Chapter 2
Exotic Annual *Bromus* Invasions: Comparisons Among Species and Ecoregions in the Western United States

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Abstract Exotic annual *Bromus* species are widely recognized for their potential to invade, dominate, and alter the structure and function of ecosystems. In this chapter, we summarize the invasion potential, ecosystem threats, and management strategies for different *Bromus* species within each of five ecoregions of the western United States. We characterize invasion potential and threats in terms of ecosystem resistance to *Bromus* invasion and ecosystem resilience to disturbance with an emphasis on the importance of fire regimes. We also explain how soil temperature and moisture regimes can be linked to patterns of resistance and resilience and provide a

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conceptual framework that can be used to evaluate the relative potential for invasion and ecological impact of the dominant exotic annual *Bromus* species in the western United States.

Keywords Fire • Resilience • Resistance • Management • Moisture regime • Temperature regime

2.1 Introduction

Numerous *Bromus* species occupy a wide range of ecosystems around the globe (Atkinson and Brown 2015; Clayton et al. 2006), including 58 species within North America (Clayton et al. 2006), approximately half of which are exotic species that are nonnative to the continent (Pavlik 1995). Exotic annual *Bromus* (*Bromus* hereafter) are of significant concern to ecologists and land managers alike (Brooks and Pyke 2001). Much of what has been reported about the environmental and ecological controls on *Bromus* and their interactions with land uses and disturbance regimes have focused on the Cold Deserts ecoregion of the western United States (Fig. 2.1) and on *Bromus tectorum* L. (cheatgrass) in particular. This chapter reaches beyond that specific ecoregion and individual species to examine the invasion potential, ecosystem threats, and management strategies for the dominant *Bromus* species within each of five major ecoregions of the western United States (Table 2.1; Fig. 2.1). Other chapters within this book that are relevant to the topics in this chapter include Chambers et al. (2015), Germino et al. (2015), Monaco et al. (2015), and Pyke et al. (2015).

2.1.1 Resistance and Resilience to Bromus *Invasions*

The invasion potential, ecosystem threats, and management strategies for *Bromus* all vary based on ecosystem resistance to invasion and resilience to disturbance. Resistant ecosystems have the capacity to retain their fundamental structure, processes, and functioning (or remain largely unchanged) despite stressors, disturbances, or invasive species (Folke et al. 2004). Resilient ecosystems have the capacity to regain their fundamental structure, processes, and functioning following stessors like drought and disturbances like wildfire and then reorganize without crossing thresholds to alternative ecosystem states (Holling 1973; Walker et al. 2004). We use resistance and resilience as explanatory concepts throughout this chapter, along with temperature and precipitation gradients which are key factors affecting resistance and resilience (Brooks and Chambers 2011; Chambers et al. 2014a, b; Fig. 1.1).

Resistance to invasion is particularly important in the context of this chapter and is related to abiotic and biotic attributes and ecological processes that limit the population growth of invading species (D'Antonio and Thomsen 2004). Ecosystem resistance to invading species is a function of both the fundamental niche, which is largely related to climate suitability, and the realized niche, which is related

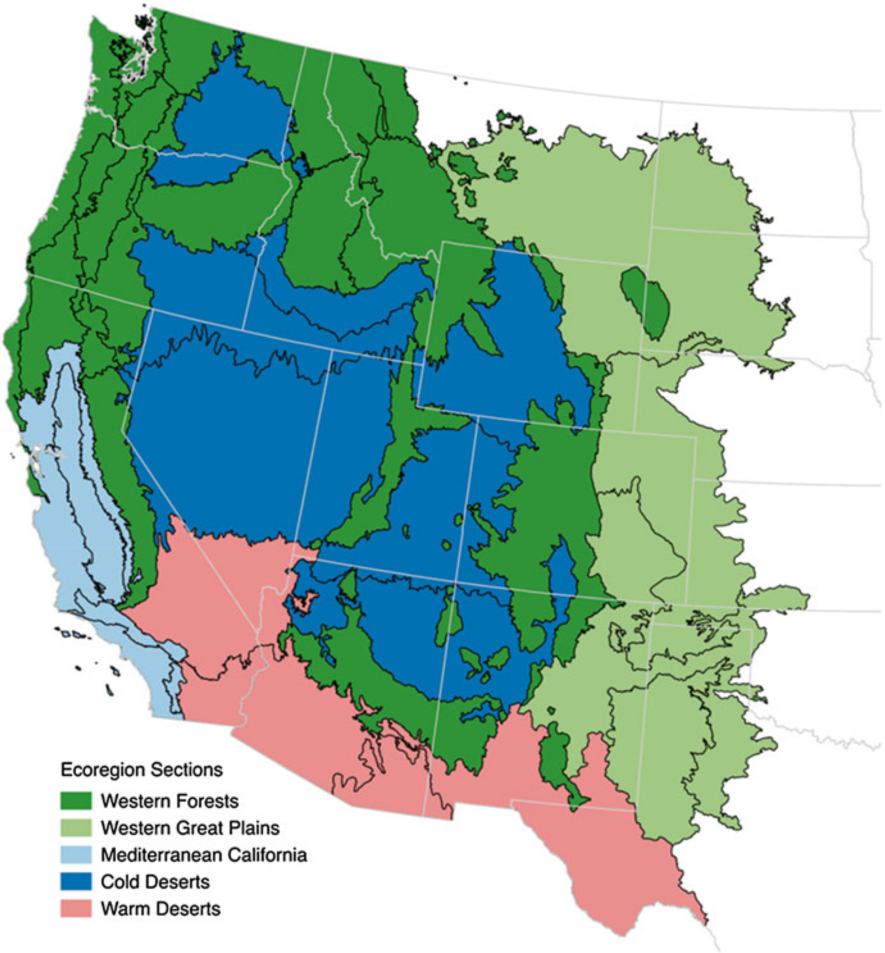

Fig. 2.1 Ecoregions of the western United States that are characterized by distinct temperature and soil moisture regimes and influence resistance to *Bromus*. Each ecoregion is an amalgam of various level I, II, and III Ecoregions of North America (http://www.epa.gov/wed/pages/ecoregions/na_eco.htm, accessed 17 Jun 2014; Wiken et al. 2011). Their specific delineations were based on breaks in soil temperature and moisture (amount and seasonality) regimes associated with ecological resistance to, and ecosystems threats posed by, *Bromus* invasions, and the availability of published information on these topics. The Western Forests ecoregion encompasses Level I ecoregions 6.0 and 7.0 (the Northwestern Forested Mountains and the Marine West Coast Forest). Mediterranean California corresponds to the Level I ecoregion 11.0 which bears the same name. The Cold Deserts and Warm Deserts correspond to Level II ecoregions 10.1 and 10.2, respectively. The Western Great Plains includes three level III ecoregions (Table 2.1) representing parts of two Level II ecoregions, the West-Central Semi-Arid Prairies and South-Central Semi-Arid Prairies (ecoregions 9.3 and 9.4)

to species interactions, both of which need to be understood to evaluate *Bromus* invasions (Chambers et al. 2014a). Temperature and precipitation amounts, and precipitation seasonality, are key attributes that influence ecosystem resistance

Table 2.1 Major ecoregions of the western United States and their most widespread dominant and subdominant exotic annual *Bromus* species

Ecoregion	Dominant *Bromus* species	Subdominant *Bromus* species	Associated EPA III Ecoregions (mean and range of annual precipitation in mm) (Wiken et al. 2011)
Warm Deserts	*B. rubens*	*B. tectorum*	10.2.1, 2, 4: Mojave (167, 50–900), Sonoran (206, 75–560), Chihuahuan (340, 200–635) 12.1.1 Madrean Archipelago (421, 260–950)
Cold Deserts	*B. tectorum*	*B. rubens*	10.1.2–8: Columbia Plateau (334, 150–600), Northern Basin and Range (351, 150–1000), WY Basin (296, 130–500), Central Basin and Range (277, 4–1000), CO Plateaus (298, 130–800), AZ/NM Plateau (293, 125–380), Snake River Plain (316, 110–350)
Mediterranean California	*B. rubens* *B. diandrus* (= *B. rigidus*) *B. hordeaceus*	*B. madritensis* *B. tectorum*	11.1.1–3: CA coastal sage/chaparral/woodlands (548, 200–1400), central valley (443, 125–760), southern California mountains (525, 220–1250)
Western Great Plains	*B. arvensis* (= *B. japonicus*) *B. tectorum*	None	9.3.3: NW great plains (393, 250–510) 9.4.1, 3: high plains (433, 305–530), southwestern tablelands (449, 255–710)
Western Forests	*B. tectorum*	*B. diandrus*	6.2.5, 7, 8, 11, 12, 13, 14: north cascades (1761, 300–6000), Cascades (824, 1150–3600), eastern cascades (649, 500–3500), Klamath mountains (1438, 500–3000), Sierra Nevada (1070, 150–2500), Wasatch/Uinta mountains (602, 150–1400), southern rockies (588, 255–1750) 7.1.7–9: Puget lowland (1400, 300–2500), coast range (2149, 1000–5000), Willamette valley (1228, 900–1600) 13.1.1: AZ/NM mountains (477, 270–2000)

and define ecological niche space (Davis et al. 2000; Miller et al. 2013; Chambers et al. 2014a, b, 2015).

Site occurrence information for *Bromus* gleaned from the GrassPortal website (www.grassportal.org, Osborne et al. 2011) indicates that resistance to invasion should vary among species based on mean annual minimum and maximum temperature and precipitation (Fig. 2.2). *Bromus rubens* L. (red brome) is clearly found at the hottest and driest sites, whereas *Bromus arvensis* L. (field brome) and to some degree *B. tectorum* occur at the coldest and wettest sites in the database. Variability among species is low at the lower end of the precipitation gradient, but very high at the upper end of the gradient (Fig. 2.2c). The preponderance of outlier sites on the high end of the precipitation gradient may represent occurrences at early successional or otherwise disturbed sites embedded within high precipitation vegetation types, especially within the Western Forests ecoregions, that would otherwise have

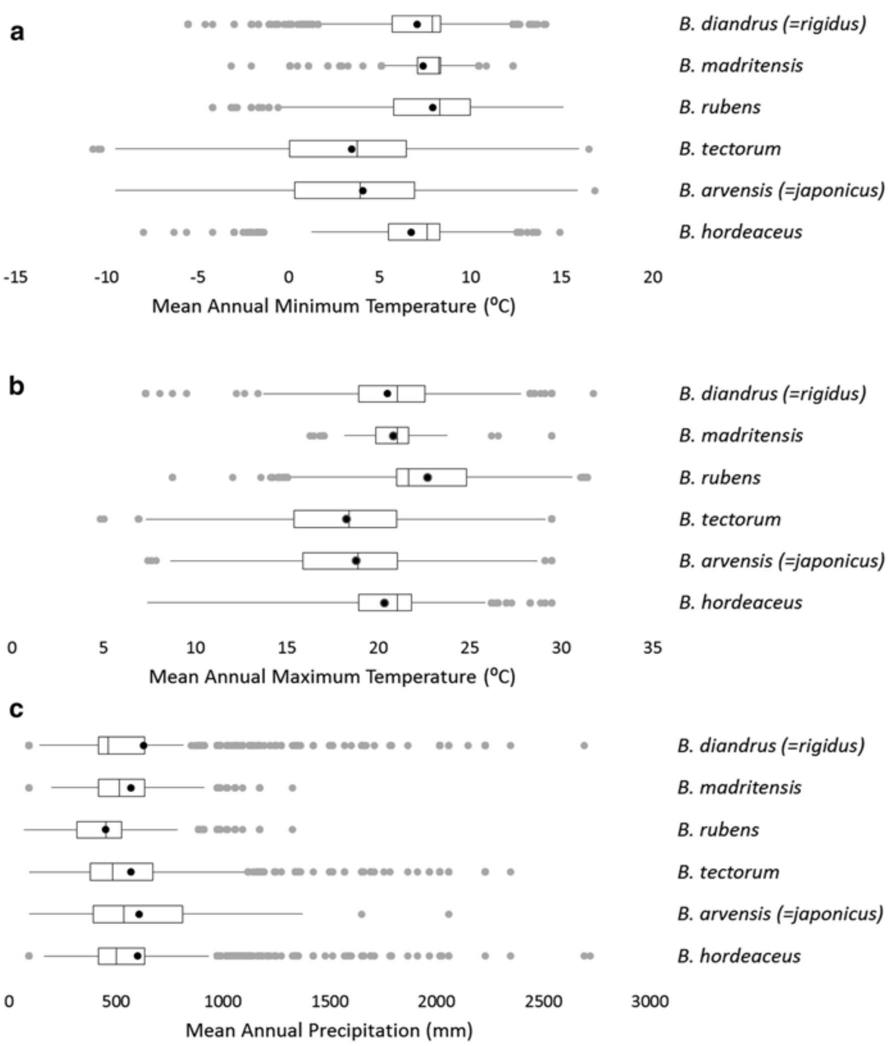

Fig. 2.2 (**a**) Annual minimum temperature, (**b**) annual maximum temperature, and (**c**) annual precipitation for site locations of *Bromus* in the western United States. Data were summarized for states intersecting the ecoregional range map (Fig. 2.1), and downloaded from www.grassportal.org (accessed 16 Feb 2015, Osborne et al. 2011). Species were only included if the database was represented by site locations in states throughout the species range (www.plants.usda.gov). Numbers of sites were as follows: *B. diandrus* (and *B. rigidus*), $n = 1241$; *B. madritensis*, $n = 226$; *B. rubens*, $n = 1568$; *B. tectorum*, $n = 2004$; *B. arvensis* (and *B. japonicus*), $n = 897$; *B. hordeaceus*, $n = 1188$. Climate data are 30-year mean annual values from 1961 to 1991; box plots show quartiles 1, 2, and 3, and upper and lower limits. Mean climate values are shown as *solid dots* and outliers as *gray dots*. Data sources and other database information are listed in Table 2.2

high resistance to *Bromus*. These data suggest that *Bromus* may be firmly established at the relatively lower precipitation sites that define one boundary of both their fundamental and realized niches. However, they additionally suggest there may be higher precipitation sites that are within their fundamental niche, but that are not currently within their realized niche due to competition from other species. The implications of this are that *Bromus* may be poised to expand and potentially dominate climatically suitable high precipitation sites in the event that land use or climate conditions change the competitive balance in their favor.

There is great interest in understanding the resistance of ecosystems to invasion by *Bromus* because of their negative ecological effects. Chief among these effects are altered fire regimes (Whisenant 1990; D'Antonio and Vitousek 1992; Brooks and Pyke 2001; Brooks et al. 2004; Balch et al. 2013; Germino et al. 2015). *Bromus* can alter fire regimes by changing fuel structure in ways that can lengthen the fire season, enhance ignition probabilities, increase fire extent, and alter fire severity (Brooks et al. 2004). The altered fire regime in turn creates conditions that promote dominance of the species that created the new fuels, thus creating a positive grass/fire feedback (D'Antonio and Vitousek 1992), the mechanisms of which are much better understood than perhaps any other potential ecosystem threat posed by *Bromus*. Important questions for evaluating the potential impacts of *Bromus* among ecoregions include the following (Brooks 2008). Has the invasion introduced a novel structure or property into an ecosystem? Has that novel feature in turn altered ecosystem processes or their controls (disturbance regimes)? Do the resultant conditions perpetuate a new, persistent ecosystem state (e.g., alternative state)?

Ecosystem resilience, and thus ecological risks posed by plant invasions, can be affected when disturbance regimes (perturbation type, timing, duration, size, and/or intensity) are altered from historical norms. Land uses are often at the root of these alterations, including inappropriate grazing of grasslands and shrublands by livestock and clear-cut harvests of forests. Plant invasions themselves may also facilitate changes in disturbance regimes in ways that increase ecological effects of the invading species, such as the grass/fire cycle.

2.1.2 Species, Ecoregions, and Chapter Structure

We focus on six widespread annual exotic *Bromus* taxa within the western United States, specifically *B. arvensis*, *Bromus diandrus* Roth (ripgut brome), *Bromus hordeaceus* L. (soft brome), *Bromus madritensis* L. (compact brome), *B. rubens*, and *B. tectorum* (Table 2.1). At times in the past, botanical taxonomic authorities have considered *B. arvensis* and *Bromus japonicus* Thunb. (Japanese brome) to be distinct species, but the taxonomic authority used in this book, namely the USDA, Natural Resources Conservation Service, Plants Database, currently considers them to be one in the same species within *B. arvensis* (http://plants.usgs.gov, accessed 21 Jul 2015). Similarly, *B. diandrus* and *Bromus rigidus* Roth (ripgut brome) have been considered by some as separate species, but are both currently subsumed within

B. diandrus in the Plants Database. Thus, where we reference *B. arvensis* or *B. diandrus* throughout this chapter we are also referencing their Plants Database synonyms.

Bromus madritensis and *B. rubens* are currently considered distinct species in the Plants Database (http://plants.usgs.gov, accessed 21 Jul 2015), although they intergrade so much in their taxonomic characteristics that they are often difficult to distinguish and may be misidentified in some publications. For example, an analysis of 28 field samples from central and southern California and southern Nevada (M. Brooks, unpublished data, 2015) indicated that every sample contained taxonomic characteristics of both species, although those of *B. rubens* were much more frequent (mean 9.1, median 9.0, of 11 characteristics).

We also identify five major ecoregions in the western United States (Fig. 2.1), each of which is characterized by a unique set of dominant and subdominant *Bromus* (Table 2.1). For each ecoregion, we recognize 3–5 major vegetation types which can be placed along hot-dry to cool-moist soil temperature and moisture gradients and which vary in their resistance to *Bromus* and resilience to disturbance. We use soil temperature and moisture regimes as indicators of relative ecosystem resistance and resilience to various *Bromus* species within each ecoregion (Chambers et al. 2014a, b, c).

Each of the five ecoregional sections in this chapter follows a common outline. For each ecoregion, we (1) describe the invasion potential of each widespread *Bromus* species; (2) explain the ecosystem threats posed by *Bromus* invasions; and (3) summarize the efficacy of typical management strategies for *Bromus*. The majority of citations focus on published studies conducted within each ecoregion. The relative resistance to invasion and resilience to fire are illustrated in a series of conceptual models for each ecoregion focusing on the dominant *Bromus* species in the ecoregion. We acknowledge that the amount of supporting science that underpins these figures varies greatly among ecoregions, and we refer to them as hypothetical resistance and resilience models.

2.2 Warm Deserts

Environmental conditions in the Warm Deserts ecoregion are the hottest and driest of anywhere in western United States (Fig. 2.3). Soil temperature regimes are either thermic (mean annual temperature 15–22 °C) or hyperthermic (≥22 °C). Soil moisture regimes are mostly aridic, meaning that the soil is dry for at least half of the growing season and moist for less than 90 consecutive days, which supports mostly desert shrubland vegetation types. Some areas are classified as ustic aridic, meaning they have slightly longer periods of moist soil during the growing season due to higher amounts of summer precipitation which is conducive to the growth of semiarid desert perennial grasslands. These warm and dry conditions result in limited anthropogenic land uses compared to other ecoregions, although mining, livestock grazing, off-highway vehicle use, and most recently wind and solar energy developments can have broad landscape effects with implications for plant invasion (Lovich and Bainbridge 1999; Brooks and Pyke 2001; Brooks 2009).

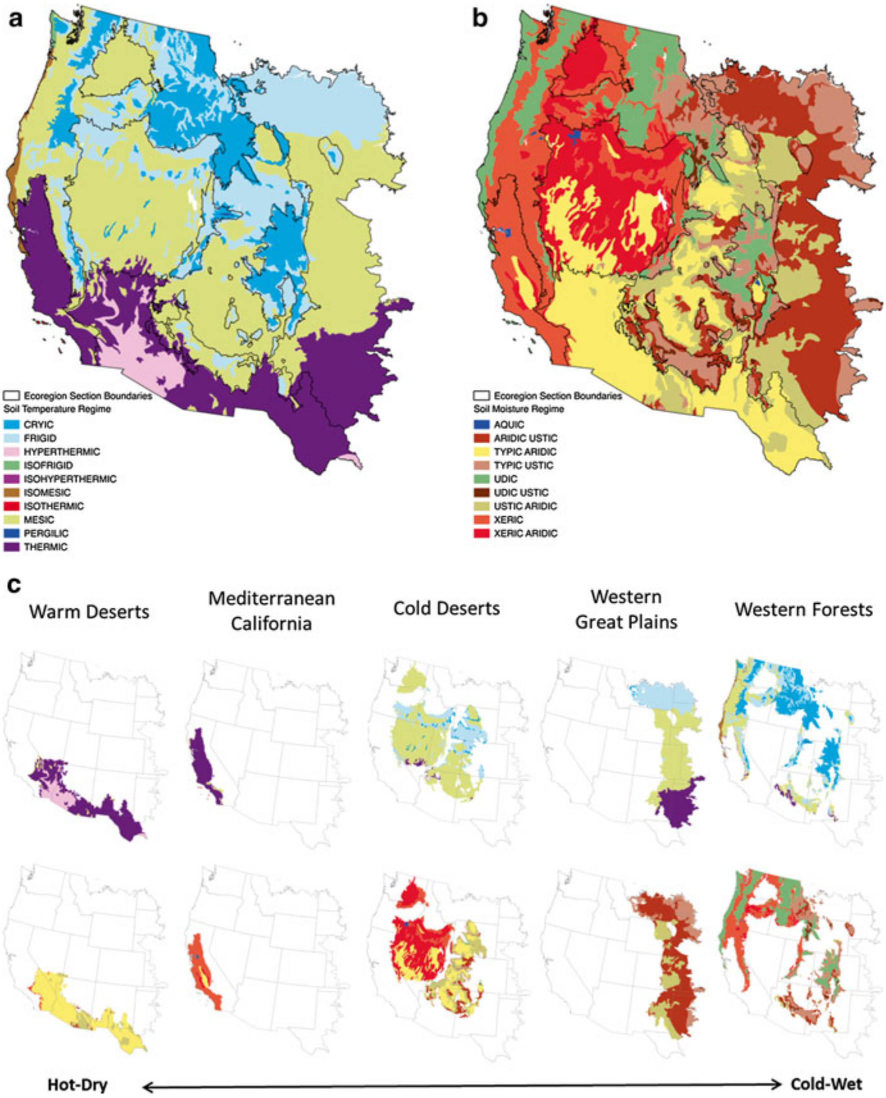

Fig. 2.3 (**a**) Soil temperature regimes, (**b**) soil moisture regimes, and (**c**) comparisons among the six major ecoregions of the western United States

Bromus rubens is the most ubiquitous *Bromus* species in the Warm Deserts ecoregion. It can occur in all but the most hyperthermic and xeric regions, but is most prevalent in middle elevations typified by creosote bush scrub and blackbrush shrubland which have the lowest resistance to its dominance (Fig. 2.4a) (Brooks and Berry 2006; Brooks 2009; Klinger et al. 2011a). *Bromus tectorum* can also be locally abundant, but is much more restricted in its geographic distribution in Warm Deserts than is *B. rubens* (www.calflora.org, accessed 8 Apr 2014). Although *B. tectorum* can

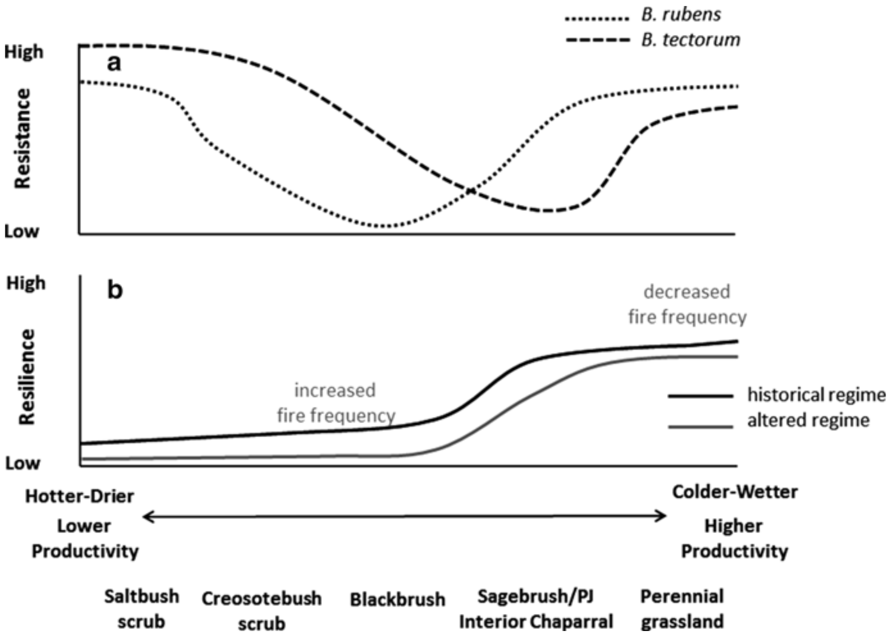

Fig. 2.4 Hypothetical (**a**) resistance to common *Bromus* species and (**b**) resilience to historical and altered fire regimes for the Warm Deserts ecoregion (primary altered regime characteristic labeled in *gray*)

appear in lower elevation areas with locally higher soil moisture such as riparian zones and roadsides (Brooks 2009), it only occurs as a dominant *Bromus* species at higher elevations, such as those within the upper blackbrush ecotone, sagebrush, piñon–juniper, and interior chaparral (Fig. 2.4b) (Klinger et al. 2011a). *Bromus trinii* Desv. (Chilean chess) has also been reported from some locations, generally within the same ecological range as *B. rubens* (www.calflora.org, accessed 8 Apr 2014), but its relative dominance is typically very low (Brooks 2009; exception is Brooks 1999). *Bromus diandrus* can also be found in the Warm Deserts (www.calflora.org, accessed 8 Apr 2014), but almost always in localized areas of higher soil moisture such as along roadsides, in riparian areas, or associated with agricultural or urban developments (Dudley 2009; M. Brooks, pers. obs.).

2.2.1 Invasion Potential of Warm Deserts by Bromus

The lowest elevation ecosystems of the Warm Deserts are characterized by hyperthermic, typic aridic soils (Fig. 2.3c) and sparse cover of creosote bush scrub or saltbush scrub. Creosote bush scrub is dominated by the type species, *Larrea tridentata* (DC.) Coville (creosote bush), and is the most widespread vegetation type. Saltbush scrub is dominated by one or more *Atriplex* species, including *Atriplex polycarpa* (Torr.) S. Watson (cattle saltbush), *Atriplex spinifera* J.F. Macbr. (spinescale saltbush), and *Atriplex canescens* (Pursh) Nutt. (fourwing saltbush). Productivity is strongly limited by low annual precipitation, and resistance to invasion by *Bromus* is generally high (Fig. 2.4a).

Blackbrush occurs on thermic and mesic soils at middle elevations above creosote bush scrub and is dominated by the type species, *Coleogyne ramosissima* Torr. (blackbrush), but may also contain *L. tridentata*, *Atriplex confertifolia* (Torr. & Frém.) S. Watson (shadscale saltbush), *Yucca brevifolia* Engelm. (Joshua tree), and *Juniperus* spp. (juniper). This vegetation type is the least resistant to invasion by *Bromus*, especially *B. rubens* (Fig. 2.4a). At higher elevations, sagebrush, piñon–juniper woodland, and interior chaparral occur on the more mesic soils of desert mountain ranges and at ecoregional ecotones along the western, northern, and north-eastern margins of the Warm Desert ecoregion. The specific ecosystem type that is present depends on local conditions associated with soils, topography, and disturbance history, but in most cases the dominant *Bromus* species at these higher elevations is *B. tectorum*.

Desert grasslands dominate the thermic soils in the monsoonal regions of the far eastern Mojave and the Sonoran and Chihuahuan deserts. Historically, these ecosystems were dominated by perennial grasses and a fire frequency of every 5–15 years (Humphrey 1958; McPherson 1995; Wright and Bailey 1982). Vigorous stands of perennial grasses with their extensive shallow roots very likely provided high ecosystem resistance to invasion by *Bromus* which share the same shallow rooting zone. During the twentieth century, overgrazing and fire suppression have allowed deeper rooting woody species to invade (McPherson and Weltzin 2000), reducing the vigor of perennial grasses and potentially the ecosystem resistance to *Bromus*. Although the exotic annuals *B. rubens* and *B. tectorum* occur in desert grasslands, they have not exhibited the widespread dominance observed for exotic perennial grasses such as *Eragrostis* von Wolf spp. (lovegrasses) and *Pennisetum ciliaris* (L.) Link (buffelgrass) which have replaced native grasses in many areas and maintain a fairly high level of resistance to *Bromus* invasion.

Bromus rubens was present at 44 % of 126 low elevation (149–1222 m) sites in the eastern Mojave Desert near Lake Mead National Recreation Area (Abella et al. 2012). It was twice as prevalent at middle elevation (800–1222 m) sites, which tended to have more precipitation, were more species rich, and were characterized by mixed perennial communities, compared to the lowest elevation sites (<800 m) which were drier, more species poor, and dominated by either *Atriplex* L. spp. or *L. tridentata*. Similar results were reported from the western Mojave Desert in lower to middle elevations ranging from 683 to 1402 m (Brooks and Berry 2006). Similar patterns were also found in post-fire landscapes of the eastern Mojave Desert (Klinger et al. 2011a), where *B. rubens* was the dominant *Bromus* species in lower elevation communities, with peak densities between 800 and 1200 m, whereas *B. tectorum* dominated higher elevation communities, with a peak density at 1800 m. Averaged over both low and high elevation sites in the eastern Mojave Desert, peak densities of

B. rubens were almost twice as high as those of *B. tectorum* (Klinger et al. 2011a). The prevalence of *B. rubens* at lower and middle elevation and *B. tectorum* at high elevations is likely a function of the lower minimum temperature tolerance of the latter (Fig. 2.2a), but may be modified by variation in the realized niches of these two species along this elevation gradient as a result of interspecific competition.

Livestock grazing may decrease resistance to *Bromus* by reducing vigor of perennial plants particularly grasses (Brooks and Pyke 2001; Brooks et al. 2007). Short-term, high-intensity grazing has been used to reduce fine fuel loads and, if applied in early spring or late summer, it can preferentially impact *B. tectorum* populations in Cold Deserts (Strand and Launchbaugh 2013). However, in most cases dominance of *Bromus* increases following cessation of grazing in both Warm Deserts and Cold Deserts, and the net long-term effects of livestock grazing are generally favorable for invasive plants (Brooks and Pyke 2001; Brooks et al. 2007).

Atmospheric nitrogen deposition may also reduce landscape resistance to *Bromus* species in Warm Deserts where deposition levels are high downwind from major urban or agricultural areas (Brooks 2003; Allen et al. 2009; Rao and Allen 2010). These studies explain that naturally low soil nitrogen levels in Warm Desert regions, along with low soil moisture availability, can hinder *Bromus* invasions, and elevated levels can reduce this resistance. Increased biomass of *Bromus* and other annual plants facilitated by nitrogen deposition may increase the potential for fire, which may further promote *Bromus* dominance (Rao et al. 2010, 2015).

2.2.2 Ecosystem Threats to Warm Deserts from **Bromus**

The role of *Bromus* in creating continuous biomass cover in the interspaces between perennial plants and increasing the size and frequency of fires represents its primary ecosystem threat in the Warm Deserts ecoregion (Brooks and Pyke 2001; Brooks and Esque 2002). This threat is most prevalent in areas with low resistance to invasion by *Bromus* and resilience of native vegetation to disturbance, typically at middle elevations dominated by mixed woody scrub and blackbrush communities, and to some degree in creosote bush scrub (Brooks and Minnich 2006; Brooks et al. 2013) (Fig. 2.4). Native perennial cover in blackbrush is already at the threshold of what can carry fire (Fig. 2.5a), and adding *Bromus* biomass can tip the balance to a more fire-prone landscape (Fig. 2.5b) (Brooks and Matchett 2006). *Bromus* dominance following fire can increase substantially after only a single fire in saltbush scrub and creosote bush communities (Fig. 2.5c), although subsequent fires can sequentially reduce cover and diversity of native perennials and promote recurrent fire (Fig. 2.5d) (Brooks 2012). This reduced resilience caused by frequent fires is operative primarily in saltbush, creosote bush scrub, and blackbrush, although it can also affect even perennial grasses in cases of extreme fire frequency (Fig. 2.4b).

This grass/fire cycle has been occurring in the Mojave Desert since at least the early 1900s, when post-fire blackbrush landscapes were recognized to be dominated

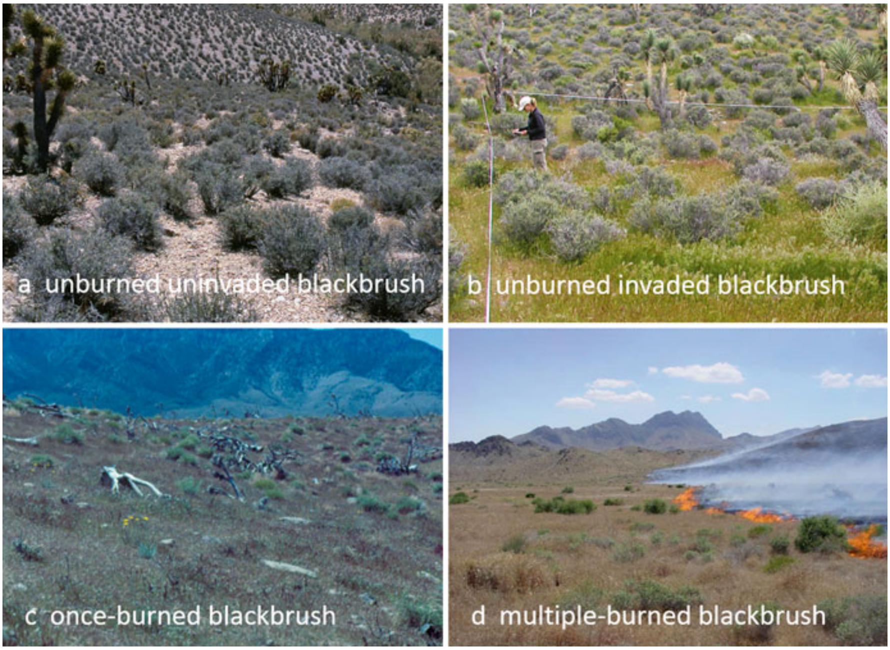

Fig. 2.5 (**a**) Unburned blackbrush stand uninvaded by *Bromus*, (**b**) unburned blackbrush stand invaded by *B. rubens*, (**c**) once-burned blackbrush stand dominated by *B. rubens*, and (**d**) multiple-burned blackbrush stand dominated by *B. rubens*

by *B. rubens* and land managers were concerned about the potential for recurrent fire (Fig. 2.6a) (Holmgren 1960; Brooks et al. 2007). Dominance by *B. rubens* in this region can be established after a single fire and may persist at least a half century even without subsequent burning (Fig. 2.6b). By some definitions this condition can be considered a type conversion from native shrubland to exotic annual grassland, even after a single fire. These fires are much more prevalent in the northeastern Mojave Desert (Brooks and Esque 2002), especially in areas of both high winter and high summer rainfall (Tagestad et al. in press). Modeled estimates of precipitation through the year 2100 forecast increased interannual variability including higher peak rainfall years (Tagestad et al. in press) which are conditions associated with increased probability of fire occurrence (Brooks and Matchett 2006). Higher elevation sagebrush, piñon–juniper, and interior chaparral ecosystems with mesic to warm frigid soils have relatively low resistance to invasion by *B. tectorum* (Fig. 2.4a), but they also have high resilience to disturbance and thus are at relatively low risk of conversion to a grass/fire cycle (Fig. 2.4b). Fire occurrences at these high elevation sites are also not associated with interannual rainfall amounts, providing further evidence that they are not significantly affected by altered fire regimes associated with exotic annual grasses (Brooks and Matchett 2006).

Fig. 2.6 (**a**) 7-year post-fire scene dominated by a carpet of *B. rubens* following a stand-replacing fire in a blackbrush shrubland that burned once in 1939 (photo by A. Croft, 12 May 1946). (**b**) A 63-year post-fire scene showing *B. rubens* persisting with early successional shrubs following a half century of no additional fire (photo by D. Oldershaw, 9 May 2002). The view is looking southwest inside the mouth of Horse Spring Basin in the northeastern Mojave Desert, Lincoln County, NV

Bromus rubens has also been shown to effectively compete with native annual (Brooks 2000; DeFalco et al. 2003) and perennial plants in the Mojave Desert (DeFalco et al. 2007). These competitive effects can influence community dynamics and resilience following disturbance (Brooks and Chambers 2011). For example, during the first 3 years following the 2005 Southern Nevada Fire Complex woody plant seedlings were almost nonexistent except where densities of exotic annuals, primarily *B. rubens* and *Erodium cicutarium* (L.) L'Hér. ex Aiton (redstem stork's bill), were exceedingly low (Klinger et al. 2011a). Reduced resilience of native perennials is a key element of the process by which a grass/fire cycle becomes established (Brooks 2008). The reduced productivity and diversity of native annuals and loss of the habitat structure provided by perennial shrubs can negatively affect wildlife, such as the federally Threatened *Gopherus agassizii* Cooper (desert tortoise) (Brooks and Esque 2002).

2.2.3 Management Strategies for Bromus *in Warm Deserts*

Bromus are already so wide ranging in the Warm Deserts that early detection and eradication is not a relevant management strategy for these taxa. Even when direct control efforts such as herbicide use are implemented, they are typically economically feasible to implement for only a couple of years and in relatively small areas. In addition, even if dominance of one *Bromus* species is effectively reduced, other exotic species may fill the void if there is no plan for facilitating the growth of other more desirable species to compete with them. In one dramatic case from the riparian zone in Zion Canyon of SW Utah at the regional ecotone between the Warm Deserts, Cold Deserts, and Western Forests, an herbicide treatment effectively controlled *B. diandrus*, but inadvertently led to dominance of *B. tectorum* by the following year (Fig. 2.7). This is an important reminder that any effort to reduce abundance of

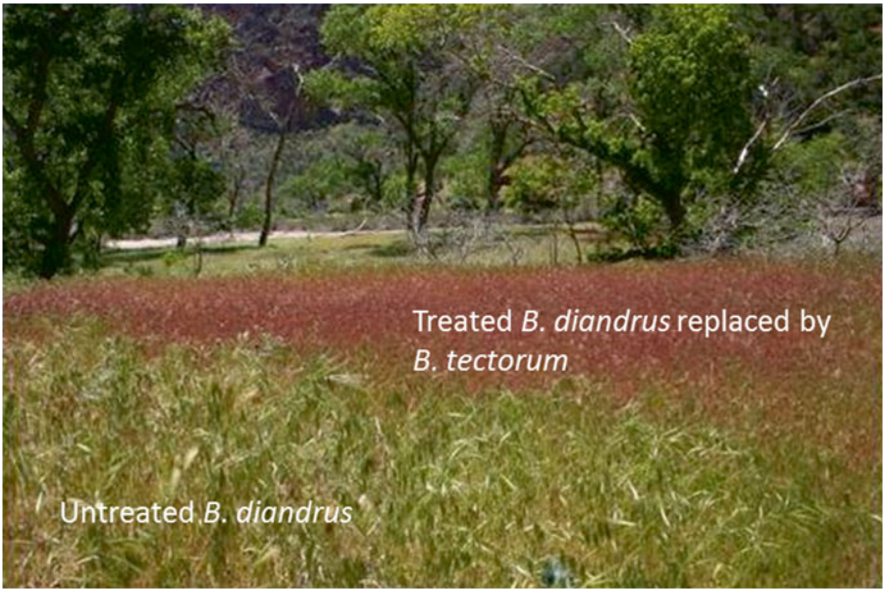

Fig. 2.7 Effects of fall Imazapic treatment of *B. diandrus* on subsequent increase in dominance by *B. tectorum* the following spring in a riparian woodland in Zion Canyon, Utah (photo by M. Brooks, Spring 2006)

Bromus in any ecosystem should consider the likely net response of the plant community and include effective contingency plans.

Restoration guidelines in Warm Deserts generally focus on maximizing abundance and diversity of native species, diversity of functional types, and groups of species important for critical aspects of ecosystem function (Brooks et al. 2013). Thus, the most effective management approach for *Bromus* in the Warm Deserts is to maximize ecosystem resilience to disturbance. In doing so, landscapes will be less prone to ecosystem type conversions and can increase resistance to dominance by *Bromus* and other invasive plant species (Brooks and Chambers 2011; Chambers et al. 2014a). This can be done proactively by minimizing the extent and frequency of major disturbances such as wildfire (Brooks et al. 2007). Once these disturbances occur, management options become much more limited. Post-fire seeding is a standard management tool in other ecoregions to promote recovery of native species and minimize dominance of undesirable invasives such as *Bromus*. However, its long-term efficacy has recently been shown to vary depending on relative resistance and resilience in both the Cold Deserts (Beyers 2004; Shinneman and Baker 2009; Pyke et al. 2013; Knutson et al. 2014) and Warm Deserts (Klinger et al. 2011b). Thus, the most effective fire management strategy is to prevent fires from starting, and suppress fires once they start, especially at middle elevations characteristic of the upper creosote bush scrub ecotones and blackbrush shrublands (Brooks et al. 2013) where resistance and resilience are both low (Fig. 2.4).

2.3 Mediterranean California

The central valley and surrounding foothills, coastal mountains, and coastal plains of California have a Mediterranean climate with a relatively cool and wet winter and spring and a hot and dry summer and autumn. Soil temperatures are mostly thermic and similar to much of the warm desert region, but moisture regimes are mostly classified as xeric, rather than drier typic aridic which characterizes the Warm Deserts (Fig. 2.3c).

The grasslands of Mediterranean California can be divided into various ecotypes dominated by different *Bromus* species, often with co-dominance by exotic annual grasses from other genera. The more arid southern and interior grasslands are defined by an abundance of *B. rubens*, although its taxonomic similarity with *B. madritensis* (Sect. 2.1.2) makes it difficult to attribute dominance to one or the other. By contrast, the coast range grassland is defined by dominance of *B. diandrus* and *B. hordeaceus* (Jackson and Bartolome 2002; Keeler-Wolf et al. 2007). Serpentine grasslands can be dominated by *B. hordeaceus*, especially following periods of high rainfall. The coastal prairie is more defined by native and invasive perennial grasses, but *B. hordeaceus* and *B. diandrus* are also common. Disturbed areas within the region's coastal sage scrub and chaparral shrublands tend to be dominated by *B. rubens*, often in association with *B. diandrus* and *B. hordeaceus.* In somewhat moister woodlands and riparian zones, these species are often replaced entirely by *B. diandrus*, and in the higher inland mountain forests with colder winters, they are replaced by *B. tectorum.*

2.3.1 Invasion Potential of Mediterranean California by Bromus

Ecosystems within the Mediterranean California ecoregion are diverse and vary in their resistance to *Bromus* invasion. Sage scrub is at the hottest and driest end of the productivity gradient in the Mediterranean California ecoregion and tends to have the lowest resistance to *Bromus* invasion particularly when it is disturbed or stressed by nitrogen addition (Fig. 2.8a). Perennial grasslands and oak woodlands tend to have moderate resistance to *Bromus* invasion (Fig. 2.8a), but only where disturbance regimes have not shifted outside of the range of historic variation due to grazing or increased fire frequency (Fig. 2.8b). Oak woodlands and oak savannas that have been grazed for many decades often have an understory of *B. diandrus* which increases in dominance after grazing ceases (Rice and Nagy 2000; Stahlheber and D'Antonio 2013). Chaparral and mixed conifer forests display the highest resistance to *Bromus* invasion due to their high canopy cover which shades the soil surface impeding annual plant growth.

Bromus species in Mediterranean California thrive best where perennial cover is slow to recover following disturbance, and their dominance is often transitory where

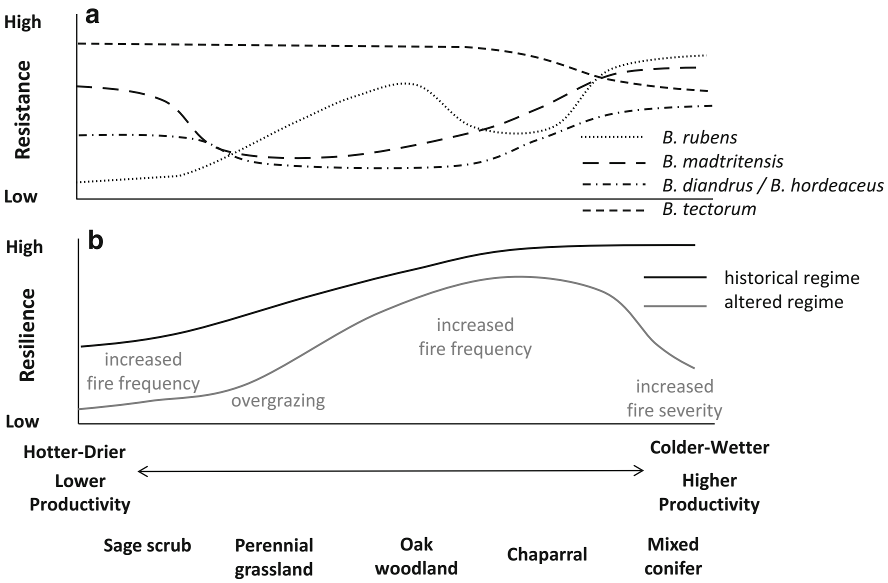

Fig. 2.8 Hypothetical (**a**) resistance to common *Bromus* and (**b**) resilience to historical and altered fire regimes for the Mediterranean California ecoregion (primary altered regime characteristic labeled in *gray*)

perennial cover recovers more quickly. In a study of 250 chaparral sites (Keeley et al. 2008), *B. madritensis* cover was negatively correlated with pre-fire stand age and previous fire severity. In addition, 5 years post-fire cover of exotic species, of which *Bromus* was a major contributor, was best predicted by shrub cover and estimated exotic seed bank at the time of fire. In essence, the extent to which *Bromus* and other exotics can invade disturbed Mediterranean shrublands is a race between exotic propagules getting to the site (since most that were there before are killed by high-intensity fire) and shrub canopy reestablishment. Under historical disturbance regimes, productivity and resilience covaried (Fig. 2.8b). However, various anthropogenic factors have altered disturbance regimes and reduced ecosystem resilience, especially at the lowest and highest ends of the productivity gradient. Because chaparral tends to be more species rich with more post-fire resprouting species compared to sage scrub, it tends to be more resilient to increased fire frequency (Fig. 2.8b).

Exotic annual grasslands, most of which have a strong component of *Bromus*, owe their origins to either (1) disturbance that converts native woody vegetation or mixed native perennial grass/shrub stands or (2) direct invasion of native grasslands (Keeley 1990). These exotic grasslands are markedly unlike native perennial grasslands in that the former are lower in functional diversity than the latter, being dominated entirely by annual grasses and forbs with a different composition of native forbs (Molinari and D'Antonio 2014). Where remnants of native grasslands persist within larger exotic annual grasslands, *Bromus* are usually only co-dominants (e.g., Molinari and D'Antonio 2014).

Fig. 2.9 Chaparral with three different fire histories in southern California. The entire scene burned in the 1970 Laguna Fire. The front and middle third burned in the 2001 Viejas Fire, and the front third burned a third time in the 2003 Cedar Fire. The background illustrates mature chaparral dominated by the native shrub *Adenostoma fasciculatum*, the middle third early seral chaparral dominated by the native shrub *Lotus scoparius*, and the front portion a 1-year post-fire scene dominated by the nonnative annual grass *B. madritensis* (photo by Richard Halsey, Spring 2004)

Fire history plays a critical role in the prevalence of exotic grasses within shrubland ecosystems of the region. Short intervals between fires can thin shrub density, which can both increase grass abundance and reduce native shrub seed banks and the vigor of potential resprouts (Zedler et al. 1983; Haidinger and Keeley 1993; Talluto and Suding 2008; Keeley and Brennan 2012). These thinned stands lead to reduced fire intensity which may further favor survivorship of exotic propagules (Keeley et al. 2008). A classic example of this dynamic is illustrated in Fig. 2.9 where a chaparral stand that burned three times over three decades was dominated by *B. madritensis* compared to areas burned only once or twice. However, in a region-wide remote sensing study only a few shrublands appeared to be undergoing type conversion via fires that occurred two times within 8 years (Meng et al. 2014), so other factors may interact with fire frequency to affect vegetation trajectories.

Atmospheric pollution in the form of nitrogen deposition has been implicated in the invasion of semiarid shrublands by annual grasses including *Bromus* (Westman 1979; Allen et al. 1998). In desert scrub, openings between widely spaced shrubs are readily invaded by invasive grasses and this is enhanced by nitrogen pollution (Brooks 2003). In contrast, within closed canopy shrublands there is no evidence that pollution alone can promote type conversion from shrubs to these grasses, but there is evidence that following a disturbance that opens up the canopy (such as fire or human disturbance), *B. diandrus* and *B. rubens* can quickly establish and suppress native shrub seedlings (Eliason and Allen 1997). Recent work suggests that nitrogen enhances competitive suppression of native shrub seedlings in the presence of abundant *Bromus* at least in part due to interactions with mycorrhizae (E. Allen, pers. comm.). Also in coastal prairies, nitrogen addition such as by cyclical growth of native lupines enhances *B. diandrus* cover (Maron and Connors 1996; Maron and Jeffries 1999; Suttle et al. 2007) at the expense of native grassland species. In serpentine grassland, nitrogen addition enhances *B. hordeaceus* dominance at the expense of native species (Huenneke et al. 1990).

Sites dominated by native perennial grasses today appear to have some resistance to invasion by annual grass species including some *Bromus*. This has been demonstrated experimentally as well as by observation (Seabloom et al. 2003; Corbin and D'Antonio 2004; Lulow 2006). Invasive bromes in these settings include B. *diandrus*, *B. hordeaceus*, and *B. madritensis*. Resistance was disrupted historically by conversion of landscape to crop agriculture and by animal disturbance such as by livestock. The interaction of grazing with native versus exotic grasses in California is controversial and varies by region. However, a meta-analysis showed that exotic grass cover, including largely *Bromus*, decreases with livestock grazing (Stahlheber and D'Antonio 2013) whereas seasonal grazing can enhance native grass cover particularly in the more coastal regions of California. Exotic forb cover tends to increase with grazing while native forb richness (but not cover) increases with grazing. Despite the use of grazing as a tool to enhance native species and reduce exotic annual grasses such as *B. diandrus*, these grasses remain an important component of virtually all of the grazing lands in California (Jackson and Bartolome 2007).

Natural disturbance factors such as gopher excavation have also been shown to promote *Bromus* abundance in grassland settings (Hobbs and Mooney 1995) as do excavations by feral pigs (Cushman et al. 2004). These *Bromus* also invade ruderal environments created by various types of disturbance that remove native vegetation and disturb the soil. Invasion success is complicated and tied to soil nutrients and belowground root competition (Brown and Rice 2010). On severely disturbed sites, *Bromus* and other exotic annuals may persist for 70 years or more in what otherwise would have been sage scrub (Stylinski and Allen 1999).

In ecosystems such as oak woodlands and mixed conifer forests that are characterized mostly by frequent surface fire regimes, decreasing fire frequency can lead to understory fuel accumulations and increased potential for higher severity crown fire and lower post-fire resilience (Fig. 2.8b). The loss of forest canopy cover can change microclimates in ways that significantly reduce resilience and improve conditions for dominance by *Bromus*. In Oak savannas, the understory of trees is well known to promote dominance of *B. diandrus* over other annual species including other *Bromus* (Rice and Nagy 2000), and this is true over a wide latitudinal range of California oak savannas (Stahlheber 2013). Thus, loss of tree cover may change the relative dominance of specific *Bromus* in this vegetation type.

2.3.2 *Ecosystem Threats to Mediterranean California from* **Bromus**

Bromus invasions have had a multitude of impacts in Mediterranean California. Their success has largely been at the cost of losing native shrublands, primarily chaparral, sage scrub, and oak woodlands, although perennial grasslands have also been affected (Molinari and D'Antonio 2014). When this type conversion occurs it affects biodiversity, hydrology, fire regimes, and the global carbon balance. However, the direction of such effects can be variable. For example, *Bromus* invasion of coastal sage scrub in southern California has been linked to increased soil carbon storage if the shrublands remain unburned. If they burn and convert to grasslands, it is likely that soil carbon storage will decline (Wolkovich et al. 2009a).

Where type conversion has occurred, the dominant functional type has been changed from deep-rooted shrubs to shallow fibrous rooted annuals. This impacts soil water holding capacity and increases erosion and debris flows following heavy winter rains but also has the potential for enhancing stream flow (Meixner and Wohlgemuth 2003). Type conversion also impacts fire regimes in a couple of important ways. Length of the fire season is greatly expanded because fuel moisture in drying herbaceous biomass is lost rapidly and this can provide available fuel during all 12 months of the year. In addition, a substantial proportion of fires in the region ignite in herbaceous fuels (Syphard and Keeley 2015), which provides a wick that carries fires into woody vegetation, promoting repeat fires that further degrades mixed grass and shrub mosaics (Fig. 2.9) (Keeley et al. 2012; Monaco et al. 2015).

This grass/fire cycle where fire regimes are altered by grass invasion is well documented for several ecosystems (D'Antonio and Vitousek 1992). However, it is important to recognize that there are very diverse ways grass invasion impacts fire regimes depending on the natural fire regime in the region. For example, fire-prone perennial grass invasion into fire-sensitive tropical forests results from increased fire intensity, which acts to open up the forest to further invasion. California annual grass invasions by *Bromus* spp., *Avena* L. spp., and others are quite different because these annuals are invading a fire-prone shrubland ecosystem, one with a natural fire regime of high-intensity fires, and such fires are in some respects detrimental to grass invasion as they kill seeds of the invaders. However, these native shrublands require decades to recover and if grasses invade in the early post-fire stages they can produce flashy fuels that readily ignite and carry repeat fires when the native vegetation is still not mature. These short-interval low-intensity fires can result in stand thinning, further grass invasion, and increased probability of a repeat fire (Fig. 2.9). Sage scrub is especially susceptible to alteration due to repeat short-interval fire compared to chaparral, largely because productivity and levels of resilience are lower (Fig. 2.8b). In these stands, fire severity is lower and exotic seed survivorship is higher. As a general rule as stand age decreases, fire severity decreases and exotic seed survivorship and vegetative dominance increase after fire (Keeley et al. 2008).

One of the predominant concerns of reserve managers in California grassland and oak savanna habitats is the apparent decline of native wildflowers (Minnich 2008) and native biodiversity in general. *Bromus*-dominated grasslands are depauperate in diversity of plant functional types and animal communities (Rochester et al. 2010; Molinari and D'Antonio 2014). An ongoing study suggests that it is the accumulated litter of *Bromus* that suppresses native forb germination and not direct competition for soil nutrients between *Bromus* and native forbs (Molinari 2014). Molinari and D'Antonio (2014) demonstrate that there are several native forbs that can coexist with *B. diandrus* and that although native forb richness is depressed where this species becomes dominant, several native forbs preferentially associate with this grass. The influence of *Bromus* invasion on native animals has been little studied. One study found that despite enhancing primary production, *Bromus* invasion into coastal shrublands caused either a decrease in or no effect on arthropod assemblages (Wolkovich et al. 2009b). Key native ant species declined as litter of *Bromus* increased (Wolkovich et al. 2009b).

2.3.3 Management Strategies for Bromus *in Mediterranean California*

Preventing further invasions of *Bromus* species is largely dependent on reducing the incidence of disturbance and maximizing ecosystem resilience (Fig. 2.8). In grasslands, this may involve manipulating livestock grazing patterns or removal of feral animals such as pigs. Where exotic grasses have invaded fire-tolerant or even fire-dependent ecosystems, it is important to appreciate that these shrublands require a particular fire regime that typically involves long fire-free intervals and high-intensity fire. Humans currently cause over 95 % of all fires in the foothills and coastal plain of California and have greatly increased the natural fire frequency (Safford and Van de Water 2014). Keeping unwanted ignitions out of these systems is a major challenge. A more tractable problem is reducing planned ignitions and resource managers in the region are beginning to appreciate that prescription burning, while possibly having some fire-hazard reduction benefit, is adding to the readily ignitable fuel load on these landscapes.

Bromus dominance may decline under passive management for some landscapes whereas other landscapes require active restoration. Sage scrub displaced by grasslands from various disturbances can return within a few decades if disturbance is reduced and native seed sources are in close proximity (Freudenberger et al. 1987; DeSimone and Zedler 1999; Callaway and Davis 1993), although some sites have proved resistant to passive restoration (Stylinski and Allen 1999). The type of disturbance associated with annual grassland appears important as soil disturbance that affects biological soil crusts (if present) can favor exotic annuals such as *Bromus* and inhibit native shrub seedlings (Hernandez and Sandquist 2011).

Native perennial grasslands invaded by exotic grasses show some promise of being restored to a greater native grass and forb composition through active management. In particular, winter/spring grazing has been shown to enhance dominance of the bunch grass *Nassella pulchra* (Hitchc.) Barkworth (purple needlegrass) while reducing dominance of *Bromus* (Stahlheber and D'Antonio 2013). It has also been suggested that spring fires, which kill the exotic seed bank while still on the plant but do not diminish the resprouting capacity of native perennial bunch grasses and forbs, have potential (DiTomaso et al. 2006), although native grasses can still be highly susceptible to mortality from fire (Marty et al. 2005). One experiment showed that high-intensity fires in mixed grasslands can improve the ratio of native versus exotic (*Bromus* and *Avena* spp.) grasses for at least 2 years (Keeley and Brennan 2015). However, a key to the success of this effort was that these native-dominated grasslands possessed substantial fuel loads because it had been many years since the last fire or other major form of disturbance. Large fuel loads contributed to extraordinary flame lengths and presumably high soil temperatures that were sufficient to kill the exotic seed bank but allowed for the survival of native perennial grasses.

Studies from other vegetation types also illustrate the importance of the fuel load in creating fire behavior that can reduce *Bromus* dominance. For example, an investigation of spring burning on *B. tectorum* understory in a ponderosa pine forest failed to displace this exotic invader (Keeley and McGinnis 2007). In that case the low nutrient availability of the soils produced rather sparse grass populations and field measures of temperatures during the fire revealed that they failed to reach high enough levels to kill seed banks. The importance of high fuel loading to make this approach effective has been noted in studies of other *Bromus* (Sweet et al. 2008). Even when prescription burning to eliminate *Bromus* has been effective for the target species, they are replaced by other exotic annuals (Keeley et al. 2011). Other studies have also shown that effects of a single fire on annual grass reduction can be short-lived and repeated burning or burning followed by grazing may be necessary for sustained reductions in annual grasses (Corbin et al. 2004).

2.4 Cold Deserts

Environmental conditions in the Cold Deserts are on average moderately warm and dry in comparison to the range of soil temperature and moisture regimes across the western United States (Fig. 2.3). However, the topographic diversity of this ecoregion results in high temperature and moisture variability associated with local elevation gradients. The lower elevations dominated by salt desert and Wyoming big sagebrush ecosystems are relatively hot and dry whereas the higher elevations typified by mountain sagebrush and mountain brush are cold and moist. The most widespread invasive *Bromus* in the Cold Deserts ecoregion is *B. tectorum* which occurs over a broad range of temperature and precipitation conditions (Fig. 2.2). *Bromus rubens* also occurs in the Cold Deserts but appears less cold tolerant (Fig. 2.2a) and occurs at lower elevations and latitudes than *B. tectorum*. Colder winter conditions, in particular, severe and sudden freeze events, are lethal to *B. rubens* but are not lethal to *B. tectorum* (Bykova and Sage 2012).

2.4.1 *Invasion Potential of Cold Deserts by* Bromus

Salt desert vegetation types typically occur at relatively low elevations and have the warmest (mesic) and driest (aridic) soil temperature and moisture regimes in the Cold Deserts. Vegetation types that characterize the salt desert are typically dominated by members of the Chenopodiaceae such as *Atriplex* L. spp. and Sarcobatus Nees spp. (West 1983a, b). Resistance to *B. tectorum* and presumably *B. rubens*, which has received less study in this vegetation type, is low to moderate (Fig. 2.10a). Under the warmest and driest regimes, establishment of *B. tectorum* is limited by frequent low and sporadic precipitation years, and longer term persistence requires either the necessary environmental conditions to maintain viable populations or high propagule pressure (Meyer et al. 2001). Resilience to disturbance is generally low due to low productivity, infrequent plant establishment, and slow recovery (Fig. 2.10b, and see Haubensak et al. 2009). Recent expansion of *B. tectorum* and *B. rubens* into marginal salt desert environments has been attributed to favorable years for establishment during El Niño–Southern Oscillation (ENSO) events (Meyer et al. 2001; Salo 2005). Rising CO_2 levels (Smith et al. 1987) and high genetic variability (Ramakrishnan et al. 2006; Haubensak et al. 2014) also may help explain increased establishment and spread of *B. tectorum* and likely *B. rubens*. Invasion of *B. tectorum* has increased fine fuels and fuel continuity in these types

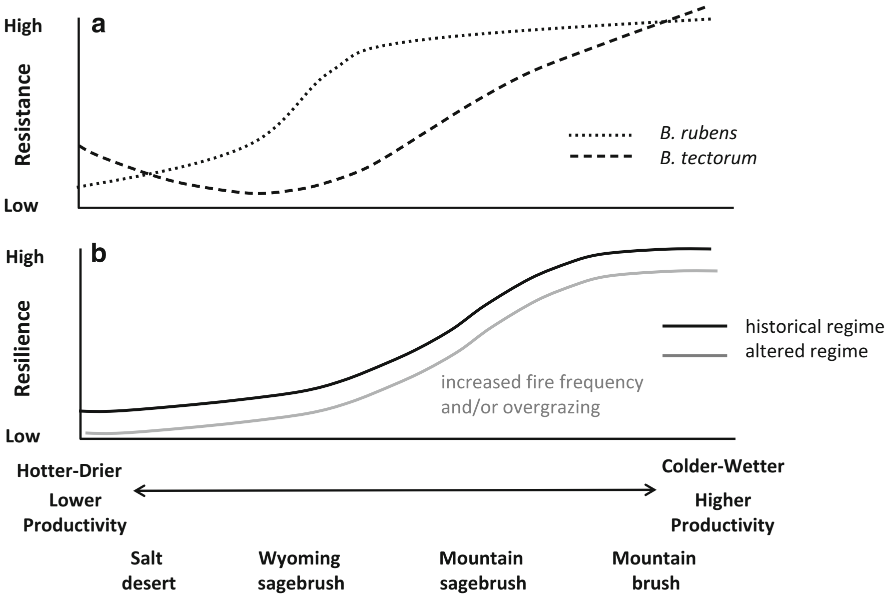

Fig. 2.10 Hypothetical (**a**) resistance to common *Bromus* species and (**b**) resilience to historical and altered fire regimes for the Cold Deserts ecoregion (primary altered regime characteristic labeled in *gray*). Figure modified from Chambers et al. (2014a)

and wildfires are burning for the first time in recorded history (Haubensak et al. 2009; Balch et al. 2013).

Low to mid elevations have warm and dry (mesic/aridic) to warm and moist (mesic/xeric) soil temperature and moisture regimes and are characterized by *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young (Wyoming big sagebrush) and to a lesser degree *A. tridentata* Nutt. ssp. *tridentata* (basin big sagebrush) vegetation types (West 1983a, b; Miller et al. 2011). Resistance to *B. tectorum* is low under these regimes, largely due to high climatic suitability for establishment and persistence (Fig. 2.10a) (Chambers et al. 2007, 2014a; Davies et al. 2012). *Bromus rubens* can occur on warmer and drier sites, especially at the lowest elevations (Salo 2005), but its distribution and relative abundance have not been well quantified. Resilience to disturbance and management treatments is low to moderately low (Fig. 2.10b) (Miller et al. 2013; Davies et al. 2012; Chambers et al. 2014a, b). Because the Cold Deserts represent more moderate climates, they also have high levels of anthropogenic disturbance (agricultural, urban and energy development, livestock, wild horse and burro grazing, off-highway vehicle and recreation use, etc.) which has increased the spread and dominance of *B. tectorum* (Knick et al. 2011). Progressive expansion of *B. tectorum* has increased fire frequency and size (Balch et al. 2013), and threshold transitions to annual grass dominance are highest in these vegetation types (Chambers et al. 2014a).

Upper elevations typically have cool and moist (frigid/xeric) to cold and moist (cryic/xeric) regimes and are characterized by *A. tridentata* Nutt ssp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush) and mountain brush (e.g., *Symphoricarpos* Duham. spp. [snowberry.], *Purshia tridentata* (Pursh) DC. [antelope bitterbrush]) vegetation types. Colder soil temperature regimes limit the amount of suitable niche space and increase resistance to *B. tectorum* invasion (Fig. 2.10a) (Chambers et al. 2007; Davies et al. 2012). Although *B. tectorum* can germinate at relatively low temperatures (Roundy et al. 2007), growth and reproduction under cool to cold (frigid to cryic) regimes are limited as indicated by low growth and reproduction (Chambers et al. 2007). At the warmer end of the gradient depletion of perennial herbaceous species due to either inappropriate livestock grazing or expansion of piñon and juniper trees can promote *B. tectorum* establishment following fire, but few of these systems become *B. tectorum* dominated (Chambers et al. 2014b). Favorable conditions for establishment and growth and relatively high levels of productivity result in moderate to high resilience on all but the coldest high elevation sites (Chambers et al. 2014a).

Slope, aspect, and soil characteristics modify soil temperature and water availability and influence occurrence of *B. tectorum* at landscape to plant community scales (Chambers et al. 2007; Condon et al. 2011; Reisner et al. 2013). At higher elevations with cooler soil temperatures, *B. tectorum* is found primarily on south facing slopes (Kulpa et al. 2012) with more solar radiation (Condon et al. 2011; Lovtang and Riegel 2012).

Seasonality of precipitation within the ecoregion also appears to influence establishment and persistence of *B. tectorum*. In the western portion of the ecoregion, most precipitation arrives in winter and spring months and climate suitability to

B. tectorum is high. Life history and physiological traits such as germination in early fall through winter (Mack and Pyke 1983) and high growth and nutrient uptake rates (James et al. 2011) make *B. tectorum* highly competitive with native plants. In the eastern portion of the ecoregion, summer precipitation is higher (ustic soil moisture regimes) and this competitive advantage appears to be greatly diminished (Bradley 2009), although establishment and persistence still can occur following disturbance (Bradford and Lauenroth 2006).

2.4.2 Ecosystem Threats to Cold Deserts from Bromus

The most widely cited effect of *Bromus* invasions in the Cold Deserts ecoregion is the alteration of fire regimes (Whisenant 1990; Brooks and Pyke 2001; Balch et al. 2013). The mechanisms of these changes in Cold Deserts are largely the same as those described for Warm Desert in Sect. 2.2 and the impacts are explained in more detail in Germino et al. (2015). Invasion of *B. tectorum* can also alter the size and dynamics of soil N pools, or the activity of the microbial community, with the type and magnitude of the effect depending on factors such as soil characteristics, plant community composition, and time since invasion (Rimer and Evans 2006; Hooker et al. 2008; Schaeffer et al. 2012). *Bromus* invasions can alter hydrologic conditions resulting in increased soil water recharge (Wilcox et al. 2012) which can decrease resistance to secondary invasion by deep-rooted forbs that mature later in the growing season (Kulmatiski et al. 2006). After wildfires, runoff and erosion can increase, particularly on steep slopes (>15 %) (Wilcox et al. 2012). Wind erosion also can occur after fire, resulting in redistribution or loss of nutrient-enriched soil fines and, under shorter fire return intervals caused by *Bromus*, homogenization of soil properties in Cold Deserts shrublands (Sankey et al. 2009).

Both resilience from disturbance and resistance to *Bromus* in the Cold Deserts are reduced by disturbances that decrease perennial species abundance and increase resource availability. Such disturbances include excessive livestock grazing and altered fire regimes, specifically increased fire frequency. Many of the dominant shrubs (e.g., *Artemisia* spp.) are not fire tolerant in the warmer and drier ecological types that are least resistant to *Bromus*. Plant establishment is often sporadic (Miller et al. 2013) even when these species are seeded (Knutson et al. 2014). More frequent fire coupled with increased competition due to invasion of *Bromus* and following livestock grazing too soon after reseeding can prevent native regeneration (Eiswerth and Shonkwiler 2006). Populations of *B. tectorum* often increase rapidly following fire or other disturbances that remove perennial native species and seed banks can grow to ≥20,000 seeds/m^2 within a few years (Humphrey and Schupp 2001; Meyer et al. 2007; Chambers et al. 2015). Typically small seed banks of most native species (Hassan and West 1986; Allen et al. 2008), coupled with low competitive ability of native seedlings with *B. tectorum* (James et al. 2011; Mazzola et al. 2011), can greatly decrease seedling establishment. Mature individuals of perennial herbaceous species, especially those with similar phenologies, are often strong competitors (Booth et al. 2003), but large individuals or populations of *B. tectorum* can reduce growth and seed production of these species. Decreases in perennial native species, especially grasses and forbs, biological soil crusts, and the distance between perennial herbaceous species (gaps) due to inappropriate livestock grazing or other disturbances are strongly associated with increases in *B. tectorum* across a range of ecological types (Chambers et al. 2007; Dettweiler-Robinson et al. 2013; Reisner et al. 2013; Pyke et al. 2015). Increasing plant community dominance of *B. tectorum* can alter species interactions, influence trophic interactions, and reduce species diversity (Germino et al. 2015). For example, increasing *B. tectorum* cover has a negative influence on nesting of *Centrocercus urophasianus* Bonaparte (greater sage-grouse) which has been considered for listing under the US Endangered Species Act of 1972 (Federal Register, 50 CFR Part 17), and on the abundance of *Spermophilus townsendii* Bachman (Townsend's ground squirrel) which is important prey for raptors and other predators (Yensen et al. 1992). Complete conversion to *B. tectorum* results in loss of shrub structure and shrubland-associated species like *Amphispiza belli* Cassin (sage sparrow) and an overall decrease in native species diversity (Earnst and Holmes 2012).

Ecosystem resilience to disturbances increases with increasing elevation, latitude, and associated primary productivity (Fig. 2.10). Because resistance to invasion follows a similar pattern, especially for *B. tectorum*, the net threat posed by this species differs with seasonality of precipitation, but is generally highest at low to mid productivity, and lowest in areas of higher productivity (Fig. 10.1, Chambers et al. 2015).

2.4.3 Management Strategies for **Bromus** *in Cold Deserts*

In the Cold Deserts, a suite of different vegetation management treatments are used to increase resilience to fire and other disturbances and to enhance resistance to invasive annuals (Chambers et al. 2014a). Primary objectives are to reduce woody fuel loads and thus fire severity and extent, decrease exotic annual species abundance and spread, and increase perennial herbaceous species dominance which both promote recovery after disturbance and compete with exotic annual plants. Treatments include various combinations of prescribed fire, mechanical treatment, and herbicide application to decrease sagebrush, piñon, and juniper abundance, herbicide application and grazing to control *Bromus*, and seeding with perennial herbaceous species and shrubs to restore native plant communities (Monsen et al. 2004; Pyke 2011). However, responses to these treatments often vary due to inherent differences in site resilience and resistance (Miller et al. 2013) and subsequent land use regimes (Eiswerth and Shonkwiler 2006). Knowledge of environmental factors, ecosystem attributes and processes, and disturbance and land use history effects that influence resilience and resistance (Fig. 1.1) can be used to determine appropriate management strategies at both site and landscape scales (Chambers et al. 2014a; Miller et al. 2013).

Fig. 2.11 (**a**) A fire that started along a major highway and burned through a sagebrush ecosystem with *B. tectorum* in the understory and into a Jeffrey pine ecosystem, Washoe County, Nevada. (**b**) Landscape conversion of a sagebrush ecosystem to *B. tectorum* and other exotic annual dominance following repeated fire, Humboldt County, Nevada. Photos by Nolan E. Preece

The degree of uncertainty increases and management options become increasingly limited with decreases in resilience to fire and management treatments and resistance to invasion. In cool and dry to cool and moist regimes with moderate to high resilience and resistance, a variety of management treatments like carefully timed grazing, prescribed fire, mechanical treatments, and herbicide applications can be used to maintain or improve ecological conditions. However, in warm and dry to warm and moist regimes, widespread invasion and increasing dominance of *Bromus* and other invaders have altered vegetation dynamics and often limit options. Largely irreversible thresholds can occur following either fire or management treatments if sufficient perennial herbaceous species for recovery are lacking (Fig. 2.11).

2.5 Western Great Plains

The Western Great Plains comprises shortgrass steppe and northern and southern mixed-grass prairie. The foothills of the Rocky Mountains form the western border (Lauenroth and Milchunas 1992; Coupland 1992) and tallgrass prairie the eastern border, which is a vegetation transition zone (Sims and Risser 2000) at approximately the 100th meridian (Van Dyne 1975). Temperatures in the ecoregion are cooler in the north than the south (frigid, mesic, thermic from north to south; Fig. 2.3c). The mean annual temperature in shortgrass steppe is 8.6 °C (Lauenroth 2008) and ranges from 8.2 °C in northern Colorado to 17.7 °C in western Texas and southeastern New Mexico (Lauenroth and Milchunas 1992). Likewise, mean annual temperatures in the mixed-grass prairie increase from north to south (3.6 °C in Saskatchewan to 12.9 °C in central Kansas) (Coupland 1992). A precipitation gradient runs perpendicular to the temperature gradient; it is drier in the west than the east (ustic aridic, aridic ustic, typic ustic from west to east; Fig. 2.3c). Annual precipitation in the shortgrass steppe of northern Colorado ranges from 300 to 400 mm on the west side to 500–600 mm on the east side (Lauenroth and Milchunas 1992) with mean annual precipitation of 321 mm (Lauenroth et al. 2008). Mean annual precipitation in the mixed-grass prairie ranges from around 300 mm near the shortgrass steppe to around 600 mm in the eastern transition zone to tallgrass prairie (Coupland 1992; Moran et al. 2014). There is a smaller gradient of precipitation from south to north ranging from around 430 mm in southern mixed-grass prairie to 340 mm in the northern mixed-grass prairie (Van Dyne 1975).

B. tectorum and *B. arvensis* are the two most common invasive *Bromus* that occur in the shortgrass steppe, although they are largely restricted to roadsides and disturbed areas such as old fields because intact native vegetation is highly resistant to invasion (Kotanen et al. 1998; Milchunas et al. 1992) (Fig. 2.13a). The shortgrass steppe is dominated by the short-stature, warm-season species *Bouteloua gracilis* Willd. ex Kunth) Lag. ex Griffiths (blue grama) and *Bouteloua dactyloides* (Nutt.) J.T. Columbus (buffalograss). The mid-height, cool-season grass *Pascopyrum smithii* (Rydb.) Á. Löve (western wheatgrass) is commonly associated with *B. gracilis* in the northern portion of the shortgrass steppe (Lauenroth and Milchunas 1992). This shifts to *B. gracilis* in association with *Sporobolus airoides* (Torr.) Torr. (alkali sacaton), *Pleuraphis jamesii* Torr. (James' galleta), and *B. dactyloides* toward the south (Lauenroth and Milchunas 1992).

Bromus tectorum and *B. arvensis* are also the most common invasive *Bromus* species in northern and southern mixed-grass prairie and are joined by *Bromus catharticus* Vahl (rescuegrass) and *Bromus secalinus* L (rye brome), but these species are of secondary dominance. *Bromus gracilis* remains a major component of the mixed-grass prairie, which comprises cool-season and warm-season species from tallgrass prairie and shortgrass steppe (Sims and Risser 2000). *Pascopyrum smithii* and *Hesperostipa* (Elias) Barkworth spp. (needlegrass) are codominant species with *B. gracilis* in the northern mixed-grass prairie (Van Dyne 1975). Other cool-season species such as *Carex* L. spp., *Elymus lanceolatus* (Scribn. & J.G. Sm.) Gould ssp. *lanceolatus* (thickspike wheatgrass), *Koeleria macrantha* (Ledeb.) Schult. (prairie Junegrass), and *Nassella viridula* (Trin.) Barkworth (green needlegrass) become more abundant in particular microsites. In the southern mixed-grass prairie, taller dominants are *P. smithii*, *Andropogon gerardii* Vitman (big bluestem), *Schizachyrium scoparium* (Michx.) Nash (little bluestem), and *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama), with *B. gracilis* and *B. dactyloides* as a lower layer in the canopy (Van Dyne 1975).

2.5.1 Invasion Potential of Western Great Plains by Bromus

The relative resistance of Western Great Plains ecosystems to invasion by exotic annual *Bromus* species can be attributed to adaptation of the native plants to the climate and characteristic disturbances of drought, fire, and grazing. Of the three subregions of the Western Great Plains, northern mixed-grass prairie appears to be least resistant to exotic annual *Bromus* invasion (Fig. 2.12). *Bromus arvensis* (Heitschmidt et al. 1995; Karl et al. 1999) and *B. tectorum* (Heitschmidt et al. 1995) can be dominant species in northern mixed-grass prairie. In Wind Cave National Park in South Dakota, occurrence of exotic annual *Bromus* species was associated with cool-season grasses such as *P. smithii* and *N. viridula* and the shrub *Symphoricarpos occidentalis* Hook. (western snowberry) and negatively associated with warm-season grasses, especially *A. gerardii*, *B. curtipendula*, and *S. scoparium*, and the shrub *Rhus aromatica* Aiton (fragrant sumac) (Ogle and Reiners 2002).

Data from the U.S. National Park Service Northern Great Plains Network indicate that higher cover of *Bromus* can be associated with lower native species richness, but only in the South Prairie region of the network where *Bromus* cover is highest (Fig. 2.14). This is especially true at Scotts Bluff National Monument in northwestern Nebraska, Badlands National Park in southwestern South Dakota, and Fort Laramie National Historic Site in southeastern Wyoming where *Bromus* cover was repeatedly measured in excess of 30 % (Fig. 2.14) as illustrated in the foreground of Fig. 2.13d. This pattern was not exhibited at Agate Fossil Beds National

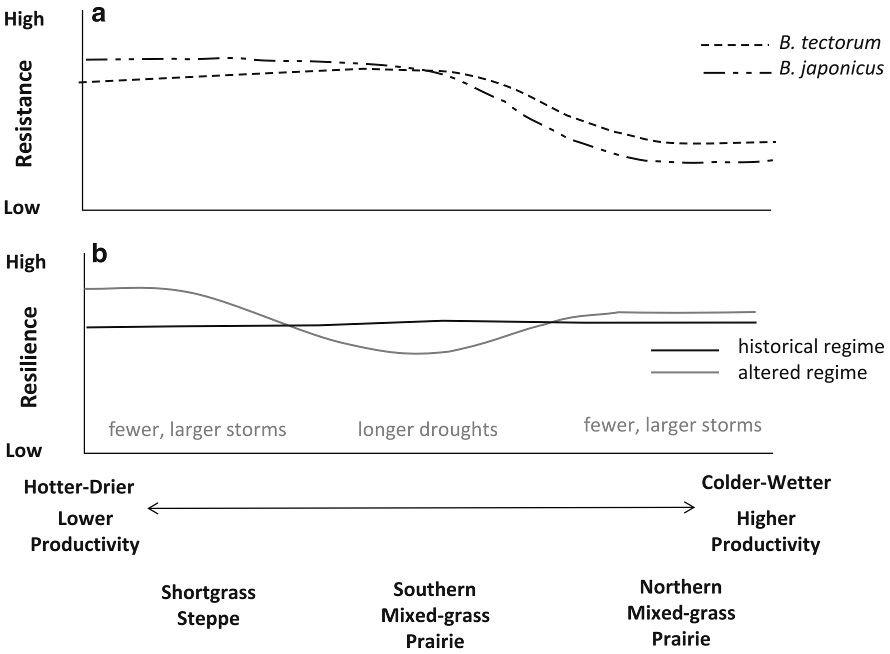

Fig. 2.12 Hypothetical (**a**) resistance to common *Bromus* species and (**b**) resilience to historical and altered fire regimes for the Western Great Plains ecoregion (primary altered regime characteristic labeled in *gray*)

Monument (Fig. 2.13c), or elsewhere in the Northern Great Plains where *Bromus* cover rarely exceeded 10 % *Bromus* cover (Fig. 2.14).

Resistance to invasion by exotic annual *Bromus* species of southern mixed-grass prairie may be as high as in shortgrass steppe (Fig. 2.12). Although *B. catharticus*, *B. arvensis*, and *B. tectorum* occur in Oklahoma (Bidwell et al. 2004), none of the fact sheets for managing invasive species published by the Oklahoma Cooperative Extension Service are about exotic annual grasses or mention them as being problems (http://www.oces.okstate.edu/extension-fact-sheets, accessed 6 Jan 2015). The invasive species of concern are all shrubs and subshrubs (Cummings et al. 2007; Bidwell et al. 2009).

Drought has been a common feature of the Western Great Plains climate (Coupland 1992), where potential evaporation exceeds precipitation (Sims and Risser 2000). Many long-term studies found weather to be a more important influence on vegetation response than grazing or burning treatments (Teague and Dowhower 2003; Teague et al. 2004, 2010; Heitschmidt et al. 2005; White and Loftin 2000; Vermeire et al. 2008, 2014). Modeling efforts by Bradford and Lauenroth (2006) indicate that climate is a stronger influence on invasion of *B. tectorum* than soil characteristics. Bradley (2009) found that two of the strongest predictors of improved habitat suitability for *B. tectorum* in the Great Basin region

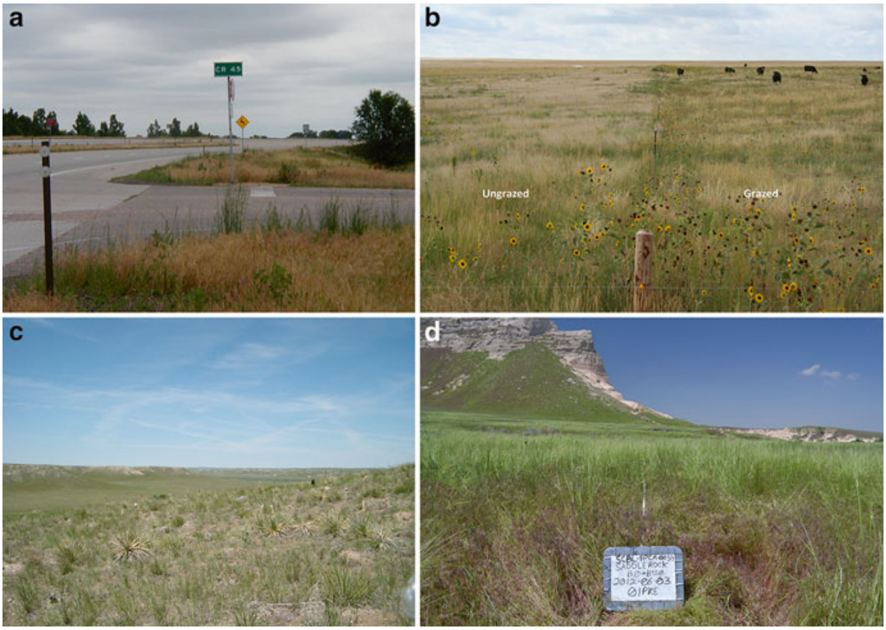

Fig. 2.13 (**a**) Typical *B. tectorum* invasion of roadsides in the shortgrass steppe ecosystem, Weld County, Colorado. Photo by CS Brown. (**b**) Conservation Reserve Program land 3 years after seeding with native species. Increased beige vegetation on *left* side of fence is *B. tectorum*. Photo by M Vandever. (**c**) Little or no *Bromus* at Agate Fossil Beds National Monument. Photo by US Geological Survey. (**d**) Aerial cover at this site in Scotts Bluff National Monument is 60 % *B. tectorum* and 10 % *B. arvensis*. Photo by US National Park Service

were decreased annual and summer precipitation. This suggests that the normal pattern of summer precipitation in the Western Great Plains creates conditions unfavorable to *Bromus* and drought could improve their success. However, it does not appear that drought alone (see Van Dyne 1975; Munson and Lauenroth 2009; Moran et al. 2014) or in combination with grazing (Heitschmidt et al. 1999, 2005; Eneboe et al. 2002) has reduced resistance of these grasslands to invasion by *Bromus*.

Grazing of ungulates has always been important in the Great Plains, which was once inhabited by 2–4 million bison (*Bison bison*) and other grazing and browsing ungulates (Van Dyne 1975). As a result, this ecoregion is resilient to grazing (Vermeire et al. 2008). The abundances of *Bromus* and other weedy plants can be reduced (Fig. 2.13b) (Milchunas et al. 1992, 2011; Harmoney 2007; Vermeire et al. 2008) or remain unaffected by grazing, even in combination with drought (Heitschmidt et al. 1999, 2005).

Fire is a natural disturbance in the Western Great Plains and has either no effect on or reduces aboveground productivity (Scheintaub et al. 2009). Herbaceous productivity of shortgrass steppe (Ford and Johnson 2006; Augustine and Milchunas

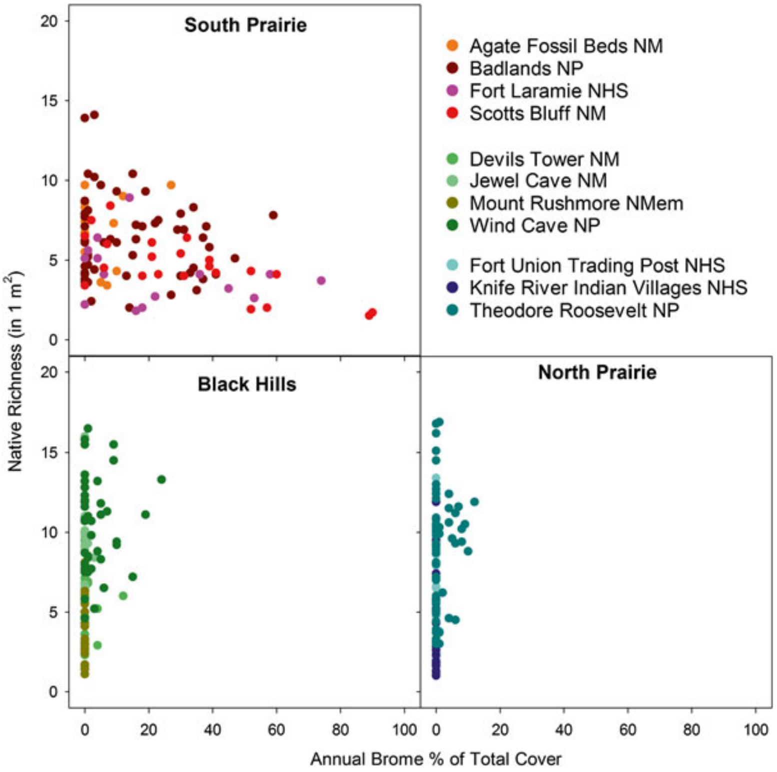

Fig. 2.14 In southern Northern Great Plains Network prairie parks, plots with high cover of *Bromus* have lower native plant species richness than plots with little *Bromus* cover. NM = National Monument; NP = National Park; NHS = National Historic Site; NMem = National Memorial. (Courtesy of the National Park Service, Northern Great Plains Network Inventory and Monitoring Program)

2009; Augustine 2010), northern mixed-grass prairie (Whisenant and Uresk 1990; Vermeire et al. 2011), and southern mixed-grass prairie (Whisenant et al. 1984; Ford and White 2007; Teague et al. 2008, 2010; Vermeire et al. 2014) may be unaffected by fire or can recover productivity and species composition within 6 months to 2 years of burning, depending on precipitation amounts during the recovery period (Teague et al. 2008; Augustine and Milchunas 2009). Grazing is often reported not to alter the effects of fire (Augustine et al. 2010; Vermeire et al. 2014). Not only do these ecosystems have high resilience to fire, but fire either reduces (Whisenant and Uresk 1990; Scheintaub et al. 2009; Teague et al. 2010; Vermeire et al. 2011, 2014) or does not affect (Teague and Dowhower 2003; Augustine and Milchunas 2009; Augustine et al. 2014) abundance of *Bromus*. However, in some cases when *Bromus* were initially reduced by spring burning, they increased in abundance the second year after the burn (Whisenant et al. 1984).

2.5.2 Ecosystem Threats to Western Great Plains from **Bromus**

Although several *Bromus* are considered invasive in the Western Great Plains, they are neither as widespread nor have they had the extensive, ecosystem altering effects documented in some other ecoregions. Even though the Western Great Plains is relatively resistant and resilient to invasion by *Bromus*, invasions can effect change in some circumstance. For example, *Bromus* can reduce the growth of native plants in northern mixed-grass prairie (Haferkamp et al. 1997, 1998; Ogle et al. 2003). Ogle et al. (2003) found *Bromus*-dominated northern mixed-grass prairie had lower above- and belowground biomass, slower decomposition, and sometimes greater litter than native vegetation. Modeling of *B. arvensis* and *B. tectorum* in northern mixed-grass prairie found non-significantly greater carbon storage with high *Bromus* cover, but the differences continued to diverge after 50 years and may become large in the future (Ogle et al. 2004).

Resilience of ecosystems to disturbance and resistance to invasion can be altered when historically normal patterns of disturbance change (Germino et al. 2015). The absence rather than presence of grazing, fire, or both represents disturbances for Western Great Plains grasslands (Milchunas et al. 1992; Haferkamp et al. 1993; Adler and Lauenroth 2000; Brockway et al. 2002; Ford and Johnson 2006; Vermeire et al. 2011) and may facilitate invasion by *Bromus* (Milchunas et al. 1992, 2011). Fire frequencies in the Western Great Plains may increase as a result of accumulation of fuels due to fire suppression (Brockway et al. 2002; Garfin et al. 2014) and increased lightning strikes due to climate warming (Romps et al. 2014).

As explained above, weather is an important determinant of productivity and composition of Western Great Plains grasslands. Thus, changes in climate may influence resistance of Western Great Plains ecosystems to *Bromus* invasion (Fig. 2.12). More frequent high temperatures and extreme heat are predicted for the region (Walsh et al. 2014). *Bromus tectorum* reportedly increases with temperature in northern mixed-grass prairie (Blumenthal et al., unpublished data). Longer periods between storms are predicted for much of Texas and Oklahoma (Walsh et al. 2014), which may decrease its resilience to disturbance and resistance to *Bromus* invasion (Fig. 2.12). Models that assume continued increases in heat trapping greenhouse gases predict that winter and spring precipitation and days with heavy rain will increase in the northern part of the Great Plains (Walsh et al. 2014). Changes such as these are not likely to reduce resilience to disturbance and may increase resilience in more water-limited shortgrass steppe (Fig. 2.12).

The drought in the early 2000s resulted in conditions similar to predicted future climates (Moran et al. 2014). Western Great Plains grasslands had linear responses to current year total precipitation and previous year productivity (Moran et al. 2014). No new species assemblages (e.g., dominance of *Bromus*) emerged in response to the drought (Moran et al. 2014). The system appears to be buffered against changes predicted in the next 50 years (Symstad et al. 2014), but it remains to be seen how far the climate system can be pushed before the biotic components of the ecosystem can no longer respond sufficiently to be sustained.

2.5.3 Management Strategies for **Bromus** *in Western Great Plains*

Bromus invasions can be prevented and minimized throughout the ecoregion by conserving intact grasslands and applying reasonable levels of grazing and burning to maintain their integrity and resistance to invasion. The Western Great Plains ecosystems are currently most threatened by large-scale disturbances such as conversion to cultivated agriculture, urban development, and oil and gas exploration and development, all of which may foster *Bromus* dominance.

Management beyond good stewardship of the ecosystem can focus first on containing and then eliminating *Bromus* where it occurs. Herbicides that control *Bromus* with minimal negative effects on native species can be effectively used alone (Hewlett et al. 1981; Haferkamp et al. 2001) or in combination with burning (Masters et al. 1992; Calo et al. 2012). *Bromus* populations can be managed by reducing seed production through well-timed grazing, mowing, or burning (e.g., Fig. 2.13b) (Vermeire et al. 2008; Milchunas et al. 2011) or application of growth regulator herbicides used for broadleaf weed control (Rinella et al. 2010a, b, 2013).

2.6 Western Forests

The Western Forests range from the Marine West-Coast Forest to the Northwestern Forested Mountains Level I EPA ecoregions and are characterized by a very diverse range of environmental conditions. Collectively, they represent some of the coolest and wettest conditions in the western United States (Fig. 2.3). Soil temperature regimes are generally cryic or frigid in the east and north, but can also be mesic and even thermic to the west and south. These conditions combined with high precipitation are conducive to the growth of forests with relatively high canopy and surface cover of perennial vegetation and high accumulations of litter and duff. Shrublands or grasslands occur as early successional patches following disturbances that remove forest canopy cover, and where productivity levels are relatively low due to shallower soils or warmer and drier soil temperature and moisture regimes (Fig. 2.15).

Bromus species are generally not considered among the highest priority invasive plants in the Western Forests. In fact, one recent review of the impacts of exotic invasive species in US forests did not even mention *Bromus* (Moser et al. 2009). The exception are patches of chaparral and grasslands (Fig. 2.15) within ponderosa pine and Jeffrey pine mixed conifer forests (Pierson and Mack 1990; Keeley and McGinnis 2007). In these situations, soils are more frequently exposed to sunlight and warmer and drier conditions facilitate establishment, growth, and reproduction of *Bromus*. *Bromus tectorum* is the most widespread and abundant *Bromus* in these ecoregions, but *B. diandrus* can also occur within grassland and chaparral forest openings.

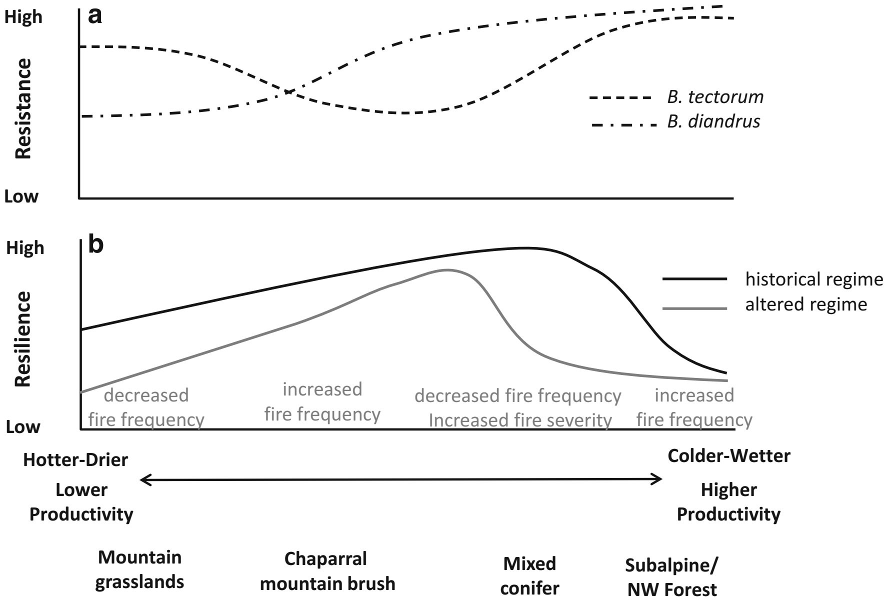

Fig. 2.15 Hypothetical (**a**) resistance to common *Bromus* species and (**b**) resilience to historical and altered fire regimes for the Western Forests ecoregion (primary altered regime characteristic labeled in *gray*)

2.6.1 Invasion Potential of Western Forests by Bromus

Forests with cool to cold temperature regimes have low climatic suitability to *Bromus*. Also, forests with high amounts of canopy cover that accumulate large amounts of litter and duff in the understory and create low light conditions at the soil surface have limited establishment and growth of annual plant species. Drier and warmer mixed conifer, Jeffrey pine, and ponderosa pine forests that have less canopy cover and lower litter and duff accumulation are generally less resistant to *Bromus* than subalpine and northwestern forests due to lower levels of productivity and higher frequency of fire (Fig. 2.15).

Fire events that remove forest canopy, especially high severity fire, are often associated with decreased resistance to *Bromus* in climatically suitable forests (Crawford et al. 2001; Keeley and McGinnis 2007; McGlone et al. 2009; Fornwalt et al. 2010; Kerns et al. 2011). Decreased resistance is partly due to increased light availability at the soil surface, but also may be affected by increased availability of soil nutrients. Biomass of *B. tectorum* beneath *Pinus ponderosa* Lawson and C. Lawson (ponderosa pine) trees can be limited by low N availability. Fire can increase available nutrients due to deposition of ash onto the soil surface, release of available P and N from organic matter, and decomposition of belowground biomass and result in increases in *B. tectorum* growth and reproduction (Covington and Sackett 1992; Monleon et al. 1997; Gundale et al. 2005, 2008). Also, charcoal generated by fire may adsorb phenolic compounds from pine litter inputs which can otherwise impede understory plant growth (Gundale and DeLuca 2006, 2007), and increase nitrification rates, further increasing the amount of plant available N in the soil following fire (DeLuca et al. 2006).

High severity human disturbances such as clear-cut logging can similarly decrease resistance of landscapes. Recruitment, survival, and reproduction of *B. tectorum* can all be higher in clear-cuts across a range of western forest types including those dominated by *P. ponderosa*, *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), *Abies grandis* (Douglas ex D. Don) Lindl. (grand fir), and *Thuja plicata* Donn ex D. Don (western redcedar) (Pierson and Mack 1990). Lower severity understory thinning can also decrease resistance to *B. tectorum* in these forest types, but only where significant understory cover of *B. tectorum* was present before thinning. Even lower severity human disturbances such as cattle grazing occurring at light intensity and short duration can lead to increased cover of *B. tectorum* in ponderosa pine forests under drought conditions (Sorensen and McGlone 2010), possibly due to competitive release of other vegetation such as *Elymus elymoides* (Raf.) Swezey (bottlebrush squirreltail) and *P. smithii* caused by preferential grazing by cattle.

Removal of litter and coarse woody debris can increase exposure of mineral soil and the probability that *Bromus* seeds can make contact with the soil and germinate (Pierson and Mack 1990; Keeley and McGinnis 2007; Gundale et al. 2008). This is partly due to the litter creating a physical barrier preventing seeds from coming into contact with mineral soil, but also may be due to phenolytic compounds in new pine litter that can inhibit germination.

Lower temperature limits may limit the upper elevation sites attainable by *Bromus* species (Fig. 2.2a), but climate change is increasingly recognized as a mechanism by which high elevation habitats such as Western Forests may become increasingly more invasible (Pauchard et al. 2009). There is evidence suggesting that *B. tectorum* already exhibits the ability to adapt to higher elevation sites (Rice and Mack 1991; Leger et al. 2009), and climatic warming may further reduce the resistance of these habitats to *Bromus* invasion (Compagnoni and Adler 2014). Rising CO_2 has also been shown to increase *B. tectorum* productivity through increased water use efficiency in Cold Deserts shrublands (Smith et al. 1987), and the operative mechanism could further promote growth at higher elevations as they warm.

2.6.2 Ecosystem Threats to Western Forests from **Bromus**

It is unclear how much of a threat *Bromus* pose to Western Forests compared to other ecoregions of the western United States. No doubt *Bromus* can have some of the same effects documented for other ecoregions, such as direct competition with other plant species. They may even affect landscape susceptibility to fire by producing continuous fuelbeds at least where the forest canopy does not overshadow and inhibit their growth (e.g., Fig. 2.16). However, the potential for *Bromus* species to alter fire regimes (i.e., fire frequency, severity, seasonality, etc.) in Western Forests is more difficult to discern.

Many of the lower elevation forests that are most susceptible to invasion by *Bromus* (e.g., ponderosa pine) are also evolutionarily suited to fire return intervals as short as once every 2 years (reviewed by Hurteau et al. 2013). So if *Bromus* species, *B. tectorum* in particular, has the potential to increase landscape flammability and promote recurrent fire, is it reasonable to think that they might promote such short intervals that even these fire-adapted forests cannot persist? The general consensus is that they could, especially in areas where anthropogenic activities increase ignition sources and promote productivity of *Bromus*, thus enhancing their competitive suppression of regenerating forest species and their contributions to highly flammable fuelbeds (McGinnis et al. 2010; Hurteau et al. 2013). As explained above in Sect. 2.6.1, as the climate increasingly warms, resistance of Western Forests to invasion by *Bromus* will likely decrease. When this decreased resistance is coupled with increased frequency of large fires (Westerling and Bryant 2008) and length of the fire season (Westerling et al. 2006), the potential for *Bromus* to alter fire regimes in Western Forests may become more likely.

Fig. 2.16 *Bromus tectorum* dominating a landscape 6 years after a high severity fire in a previous conifer forest stand (Star Fire, Tahoe National Forest, 2001). Note the conifer recruitment in the *upper right* side of this image despite the high cover of *B. tectorum* (photo by Jon Keeley, 22 June 2007)

2.6.3 Management Strategies for **Bromus** *in Western Forests*

Prevention and control of *Bromus* in the Western Forests have not be evaluated to the degree they have in other ecoregions, most notably in the Cold Deserts and Mediterranean California. Strategies developed in those regions should be generally applicable to the Western Forests, although there are some unique characteristics of Western Forests that lend themselves to approaches only possible in this ecoregion. For example, litter and duff can rapidly accumulate on the forest floor, which can suppress *B. tectorum* germination (Keeley and McGinnis 2007). However, some of the principles that have been applied to restore historical fire regimes where fire suppression and fuel accumulation have altered them may reduce litter and forest canopy cover, which could inadvertently improve conditions for *Bromus* species. Some of these include reducing surface and ladder fuels, decreasing crown density, and maintaining widely spaced large trees. Forest managers are challenged to find an effective balance between the restoration of historical fire regimes and the suppression of invasive plants such as *Bromus*, thus maximizing resilience to fire and resistance to invasion. Management of *Bromus* invasion should be linked with maintaining historical ecosystem structure and function, which may entail suppressing or facilitating fire, or reducing fire severity (e.g., by pre-fire fuels manipulations), as dictated by the historical fire regimes and current condition of local areas.

2.7 Management Implications

This chapter explained that invasion potential, ecosystem threats, and management strategies for *Bromus* vary both within and among ecoregions and vegetation types, and among *Bromus* species. In particular, it should not be assumed that just because a particular *Bromus* is documented to pose a significant threat in one ecoregion or vegetation type, that other *Bromus* will pose similar threats to other ecoregions or vegetation types. Variation among ecoregions and vegetation types in ecosystem resistance to *Bromus* invasion, and resilience to disturbance, can be used to explain the conditions associated with high probability of ecosystem impacts such as an altered fire regime caused by a grass/fire cycle.

A strategic, landscape-scale management approach that includes protection, prevention, and restoration (e.g., Brooks and Chambers 2011; Chambers et al. 2014a) can be used to better focus management activities across the environmental/productivity gradients in the western United States. Protection focuses on maintaining or increasing the resilience and resistance of ecosystems with high conservation value by eliminating or minimizing current and future stressors. Protection is a viable strategy for intact communities within ecosystem types that have inherently low resistance and resilience such as blackbrush ecosystems in the Warm Deserts and salt desert and warmer Wyoming big sagebrush ecosystems in the Cold Deserts. Protection may also be a viable strategy for critical habitat for threatened and endangered species that are sensitive to *Bromus* invasions and their associated impacts.

Prevention involves increasing both resilience and resistance of ecosystems that have not crossed thresholds, but that exhibit declining conditions and are at risk of high severity fire and invasion (Miller et al. 2013). The focus is on ecosystems with higher resilience, like cooler and moister *A. tridentata* ecosystems in the Cold Deserts (Fig. 2.10) and mixed conifer ecosystems of the Western Forests (Fig. 2.15). Management objectives are to improve or maintain ecosystem attributes and processes by reducing woody species dominance and promoting a functionally diverse community of shrubs, perennial grasses, and forbs.

Restoration involves increasing resilience and resistance of disturbed, degraded, or invaded areas by reestablishing functionally diverse plant communities. Integrated management strategies that include using herbicides to control/suppress *Bromus* and seeding perennial herbaceous and shrub species adapted to local conditions may be used to restore priority areas dominated by *Bromus* and other annual invaders (Monaco and Sheley 2012). Restoration activities that target relatively moister sites are likely to be more successful, and even then repeated intervention may be required. As the climate warms, it may be necessary to consider transformative restoration in areas with novel climates in which species are established that are climatically suitable but that have not occurred on a given landscape historically (Bradley et al. 2010).

2.8 Research Needs

This chapter indicates that patterns of ecological resistance to *Bromus* invasions have been well documented in the western United States, especially related to presence/absence of *B. tectorum* and *B. rubens* in the Cold Deserts, Mediterranean California, and Warm Desert Ecoregions. What is less understood are the patterns of relative abundance (e.g., cover or biomass) of these and other *Bromus*, and the ecological mechanisms associated with these patterns. Also, the range of conditions associated with the grass/fire cycle have only been studied in depth within these same three ecoregions, and even within them there is limited capacity to predict when and where they will establish. A framework exists for objectively evaluating the grass/fire cycle potential (Brooks 2008) which can be systematically applied to each major vegetation types within each ecoregion to better understand when and where *Bromus* invasions pose the threat of altering fire regimes. This information is needed to more reliably predict potential future conditions of spread, dominance, and ecological impact by *Bromus* species within each ecoregion of the western United States.

The relative resistance to invasion by the dominant *Bromus* species and resilience to fire of each of five major ecoregions in the western United States were presented in Figs. 2.4, 2.7, 2.9, 2.11, and 2.14. In the introduction to this chapter, we emphasized that the degree to which scientific studies supported these models varies widely among ecoregions, and we suggested that the conservative approach would be to consider them hypothetical models. We feel confident with the scientific support for the Cold Desert and Warm Desert models, but encourage others to develop studies to test the predictions of all five ecoregional models. The refinement and validation of these models would improve their reliability and utility in evaluating the relative potential for invasion and ecological impact of *Bromus* in the western United States.

Appendix

See Table 2.2.

Table 2.2 GrassPortal (www.grassportal.org, accessed 16 Feb 2015, Osborne et al. 2011) site localities used to construct Fig. 2.2

	B. arvensis (=*japonicus*)	*B. hordeaceus*	*B. diandrus* (=*rigidus*)	*B. madritensis*	*B. rubens*	*B. tectorum*
Arizona	82	36	108	4	377	183
California	104	979	934	220	1109	664
Colorado	59	3	1	0	1	121
Idaho	31	16	2	0	10	48
Kansas	220	7	0	0	0	266
Montana	45	14	0	0	0	77
Nebraska	50	0	0	0	0	98
Nevada	8	7	9	0	4	25
New Mexico	45	1	9	0	11	61
North Dakota	0	0	0	0	0	34
Oklahoma	36	0	0	0	0	22
Oregon	40	55	71	2	35	141
South Dakota	7	1	0	0	0	36
Texas	89	8	6	0	4	30
Utah	31	10	9	0	13	45
Washington	27	12	92	0	4	113
Wyoming	23	39	0	0	0	40
Sum	897	1188	1241	226	1568	2004

Data Provider	**Dataset**
USDA PLANTS	USDA PLANTS Database
Consortium of California Herbaria	Consortium of California Herbaria
University of Arizona Herbarium	UA Herbarium
Arizona State University, International Institute for Species Exploration	Arizona State University Vascular Plant Herbarium
University of Connecticut	CONN GBIF data
Berkeley Natural History Museums	University and Jepson Herbaria DiGIR provider
New Mexico Biodiversity Collections Consortium	New Mexico Biodiversity Collections Consortium database

(continued)

Table 2.2 (continued)

Data Provider	Dataset
Missouri Botanical Garden	Missouri Botanical Garden
Utah Valley State College (UVSC)	Utah Valley State College Herbarium
University of Kansas Biodiversity Research Center	Botany Vascular Plant Collection
Oregon State University	Vascular Plant Collection
University of Washington Burke Museum	Vascular Plant Collection – University of Washington Herbarium (WTU)
Bernice Pauahi Bishop Museum	Bishop Museum Natural Sciences Data
University of Alabama Biodiversity and Systematics	Herbarium (UNA)
Colorado State University Herbarium (CSU)	Colorado State University Herbarium
National Museum of Natural History	NMNH Botany Collections
Canadian Museum of Nature	Canadian Museum of Nature Herbarium
University of Colorado Museum of Natural History	Specimen Database of Colorado Vascular Plants
The New York Botanical Garden	Herbarium of The New York Botanical Garden

The 17 states represent the ecoregions of the western United States (Fig. 2.1). The seven *Bromus* species are represented by state site records spanning their current distributional range as indicated by the USDA Plants database (www.plants.usda.gov, accessed 18 Feb 2015). The 19 data providers represent the original sources of information for the database used in Fig. 2.2

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