BLACKBRUSH (*COLEOGYNE RAMOSISSIMA* TORR.)

State of Our Knowledge and Future Challenges

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ABSTRACT

Blackbrush (*Coleogyne ramosissima* Torr.) is a regionally dominant shrub species found in the transition zone between North American warm and cold deserts where it occupies millions of hectares on National Park Service, Bureau of Land Management, and National Forest lands. Blackbrush habitat is under severe threat of loss from the combined effects of exotic annual grasses, increased fire frequency, and rapid climate change. Attempts to restore blackbrush habitat have met with limited success. This research synthesizes existing information on blackbrush biology and ecology. Our goal is to guide successful restoration efforts. Recent genetic work has revealed the existence of two metapopulations corresponding to the Mojave and Colorado Plateau regions. This work, along with germination and reciprocal transplant studies, demonstrates the need to use appropriate seed sources. Blackbrush plants produce large seed crops infrequently; however, seed can be stored for 10–12 years with minimal loss of viability. Establishment success may be enhanced by planting seeds in the fall to meet chilling requirements, and in small groups at 2.5–4.0 cm in depth to mimic rodent caches. Current observations and projected changes in climate suggest that attempts to restore blackbrush at lower elevations than its current distribution would be unlikely to succeed. Common garden experiments under multiple climate conditions will give us a better understanding of climatic tolerances. Further research is needed to develop new and better restoration techniques.

INTRODUCTION

Blackbrush (*Coleogyne ramosissima* Torr.) occurs in an ecotonal band between warm and cold desert regions extending from California through Utah and Arizona (Meyer and Pendleton 2005). It is an iconic landscape dominant in many of the national parks and monuments. In the Colorado Plateau, blackbrush is found throughout much of southeastern Utah primarily in upland areas along the Colorado and San Juan River drainages and into the desert canyon areas of northern Arizona. Blackbrush communities of the Colorado Plateau are bounded by salt desert shrub (*Atriplex* sp.), sand sagebrush (*Artemisia filifolia*), and grass communities at lower elevations and by pinyon-juniper (*Pinus edulis–Juniperus* sp.) and sagebrush-grass at higher elevations. Blackbrush communities also occur in the Mojave, where they are bounded by the creosote-bursage (*Larrea tridentata–Ambrosia dumosa*) community at lower elevations and by pinyon-juniper-sagebrush at upper elevations (Lei and Walker 1995). Blackbrush is found in some of the most scenic areas of the Southwest, and it provides cover and food for a number of wildlife species, most notably heteromyid rodents (Auger 2005), nongame birds, deer, and desert bighorn (Bradley 1965; Brown and Smith 2000).

The blackbrush community is currently under threat from the combined effects of exotic species, large-scale fires, and climate change. Predicted effects of climate change on recruitment of blackbrush make it unlikely that blackbrush will persist in place. Blackbrush has little resistance to invasion by exotic species and very little resilience to subsequent large-scale fires. Blackbrush itself is not fire adapted and does not resprout when burned (Brooks 2009). Large areas of the blackbrush community have burned in the last decade, although primarily in the Mojave. Natural recovery from these and other large-scale disturbance events is apparently not possible, and the resulting vegetation then becomes dominated primarily by exotic weed species (Brooks 2009).

In this chapter, we summarize the current state of knowledge of blackbrush biology, including reproductive biology, establishment ecology, interaction with herbivores, response to disturbance, and genetic structure. We report on current studies of interpopulation variation and potential response to climate change. Finally, we assess current efforts at restoration and identify needs for additional research.

DISTRIBUTION AND GENETIC STRUCTURE

Prior to the early 1970s, very little was known about blackbrush, despite its occurrence as a landscape dominant on over three million hectares (Pendleton and Meyer 2004). The first intensive study of blackbrush biology was done by Jim Bowns as part of his PhD research (Bowns 1973). Most of Bowns' dissertation was subsequently published as a research report (Bowns and West 1976), which included a distribution map for blackbrush compiled from a number of sources. More recently, Richardson and Meyer (2012) developed a map of predicted distribution based on bioclimatic profiles (figure 10.1). Unlike the map of Bowns and West (1976), the newer map shows a distinct break between Colorado Plateau and Mojave Desert populations.

This break in distribution is reinforced by genetic analysis (Richardson and Meyer 2012), which revealed the existence of two metapopulations corresponding to Colorado Plateau and Mojave Desert regions. This same study also refuted the long-held assumption that blackbrush was a paleoendemic species, generally lacking in genetic variation (Stebbins 1972; Stebbins and Major 1965). The assumption was based primarily on the fact that the genus is monotypic with few close relatives (see Potter et al. 2007). Current distribution was thought to represent a restriction from a much wider distribution during the Cretaceous period to xeric "islands" during the onset of more mesic Tertiary conditions during which the gene pool became depauperate (Stebbins 1972). In contrast, studies have now revealed a relatively high level of genetic diversity within blackbrush populations, as well as significant population differentiation (Richardson and Meyer 2012; Schuster et al. 1994). The existence of two metapopulations also provides context for prior work demonstrating that the two population groups differ in other important ways related to their germination characteristics and establishment strategies (Meyer and Pendleton 2005; Pendleton and Meyer 2004).

SOILS AND SOIL MICROORGANISMS

Blackbrush stands typically occur on upland terraces, ridges, open plains, and alluvial slopes (Bowns 1973; Bowns and West 1976; Turner 1994). Edaphic conditions largely

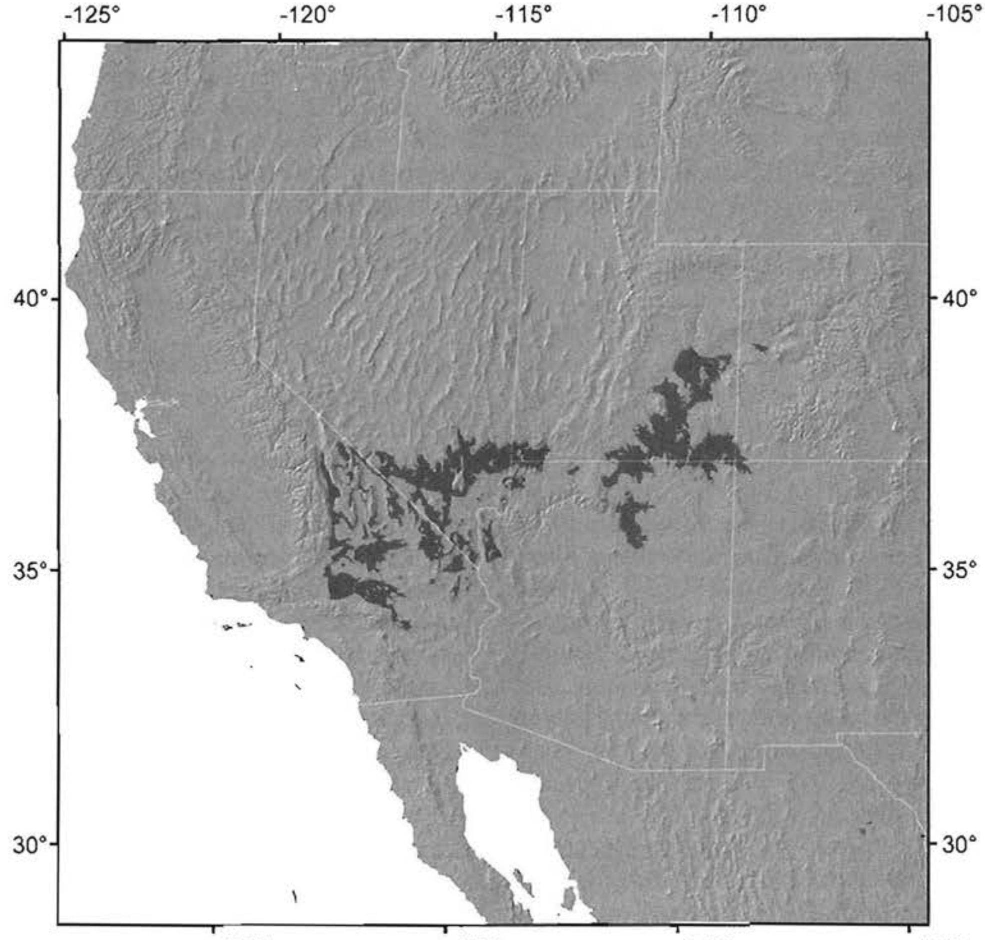

Figure 10.1. Predicted distribution of blackbrush based on a bioclimatic profile from Richardson and Meyer (2012).

control the amount of blackbrush present within a vegetative community (Thatcher 1975). Soils are generally described as coarse, shallow, poorly developed, and calcareous (Anderson 2001; Kearney and Peebles 1960; Shreve 1942). However, more specific descriptions are needed. Parent materials in the Colorado Plateau frequently consist of sandstone or siltstone, whereas mixed alluvium and basalts are more common on Mojave sites, and often they have a pronounced petrocalcic layer (Bowns 1973). Blackbrush is saline sensitive (Wallace and Romney 1972) and does not occur on soils with high salt content (Bowns and West 1976; Shreve 1942). A more comprehensive description of blackbrush soil relationships across the geographic range is sorely needed, as available soils data are somewhat limited.

In the Colorado Plateau, blackbrush sites characteristically exhibit well-developed biotic crusts, which help to stabilize sandy soils in the relatively large perennial plant canopy interspaces (Belnap and Lange 2003; Munson, Belnap, and Okin 2011). Soil crusts in the Mojave are less developed

Figure 10.2. Photograph of a pedestalled blackbrush plant showing the high degree of soil erosion that often follows destruction of biological soil crusts on the Colorado Plateau.

and are dominated by cyanobacteria with occasional patches of lichen and moss. Soil organic matter, nitrogen, and phosphorus are reportedly higher under blackbrush plants than in interspaces, which is consistent with the fertile island effect common to shrublands (Bowns and West 1976; Thompson et al. 2005). Wallace and Romney (1972) attributed the increase in nitrogen to symbiotic nitrogen fixation within the shrub rhizosphere. However, biological soil crusts are the predominant source of nitrogen in many arid ecosystems (Evans and Ehleringer 1993), and nitrogen fixed by soil crust cyanobacteria can be translocated to plant roots through mycorrhizal and dark septate fungal associations (Green, Porras-Alfaro and Sinsabaugh 2008; Hawkes 2003). This mechanism may well be operating in the well-defined soil crusts of the Colorado Plateau and, to a more limited extent, in the Mojave. In greenhouse studies, blackbrush seedlings exhibited a positive growth response to the presence of arbuscular mycorrhizae and biological soil crusts (Pendleton, Pendleton, and Howard 1999). Large-scale hot fires can disrupt these soil relationships, and loss of soil crust from any kind of disturbance can lead to significant erosion (figure 10.2; Belnap and Lange 2003; Munson et al. 2011).

REPRODUCTIVE BIOLOGY

Flowering in blackbrush typically occurs during April and early May and is induced by moderate to heavy winter precipitation. The timing and degree of flowering varies significantly from year to year (Beatley 1974). Population flowering occurs over a period of 2–3 weeks (Pendleton and Meyer 2004). Individual flowers are open 4–5 days, and most of the anthers dehisce within the first 24 hours (Pendleton and Pendleton 1998). Flowers are perfect and regular, with a perianth usually consisting of four persistent yellow petaloid sepals (Welsh et al. 1993). The fruit is a glabrous chestnut-brown achene. Blackbrush is wind-pollinated and largely self-incompatible, but it exhibits characteristics indicative of evolution from an insect-pollinated ancestor. In addition to the showy petaloid sepals, rare individuals with 1–4 yellow petals have been observed in most populations, and plants occasionally produce more than one fruit per flower (Pendleton and Pendleton 1998).

Blackbrush is mast-seeding, which is defined as the "synchronous intermittent production of large seed crops in perennial plants" that "results from weather conditions or is an evolved plant reproductive strategy" for satiating predators (Kelly and Sork 2002, 427). Mast-seeding in blackbrush is a composite of both forces. The size of the seed crop is related to precipitation and plant resource reserves, which accumulate slowly in woody desert species (Pendleton, Meyer, and Pendleton 1995). Mast-seeding events deplete resource reserves such that, even when adequate winter precipitation occurs in successive years, blackbrush does not produce successive large fruit crops. A mast-year's crop comprises almost all of the seed production at low elevations, whereas some seeds are produced in more mesic higher-elevation sites in all but the driest intermast years (Pendleton, Meyer, and Pendleton 1995). Periods between mast-seed crops often exceed five years. Late frosts can reduce or eliminate flowering and fruit production (Pendleton 2008; Pendleton, Meyer, and Pendleton 1995).

Blackbrush fruits ripen between late May and the third week of July depending on elevation and weather conditions (Pendleton 2008). Natural seed-fall is correlated with rain showers, which dislodge the achenes from the floral cup (Auger 2005). Achenes have no special morphological traits that would aid in dispersal, but they are gathered and cached by heteromyid rodents (Auger 2005; Bowns and West 1976). In the Colorado Plateau (Auger 2005), these consist primarily of Ord's kangaroo rat (*Dipodomys ordii*) and the plains pocket mouse (*Perognathus flavescens*). In the Mojave, the chisel-toothed kangaroo rat (*D. microps*) is the major disperser (Beatley 1976).

GERMINATION AND ESTABLISHMENT

Freshly collected seed of blackbrush is largely dormant. Dry after-ripening under summer field conditions may reduce initial dormancy, and winter chilling removes any remaining dormancy (Meyer and Pendleton 2005; Pendleton and Meyer 2004). The amount of chill required to break dormancy is correlated with collection site's elevation. Seeds from low-elevation sites have shorter chilling requirements than seeds from higher elevation sites. Also, seeds from higher, colder sites, where winter snow regularly occurs, have a lower optimum temperature for chilling and can germinate faster when incubated at near-freezing temperatures (Pendleton and Meyer 2004). In the field, germination takes place in late winter, under winter rain conditions at warm desert Mojave sites, and under snow at colder Colorado Plateau sites (Meyer and Pendleton 2005). This ecotypic variation functions to time germination optimally in habitats with contrasting chilling regimes (Pendleton and Meyer 2004).

Blackbrush does not form a persistent seed bank, and recruitment depends on seed produced during the previous summer. Seeds are collected by heteromyid rodents (kangaroo rats and pocket mice) and cached in scatter hoards (Auger 2005). Scatter hoarding is the collection of seed by heteromyid rodents and subsequent burial in small surface caches (Longland et al. 2001). The rodents later return to recollect the seed and store it in their burrows (larder hoards). Larder-hoarded seeds are removed from the seed bank, but scatter hoards that were not recollected form a short-term seed bank. Burial by rodents is generally required for blackbrush seed to germinate and for successful seedling establishment.

Following germination, several weeks of root growth occurs prior to shoot emergence in early spring (Pendleton 2008). Timing of emergence varies with region: February for warm winter Mojave Desert populations and March for Colorado Plateau populations. Seeds and emerging seedlings are very palatable to heteromyid rodents, and therefore, successful recruitment is primarily limited to periods following a mast-seed crop when some of the cached seed can escape predation (Auger 2005). Successful establishment is a relatively rare event, requiring two years of above-average precipitation—one to produce a seed crop of sufficient size and another for seedlings to get through the summer. Emerged seedlings have very low survivorship over time due to herbivory and summer moisture limitation (Bowns and West 1976). Meyer and Pendleton (2005) found establishment success to be greatest for seeds from local populations, indicating ecotypic differentiation in emergence and establishment strategies for Mojave and Colorado Plateau populations. Overall establishment success, however, was much greater on the Colorado Plateau where cooler temperatures and more dependable summer moisture prevail (figure 10.3).

RESPONSE TO DISTURBANCE AND CLIMATE CHANGE

Blackbrush communities are under threat from the combined effects of climate change, invasive grasses, and increased fire frequency. Global climate change models predict higher temperatures and an increase in extreme drought events for the Southwest (Archer and Predick 2008; Cayan et al. 2010; Seager et al. 2007). Drought has multiple effects on seed set and seedling recruitment. Increased drought during seed fill can negatively affect seed production of long-lived mast-seeding woody species (Pérez-Ramos 2010), and the stress period for seedlings is the time between the loss of winter soil moisture and the onset of monsoonal moisture in July–September. While mature plants undergo dormancy during this time, the majority of seedling mortality occurs during this period. Greater than normal precipitation during this usually dry period appears to be the key to seedling survival. Predicted increases in summer temperatures, coupled with a higher incidence of drought, will exacerbate seedling stress and make successful recruitment an even rarer event.

Predicted effects of climate change on recruitment of blackbrush make it unlikely that blackbrush will persist in place. Current observations suggest an upward elevational shift in distribution for this species in response to a long-term warming trend (Meyer and Pendleton 2005). Data from packrat middens reveal past migration of the blackbrush ecotone. Blackbrush has been reported from Late Pleistocene midden sites along the lower Colorado River Valley, far to the south of its current range, as well as at lower elevations of the Grand Canyon (Cole 1990a, 1990b; Hunter and McAuliffe 1994; King and Van Devender 1977; Van Devender 1990). During the late Pleistocene and early Holocene, blackbrush migrated northward and upward in elevation into the Mojave Desert and Colorado Plateau, likely reaching its historic distribution in the late Holocene (Coates, Cole, and Mead 2008; Cole 1990a, 1990b; Hunter and McAuliffe 1994). The paleo records, therefore, indicate that blackbrush has the ability to migrate in response to changes in climate; however the speed at which future changes occur may

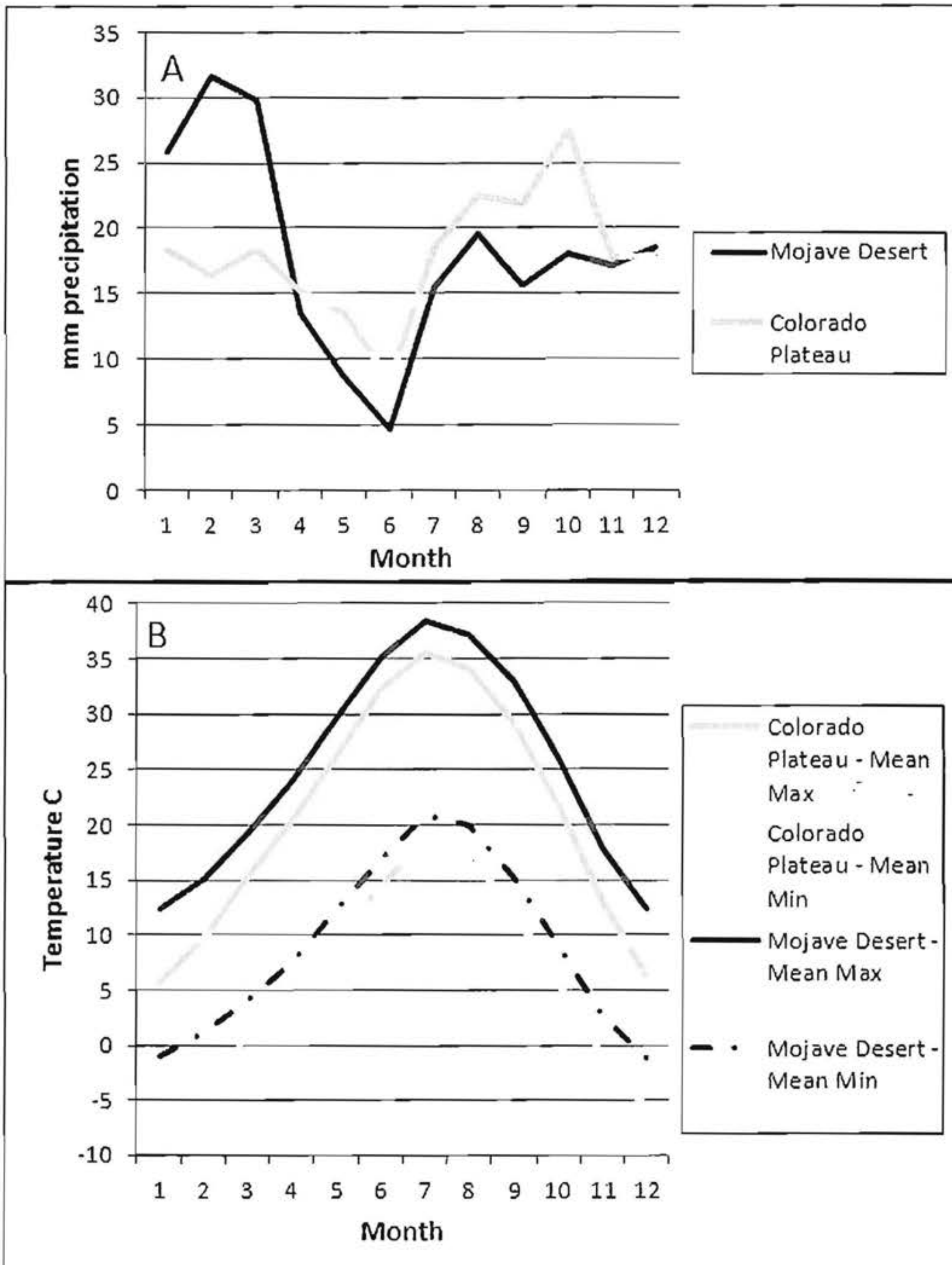

Figure 10.3. Long-term average precipitation (A) and temperature (B) profiles for Colorado Plateau and Mojave Desert blackbrush habitats. For temperature, heavy lines depict mean monthly highs, while broken lines depict mean monthly lows. Graphs represent composite averages for six locations in each region. (Modified from Pendleton et al. 2012.)

preclude natural migration for long-lived species with episodic recruitment.

By far the greatest threat to the blackbrush community comes from the combination of exotic grasses and accompanying changes in the fire regime. Climate change models predict an increase in the incidence of large-scale wildfire (Marlon et al. 2009). As stated earlier, the blackbrush community has little resistance to invasion by exotic annual grasses and is extremely vulnerable to fire (Brooks and Chambers 2011; Brooks and Matchett 2006). Historically, low amounts of fine fuels present in shrub interspaces limited the spread of fires except under extreme conditions (Brooks, Esque, and Duck 2007), and recovery often occurred within a few decades (Brooks and Matchett 2006). Natural fire-return intervals were likely on the order of centuries (Webb et al. 1987). Extensive burning of blackbrush stands in the mid-1900s to improve livestock production had unpredictable outcomes and mostly resulted in less desirable vegetation (Bowns and West 1976; Brooks, Esque, and Duck 2007). Burned blackbrush stands took many years to recover, if at all.

Exotic grasses now present in most blackbrush stands in the Mojave create large amounts of fine fuels following years of high rainfall (Brooks and Matchett 2006). Ensuing fires can burn large areas and encourage dominance by early-seral exotic annuals that, in turn, perpetuate shorter fire-return intervals (Brooks 2009; Brooks and Pyke 2002; Engel and Abella 2011). For example, Esque (2009) modeled blackbrush habitat and fire perimeters in the Mojave immediately following years of high rainfall. Their study revealed that nearly 7,700 km^2 of blackbrush habitat burned in 2005–2006 alone. The Ely Bureau of Land Management District had the highest impact, with about 40% (112,502 ha) of the district's blackbrush communities burned during the 2005 and 2006 fire seasons.

Recruitment following fire is seed limited. Partially burned adult plants may recover to some extent, but most large-scale fires are stand-replacing. Seedlings are not fire-tolerant, but if a fire occurs in the summer after seeds are cached (June), seeds may survive the fire and emerge in the winter and spring (Zitzer 2009). Rodent behavior is at least partially responsible for the lack of recovery following large fires, as seed movement by granivores into a burned area is restricted (Beatley 1976). In the Mojave, the kangaroo rat (*D. microps*), which occupies the unburned blackbrush community, does not cache seeds in open areas, such as burns, due to predation threat. On the other hand, small-scale disturbances, such as pipelines, road cuts, and rights-of-way, can be revegetated with seed caches and will recover in time (Beatley 1976).

While concern over loss of blackbrush habitat has centered around Mojave populations, the Colorado Plateau is not immune from similar losses. There are many reports of dramatic increases in exotic annual grass cover in grasslands of the Colorado Plateau (Belnap, Phillips, and Troxler 2006; Enserink 1999; Hanson 1999; Rimer and Evans 2006; Schwinning et al. 2008). Although cheatgrass (*Bromus tectorum*) does not currently occur extensively in blackbrush habitat, new strains of cheatgrass may be able to adapt and persist. Furthermore, the impact that climate change will have on invasive species in general and annual grasses specifically is not well understood. Predictions range from an increase in the number of invasive species and the expansion of exotic annual grasses (e.g., Abatzoglou and Kolden 2011; D'Antonio and Vitousek 1992) to a decrease in potential habitat for cheatgrass, at least, in the Southwest (Bradley 2009). Consequently, while blackbrush communities in the Colorado Plateau have not yet experienced the same kind of fire-cycle increase that has occurred in the Mojave, it is possible that new introductions of invasive species, combined with predicted alterations in temperature and precipitation patterns that will accompany climate change, could alter fire patterns on the Colorado Plateau.

RESTORATION POTENTIAL AND GUIDELINES

Blackbrush is considered to be one of the most challenging ecosystems to restore (Brooks and Matchett 2006; Hansen and Ostler 2008). There have been attempts to seed blackbrush (Abella and Newton 2009), but success has been limited. Transplants have also met with mixed success (Monsen, Stevens, and Shaw 2004). It is our hope that an understanding of the biology of blackbrush will increase the success of future restoration efforts.

Blackbrush mast-seed crops are produced infrequently and, therefore, seed availability is likely to be a limiting factor in restoration. However, blackbrush seed does maintain viability in storage. Germination and emergence tests on 32 seed collections that had been kept at room temperature for 12–27 years revealed that seed lots with good initial viability maintained a viability of greater than 80% for 10–12 years (Pendleton et al. 2012). Large quantities of good quality seed can easily be collected in mast-years and stored for future use. For example, in 2008, volunteers collected a large mast crop of Mojave blackbrush seed for use in future plant production and seeding projects. This volunteer-collecting effort is a good example of a cost-effective method of providing a supply of seed for use after fire or other disturbances (Brean 2008).

Germination and establishment success may be enhanced by planting seeds in the fall to meet chilling requirements and at a depth of 2.5–4.0 cm to mimic rodent cache depth. It may also be necessary to protect emerging seedlings from rodent predation (Jones 2012). In emergence experiments in the Mojave and Colorado Plateau, protective hardware cloth cages were effective in reducing seed and seedling predation, which resulted in higher survivorship than for uncaged seeds (Meyer and Pendleton 2005). Seeding in groups (caches) also seems to improve survival. Blackbrush is adapted to growing in clusters, and natural recruitment often occurs under established nurse plants (Jones 2012; S. Kitchen unpublished data). It may therefore be useful to establish nurse plants on large burned areas by including other species that have high seedling success rates in a seed mix (Abella and Newton 2009), or through the use of transplants to establish shrub islands. It is important, too, to use an appropriate seed source, as Mojave and Colorado Plateau populations differ in their germination and establishment strategies (Meyer and Pendleton 2005; Pendleton and Meyer 2004). There are also elevational differences among populations in chilling requirements.

Restoration may also be accomplished through the use of transplants. Production of blackbrush plants for transplanting is not difficult (Pendleton 2008), but use of a well-drained soil medium is necessary as seedlings are susceptible to overwatering (Pendleton 2008; Wallace and Romney 1972). Even older, stored seed can be successfully used to produce seedlings. We have successfully produced seedlings from seed stored for 27 years by first germinating seeds in a growth chamber (Pendleton et al. 2012). In the Mojave, transplants would need additional water to become established, likely for multiple years (Winkel et al. 1995; Pendleton unpublished data). In contrast, Colorado Plateau plantings have been established without second year supplemental water due to the more predictable summer moisture (Hughes and Weglinski 1991).

Whether by seedings or transplants, restoration efforts will meet greater success at the upper blackbrush ecotone or above. Predicted climate change variables of increasing CO_2, higher nighttime winter temperatures, and lack of spring and early summer moisture all suggest that attempts to restore blackbrush communities at lower elevations would be unlikely to succeed. A recent restoration study using blackbrush seed reported larger and more numerous seedlings at mid and high elevations (Jones 2012), which is a result that supports our own observations.

Additionally, an understanding of how genetic variation is arrayed across the landscape is necessary for successful restoration and conservation efforts. Restoration of a viable blackbrush community must take into account the existence of the Mojave and Colorado Plateau metapopulations (Richardson and Meyer 2012) and use genetically appropriate sources for blackbrush seed. Further development of seed transfer zones will aid in this effort.

RESEARCH NEEDS

Despite 40 years of active research on the biology and ecology of blackbrush, questions remain. Would use of a pre-emergent herbicide prior to seeding increase success? In the Mojave, the lack of moisture between emergence and the monsoon cannot be overcome without irrigation. Might the use of hydrogels overcome this need? Could the establishment of appropriately placed shrub islands within large disturbances influence rodent caching behavior? How do soil characteristics affect invasibility? What is the frequency of successful seedling establishment, and how might this change under future climate conditions? The growth chamber experiments (Pendleton et al. 2012) were an initial step in determining viability of seed in long-term storage, but field trials with older seed are needed along with additional work on seed transfer zones, seeding rates, and appropriate seed mixes for a given location. Field studies are needed to test the guidelines given above, including the effectiveness of nurse plants of various species (e.g., Jones 2012; Scoles-Sciulla, DeFalco, and Esque 2014) and seeding techniques that improve establishment success. Restoration of the blackbrush ecosystem presents a major challenge that requires further research, as well as the development of new and better restoration techniques.

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