# Chapter 3
# Ecosystem Impacts of Exotic Annual Invaders in the Genus *Bromus*

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**Abstract** An understanding of the impacts of exotic plant species on ecosystems is necessary to justify and guide efforts to limit their spread, restore natives, and plan for conservation. Invasive annual grasses such as *Bromus tectorum*, *B. rubens*, *B. hordeaceus*, and *B. diandrus* (hereafter collectively referred to as *Bromus*) transform the structure and function of ecosystems they dominate. Experiments that prove cause-and-effect impacts of *Bromus* are rare, yet inferences can be gleaned from the combination of *Bromus*-ecosystem associations, ecosystem condition before/after invasion, and an understanding of underlying mechanisms. *Bromus* typically establishes in bare soil patches and can eventually replace perennials such as woody species or bunchgrasses, creating a homogeneous annual cover. Plant productivity and cover are less stable across seasons and years when *Bromus* dominates, due to a greater response to annual climate variability. *Bromus'* "flash" of growth followed by senescence early in the growing season, combined with shallow rooting and annual habit, may lead to incomplete use of deep soil water, reduced C

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sequestration, and accelerated nutrient cycling. Litter produced by *Bromus* alters nearly all aspects of ecosystems and notably increases wildfire occurrence. Where *Bromus* has become dominant, it can decrease soil stability by rendering soils bare for months following fire or episodic, pathogen-induced stand failure. *Bromus-invaded* communities have lower species diversity, and associated species tend to be generalists adapted to unstable and variable habitats. Changes in litter, fire, and soil properties appear to feedback to reinforce *Bromus'* dominance in a pattern that portends desertification.

**Keywords** *Bromus* • Annual exotic grasses • Ecosystems • Desertification • Feedbacks

## 3.1 Introduction

Exotic annual grasses in the genus *Bromus* that are invading semiarid and arid landscapes in the Western USA (hereafter "*Bromus*") have significant impacts on ecosystem structure and function where they dominate plant community cover (Fig. 1.1 in Germnio et al. 2015). This chapter aims to give an overview of these impacts, with some treatment of *Bromus rubens* L. (red brome), *B. diandrus* Roth (ripgut brome), and *B. hordeaceus* L. (soft brome) but a primary focus on *B. tectorum* L. (cheatgrass, downy brome). *B. tectorum* has become the most widespread exotic annual grass in the Western USA and has also attained the greatest local dominance of communities, often occurring in vast and nearly monocultural patches (Brooks et al. 2015). Nearly 10 % of the many publications on invasive plant impacts are on *Bromus* (specifically *B. tectorum*; Hulme et al. 2013), and an exhaustive review of the studies on ecosystem impacts of *Bromus* invaders is beyond the scope of this chapter. Several previous reviews have suggested ways that *Bromus* can transform ecosystem structure and function (Hulbert 1955; D'Antonio and Vitousek 1992; Allen et al. 2011), particularly *B. tectorum* (Stewart and Hull 1949; Klemmedson and Smith 1964; Mack 1981; Billings 1990). We begin with a short overview of how the plant community is altered by *Bromus* invasion. Then, we describe how disturbance interacts with *Bromus*, focusing on fire because it is a key disturbance for most landscapes in western North America and is a key aspect of *Bromus* invader's impacts (Brooks et al. 2004). We evaluate *Bromus'* impact on fire frequency and extent and the influence of *Bromus* on ecosystem characteristics such as site and soil stability and flow or cycling of energy, water, carbon (C), and nutrients. Last, we discuss impacts on invertebrate and vertebrate communities, including wildlife and domestic livestock.

We focus on comparisons between native- and *Bromus*-dominated communities where there is supporting literature, although few studies can truly separate *Bromus* invader effects from those of native species (Stark and Norton 2015). Many of the native plant communities impacted by *Bromus* have native perennial grasses that increase after disturbance in the absence of *Bromus* invasions, followed by increases in abundance of woody species over time. Thus, we assess *Bromus* impacts by comparing *Bromus* effects relative to both native perennial grasses and later-successional plants, as well as to plant communities created by land treatments (e.g., seedings) designed to counter threats of *Bromus* invasion. As our review demonstrates, no single study has distinguished the influence of *Bromus* from effects of associated land uses and disturbances or compared *Bromus* impacts among various native community states.

## 3.2 Impacts on Plant Communities

Where *Bromus* occur with native perennials, they often have inverse relationships to density or cover of natives or may have a patchy distribution among perennial plant, bare interspace, or biological soil crust microsites, as shown for sagebrush steppe in the Northern Basin and Range and Wyoming Basin (Anderson and Inouye 2001; Gasch et al. 2013; Reisner et al. 2013), Mojave and Sonoran Deserts (Brooks 2000; Salo et al. 2005; DeFalco et al. 2001, 2007), Colorado Plateau (Belnap and Phillips 2001), and Mediterranean California Grasslands (Corbin et al. 2007). *Bromus* typically attains dominance following disturbances such as fire and/or grazing, in those areas having suitable climate (Chambers et al. 2014, 2015). *Bromus* invasions can transform communities that have a relatively high proportion of perennials or mosses and lichens that cover plant interspaces into exotic annual and ephemeral native communities (Brooks et al. 2015). Such invasions can also change the most basic spatial and temporal structure of the plant community depending on factors such as seasonality of precipitation and community productivity and composition (Fig. 10.1 in Chambers et al. 2015). For example, *Bromus* impacts are greater in the less productive mix of shrubs and forbs in the Mojave Basin and Range compared to the relatively productive shortgrass steppe, as we describe below. Few native species are able to establish in dense stands of *Bromus* (e.g., Humphrey and Schupp 2004), and loss of native species richness and diversity often leads to either *Bromus* monocultures or exotic annual/biennial communities (Fig. 3.1). However, *Bromus* invasion into relatively undisturbed and protected communities or regions does occur, typically at subdominant levels (*Bromus* comprising <20 % relative cover). Examples of undisturbed but invaded areas include perennial grasslands of the Colorado Plateau (Belnap and Phillips 2001), islands of sagebrush steppe in the Northern Basin and Range isolated by rugged/impassable lava where native species richness declined (“kipukas”, Bangert and Huntly 2010), a ~1000-km$^2$ grazing exclosure at the Idaho National Lab (Anderson and Inouye 2001; Bagchi et al. 2013), undisturbed *Coleogyne ramosissima* Torr. (blackbrush) shrubland (Brooks and Matchett 2003), and coastal sage scrub subject to anthropogenic nitrogen (N) deposition in southern California (Cox et al. 2014).

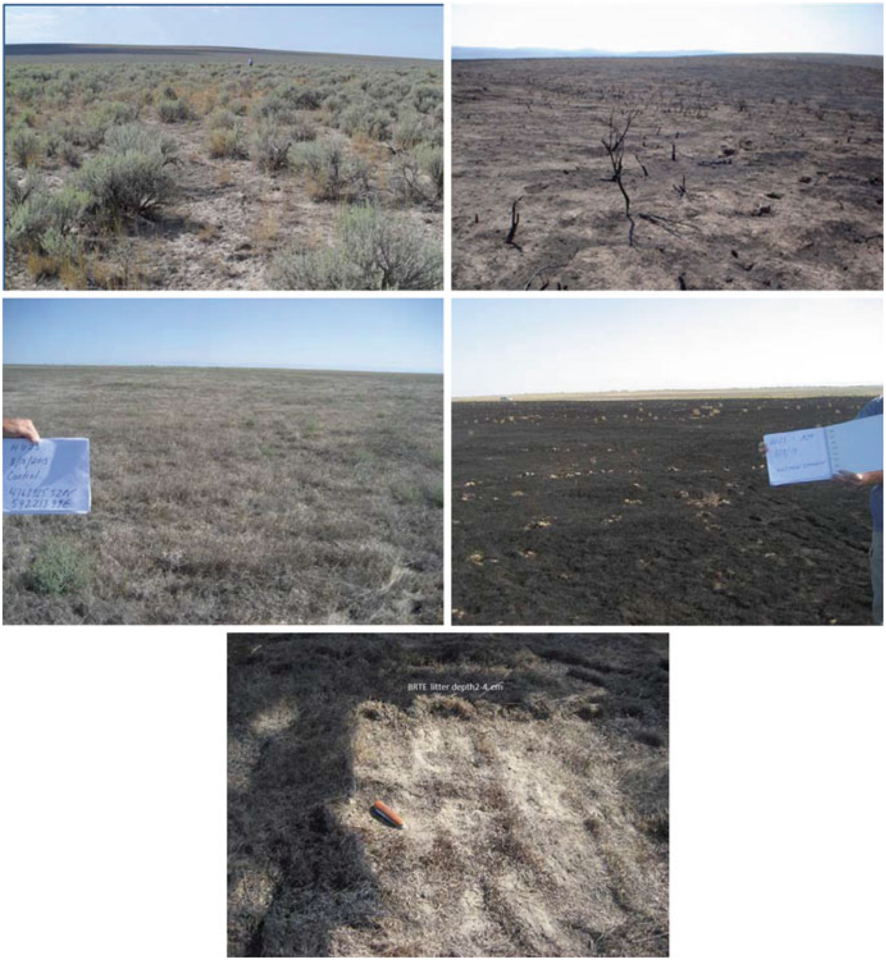

**Fig. 3.1** Photos of a Wyoming big sagebrush site that had no *B. tectorum* before fire (*top left*) and the resulting "clean burn" typical of such sites (*top right*), a site dominated by *B. tectorum* before fire (*middle left*), and the resulting "dirty burn" and dense *Bromus* litter (*middle right*). The *bottom panel* shows a close-up view of the charred but incompletely combusted *Bromus* litter occluding the soil. Postfire photos were taken approximately 1 month after summer wildfire. Photo credits: *top row*, M. Germino; lower three, A. Halford

### 3.2.1 Changes to Above- and Belowground Community Structure

Invasion of *Bromus* in the absence of fire often occurs through establishment in bare soil interspaces between perennials, creating a homogeneous herbaceous layer, such as for *B. tectorum* in grazed sagebrush steppe (Reisner et al. 2013). However, greater establishment under shrubs or trees than interspaces is also evident in some communities, such as for *B. rubens* in the Mojave Basin and Range (Brooks 1999;

Abella et al. 2011), *B. tectorum* in ponderosa pine forest of the Northern Rockies, or sagebrush steppe in the ecotone between the Sierra Nevada and Central Basin and Range (Gundale et al. 2008 and Griffith 2010, respectively). Following fire, many of the dominant shrub species are killed, further promoting the shift toward homogenous cover of *Bromus* (Fig. 3.1). Belowground, the native diversity of deep/tap rooting and shallow/fibrous-rooting plant species and the associated soil-resource partitioning that is fundamental to sagebrush steppe (Ryel et al. 2008) is lost when *Bromus* dominate sites, often leaving a dense, continuous, and shallow dispersion of fine, annual roots (reviewed in Wilcox et al. 2012). Specifically, many of the native communities impacted by *Bromus* have a mix of woody species that have tap roots extending 1–3 or more meters deep into the soil profile, while neighboring herbs and particularly grasses typically have their highest densities of roots in shallower soils (i.e., 10–50-cm depths). Following conversion to *Bromus* grasslands, these sites are left with only a dense proliferation of roots in the shallow soil horizons (typically above 30–40-cm depth although their roots can extend to 1 m or deeper; Wilcox et al. 2012).

*Bromus* invasions strongly affect the phenology of the plant community because of *Bromus'* capacity for fall germination, rapid growth, and senescence by spring or early summer. *Bromus* cover also exhibits relatively high interannual variability compared to perennial vegetation, primarily due to its response to precipitation in fall and early spring (e.g., for *B. tectorum*, West and Yorks 2006). Communities that are dominated by *Bromus* are often also comprised of other annual or biennial exotics that have highly variable presence from year to year (Piemeisel 1951; Prevey et al. 2010). Few native plants impart spatiotemporal effects as strong as *Bromus*. One example is *Poa secunda* J. Presl (Sandberg bluegrass), a small bunchgrass that can create vast expanses of homogenous cover with early-season green up and senescence, often in sagebrush steppe that has been repeatedly disturbed.

Significant instability in community cover results when *B. tectorum* exhibits large-scale, periodic stand failure in response to fungal pathogens on sites it otherwise dominates (Stewart and Hull 1949; Klemmedson and Smith 1964, Meyer chapter on Pathogens, see maps in Fig. 3.2). The absence of vegetation cover prior to recolonization can result in extensive wind erosion, depletion of topsoil organic matter, and other key attributes of these ecosystems (Fig. 3.3, Sect. 3.4). Die-offs of *B. tectorum* lasting at least 2 years apparently occurred on approximately one million hectares per year from 2000 to 2010 in the Northern Basin and Range, and 10 % of *Bromus*-invaded areas had a >80 % chance of stand failure (Wylie 2012).

### 3.2.2 Effects of Litter Accumulation on Community Structure

Dense layers of fine-textured, straw-like litter (including standing dead tissue) produced from senesced stems, leaves, and reproductive tissue of *Bromus* are an important impact at either patch (interspace) or landscape scales (Fig. 3.1). The litter layers can either be mats laying on soil and/or standing dead tissue. Factors such as

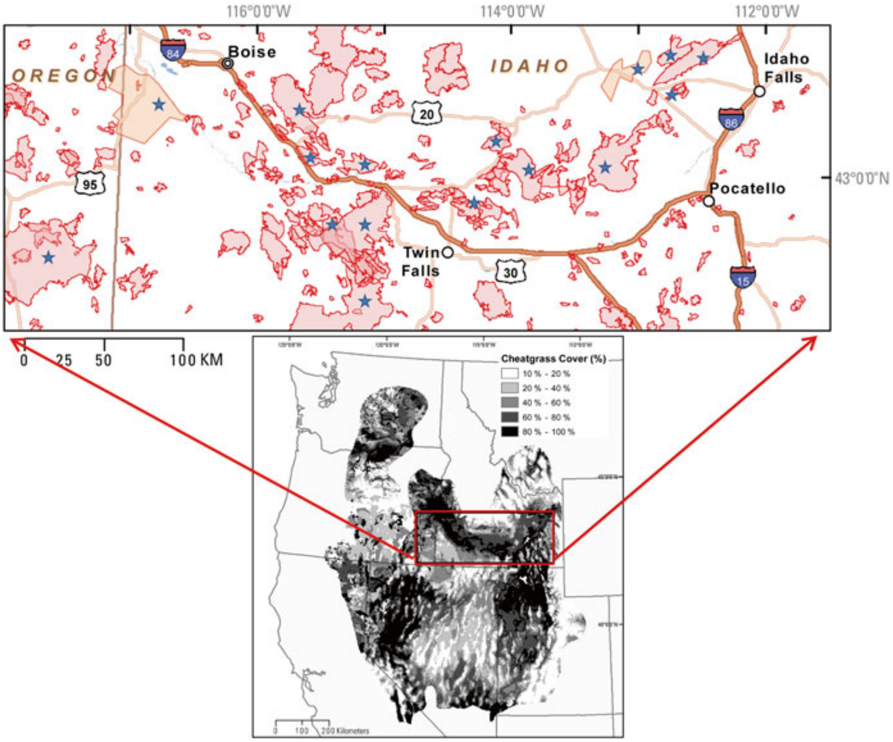

**Fig. 3.2** Distribution and abundance of *Bromus tectorum* as detected in satellite imagery from Wylie (2012) and expanded map of wildfire boundaries (2002–2015) of the *red-highlighted region* in the *B. tectorum* map, obtained from the Monitoring Trends in Burn Severity (www.mtbs.gov) and also www.geomac.gov. Stars show fires that were followed by wind erosion based on publications, direct observations, and/or geomorphic indicators

erosion, grazing, climate and soils, and decomposition rates likely contribute to variability in density and form of the litter, but most have not been formally studied. Dense *Bromus* litter acts like mulch and can insulate soil from solar and terrestrial radiation and wind, intercept precipitation, prevent seeds from contacting soil, alter biogeochemistry, and increase combustibility and continuity of wildfire fuels (described further in Sects. 3.3 and 3.7 below). Furthermore, alteration of litter characteristics could promote “legacy effects” of *Bromus* on soil or plant community properties, which in turn may favor *Bromus* and discourages natives. However, evidence is equivocal for the importance of *Bromus’* soil-legacy effects in light of other ways *Bromus* impacts native plants (see Sects. 3.4–3.8; Rowe and Brown 2008; Belnap and Phillips 2001; Evans et al. 2001; Gill and Burke 1999; Sperry et al. 2006; Bansal et al. 2014). Litter produced by nonnatives is typically considered to selectively benefit the nonnatives and often inhibits establishment of native plants due to excessive shading or preventing seed from reaching the soil. However, larger established native shrubs can benefit from litter mulch beneath them due to

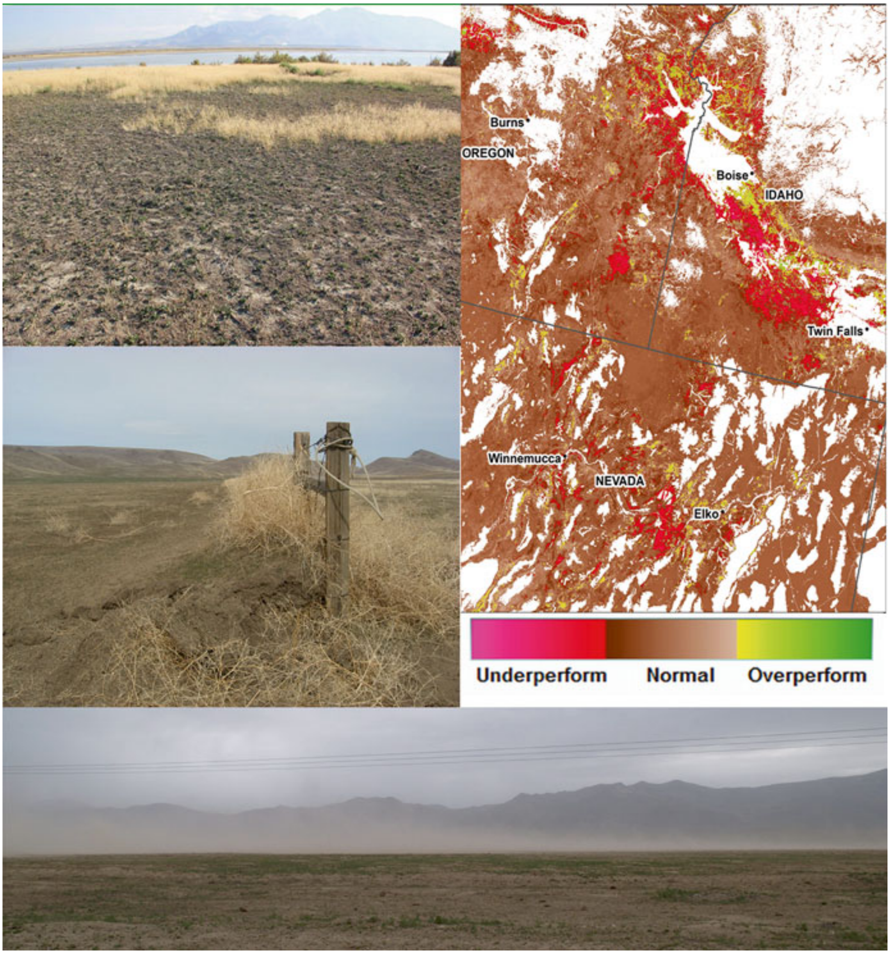

**Fig. 3.3** Examples of extent and impact of *B. tectorum* die-off in the Northern Basin and Range. The map in the *top right* shows estimated die-off patterns during 2010 based on MODIS imagery [*red* shows areas in which growth potential of *B. tectorum* based on its mapped presence and climate/weather is not materialized, from Wylie (2012)]. *Upper left* photo shows a die-off in 2014 (dark ground is died off, blond grasses survived and senesced normally, photo courtesy of Mindy Wheeler). *Middle right* photo shows large deposition of soil eroded from a 2010 die-off (photo, Megan Hynes). Photo on bottom shows high bare soil exposure and a dust plume originating from a site that experienced stand failure of *B. tectorum*, a site classified as "Loamy with 5–8 inches of precipitation" in August 2012 (photo, Tamzen Strigham). Other BLM staff reported complete loss of visibility on similarly afflicted sites due to dense dust clouds in the same summer (M. Pellant, pers. comm.)

increased soil resources, particularly water (e.g., for *Bromus* species in central California shrublands; Wolkovich et al. 2009). Other studies show biomass production of *B. hordeaceus* to be negatively related to its own litter (Amatangelo et al. 2008). Litter removal increased plant-available N and abundances of *B. tectorum* and other exotic annuals in a cool and wet summer but led to decreases in a warm and dry year (Bansal et al. 2014; Jones et al. 2015a). High variability in conclusions among studies addressing litter effects of *Bromus* may relate to the timing of experimental litter removal treatments, density/thickness of experimental litter layers, nonlinear effects of litter amount (e.g., positive effects of small amounts, negative effects of large amounts), and weather events that affect soil microclimate, plant establishment and productivity, and decomposition and nutrient cycling.

## 3.3 Impacts on Landscape Disturbance, Specifically Fire

Increased incidence of fire due to greater and more spatially continuous fuel (litter) production by *Bromus* has been recognized since the early 1900s. Fires have been abundant recently in regions that have large areas of *Bromus*, such as the Northern Basin and Range and Snake River Plain or the ecotone between the Central and Mojave Basin and Ranges (Fig. 3.2, Brooks and Matchett 2006).

Within particular ecoregions, fire-return intervals on *B. tectorum*-dominated areas are considered to have been markedly reduced (e.g., Stewart and Hull 1949; Whisenant 1990), although little evidence exists to substantiate the commonly cited 3–5-year fire-return interval. Over the whole 650,000 km$^2$ of Great Basin dominated by *B. tectorum*, annual probabilities of burning were 1–2 %, compared to <1 % for areas mapped as sagebrush habitat, using USGS fire records from 1980 to 2007 (Balch et al. 2013, estimates vary by data source). Fire-return intervals summarized by decade were 50–82 years for *B. tectorum* sites, compared to 97–313 years for sagebrush sites (Balch et al. 2013). *Bromus tectorum* sites were ~250 % more likely to burn than sagebrush sites, compared to 4 % and 25 % more likely to burn than pinyon-juniper and desert shrub sites, respectively (Balch et al. 2013). Balch et al. (2013) also found that 65 % of fires from 2000 to 2009 started on *B. tectorum-dominated* sites, and a substantial fraction of these spread onto sites that were not dominated by *B. tectorum*. Climate- and weather-fire relationships are strengthened where *B. tectorum* dominates (Knapp 1996). For example, 22–27 % of the variation in fire frequency and fire size in the Great Basin was positively related to precipitation of the previous calendar year on *B. tectorum* sites, compared to only 12–13 % on sagebrush sites or no correlation found over all vegetation types combined (Balch et al. 2013). Probability of increased fire size increased steeply above a threshold of 125 g/m$^2$ of fine fuel in the Mojave Desert, driven by prior year precipitation and N deposition. In this case, fine fuel included *B. rubens* at higher elevations and the exotic annual grasses *Schismus* spp. P. Beauv (Mediterranean grass) at lower elevations (Rao et al. 2015).

### *3.3.1 Mechanisms Underlying Altered Fire Regime*

Increases in fire occurrence and rate of spread with dominance of *Bromus* are due to the increase in fine fuel abundance and continuity caused by *Bromus* replacing more widely spaced, native perennial fuels (described in Sect. 3.2 and Fig. 3.1, Brooks and Zouhar 2008). More specifically, species such as *B. tectorum* increase surface-to-volume ratio, horizontal continuity (size and abundance of grass fuel patches per unit area), and the packing ratio (amount per unit volume) of fire fuels compared to perennial vegetation, thereby increasing likelihood of ignition and spread (Brooks et al. 2004; Davies and Nafus 2013). Link et al. (2006) furthermore demonstrated that these attributes of *Bromus* increase combustibility, specifically the probability of ignition and fire spread. Rapid curing is also important; litter in *B. tectorum* plots is completely depleted of moisture (reportedly 0 % water content) at least a month prior to several bunchgrasses drying to their minimum seasonal water content (about 20 % of dry mass, Davies and Nafus 2013).

Although *Bromus* increases fire occurrence, it is a common misconception that *Bromus* increases fire intensity in terms of temperatures reached and duration of heating; loss of woody fuel or large herbaceous perennials actually reduced fire intensity (Brooks et al. 2004). Fires on *Bromus*-dominated sites are characterized by low temperatures and often do not completely combust the litter layer (Jones et al. 2015b), leaving what rangeland managers sometimes refer to as a “dirty burn” that contrasts with the completely combusted, charred ground where fire has occurred in uninvaded sagebrush steppe (“clean” burn, Fig. 3.1). “Dirty burn” conditions are perceived to complicate postfire recovery and seeding success, mainly due to insufficient heating during fire to kill *Bromus* seeds and reduced seed-soil contact of seeded native species due to residual litter.

## 3.4 Impacts on Soil Stability

Soil stability, or resistance to erosion by water or wind, is an important concern for semiarid landscapes because relatively sparse vegetation cover increases exposure of soil and erosion by removing the thin layer of topsoil and the organic matter, nutrients, and seed banks that are concentrated in it (Hasselquist et al. 2011). These losses can push ecosystems toward primary succession conditions. Temporary losses of biological soil crust and plant cover through fire or stand failure (Fig. 3.3) are key ways that *Bromus* increases erosion risks. However, rapid establishment of *Bromus* in disturbed sites with low abundance of native perennial herbaceous species may confer some site stabilization by the second or third year after disturbances like wildfire (Stewart and Hull 1949; Klemmedson and Smith 1964; Miller et al. 2012).

Fire can increase water erosion >100-fold on steep slopes to the detriment of entire watersheds, and two growing seasons are usually required before stabilization is observed (reviewed in Wilcox et al. 2012). Wind erosion in the year after fire can transport several cm or more of topsoil from large burn areas in sagebrush steppe (Sankey et al. 2010), and the resulting dust clouds can be so dense that they exceed measurement capacity of air-quality instrumentation and air-quality standards over vast air sheds (>65 mg/m$^3$; Wagenbrenner et al. 2013). Postfire dust impacts human health and safety, radiation balance, precipitation, and contaminant transport. The herbicide Oust© applied to inhibit the emergence of *B. tectorum* on burned areas was blown long distances (10–100’s of km) with the soil onto downwind crop fields

(Paez 2011). The resulting litigation has discouraged the use of herbicides on many US Bureau of Land Management lands and affected control of *B. tectorum* and other exotics in the critical postfire window across millions of hectares of sagebrush steppe in the Snake River Plain.

### *3.4.1 Direct Effects on Erosion*

Aside from fire or stand failure, there are a number of ways that *Bromus* could decrease or increase water erosion depending on the type and amount of vegetation cover, slope, and soil type. Craddock and Pearse (1938) conducted many simulated rain experiments on steep slopes, and although they did not control for the amount of plant cover, their data suggest that erosion under *B. tectorum* was greater than under *Pseudoroegneria spicata* Pursh. A. Löve (bluebunch wheatgrass) but less than where native or exotic forbs dominated. Wilcox et al. (2012) used simulation models to separate the confounding factors of amount of vegetation cover, slope, and burn severity in determining *B. tectorum* grassland effects on water erosion (HYDRUS to partition rain into infiltration, storage, evapotranspiration, or runoff; MAHLERAN to simulate sediment transport). Their models predicted water erosion to double on steep slopes (20–40 %) dominated by *B. tectorum* (<50 % of community cover) compared to native sagebrush steppe, although high abundances of *B. tectorum* (>66 % of community cover) reduced erosion compared to native sagebrush steppe (46 % community cover) on intermediate slopes (10–20 % pitch). The *Bromus*-induced increase in erosion hinged on the assumption that *Bromus* grasslands altered particle-size distributions and decreased hydraulic conductivity of soil (infiltration)—an assumption based on potentially confounded findings from Boxell and Drohan (2009; discussed in Sect. 3.5 below). Regardless, the water-erosion rates where *Bromus* or natives are present and differences in erosion between them are much smaller than the water-erosion rates after wildfire.

Few data sources are available to assess direct effects of *Bromus* on wind erosion. Wind erosion was greater on a *Bromus*-invaded site compared to native sagebrush steppe in only 1 of 5 years in the Snake River Plain (Fig. 3.4, M. Germino). In that study, total and relative cover of *B. tectorum* sites ranged from 40 to 100 % of ground area across sampling periods, and plant heights were typically about 20 cm. The native site had *A. tridentata* ssp. *wyomingensis* Beetle & Young (Wyoming big sagebrush) with a *P. secunda* and *Elymus. elymoides* Raf. Swezey (squirreltail) understory; its cover in June 2014 was 18 % bare soil, 5 % herbs, 45 % litter/wood, and 30 % shrub, and plant heights were up to 90 cm. The absolute levels of soil movement on both sites were small compared to the very large annual flux observed on a severe postfire wind erosion site using the same measurement devices (442 kg/m/day equates to ~100 gallons of soil flowing through an area the size of a door, daily for a year; Germino, unpublished for the site observed in Wagenbrenner et al. 2013). Like for water erosion, these data suggest that indirect effects of *Bromus* on wind erosion following fire vastly exceed any direct effects of the *Bromus* on erosion.

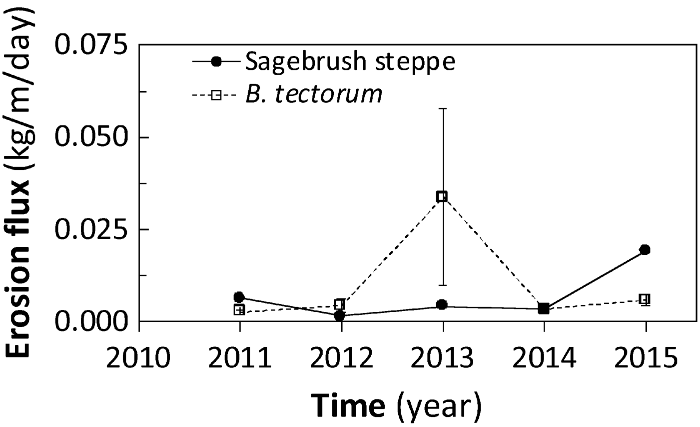

**Fig. 3.4** Annual horizontal flux of soil on sites dominated by *B. tectorum* (*open symbols*) or intact sagebrush (*solid symbols*, *Artemisia tridentata* ssp. *wyomingensis*, *Poa secunda*, and *Elymus elymoides*) near Twin Falls, Idaho. Data were collected on four towers of Big Springs Number Eight collectors (5 collectors/tower) in June of each year, and fluxes were determined from the integral of the relationship of mass of soil captured to height aboveground. Measurement of saltation activity in 2013 on the *B. tectorum* sites indicates that the erosion occurred when average wind speeds (5-min periods) were 6–10 m/s. From M.J. Germino, unpublished data

## 3.5 Impacts on Soil Hydrology and Water Balance

The domain of *Bromus* in the Western USA is semiarid and, by definition, limited by precipitation. Thus, the effects of *Bromus* on how precipitation is partitioned into infiltration, runoff, evapotranspiration, or deep soil-water storage could heavily impact ecosystems. Craddock and Pearse (1938) found greater runoff and thus less infiltration, on sites with more *B. tectorum* than bunchgrasses. The hydrology simulations of Wilcox et al. (2012, see Sect. 3.4.1 above) suggest runoff is about twice as large from *B. tectorum* grasslands compared to sagebrush steppe on slopes greater than 20 %. In addition to reduced plant cover, reductions in soil hydraulic conductivity and infiltration (determined by Boxell and Drohan 2009, Sect. 3.4) were pivotal model parameters predicting greater runoff of *B. tectorum* grasslands compared to native conditions in Wilcox et al.'s (2012) simulations. *Bromus* could decrease infiltration if they reduce organic matter inputs (Gill and Burke 1999; Evans et al. 2001; Norton et al. 2004) because organic matter inhibits formation of hard physical soil crusts and enhances aggregate formation, infiltration, and water retention of desert soils (Singer and Shainberg 2004). Loss of shrub cover and replacement by *Bromus* spp. in southern California led to reduced percolation of water through the 150-cm shrub rooting depth and thus shallow soil-water availability (Wood et al. 2006). Physical soil crusts harden as they dry, and their permeability resumes only after prolonged wetting (Hoover and Germino 2012); thus, drying of surface soils by *Bromus* likely increases the duration that soils are hard and impermeable each year. In contrast, infiltration was greater on burned sites where dense invasion of *B. tectorum* and *B. arvensis* (L. field brome; >80 % total cover of *Bromus*) was observed compared to burned sites where native *A. t. tridentata* recovered, hypothetically due to greater porosity created by the high density of near-surface root channels in *Bromus* roots (Gasch et al. 2013; in the Wyoming Basin; authors referred to *B. japonicus* Thunb., Japanese Brome).

Several considerations for the discrepancies or uncertainties in these studies point to additional research needs, especially accounting for initial soil properties prior to invasion. For example, Boxell and Drohan (2009) examined four areas in the Northern Basin and Range that burned up to 20 years prior to sampling and were subsequently invaded by *B. tectorum* and four adjacent areas that were undisturbed sagebrush steppe. The burned and invaded areas had slightly coarser soil textures, greater stability of soil aggregates, and smoother soil surfaces but had harder and less permeable soil surfaces compared to nearby unburned sagebrush communities (Boxell and Drohan 2009). Fire heating, combustion of soil organic matter, and erosion of topsoil all could have occurred prior to *Bromus* invasion and contributed to the altered soil properties that were attributed to *B. tectorum*—similar to other studies that did not have before/after fire and invasion measurements or other experimental control of confounding factors. Furthermore, Boxell and Drohan (2009) compared soils under shrubs from unburned and uninvaded sites to all microsite types (undershrub plus interspaces) in burned and invaded sites. *Bromus tectorum* can establish on hard, often-impermeable interspace physical crusts where cracks in the crust or litter facilitate its establishment (Evans and Young 1970, 1972), even though it typically exhibits greater growth where shrubs create islands of fertility (like most herbs; Chambers et al. 2007; Hoover and Germino 2012). Thus, the association of *B. tectorum* and altered soil permeability in both Boxell and Drohan's (2009) and Gasch et al.'s (2013) studies could have resulted from fire effects or *Bromus'* microsite selection of initial soil properties, in addition to *Bromus'* influence on the soils. To our knowledge, there is no information available on direct effects of invasive *Bromus* on physical properties of soil surfaces and infiltration/runoff in California grasslands, Mojave Basin and Range, Colorado Plateau, or High Plains.

### 3.5.1 Spatial and Temporal Patterns of Soil-Water Use

*Bromus* typically has fibrous and relatively shallow rooting systems (about 5-cm to 35-cm depths), although in some ecosystems (e.g., Palouse prairie, tallgrass prairie, and Great Basin sagebrush), studies have shown that some roots may penetrate to 1–2 m (Hulbert 1955; Hironaka 1961; Peek et al. 2005). This high concentration of *Bromus* roots in surface soil layers combines with their rapid growth and winter-annual phenology to strongly alter community soil-water use (reviewed in Klemmedson and Smith 1964; Reever Morghan et al. 2007; Wilcox et al. 2012). Detailed field data on soil-water profiles in soils under *Bromus* compared to analog native grasses or later seral communities are surprisingly scarce given how commonly the early depletion of soil moisture by *Bromus* is cited.

*Bromus tectorum* appears less capable of extracting water from dry soils compared to natives; instead this species uses freely available water in shallow soils and then senesces as this resource is depleted. Water status at predawn (i.e., maximum daily hydration) or even midday remained above −1 MPa in *B. tectorum*, which is considerably wetter than the permanent wilting point for many crops −1.5 MPa and for *P. secunda* growing under the same conditions (nearly −3 MPa, Link et al. 1990). Transpiration rates were considerably greater on a per leaf-area basis in *B. tectorum* compared to *P. secunda* (Link et al. 1990), which, combined with a high capacity for leaf-area production, enables rapid soil-water depletion by *B. tectorum*.

*Bromus* may deplete shallow soil water early in growing seasons, but they do not efficiently deplete shallow water across the entire year nor do they utilize deep soil water efficiently. Norton et al. (2012; Fig. 3.7) found consistently wetter surface soils beneath *B. tectorum* in the Great Basin compared to sagebrush vegetation throughout much of the growing season, which could be due to reduced rainfall interception by foliage (greater throughfall) in the *Bromus* stands. At midsummer, deep soil-water depletion by the *Bromus*-invaded plant community is greatly diminished compared to early or late-seral bunchgrasses and the evergreen sagebrush (sagebrush depletes soil water to –5 MPa or perhaps drier; Cline et al. 1977; Peek et al. 2005; Ryel et al. 2008). The lack of deep soil-water extraction by *Bromus* could lead to increases in deep soil-water accumulation of 60–70 mm/year in coarse soils, as shown in the Central and Northern Basin and Ranges and Central California Valley (reviewed in Wilcox et al. 2012 and Reever Morghan et al. 2007, respectively). Soil-water wetting fronts under *Bromus* grasslands were predicted to become deeper at rates up to 2 m/year in coarse soils or 0.2 m/year in loam soils, in a winter-wet/summer-dry climate typical of the Great Basin (Wilcox et al. 2012). Ultimately, contact of the wetting front could link vadose and groundwater systems in those rare situations where weather, climate, geology, and topography result in shallow water tables,such as in some ancient lacustrine basins.

## 3.6 Impacts on Ecosystem Fluxes and Energy Partitioning

Plants have a primary role in regulating the flow or storage of C, water, and energy through ecosystems, and field observations suggest that *Bromus* likely impacts net ecosystem exchange of $CO_2$ (NCE) and water (evapotranspiration, ET) and energy balance (Prater et al. 2006; Prater and DeLucia 2006; Germino et al., unpublished data). Energy balance of plant and soil surfaces refers to the partitioning or dissipation of net radiation (solar and thermal) into latent heat (LE; vapor flux dominated by evapotranspiration, ET), sensible heat (conductive and primarily convective heat exchange), and storage of heat in soil. Semiarid ecosystems generally have high net radiation fluxes as a result of cloudless skies and low ET and thus $CO_2$ exchange on an annual basis (given water scarcity and the water-for-C tradeoff in leaf gas exchange). The effect of conversion of diverse perennial ecosystems to exotic annual grasslands on these fluxes is of interest because vast areas are likely to have strongly altered radiation due to greater albedo, reduced NCE, and changes to nearly all aspects of energy balance.

Three studies provide insights into the changes in energy balance on *B. tectorum-invaded* sites and intact sagebrush steppe in the Central Basin and Range and Snake River Plain (*A. tridentata* ssp. *wyomingensis*). These studies ranged in spatial and temporal scale as follows: (1) plot-level chamber measurements of NCE and ET over 3 years on a variety of burned and unburned sagebrush sites (Prater et al. 2006), (2) short-term landscape flux-tower measurements that provide indirect, snapshot estimates of ET and associated energy balance on a burned and an unburned site (7 sampling days over a 3-month period, using gradient method, Prater and DeLucia 2006), and (3) long-term landscape flux-tower measurements of NCE, ET, and energy balance on a *B. tectorum*-dominated site (mean *Bromus* cover ranged 40–100 %) and an *A. tridentata* ssp. *wyomingensis* site with *P. secunda* and *E. elymoides* understory (5 years, using replicate eddy covariance towers dispersed over 1–2 km in each site type; Germino et al., unpublished data). Although the Prater and DeLucia studies have been cited as isolating flux impacts of *B. tectorum* (e.g., Bradley et al. 2006; Wilcox et al. 2012), *B. tectorum* tended to comprise only about 20 % of relative cover in both the burned and sagebrush site. Abundance of *Agropyron cristatum* L. Gaertn. (crested wheatgrass) actually varied more consistently and appreciably between Prater and DeLucia's (2006) sites. Their study also relied on the Bowen-ratio approach, in which a determination of the ratio of sensible to latent heat is combined with measurement of often miniscule (and difficult to detect) gradients in temperature and vapor in air aboveground to indirectly estimate evapotranspiration (ET).

Prater and DeLucia's (2006) data suggested overall lower ET occurred in the burned site dominated by exotic grasses, in spite of "flashes" of greater ET during wet-soil periods in late spring. Lower ET in their study appeared to result from lower ability of *Bromus* to extract water from dry soils combined with a hypothetically greater albedo (reflectance) and thermal radiation emitted from warmer soils. Consistent with these hypotheses, reflectance of solar radiation could be up to 50 % greater for the *B. tectorum* compared to sagebrush community at spring and midsummer (mean ± SD daily values were 0.21 ± 0.05 for *Bromus* vs. 0.16 ± 0.03 for the sagebrush community over 11 representative clear-sky days, Fig. 3.5, bottom panel from Germino et al. unpublished data). Ecosystem surface temperatures were 2 °C warmer on the *B. tectorum* compared to sagebrush community across all days and nights (Fig. 3.5, middle panel), which could increase emission of longwave radiation relative to incoming radiation. Consequently, the *Bromus* community had about 10 MJ/m$^2$ less net radiation (not shown). Over 4 years and in the particular case year shown in Fig. 3.6, evapotranspiration (latent heat flux) was never greater for the *Bromus* community, at least on a monthly basis. The dissipation of greater energy and warmer surfaces contributed almost 50 MJ/m$^2$ more sensible heat loss to the air (i.e., warming air, not shown) for the *Bromus* compared to sagebrush community during the particular period shown in Fig. 3.5 (mostly senesced *Bromus*). Changes in these surface energy balance parameters have the potential to feedback on climate of the ecosystem, and they relate to hydrological differences between the sites.

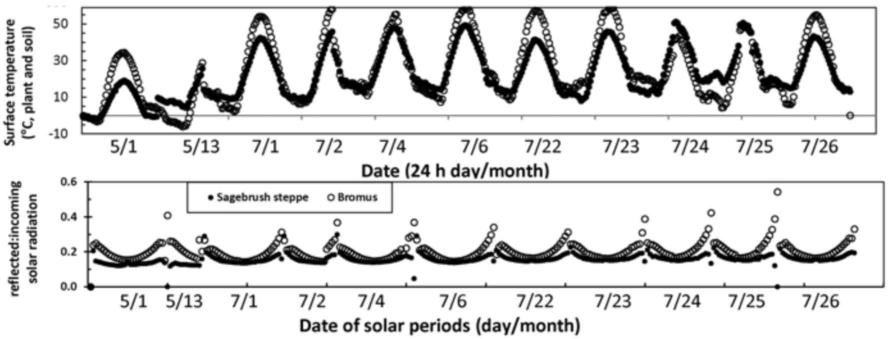

**Fig. 3.5** Representative parameters affecting net radiation balance on a *Bromus tectorum* landscape over 11 days during the green (May) and senesced (July) months. Parameters were measured by duplicate sensors separated by about 1 km and positioned at 4-m height and are reported on 30-min intervals. Ecosystem surface temperature of about 10–100-m$^2$ patches was measured with infrared thermometers (Apogee, narrow and wide focus sensors), and the ratio of solar radiation reflected off the plant/soil surface to incoming (direct and diffuse) solar radiation (i.e., albedo, measured with two Hukseflux NR01 4-way sensors per site). From MJ Germino, R Allen, W Zhao, and C Robison, unpublished data

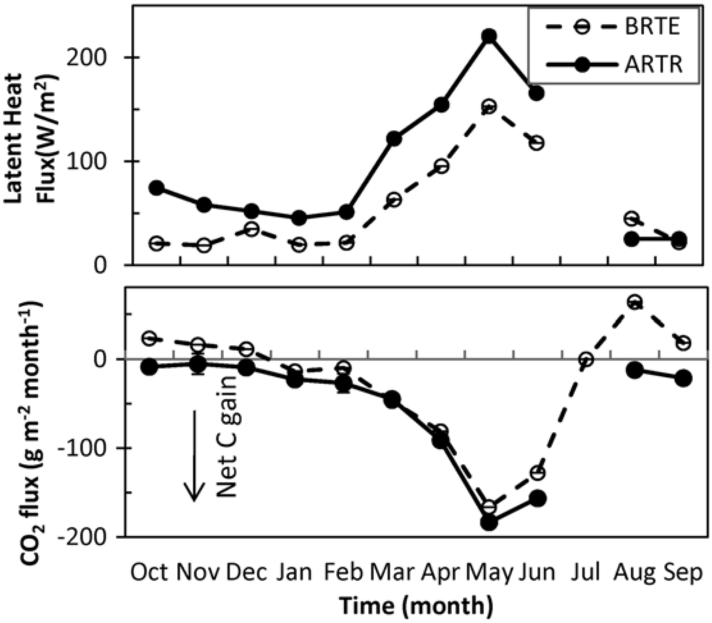

**Fig. 3.6** Monthly ecosystem fluxes of latent heat and $CO_2$ on *Bromus tectorum (BRTE)*-dominated or sagebrush-steppe communities (ARTR). Data are for two RM Young 8100 and Campbell CSAT 3D sonic anemometers and LiCOR 7500 open-path gas analyzers per site. SE are smaller than symbols. MJ Germino, R Allen, W Zhao, J Greth, C Robison, unpublished data

The *Bromus* site had substantially less ET in spite of receiving similar precipitation in the study year (2011; ~240 mm), thereby corresponding with considerably less NCE and C rain-use efficiency (NCE/ET, Fig. 3.6, bottom). While the sagebrush-steppe site was a net sink for 581 g C/m$^2$ over the year sampled, the *Bromus* site was a net sink for 313 g C/m$^2$ and was a net source of C in late summer months (calculated for Fig. 3.6).

Further evidence of reduced NCE and ET on *B. tectorum* sites compared to native communities comes from plot-scale field chambers (Prater et al. 2006) and large-pot microcosms in a greenhouse setting (Verburg et al. 2004) that suggest reduced NCE where *B. tectorum* dominates. For example, in Prater et al. (2006), the plot with the greatest cover of *B. tectorum* (up to 70 % cover of *B. tectorum*) had lower NCE and ET than all other plots with less *B. tectorum*. In Verburg et al. (2004), indoor microcosms containing Kansas soils (presumably C-rich loess) and planted with *B. tectorum* had very high respiration rates and negative annual NCE (300 g C m$^{-2}$). These smaller-scale findings combine with the landscape-level data to suggest C sequestration at the ecoregional level would also be reduced by *Bromus* invasion. The potential switch of ecosystems from sinks to sources of C to the atmosphere is an important impact of *Bromus*. An estimated 8 Tg of the aboveground standing crop of C in perennial vegetation (including wood) has already been released where *B. tectorum* has dominated the Western USA, and another 50 Tg C of losses are likely with its continued invasion into all suitable habitats (Bradley et al. 2006). Changes in soil C storage have also occurred with *Bromus* invasion (Sect. 3.7.1).

## 3.7 Impacts on Soil Nutrients

An abundance of correlative studies on *Bromus* impacts on soil nutrients exist, and their conclusions vary as to whether *Bromus* has net positive, negative, or null effects on soil nutrients. This variability is likely due to differences in site context (vegetation type, soils, climate), the spatial and temporal patterns of sampling, and factors such as whether top soils were eroded in disturbances associated with *Bromus* invasion. It is beyond the scope of this chapter to identify why the studies might differ, as the sampling regime of each would need to be described, but it is useful to evaluate representative cases. *Bromus* might accelerate elemental cycling—provided their biomass is not removed by grazers or erosion—because they annually return all nutrients to the soil as they senesce and decompose and they might change the quality and quantity of plant inputs into soil. *Bromus* may also temporarily deplete soil nutrient pools while they are in their rapid growth phase. The disturbances and soil factors associated with *Bromus* may also influence soil nutrients (e.g., fire affects net N mineralization, soil texture affects, and soil nutrient content).

### 3.7.1 Effects on Soil C in Topsoil Versus Subsoil

In ecosystems where NCE and spatial and temporal patterns of litter and root distribution differ between *Bromus* and native communities, corresponding differences in soil organic matter C may be expected. Inorganic and particularly organic C (SIC and SOC, respectively) are important for nutrient cycling. SOC is the primary source of plant-available N and can be an important source of phosphorus (P; Belnap et al. 2015), and it also enhances water infiltration and retention in semiarid soils. In addition to altering litter inputs and organic matter, *Bromus* may influence SOC by altering soil aggregates, which increase C storage by shielding SOC.

Several studies suggest that soil organic matter is reduced and tends to be shallower and cycle more rapidly where *B. tectorum* dominates (Norton et al. 2004; Gill and Burke 1999; Evans et al. 2001). However, other studies, which examined *B. tectorum*-dominated sites that had not recently burned, have shown no difference or greater SOC under *B. tectorum* (Hooker et al. 2008; Norton et al. 2012; Stark and Norton 2015). The immediate effects of fires on *Bromus*-dominated sites are reductions in vegetation and litter C by combustion. Soil C may be lost through erosion of topsoil, while vegetation recovers in those areas that lack a significant litter layer. Aside from these fire or erosion effects, longer-term decreases in litter C contents on *Bromus* sites may occur only with repeated fire, as neither vegetation nor soil C contents decrease over time (Jones et al. 2015a). Fires in *Bromus*-dominated ecosystems are generally characterized by soil temperatures that are too low to volatilize either soil N or C (Jones et al. 2015a), and longer-term variation in C after fires likely relates more to differences in decomposition and nutrient cycling (Jones et al. 2015a).

Deep soil (i.e., deeper than 20–30 cm) had less SOC where *B. tectorum* had invaded compared to uninvaded sagebrush steppe in the Central and Northern Basin and Ranges, as would be expected from loss of deep rooting in the invaded community (Norton et al. 2004; Rau et al. 2011). Reductions in SOC in deep soils with *Bromus* invasion may be a function of the interaction between root inputs, soil aggregates, and decomposition. Austreng (2012) found less SOC in *B. tectorum-dominated* compared to *A. cristatum*-dominated stands, 27 years after fire (SOC was 23 and 33 Mg/ha, respectively, and 44 Mg/ha in undisturbed sagebrush steppe). Notably, soil aggregates >250 μm, an important form of C storage, were absent on Austreng's burned/grassland sites. In contrast, Hooker et al. (2008) found that at a Great Basin rangeland site, 10 years after fire converted sagebrush to *B. tectorum* and adjacent sites were seeded to *A. cristatum*, SOC contents to a 1-m soil depth were 72, 69, and 62 Mg C/ha in *B. tectorum*-, *A. cristatum*-, and *A. tridentata* ssp. *wyomingensis*-dominated stands, respectively. While root C below 20 cm was substantially lower in *B. tectorum* soils, there were no detectable differences in deep SOC 10 years after vegetation conversion. Over longer time periods, replacement of native perennial shrubs and herbaceous vegetation with exotic annual grasses could release 6–9 Mg/ha. of root and SOC over the whole soil profile, more than double the aboveground losses (Rau et al. 2011; Bradley et al. 2006).

Decreases in SOC in deep soils may be an important driver of changes in the overall soil profile, as several studies suggest that SOC can be greater in near-surface soils under *Bromus*. In the Northwestern Great Plains, subtle increases in SOC in shallow soils (top 20 cm) became significant only after 50 years of *Bromus* cover, according to computer simulation models [40 % *B. tectorum* plus *B. arvensis* (authors referred to *B. japonicus*) cover, CENTURY model, Ogle et al. 2004]. Rapid increases in SOC following *B. tectorum* invasion of *Krascheninnikovia lanata* A. Meeuse & Smit (winterfat) stands were detected to 1-m soil depth by Blank (2008) in the Central Basin and Range. Although SOC differences may have been at least partly present before invasion in Blank's sites (2008; see Sect. 3.7.2), they are corroborated by greater SOC in shallow soils of invaded sagebrush steppe of the Northern Great Basin (Norton et al. 2004; Hooker et al. 2008). Similarly, surface SOC (top 10 cm) in southern California chaparral was greater where *B. rubens* and *B. diandrus* invaded and dominated after fire (Dickens and Allen 2014a). By contrast, mean SOC was no different (but was less variable) where *Bromus* had invaded coastal sage scrub in California (Dickens et al. 2013). The differences in SOC-*Bromus* relationships between these ecosystems likely relate to a tendency for chaparral to have coarse and deep roots compared to a high density of fine shallow roots in coastal sage scrub.

### *3.7.2 Effects on Soil Nitrogen Cycling*

Soil N is generally considered the most limiting of macronutrients in semiarid soils. The effect of *Bromus* invasion has been evaluated in many studies, but findings have been mixed. *Bromus* is associated with soils higher in N in a number of correlative field studies, like many invasive plant species (e.g., Liao et al. 2008). Several studies were able to evaluate soil N before and after invasion of undisturbed grasslands of the Colorado Plateau. *Bromus tectorum* did not affect N pools 2–4 years following invasion where *Achnatherum hymenoides* (Roem. & Schult.) Barkworth (Indian ricegrass) and *Stipa comata* (Trin. & Rupr.) Barkworth (needle and thread) dominated. However, *B. tectorum* initially increased total soil N from by 0.04 to 0.12 g/kg at 0–10-cm depth where *Pleuraphis jamesii* Torr. (James' galleta) dominated, which is equivalent to an increase of 13 and 40 kg N/ha/year (Evans et al. 2001; Rimer and Evans 2006; Miller et al. 2006; Schaeffer et al. 2012). In addition, the *P. jamesii* sites invaded by *Bromus* had greater N before the invasion, which was magnified by *Bromus* (Kleiner and Harper 1977). While the higher of the two rates exceeds ecosystem N inputs in this region by four- to tenfold, redistribution of N into the surface soil following extraction of N from deeper in the soil profile might explain the increase in the surface soil in this study (Sperry et al. 2006). Eight years after the invasion, extractable N ($NO_3^-$ plus $NH_4^+$) was still no greater where *B. tectorum* was present compared to *Stipa*-dominated patches (only 1 of 21 sampling events), whereas it was greater for 5 of 21 sampling events compared to *P. jamesii-dominated* patches (Schaeffer et al. 2012). In southern California where *Bromus* spp. had invaded coastal sage scrub, there were no differences in organic N, but extractable mineral N was higher during the dry season and lower during the growing season (Dickens and Allen 2014b). This result was attributed to high rates of N uptake by rapidly growing *Bromus* during the rainy season and rapid N mineralization upon senescence. In the Central Basin and Range, Blank (2008) found N was 1380 kg/ha greater at a *K. lanata* site that had been invaded by *B. tectorum* 3 years prior to sampling compared to an uninvaded *K. lanata* stand, but the annual inputs of 460 kg N/ha/year required to create the enrichment does not seem possible via *Bromus* alone. Thus, similar to the Utah site, *Bromus* may have selectively invaded N-rich soils.

A few carefully controlled field experiments provide less ambiguous evidence for the direct enhancement of soil N by *Bromus*. Soil net N mineralization, net nitrification, inorganic N concentrations, and denitrifier population size were positively correlated with variations in abundance of *B. rubens*, *B. hordeaceus*, and another exotic annual grass, *Hordeum murinum* L. (mouse barley), among other perennial grasses, in an experiment in which the species were planted 5–7 years prior to evaluating species effects (Parker and Schimel 2010). In sagebrush steppe of northwest Colorado, net N mineralization and net nitrification rates were 50 % and 28 % faster in surface soils of plots seeded 24 years earlier with *B. tectorum* compared to *A. tridentata* ssp. *wyomingensis* and native perennial grasses, respectively (Stark and Norton 2015). Soil nitrate, organic C and N, and respiration were also greater while C:N of organic substrates consumed by microbes was lower in *B. tectorum* compared to native plots (C:N ratios of 7.7:10.4 compared to 9.8:15.6, respectively; Stark and Norton 2015)—all of which are consistent with accelerated N cycling. After just 8 weeks following planting, greenhouse mesocosms of *B. tectorum* contained a third more soil C and N and twice as much N leakage from plant roots into soil than mesocosms containing *A. cristatum* (Morris et al. accepted).

*Bromus* can affect soil N in multiple ways that may be site specific. Annual return of tissue N early in the growing season will affect N cycling, although this effect likely differs across ecoregions or sites (e.g., on the Colorado Plateau, soil fauna that bury litter is scarce and thus litter input enhancement by *Bromus* may be less). *Bromus* can release lower C:N detritus or exudates, as has been observed for *B. tectorum* in sagebrush steppe of the Central and Northern Basin and Ranges and Wyoming Basin, C3/C4-shortgrass steppe, and Colorado Plateau grasslands (Bolton et al. 1990; Evans et al. 2001; Booth et al. 2003; Saetre and Stark 2005; Hooker and Stark 2008; Adair and Burke 2010). Shifts in phenology and soil-water availability appear to be important modifiers of the influence of *Bromus* on N cycling: increases in $NO_3^-$ are pronounced as seasonal (summer) drying and senescence of *Bromus* occurs (Fig. 3.7; Svejcar and Sheley 2001; Booth et al. 2003; Norton et al. 2004, 2008; Hooker et al. 2008; Dickens and Allen 2014b, but see Schaeffer et al. 2012). *Bromus* may create warmer soil conditions (Sect. 3.7.3) that could increase microbial enzyme kinetics given sufficient available soil water. Also, invasion can alter N inputs through loss of biological soil crusts (Evans and Belnap 1999; Belnap 2003). Moreover, greater total N concentrations are usually associated with faster rates of N cycling induced by recent SOC inputs and associated with greater labile soil N pools such as $NH_4^+$, $NO_3^-$, microbial N, and readily mineralizable organic N (Booth et al. 2005; Morris et al. accepted).

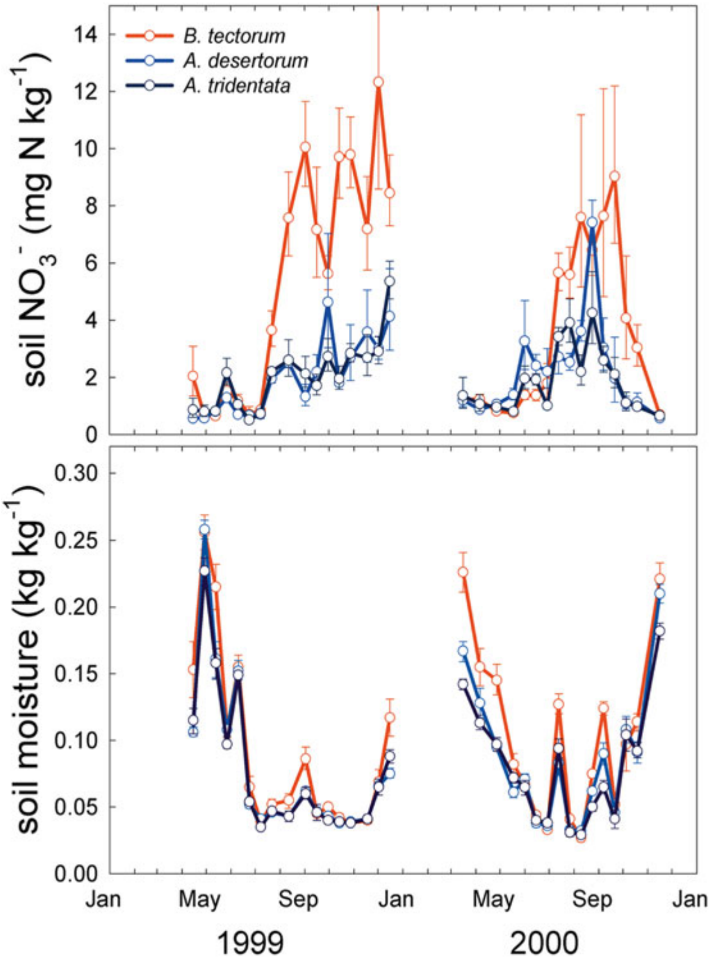

**Fig. 3.7** Seasonal changes in soil nitrate concentrations in the surface soils (0–10-cm layer) beneath *Bromus tectorum*, *Agropyron desertorum*, and *Artemisia tridentata* ssp. *wyomingensis* vegetation in Rush Valley, UT. Values represent means and SE ($n=4$) for each vegetation type (compiled from Stark et al. 2006; Norton et al. 2012; Morris et al. accepted)

*Bromus* may affect N fixation, redistribution of N in soil, leaching losses of N, and denitrification and could thereby influence longer-term trends of soil N where it has become dominant. High rates of N mineralization and nitrification relative to rates of N immobilization in mesic ecosystems typically lead to increased N loss through leaching or trace N gas emissions (Stark and Hart 1997). However, this pattern may not occur in semiarid and arid ecosystems because high nitrification could conserve N by depleting $NH_4^+$, which is otherwise readily lost as $NH_3$ in high pH soils. Also, while nitrification is normally a key step toward denitrifying losses of NO, $N_2O$, or $N_2$ gases, denitrification is suppressed by the low C and water availability in semiarid soils (Smart et al. 1999). Moreover, precipitation is scarce enough in the area impacted by *Bromus* to minimize leaching of $NO_3^-$ from soils but is sufficient to redistribute it to depths where denitrification is less likely (Sperry et al. 2006; Hooker et al. 2008). *Bromus* decreases ecosystem fixation of $N_2$ by displacing N-fixing plants or biological soil crusts (Evans et al. 2001). Promotion of fire by *Bromus* does not appear to result in mineral N losses through volatilization but rather may result in short-term increases in mineral N availability through deposition of N-rich ash (Jones et al. 2015a, b). Weather, specifically precipitation and minimum winter temperature, had stronger effects on soil N availability and *B. tectorum* success than litter removal or seeding a competitor over four consecutive repeated burns (Jones et al. 2015a, b). Thus, studies evaluating effects of *Bromus* on mineral N should monitor weather variables and soil water availability and examine differences among years.

### 3.7.3 Phosphorus and Other Nutrients

In high pH soils, such as found in deserts, phosphorus (P) and calcium (Ca) combine to form moderately to highly insoluble calcium phosphate minerals that are unavailable for plant uptake (Lajtha and Schlesinger 1988). These Ca-bound forms of refractory P are the dominant mineral P pool in deserts. However, there are multiple lines of evidence showing that the presence of *B. tectorum* can result in the conversion of recalcitrant P (bio-unavailable) to bio-available P. Extractable P was much higher in *Bromus*-invaded plots than adjacent uninvaded plots (Hansen 1999) despite no significant differences in soil P before invasion (Kleiner and Harper 1977, see also Blank 2008). Furthermore, extractable P was positively correlated with *B. tectorum* cover (0 %, 10 %, and >40 % *Bromus* cover associated with 14.6, 19.5, and 28.2 μg P/g soil, respectively; Hansen 1999). In a controlled greenhouse setting, *B. tectorum* decreased recalcitrant P and doubled soil extractable P in several sandy soils (Gopalani 2004). Phosphorus availability is highly correlated with precipitation in the months preceding measurement, and *B. tectorum*'s enhancement of P availability follows wet periods (Belnap 2011). Furthermore, elevated foliar P of *B. tectorum* following experimental watering on loam soils in the Colorado Plateau and correlations of *B. tectorum* growth and pH buffering capacity suggest a role for root exudates in liberating P (Miller et al. 2006). Greater soil moisture following experimental watering would provide *B. tectorum* more resources to increase exudates and stimulate microbial activity. Root exudates could include $H^+$ ions that acidify the soils, changing solubilities of ions that precipitate P (Frossard et al. 1991), phosphatase enzymes that release organic P, organic chelates that bind metal ions and mobilize P, and/or organic substrates that stimulate microbial activity. Microbes produce phosphatases (Blank 2008; Dighton 1983) and oxalates (Jurinak et al. 1986; Knight 1991; Knight et al. 1992), which can dissolve Ca–P bonds. Alkaline phosphatase was 38 % greater in soils under *B. tectorum* compared to interspace soils occupied by *K. lanata* (Blank et al. 2013).

The mechanisms by which *B. tectorum* could increase the availability of other nutrients are the same as for soil P; root exudates can directly dissolve chemical bonds that make them bio-unavailable, or the release of C can stimulate microbes to indirectly increase their availability. Manganese (Mn) increased while potassium (K), calcium (Ca), and magnesium (Mg) concentrations were unchanged after 7 years of dominance by *B. tectorum* in sandy loam soils (Belnap et al. 2005). In contrast, K, Ca, Fe, Mn, and copper availability doubled in soils on a *B. tectorum-invaded* site (Blank 2008); however, this may be due to preexisting soil differences. Elevated Cl, Na, and Zn also occurred during the growing season following invasion of the *K. lanata* community by *B. tectorum* (Blank et al. 2013).

## 3.8 Impacts on Soil Microbiological and Microfaunal Communities

Changes in soil communities following *Bromus* invasion seem likely given the biogeochemical changes described above and may be part of a self-perpetuating feedback that *Bromus* imposes on its environment. Alteration of key soil food web components, such as the loss of biological soil crusts, which contribute to soil fertility and stability, and arbuscular mycorrhizal fungi (AMF) that form mutualisms essential for many native plants in the impacted habitats (Allen 1988, reviewed in Knapp 1996), are examples. AMF in the genus *Glomulus* are particularly important for natives such as *A. tridentata* because their glomalin glycoproteins stimulate formation of beneficial soil aggregates (reviewed in Weber et al. 2015).

Several studies have revealed appreciable differences in microbial communities in soil under *Bromus*-invaded compared to non-invaded communities. The ungrazed and unburned grasslands of Belnap and Phillips (2001) invaded by *B. tectorum* had lower species richness and abundances of fungi and invertebrates and greater abundances of active bacteria than uninvaded patches. Their sampling included soil bacteria, fungi, detritivores, algivores, and mites and microarthropods of various trophic levels. Notable shifts with *B. tectorum* invasion were increases in generalist, non-mycorrhizal, saprophytic fungi compared to mycorrhizal fungi (Belnap and Phillips 2001). Furthermore, losses of key taxa such as the AMF found in the *Glomus* genus were revealed in the *B. tectorum* soils using restriction fragment length polymorphism (RFLP, Hawkes et al. 2006). Although *B. tectorum* supports AMF, it is a relatively poor host compared to species such as sagebrush (Busby et al. 2012), perhaps due to lapses in photosynthetic C when *Bromus* is senescent. *Bromus hordeaceus* has also supported very few RFLP types compared to native herbs (Hawkes et al. 2005). Wyoming Basin soils invaded by *Bromus* had very low abundances of all microbial groups according to phospholipid fatty acid analysis, which detects only live microbes (Gasch et al. 2013). Fewer taxonomic orders and a greater presence of pathogenic, opportunistic, and saprotrophic taxa and an absence of AMF *Glomus* fungi occurred in soils dominated by *B. tectorum* following sagebrush removal from a plot 14 years following experimental sagebrush removal (Weber et al. 2015). In studies of coastal sage scrub, *Artemisia californica* Less. (coastal sagebrush) benefitted from a greater diversity of AMF fungi, while *B. rubens* was associated primarily only with the fine endophyte *Glomus tenue* Greenhall (I. R. Hall) (Egerton-Warburton and Allen 2000; Sigüenza et al. 2006). Although *Bromus*-induced changes in soil biota would likely have substantial effects on plants and overall ecosystem functions, such effects have seldom been experimentally identified such as through reciprocal soil transplant studies. Altered soil food webs where *Bromus*-invaded *P. jamesii* grasslands on the Colorado Plateau did not translate to appreciable shifts in decomposition, mineralization, or demographics of *P. jamesii* (Belnap et al. 2005). Conversely, Sigüenza et al. (2006) showed that *G. tenue* was a more effective mutualist for *B. rubens* than the diverse AMF fungi were for *A. californica*.

## 3.9 Impacts on Higher Trophic Levels, Aboveground

The habitat transformation of diverse plant communities into *Bromus*-invaded grasslands over vast areas leads to marked changes in invertebrate and vertebrate animal populations. Animals dependent on native plant species such as sagebrush or native forbs are lost from sites as a result of *Bromus* invasion or become scarcer, and the resulting animal communities are dominated by generalist species. *Bromus* is cited as a key stressor for several species that have become imperiled. For example, *B. rubens* adversely impacts *Gopherus agassizii* Cooper (Mojave desert tortoise; Brooks and Esque 2002) and *Euphydryas editha quino* Behr (Quino checkerspot butterfly (USFWS 2003), and *B. tectorum* adversely affects *Centrocercus urophasianus* Bonaparte (greater sage grouse), *Brachylagus idahoensis* Merriam (pygmy rabbits), and other sagebrush obligates.

Although *Bromus* have some forage value, they provide relatively unstable habitat for most animals, in terms of food, shelter, and increased fire. Generally, forage quality of *Bromus* declines rapidly following its short green-up period during each year, which combines with its high year-to-year variability to detract from its reliability as a food source. *Bromus tectorum*, *B. rubens*, and *B. diandrus* impose major irritants to animals who contact or ingest floral parts, due to their stiff, barbed awns on florets, and sharp or barbed seeds (e.g., Medica and Eckert 2007). Ailments directly attributed to reproductive parts of *Bromus* include mouth sores, abscesses, corneal abrasions, skin and genital infections, and respiratory distress including coughing and gagging (reviewed in Zouhar 2003).

### *3.9.1 Impacts on Invertebrates and Small Vertebrates*

Changes in diversity and abundance of insects, small mammals, and reptiles form one of the most distinctive and tractable impacts of *Bromus* on ecosystems. Insects and small mammals, particularly ants or ground squirrels, can be important ecosystem engineers due to their herbivory, granivory, and soil disturbances that accompany colony development. Seed-harvesting genera, such as the mound-forming *Pogonomyrmex occidentalis* L (harvester ant), became more abundant in *B. tectorum-dominated* plots compared to native sagebrush steppe and would likely impose seed predation problems for restoration seedings (Ostoja et al. 2009).

Loss of native forbs and the pollinator community associated with them is an important but understudied impact of *Bromus*, considering that loss of pollinator services (e.g., from bees) could greatly impact efforts to restore native plants. Population stability of *Lepidium papilliferum* L.F. Hend. A. Nelson & J.F. Macbr. (Idaho pepperweed) was related to diversity and pollination activity of insect pollinators, in a region of southwest Idaho that is heavily impacted by *Bromus* (Robertson and Klemash 2003).

A number of studies demonstrate negative relationships in overall abundance and species richness and diversity of small mammals with *Bromus* invasion (e.g., Great Basin studies: Larrison and Johnson 1973; Gano and Rickard 1982; Ostoja and Schupp 2009; Hall 2012; see Fig. 3.8 from Freeman et al. 2014). Omnivorous species that can tolerate a wide range of physical conditions and are generalists, such as *Peromyscus maniculatus* Wagner (deer mice), tend to dominate the animal communities of *B. tectorum*-invaded landscapes (it was one of the few species in Bromus-dominated plots in Fig. 3.8).

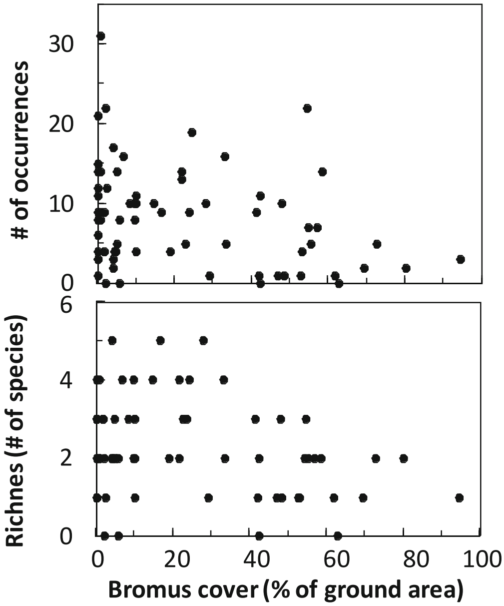

**Fig. 3.8** Relationship of *Bromus tectorum* percentage cover to total abundance and species richness of all small mammals detected in 10,437 trap nights on 70 sites throughout NE Utah over 2 years. Animal communities included the following (in decreasing abundance): *Peromyscus maniculatus* (deer mouse), *Dipodomys ordii* (Ord's kangaroo rat), *Dipodomys microps* (chisel-toothed kangaroo rat), *Ammospermophilus leucurus* (white-tailed antelope squirrel), *Chaetodipus formosus* (long-tailed pocket mouse), *Perognathus parvus* (Great Basin pocket mouse), *Onychomys leucogaster* (northern grasshopper mouse), *Neotoma lepida* (desert wood rat), *Perognathus longimembris* (little pocket mouse), *Microtus montanus* (montane vole), *Tamias minimus* (least chipmunk), and *Microdipodops megacephalus* (dark kangaroo mouse). From data in Freeman et al. (2014)

Ground squirrel relationships to *Bromus* are particularly noteworthy because of their close link as important prey (Van Horne et al. 1997). For example, ground squirrels are important food for hawks, *Taxidea taxus* Long (American badger), and snakes and are critical for nesting *Falco mexicanus* Schlegel (prairie falcons, Yensen et al. 1992). Their burrowing strongly affects infiltration, biogeochemistry, and plant community dynamics (e.g., Blank et al. 2013). Burrow densities (number/ha) of *Spermophilus townsendii* Bachman (Townsend's ground squirrels) and abundances and body condition of *Spermophilus mollis* Kennicott (Piute ground squirrels) were inversely related to *B. tectorum* abundances in sites otherwise dominated by *P. secunda* in southern Idaho (Yensen et al. 1992; Steenhof et al. 2006). Abundances of *S. townsendii* were not reduced in *Bromus*-invaded sites, but they were highly variable over time in a "boom-bust" fashion, ranging from 25 to 350 burrows/ha from 1 year to the next compared to consistent <100 burrows/ha per year in intact vegetation (Yensen et al. 1992).

#### 3.9.1.1 Impacts on Nutrition, Shelter, and Locomotion

Although Kelrick and MacMahon (1985) suggested that *Bromus* is not a preferred food, some small mammals consume it (Zouhar 2003), and *B. tectorum* even comprised 100 % of stomach contents of species like *Perognathus parvus* Peale (Great Basin pocket mouse, Richardson et al. 2013). Sylvilagus spp. (cottontail rabbits) prefer *B. tectorum* over other forage options in winter (Turkowski 1975), but ground squirrel preference for *B. tectorum* was very low compared to *P. secunda* and or other shrubs and forbs (Van Horne et al. 1998). *Bromus rubens* is an important food source for *Dipodomys microps* Merriam (chisel-toothed kangaroo rat, Rowland and Turner 1964) and can provide some nutritional benefit when green to *G. agassizii* (Esque et al. 2014), although they generally prefer a diverse diet that is usually not available in *Bromus*-dominated areas (Esque 1994; Jennings 2002). *Bromus rubens* alone is unable to provide the energy and nutrients required by *G. agassizii* and is an irritant to mouth tissues and thus is not preferred over other forages (McArthur et al. 1994; Nagy et al. 1998; Medica and Eckert 2007).

Cover and navigability for small animals is transformed by the loss of relatively tall perennials, such as sagebrush or taller bunchgrasses with high crown-to-basal area ratios, and the bare or crusted soil that normally separates them and facilitates animal movement (Bachen 2014). Spacing between stems or litter in dense *Bromus* canopies becomes smaller than animal sizes, and experiments show movements made for foraging or escaping predation become slower and noisier, and thus risks of predation are increased for a number of rodents such as mice and reptiles such as lizards (Esque et al. 2002; Newbold and Carpenter 2005; Rieder et al. 2010; Bachen 2014). Mice avoid moving through noisy substrates, and acoustic cues are important for hunting by *Vulpes* spp. (fox), *Canis latrans* Say (coyotes), and birds of prey, particularly nocturnal hunters such as owls (reviewed in Bachen 2014). However, tall and dense *Bromus* canopies might also obscure small animals from predation, offsetting negative effects of *Bromus* on small mammals, although few studies have separated these mechanisms.

### *3.9.2 Changes in Bird and Large-Mammal Communities*

Although *Bromus* provides import forage and cover for introduced game birds such as the nonnative *Alectoris chukar* Gray (chukar partridge; reviewed in Zouhar 2003), the loss of perennials such as sagebrush is a notable detriment to many bird species such as greater sage-grouse. Sage-grouse benefits from the structural protection sagebrush provides throughout all life stages (Connelly et al. 2011). The grouse feed exclusively on sagebrush leaves in winter (Patterson 1952; Wallestad and Eng 1975), and chicks and adults depend on forbs often displaced by *Bromus* for a major portion of their diet in spring and early summer (Johnson and Boyce 1990; Schroeder et al. 1999). Direct negative effects of *Bromus* have also been noted on birds including sharp florets of *B. rubens* scratching eyes of hawks and causing infections, loss of vision, and thus starvation (McCrary and Bloom 1984). Birds associated with grasslands tended to use bunchgrass more than *B. tectorum* sites: *Eremophila alpestris* L. (horned lark) and *Ammodramus savannarum* Gmelin. (grasshopper sparrow) visits and densities were greater on *B. tectorum* sites than native perennial grasslands (Earnst and Holmes 2012). Fire effects on birds include loss of nesting and temporary removal of food and protection provided by vegetation.

*Bromus* can contribute to the diet of native and domestic ungulates but generally are considered low-quality forage. *Odocoileus hemionus* Rafinesque (mule deer) diets can have a large portion of *B. tectorum* in winter if the grasses are accessible, and it is also an important forage before native herbs emerge in spring (reviewed in Zouhar 2003). In Arizona, *B. rubens* comprised <1 % of seasonal diet of desert mule deer, but this grass species is grazed by *Ovis canadensis nelsoni* Merriam (desert bighorn sheep; reviewed in Zouhar 2003). Predators such as coyotes and fox were less abundant on *Bromus*-invaded sites than in sagebrush steppe in Utah (Arjo et al. 2007). Like wildlife, livestock will utilize *Bromus*, especially in winter and particularly spring when livestock preferences and weight gain suggest that it has good nutritional value (for *B. tectorum*: Murray and Klemmedson 1968; Murray 1971). While some livestock operations are able to make extensive use of *Bromus-dominated* pastures in spite of mechanical irritants caused by stiff awns, the forage lost in frequent wildfire and additional year(s) of grazing deferment that often follow wildfire detracts considerably from Bromus' appeal for livestock operations (Pyke et al. 2015).

## 3.10 Management Implications

Assessments of ecosystem impacts of exotic invaders are important for ensuring that resources are allocated toward the most problematic species and that restoration addresses processes that we have the capacity to modify (Hulme et al. 2013). *Bromus* has biological and physical impacts on the environment that justify efforts to control them where they can dominate the plant community. Impacts of *Bromus* on fire regimes and plant community conditions, hydrologic functioning, and soil stability are difficult to mitigate. These impacts all reduce ecosystem productivity and portend a pattern of desertification. However, some of the perceived impacts of *Bromus* are not clearly and scientifically demonstrated or have been demonstrated only under a narrow set of responses (e.g., as described above for infiltration and erosion).

Allowing *Bromus* to reestablish may seem more desirable in some cases than a bare landscape that can lead to wind or water erosion following its eradication (e.g., with post-fire herbicide). Where *Bromus* are dense, restoration of desired plants will likely only be possible following its eradication and clearing of accumulated litter in order to ameliorate the microclimate and the hydrological and biogeochemical conditions required by native or naturalized restoration species (see Monaco et al. 2015). The homogenization and loss of microsite structure with *Bromus* invasion into otherwise patchy perennial communities can reduce the availability of safe sites for establishment of restoration plantings or seedings (Davies et al. 2009), and techniques to replicate or restore this microsite variability may also enhance restoration. Management practices that conserve or reintroduce appropriate root symbionts, such as mycorrhizae, may overcome putative feedbacks that otherwise inhibit native plant recolonization of *Bromus*-invaded sites.

## 3.11 Research Needs

Studies that identify how relative cover of *Bromus* compared to that of other exotic invaders affect ecosystem structure and function are scarce in the literature but are needed to identify tolerances for *Bromus* abundance in land use planning. For several ecosystem impacts, such as reduced infiltration, controlled studies that manipulate abundances of *Bromus* and evaluate ecosystem outcomes under a range of soil and climate contexts are still needed. Similarly, comparisons of impacts caused by *Bromus* with the impacts of native or naturalized species that otherwise would dominate the ecosystems in the years as well as decades following disturbance (e.g., *P. secunda* and *Artemisia* spp.) would be most meaningful for both assessing impacts and guiding restoration.

Comparing impacts of *Bromus* to other exotics is important considering the emergence and continuing spread of other annual exotic grasses in the Western USA, such as *Taeniatherum caput-medusae* (L.) Nevski (medusahead) and *Ventenata dubia* (Leers) Coss. (North Africa grass) that could occupy sites currently dominated by *Bromus*. Furthermore, comparison of plant communities resulting from management actions targeting *B. tectorum* (e.g., communities dominated by introduced species such as *A. cristatum* used in restoration) with unmanaged *B. tectorum* communities is increasingly important given the past and future extent of these exotic grasses seedings and the difficulty in restoring them to native communities (Davies et al. 2011).

Overall, research is needed that enables *Bromus*-ecosystem relationships to be both generalized and applied to specific sites. Variability among studies of *Bromus* impacts was apparent for key topics such as *Bromus* effects on infiltration and nutrients. The variability is likely due to local site differences and to temporal factors such as weather or time since disturbance or invasion. Transferability of information on *Bromus* impacts can be done more reliably if studies can (1) incorporate environmental gradients that characterize these largely arid and semiarid ecosystems at both local and larger scales and (2) determine mechanisms by which *Bromus* impact their environment across these gradients. Because of the aridity associated with *Bromus*, research needs to include longer time frames to identify how weather modulates *Bromus* impacts and its implications for management. For example, understanding how drought modulates the impact of *Bromus* on soil fertility will help restoration assessment and planning. Broadscale studies that use similar methodology and hold factors constant across the large spatial extents affected by *Bromus* will typically require collaborative approaches and are clearly needed to provide information useful to both ecologists and managers.

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