Chapter 10
Plant Community Resistance to Invasion by *Bromus* Species: The Roles of Community Attributes, *Bromus* Interactions with Plant Communities, and *Bromus* Traits

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Abstract The factors that determine plant community resistance to exotic annual *Bromus* species (*Bromus* hereafter) are diverse and context specific. They are influenced by the environmental characteristics and attributes of the community, the traits of *Bromus* species, and the direct and indirect interactions of *Bromus* with the plant community. Environmental factors, in particular ambient and soil temperatures, have significant effects on the ability of *Bromus* to establish and spread. Seasonality of precipitation relative to temperature influences plant community

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M.J. Germino et al. (eds.), *Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US*, Springer Series on Environmental Management,
DOI 10.1007/978-3-319-24930-8_10

resistance to *Bromus* through effects on soil water storage, timing of water and nutrient availability, and dominant plant life forms. Differences among plant communities in how well soil resource use by the plant community matches resource supply rates can influence the magnitude of resource fluctuations due to either climate or disturbance and thus the opportunities for invasion. The spatial and temporal patterns of resource availability and acquisition of growth resources by *Bromus* versus native species strongly influence resistance to invasion. Traits of *Bromus* that confer a "priority advantage" for resource use in many communities include early-season germination and high growth and reproductive rates. Resistance to *Bromus* can be overwhelmed by high propagule supply, low innate seed dormancy, and large, if short-lived, seed banks. Biological crusts can inhibit germination and establishment of invasive annual plants, including several annual *Bromus* species, but are effective only in the absence of disturbance. Herbivores can have negative direct effects on *Bromus*, but positive indirect effects through decreases in competitors. Management strategies can be improved through increased understanding of community resistance to exotic annual *Bromus* species.

Keywords Ecosystem resilience • Plant traits • Resource dynamics • Species interactions • Herbivory

10.1 Introduction

The resistance or conversely susceptibility of plant communities to exotic annual *Bromus* species (*Bromus* hereafter) and other invasive species is a function of environmental factors, community attributes and processes, life history and ecophysiological traits of the invader, and direct and indirect interactions of the invader (see reviews in Chesson 2000; Shea and Chesson 2002). Resistance to invasion varies both spatially and temporally (Chesson 2000; Seabloom et al. 2003) and is closely related to the resilience of a community (Chambers et al. 2014a). Resilience is the capacity of a community to *regain* its fundamental structure, processes, and functioning when altered by stressors like drought, and disturbances like inappropriate grazing and altered fire regimes (Holling 1973; Folke 2006); resistance is the capacity of a community to *retain* its fundamental structure, processes, and functioning despite stresses, disturbances, or invasive species (Folke et al. 2004). While resilience is a measure of the recovery potential of a community following stress or disturbance (Chambers et al. 2014a), resistance to invasion is a measure of the capacity of a community to limit the population growth of an invading species (D'Antonio and Thomsen 2004). The relationships of environmental factors, including climate, topography, and soils, to the abiotic and biotic attributes of communities, and to resilience to disturbance and resistance to *Bromus*, are illustrated in Fig. 1.1 (Germino et al. 2015).

In this chapter, we examine the interactions of four focal, invasive annual *Bromus* species—*B. diandrus* Roth (ripgut brome), *B. hordeaceus* L. (soft brome), *B. rubens*

L. (red brome), and *B. tectorum* L. (cheatgrass or downy brome)—with plant communities in the Western USA. We emphasize the factors that influence plant community resistance to invasion, specifically, environmental characteristics, community attributes and processes, life history and ecophysiological traits of the invader, and direct and indirect interactions of the invader with the community. We integrate the role of disturbance and stressors in influencing community interactions with *Bromus* into each section. We address the implications for management and research needs in the final sections.

10.2 Effects of Environmental Factors on Plant Community Resistance to *Bromus*

Resistance of plant communities to *Bromus* is strongly affected by environmental factors such as climate and soils. Environmental factors affect (1) the ability of *Bromus* to establish and persist, (2) the interactions of *Bromus* with the plant community, and (3) the attributes of plant communities such as life form dominance and productivity that determine their capacity to resist *Bromus* invasion. *Bromus* species differ in the climatic regimes where they can establish and persist, and these differences are well illustrated by soil temperature and moisture regimes (Brooks et al. 2015). For example, resistance to *B. tectorum* in the cold desert varies strongly over elevation gradients. *Bromus tectorum* germination, growth, and/or reproduction is limited in relatively hot and dry environments by low and sporadic precipitation (thermic to xeric/aridic soils), constrained in cold and moist environments by low soil temperatures (frigid to cryic soils), and optimal under relatively moderate temperature and water availability (xeric/aridic to xeric/mesic soils) (Meyer et al. 2001; Chambers et al. 2007; Leger et al. 2009). In contrast, *B. rubens* L. (red brome) is less cold tolerant than *B. tectorum*, and *B. rubens* establishment and persistence occurs primarily at lower latitudes and altitudes characterized by warmer environments (thermic to xeric soils) (Salo 2005; Bykova and Sage 2012).

At the scale of the western USA, differences in overlap between seasonality of precipitation and temperature, and onset of the dry season have important consequences for plant functional type dominance (Sala et al. 1997), and competitive interactions with *Bromus* (Bradford and Lauenroth 2006). Amount of precipitation that is received during the period when temperature, and thus potential evapotranspiration, is low influences the amount of water stored in deep soil layers and therefore the balance between woody and herbaceous species (Sala et al. 1997). Areas that receive more winter/spring precipitation typically have greater deep soil water storage and are dominated by woody species, which are more effective at using deep soil water (Fig. 10.1a, b). In contrast, areas that receive predominantly summer precipitation are dominated by grasses. Also, seasonality of wet soil during the period when temperatures are favorable for plant growth is an important control on the balance between C3 and C4 species with C3 species dominating in areas with cool, wet springs and C4 species dominating in areas with warm, wet summers

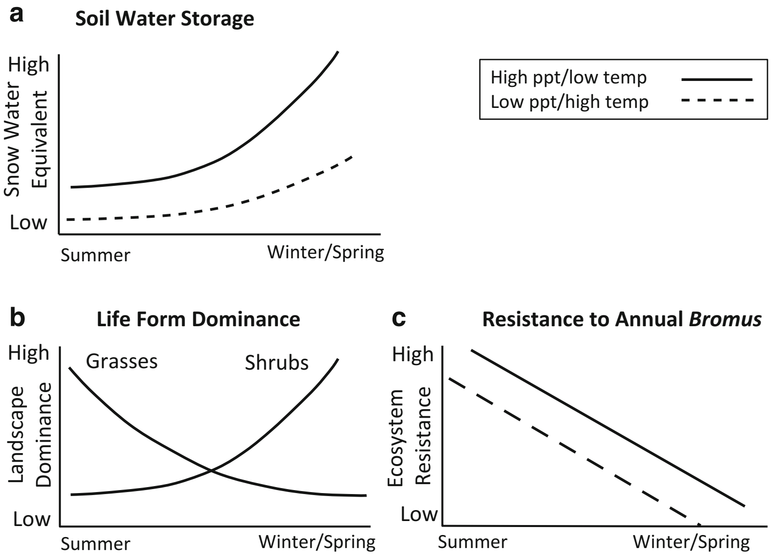

Fig. 10.1 Changes in soil water storage, life form dominance, and resistance to annual *Bromus* as seasonality of precipitation transitions from primarily summer to winter. (**a**) Soil water storage increases as winter/spring precipitation and snow water equivalent increase and these changes are relatively greater for areas with relatively high precipitation and low temperature. (**b**) Landscape dominance of grasses is highest with primarily summer precipitation; shrub dominance is greatest with primarily winter/spring precipitation. (**c**) Resistance to *Bromus* is higher in areas where soil water storage is low and grasses dominate largely due to strong resource competition. Decreases in effective precipitation can increase resource fluctuations and lower resistance to *Bromus*. At more local scales, resistance also is influenced by nutrient availability and disturbance

(Paruelo and Lauenroth 1996; Sala et al. 1997). Resistance to *Bromus* generally increases with increasing summer precipitation (Fig. 10.1c) as a function of increasing grass dominance. This appears to be due to less favorable conditions for establishment of *Bromus* and strong competition from grass species that dominate under this precipitation regime (Bradford and Lauenroth 2006; Bradley 2009). *Bromus* also may be constrained in regions with predominant summer precipitation due to low soil phosphorus availability (Belnap et al. 2015).

At more local scales, resistance to *Bromus* varies over environmental gradients. Increases in effective precipitation are typically associated with greater resource availability and more favorable environmental conditions for plant growth and reproduction. Higher resource availability and plant productivity are associated with higher resilience to disturbance or recovery potential in the cold desert (Chambers et al. 2014a). These conditions translate into greater plant community resistance to *B. tectorum* on more mesic sites in the cold desert (Chambers et al. 2014b) and to *B. diandrus* and *B. hordeaceus* in California grasslands (Corbin et al. 2007). Resistance is likely decreased by low precipitation or high temperatures, which decrease soil water availability and plant productivity regardless of seasonality of precipitation. Low effective precipitation can result in increases in water and nutrient resource fluctuations and decreased resistance to invasion in arid and semiarid ecosystems (Davis et al. 2000). This has been observed following El Niño years for *B. rubens* in the Mojave Desert (Salo 2005) and *B. tectorum* in salt desert ecosystems of the cold desert (Meyer et al. 2001), as well as over elevation gradients in the central Basin and Range (Chambers et al. 2007).

10.3 Interactions of *Bromus* with Plant Communities

10.3.1 Bromus *Plant Traits and Resource Dynamics*

Community resistance to *Bromus* invasion is strongly influenced by spatial and temporal patterns of resource availability that result from differences in temperature and precipitation regimes, and by effects of these patterns on acquisition or use of growth resources by *Bromus* and natives. Like many invasive annuals, *Bromus* is generally more effective than native species at using limiting soil resources on short timescales largely due to its life history strategies and rapid growth rates. Soil resource uptake can vary between *Bromus* and competitors as a function of differences in root growth and surface area, rooting depth, spatial distribution or timing of activity, uptake capacity, or resource use efficiency (RUE) (see Smith et al. 1997; Leffler and Ryel 2012).

In communities dominated by winter/spring precipitation, which often exhibit the greatest impacts of *Bromus*, the spring growth period and shallow soil layers are the most significant factors for nutrient uptake and growth of all species, including *Bromus*. Nutrients are typically concentrated in shallow soils, and soil water availability that is sufficient for mineralization and transport of nutrients to plant roots occurs at these depths primarily in spring (Ryel et al. 2008). High growth rates, early-season root growth, and use of this shallow resource pool are important aspects of the "seasonal priority advantage" of *Bromus* compared to a wide range of native perennials, but competitive outcomes depend on life form, life stage, and season of growth. For example, although *B. tectorum* roots occur at depths of nearly 2 m in some situations, *B. tectorum* root densities are typically highest in the top 20–30 cm of soil (see Thill et al. 1984). Roots of *Bromus* tend to grow more rapidly and at lower temperatures than those of native species, as shown for *B. tectorum* compared to bunchgrasses (Aguirre and Johnson 1991). Consequently, *Bromus* has relatively higher water use from shallow soils (e.g., 0–30 cm vs. 30–200 cm depth) than many native perennials, which often have deeper roots and also extract soil water from greater depths (see Wilcox et al. 2012; Leffler and Ryel 2012). *Bromus tectorum* has been shown to compete effectively with woody plants such as *Chrysothamnus* Nutt. spp. (rabbitbrush) and *Artemisia tridentata* Nutt. (big sagebrush) for near-surface soil water and nutrients (e.g., nitrogen and phosphorus) during spring (Melgoza et al. 1990; Booth et al. 2003). However, uptake of soil water by deeper-rooted woody plants from greater depths during summer drought can facilitate their persistence (Leffler and Ryel 2012). This growth/maintenance resource pool helps explain coexistence of *B. tectorum* and woody species in areas with deep-water storage, but intensity of competitive interactions likely depends on temperature and precipitation regimes and shrub rooting depths. Use of shallow soil water by *B. tectorum* also helps explain its coexistence with deep-rooted exotic forbs in areas with deep-water storage as shown in *Bromus*-dominated areas using soil and plant water balance (Hill et al. 2006), in shrub steppe with winter rainout shelters (Prevey et al. 2010) and stable isotope tracers of soil water use (Kulmatiski et al. 2006), and in California grasslands with water balance studies (Enloe et al. 2004).

Mature, perennial grasses with relatively high densities of roots in shallow soils and with similar phenologies are typically strong competitors with *Bromus* for shallow resource pools as shown for *B. tectorum* (Booth et al. 2003; Blank and Morgan 2013). However, competitiveness of *Bromus* against these grasses appears to increase with soil nitrogen as illustrated in the central Basin and Range (Beckstead and Augspurger 2004), short-grass steppe (Lowe et al. 2003), and California grasslands (Corbin et al. 2007). Also, *B. tectorum* and other *Bromus* often preempt establishment of shallow-rooted native seedlings. A meta-analysis of studies that examined effects of nitrogen manipulation (fertilizer, straw, sawdust) on seedling growth of annual *Bromus* and native perennial species in a wide variety of ecological types showed that *Bromus* maintained higher growth rates, biomass, and tiller production than natives under both low and high nitrogen availability (James et al. 2011). Greenhouse studies with *B. tectorum* and *B. rubens* further showed that *Bromus* tends to have greater root length and root biomass (James et al. 2008) and nitrogen content (Defalco et al. 2003; Monaco et al. 2003) than seedlings of native species over a range of nitrogen availability if other nutrients are not limiting. Effects of phosphorus and potassium on *Bromus* interactions with native species are detailed in Belnap et al. (2015).

Aboveground canopy and litter effects also influence interactions of *Bromus* with its plant community. *Bromus* are high-light adapted and generally exhibit low acclimation and tolerance of shade under dense overhead canopies (Pierson et al. 1990). Overhead canopy and standing litter can have either negative or positive effects on *B. tectorum*, depending on factors such as weather and species (Newingham et al. 2007; Bansal et al. 2014). Where *B. diandrus* and *B. hordeaceus* dominate community cover, increased competition for light during spring when growth of annuals is most rapid suppresses growth and reproduction of perennial native species (Dyer and Rice 1999). Litter accumulation in *Bromus*-dominated areas appears to have a positive feedback effect on *B. tectorum* growth through decreases in soil water loss, changes in nutrient cycling, and effects on seed entrapment and germination (e.g., Bansal et al. 2014). *Bromus* litter can promote emergence of *B. tectorum* on smooth, hard surfaces of fine-textured soils (Young and Evans 1975). However, thick *Bromus* litter likely prevents germination and establishment of small-seeded native species (Chambers 2000).

10.3.2 Interactions of **Bromus** *with Perennial Grasses*

Competitiveness of established perennial grasses with *Bromus* differs among and within ecoregions as a function of environmental attributes and resource availability and is strongly affected by disturbance. Invasive *Bromus* cover is typically negatively related to the amount of cover of native species, such as grasses of the cold desert and western Great Plains. An inverse relationship of *B. tectorum* to native or naturalized bunchgrass cover (Reisner et al. 2013; Chambers et al. 2014b) and increases in *B. tectorum* biomass upon experimental reduction of native perennial herbaceous species have been observed across the elevation range with suitable climate for *B. tectorum* in the Great Basin (Chambers et al. 2007). At local scales, *B. tectorum* cover is positively related to size of bare soil gaps separating bunchgrasses, negatively correlated with biological soil crust (biocrust) cover, and increases with grazing pressure or soil water deficits (Reisner et al. 2013). At landscape scales, *B. tectorum* cover generally increases with fire. However, *B. tectorum* cover varies depending on topographic position and is positively associated with solar radiation and negatively associated with perennial herbaceous species (Condon et al. 2011).

In areas dominated by winter/spring precipitation, where *B. tectorum* is often most problematic, cool-season, early-seral bunchgrasses, such as *Elymus elymoides* Raf. (Swezey) (squirreltail) that have traits similar to *Bromus*, can quickly occupy disturbed sites and appear to have a better overall ability to compete against *B. tectorum* than other native grass species (Booth et al. 2003; McGlone et al. 2011). Greenhouse studies show that mature plants of long-lived, cool-season grasses that occur over a range of soil temperature and moisture regimes, including *Elymus wawawaiensis* J. Carlson & Barkworth (Snake River wheatgrass), *Achnatherum hymenoides* (Roem. & Schult.) Barkworth (Indian ricegrass), and *Leymus triticoides* Buckley Pilg. (creeping wild rye), strongly suppress growth of *B. tectorum*, likely due to co-opting biological soil space and reducing nitrogen availability (Blank and Morgan 2012). As with all plant types, seedling recruitment of native grasses is very low in dense, established *Bromus* stands, regardless of native seed abundance as seen for *B. tectorum* (Mazzola et al. 2011). Introduced bunchgrasses, such as *Agropyron cristatum* (L.) Gaertn. (crested wheatgrass), are often more competitive with *B. tectorum* in the seedling stage than native bunchgrasses (e.g., James et al. 2008). This has led to widespread efforts to seed introduced bunchgrasses such as *A. cristatum* following fires or other disturbances, even though these introduced species also outcompete native seedlings over a wide range of climate conditions in the cold desert (Knutson et al. 2014).

In Mediterranean California grasslands characterized by winter/spring precipitation and cool-season grasses, both above- and belowground factors help explain competitive interactions of *Bromus* with native bunchgrasses. Established perennial grasses preempt sunlight for exotic annual seedlings, including *B. diandrus* and *B. hordeaceus*, and inhibit carbon gain, growth, and rooting depth to the degree that plants cannot survive the onset of later spring and summer soil drying (Corbin and D'Antonio 2004; Seabloom et al. 2003). The same effect occurs for perennial seedlings in *Bromus*-dominated grassland (Dyer and Rice 1999). All life stages of *Nassella pulchra* Hitchc. (Barkworth) (purple needlegrass) respond negatively to *Bromus* and other invasive annuals in the relatively dry Central Valley, but *N. pulchra* and other perennial native grasses have greater resistance in areas with higher precipitation (Corbin et al. 2007). Competition also occurs among *Bromus* in annual grasslands of California. *B. diandrus* is able to exclude *B. hordeaceus* in fertile microsites (see Callaway 2007). Short-grass steppe is dominated by summer precipitation and warm-season grasses such as *Bouteloua* Lag. spp. (grama). In the high plains east of the Colorado Front Range, short-grass steppe is largely resistant to *B. tectorum* (Kotanen et al. 1998), but nitrogen addition increases the competitive ability of *B. tectorum* (Lowe et al. 2003) and disturbance can promote invasion (Bradford and Lauenroth 2006). In the northwestern Great Plains, which is also dominated by winter precipitation but has cooler soils and both warm- and cool-season grasses, species are active throughout the growing season and soil nitrogen fluctuations are minimal (McCulley et al. 2009). Despite this, *B. tectorum* and *Bromus japonicus* (syn. *Bromus arvensis* L. [field brome]) are common invaders in areas used for forage production (Ogle et al. 2003).

On the Colorado Plateau, which has a mixed precipitation regime, perennial grasslands dominated by another warm-season, rhizomatous grass, *Pleuraphis jamesii* Torr. (syn. *Hilaria jamesii*; James' galletta), showed a significant negative association with *B. tectorum* after fire (Getz and Baker 2008). However, in another location with sandy loam soils that receives about 35 % of annual precipitation in summer, grasslands dominated by cool-season *A. hymenoides* and *Hesperostipa comata* (Trin. & Rupr.) Barkworth (needle-and-thread grass) remained uninvaded while adjacent communities dominated by *P. jamesii* were highly invaded. Soils in cool-season grasslands that lacked *B. tectorum* were slightly coarser and less fertile and contained less soil biotic richness than invaded soils (Belnap and Phillips 2001).

10.3.3 Interactions of **Bromus** *with Woody Plants*

Environmental factors, particularly temperature, strongly influence resistance of plant communities dominated by woody plants to *Bromus*. In the cold desert, a seeding experiment demonstrated that *B .tectorum* growth and reproduction were consistently higher at low-elevation *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young (Wyoming big sagebrush) sites with warmer soils, were variable and dependent on growing season temperatures at mid-elevation *A. tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush) sites, and were lowest at high-elevation *A. tridentata* ssp. *vaseyana* /mountain shrub sites (Chambers et al. 2007). These differences were apparent in a regional study of management treatments (prescribed fire, *Pinus monophylla* Torr. & Frém. [singleleaf pinyon] and *Juniperus* L. spp. [juniper] cutting, and *A. tridentata* mowing) where resistance to *B. tectorum* and thus capacity to recover was higher on sites with lower soil temperatures (Chambers et al. 2014b). Similarly, undisturbed conifer forests in the northern Rockies tended to exhibit progressively higher resistance to introduced *B. tectorum* as elevation increased (*Pinus ponderosa* Lawson and C. Lawson [ponderosa pine], *Pseudotsuga menziesii* Mirb. Franco [Douglas-fir], *Abies grandis* Douglas ex D. Don Lindl. [grand fir], *Thuja plicata* Donn ex D. Don [western redcedar]) due to limitations on its growth and reproduction at lower temperatures (Pierson and Mack 1990).

Within plant communities, a variety of factors influence whether *Bromus* has negative or positive associations with woody plants, including direct interactions between species, moderated microclimate, enhanced nutrients or higher litter under shrubs, and livestock grazing that alters species composition and spatial distribution. In the cold desert, *B. tectorum* frequently occurs under *A. tridentata* and appears to be facilitated by the shrub at the scale of the individual plant. In an experimental seeding study in the Basin and Range, Chambers et al. (2007) found that *B. tectorum* had higher biomass and seed production in under-shrub microsites than in interspace microsites on a per plant basis, likely due to higher resource availability. However, interspaces typically had higher emergence and plant densities and thus greater total biomass and seed production than under-shrub microsites likely due to experimental seed burial. In an observational study in the eastern Sierra Nevada, Griffith (2010) found that *B. tectorum* plant density and seed production were naturally greater under *A. tridentata* Nutt. ssp. *tridentata* (basin big sagebrush) and *Purshia tridentata* Pursh DC. (antelope bitterbrush) compared to bare interspaces, probably because conditions for seed burial were lacking in interspaces. Seedling survival of *B. tectorum* is generally high following emergence (Mack and Pyke 1983). However, seed production and root growth of *B. tectorum* can be suppressed by *A. tridentata* ssp. *wyomingensis*, as revealed by experimental exclusions (Reichenberger and Pyke 1990), and removal of *A. tridentata* can result in large increases in *B. tectorum* (Chambers et al. 2007; Prevey et al. 2010). Thus, establishment of *Bromus* in association with shrubs in the cold desert is determined by factors that affect seed burial and seedling emergence, such as location and depth of litter or occurrence of biocrusts, while *Bromus* biomass and seed production are strongly influenced by soil nutrients, which are typically more available under shrubs even in competitive environments.

Indirect influences of shrubs on *B. tectorum* include soil and vegetation legacy effects in which microsite conditions created by the shrub continue to affect the plant community beyond the life of the shrub (Sankey et al. 2012). In historically grazed areas of the Basin and Range, native bunchgrasses (e.g., *Pseudoroegneria spicata* (Pursh) Á. Löve [bluebunch wheatgrass] and *Achnatherum thurberianum* (Piper) Barkworth [Thurber's needlegrass]) often have greater association with shrub coppice mounds than *B. tectorum*, which is more evenly distributed among mounds and interspaces (Hoover and Germino 2012; Reisner et al. 2013). Bunchgrass mortality during fire is typically higher under shrubs, especially in dense stands with high levels of woody fuels (Miller et al. 2013). *Bromus tectorum* exhibits a greater growth response than bunchgrasses to fertile shrub mounds compared to interspace soils (Hoover and Germino 2012), especially after removal of native herbaceous species and burning (Chambers et al. 2007). Consequently, *B. tectorum* can rapidly dominate shrub islands after burns in the absence of adequate cover of perennial herbaceous competitors.

In the warmer and drier Mojave Desert, competitive and facilitative relationships with *B. rubens* vary among shrub species (Abella et al. 2011) and over environmental gradients (Brooks 2009). In a survey of seven Mojave Desert sites (710–1367 m), *B. rubens* was more common under shrubs than in interspaces but had relatively lower cover under *Encelia farinosa* A. Gray ex Torr. (brittlebush) and *Bebbia juncea* (Benth.) Greene (sweetbush) and higher cover under *Krameria erecta* Willd. ex Schult. (littleleaf ratany) (Abella et al. 2011). However, in another study, biomass of *B. rubens* beneath canopies of perennial plants generally increased with elevation likely due to more mesic conditions rather than any specific local conditions created by the perennial species (Brooks 2009). Positive effects of *Ambrosia dumosa* (A. Gray) Payne (burrobush) on *B. rubens*' survival and especially reproduction have been attributed mainly to canopy effects with little evidence for belowground competition (Holzapfel and Mahall 1999).

Trees and forest canopies also can exert either positive or negative effects on *Bromus*. *Juniperus* spp., *P. monophylla*, and *P. edulis* Engelm. (two-needle pinyon) on warmer and drier soils typically inhibit herbs, including *Bromus*, underneath their crowns and canopies, but invasion and prolific growth often occurs after the tree has died or burned (e.g., Kane et al. 2011). Similarly, *B. tectorum* increases rapidly after fire in *P. ponderosa* forests in the southern Sierra Nevada (Keeley and McGinnis 2007), on the Colorado Plateau (McGlone et al. 2011), and in the Northern Rockies (Gundale et al. 2008). In contrast, in the coastal mountains and inland foothill woodlands of California, *B. diandrus* and *B. hordeaceus* densities are enhanced by living oak crowns due to greater soil fertility (reviewed in Callaway 2007).

10.3.4 Interactions of **Bromus** *with Forbs*

Only a few studies have focused on interactions between native forbs and *Bromus*, and they indicate that forbs can affect various aspects of *Bromus* growth and reproduction through competition or facilitation. In the greenhouse, *B. rubens* used water more rapidly and had greater biomass and nitrogen content than two native Mojave Desert annuals, the grass *Vulpia octoflora* (Walter) Rydb. (6 weeks fescue) and forb *Descurainia pinnata* (Walter) Britton (western tansymustard), partly because of *B. rubens*' greater root-surface area and exploitation of deeper soils (DeFalco et al. 2003). In the Mojave Desert and central Basin and Range, native annual forbs, such as *Amsinckia tessellata* A. Gray (bristly fiddleneck), decreased biomass or seed density of *B. tectorum* when forbs were grown at similar densities with *B. rubens* in a greenhouse (Abella et al. 2011) and when grown at higher densities than *B. tectorum* in greenhouse and field settings (Leger et al. 2014). Also, relatively high transplant densities of *Sphaeralcea ambigua* A. Gray (desert globemallow, a short-lived perennial forb) in the Mojave Desert significantly decreased *B. rubens* biomass when compared to controls (Abella et al. 2012). Ability of these native annual or short-lived forbs to compete with *Bromus* has been examined to determine their potential as restoration species, but difficulty in routinely establishing these forbs makes their use in restoration problematic.

Interactions between perennial forbs and *Bromus* can be complex. A field experiment in the Basin and Range indicated that litter of adult *Lupinus argenteus* Pursh (silvery lupine) increased soil nitrogen and resulted in higher *B. tectorum* biomass and reproduction, despite overall negative effects of *L. argenteus* on emergence and survival (Goergen and Chambers 2012).

Several studies describe interactions between exotic forbs and *Bromus*. In sagebrush shrublands of the central California foothills, *Bromus* can form a competitive hierarchy with exotic forbs that leads to exclusion of native forbs (Cox and Allen 2011). In California grassland, annual grass and forb dominance varies over time and is weather dependent (Corbin et al. 2007). In the cold desert, *B. tectorum* can replace exotic mustards (e.g., *Sisymbrium* L. spp. [hedge mustard]) or *Salsola kali* L. [Russian thistle]) on disturbed sites over time, but in other cases dominance depends on weather, fire or other disturbance (Piemeisel 1951; Chambers et al. 2014b), or die-off events caused by pathogens (see Meyer et al. 2015). Many exotic, tap-rooted perennial forbs are particularly invasive in mid- to high-elevation cold desert communities that are disturbed and otherwise colonized by *B. tectorum* or other *Bromus*. These secondary, tap-rooted invaders include *Cirsium* L. spp. (thistles), *Centaurea* L. spp. (knapweeds), *Chondrilla* L. spp. (chondrilla), and nearly 50 other perennial or biennial species (Hill et al. 2006; Kulmatiski et al. 2006). Similarly, *Centaurea solstitialis* L. (yellow star-thistle) has invaded annual (including *Bromus*) grasslands in central California (Enloe et al. 2004). This secondary invasion by tap-rooted forbs or the metastable coexistence of biennial or annual forbs with *Bromus* appears related to soil water partitioning as described earlier.

10.4 *Bromus* Reproductive Traits, Propagule Supply, and Priority Advantage

10.4.1 Seed Production and Propagule Supply

Bromus exhibits highly plastic growth and reproduction, which enables it to produce sufficient seeds to maintain low, persistent populations under marginal conditions and to increase seed production under favorable conditions. Plant biomass and seed production differ among communities with different environmental conditions and among growing seasons within communities (Mack and Pyke 1983; Chambers et al. 2007). In a relatively dry *A. tridentata* ssp. *wyomingensis* community on the Columbia Plateau, most *B. tectorum* plants produced between 0 and 70 viable seeds, but one individual produced 555 viable seeds (Mack and Pyke 1983). During the subsequent growing season, the maximum number of seeds produced by any one plant was 32. In comparison with warmer and drier communities, higher elevation communities with cool to cold soil temperature regimes routinely produce the least seeds per plant (Mack and Pyke 1983; Chambers et al. 2007). Local adaptations may exist in populations from communities with environmental extremes as shown for an arid saline site dominated by *Sarcobatus vermiculatus* (Hook.) Torr. (greasewood) and for clearings within a cool, mesic *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) forest habitat (Rice and Mack 1991).

High densities of *Bromus* seedlings can result in intraspecific competition and thinning, although this may vary among *Bromus* species. *Bromus rubens* exhibits less plasticity in its response to canopy crowding (i.e., shade intolerance) than *B. hordeaceus* leading to greater density-induced mortality of individuals albeit without loss of seed production at the population level (Wu and Jain 1979). Seedling survival of *B. tectorum* is seldom density dependent, particularly in populations from mesic habitats, but plant and seed mass decrease with greater plant density (Rice and Mack 1991). In high-density stands of *B. tectorum*, plants have only 1–2 culms and do not form basal rosettes, but in low-density stands, plants can resemble small bunchgrasses (Mack and Pyke 1983). This same effect on plant mass and, consequently, seed production is seen when *B. tectorum* is growing in intact *Artemisia* communities with high densities of native perennial herbaceous species (Chambers et al. 2007).

Seed production of *Bromus* can increase dramatically with increased resource availability. Nitrogen (N) fertilization increased the number of *B. tectorum* seeds from 350 seeds/dm^2 without added N to 1200 seeds/dm^2 with 7.2 g N/m^2 (Hulbert 1955). In warm and cold deserts, disturbances that increase available water and nutrients are wildfire and removal of native perennial grasses and forbs through inappropriate grazing by livestock. Experimental removal of native perennial grasses and forbs in big sagebrush communities can increase *B. tectorum* seed production 2- to 3-fold, burning 3- to 6-fold, and removal combined with burning 10- to 30-fold (Chambers et al. 2007). These studies underscore the importance of perennial grasses and forbs as competitors with *Bromus* that decrease not only growth but also seed production.

10.4.2 Seed Characteristics and Dispersal

All four focal *Bromus* species have lemma awns that can facilitate seed dispersal to new locations and subsequent seed burial. Lemma awns are wirelike appendages attached to the lemma, the membrane that surrounds the caryopsis on the dorsal side (Hitchcock 1971). Species in section Genea, which include *B. diandrus*, *B. rubens*, and *B. tectorum*, have “sharp calluses and barbed lemmas and awns” (Hulbert 1955, p 183). Lemmas of species in section Bromus, which includes *B. hordeaceus*, lack barbs on lemmas and awns and their calluses are not as sharp (Hulbert 1955).

Diaspores of *B. tectorum* may include one or more florets in what are essentially multiple-awned seed units. Awns can promote adhesion of seeds to animal fur and wool and human clothing (Mack 1981), but they often function primarily to anchor seeds to soil and facilitate germination (Sorensen 1986). Awns can assist seed burial due to hygroscopic characteristics that result in twisting with wetting and drying cycles (Peart 1979). On the Colorado Plateau, most *B. tectorum* diaspores had either a single floret with an awn and filled seed (simple diaspore) or one or more sterile florets with awns that were attached to the floret with the filled seed (complex diaspores) (Monty et al. 2013). Even though complex diaspores were slightly heavier, they traveled more than five times farther and their maximum dispersal distance was more than 15 times greater than simple diaspores. Increased surface area created by sterile florets likely resulted in greater lift forces to carry them longer distances. Similarly, Chambers (2000) found that seeds with greater surface area were transported longer distances despite having structures that appear designed to promote burial (e.g., hygroscopic awns) and retention (e.g., sharp tip of diaspore and directional hairs that encourage movement into materials such as fur and fabric as in many *Bromus* species).

Both physical and biotic factors influence *Bromus* dispersal. Wind and water are important dispersal agents of *Bromus* (Kelrick 1991), especially over short distances (Hulbert 1955). Wind usually carries *Bromus* diaspores across soil surfaces, moving seeds 1–2 m from parent plants (Kanarek and Kao 2011). At times, “dust whirls” may carry diaspores longer distances (Hulbert 1955). Johnston (2011) found *B. tectorum* diaspores traveled 2.4 m on average over bare, mostly level soil with depressions less than 10 cm deep. Only 5 % of seeds traveled farther than 7.6 m and maximum dispersal distance was 20.8 m.

Diaspores accumulate with litter in cracks and depressions in soil and near obstacles that slow wind speed like shrubs (Kelrick 1991). In *P. edulis* and *Juniperus osteosperma* (Torr.) Little (Utah juniper) plant communities, *B. tectorum* seeds traveled more than five times farther on average in burned areas with little vegetation to obstruct seed movement compared to unburned areas (Monty et al. 2013). Higher *B. tectorum* recruitment can occur under *A. tridentata* shrubs where more litter and seeds accumulate than in bare interspaces (Kelrick 1991). Favorable moisture and temperature conditions where seeds and litter are deposited may enhance germination (Reichman 1979; Chambers 2000). Burial in relatively bare soil may be facilitated by precipitation events. Johnston (2011) reported that *B. tectorum* diaspores were visible only by their awns protruding from the soil after a 3.2 mm rainfall event.

Animals are likely to play a role in dispersal of *Bromus* over distances farther than a few meters (Hulbert 1955; Klemmedson and Smith 1964). Although *Bromus* diaspores lack adaptations to facilitate adhesion such as barbs or hooks (Sorensen 1986), the sharp callus and backward directed hairs that some *Bromus* species possess can facilitate attachment to animals and humans (Mack 1981). Diaspores remain attached until they are discovered and removed by the animal or fall off passively (Sorensen 1986). When and where detachment from the animal occurs is important to understanding long-distance dispersal of *Bromus* and other plant species, but is difficult to study.

Seeds of *Bromus* species are dispersed by humans intentionally and unintentionally. Common gardens with ecotypes of *B. tectorum* from different regions of the world planted in Pullman, WA, and Lewiston, ID, USA, may have been one origin of future spread (Mack 1981). Although animals and humans disperse seeds of *Bromus* through adhesion, this mechanism is likely minor compared to the scale and extent of spread through contamination of hay and crop seed, in particular seed of forage and small grain crops such as wheat (Mack 1981).

Grass seed can survive digestive tracts of herbivores. Survival seems to be related to hard seededness (hard-seeded species have higher survival) (Gardener et al. 1993a, b), seed size (Pakeman et al. 2002), and transit time through the gut (the shorter the transit time, the greater the survival) (Janzen 1984). In general, *Bromus* do not have characteristics associated with high survival after bovine ingestion. Despite this, Wells and Lauenroth (2007) found that *B. tectorum* seedlings emerged from recent horse manure collected from a trail used for backcountry access in the Colorado Rocky Mountains.

Birds eat seeds of *Bromus* species and could serve as dispersal vectors should the seed survive, although information as to this possibility is lacking. In western Utah, *Alectoris chukar* (chukars), an exotic game bird species widely introduced in the western USA, had *B. tectorum* seed in 76.3 % of their crops with an average of 522 *B. tectorum* seeds per crop (Larsen et al. 2007). Despite this, no *B. tectorum* germinated from chukar fecal samples after being treated to break seed dormancy.

La Tourrette et al. (1971) studied the role of heteromyid rodents in seed dispersal in degraded *A. tridentata* communities. Cheek pouches of *Dipodomys* spp. (kangaroo rats) contained over 1500 *B. tectorum* seeds on average, more than any other species, although an introduced forage grass had higher seed mass. Cheek pouches of *Perognathus parvus* (pocket mice) also contained *B. tectorum* seeds. Rodents stored caryopses of *B tectorum* in soil depressions approximately 5 cm deep and 3 cm wide, and *B. tectorum* seeds in caches germinated earlier than non-cached seed. Likewise, Reichman (1979) found that nearly twice as many seedlings grew from seed caches than from nearby soils. Higher seedling emergence was attributed primarily to higher seed densities in caches compared to controls, but microsite conditions of seed caches also may have contributed to enhanced germination (Reichman 1979). Emergence of *B. tectorum* was 100 times higher for seeds placed in 9 mm depressions in soil compared to seeds placed on bare soil (Evans and Young 1987 in Chambers and MacMahon 1994).

10.4.3 Seed Banks

A seed bank is a reserve of mature viable seeds located in fruits (or cones) on the plant (aerial seed bank), on the soil surface, or buried in soil, duff, or litter (Roberts 1981). In annual *Bromus* the majority of the seed bank is stored on the soil surface or in litter. Seed burial studies show that most seeds of *B. tectorum* germinate in the first year after dispersal. Few *B. tectorum* seeds are viable after 2–3 years of burial, but some seeds survive as long as 5 years (Thill et al. 1984).

Seed bank information is limited for *B. diandrus* and *B. hordeaceus*, but in heavily invaded communities seed bank densities of all four *Bromus* species often reach numbers in the thousands following dispersal. More intact communities with minimal *Bromus* also can have significant *Bromus* in the seed bank. In southern California annual grasslands, *B. diandrus* seed density estimates range from 569 to 1473 m^{-2}, some of the lowest peak densities of the four species (Moyes et al. 2005; Cox and Allen 2008). *Bromus rubens* seed bank densities range from 2837 to 4085 m^{-2} in southern California annual grasslands (Cox and Allen 2008) and >3000 to >5800 m^{-2} in Mojave Desert communities (Abella et al. 2009; Esque et al. 2010; Jurand and Abella 2013). Estimates of *B. hordeaceus* seed bank densities span the greatest range, from >1900 seeds m^{-2} in southern California to >103,500 seeds m^{-2} in the northern California's Central Valley (Young and Evans 1989; Cox and Allen 2008). *Bromus tectorum* seed banks are highly variable in invaded ecosystems, with a low of 35 seeds m^{-2} in northern mixed prairie of Montana (Karl et al. 1999) and a high of >30,000 seeds m^{-2} in a shadscale ecosystem in the Great Basin (Meyer et al. 2007), with frequent counts from 2000 to 20,000 seeds m^{-2} (e.g., Mack and Pyke 1983; Humphrey and Schupp 2001; Meyer et al. 2007). Even in more intact communities, *Bromus* are in the seed bank in low (e.g., <50 seeds m^{-2} for *B. tectorum* in the Great Basin; Hassan and West 1986; Allen et al. 2008) to moderate (e.g., 806 seeds m^{-2} for *B. hordeaceus* in coastal sage scrub of southern California; Cox and Allen 2008) densities. Higher densities in relatively intact communities appear due to high propagule pressure from adjacent heavily invaded communities (Cox and Allen 2008).

Peak seed densities are short lived, and the seed bank is rapidly depleted, primarily by germination but also by seed predation (Borchert and Jain 1978; Beattie 1989) and pathogens (Crist and Friese 1993; Meyer et al. 2007, 2015). Consequently, seed bank carryover to the following year is frequently less than 10 % for *B. tectorum* in the Great Basin (Meyer et al. 2007; Smith et al. 2008), *B. rubens* in the Mojave Desert (Jurand et al. 2013), and *B. hordeaceus* in the northern Central Valley, California (Young and Evans 1989). However, the actual proportion surviving depends on the environment, and carryover of *B. tectorum* in the Great Basin can be greater in drier years and on drier sites due to reduced germination (Smith et al. 2008), or less on drier sites due to ungerminated seeds having longer exposure to pathogens (Meyer et al. 2007). Nonetheless, high levels of yearly loss from the seed bank mean that survival for more than 3 years is unlikely (Meyer et al. 2007). Although no studies have been conducted on carryover for *B. diandrus*, germination patterns suggest it also has little carryover (Harradine 1986).

Abiotic and biotic factors contribute to variation in seed bank densities, although relative strengths of different factors are unknown. *Bromus* must largely refill the seed bank annually, and ability to refill depends largely on precipitation—*B. tectorum* input to a seed bank in western Utah varied from 3567 seeds m^{-2} in a drier year to 13,942 seeds m^{-2} in a wetter year (Smith et al. 2008). Prescribed burns and wildfires frequently reduce *Bromus* seed bank densities by 94–99 % (Humphrey and

Schupp 2001; Allen et al. 2008; Cox and Allen 2008; Diamond et al. 2012), although reductions can be less depending on timing of fire relative to seed shatter (Hassan and West 1986; Rasmussen 1994). *Bromus tectorum* seed bank densities in the Great Basin can completely recover to pre-burn densities in two growing seasons (Humphrey and Schupp 2001; Allen et al. 2008). In contrast, recovery of *B. rubens* seed banks in the Mojave Desert appears to take 4 or more years (Brooks 2002; Abella et al. 2009). Livestock grazing also influences seed banks and targeted grazing by livestock can reduce *B. tectorum* inputs to the seed bank (Diamond et al. 2012), but may not be sufficient to influence *B. tectorum* populations (Hempy-Mayer and Pyke 2008). At cheatgrass-dominated sites in the Basin and Range, plants clipped short at the boot stage and again 2 weeks later had among the lowest mean seed densities, but still had 123–324 seeds m^{-2} at one site, and 769–2256 seeds m^{-2} at a second site (Hempy-Mayer and Pyke 2008).

In highly invaded areas, *Bromus* often dominate the seed bank. In a degraded *B. tectorum*-dominated community in western Utah, over 90 % of the seed bank was *B. tectorum*; in contrast to >12,800 *B. tectorum* seeds m^{-2}, there were <3 native perennial seeds m^{-2} (Humphrey and Schupp 2001). Similarly, in a Mojave Desert community, *B. rubens* comprised >90 % of the seed bank (Jurand and Abella 2013). In highly invaded areas, when *Bromus* do not dominate the seed bank, it is often because other invasive annuals, not natives, are more dominant (Cox and Allen 2008; Esque et al. 2010). Low densities of *B. tectorum* in Montana grasslands (35 m^{-2}) are likely at least partially a consequence of site domination by *B. japonicus*, with >10,000 seeds m^{-2} (Karl et al. 1999). Even more intact communities can have significant representation of *Bromus* in the seed bank. In an *A. tridentata*/*J. osteosperma* community in western Utah, *B. tectorum* seed densities were low but still comprised 47 % of the seed bank (Hassan and West 1986). In an intact Wyoming big sagebrush community in Utah, *B. tectorum* comprised only 7.5 % of the seed bank, but was the fourth most abundant species (out of 47) with higher density than all but one native (Pekas and Schupp 2013).

10.4.4 Seed Germination

Seeds of all four species are nondormant following a period of after-ripening and readily germinate when soil water and temperature are not limiting (Corbineau et al. 1992; Andersson et al. 2002; Beckstead et al. 1996; Del Monte and Dorado 2011). Differences in length of dormancy and germination responses to environmental conditions exist among annual *Bromus* species and influence competitive interactions (e.g., Andersson et al. 2002), but are not well quantified. Adaptive germination and growth responses in *B. tectorum* populations from contrasting habitats indicate both genetic and environmental controls on germination response (Beckstead et al. 1996; Dyer et al. 2012), thus partially explaining invasibility of this and likely other invasive annual *Bromus* species.

Timing of germination and seasonal activity (phenology) of *Bromus* allows these invaders to use different resource pools than species in many of the native communities where they are most problematic. In those ecoregions where most precipitation arrives in winter and spring, invasive *Bromus* species that germinate and grow early in the growing season may preempt resources and attain competitive dominance. This aspect of the "seasonal priority advantage" of *Bromus* has been shown for *B. diandrus* and *B. hordeaceus* in Mediterranean California annual grassland (Dyer and Rice 1999; Abraham et al. 2009; Wainwright et al. 2012), *B. tectorum* in the cold desert (Mack and Pyke 1983; Booth et al. 2003; Kulmatiski et al. 2006), and *B. rubens* in the Mojave Desert (DeFalco et al. 2007). Timing of germination depends on having adequate soil water availability when temperatures are high enough for physiological activity and consequently varies among ecoregions and over environmental gradients. In cold desert sagebrush steppe, germination of *B. tectorum* was predicted to occur more often in spring than in fall and much more often than in winter based on simulated soil moisture availability from historical climate records (Bradford and Lauenroth 2006) and soil temperature and water data measured over elevation gradients in the central Basin and Range (Roundy et al. 2007). However, on the Columbia Plateau germination was higher in late summer and fall than winter or spring (Mack and Pyke 1983). Earlier germination in fall or winter vs. spring may increase competitiveness of *Bromus* with natives, as shown for *B. rubens* and native annual species in the Mojave Desert (DeFalco et al. 2007). However, *B. diandrus* and *B. hordeaceus* in California coastal sage scrub had higher mortality when emergence resulted from a late-summer watering event than when emergence followed ambient winter rainfall due to factors such as increased herbivory (Wainwright et al. 2012).

10.5 Effects of Biological Crusts on Seed Dispersal and Germination

Roughness, texture, cracking, and other aspects of the soil surface influence the ultimate destination of plant seeds and most of these variables are heavily affected by biocrusts. There are two general morphologies of biocrusts: smooth biocrusts found in warm deserts or recently disturbed areas and pinnacled biocrusts found in cold deserts. Smooth biocrusts are found in regions where soils do not freeze; they are characterized by a heavy dominance of cyanobacteria and physical/chemical crusting. Because these biocrusts actually smooth the soil surface, most seeds are easily moved across plant interspaces by wind or water unless the seed has specialized mechanisms for adhesion to smooth soil surfaces (e.g., mucilaginous coats) (Gutterman 1994). *Bromus* seeds lack these adaptations and *Bromus* seeds and plants are typically found under or near obstacles such as rocks or plants rather than in plant interspaces.

In contrast, surfaces in cold deserts are characterized by lichen-moss biocrusts, which, combined with soils that freeze in winter, create a highly roughened and cracked soil surface. Many studies have shown that these rough surfaces trap seeds more effectively than smooth soil surfaces (Harper and St. Clair 1985; Eckert et al. 1986; Harper and Marble 1988; Mücher et al. 1988; Prasse 1999). In such settings, *Bromus* seeds can often be seen on the soil surface in both plant interspaces and under plant canopies. This surface effect was verified using a portable wind tunnel where seeds with large appendages, including *B. tectorum*, quickly left smooth interspace soils but were retained by roughened biocrusted surfaces (Belnap, unpubl. data).

Multiple studies in warm and cold deserts show that well-developed biocrusts can inhibit germination and establishment of invasive annual plants including several *Bromus* species in the USA and Israel (Evans and Young 1984; St. Clair et al. 1984; Eckert et al. 1986; Kaltenecker et al. 1999; Larsen 1995; Howell 1998; Prasse 1999). In contrast, crushed biocrusts can stimulate growth of invasive annual plants when left in place (Crisp 1975; Larsen 1995; Howell 1998). It has been speculated in the literature that *Bromus* and *Schismus* P. Beauv (Mediterranean grass) evolved with animal herds whose hooves break up biological and physical soil crusts facilitating seed burial and annual grass success (Mack and Thompson 1982).

The mechanism by which intact biocrusts inhibit *Bromus* and other annual plants is not known, but several factors are likely involved. Germination and emergence are facilitated in arid systems when seeds are buried due to a higher probability of sufficient soil moisture for germination. Also, buried seeds are hidden from consumers, potentially reducing predation. Small cracks found in biocrusts allow small seeds to enter the soil, but seeds with large appendages, such as many *Bromus*, are prevented from entering these cracks. Well-developed biocrusts also stabilize soils and thus prevent moving sediment from burying seeds (Belnap 2003).

Biocrusts cannot protect all areas from *Bromus* invasion. In a southeast Utah grassland covered by well-developed biocrusts, a combination of low seed predation and unusual climate conditions facilitated a large *B. tectorum* invasion (Belnap and Phillips 2001). Extremely low (<0.01 %) cover of *B. tectorum* was first documented in this grassland in 1964 (Kleiner and Harper 1977) and stayed at a low level until 1995. In late August-early September 1995, almost daily rain events resulted in *B. tectorum* establishment and invasion over a 50 ha area. This “instant” large-scale invasion implied that sufficient seed were in the seed bank to facilitate plant establishment and population growth under favorable weather conditions despite the presence of biocrusts.

10.6 Herbivory

Most of the available information on herbivory is from research on *B. tectorum*, and there is still much to learn about the other three focal species. Soil and plant community disturbance often precede and reinforce *Bromus* invasions. Herbivory often has less immediately apparent effects on *B. tectorum* establishment and expansion than fire, but its influence can vary depending on the intensity and timing of herbivory and climate conditions. Negative effects of herbivory on *B. tectorum* can be exceeded by indirect positive effects through competitive release when herbivores preferentially target native grasses and forbs over *B. tectorum*.

10.6.1 Grazing Impacts on **B. tectorum**

There has been interest in livestock grazing effects on *B. tectorum* because of its potential as a biocontrol. Livestock and wildlife forage on *B. tectorum* particularly during the winter and spring vegetative period (Murray 1971; Wikeem and Pitt 1992). *Bromus tectorum* has good nutritional value during winter/spring as indicated by feeding preference by wildlife (Austin et al. 1994) and livestock weight gain in *B. tectorum*-dominated pastures (Murray and Klemmedson 1968). However, preference for *B. tectorum* tends to decrease during dry years (Murray 1971) and in late spring/summer when senescence and seed production reduce its nutritional quality and palatability (Cook and Harris 1952; Wikeem and Pitt 1992).

Intensive grazing of *B. tectorum* by cattle (80–90 % removal) or experimental clipping reduces *B. tectorum* biomass and seed production, particularly when defoliation is repeated or occurs early in development (Hempy-Mayer and Pyke 2008; Schmelzer 2009; Diamond et al. 2012). However, clipping plants to a 2.5 cm height at the boot stage and again 2 weeks later still resulted in 123–324 seeds m^{-2} at one site and 769–2256 seeds m^{-2} at a second site, calling into question the potential for using livestock grazing as a biocontrol in *B. tectorum*-dominated areas (Hempy-Mayer and Pyke 2008). Grazing tolerance in *B. tectorum* may result from continued growth of its root system despite defoliation (Arredondo and Johnson 2009).

Available data indicate that the response to high-intensity grazing is generally negative, but that the magnitude of change and degree of recovery depends on climate and site conditions. In a high-elevation, semiarid grassland near Flagstaff, AZ, high-intensity grazing had strong directional effects that led to a decline in perennial forb cover and an increase in annual plants, particularly *B. tectorum* (Loeser et al. 2007). Following a severe drought in the sixth year of the study, plant cover of exotic species increased significantly and this increase was greatest in the high-impact grazing plots where native cover had been reduced by one-half (Loeser et al. 2007). A multivariate study in *A. tridentata* ssp. *wyomingensis* communities in the Basin and Range showed that cattle grazing reduced resistance to invasion by decreasing bunchgrass cover, increasing the size of gaps between perennial herbaceous plants, and reducing biological soil crusts (Reisner et al. 2013). Cheatgrass cover was positively associated with sandy soils and negatively associated with high heat loads due to negative effects on bunchgrass cover (Reisner et al. 2013). Analyses of long-term datasets from sagebrush steppe in the Northern Basin and Range clearly indicate that site conditions and climate influence *B. tectorum* abundance and plant community dynamics over time regardless of grazing history (West and Yorks 2002; Bagchi et al. 2013).

Grazing history can interact with herbivory to modulate its influence on *B. tectorum* success. A factorial study in an *A. tridentata* ssp. *vaseyana* site that examined effects of grazing and fire showed that long-term grazing exclusion followed by fire stimulated much higher levels of *B. tectorum* cover, density, and biomass than grazing exclusion without recent fire or grazing followed by fire due to higher fuel biomass and fire severity (Davies et al. 2009).

10.6.2 Native Herbivores and Community Resistance

Native herbivores consisting primarily of small mammals and insects can decrease invasive plant establishment and performance and thus increase community resistance to invasion (Levine et al. 2004). In a sagebrush community, folivory (leaf eating) by small mammals had little effect on seedling survival of *B. tectorum*, but significantly reduced biomass and seed production (Pyke 1986). In a follow-up study, small mammal folivory strongly increased *B. tectorum* seedling mortality, but tolerance to herbivory increased as seedlings matured (Pyke 1987). Grasshoppers consume *B. tectorum* (Rogers and Uresk 1974; Beckstead et al. 2008), but their preference for it decreases from late spring to summer (Fielding and Brusven 1992). Harvester ants can be very efficient at controlling *B. tectorum* establishment around their mounds by removing seedlings, but their influence outside of their nest area is not well studied (Clark and Comanor 1975). Better understanding of the relationships between *B. tectorum* and native folivores could result in management approaches that strengthen community resistance to *B. tectorum* establishment and expansion.

Herbivory can promote establishment and expansion on *B. tectorum* through competitive release if herbivores preferentially target other plant species (Strand et al. 2014). Studies of insect and ungulate herbivory demonstrate preference for native plant species over *B. tectorum* (Rogers and Uresk 1974; Loeser et al. 2007). Also, there is evidence of indirect competition between *B. tectorum* and native grasses in which high-density *B. tectorum* populations increase grasshopper populations that consume native grasses more intensively than *B. tectorum* (Beckstead et al. 2008).

10.6.3 Potential Effects on Disturbance Regimes and Community Resilience

Herbivory in *B. tectorum*-dominated communities has the potential to mitigate invasive grass-fire regimes by altering biomass composition, and reducing fine fuels and their continuity (Strand et al. 2014). High-impact cattle grazing in successive post-fire years reduced *B. tectorum* biomass and cover resulting in reduced flame lengths and fire spread in subsequent years (Diamond et al. 2010). However, given the size of recent wildfires in the western USA (e.g., 80,000 ha and larger; Murphy et al. 2013) relative to the size of areas where high-impact grazing can be successfully implemented, applicability is likely limited to fuel breaks or protecting property. Because of the central role that fire has in *B. tectorum* invasions, reducing fire severity and extent has the potential to increase resilience of the plant community to invasion (Chambers et al. 2014a). However, any potential gains resulting from fine fuel removal by livestock may be counterbalanced by decreased resistance to

B. tectorum due to herbivory of native plants that compete with *B. tectorum*, increased soil disturbance, and damage to biocrusts (Reisner et al. 2013).

10.7 Management Implications

This chapter illustrates that environmental factors, community attributes and processes, life history and ecophysiological traits of the invader, and direct and indirect interactions of the invader with the plant community are important determinants of community resistance to *Bromus*. Understanding the effects of climate and soils, especially soil temperature and moisture regimes, on interactions of *Bromus* and plant communities can be used to prioritize management activities across the landscape and determine appropriate activities at local scales (Miller et al. 2013; Chambers et al. 2014a, c). For example, in higher elevation communities with cooler soil temperatures and greater resistance to *B. tectorum*, it may be possible to successfully use treatments like prescribed fire that likely would result in *B. tectorum* dominance in communities with warmer soil temperatures and lower resistance. Also, recognition of the importance of community attributes and processes on *Bromus* invasion, such as the role of biocrusts in preventing *Bromus* seed entrapment and seedling establishment, can be used as management incentives to conserve communities where these attributes and processes are still intact and to restore those where they have been degraded.

Rethinking effects of resource availability on competitive interactions within plant communities may allow development of more effective management strategies. *Bromus* is generally more effective than native species at using limiting soil resources on short timescales, and manipulating soil nitrogen through carbon additions or repeated fire is largely ineffective in more arid ecosystems (Monaco et al. 2003; James et al. 2011; Jones et al. 2015a, b). However, perennial herbaceous species, especially those with similar phenologies, are highly effective competitors (Booth et al. 2003; Blank and Morgan 2012). This indicates that in more highly invaded areas and areas with high climate suitability to *Bromus*, restoration species need to have the capacity to both establish and compete, specifically similar phenology and use of shallow resource pools. In less highly invaded areas and areas with lower climate suitability to *Bromus*, both passive and active management activities may need to focus on increasing perennial herbaceous species, especially grasses.

Recognition of the importance of propagule supply as influenced by seed production and seed banking, seed dispersal, and priority effects also informs management. In highly invaded areas where restoration/rehabilitation or fire prevention are objectives, herbicides and high-impact livestock grazing can decrease seed production and seed banks. However, caution is advised in applying these management strategies because native species can also be negatively affected by preemergent herbicides (Pyke et al. 2014) and heavy livestock grazing (Reisner et al. 2013).

10.8 Research Needs

Understanding community resistance to invasion is complex because it is affected by many interacting variables about which we are still learning. Both manipulative studies and longer-term observational studies that examine a suite of variables are needed in order to better clarify the environmental characteristics and community attributes and processes that influence resistance to *Bromus.* Although most research to date has focused on *B. tectorum*, in a warming environment other invasive species adapted to warmer temperatures such as *B. rubens* may become more problematic (see Bradley et al. 2015). An experimental approach that examines broad-scale environmental gradients and multiple species is likely to provide the most useful information. Research is needed in several areas to improve our understanding of resistance to *Bromus*, and our ability to develop more effective management strategies for increasing resistance. These needs include:

- Better define the climate suitability (space) of *Bromus* species and of co-occurring native species to understand (1) effects of environmental factors on community resistance at both large landscape scales and local scales and (2) potential expansion in a warming environment.
- Increase our understanding of resource pools (sensu Leffler and Ryel 2012) and their influence on resistance to *Bromus*. How does resource availability vary across environmental gradients and in response to disturbance and management treatments? How do changes in resource availability across environmental gradients and in response to disturbance and management treatments influence interactions of *Bromus* with plant communities?
- Increase our understanding of how native species' life history and ecophysiological traits influence competitive interactions with *Bromus*.
- Increase our understanding of community processes, such as herbivory by native herbivores and livestock, on resistance to *Bromus*.

Acknowledgments Jayne Belnap was supported by the USGS Ecosystem Invasives Program. Any use of trade names is for descriptive purposes only and does not imply endorsement by the US Government.

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