0.05$), but the combined presence of *B. tectorum* and grasshoppers had no effect (Figure 7).

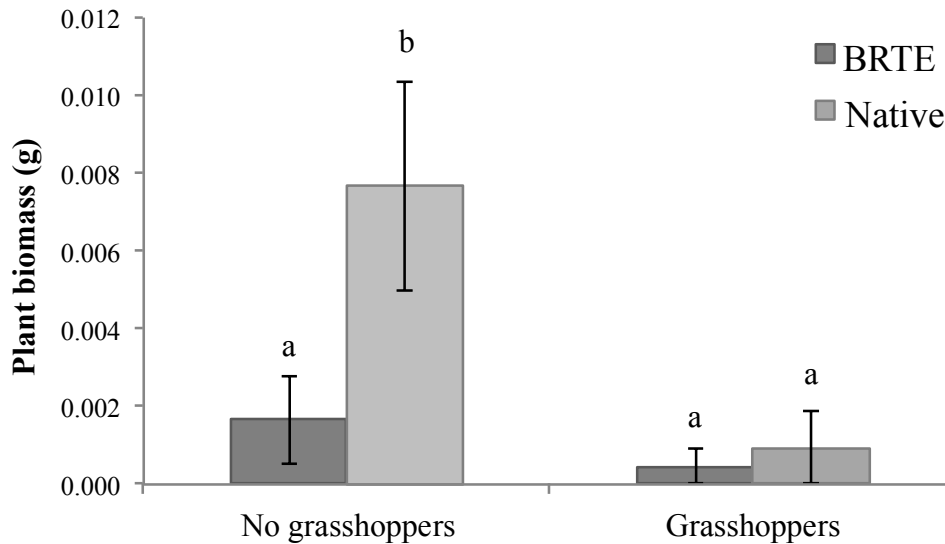


Figure 7. *Artemisia tridentata* biomass, in a study testing effects of grasshopper herbivory in a context of *Bromus tectorum* invasion. Plant biomass was collected from all-native (“Native”) vs. native-plus-*B. tectorum* (“BRTE”) field mesocosms with and without grasshoppers. Means with the same letter are not significantly different at $\alpha = 0.05$.

Discussion

I hypothesized that grasshopper herbivory would have a greater impact on natives where *B. tectorum* was present, due to grasshopper feeding preference for native plants. My data did not support this hypothesis. I found no significant difference in native biomass in mesocosms with

vs. without *B. tectorum*. Grasshoppers significantly reduced biomass in most SSE (sagebrush steppe ecosystem) natives but *B. tectorum* “invasion” in my experimental communities did not appear to increase feeding pressure on most native plants and in fact slightly relieved feeding pressure on some species.

An unexpected result was observed for *Elymus elymoides* and *Machaeranthera tenacetifolia* in the absence of grasshoppers. Both species had significantly greater biomass where *B. tectorum* was present. For these species, *B. tectorum* apparently had a facilitative effect, despite the fact that plants were grown in separate containers and therefore were not interacting below ground. Notably, grasshoppers eliminated this benefit and significantly reduced biomass of both species, as well as increased mortality in *M. tenacetifolia*.

Grasshoppers significantly increased mortality in native species as a group. Mortality was highest in forbs and shrubs, including the SSE keystone species *A. tridentata*. Mortality in *B. tectorum* also increased significantly where grasshoppers were present, but was approximately the same as “background” native plant mortality (i.e., mortality when grasshoppers were absent).

Grasshoppers did not increase mortality in three of the five grass species studied (*Elymus elymoides*, *Leymus cinereus*, *Pascopyrum smithii*). A fourth species, *Poa secunda*, showed significantly *decreased* mortality when both *B. tectorum* and grasshoppers were present, suggesting *B. tectorum* is a preferred food plant for grasshoppers compared to this species. Other species with results indicating resistance to herbivory were *Purshia tridentata* (grasshoppers reduced biomass, but not mortality), and *Oenothera pallida* (grasshoppers did not reduce biomass and no plants died in any treatment; suggesting *O. pallida* is not a preferred food).

My intention was to allow the greenhouse mesocosm trial to continue until all grasshoppers were at least two weeks into adult stage, so that effects of herbivory could be observed over the course

of an entire growing season. Instead, plants were defoliated so quickly I ended the trial well before grasshoppers reached maturity. I do not expect that confinement in mesocosms affected herbivory rates since, given adequate resources, grasshoppers tend to remain within a relatively small area (mean movement < 4 m per 36 hour period) (Narisu et al. 1999). However, despite a gradual reduction in insect density, plant regrowth did not keep pace with biomass loss via herbivory. I surmise that the retractable shading system used to regulate temperature in the CSU Plant Growth Facility reduced sunlight enough to prevent vigorous plant regrowth. Further evidence for this was the slow rate of grasshopper development as the experiment proceeded. Normal growth rates (about one week per instar) are slowed at lower temperatures (Fry 1927; Langford 1930). Most grasshoppers in the greenhouse mesocosms (92%) had only reached third instar when the trial was terminated at week six.

Field mesocosm data supported my hypothesis for some but not all native plants tested. For native plants as a whole, only the effect of grasshoppers was statistically significant. Presence of *B. tectorum* did not significantly affect herbivory outcomes except in certain species.

Examining individual species responses revealed several different patterns. The keystone shrub *Artemisia tridentata* is of particular concern in SSE restorations and has high value as a food plant for greater sage grouse (Patterson 1952; Rogers 1964). In my study, *Artemisia* seedling biomass was significantly reduced where either grasshoppers or *B. tectorum* were present, suggesting both factors have the potential to inhibit sagebrush regeneration and both should be considered in SSE restoration planning. Another SSE shrub, *Chrysothamnus viscidiflorus*, was also significantly impacted by herbivory, appearing only in plots where grasshoppers were absent. Competition with *B. tectorum* does not appear to be an important factor. For restoration purposes in areas where grasshoppers are prevalent, my results indicate that *Krascheninnikovia*

lanata (winterfat) germinates reliably and is either a less preferred food plant or more tolerant of herbivory than the other two shrubs examined, with no significant reduction in biomass across treatments.

Native annual forbs were included in the species tested because their rapid growth rates and tolerance of post-disturbance conditions makes them potential competitors to *B. tectorum*. All three native annuals performed fairly well in field mesocosms. Analysis of *Helianthus* data suggested the species can perform well in competition with *B. tectorum* — there was no significant reduction in *Helianthus* biomass where *B. tectorum* was present. *Helianthus* also tolerates herbivory well, with no significant reduction in average biomass with vs. without grasshoppers. However, it appears grasshoppers strongly prefer *Helianthus* to *B. tectorum*: Despite the large amount of *Helianthus* biomass present, grasshoppers significantly reduced *Helianthus* biomass in plots where *B. tectorum* was present. Another annual forb, *Coreopsis tinctoria*, also competed fairly well with *B. tectorum* (no reduction in biomass where *B. tectorum* was present). But in contrast to *Helianthus*, it appears grasshoppers not only prefer *Coreopsis* to *B. tectorum* but *Coreopsis* is less tolerant of grasshopper herbivory, appearing in only one plot where grasshoppers were present vs. all but one plot where grasshoppers were absent. The best-performing annual in my study was *Machaeranthera tenacetifolia*. This species appeared with equal frequency in plots with and without both *B. tectorum* and grasshoppers, with no difference in biomass across treatments. Forbs are another important component of the sage grouse diet (Klebenow & Gray 1968). The resilience of *M. tenacetifolia* to both grasshopper herbivory and *B. tectorum* competition indicates the species could be a key forb in SSE restoration seed mixes. Because most native grasses performed well in greenhouse mesocosms, the only native grass I included in field mesocosms was *Poa secunda*. This species had significantly lower mortality in

greenhouse mesocosms with grasshoppers when *B. tectorum* was present, suggesting grasshoppers could strongly prefer *B. tectorum*. In field mesocosms, there was no significant difference across treatments in *P. secunda* biomass. This result doesn't rule out grasshopper preference for *P. secunda* as a food plant, but suggests the species can better withstand herbivory in good growing conditions.

Finally, there was no significant reduction in *B. tectorum* biomass where grasshoppers were present. As I expected, abundant sunlight in the field mesocosms compared to the greenhouse setting apparently supported vigorous regrowth in *B. tectorum* plants, allowing them to recover from grasshopper feeding. In addition, *B. tectorum* was the only seeded species that appeared in 100% of plots where it was sown. Though the experiment was not a test of seedling competition, this result is another indication of competitive advantage in *B. tectorum* compared with SSE restoration natives.

My results do not allow me to make generalized statements that would either support or dispute hypotheses regarding exotic species invasions. The enemy release hypothesis predicts greater impact of generalist consumers on native species (Keane & Crawley 2002). Data from my greenhouse mesocosms suggest the opposite for some species. Generalist grasshoppers significantly reduced *B. tectorum* biomass but did not significantly reduce biomass in certain natives (mostly grasses). Grasshopper herbivory also led to significantly greater mortality in *B. tectorum* while causing low or no mortality in several natives. The mortality outcome suggests growth form does not factor strongly in *B. tectorum*'s success. Grasses (including *B. tectorum*) may be more resistant to herbivory than forbs and shrubs, since basal meristems are less accessible to herbivores, but native grasses in my study either had better resistance to herbivory than *B. tectorum* or were less preferred.

On the other hand, my results also do not unequivocally support the biotic resistance hypothesis, which predicts generalist enemy impact on exotics will limit invasions (Parker & Hay 2005). Despite widespread, abundant grasshopper distributions and multiple indications of *B. tectorum* consumption by grasshoppers in this and other studies, grasshopper herbivory does not appear to have appreciably curtailed *B. tectorum* spread in sagebrush steppe communities. Potential impacts of *B. tectorum* invasion were illustrated by my study results in shrubs and forbs. For most SSE restoration shrubs and forbs in my study, presence of *B. tectorum* did not significantly increase native plant biomass or reduce native plant mortality. In other words, even though *B. tectorum* is evidently an acceptable food plant for generalist grasshoppers, its availability either did not relieve feeding pressure on native plants or did not relieve it enough for natives to benefit. Finally, in field mesocosms, biomass for native species as a whole significantly decreased where grasshoppers were present, whereas *B. tectorum* biomass was unaffected. I obtained no evidence that generalist grasshoppers may provide “biotic resistance” of SSE to *B. tectorum* invasion. This finding is in agreement with other researchers’ observation that (compared with vertebrates) invertebrate herbivores may have modest impacts on exotic plant invasions (Parker et al. 2006).

Only one result from my study supports the apparent competition hypothesis: There was a significant effect of interaction between community and herbivory for *Helianthus annuus*, i.e., grasshoppers did not significantly decrease *Helianthus* biomass except in mesocosms where *B. tectorum* was present. For other species, competition with *B. tectorum* and intolerance of herbivory may be more important factors limiting restoration success and sustaining *B. tectorum* dominance. Taken together, my data suggest invasion resistance at the community scale may largely depend on traits of individual species and how they are distributed.

Management Recommendations

An encouraging result for SSE restoration in areas with high grasshopper densities was the resilience of native grass species to herbivory. Four of the five grasses I studied (*Elymus elymoides*, *Leymus cinereus*, *Pascopyrum smithii*, *Poa secunda*) were highly tolerant of grasshopper herbivory. The fifth native grass species in my study, *Pseudoroegneria spicata*, was historically the dominant SSE bunchgrass (Mack & Pyke 1983) and is commonly recommended for use in SSE restorations as one of the most ecologically and economically important native grasses (Monsen et al. 2004). But my results affirm what others have found: Compared to other native grass species, *P. spicata* is particularly sensitive to herbivory and therefore likely a poor choice in restoration seed mixes where grasshoppers are common. (*cf.* Daubenmire 1940). Studies of food plant selection in a grasshopper species closely related to *M. bivittatus* (*M. sanguinipes*) indicated *P. spicata* is a preferred food plant (Rogers & Uresk 1974), a finding in agreement with my results (see Chapter 3). The combined impact of low tolerance to herbivory and high desirability as a food plant may help explain why introduced species have overtaken much of *P. spicata*'s historical range (Zlatnik 1999).

Results from my study indicate that the shrubs *Purshia tridentata* and *Krascheninnikovia lanata* and the forbs *Oenothera pallida* and *Machaeranthera tenacetifolia* are resistant to grasshopper herbivory. These species are either not preferred food plants for *M. bivittatus*, are more tolerant of herbivory than other native plants, or are able to establish and survive in competition with *B. tectorum* as well as tolerate grasshoppers. *P. tridentata* and *K. lanata* are particularly valuable forage species for wildlife and livestock in SSE rangeland (Vallentine 1989); along with the other natives mentioned, these species would make good candidates for SSE restoration in areas with high grasshopper densities or where grasshopper control programs are cost-prohibitive.

The objective of this research was to contribute to an understanding of the ecological impacts of an invasive species. Extensive research has been conducted exploring the implications of *B. tectorum* invasion, yet there has been little focus on how it might affect feeding patterns in native grasshoppers — often the dominant consumers in its host range. Likewise, effects of grasshopper herbivory have mostly been investigated out of concern for how grasshoppers might negatively impact agricultural crops or rangeland forage; their effect on wildland plant distributions and potential role in the spread dynamics of invasive species has received minimal attention (but see Branson & Sword 2009). Results of my research suggest generalist grasshoppers readily consume *B. tectorum*, though likely more readily before the plant reaches bolt stage, and certainly less readily than they consume preferred natives. Consequences of grasshopper herbivory are not equal for all species: Half the species in my study were significantly impacted by either *B. tectorum*, grasshoppers, or both; some plants were not affected by grasshopper herbivory but unfortunately *B. tectorum* was among them. My results suggest grasshoppers have the capacity to influence SSE restoration success, grasshopper herbivory may alter SSE plant community composition as *B. tectorum* invasion progresses, and availability of *B. tectorum* as a food plant could influence grasshopper distributions.

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Chapter 3. Interactions between *Bromus tectorum*, grasshoppers and sagebrush steppe restoration plants: laboratory and field studies

Introduction

Among the many plants introduced to Western North America, the most successful has been the annual grass *Bromus tectorum* (cheatgrass), which was introduced from Eurasia numerous times, beginning in the late 1800s (Huttanus et al. 2011). As of 1981, *B. tectorum* was common — and in many areas dominant — over an estimated 400,000 km² of sagebrush steppe (Mack 1981). *Bromus tectorum* invasion has had profound impacts on sagebrush steppe ecosystem function through altering fire regime, modifying soil nutrients, and outcompeting SSE plant species for space and resources (Knapp 1996; Whisenant 1990). *Bromus tectorum* density is negatively correlated with native plant abundance (Davies et al. 2011; Rau et al. 2011).

As *B. tectorum* invasion progresses and the proportion of native plants in sagebrush steppe ecosystems is reduced, herbivores will experience alterations to their food resources. There is evidence — especially for insects colonizing new plant hosts — that herbivorous insects may quickly adapt to utilize novel food sources (Strauss et al. 2006). However, not all species will benefit from the new arrival. Instead it can be expected that plant invasions will benefit some insect herbivores disproportionately. A widespread and dominant invasive thus has the potential to rearrange food webs and impact insect community composition.

In North American rangelands, grasshoppers are often the dominant herbivores in terms of biomass consumed (Belovsky & Slade 2000; Branson et al. 2006). *Bromus tectorum* is consumed by grasshoppers, though not necessarily in proportion to its availability. Rogers & Uresk (Rogers & Uresk 1974) found *B. tectorum* appeared with 100% frequency in survey areas but only 11%

frequency in grasshopper (*Melanoplus sanguinipes*) crop contents. Plant nutrient concentration likely played a role; plants appearing with greatest frequency in grasshopper crops were biennial forbs (Rogers & Uresk 1974). Forbs generally have higher nutrient concentration than grasses (Randolph et al. 1991).

Since nitrogen availability is limited in most ecosystems, it would seem plausible that grasshoppers would choose to consume high-protein plants (~ high nitrogen concentration). Nitrogen is a key nutrient; however, grasshoppers do not select exclusively for nitrogen but rather for a particular balance of nutrients from their foods (Simpson & Raubenheimer 1999). Insects cannot generally compensate for poor food quality by feeding at higher rates, due to physiological constraints (Crawley 1989). Grasshoppers' preferred food plants are those that produce the best growth, survival and reproductive outcomes (Mulkern 1967). If SSE plants provide nutritionally balanced food sources for grasshoppers, an abundance of *B. tectorum* will not necessarily make up for an absence of SSE plants in their diet. For instance, nymphs of a mixed-feeding grasshopper species given a 100% brome grass (*B. inermis*) diet fed on it, but none lived beyond third instar (MacFarlane & Thorsteinson 1977).

Investigations have been made into the comparative nutritional value of *B. tectorum* vs. native plants. In one study, young *B. tectorum* had much higher protein concentration (18.6% crude protein overall) than a common SSE shrub, bitterbrush (*Purshia tridentata*) (approximately 7% crude protein) (Bishop et al. 2001). But protein concentration in annual grasses declines as the growing season progresses (Hart et al. 1932). In another comparison, *B. tectorum* contained significantly higher nitrogen concentration than native species (mostly perennial grasses) only until seed-ripening stage. After seed-ripening, *B. tectorum* nitrogen concentration was significantly lower than the natives' (Beckstead et al. 2008). If grasshoppers consume

B. tectorum, their consumption would likely fluctuate over the season in response to changing nutrient levels.

Studies of population-scale impacts of *B. tectorum* invasion on grasshoppers are limited, but there is evidence that *B. tectorum* affects species distributions. Fielding & Brusven (1992) found that sites dominated by exotic grasses (primarily *B. tectorum*) had high grasshopper densities but low diversity. Beckstead, et al. (2008) found grasshopper density was twice as high in high-density *B. tectorum* patches than in low-density patches. Grasshopper species that are able to utilize *B. tectorum* may be selected for through a variety of mechanisms. Young *B. tectorum* has high nitrogen concentration, a limiting factor in grasshopper egg production (Branson et al. 2006). *Bromus tectorum* outcompetes native plants for water; low water content in food plants may decrease grasshopper egg production (Bailey & Mukerji 1976). These and other aspects of *B. tectorum* physiology and competitive ability could promote higher nymphal survival early in the growing season and / or higher reproductive rates late in the season for *B. tectorum* consumers.

The purpose of this study was to investigate whether *B. tectorum* is associated with grasshoppers in natural settings as well as whether *B. tectorum* is a preferred food source for grasshoppers relative to native plants, and if so, whether *B. tectorum* consumption improves grasshopper fecundity. Insects tested were two-stripe grasshoppers (*Melanoplus bivittatus*; Orthoptera: Acrididae: Melanoplinae), a widespread, mixed-feeding generalist species. Native plants tested were either (or both) 1) species commonly utilized in sagebrush steppe restoration projects or 2) species that have shown potential, in experimental trials, to compete well with *B. tectorum* (and thus are plausible SSE restoration candidates).

I assumed life history traits of plants tested would factor in grasshopper food choices and fecundity outcomes. Since many SSE natives (primarily forbs) have higher nutrient concentration than *B. tectorum* and remain green and thus relatively palatable after *B. tectorum* has bolted (Rogers & Uresk 1974), I hypothesized that grasshoppers would choose native restoration plants more often overall, and would ultimately consume greater amounts of native vs. *B. tectorum* biomass. However, I expected grasshoppers would exhibit equal or even greater preference for *B. tectorum* in early fall — during grasshopper reproductive stage — when native plants have either senesced or developed chemical / structural defenses and fresh *B. tectorum* seedlings are available. Results of this research may contribute to a better understanding of the impacts of *B. tectorum* invasion on SSE food webs, as well as guide efforts to restore native plant communities in areas with high local densities of grasshoppers.

Materials and methods

Paired-Choice Preference Trials

(i) Objectives. Determine whether native, generalist grasshoppers preferentially consume native plants compared to *B. tectorum*.

(ii) Experimental insect. I collected adult *Melanoplus bivittatus* weekly from mid-September through late October 2011 at Colorado State University's Environmental Learning Center (13T 498232 4489414) and brought them to the CSU Restoration Ecology Laboratory (REL) (Fort Collins, Colorado, USA). Grasshoppers were caged in Precision[®]-818 illuminated incubators at 35/30 °C with a 14-h photoperiod. All insects were given romaine lettuce, wheatgrass held in a water-filled beaker, brewers yeast, and wheat bran. This diet is a common and effective preparation for successful laboratory rearing of *M. bivittatus* (Jonas & Joern 2013).

Each cage contained an egg-laying substrate (700-ml plastic container filled with moist sterilized sand). Egg containers were removed after 7–10 days and held at diapause temperature (4 °C) (Fisher 1994) from November 2011 until May 2012. Hatchlings from these eggs were used for preference trials. Ten insects were tested per trial. Each insect was tested once.

(iii) Test plants. Testing took place in the REL. I assessed grasshopper food preferences using cut samples of *B. tectorum* paired against each of 17 native plant species commonly used in sagebrush steppe restoration (Table 3). I established test plants in early spring (February 2012–April 2012) at the CSU Plant Growth Facility. Plants were grown in well-draining media (potting soil:sand, 2:1 v/v) with no fertilization and no more than adequate water, and given a 16-h day / 8-h night photoperiod with average day / night temperatures of 25.9/ 20.2 °C.

Table 3. Native plant species commonly used in sagebrush steppe ecosystem restoration, in a test of grasshopper food preferences. Duration indicates annual (A), biennial (B) or perennial (P) lifespan (USDA 2013).

Botanical Name	Common Name	Life form	Duration
<i>Amsinckia menziesii</i>	Menzies' fiddleneck	forb	A
<i>Coreopsis tinctoria</i>	golden tickseed	forb	A/B/P
<i>Helianthus annuus</i>	common sunflower	forb	A
<i>Machaeranthera tanacetifolia</i>	tanseyleaf tansyaster	forb	A/B
<i>Oenothera pallida</i>	pale evening primrose	forb	B/P
<i>Elymus elymoides</i>	squirreltail	grass	P
<i>Leymus cinereus</i>	basin wild rye	grass	P
<i>Pascopyrum smithii</i>	western wheatgrass	grass	P
<i>Poa secunda</i>	Sandburg bluegrass	grass	P
<i>Pseudoroegneria spicata</i>	bluebunch wheatgrass	grass	P
<i>Artemisia tridentata</i>	big sagebrush	shrub	P
<i>Artemisia frigida</i>	prairie sagewort	shrub	P
<i>Atriplex canescens</i>	fourwing saltbush	shrub	P
<i>Chrysothamnus viscidiflorus</i>	yellow rabbitbrush	shrub	P
<i>Eriogonum umbellatum</i>	sulphur flower buckwheat	subshrub, shrub	P
<i>Krascheninnikovia lanata</i>	winterfat	subshrub, shrub	P
<i>Purshia tridentata</i>	antelope bitterbrush	shrub	P

(iv) Trials. Grasshopper food preferences can change depending on prior feeding (Otte 1975) and nutritional status of plants and insects (Simpson & Raubenheimer 2000). To maintain uniform influence on food choice, all insects were raised on the diet described above until they were tested. Preference testing took place from May–July 2012 and was conducted in a Percival® E-36HO growth chamber at 35 °C. Relative humidity was kept at 70% to maintain leaf turgor.

Test insects were starved for 24–28 hours before each trial, then placed in individual ventilated plastic observation boxes (15-cm L × 8.5-cm W × 10-cm H) containing two petri dishes with *B. tectorum* in one dish and a native plant species in the other. Dishes contained similar amounts of material. Trials lasted 15 minutes, the length of an average feeding bout for this species (Langford 1930). Since grasshoppers may select food plants based on visual cues, I cut plant material into similar-size pieces, about 5 mm × 3 mm. Prior studies of food preference in a closely related species (*M. sanguinipes*) found that although chopping leaves increased the amount of volatile substances released, this did not influence choice (Kang & Hopkins 2004).

Newly hatched grasshoppers with no prior experience are able to detect and orient to host plants by tracking odor, and these responses become stronger as insects mature (Kang & Hopkins 2004). To determine whether food preferences change over the insects' lifespan, I conducted choice tests at each instar. I avoided testing insects for at least 24 hours following ecdysis. Results from insects that molted during feeding trials were discarded. Because of the nutritional demand of egg production, it is possible that adult female grasshoppers have different food preferences from adult males; in addition, females eat up to three times as much as males (Langford 1930), so I tested adult males and females separately.

(v) Data collection. Plant material was clipped and weighed immediately before each trial. Approximately equal samples of both species were prepared for each trial as controls for

calculating evaporative mass loss and wet-to-dry mass conversions. Samples were weighed again immediately upon completion of the trial. After accounting for water loss and converting wet mass to dry mass, difference in dry plant mass before and after exposure to feeding by grasshoppers (to the nearest 0.01 mg) was recorded as the amount consumed.

(vi) Statistical analysis. Treatment effects were analyzed using SAS 9.3 (SAS Institute, Cary, NC, USA). I conducted paired t-tests (SAS TTEST procedure) to determine whether there was a statistically significant difference in mean amount of *B. tectorum* vs. native plant material consumed per trial. A species was considered preferred if the amount consumed was significantly greater than the amount consumed of the other species given in the trial (native consumed - *B. tectorum* consumed \neq 0) at $\alpha = 0.05$.

Field Surveys

(i) Objectives. Determine whether grasshopper density and species richness is correlated with percent cover of *B. tectorum* in SSE.

(ii) Survey protocol and data collection. In May and August 2012, I surveyed 37 sites across five states in the Intermountain West (Colorado, Utah, Nevada, Idaho and Wyoming) (Appendix, Table 9). Sites were selected to represent a range of soil types, elevations, and prevailing soil moisture conditions, but vegetation at all sites included either SSE shrubs (primarily *Artemisia tridentata*), *B. tectorum*, or both. Where possible, sites with high *B. tectorum* cover were matched with nearby sites with low to no *B. tectorum* cover but otherwise similar vegetation.

The survey team consisted of three members with two tasks: site data collection and grasshopper counts. The first team member photographed the site, recorded date, time, slope, aspect and

weather data (temperature, windspeed, cloud cover), and entered the site location on a portable GPS unit (NAD 84 Datum). In addition, this team member took a sweep net sample along a 100-m transect through the center of the site for the purpose of determining relative species abundances and obtaining a voucher sample of grasshoppers at the location. Sweep net contents were placed in a labeled plastic storage bag and immediately frozen. On the first visit to each site, after surveying and sweep netting, the survey team recorded vegetation cover (by species) at 1-m intervals along the 100-m sweep-net transect using the point-intercept method.

Grasshopper density was estimated using the 18-point survey method developed by the USDA Animal and Plant Health Inspection Service (USDA-ARS 2008). Using this method, surveyors counted the number of grasshoppers fleeing a visually estimated 0.09-m² area approximately 3–4.5 meters ahead as they walked a 54–80-m transect. Eighteen such counts were made along each transect for a total of 1.62 m² sampled per transect. Grasshoppers jumping into the sample area were not counted. Upon reaching the sample area, surveyors probed the area with a stake to make sure all grasshoppers had flushed and been counted.

Two surveyors conducted density counts, each walking a separate density transect at each site. Density transects were placed in areas typical of the site making sure transects did not intersect and were located at least 20 paces away from the sweep-net transect line. I avoided sampling near roads, livestock trails, ditches, fence lines, or other features not representative of the general vegetation pattern. Surveys were conducted only on dry days well after sunrise (about 9:00 am) when temperature rose above 20 °C. In strong sunlight where the sampler's shadow was a factor, surveyors approached the sample point so their shadow did not flush grasshoppers prematurely.

(iii) Statistical analysis. I examined relationships between measurements using linear regression (SAS REG procedure). Data were transformed where necessary to meet the testing assumption of normal distribution.

Fecundity Trials

(i) Objectives. Determine whether availability of seedling *B. tectorum* at adult female reproductive stage affects fecundity in native, generalist grasshoppers.

(ii) Experimental insect. I collected adult *M. bivittatus* weekly from mid-September through late October 2012 at the Environmental Learning Center and brought them to the REL. Grasshoppers were caged, fed, and given an egg-laying substrate using the same methods as for Preference Trials. Egg containers were removed from cages after 7–10 days and held at diapause temperature (4 °C) (Fisher 1994) from November 2012 until June 2013. Hatchlings from these eggs were used for fecundity trials.

(iii) Site Description. This experiment was conducted at a 130-hectare grassland site north of Fort Collins, Colorado (13T 0491505 4506630), owned by CSU. Elevation is approximately 1,525 m; topography is relatively flat (1–3% slopes). Soil type is Stoneham loam derived from mixed alluvium parent material (NRCS 2013). Dominant plants are *Agropyron cristatum* L. Gaertn. (Crested Wheatgrass) and *Ericameria nauseosus* (Rubber Rabbitbrush). Winds are generally from the northwest at 4–5 ms⁻² average windspeed (U.S. Dept. of Energy 2013). Average monthly precipitation and maximum daily temperatures during the growing season at the site are approximately 3.75 cm and 19.7 °C (1994 to 2012, High Plains Regional Climate Center 2013). The site received 14.58 cm precipitation over the course of the experiment (August

20–October 4). Average daily temperature ranged from 7.66 to 25.78 °C during this period (recorded on a Campbell® Scientific CR1000 Weather Data Logger installed on site).

(iv) Site Preparation. In February 2013, existing vegetation was removed from the site using a tractor-mounted mower followed by a box scraper. The site was rototilled several times, lengthwise and crosswise, to 10-cm depth. Root wads and large rocks were removed. Rabbits were excluded from the site with poultry fencing around the perimeter (2.5-cm mesh approximately 1 m high, buried 10–15 cm below the soil surface).

(v) Mesocosms. I established field mesocosms using *B. tectorum* and eight native plant species. *Bromus tectorum* seed was collected in August 2011 from a site in Fort Collins. Native plant seeds were obtained in 2013 from Granite Seed Company. I established forty plots (1.25- × 2-m) with 1-m rows between plots and a 2-m buffer around the entire plot layout. Plots were seeded in February 2013 with one of two seed mixes (Table 4). Twenty plots were randomly selected to receive a native-only mix (“Native”) with equal proportions of all species for a total of 3,000 PLS (pure live seeds) m⁻². The other 20 received a native-plus-*B. tectorum* mix (“BRTE”) using the same seeding rates as native-only plots, plus *B. tectorum* at 1,000 PLS m⁻² for a total of 4,000 PLS m⁻². Per-species seeding levels were adjusted to offset variable germination rates and accomplish approximately equal cover of each native in all plots, as well as 50% *B. tectorum* cover in native-plus-*B. tectorum* plots. I established 15 replicates of each treatment. Immediately after seeding, plots were harrowed to increase seed-soil contact, rolled to firm the seedbed, watered to 2.5-cm depth to promote germination, and covered with a layer of wood straw. Plants were watered twice per month if necessary to approximate 18-year average precipitation conditions (HPRCC 2013). To ensure late-summer / early fall *B. tectorum* production, I again

added *B. tectorum* seed at 1,000 PLS m⁻² to treatment 2 and rearing cage plots on August 2, 2013, after *B. tectorum* plants had bolted.

Table 4. Seed mixes and seeding rates (pure live seed, PLS m⁻²) used in field mesocosms to test effects of plant community composition on grasshopper fecundity. Seed mix used in native-plus-*B. tectorum* plots included the same species and seeding rates as all-native plots, plus *Bromus tectorum*. Duration indicates annual (A), biennial (B) or perennial (P) lifespan (USDA 2013).

Botanical name	Common name	Life form	Duration	PLS m ⁻²
Species and seeding rates used in all-native plots:				
<i>Artemisia frigida</i>	Fringed sagebrush	shrub	P	420
<i>Artemisia tridentata</i>	Big sagebrush	shrub	P	600
<i>Chrysothamnus viscidiflorus</i>	Low rabbitbrush	shrub	P	300
<i>Coreopsis tinctoria</i>	Plains coreopsis	forb	A/B/P	375
<i>Helianthus annuus</i>	Common sunflower	forb	A	345
<i>Krascheninnikovia lanata</i>	Winterfat	shrub, subshrub	P	375
<i>Machaeranthera tenacetifolia</i>	Tanseyleaf tansyaster	forb	A/B	375
<i>Poa secunda</i>	Sandberg bluegrass	grass	P	210
Species and seeding rates used in native-plus- <i>B. tectorum</i> plots included the above plus:				
<i>Bromus tectorum</i>	cheatgrass	grass	A	1000

Grasshopper cages were constructed using Lumite[®] insect screening attached to a PVC frame (0.5 m L × 0.5 m W × 1 m H). Vinyl flaps along the bottom edge of the cage were partially buried and weighted with sandbags to prevent insect escape and entry. Cages were installed in plots in one of six randomly chosen positions.

An egg-laying substrate (700-ml plastic container filled with moist sterilized sand) was provided in each cage. Adult grasshoppers were moved from rearing cages to experimental cages on August 20, 2013. One adult female and two adult male grasshoppers were placed in each experimental cage. Phase I of the trial ran for 6 weeks and ended when *B. tectorum* seedlings appeared (September 17, 2013). At this point, egg containers were collected and replaced. Phase II of the trial ran for 2.5 weeks and ended when all grasshoppers were at least 45 days into adulthood (October 6, 2013). Egg cups removed from cages were stored at 4 °C.

Grasshoppers were censused twice per month and maintained at uniform densities for the duration of the experiment. Females were not replaced unless a dead female was found. Replacement grasshoppers were reared in additional cages in separate plots sown with the same seed combinations used in treatment cages.

(vi) Data collection. Egg pods were removed from the sand with a 5.6-mm soil sieve, cleaned with a brush to remove excess sand and weighed to the nearest 0.01 mg.

(vii) Statistical analysis. Egg pod mass data (log transformed) were analyzed using one-way analysis of variance (SAS GLIMMIX procedure).

Results

Paired-Choice Preference Trials

Grasshoppers showed no significant plant species preference in 64% of comparisons (17 native plant species \times 7 grasshopper life stages = 119 total comparisons). Early-instar grasshoppers exhibited statistically significant preferences more often than adults (Table 5).

Table 5. Count of significant preferences for *B. tectorum* vs. native plants in paired-choice feeding preference trials. Grasshoppers (*Melanoplus bivittatus*) at different life stages were given samples of native plant material alongside samples of *Bromus tectorum*. Trials were conducted on each nymphal instar (I–V), adult males (AM), and adult females (AF). Only statistically significant results are shown ($\alpha = 0.05$).

Instar	Plant species	
	<i>B. tectorum</i>	Native
II	10	4
III	4	3
IV	5	1
V	1	3
AM	3	0
AF	2	0
Total:	25	11

Where preference was significant (36% of comparisons), it was more often for *B. tectorum* (25%) than for native plants (11%) (Table 6a). Examining preference across all life stages indicated grasshoppers preferred *B. tectorum* in five out of 17 comparisons and preferred one native species (*Krascheninnikovia lanata*) to *B. tectorum* (Table 6b).

Table 6a. Results from t-tests of differences between mass of *B. tectorum* vs. mass of native plant consumed in paired-choice feeding preference trials. Grasshoppers (*Melanoplus bivittatus*) at different life stages were given samples of native plant material alongside samples of *B. tectorum*. Trials were conducted on each nymphal instar (I–V), adult males (AM), and adult females (AF). Negative t-values denote greater amount (dry weight) of *B. tectorum* consumed compared to native plant material; positive t-values denote greater amount of native plant material consumed compared to *B. tectorum*.

Only statistically significant results are shown ($\alpha = 0.05$).

Species	Instar	tValue	DF	Probt
Significant preference for cheatgrass over native				
<i>Amsinckia menzeisii</i>	II	-12.11	8	0.0000
<i>Artemisia frigida</i>	II	-4.14	9	0.0025
<i>Atriplex canescens</i>	II	-2.49	9	0.0342
<i>Elymus elymoides</i>	II	-3.68	9	0.0051
<i>Eriogonum umbellatum</i>	II	-3.41	9	0.0077
<i>Machaeranthera tenacetifolia</i>	II	-4.78	9	0.0010
<i>Pascopyrum smithii</i>	II	-7.79	9	0.0000
<i>Poa secunda</i>	II	-11.01	9	0.0000
<i>Pseudoroegneria spicata</i>	II	-4.45	9	0.0016
<i>Purshia tridentata</i>	II	-3.15	9	0.0117
<i>Chrysothamnus viscidiflorus</i>	III	-2.78	9	0.0214
<i>Eriogonum umbellatum</i>	III	-2.65	9	0.0264
<i>Oenothera pallida</i>	III	-2.83	9	0.0197
<i>Poa secunda</i>	III	-3.04	9	0.0140
<i>Chrysothamnus viscidiflorus</i>	IV	-5.85	9	0.0002
<i>Pascopyrum smithii</i>	IV	-2.27	9	0.0497
<i>Poa secunda</i>	IV	-3.67	9	0.0051
<i>Pseudoroegneria spicata</i>	IV	-2.35	9	0.0430
<i>Purshia tridentata</i>	IV	-6.06	9	0.0002
<i>Machaeranthera tenacetifolia</i>	V	-2.52	9	0.0329
<i>Helianthus annuus</i>	AM	-4.20	19	0.0005
<i>Pascopyrum smithii</i>	AM	-3.03	9	0.0143
<i>Purshia tridentata</i>	AM	-4.48	9	0.0015
<i>Artemisia frigida</i>	AF	-2.80	9	0.0206
<i>Eriogonum umbellatum</i>	AF	-3.34	9	0.0087

Table 6a, continued.

Species	Instar	tValue	DF	Probt
Significant preference for native over cheatgrass				
<i>Artemisia tridentata</i>	II	4.80	9	0.0010
<i>Coreopsis tinctoria</i>	II	3.39	9	0.0080
<i>Helianthus annuus</i>	II	16.80	9	0.0000
<i>Krascheninnikovia lanata</i>	II	3.34	9	0.0086
<i>Coreopsis tinctoria</i>	III	5.91	9	0.0002
<i>Krascheninnikovia lanata</i>	III	4.55	9	0.0014
<i>Machaeranthera tenacetifolia</i>	III	8.28	9	0.0000
<i>Machaeranthera tenacetifolia</i>	IV	2.37	9	0.0416
<i>Amsinckia menzeisii</i>	V	2.29	9	0.0480
<i>Krascheninnikovia lanata</i>	V	3.81	9	0.0042
<i>Pascopyrum smithii</i>	V	3.25	9	0.0101

Table 6b. Results from t-tests of differences between amount of *B. tectorum* vs. amount of native plant consumed in paired-choice feeding preference trials. Grasshoppers (*Melanoplus bivittatus*) at different life stages were given samples of native plant material alongside samples of *B. tectorum*. Trials were conducted on each nymphal instar (I–V), adult males (AM), and adult females (AF). Negative t-values denote greater mass (dry weight) of *B. tectorum* consumed compared to native plant material; positive t-values denote greater amount of native plant material consumed compared to *B. tectorum*.

Only statistically significant results are shown ($\alpha = 0.05$).

Species	tValue	DF	Probt
Significant preference for cheatgrass over native			
<i>Eriogonum umbellatum</i>	-3.42	59	0.0011
<i>Oenothera pallida</i>	-3.92	59	0.0002
<i>Pascopyrum smithii</i>	-2.43	59	0.0180
<i>Poa secunda</i>	-2.43	59	0.0182
<i>Purshia tridentata</i>	-2.71	59	0.0089
Significant preference for native over cheatgrass			
<i>Krascheninnikovia lanata</i>	2.03	59	0.0472

Field Surveys

At survey sites, grasshopper density and *B. tectorum* cover were positively correlated ($p < 0.01$, $R^2 = 0.11$). Grasshopper species richness and *B. tectorum* cover were also positively

grasshoppers in *B. tectorum* communities did not significantly differ from pods produced by grasshoppers in native plant communities (Figure 9).

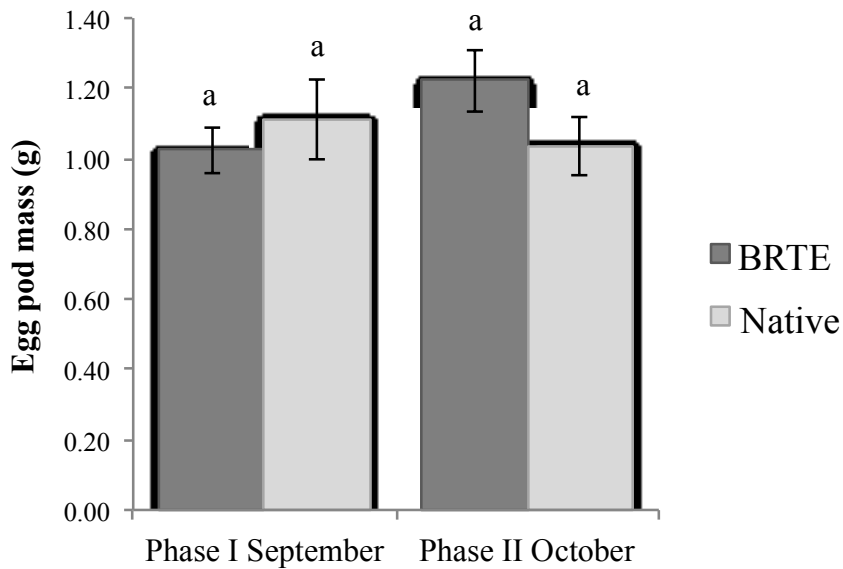


Figure 9. Mean egg pod weight produced by grasshoppers in *B. tectorum* (“BRTE”) vs. native plant (“Native”) communities over time. Phase I (September) was 4 weeks long; Phase II (October) was 2.5 weeks. Means with the same letter are not significantly different at $\alpha = 0.05$.

Discussion

I predicted native grasshoppers would generally prefer native plants to *B. tectorum*. Preference trial data did not support this hypothesis. First, grasshoppers showed no significant preference in most comparisons. Second, where grasshoppers did show a significant preference, it was more often for *B. tectorum* than for native plants.

I also expected that preferences would change as a factor of insect life-stage. Preference trial data support this prediction. Early-instar insects exhibited significant preferences more often than adults, particularly for *B. tectorum*. Adults, especially females, appear to have wider feeding tolerances. An unforeseen result was an increase in preference for native plants at instar V. This is the longest grasshopper developmental stage, during which reproductive and flight organs are

maturing, and could require nutrients more likely to be obtained from native plant sources. Measuring preference over a sustained period of herbivory by this age group (as opposed to 15-minute feeding bouts) could clarify whether this increase was simply chance variation.

One possible outcome resulting from a preference for *B. tectorum* by early-instar grasshoppers is that *B. tectorum* could boost survival to adulthood in species that hatch earlier in the season when *B. tectorum* nitrogen concentrations are at their peak (Beckstead et al. 2008). However, the net impact of *B. tectorum* for *M. bivittatus* could be that it presents an evolutionary trap, because it is highly palatable to early instars, yet the insect may not be able to complete its life cycle on this resource (Schlaepfer et al. 2005). This possibility is suggested by my data indicating an increase in native plant preferences at instar V.

In field surveys, I found a significant, positive correlation between *B. tectorum* cover and grasshopper density and species richness, but the low correlation coefficients in my results indicate grasshopper density and richness cannot be reliably predicted from *B. tectorum* cover and could be accounted for by other factors.

The response variable driving the correlation between *B. tectorum* and grasshoppers was density in the subfamily Cyrtacanthacridinae. Over half of USDA-identified crop and rangeland pest species (including *M. bivittatus*) are in this subfamily (USDA-ARS 2012). Other researchers have also observed a correlation between pest grasshopper species and annual grassland vegetation (Fielding & Brusven 1992).

I was not able to test the fecundity trial hypothesis precisely. The study design called for newly molted adults to be placed in cages with young *B. tectorum* present, but most grasshoppers had reached adulthood before *B. tectorum* germinated. This led to my decision to split the trial into phases (phase I: seedling *B. tectorum* absent; phase II: seedling *B. tectorum* present). Female

grasshoppers have a preoviposition period of one to two weeks before producing their first clutch of eggs (Pfadt 1994), so it is likely there was no egg production in either community type until the second half of phase I. But even taking this delay into account, effects of *B. tectorum* on female fecundity could only be observed from phase II results, because conditions for hypothesis testing were present only during phase II rather than the entire 6.5-week duration.

Despite this misalignment in plant and insect development, data from the fecundity trial suggest this hypothesis merits reinvestigation. A longer period of *B. tectorum* availability may have clarified the result. Female *M. bivittatus* have been observed laying eggs in the Fort Collins area into late October (personal observation; Langford 1930). A proper test of the hypothesis (given 2013 weather conditions) could have been obtained by introducing newly molted adults approximately three weeks later than I did.

In summary, I found several lines of evidence for utilization of *B. tectorum* by *Melanoplus bivittatus*. Field surveys indicate grasshoppers are responding to *B. tectorum* in sagebrush ecosystems. Preference trials show *M. bivittatus* not only consumes *B. tectorum* but prefers it in comparison to some native plants. Results from tests of fecundity impacts, though inconclusive, indicate that the question (whether *B. tectorum* could promote grasshopper reproductive success) warrants further investigation. Taken together, these results suggest *B. tectorum* invasion could be a factor structuring grasshopper communities. Rangeland and crop pest species that consume *B. tectorum* may already have gained competitive advantage. However, a certain proportion of native (or non-*B. tectorum*) plants probably needs to persist in the SSE plant community in order to sustain grasshopper diversity. A *Bromus tectorum* monoculture may ultimately be an evolutionary trap even for insects that readily consume it.

In addition, outcomes of interactions between grasshoppers, *B. tectorum* and native plants could cascade to other trophic levels. For example, juvenile sage grouse (<21 days old) require insects in their diet for survival and optimum growth (Johnson & Boyce 1990). Grasshoppers, ants and beetles compose up to 75% of foods consumed (Patterson 1952). However, after the first few weeks of life, forbs become the most important food for sage grouse; a pattern which continues into adulthood (Klebenow & Gray 1968). Sagebrush is another key food plant, comprising approximately 25% of the sage grouse summer diet (Patterson 1952; Rogers 1964). High grasshopper densities arising from *B. tectorum* availability could promote survival of sage grouse chicks. But declines in forb and sagebrush density — resulting from competitive suppression via *B. tectorum* and selective grasshopper herbivory — could establish another evolutionary trap, this one affecting sage grouse. An alternate pathway into the trap could arise if *B. tectorum* promotes outbreaks in pest grasshopper species, triggering control programs (pesticide applications). While not directly harmful to birds, spraying occurs during summer, when consumption of insects by juvenile sage grouse is at its peak (Johnson & Boyce 1990). Other sagebrush-associated avifauna, e.g., Sage Sparrow (*Amphispiza belli*), Sage Thrasher (*Oreoscoptes montanus*) and Grasshopper Sparrow (*Ammodramus savannarum*) may also be sensitive to *B. tectorum*-induced changes in SSE plant and invertebrate community composition (Knick et al. 2003; Slater 2004).

Other studies have examined interactions between introduced plants, grasshoppers and native plants. Branson and Sword (2009) noted that sites dominated by crested wheatgrass (*Agropyron cristatum*) often have high grasshopper densities; the authors hypothesized that selective grasshopper herbivory on native plants in *A. cristatum*-invaded grassland would promote *A. cristatum* dominance. They found generalist grasshopper herbivory reduced native forb richness,

abundance, and diversity in three of four years in *A. cristatum*-dominated sites, and suggested grasshoppers could impede efforts to restore *A. cristatum* sites to native grassland. Beckstead, et al. (2008) found evidence of associational herbivory / apparent competition in a Great Basin plant community invaded by *B. tectorum*, wherein a native grass (*E. elymoides*) experienced greater cumulative grasshopper herbivory and reduced reproductive potential in high- vs. low-density *B. tectorum* patches.

Results from my research affirm the essential findings of these prior studies. Grasshopper herbivory is likely influencing competitive outcomes between native and invasive plants; their impacts, especially at seedling stage, can influence plant community composition. Since large-scale grasshopper control efforts may have unwanted ecological consequences, considering the potential impacts of grasshopper feeding preferences when planning restoration efforts may improve SSE restoration success.

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Chapter 4. Conclusion and synthesis

This research investigated interactions between an exotic plant, *Bromus tectorum*, and plant competitors and generalist consumers in its new host range. Since little is known about impacts of *B. tectorum* invasion on relationships between native plants and insect herbivores, my studies (field surveys, laboratory trials, greenhouse and field experiments) gathered coarse-scale information to assess three potential mechanisms (enemy release, biotic resistance and apparent competition) that may be driving plant-insect interactions in an invaded ecosystem.

Field study results from this research provided limited support for the enemy release hypothesis: Average biomass in native plants as a whole was significantly reduced where herbivores were present, while *B. tectorum* biomass was unaffected. But a more accurate picture can be obtained by examining species responses on a case-by-case basis. For example, laboratory and greenhouse results suggested *Krascheninnikovia lanata* (winterfat) was highly preferred compared to *B. tectorum*, and *K. lanata* incurred significantly increased mortality when herbivores were present. However, in a field setting with better light conditions and other food plants available for grasshoppers, *K. lanata* emerged as a strong competitor, occurring with equal frequency across all treatments. In contrast, another SSE shrub species, *Chrysothamnus viscidiflorus* (yellow rabbitbrush), was not significantly preferred to *B. tectorum* in feeding trials, yet only appeared in field plots when grasshoppers were absent, suggesting it is strongly preferred in comparison with other plants. A third pattern appeared in *Helianthus annuus* (common sunflower) and *A. tridentata*. Both were preferred over *B. tectorum* by early-instar insects and significantly impacted by *B. tectorum* presence, grasshopper herbivory, or both. Given this variability in individual species interactions it may be meaningless to characterize enemy release as occurring for *B. tectorum* across native plant communities as a whole.

I also found no support for the biotic resistance hypothesis. *Bromus tectorum* is readily consumed by grasshoppers, and herbivory significantly increased *B. tectorum* mortality in my greenhouse study, but grasshoppers had no effect on *B. tectorum* biomass in field settings. This suggests that with adequate resources, *B. tectorum* can regrow at rapid enough rates to offset herbivory impacts. If so, *B. tectorum* could increase grasshopper abundances (possibly pest species) yet remain unconstrained by those same grasshoppers' feeding impacts. My results support other researchers' conclusion that (compared with vertebrates) invertebrate herbivores may have modest effects on exotic plant invasions (Parker et al. 2006).

Finally, I did not find general support for the apparent competition hypothesis. With the exception of *Helianthus annuus*, *B. tectorum* presence did not significantly increase feeding pressure on native species tested. One species (*Poa secunda*) even appeared to benefit from the exotic, showing significantly reduced mortality when *B. tectorum* was present in greenhouse mesocosms compared to when it was absent. In contrast, other studies have shown effects of apparent competition ("associational herbivory") between *B. tectorum* and native plants: Grasshoppers in a Great Basin saltbush (*Atriplex* spp.) community inflicted greater damage on a native bunchgrass (*E. elymoides*) in high-density *B. tectorum* patches than in low-density patches (Beckstead et al. 2008). Notably, effects on *P. secunda* from the same study are consistent with my field mesocom results, providing further indication that effects of herbivory are context-dependent. In other words, *E. elymoides* may have suffered associational herbivory in the Beckstead et al. (2008) study mainly because it was preferred by grasshoppers to *P. secunda*. Had more preferred food plants been present, *E. elymoides* might have performed as it did in my greenhouse mesocosms, in which it showed no effect of associational herbivory resulting from *B. tectorum* presence.

My results suggest *B. tectorum* has the potential to restructure grasshopper communities by providing a food source that can be utilized by (and promote population increase in) certain species. Field surveys revealed a significant relationship between *B. tectorum* cover and grasshopper density; this association was driven by the subfamily (Cyrtacanthacridinae) containing many rangeland and crop pest species. In laboratory trials, native, generalist grasshoppers (*Melanoplus bivittatus*) exhibited distinct feeding preferences that could influence competitive outcomes between *B. tectorum* and native plants. Though early-instar insects preferred *B. tectorum* more often than native plants, preferred natives included big sagebrush — the keystone shrub and focal species in sagebrush steppe restoration efforts. Studies have shown sagebrush is a key food for greater sage grouse, comprising approximately 25% of the species' summer diet (Patterson 1952; Rogers 1964). In my study, sagebrush biomass was significantly reduced either through competition with *B. tectorum* or grasshopper herbivory, which suggests successful sagebrush restoration may require controlling both *B. tectorum* and grasshopper densities.

In addition, I observed significantly increased plant mortality resulting from grasshopper herbivory in the majority of other natives tested. For restoration purposes, the effects of grasshopper herbivory are probably most critical at seedling stage. Seedling resistance to herbivory is a key predictor of relative species abundances and determinant in eventual plant community structure (Burt-Smith et al. 2003). Grasshopper food choices (especially by early instars, the likeliest grasshopper life-stage to encounter restoration seedlings) should be considered in restoration planning.

Survival outcomes for native plants susceptible to grasshopper herbivory should also be taken into account. For example, I found no significant effect of grasshoppers on biomass or mortality

in most native grasses. I tested perennial grass species, so this result may simply indicate greater resistance to herbivory in perennials, but the exotic annual was either less resistant or more preferred. Grasshopper-tolerant natives (grasses and shrubs) could be seeded in an initial restoration phase to stabilize disturbed sites, establish a positive trajectory in the soil biotic community, and provide nursery sites that could shelter more sensitive natives to be seeded in later phases (for example using an alternate-furrow method to seed phases separately). Pale evening primrose (*Oenothera pallida*), basin wildrye (*Leymus cinereus*) Western wheatgrass (*Pascopyrum smithii*) and antelope bitterbrush (*Purshia tridentata*) would be good restoration candidates in *B. tectorum*-invaded areas having high densities of grasshoppers because they were less preferred, more tolerant of herbivory (no increase in mortality despite significant reduction in biomass), or both.

My results suggest that despite periods of equal or even greater preference for *B. tectorum*, grasshoppers may choose native plant foods at particular developmental stages, or may reject *B. tectorum* regardless of life stage when *B. tectorum* plants have gone to seed. Further study is needed to determine whether *B. tectorum* invasion could boost populations of generalist grasshoppers or if it instead sets up an evolutionary trap, wherein early instars are more likely to survive but later instars can't obtain the balance of nutrients necessary to complete their life cycle (either because *B. tectorum* has bolted or because it has outcompeted native plants that could supply adequate nutrition). Also, adult female grasshoppers showed the least choosiness in their feeding preferences. Their acceptance of *B. tectorum* as a food source suggests fecundity could improve where green *B. tectorum* is obtainable by reproducing females (i.e., in early fall, when *B. tectorum* typically germinates). Elucidating the relative importance of

B. tectorum consumption at different grasshopper life stages could further our understanding of population dynamics in both an invasive exotic plant and generalist pest insect species.

Invasive species have been identified as one of the biggest threats to biodiversity worldwide (Higgins et al. 1999). Yet studies of *B. tectorum* invasion have thus far focused on impacts to plant- and soil-community diversity, with little attention paid to effects on herbivores other than domesticated livestock (but see Beckstead et al. 2008). My results indicate that interactions between native plants, generalist grasshoppers and this highly successful invasive could produce a range of physiological, ecological and evolutionary outcomes at multiple trophic levels in SSE communities.

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Appendix

Table 7. Biomass of greenhouse mesocosm plants (g/mesocosm), in a study testing effects of grasshopper herbivory in a context of *Bromus tectorum* invasion. All-native mesocosms (“Native”) contained 15 native plant species commonly used in sagebrush steppe ecosystem restoration. Native-plus-*B. tectorum* mesocosms (“BRTE”) contained the same native species as all-native mesocosms, plus *Bromus tectorum*. Means with the same letter are not significantly different at $\alpha = 0.05$.

Species	Without grasshoppers					With grasshoppers						
	Native	standard error		BRTE	standard error	Native	standard error		BRTE	standard error		
AMME	0.0257	0.0040	a	0.0276	0.0056	a	0.0055	0.0018	b	0.0059	0.0022	b
ARFR	0.0080	0.0008	a	0.0078	0.0010	ab	0.0041	0.0007	c	0.0042	0.0011	bc
ARTR	0.0043	0.0008	a	0.0032	0.0006	ab	0.0005	0.0002	c	0.0009	0.0005	bc
CHVI	0.0050	0.0007	a	0.0053	0.0006	a	0.0013	0.0004	b	0.0009	0.0003	b
COTI	0.0286	0.0024	a	0.0256	0.0030	a	0.0066	0.0018	b	0.0004	0.0002	b
HEAN	0.0893	0.0101	a	0.0756	0.0088	a	0.0269	0.0077	b	0.0163	0.0051	b
KRLA	0.0221	0.0017	a	0.0183	0.0026	ab	0.0096	0.0015	c	0.0117	0.0023	bc
POSE	0.0101	0.0010	a	0.0107	0.0011	a	0.0034	0.0007	b	0.0042	0.0019	b
PSSP	0.0258	0.0024	a	0.0232	0.0024	a	0.0073	0.0010	b	0.0036	0.0007	b
PUTR	0.0490	0.0019	a	0.0491	0.0031	a	0.0425	0.0017	ab	0.0384	0.0036	b
BRTE				0.0648	0.0018	a				0.0340	0.0014	b
ELEL	0.0181	0.0015	a	0.0322	0.004	a	0.0089	0.0011	a	0.0097	0.0018	a
LECI	0.0218	0.0016	a	0.0249	0.0017	a	0.0318	0.0017	a	0.0193	0.0029	a
MATA	0.0185	0.0013	a	0.0388	0.0041	a	0.0042	0.001	a	0.0015	0.0006	a
OEPA	0.0434	0.0018	a	0.0464	0.0034	a	0.0494	0.002	a	0.0487	0.0025	a
PASM	0.0516	0.0023	a	0.0475	0.0033	a	0.0595	0.0087	a	0.0494	0.0031	a

Table 8. Biomass of field mesocosm plants (g/mesocosm), in a study testing effects of grasshopper herbivory in a context of *Bromus tectorum* invasion. All-native mesocosms (“Native”) contained 8 native plant species commonly used in sagebrush steppe ecosystem restoration. Native-plus-*B. tectorum* mesocosms (“BRTE”) contained the same native species as all-native mesocosms, plus *Bromus tectorum*. Means with the same letter are not significantly different at $\alpha = 0.05$.

Species	Without grasshoppers						With grasshoppers					
	Native	standard error		BRTE	standard error		Native	standard error		BRTE	standard error	
ARTR	0.0084	0.0014	a	0.0017	0.0006	b	0.0009	0.0005	b	0.0005	0.0002	b
CHVI	0.3192	0.1391	a	0.1000	0.0423	ab	0.0000	0.0000	b	0.0000	0.0000	b
COTI	0.8990	0.1618	a	0.7350	0.0927	ab	0.0670	0.0335	bc	0.0000	0.0000	c
HEAN	148.05	8.79	a	133.25	5.85	ab	164.76	6.67	a	81.69	10.77	b
ARFR	0.0000	0.0000	a	0.0046	0.0014	a	0.0000	0.0000	a	0.0015	0.0008	a
KRLA	0.4181	0.0727	a	0.2902	0.0493	a	0.3482	0.0423	a	0.2614	0.0377	a
MATA	4.8937	0.9780	a	4.0895	0.3961	a	3.0150	0.2845	a	2.0437	0.4058	a
POSE	0.1502	0.0553	a	0.0551	0.0202	a	0.0074	0.0037	a	0.0293	0.0099	a
BRTE				10.30	1.03	a				10.85	1.15	a

Table 9. UTM coordinates of 37 field survey locations in five states (Colorado, Utah, Nevada, Idaho, Wyoming). Sites were surveyed in May and August 2012 to assess grasshopper density and richness in relation to varying proportions of *B. tectorum* and native shrub cover.

Site number	UTM zone	Easting	Northing
GH01	12 S	739472	4418221
GH02	13 S	258403	4394183
GH03	13 S	258442	4394112
GH04	13 S	258813	4388589
GH05	12 S	731102	4412121
GH06	12 T	673175	4448325
GH07	12 T	611252	4462217
GH08	12 T	613967	4465555
GH09	12 S	528862	4421449
GH10	12 S	417257	4292364
GH11	12 S	416564	4291957
GH12	12 S	328182	4240529
GH13	11 S	753177	4316950
GH14	12 S	248198	4285667
GH15	11 S	724165	4338060
GH16	11 S	715673	4325385
GH17	11 S	692520	4384691
GH18	11 T	643275	4548411
GH19	11 T	680798	4564475
GH20	11 T	681674	4619052
GH21	11 T	686676	4626620
GH22	11 T	697071	4674160
GH23	11 T	699826	4690361
GH24	11 T	710169	4750976
GH25	11 T	709060	4750339
GH26	12 T	270260	4802187
GH27	12 T	369480	4800185
GH28	12 T	589311	4639644
GH29	12 T	599185	4637554
GH30	13 T	341832	4665712
GH31	13 T	339918	4664038
GH32	13 S	260781	4392948
GH33	12 S	351690	4214328
GH34	11 S	692044	4379235
GH35	11 T	718287	4790336
GH36	13 T	421924	4622019
GH37	13 T	416945	4623819

Table 10. Grasshopper species and *Bromus tectorum* densities at field survey locations in five states (Colorado, Utah, Nevada, Idaho, Wyoming) (see Table A3). Only sites with grasshoppers are shown. Sites were surveyed in May and August 2012 to assess grasshopper density and species richness in relation to varying proportions of *B. tectorum* and native shrub cover. Grasshopper subfamilies: C = Cyrtacanthacridinae, G = Gomphocerinae, O = Oedipodinae.

Plot ID	<i>B. tectorum</i> cover (%)	Date	Subfamily	Species	Count	Instar range	Total species at site
GH01	0	May	C	<i>Melanoplus femurrubrum</i>	1		1
GH02	34	May	C	<i>Melanoplus femurrubrum</i>	7	I–VI	
	"	May	O	Unknown 1	1		
	"	Aug	C	<i>Melanoplus sanguinipes</i>	1	VI	
	"	Aug	C	Unknown 2	1		4
GH03	37	May	C	<i>Melanoplus femurrubrum</i>	2	I–VI	
	"	May	G	Unknown 3	5	I–II	
	"	May	G	Unknown 4	6	I–II	
	"	Aug	G	<i>Ageneotettix deorum</i>	1	VI	
	"	Aug	C	<i>Melanoplus femurrubrum</i>	1	VI	4
GH05	0	May	G	Unknown 5	1	VI	1
GH06	30	May	C	<i>Melanoplus femurrubrum</i>	3	II	1
GH08	7	May	G	<i>Ageneotettix deorum</i>	5	I–II	
	"	May	O	<i>Xanthippus corallipes</i>	1	VI	
	"	May	C	Unknown 6	3	I–III	
	"	Aug	G	Unknown 7	1	VI	4
GH09	0	May	G	Unknown 8	1	I	
	"	May	O	Unknown 9	1	I	2
GH10	32	May	C	<i>Melanoplus confusus</i>	16	I–VI	
	"	May	C	<i>Melanoplus femurrubrum</i>	8	II–VI	
	"	May	C	Unknown 10	1	III	
	"	May	C	Unknown 11	2	I	
	"	May	O	Unknown 12	1	III	
	"	Aug	C	<i>Melanoplus femurrubrum</i>	7	VI	
	"	Aug	G	<i>Orphulella pelidna</i>	1	I	6
GH11	36	May	C	<i>Melanoplus confusus</i>	28	I–VI	
	"	May	C	<i>Melanoplus femurrubrum</i>	1	I	
	"	May	G	<i>Orphulella pelidna</i>	1	I	
	"	May	C	Unknown 13	1	Unknown	
	"	May	C	Unknown 14	1	I	
	"	Aug	C	<i>Melanoplus confusus</i>	2	VI	
	"	Aug	C	<i>Melanoplus sanguinipes</i>	1	VI	6

Table 10, continued.

Plot ID	<i>B. tectorum</i> cover (%)	Date	Subfamily	Species	Count	Instar range	Total species at site
GH12	15	May	C	<i>Melanoplus femurrubrum</i>	1	I	2
		May	G	<i>Orphulella pelidna</i>	1	II	
GH13	13	May	C	<i>Melanoplus confusus</i>	6	V–VI	5
		May	G	<i>Orphulella pelidna</i>	1	IV	
		May	G	Unknown 15	1	IV	
		May	G	Unknown 16	1	III	
		May	G	Unknown 17	1	V	
GH14	16	Aug	G	<i>Ageneotettix deorum</i>	2	VI	1
GH15	23	May	G	Unknown 18	2	III–IV	3
		Aug	C	<i>Melanoplus bowditchi</i>	1	VI	
		Aug	C	<i>Oedaleonotus enigma</i>	2	VI	
GH17	0	May	C	<i>Melanoplus</i> sp.	1	I	1
GH18	10	May	G	<i>Ageneotettix deorum</i>	1	VI	5
		May	C	<i>Melanoplus</i> sp.	1	I	
		May	G	Unknown 19	2	I	
		May	G	Unknown 20	1	II	
GH20	9	Aug	C	<i>Melanoplus complanatipes</i>	3	VI	1
GH23	50	May	C	Unknown 21	1	I	2
		Aug	C	<i>Melanoplus sanguinipes</i>	2	VI	
GH24	49	Aug	C	<i>Melanoplus sanguinipes</i>	1	VI	1
GH29	0	May	G	<i>Ageneotettix deorum</i>	1	VI	3
		May	G	Unknown 22	1	IV	
		Aug	G	<i>Amphitornus coloradus</i>	1	IV	
GH31	13	May	C	<i>Melanoplus</i> sp.	2	I	1
GH32	12	Aug	C	<i>Melanoplus sanguinipes</i>			2
		Aug	O	<i>Trachyrhachys kiowa</i>	2	VI	
GH34	21	Aug	O	<i>Derotmema haydeni</i>	2	IV	2
		Aug	C	<i>Melanoplus sanguinipes</i>			
GH35	7	Aug	C	<i>Melanoplus femurrubrum</i>	2	VI	2
		Aug	C	<i>Melanoplus sanguinipes</i>	2	VI	