

Chapter 8

Soil Moisture and Biogeochemical Factors Influence the Distribution of Annual *Bromus* Species

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Abstract Abiotic factors have a strong influence on where annual *Bromus* species are found. At the large regional scale, temperature and precipitation extremes determine the boundaries of *Bromus* occurrence. At the more local scale, soil characteristics and climate influence distribution, cover, and performance. In hot, dry, summer-rainfall-dominated deserts (Sonoran, Chihuahuan), little or no *Bromus* is found, likely due to timing or amount of soil moisture relative to *Bromus* phenology. In hot, winter-rainfall-dominated deserts (parts of the Mojave Desert), *Bromus rubens* is widespread and correlated with high phosphorus availability. It also responds positively to additions of nitrogen alone or with phosphorus. On the Colorado Plateau, with higher soil moisture availability, factors limiting *Bromus tectorum* populations vary with life stage: phosphorus and water limit germination, potassium and the potassium/magnesium ratio affect winter performance, and water and potassium/

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magnesium affect spring performance. Controlling nutrients also change with elevation. In cooler deserts with winter precipitation (Great Basin, Columbia Plateau) and thus even greater soil moisture availability, *B. tectorum* populations are controlled by nitrogen, phosphorus, or potassium. Experimental nitrogen additions stimulate *Bromus* performance. The reason for different nutrients limiting in dissimilar climatic regions is not known, but it is likely that site conditions such as soil texture (as it affects water and nutrient availability), organic matter, and/or chemistry interact in a manner that regulates nutrient availability and limitations. Under future drier, hotter conditions, *Bromus* distribution is likely to change due to changes in the interaction between moisture and nutrient availability.

Keywords Climate • Geomorphology • Nitrogen • Nutrients • Phosphorus • Soils

8.1 Introduction

Despite much research, we still know little about what makes arid and semiarid (hereafter referred to as dryland) ecosystems susceptible to invasion by exotic annual grasses such as *Bromus tectorum* (L.) and *Bromus rubens* (L.) (Fig. 8.1). Because annual grasses are often associated with soil surface disturbance, this is

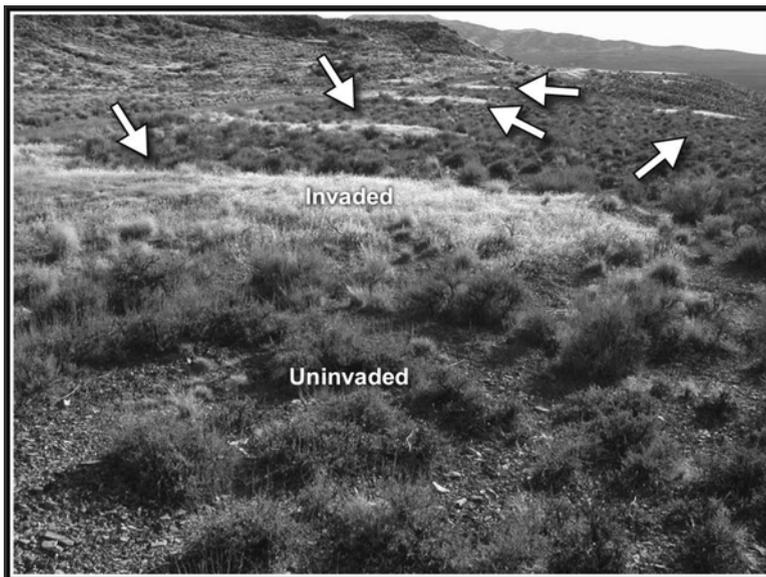


Fig. 8.1 Unless the invasion is a result of fire, annual grass invasions in the drier parts of the Western USA often occur in distinct patches (as indicated by *arrows*) as can be seen in this photo (taken adjacent to the Great Salt Lake on lacustrine sediments from Lake Bonneville)

thought to be the factor most responsible for such invasions (Hobbs and Huenneke 1992). However, invasive annual grasses are also able to establish in relatively undisturbed communities yet not always occur in disturbed sites (Tausch et al. 1994; Belnap and Phillips 2001), indicating there are other factors influencing ecosystem invasibility.

In this chapter, we explore the potential role of soil biogeochemical factors in controlling the distribution of *B. tectorum* and *B. rubens* (*B. madritensis* ssp. *rubens*) in the mid- and lower-elevation semiarid and arid lands of the Western USA. We review the literature and other data on how water and nutrient availability, as influenced by climate, controls the spread and range extent of exotic annual *Bromus* (*Bromus* hereafter). We examine studies correlating *B. tectorum* and *B. rubens* distribution in five regions where these plants occur in the Western USA: the Chihuahuan Desert, the Mojave Desert, the Colorado Plateau Desert, the Great Basin/Columbia Plateau Deserts, and the California coastal sage scrub. All these regions have different climatic regimes, which likely influence the ability of these species to establish and thrive (Table 8.1). The Chihuahuan is a hot desert with the majority of rainfall occurring during summer, whereas the Mojave Desert is a hot desert with predominantly winter precipitation. The Colorado Plateau and Great Basin/Columbia Plateau Deserts are both much cooler. The Colorado Plateau receives both summer and winter precipitation, whereas the Great Basin/Columbia Plateau regions receive almost exclusively winter precipitation. We end the chapter with a hypothesis on how soils and climate may interact to limit cover of *Bromus* throughout the low elevations of the Western USA.

8.2 Soil Nutrient Availability and Water in Dryland Settings

Plants require nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), sulfur (S), and calcium (Ca) in large amounts, which are thus considered macronutrients, whereas essential nutrients needed in small quantities (e.g., manganese [Mn], zinc [Zn], copper [Cu], and iron [Fe]) are called micronutrients (Marschner 1995).

Table 8.1 Climate regimes of the different regions of Western US semiarid and arid lands

	Mean annual temperature (C)	Mean annual precipitation (mm)	Timing of most precipitation
Columbia Plateau	4–14	230–380	Spring and fall
Colorado Plateau	5–17	150–400	Summer and winter/early spring
Great Basin	6–11	150–300	Winter
California coastal sage scrub	17–22	260–300	Late fall to early spring
Mojave	17–33	130–160	Winter
Chihuahuan	19–24	150–400	Summer

Years of research on plant nutrition has demonstrated that annual plants, including annual *Bromus*, require higher levels of available soil nutrients on a shorter timescale than perennial plants, because annuals require all of the nutrients necessary to complete their life cycle within a single season, whereas perennial plants can store and recycle nutrients in plant tissue for use during successive years (Epstein 1961). Because many soils in dryland regions contain low levels of many essential nutrients, they may be less or not invasible by annual *Bromus* plants compared to other sites with higher levels of soil nutrients.

Dryland soils generally have low levels of N. As N is often limiting to plants, most studies have focused on N as the nutrient likely to be most limiting for *Bromus*. Higher N in both lab and field settings (e.g., postfire or removal of perennials) has generally elicited a positive response in *Bromus* (see below; Chambers et al. 2007; Rau et al. 2014). Nitrogen can be measured as total or available pools (e.g., nitrate, ammonium), and the relationship with *Bromus* has been shown to be positive and negative regardless of the form measured (see text below). Desert soils can also have low levels of total P, or the P present can be biotically unavailable to plants as it readily forms insoluble precipitates with calcium, often found in great abundance in desert soils as calcium or magnesium carbonates (CaCO_3 , MgCO_3 , respectively; we refer to CaCO_3 and MgCO_3 collectively in terms of their acid-neutralizing potential or ANP). As P is an essential macronutrient, low P availability can also be highly limiting to desert plants (Schlesinger et al. 1989; Parker 1995). Many fewer studies have addressed the role of P in *Bromus* compared to N. Micronutrients can also be very important in dryland soils; for instance, Mn can alleviate salt stress in plants (Krishnamurti and Huang 1988), yet almost no studies have addressed the role of micronutrients in *Bromus* invasions. Interactions among nutrients can also be critical in determining their bioavailability. Higher K can increase N uptake (Dibb and Thompson 1985) and is also linked to increased Mn availability (Krishnamurti and Huang 1988). These nutrient interactions may be especially important to annual plants. For example, Scott and Billings (1964) observed that soils with high K/Mg ratios were dominated by annual plants, whereas soils with low K/Mg ratios were dominated by perennials.

Soil texture has several ways in which it regulates water and nutrient availability that can influence establishment and growth of annual *Bromus* (Miller et al. 2006a, b). First, it affects soil moisture availability. When rain events are large, infiltration can be greater in sandy soils than fine-textured soils, as incoming water drains down and away from the surface, thus out of the evaporative zone, whereas in finer-textured soils, water is held closer to the surface and thus evaporates more readily (Sala et al. 1988). This increased evaporative loss of water from fine-textured soils can also concentrate salts at the soil surface, which can increase plant water stress. Decomposition and nutrient transformations that increase soil nutrient bioavailability require moisture. Nutrient uptake by plants can only occur when soils are moist (Leffler and Ryel 2012). Water is required by plants and very high temperatures that result in high evapotranspiration rates and thus low soil moisture limit where plants grow, especially annuals with shallow root systems. Precipitation timing also interacts with soil texture to determine soil moisture, as rain falling at high summer

temperatures evaporates more quickly than rain falling during cooler winter temperatures.

On the other hand, finer-textured soils are usually more fertile than sandy soils, as nutrients adsorbed to the fine particles are prevented from leaching downward out of plant root zones. In addition, finer-textured soils tend to accumulate greater concentrations of soil organic matter (SOM) (Nichols 1984), which acts as a reservoir for plant nutrients.

Soils form from weathered parent material present *in situ* (i.e., bedrock) and include materials deposited by wind or water. Soil characteristics (e.g., texture, nutrients) thus depend to a large degree on parent material type and degree of weathering. Soils from parent materials with high nutrient content may initially have similar nutrient levels; however, over time, many nutrients may leach downward into the subsoil, where they precipitate as insoluble and plant-unavailable forms, or they may be transported downslope by erosional processes. Longer weathering times result in finer-textured soils. Soils farther from mountain sources also tend to be finer textured than upslope soils because the finer, lighter particles stay suspended longer in water and are transported farther downslope. Therefore, depositional zones, such as depressions and the base of hillslopes, have finer, deeper, more fertile soils than upslope soils. Because *B. tectorum* and *B. rubens* are annual plants, we would expect them to favor more fertile sites. Thus, we would predict these species to be more successful on geomorphic units where soils are derived from parent materials with more nutrients, those that weather to a finer texture, and/or those that occur in depositional settings (e.g., downslope, depressions). Slope aspect can also affect distribution patterns, although there is little data from which to draw conclusions among regions.

The interactions among parent materials and soil formation and geomorphic processes (e.g., landslides, overland flow, aeolian [wind-blown] deposition) create a mosaic of unique geomorphic units, highly variable in space and often in time (McAuliffe and McDonald 1995; Hamerlynck et al. 2002). As these units determine plant distribution, they create a mosaic of vegetation communities as well (Webb et al. 1988). However, even within the framework of local to regional settings, the occurrence of *Bromus* can be highly heterogeneous at various scales. The legacy of previous vegetation can result in patchy distributions of SOM (e.g., islands of fertility) that persist long after the vegetation has changed. Dryland soils have inherently low SOM contents and thus are low in nutrients that are tightly associated with SOM (e.g., N, S, and to a lesser extent P); however, it is at this low end of the nutrient availability spectrum where plants are most responsive to changes in nutrients and where heterogeneity is most strongly expressed in terms of its effect on plant growth (Stark 1994). The high soil moisture and nutrient requirements of annual plants may restrict them to microhabitats where these resources are more abundant, such as the depositional zones mentioned above or under shrub canopies (or where shrub canopies previously existed), especially in hotter and drier regions (Abella et al. 2011). Even when annual grasses are able to invade the interspaces between the native perennials, these invaded patches can be directly adjacent to seemingly similar, but uninvaded, interspace areas (Fig. 8.1). This patchwork pattern is often

repeated across a given landscape. When highly localized, these small patches of *Bromus* suggest that these invasions are not always controlled by climate, seed availability, herbivory, or soil disturbance. Instead, these patterns support the hypothesis that invasion at the local scale is most likely controlled by microclimate and/or soil characteristics. Larger-scale invaded patches can be a result of disturbance and/or removal of native competitors through processes such as fire or heavy grazing. There are exceptions to this patchy distribution pattern where large areas are covered by *Bromus*, such as areas covered by highly fertile loess, lacustrine soils (e.g., Snake River Plain in southern Idaho, areas of northern Nevada, Lake Bonneville sediments in Utah, Mancos Shale on the Colorado Plateau) or invasions following chronic (e.g., excessive grazing) or acute (e.g., fire) disturbance. In these areas, the cover of annual grasses often is, or has the potential to be, quite high and homogenous.

8.3 Studies on the Potential Soil Controls on *B. rubens* and *B. tectorum* Distribution

There are only a handful of studies examining how soil characteristics influence *B. rubens* and *B. tectorum* invasion into low-elevation dryland ecosystems, except after major disturbance (e.g., fire, plowing). The majority of studies examining *Bromus* distribution are correlative, not mechanistic, and thus, it is important to recognize that unless soil chemistry was analyzed prior to invasion, these studies cannot determine whether the particular soil characteristics were present before the invasion and caused the invasion or if they were due to plant-soil feedbacks by *Bromus* (e.g., Germino et al. 2015). In addition, many soil characteristics are frequently correlated with each other. For example, changes in pH change the solubilities of multiple nutrients simultaneously; SOM, water, and nutrient availability are frequently associated with higher silt and clay contents. Therefore, it is not possible to conclusively identify the actual limiting factor based on plant-soil correlations. Nevertheless, we will discuss the soil factors most frequently associated with the presence of *Bromus* in an attempt to identify factors that may regulate its distribution. Below, we divide this discussion into five climatic regions: Chihuahuan Desert, Mojave Desert, Colorado Plateau Desert, Great Basin Desert, and California coastal sage scrub.

8.3.1 Chihuahuan and Mojave Deserts

Chihuahuan Desert An extensive field survey (Soil Interactions with *Bromus* [SIB] study; Belnap et al., unpublished data) found no invasive exotic annual-grass patches (of any species, including *Bromus*) on any soil type. This was despite the fact that total vegetation cover and the major soil nutrients of interest at these sites were similar to those found in the other deserts (Table 8.1).

Mojave Desert There are several studies from the Mojave Desert that examine the correlation between soil characteristics and *B. rubens* cover. The SIB study compared soil (0–10 cm in depth) in randomly selected patches invaded by *B. rubens* with adjacent uninvaded patches (Fig. 8.2) at 172 sites across the eastern Mojave Desert on multiple parent material types (Table 8.2). When all sites were combined, multiple regression analysis showed a significant positive relationship between *B. rubens* cover and the ratio of bicarbonate-extractable P (P_{bc}) to the acid-neutralizing potential (which binds P, making it bio-unavailable) (P_{bc}/ANP) ($R^2=0.36$) (for all results reported from this study, significance was defined as $P<0.05$). A more resolved model resulted when only sites with $>4\%$ *B. rubens* cover were considered ($P_{bc}/ANP=R^2$ of 0.83). These results indicate that overall, *B. rubens* cover may be limited by P availability in this desert. Because soil factors affecting *B. rubens* distribution could vary with available precipitation, this dataset was also analyzed by elevation classes of 200–500, 500–950, 950–1100, and 1100–1775 m height above sea level (Table 8.3). For 200–500 m, extractable calcium (Ca_{ex}), Zn_{ex} , and Na_{ex} were negatively correlated, and Mn_{ex} was positively related, to *B. rubens* cover (total $R^2=0.73$). *Bromus rubens* cover at 500–950 m was positively related to P_{bc}/ANP and K_{ex}/Mg_{ex} and negatively related to copper (Cu_{ex} ; total $R^2=0.62$). The 950–1100 m sites showed a very weak positive relationship between *B. rubens* cover, and Mn_{ex} ($R^2=0.08$). *Bromus* cover at sites above 1100 m had a positive relationship with both P_{bc}/ANP and silt (total $R^2=0.41$).

Three other studies in the Mojave Desert addressed the relationship between soil characteristics and invasive *B. rubens*. The first study examined the effects of N fertilization on response of *B. rubens* and native forbs at Joshua Tree National Park (Allen et al. 2009, unpublished data). N fertilization experiments were done at two pinyon-juniper woodlands with lower and higher levels of anthropogenic N deposition, 6 and 12 kg N ha⁻¹ year⁻¹ (Tonnesen et al. 2007; Fenn et al. 2010, unpublished data). The site with low N deposition had initial low cover and low seed bank density of *B. rubens*, and the site with high deposition had higher cover of *B. rubens* with high seed bank density (Allen et al. 2009; Schneider and Allen 2012). Plots were fertilized with 0, 5, or 30 kg N ha⁻¹ as NH₄NO₃ each fall 2002–2004 and percent cover assessed in spring 2005. Experimental N fertilization promoted increased cover of brome grasses at the high N deposition site with a subsequent decrease in native forb cover (Fig. 8.2). However, grass cover was both low and highly variably at the low deposition site and grasses did not respond significantly. In contrast, native forb cover was initially high at the low deposition site, and native forbs respond to N fertilizer. This implies that native forbs are able to respond to N fertilizer when there is reduced competition from exotic grasses (Allen et al. 2009, unpublished data). However, *B. rubens* had a sufficiently large seed bank even at the lower N site and could eventually increase with high inputs of N (Schneider and Allen 2012). Thus, increasing N deposition appears to make these ecosystems more invisable by brome grasses. These invasions (Fig. 8.2, Allen et al. 2009) occurred in soils with moderate resin-extractable P (P_{re}) concentrations (~3–10 mg kg⁻¹) and pH of 6.5–8 (Rao and Allen 2010). In two additional Mojave Desert studies, Brooks (1999) showed that *B. rubens* cover was higher in lower micro-topographic positions where total N, P, and water were higher than elevated hummocks, but this

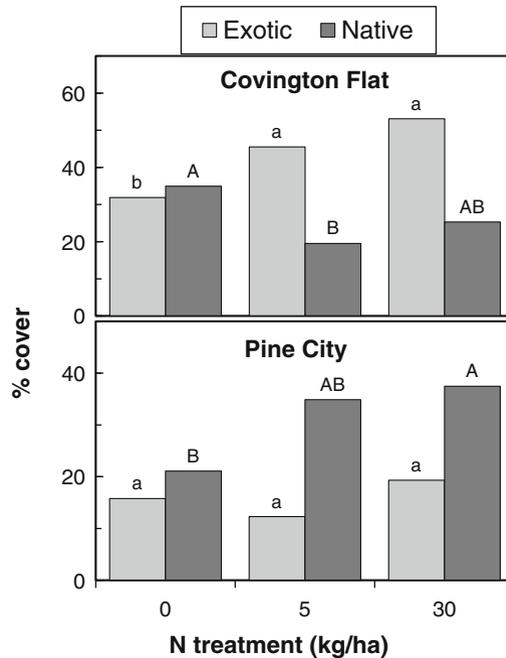


Fig. 8.2 Cover of exotic grass *B. rubens* and native forbs (~25 species) in 2005 at two sites in Joshua Tree NP. Covington Flat has relatively higher anthropogenic N deposition with ~12 kg N ha⁻¹ year⁻¹ and Pine City has ~6 kg N ha⁻¹ year⁻¹ (Tonnesen et al. 2007; Fenn et al. 2010, unpublished data). Plots were fertilized with 0, 5, or 30 kg N ha⁻¹ as NH₄NO₃ each fall 2002–2004 and percent cover of herbaceous vegetation assessed in spring 2005 (redrawn from Allen et al. 2009, unpublished data). Different letters above columns indicate significant differences within exotic or native species.

study did not distinguish among these three soil factors. However, an N fertilization experiment confirmed that N was limiting *B. rubens* productivity (Brooks 2003).

8.3.2 Colorado Plateau Desert

The interaction of *Bromus* with soil factors for the Colorado Plateau region has only been addressed by the SIB study. This study sampled 195 sites for soil chemical characteristics and *B. tectorum* cover at small (80 ha), intermediate (8000 ha), and large scales (80,000 ha). At the 80 ha scale, three uninvaded and three *B. tectorum*-invaded areas were randomly selected, and within each area, a block of 30 plots were randomly placed for sampling. Multiple regression showed a significant correlation between *Bromus* cover and higher soil K_{ex}, K_{ex}/Mg_{ex}, K_{ex}/Ca_{ex}, and soil CEC, with the strongest relationship being a positive correlation with K_{ex}/Mg_{ex} (R²=0.80; Table 8.3). Soil nutrients were measured at this site before the invasion

Table 8.2 Ranges of nutrients, nutrient ratios, and annual and perennial plant cover in the different deserts sampled

	Mojave (<i>n</i> = 172)		Colorado Plateau (<i>n</i> = 195)		Great Basin (<i>n</i> = 30)		Chihuahuan (<i>n</i> = 14)	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
Sand (%)	42	95	22	93	13	77	33	70
Very coarse sand (%)	0	49	0	14	0	10	0	20
Coarse sand (%)	0	36	0	21	0	21	1	22
Medium sand (%)	2	58	0	39	0	34	1	60
Fine sand (%)	8	51	4	72	1	34	5	47
Very fine sand (%)	4	35	3	42	5	25	3	29
Clay (%)	4	28	4	51	12	40	14	35
Silt (%)	1	40	0	52	11	59	21	40
pH	6.4	8.0	7.0	9.0	4.9	8.1	7	8.0
ANP (%)	<1	27	0	63	0	28	<1	35
Ca _{ex}	500	5796	1012	26,880	960	4842	2384	54,620
Cu	0.12	1.7	0.05	5.2	0.88	3.7	0.01	1.5
Fe	0.9	14	1	63	3.8	84	0.4	3.1
Mg _{ex}	29	692	31	820	120	849	10	7272
Mn	<1	14	<1	32	6	113	<1	10
Total N	1	1463	39	6994	369	2551	33	1427
Na _{ex}	0.1	1013	0.2	912	52	980	26	30,180
K _{ex}	30	1053	26	887	270	1724	<1	1554
K _{be}	40	529	38	816	125	1130	10	1004
P _{be}	0.8	27	0.9	37	11	60	0.1	26

(continued)

Table 8.2 (continued)

	Mojave (<i>n</i> = 172)		Colorado Plateau (<i>n</i> = 195)		Great Basin (<i>n</i> = 30)		Chihuahuan (<i>n</i> = 14)	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
Zn	0.12	0.81	0.06	3.5	0.4	8.2	0.02	1.6
K _{be} /Mg	0.64	6.2	0.13	4.6	0.46	4.3	0.04	5.2
P/ANP	<1	166	<1	391	<1	528	<1	1.5
Perennial plant % cover	0	57	0	80	12	80	14	50
Annual plant % cover	0	48	0	50	0	75	0	0

Subscripts indicate the extracting agent. Phosphorus (P_{be}) and K (K_{be}) were extracted with NaHCO₃, and exchangeable cations (Na_{ex}, Ca_{ex}, K_{ex}, and Mg_{ex}) were extracted with NH₄C₂H₃O₂ buffered to pH 8.5 to match the soils. Micronutrients (Cu_{ex}, Fe_{ex}, Zn_{ex}, and Mn_{ex}) were extracted with diethylenetriaminepentaacetic acid (DTPA). P/ANP is the ratio of P_{be} to the acid-neutralizing capacity of the soil (ANP). Concentrations of elements are expressed as mg element/kg dry soil. Subscripts av = available; ex = exchangeable; be = bicarbonate extractable. Total N was measured using the Kjeldahl method

Table 8.3 Results of stepwise regression models for Mojave, Colorado Plateau, and Great Basin sites with percent cover of exotic annual grass as the dependent variable

	Predictor	R ²	Correlation sign
Mojave Desert (n = 172)			
All sites combined	P/ANP	0.36	+
>4 % annual grass (n = 37)	P/ANP	0.83	+
Elevation 200–500 m (n = 24)	Ca _{ex}	0.26	–
	Mn	0.46	+
	Zn	0.64	–
	Na _{ex}	0.73	–
Elevation 500–950 m (n = 85)	P/ANP	0.47	+
	K/Mg	0.55	+
	Cu	0.62	–
Elevation 950–1100 m (n = 31)	Mn	0.08	+
Elevation 1100–1775 m (n = 32)	P/ANP	0.25	+
	Silt	0.41	+
Colorado Plateau (n = 195)			
All sites combined	K/Mg	0.20	+
Elevation 1200–1400 m (n = 22)	Soil depth	0.69	+
	K/Mg	0.94	+
	P	0.99	+
Elevation 1400–1585 m (n = 124)	P/ANP	0.29	+
	Soil depth	0.41	+
Elevation 1585–2160 m (n = 49)	P/Ca ^a	0.63	+
	Fine sand	0.73	–
	Very fine sand	0.78	+
Great Basin (n = 30)			
All sites combined	K _{av}	0.24	+
	Survey clay	0.35	–
	Mn	0.48	+
Elevation 865–1400 m (n = 14)	Very fine sand	0.46	+
	Mg	0.61	+
	Survey clay	0.80	–
Elevation 1400–2159 m (n = 16)	Mn	0.35	+
	ANP	0.61	+
	Survey clay	0.76	–

The reported R² values are cumulative. “Survey clay” refers to data obtained from Natural Resources Conservation Service soil surveys, rather than from analyses of collected soil. Subscripts av = available; ex = exchangeable

^aThis ratio was used in place of P/ANP, as we did not have ANP values for these sites

occurred (Kleiner and Harper 1977) and at that time, K_{ex} , K_{ex}/Mg_{ex} , and soil CEC were higher in the plots that were invaded; thus, the correlation between invasion and soil chemistry was not due solely to post-invasion plant-soil feedbacks. In addition, soil chemistry has been measured in invaded and uninvaded plots since the invasion and shows no consistent directional changes in total soil N, nitrate (NO_3), ammonium (NH_4^+), P_{be} , K_{ex} , K_{be} , Ca_{ex} , or micronutrients (Belnap et al. 2005, 2006; Schaeffer et al. 2012), further supporting the idea that soil chemistry differences existed pre-invasion.

At the intermediate scale (8000 ha), soil maps were used to identify different map units, and within each unit, a sample point was randomly selected. If this point was uninvaded, then the nearest invaded site (if present within 200 m) was also sampled; if invaded, then the nearest uninvaded site (if present within 200 m) was sampled as well. Similarly to the 80 ha area, sites dominated by *B. tectorum* had higher K_{ex}/Mg_{ex} than uninvaded sites. At the larger (80,000 ha) scale, the same approach was adopted but over the larger area. Again, K_{ex}/Mg_{ex} was significantly positively related to *B. tectorum* cover, but the relationship was weaker than at the small scale ($R^2=0.20$ vs. 0.80, respectively, Table 8.3). When sites from the largest region were divided into elevation classes, *B. tectorum* cover at sites with an elevation of 1200–1400 m was positively correlated with soil depth, K_{ex}/Mg_{ex} and P_{re} (total $R^2=0.99$; Table 8.3). As seen in the Mojave, *B. tectorum* cover at sites of intermediate elevation (1400–1585 m) was positively correlated with P_{be}/ANP and soil depth (total $R^2=0.41$). *Bromus tectorum* cover at 1585–2160 m sites was correlated with P_{re}/Ca_{ex} (+), fine sand (–), and very fine sand fractions (+, total $R^2=0.78$).

8.3.3 Great Basin/Intermountain Region and Columbia Plateau

Despite a great deal of research on *B. tectorum* in the Great Basin/Intermountain-Columbia Plateau regions, few studies have used a field approach to examine how a suite of soil characteristics may control this species. Belnap's SIB survey visited 30 sites in the Great Basin. Multiple regression analysis found that *B. tectorum* cover was positively correlated with K_{ex} and Mn_{ex} and negatively correlated with soil survey clay data (obtained from the Natural Resources Conservation Service soil surveys rather than analyzed soil; NRCS 2004) (total $R^2=0.48$; Table 8.3). When divided into elevation groups, *B. tectorum* cover at lower elevations (865–1400 m) was positively related to very fine sand content and Mg_{ex} and negatively related to soil survey clay (total $R^2=0.80$). At higher elevations (1400–2159 m), *B. tectorum* cover was positively related to Mn_{ex} , ANP, and survey clay (total $R^2=0.76$; Table 8.3).

Rau et al. (2014) sampled 72 plots at four sites in Utah, Idaho, Oregon, and Washington. Soils were sandy or silt loams, all supporting intact sagebrush communities with a *B. tectorum* understory that ranged from 0 to 50 % areal cover. Across all plots, P_{re} was the factor most strongly (and positively) correlated with *B. tectorum* cover pre-disturbance ($R^2=0.57$). Measurements immediately after

severe experimental disturbances (fire, mowing) showed P increased across all treatments and became less important than water and soil texture. Bashkin et al. (2003) also found a landscape-level correlation between *B. tectorum* biomass and P_{re} . Chambers et al. (2007) found no relationship between *B. tectorum* biomass and soil N in experimentally seeded plots but did find that soil water was limiting to *B. tectorum* establishment, biomass, and seed production at low-elevation sites. Blank et al. (2013) found that areas invaded by *B. tectorum* had significantly more phosphatase activity and more solution-phase ortho-P than uninvaded areas. Neither study found a relationship with N.

In contrast, Jones et al. (2015) did find a correlation between soil N and *B. tectorum* biomass and seed production. Stark and Norton (2015) used a common garden study to examine growth of *B. tectorum* in intact soil cylinders (23 cm diam. \times 45 cm deep) collected from high-elevation (2020 m) field plots in a sagebrush-steppe ecosystem western Colorado. The soil cylinders were collected from field plots planted to different plant communities 24 years earlier (Stevenson et al. 2000). In the field, without supplemental water, *B. tectorum* biomass was lowest when grown on soil that had been scraped and planted to sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) and native perennial grasses 24 years earlier. Biomass was moderate when grown on soil scraped and seeded to *B. tectorum* 24 years earlier and was highest on soil collected from mature, undisturbed *A. tridentata* communities. Analyses of plant tissue concentrations showed that N availability regulated *B. tectorum* production across the three soil types. Other studies in the Great Basin and elsewhere have also shown that sites invaded by *B. tectorum* have greater soil N and N availability than adjacent uninvaded sites (Booth et al. 2003b; Norton et al. 2004; Hooker et al. 2008; Adair and Burke 2010). In SE Oregon, Bansal et al. (2014) found a strong interaction of time of sampling and community type (invaded, mixed, native) and total resin-extractable N, resin NH_4 , and resin NO_3^- . Many of these studies assume that *B. tectorum* created the greater N availability following invasion; however, as discussed earlier, with these correlative studies it is difficult to know whether *B. tectorum* invaded sites that already had greater N availability or it created the greater soil N post-invasion. In at least one study, the additional soil N in the invaded site was far in excess of ecosystem N input rates during the time since invasion by *B. tectorum* (e.g., Blank 2008), and we can reasonably assume that the differences in soil N existed prior to invasion (see also Germino et al. 2015). In this case, greater N availability may have promoted invasion. In other cases, the answer is not as obvious, and in fact, *B. tectorum* may have both invaded because of greater soil N and subsequently contributed to greater N availability.

8.3.4 Coastal Sage Scrub

The impacts of anthropogenic N deposition were assessed on coastal sage scrub vegetation in western Riverside County, CA, USA. This vegetation type has been extensively invaded by annual *Bromus* species. Greenhouse experiments indicated

Table 8.4 Abundance (% cover) and richness (species/3 ha) of plant groups along a nitrogen deposition gradient in western Riverside County, CA

Site	Exotic grass (% cover)	Native forb (% cover)	Shrub (% cover)	Native forbs no. of species per 3 ha	Soil N (mg kg ⁻¹)	N dep (kg ha ⁻¹ year ⁻¹)
Jurupa Hills	63.5	4	2.2	16	37.7	19.6
Box Springs	69.2	18.5	2.4	31	32.6	14.7
Botanic Garden	36.0	25.4	0.2	20	28.9	13.4
Lake Perris	0.5	26.1	2.8	30	20.3	11.1
Mott Reserve	6.7	14.3	11.2	37	30.6	11.1
Lopez Canyon	11.1	19.6	19.3	67	9.6	9.0
Tucalota Hills	1.5	35.7	35	50	10.5	8.7

Sites along an urban to rural gradient in southern CA. Soil N is extractable nitrate plus ammonium. N deposition is from the CMAQ model. Table adapted from Fenn et al. (2010)

B. rubens would respond to atmospheric N deposition (Padgett and Allen 1999; Yoshida and Allen 2001, 2004). Along an urban to rural gradient, N deposition ranged from 19.6 to 8.6 kg N ha⁻¹ year⁻¹, based on the Community Multiscale Air Quality (CMAQ) (Tonnesen et al. 2007) model (Table 8.4), whereas other variables (soils, elevation, and rainfall) were all similar. Extractable soil N (NO₃+NH₄) ranged from 39 mg N kg⁻¹ at the urban end of the gradient to 10 mg kg⁻¹ at the rural end. Exotic grass cover was positively correlated with soil N and atmospheric N deposition, while cover of native shrubs and forbs was negatively correlated with N ($p < 0.001$). Exotic grass cover was dominated by *B. rubens* (up to 7.7 % cover) and *Bromus diandrus* Roth (ripgut brome) (up to 61 %) with <1 % cover of *Bromus hordeaceus* L. (soft brome) and *B. tectorum*. Exotic grass cover generally increased with higher N deposition (Table 8.4).

8.4 Manipulative Studies

8.4.1 Nitrogen

Multiple greenhouse and field studies have examined how N additions influence *Bromus* performance. In the field where *B. tectorum* already exists, N fertilization can increase *Bromus* production, especially in areas or years of higher precipitation and cooler temperatures. Kay (1966) showed that application of ammonium nitrate (NH₄NO₃) to field plots in northeastern California increased production in all but the driest years. Similarly, Brooks (2003) and Rao and Allen (2010) found that in the Mojave Desert, addition of NH₄NO₃ increased production of *B. rubens*, with the

greatest increases occurring during years with the highest precipitation. Interestingly, Gundale et al. (2008) examined nutrient limitations to *B. tectorum* growth in a greenhouse study and found that N was limiting to *B. tectorum* growth in soil collected from beneath the canopy of ponderosa pine trees, but P was limiting to *B. tectorum* growth in soil collected from nearby bunchgrass patches. In another greenhouse study, Monaco et al. (2003) found that while N fertilization stimulated *B. tectorum* production, it was primarily NO_3 that produced the greatest response in shoot biomass. A number of studies have also found that lowering N availability by adding labile C (such as sucrose) to soils to promote N immobilization has the effect of lowering *B. tectorum* production: in a Wyoming big sagebrush community (McLendon and Redente 1991), in a shortgrass steppe (Paschke et al. 2000), and in soil from a sagebrush community in northern Utah (Monaco et al. 2003). Most studies suggest that *B. tectorum* production is favored by high N availability.

Many fertilization studies have shown N additions stimulate *Bromus* production while often increasing perennials as well. For example, on the Columbia Plateau, James (2008) showed that N fertilization increased both *B. tectorum* and perennial grass production. More importantly, James et al. (2011) showed that while low N availability reduced *B. tectorum* production, *B. tectorum* still outproduced the native perennial grass seedlings even at low N availability. Because *B. tectorum* appears to outperform native perennial grass seedlings under both high and low N availabilities, they proposed that manipulation of N availability may not be an effective restoration practice for shifting the competitive balance in favor of native grasses during seedling establishment. Outcomes are life-stage dependent, and in intact ecosystems, N uptake in mature, native perennial grasses is strongly coupled with N availability, and the mature, perennial grasses that dominate these systems may keep N and other resources at such low concentrations that *Bromus* seedlings are not competitive. However, any disturbance that decouples this relationship by eliminating established grasses results in an ecosystem highly vulnerable to invasion (Chambers et al. 2007).

In addition, other studies have shown that manipulating N availability does shift community composition where *B. tectorum* has already become established because of stronger relative responses of *B. tectorum* to N availability. Studies in a relatively warm and dry *A. tridentata* ssp. *wyomingensis* community in western Colorado (McLendon and Redente 1991, 1992) and in a shortgrass steppe in central Colorado (Paschke et al. 2000) found that addition of N fertilizer to mixed stands of annual and perennial vegetation stimulated production by *B. tectorum* to a much greater degree than perennials and shifted the community composition in favor of *B. tectorum* dominance. While N additions frequently increase *B. tectorum* production, the effect on native perennials appears to be highly dependent on the plant species and life stage and the characteristics of the soils and climate. For example, in a meta-analysis examining studies from sagebrush, shortgrass steppe, tallgrass prairie, mixed grass prairie, and coastal California grasslands, Blumenthal et al. (2003) found that of nine studies using C addition to reduce N availability, seven showed suppression of weeds while not affecting native perennials, whereas two studies showed no effect on weeds or natives.

While a number of studies have examined the effect of N availability on production of *B. tectorum* and perennial grasses in semiarid and arid lands, very few have examined the effect of N availability (or other nutrients) on the initial establishment of *B. tectorum* into existing stands of perennial grasses. In a study in the shortgrass steppe of central Colorado, Paschke et al. (2000) reported that lowering N availability by adding sucrose reduced recruitment of weedy annuals into established perennial grass communities. Similarly, Beckstead and Augspurger (2004) found that in western Utah, addition of sucrose to field plots with high *B. tectorum* densities reduced *B. tectorum* density and biomass during the establishment and active growth phases; however, in low-density *B. tectorum* stands, N addition had no effect on establishment density or overall biomass. More future research should focus on the effect of nutrients on this aspect of *B. tectorum* invasion.

There is also the intriguing possibility that while soil N may influence annual-grass production directly, it also may do so via interactions with other nutrients. For example, studies have shown that N addition stimulates soil phosphatase concentrations and activity, thus likely increasing available P (Phuyal et al. 2008; Collins et al. 2008). As *B. tectorum* produces and secretes phosphatases (Bolton et al. 1993), a stimulation of *B. tectorum* by N could enhance its phosphatase production as well.

8.4.2 Phosphorus and Others Nutrients

Multiple studies have experimentally addressed the effect of nutrients other than N on *Bromus* performance. Manganese (Mn) can stimulate the growth of *B. tectorum* and other annual grasses (Bildusas et al. 1986; Cramer and Nowak 1992; Miller et al. 2006a, b). With burning, soil Mn doubled in low P/ANP soils and increased almost four times in high P/ANP soils (Belnap, unpublished data). Rau et al. (2008) found burned soils contained 21 kg Mn ha⁻¹ compared to 12 kg Mn ha⁻¹ in unburned soils, which may at least partially explain *Bromus* success in invading burned areas, as burning does not always elevate other nutrients such as N or P. Potassium has been found to stimulate *B. tectorum* growth in the greenhouse (Howell 1998; Morrison 1999) and in the field on the Colorado Plateau (Miller et al. 2006a, b). Using manipulative experiments and correlations, Miller et al. (2006a, b) found that in the field, the limiting soil factors for *B. tectorum* can vary with different life stages: P and water limited germination in the fall and K_{ex} and K_{ex}/Mg_{ex} were positively correlated with winter performance. A combined analysis of winter + spring performance showed that growth was negatively correlated with ANP and CaCO₃ (both negatively affect P_{be} availability) and Mg_{ex} and positively correlated with P_{be} , silt, clay, and dust content (in addition to the Mn_{ex} and K_{ex} , mentioned above). In greenhouse experiments, addition of P has been shown to stimulate production of *B. tectorum* biomass (e.g., Dakheel et al. 1993; Blackshaw et al. 2004; Cherwin et al. 2009), but, in some cases, not as much as N (Dakheel et al. 1993). Belnap and Sherrod (2009) showed in a greenhouse experiment that *B. tectorum* germination

was suppressed when P availability was reduced. DeLucia et al. (1989) found that *B. tectorum* biomass was reduced by over 90 % when growing in P-limited soils. Schlesinger et al. (1989) in the Great Basin Desert and Parker (1995) the Sonoran Desert reported P was limiting to plants in desert settings. In contrast, McLendon and Redente (1991) saw no effect on *B. tectorum* when field plots in western Colorado were amended with P.

8.4.3 Soil Moisture

Soil moisture has an important influence on *Bromus* performance directly, and it also can influence *Bromus* success indirectly through its effect on the availability of soil nutrients. Soil water and nutrient pools are not independent of each other, because plants must obtain soil nutrients in solution (Barber 1995; Leffler and Ryel 2012 and references therein). To date there have been very few studies which examine the interaction between soil water, nutrients, and *Bromus* growth, despite the importance of understanding these interactions. The greatest productivity of *B. rubens* occurred under the combination of high water and N in the Mojave Desert in a garden plot and also in experimentally fertilized natural vegetation that was measured during a series of dry to wet years (Rao and Allen 2010). Using intact monoliths obtained from a *B. tectorum*-infested site on the Columbia Plateau, Link et al. (1995) determined that the addition of water or N alone had no influence on *B. tectorum* growth, but when the two were added together, biomass production and leaf area were nearly twice that of any other treatment (control, water alone, or N alone), indicating that water and N were co-limiting. On the Colorado Plateau, Miller et al. (2006a) reported that water additions alone significantly increased establishment and plant density of *B. tectorum*. In contrast, Beckstead and Augspurger (2004), Link et al. (1995), and Cline and Rickard (1973) all reported that at Great Basin sites, water additions had no influence on *B. tectorum*; however, Beckstead and Augspurger did show N additions alone significantly increased *B. tectorum* biomass and plant density. In addition to these direct water and nutrient manipulations, several studies have shown that removal of competing vegetation significantly increases *B. tectorum* performance, predominantly due to increased moisture availability (Melgoza et al. 1990; Dodd et al. 1998; Beckstead and Augspurger 2004; Chambers et al. 2007). However, given that many areas have *Bromus* spp. occurring in patches directly adjacent to uninvaded patches, water alone is likely not the sole driver in many situations. Lastly, nutrients such as NO_3^- and sulfate move to the root largely by mass flow, and uptake is thus less constrained by soil water content than more diffusion-limited nutrients such as P and NH_4^+ . Thus, soil moisture conditions may constrain nutrient uptake by plants, with P and NH_4^+ possibly more limiting than NO_3^- or S in dry desert soils, despite being present in sufficient amounts.

8.5 Discussion

8.5.1 *How Soil Texture and Biochemistry Can Limit Bromus*

Based mostly on experimental additions of N to field plots and greenhouse plants, and increases in available N following disturbance or management treatments, elevated soil N has long been generally believed to be the most important soil factor controlling the invasion and success of annual exotic plants (Smaydohlgren et al. 1999; Ehrenfeld 2003). In our literature review, we found that the influence of N depend on which climatic region is being considered. Under hotter and drier soil temperature and moisture regimes, extensive field surveys (172 sites in the Mojave Desert, 195 sites on the Colorado Plateau) and several experimental studies showed that nutrients other than N were the most correlated with *Bromus* occurrence. However, N additions did stimulate *B. rubens* performance in greenhouse pots, in field plots, and along two N gradients in the Mojave Desert (Padgett and Allen 1999; Yoshida and Allen 2001, 2004; Allen et al. 2009). This may have been due to the soil pH at these sites, which was relatively acidic (Table 8.2) compared to most dryland soils, which are generally >7.5. Low pH can result in less co-limitation by other nutrients than generally occurs in more alkaline soils.

Many field and greenhouse studies in the wetter and cooler Great Basin/ Intermountain region showed a correlation between soil N and an increase in *B. tectorum* production, especially during wetter years. However, other greenhouse and field studies found the strongest correlation with *B. tectorum* occurrence or performance to be with K, P, or Mn (e.g., DeLucia et al. 1989; Miller et al. 2006a, b). As nutrient availability can vary widely with pH, soil moisture, and other factors, these results may not be conflicting but instead reflect unmeasured site conditions (e.g., soil pH, depth, moisture) or sampling time (e.g., wet versus dry years or life cycle stage). Unfortunately, despite the amount of data we have on factors correlated with *Bromus* occurrence and production, we have far less information on nutrients correlated with its initial germination and establishment phases.

The idea that P may limit *Bromus* invasion success is fairly recent and, from our review, may be an important driver in the hotter regions (thus having lower soil moisture) such as the eastern Mojave and Colorado Plateau Deserts and also sometimes in cooler regions (thus having higher soil moisture), such as the Great Basin. This might be due to the low availability of P in highly alkaline soils due to several interrelated factors: (1) carbonate (CaCO_3 , MgCO_3) can complex with P, reducing its availability; thus, P availability can change with factors that alter the interaction of these compounds and P; (2) marginally soluble calcium phosphate compounds can precipitate out of solution; and (3) high levels of Ca and HCO_3 can reduce or prevent the dissolution of carbonate and Ca-P compounds, thus reducing amounts of available P via common ion effects: the neutralization of acids secreted by plants, mycorrhizal symbionts, other rhizosphere microbes, and/or root-respired CO_2 , all of which would otherwise increase P solubility (Barber 1995). Other factors that are also likely to contribute to lower P availability in these soils is the low level of soil

organic matter, which can be the dominant source of plant available P when soil physiochemical processes tie up P (Stevenson 1986) and low initial concentrations of P in the soil parent material, which in these regions is often aeolian material derived from sandstone.

Climate may also affect the bioavailability of P via changes in CaCO_3 solubility (as postulated by Miller et al. 2006a, b). In high-pH desert soils, most P is bound to CaCO_3 , rendering it unavailable for plant uptake. The generation of H_2CO_3 facilitates carbonate dissolution and thus the transition of solid-phase P to solution-phase P (Jungk and Claassen 1997). The rate of H_2CO_3 formation is partially controlled by soil water content and the solubility of CO_2 in that water (Krauskopf and Bird 1995). The solubility of CO_2 in water, like that of other gases, is greater at cold than warm temperatures, and thus a theoretical maximum in H_2CO_3 production should occur when soils are cool and wet. Therefore, release of CaCO_3 -bound P should also be highest under cool and wet soil conditions. Root growth can also contribute respiratory CO_2 , facilitating the release and therefore acquisition of carbonate-bound nutrients, and *B. tectorum* shows relatively high levels of winter root growth when soils are cold and moist (Harris 1967). Therefore, under the above scenario, winter would be the time when P would be most available in dryland soils. This is supported by several studies. Results from in situ resin bags at Colorado Plateau sites indicate an increase in available P during the cold, moist conditions found in winter (Miller et al. 2006a, b). *Bromus tectorum* growth rates were greatest at these sites in winter and were positively related with P/Ca and inversely related with ANP. Lajtha and Schlesinger (1988) also found that in situ resin bag P concentrations peaked in cool winter conditions in the Chihuahuan Desert. Magid and Nielsen (1992) showed that laboratory extractions done at 4 °C recover significantly more P than those done at 25 °C. In general, lower diffusion rates at decreased temperatures may partially counteract the increase in available soil P. However, the situation may be different in calcareous soils, as diffusion rates may actually increase with decreasing temperatures (but above freezing) (Jungk and Claassen 1997). Increased solubility of P at lower temperatures may also play a large role. In addition, *Bromus* establishes in the fall and is active through winter in many areas. During this time, the roots can actively uptake P when soil temperatures and soil water content are high enough to allow efficient transport of P to the roots.

Increased soil moisture due to climate factors (higher precipitation and lower temperatures) may also impact biotically mediated ways that free bound P. Soil fungi and plants, including *Bromus*, secrete phosphatases which can make bound P available, and increased soil moisture, both in space and time, can stimulate this production. As mentioned above, root-respired CO_2 can acidify the root environment and thus increase levels of available P.

Other cations, including micronutrients, may influence invasions as well (e.g., Blank et al. 2007). In contrast to N and P, much less work has been done with K as a limiting nutrient in dryland soils. Plant species differ in their K uptake (Gray et al. 1953), and uptake is positively and highly related with plant root cation-exchange capacity (CEC) ($r=0.78$; Croke and Knight (1962). Root CECs vary widely among plant functional types: annuals have higher root CECs than perennials, and grasses

have higher CECs than herbaceous and woody species (Crooke and Knight 1962; Scott and Billings 1964; Woodward et al. 1984). Therefore, annual grasses should generally have the highest CECs of all plants. Possibly due to high root CECs that are found in *Bromus* (Belnap, unpublished data), they can have higher tissue concentrations of K than adjacent native perennial plants (Blank et al. 2002), which may also indicate they have a higher requirement for K than the native grasses (Tilman 1982). Tilman et al. (1999) also reported K to be limiting in the field for the perennial *Taraxacum officinale*. Traditionally, agriculture has regarded exchangeable K values of 140 ppm to be the minimum required for adequate plant growth (Marschner 1995; Leigh and Storey 1991). Using this standard, most of the soils sampled in the regional field surveys (Belnap, unpublished data) were K deficient.

Potassium interacts with other cations and micronutrients, which may also explain its importance to annual grasses. Osmoregulation in plants is mediated by K (Mäser et al. 2002; Wang et al. 2002). The presence of high Na can be toxic to many plants, and there are multiple studies showing that K ameliorates Na toxicity in plants (Mäser et al. 2002) and other organisms such as bacteria (Kraegeloh and Kunte 2002). The preferential transport of K over Na is especially pronounced in actively photosynthesizing tissues such as young leaves and developing seeds (Wang et al. 2002). The extent to which plants utilize K to avoid Na stress varies among species (Mäser et al. 2002). In addition, K has been implicated in plant avoidance of water stress (Xu et al. 2002). Multiple studies support the observation that high levels of Mg and Ca can restrict plant uptake of K in both the laboratory and the field (Epstein 1961; Sinanis et al. 2003). Additions of K can also enhance Mn availability to plants, which may be very important in understanding the distribution of exotic annual grasses (see below; Krishnamurti and Huang 1988). Crooke and Knight (1962) and Scott and Billings (1964) were the first to note that soils with high K_{ex}/Mg_{ex} ratios were dominated by annual plants. This finding was followed up by Harner and Harper (1973), Pederson and Harper (1979), and Woodward et al. (1984) to explain patterns of plant distribution in the arid Western USA.

Micronutrients are seldom considered in studies of native plant distribution and/or performance. However, studies in the Western USA have found that micronutrients are important in predicting the distribution of disparate organisms such as soil lichens, annual grasses, and perennial shrubs (Cramer and Nowak 1992; Bowker et al. 2005). There is very little information on how micronutrients may influence plant distribution patterns in dryland soils characterized by high pH, low SOM, and high $CaCO_3$ levels, as almost all studies have been conducted in agricultural settings. That said, it is known that the bioavailability of Zn, Mn, and Fe is very low in alkaline soils that are commonly found in dryland regions and can thus be limiting to plants under these conditions (Clark and Baligar 2000). Although these nutrients are only required in very small amounts, they are essential for plant growth. These micronutrients also form oxides that bind P, reducing its availability in soils. In the field surveys reported here, Mn_{ex} was often found to be positively related to *Bromus* cover, indicating there are places where this micronutrient may be limiting. Greenhouse studies have found that Mn_{ex} can stimulate the growth of annual grasses (Bildusas et al. 1986; Cramer and Nowak 1992). Perhaps analogously,

soil lichens are associated with soils containing higher Mn (Blank et al. 2001; Bowker et al. 2005).

Soil depth and texture were also important in characterizing invaded sites in all the deserts. At some sites in the Great Basin, deep loamy (fine sand to silt) soils with high water-holding capacity appear best able to retain a mix of *B. tectorum* and perennial grasses, in contrast to shallow coarse sandy soils that can have greater abundance of *B. tectorum* (e.g., Rau et al. 2014). This may be because the deep loams have and hold resources longer throughout the growing season than shallower coarse soils. Consequently, although *B. tectorum* uses much of the surface soil water to complete its life cycle, sufficient amounts are left, especially in subsoils (Ryel et al. 2010) for native herbaceous perennials to persist. Conversely, shallow sandy soils with low water-holding capacity may be more prone to *B. tectorum* dominance, as this plant can more fully utilize what soil moisture is present, depleting the resources that natives need (Melgoza et al. 1990). Thus, when sites experience several water-limited growing seasons, repeated herbivory, or disturbance such as fire, native perennial herbaceous species may experience sufficient stress that they can no longer produce adequate carbohydrate stores to survive, leaving the site open to *B. tectorum* dominance. Once *B. tectorum* is dominant on these sites, native seedlings cannot compete even when adequate resources are available (Booth et al. 2003a; Monaco et al. 2003). Surprisingly, though, an opposite phenomenon appears to occur on the Colorado Plateau, where *B. tectorum* only dominates deeper but finer-textured (fine sandy loam to clay loam) soils rather than shallow coarser sandy soils. The reason for this contrast to the Great Basin is not fully understood. It is possible that *B. tectorum* cannot invade the coarser shallow soils of the Colorado Plateau because of their very low fertility and instead require finer-textured soils where nutrients are sufficient to support a high cover of annual plants. In contrast, the Great Basin and Columbia Plateau soils are generally more fertile and thus competition with other plants and water-holding capacity may be the main drivers behind *B. tectorum* dominance.

8.5.2 Why Were Different Nutrients Limiting in Different Regions and What Does This Mean for Predicting Annual Grass Distribution in Western US Semiarid and Arid Lands?

Figure 8.3 presents a conceptual model of how different nutrients may limit *Bromus* occurrence among different dryland regions of the Western USA, depending on climate (Belnap 2011). This hypothesis is based on the supposition that climate can alter the availability of soil nutrients, especially those made bio-unavailable by soil carbonates (e.g., P and micronutrients). This model suggests that in regions where such nutrients are limiting to *Bromus*, climatic factors can determine whether this genus is able to invade and persist. This model proposes that the ratio of the average

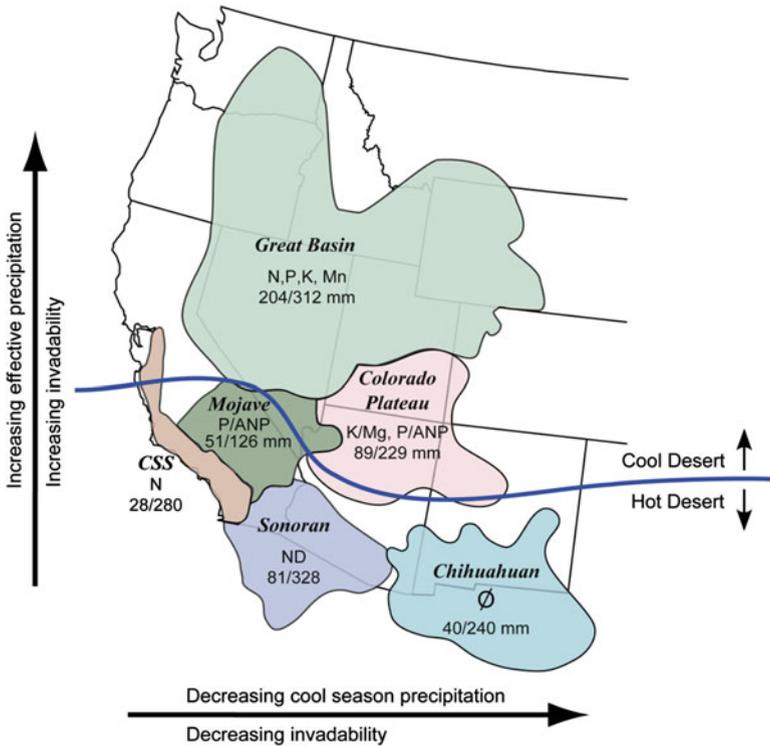


Fig. 8.3 A hypothesized relationship between climate and soil factors (nutrients and water) limiting *Bromus* cover in the different deserts of the Western USA. Limiting nutrients are listed in suggested order of importance within regional boundaries. The numbers within the regional boundaries indicate the average annual amount of precipitation (mm) when mean daily air temperatures are below 10 °C relative to total precipitation. We suggest that as this ratio and the total amount of cool season precipitation increase, so do conditions that allow the conversion of bio-unavailable phosphorus (P) into bioavailable P. As P becomes less limiting, other nutrients such as N nitrogen (N), potassium (K), manganese (Mn), and water become more important to *Bromus* establishment. We do not have data on the soil factors constraining invasive annual grasses in the Sonoran desert. Based on this model, P is expected to be most limiting to *Bromus* in hotter and drier regions

amount of precipitation that falls when air temperatures are below 10 °C (winter) relative to total precipitation (winter/total precipitation; W/T), as well as the total amount of cool season precipitation, indicates the frequency with which conditions occur that allow the conversion of bio-unavailable P into bioavailable P, as discussed in the P section above. The desert regions discussed occur along a gradient of a W/T ratio and total winter precipitation. The Chihuahuan Desert occurs at one end of the gradient, as it has the lowest total winter precipitation, the lowest proportion of winter rain, and the highest winter temperatures of the deserts we sampled. Under these conditions, it is expected that P is seldom freed from carbonates and thus available P in the soils remains extremely low most of the year. The Mojave has the next lowest winter precipitation and W/T ratio and the next highest winter

temperatures, followed by the Colorado Plateau. The Great Basin/Columbia Plateau is at the other end of the gradient, with the highest winter precipitation, the highest W/T ratio, and the lowest winter temperatures of all deserts sampled. Therefore, we suggest that P is likely the most limiting at the Chihuahuan Desert end of the gradient, becoming less so in the Mojave, even less on the Colorado Plateau, and finally the least limiting in the Great Basin. Studies in this review generally support this pattern, as invasive annual grasses are less common (or even absent, as in the SIB data) where winter precipitation is low and temperatures high (Chihuahuan Desert), and thus P is theoretically the least available, despite adequate levels of all soil nutrients in the soil at these sites. At slightly higher winter precipitation and cooler winter temperatures (the Mojave Desert), annual grasses can still be most limited by factors associated with P availability. As total winter precipitation increases and temperatures decrease (going northward to the Colorado Plateau), factors associated with P availability may become less limiting and other factors (K and water availability) become important, although P availability is still part of the regression model. At the Great Basin sites, factors influencing N, P, K, and water availability become most important. Soils of the Mediterranean climate region of southern California should show the least P limitation of all, with its cool, wet winter. Soil organic matter also increases along this gradient from dry, hot desert regions to the cooler wetter semiarid lands and is important in providing nutrients to plants. Therefore, SOM levels are important in understanding nutrient limitations. However, there are exceptions to this model at the site or landscape level. For instance, P is highly available on soils with a pH of 6.5 or less (Marschner 1995). Such soils can be found in many areas of the Mojave Desert (Rao and Allen 2010) and the California sage scrub habitat (Padgett and Allen 1999). Further research is needed to verify this hypothesis and to refine its application to various landscapes.

The role of N, P, or other nutrients in promoting *B. tectorum* and *B. rubens* invasion and dominance is also likely to depend on the perennial plants involved (e.g., grasses versus shrubs) and the role of fire. For example, for fire to be carried through vegetation, there must be sufficient fuel loads. In some communities, sufficient fuels are only achieved during very wet years; however, high nutrient availability may also stimulate *B. tectorum* and *B. rubens* production such that even under moderately wet years, there is sufficient grass biomass to carry fire. This is undoubtedly a major contributor to the well-known annual-grass fire cycle that has allowed huge areas in the Western USA to be converted to monocultures of *Bromus*. For example, fire probability was modeled to increase above $3.9 \text{ kg ha}^{-1} \text{ year}^{-1}$ (*Bromus* and *Schismus*) because of increased fine fuel production under moderate precipitation in the Mojave Desert (Rao et al. 2010). Balch et al. (2012) found cheatgrass dominates ~6 % of the Great Basin, with 13 % of these areas burning from 1980 to 2009, double that of other vegetation types. A historic record of 582 fires in the Mojave Desert was compared with N deposition rates and showed overall more area burned than expected when N deposition rates exceeded $7 \text{ kg ha}^{-1} \text{ year}^{-1}$ (Rao et al. 2014). Fires driven by annual grasses in the Mojave Desert reduce both native shrub recovery and native forb diversity, resulting in persistent dominance by exotic grasses (Steers and Allen 2011, 2012). If fire occurs in a stand of perennial grass, it may be of little

consequence. But if the fire occurs in a stand of fire-intolerant shrubs such as *A. tridentata*, postfire increases in N availability and the loss of *A. tridentata* could make lower precipitation areas open to invasion by *Bromus*.

This broad pattern of relationships, however, will have limits and exceptions when applied to particular soil types and across large areas. For instance, P availability appears limiting at higher-elevation sites in all regions in the SIB study. This seems to be contrary to the P-limitation model presented above and may show one of its limitations. However, it may also be that temperatures at the higher elevations are often below freezing, at which point the dissolution of the bonds between P and other elements would not occur. Soil texture and depth will also modify the applicability of this model at the site level as well. In addition, the water requirement of *Bromus* at various points in its life cycle likely plays a major role in determining the degree to which it can dominate a site. For instance, although *B. tectorum* is found in nearly every US state and southern Canadian provinces west of Quebec, it has only become dominant over large landscapes in semiarid regions dominated by wet winter-spring and dry summer precipitation regimes (Pyke and Novak 1994; Bradley 2009; Mack 2011). This may be because the most favorable conditions for germination and establishment within this region occur where spring precipitation is relatively abundant and temperatures are relatively warm (10–20 °C), but not hot (Roundy et al. 2007; Bradley 2009). In contrast, on the Colorado Plateau and hotter deserts, *Bromus* is generally dominant in relatively small patches.

8.6 Management Implications

The current state of knowledge suggests that there are critical interactions that occur among climate regimes, soil texture, nutrient availability, and soil surface disturbance which determine *Bromus* success in different settings. Even with our currently incomplete understanding, managers can utilize soil and climate maps to make initial assessments of the settings (parent material, soils, geomorphic settings, climate) more or less resistant and/or resilient to *Bromus* invasion. In addition, this understanding can aid in prioritizing sites for restoration or protection. Advancement of the understanding of *Bromus*-soil relationships is also needed to aid land managers in better predicting where *Bromus* can invade under future conditions as well as the resultant effects on native communities.

8.7 Research Needs

Additional research is needed to further refine our knowledge on how various factors affect *Bromus* establishment, such as (1) the less studied nutrients (e.g., Mg, K, micronutrients); (2) the presence of different native species, as they can utilize soil nutrients differently among each other; (3) the distribution of different soil

acid-neutralizing capacities because it is not often measured in soils; and (4) how the interactions of these soil factors are expected to change among regions as climates fluctuate and type, intensity, and timing of surface disturbances change. The latter is increasingly important with future moisture and temperature changes, and if our hypothesis is correct, large changes in *Bromus* distributions could occur. In addition, soils in many areas of the Western USA are unmapped or maps are inadequate for this purpose. Therefore, more effort is needed in this arena as well.

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