



Male Greater Sage-Grouse displaying on their lek near St Anthony, Idaho. Photo by Brian Perkes

Conserving and restoring habitat for Greater Sage-Grouse and other sagebrush-obligate wildlife: the crucial link of forbs and sagebrush diversity

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ABSTRACT

In the western US, Greater Sage-Grouse (*Centrocercus urophasianus* Bonaparte [Phasianidae]) have become an indicator species of the overall health of the sagebrush (*Artemisia* L. [Asteraceae]) dominated communities that support a rich diversity of flora and fauna. This species has an integral association with sagebrush, its understory forbs and grasses, and the invertebrate community dependent on that flora. Adult birds and their growing chicks consume a wide variety of understory species, and the invertebrates that develop on this flora are an important source of protein, especially for developing broods. Restoration plans for degraded sagebrush communities must consider outplanting the correct species and seed source of sagebrush and its diverse array of native forbs. Changes in climate and the problem with invasive species, especially annual grasses that spawn large-scale fires, will need to be addressed so that restoration efforts can succeed.

Dumroese RK, Luna T, Richardson BA, Kilkenny FF, Runyon JB. 2015. Conserving and restoring habitat for Greater Sage-Grouse and other sagebrush-obligate wildlife: the crucial link of forbs and sagebrush diversity. *Native Plants Journal* 16(3):277–299.

KEY WORDS

Centrocercus urophasianus, *Artemisia*, habitat, restoration, forbs, invasive species

NOMENCLATURE

Plants: USDA NRCS (2015)

Fungi: Farr and Rossman (2015)

Animals: ITIS (2015)

Birds: AOU (2015)

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Once covering 69 million ha (170 million ac) in 16 states and 3 provinces, quality sagebrush (*Artemisia* L. [Asteraceae]) habitat is now an imperiled ecosystem in the US (Noss and others 1995). Native floras of the sagebrush biome are remarkably diverse and species rich, with numerous endemic genera and species (Figure 1). Collectively, these areas contain more than 5000 plant taxa (Cronquist and others 1972–2012; Hitchcock and others 1987; Baldwin and others 2002, 2012). They are centers of diversity for a significant number of monotypic and species-rich genera (Table 1), many of which are narrow or regional endemics, and new species are still being discovered, such as *Lomatium ochocense* Helliwell & Constance (Apiaceae) from central Oregon (Helliwell 2010).

This diverse flora in turn supports a diverse invertebrate community including herbivores, predators, detritivores, important pollinators of regional flora, and the western population of the monarch butterfly (*Danaus plexippus* L. [Lepidoptera: Nymphalidae]). Together, the diverse flora and invertebrate community support numerous obligate wildlife species such as the pygmy rabbit (*Brachylagus idahoensis* Merriam [Leporidae]), sagebrush vole (*Lemmiscus curtatus* Cope

TABLE 1

Forb genera with high species diversity within the sagebrush biome of western North America.

Genus and authority	Family
<i>Allium</i> L.	Liliaceae
<i>Astragalus</i> L.	Fabaceae
<i>Calochortus</i> Pursh	Liliaceae
<i>Castilleja</i> Mutis ex L.f.	Scrophulariaceae ^z
<i>Eriogonum</i> Michx.	Polygonaceae
<i>Lomatium</i> Raf.	Apiaceae
<i>Lupinus</i> L.	Fabaceae
<i>Penstemon</i> Schmidel	Scrophulariaceae ^z
<i>Phlox</i> L.	Polemoniaceae
<i>Trifolium</i> L.	Fabaceae
Multiple genera	Asteraceae

^z ITIS (2015) places *Castilleja* in the Orobanchaceae and *Penstemon* in the Plantaginaceae.



278 Figure 1. Greater Sage-Grouse habitat in the Virginia Mountains of Nevada. Photo by Steven Schwarzbach, US Geological Survey

[Cricetidae]), pronghorn (*Antilocapra americana* Ord [Antilocapridae]), Sagebrush Sparrow (*Artemisiospiza nevadensis* Bruant des armoises), Sage Thrasher (*Oreoscoptes montanus* JK Townsend [Mimidae]), and more than 200 species of other resident and migratory birds.

Of the birds of the sagebrush biome, the Greater Sage-Grouse (*Centrocercus urophasianus* Bonaparte [Phasianidae]) and Gunnison Sage-Grouse (*Centrocercus minimus* Young and others) have become “canaries in the coal mine” as indicators for the health of the North American sagebrush landscape. These 2 species of sage-grouse have a remarkable life history entwined with sagebrush. Males assemble in areas called “leks” during the breeding season (late winter through spring) to court females with their spectacular mating displays (Figure 2). Nesting hens, brooding females, and chicks rely directly on a high diversity of annual and perennial forbs; sage-grouse diet of those forbs and the biodiverse, high-protein invertebrates associated with the plants is critical for the species survival.

In 1805, near the confluence of the Marias and Missouri Rivers, Meriwether Lewis remarked, *I saw a large flock of the mountain cock, or a large species of heath hen with a long pointed tail that the Indians informed us were common to the Rocky Mountains, and later that winter, the Cock of the Plains is found in the Plains of the Columbia and are in great abundance from the s.e. fork of the Columbia to that of Clark's River [Clark Fork River].*

Today, the Gunnison Sage-Grouse roams the Colorado Plateau, whereas the Greater Sage-Grouse (GRSG) occurs in just half of its original range in the Great Basin, Columbia River Basin, and Wyoming Basin and some areas of the northern and western Great Plains. Gunnison Sage-Grouse was listed as



Figure 2. A displaying male Greater Sage-Grouse on a lek in Butte County, South Dakota. Photo by Steve Fairbairn, US Fish & Wildlife Service

threatened under the Endangered Species Act (ESA) in 2014 (Federal Register 2014). Although listing GRSG under the ESA was recently deemed not warranted, its status will be re-evaluated in 5 y (USDI 2015). Today, most remaining GRSG populations are associated with habitats at more northern latitudes or higher elevations, and (or) within more mesic or colder sagebrush environments (Connelly and Braun 1997).

Because Gunnison Sage-Grouse and GRSG are believed to have similar life histories and habitat requirements and because most literature concentrates on GRSG, the focus of this paper will be on GRSG, recognizing that key points are most likely applicable to Gunnison Sage-Grouse, too. Our objectives are to demonstrate to nursery managers, seed producers, and land managers the importance of floral diversity to sustainable populations of both sage-grouse species (Gunnison and Greater) and to encourage those professionals to produce and deploy more native plants, especially forbs, in habitat restoration efforts.

THREATS TO SAGE-GROUSE

A suite of threats are affecting sage-grouse; these threats are often broadly lumped together as the loss, fragmentation, and degradation of sagebrush ecosystems, which are primarily driven by human activities (Connelly and others 2011). These anthropogenic activities are now interacting in complex ways (see Finch and others 2015 for a concise review), and important drivers include invasive annual grasses, encroachment by trees, altered fire cycles, grazing, and climate change (Davies and others 2011). The decades of chronic loss, fragmentation, and degradation within the sagebrush ecosystem has led to the acute potential problem of several sagebrush obligate wildlife species being considered for threatened or endangered status at the state and federal levels, which would have a large implication on the management and use of western rangelands. Two other drivers in the current discussion are pesticides and energy development.

By the 1970s, more than 2 million ha (nearly 5 million ac) of sagebrush had been mechanically treated, sprayed with herbicides, or burned to improve grazing (Hull and others 1952; Schneckas 1967; Vale 1974), often during spring and early summer at the height of GRSG nesting and brood rearing, resulting in declines in sage-grouse populations and habitat quality (Connelly and others 2000; Beck and others 2003, 2012; Crawford and others 2004). These treatments also negatively affected populations of understory native floras, health of biological soil crusts, and persistence of native seedbanks (Belnap and Eldridge 2003; Thacker and others 2012).

Herbicide use is a factor for GRSG survival. 2,4-D is a very commonly used phenoxy herbicide used for control of broadleaf plants in rangelands. Perennial forbs important to the dietary requirements of pre-laying hens, chicks, and juveniles, such as those in the species-rich Asteraceae, Liliaceae, Rosaceae,

Plantaginaceae, Orobanchaceae, and Fabaceae that support entire communities including a web of regional pollinators, are severely damaged or killed by 2,4-D. In addition, modern formulations of 2,4-D are highly toxic to bees (Hymenoptera) (Dow Chemical Company 2015), which may have long-term implications for forb reproduction if pollination services are hindered. It may take several years for annual plant recovery or recruitment following 2,4-D application (Thacker and others 2012). Broadleaf herbicides can also have long-term effects on remaining native perennials. Picloram, for example, reduced flowering of established arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt. [Asteraceae]) plants and occurrence of new seedlings for at least 4 y after application (Crone and others 2009). Sites with herbicide-reduced cover of native vegetation are vulnerable to infestation by invasive annual grasses, such as cheatgrass (*Bromus tectorum* L. [Poaceae]).

Insecticides, such as those used to control grasshoppers (Orthoptera: Acrididae) (Johnson and Boyce 1990) and Mormon crickets (*Anabrus simplex* Haldeman [Orthoptera: Tettigoniidae]), can be toxic to adult birds (Blus and others 1989), and low rates of annual GRSG recruitment, especially in areas where sagebrush habitat interfaces agricultural fields, may be attributable to insecticides. Juveniles are attracted to agricultural fields during late summer months (Peterson 1970) after many preferred native forbs have senesced for the season.

In addition, oil, gas, coal, and wind energy development in sagebrush-dominated habitats during the past 20 y has nega-

tively affected GRSG. Holloran (2005) noted that the number of producing wells has more than doubled, and this development in sagebrush habitat far exceeds GRSG tolerance thresholds. Unfortunately, current energy expansion is occurring in some of the best remaining sagebrush communities and within areas having the highest density populations of GRSG and other sagebrush-obligate species (Knick and others 2003; Crawford and others 2004; Kaiser 2006; Bergquist and others 2007). Threats to GRSG associated with energy development include a number of detrimental effects: increased fragmentation leading to disrupted habitat use patterns (Lyon and Anderson 2003; Ingelfinger and Anderson 2004; Aldridge and Boyce 2007; Walker and others 2007; Doherty and others 2008; Blickley and others 2012; LeBeau 2012), increased chick mortality proximate to oil and gas projects (Aldridge and Boyce 2007), increased invasive plant establishment along roads (Gelbard and Belnap 2003), and problems associated with wastewater holding ponds, such as potential facilitation of the spread of West Nile virus (Schrag and others 2011).

SAGEBRUSH COMMUNITIES

At first glance, sagebrush may appear to be homogenous (Figure 3); closer inspection has, however, revealed an intricate, species-rich mosaic of sagebrush taxa that are largely defined by climate and soil properties (Barker and McKell 1983; Mahalovich and McArthur 2004; Miglia and others 2007; Still and



280 Figure 3. *Artemisia tridentata* ssp. *tridentata* in the Centennial Valley of southwestern Montana. Photo by Bebe Crouse, The Nature Conservancy

Richardson 2015). Moreover, ecotones between these mosaics often harbor sagebrush derived from hybridization (McArthur and others 1988), some of which have been recognized by researchers as subspecies (Garrison and others 2013). These mosaics in turn foster various assemblages of flora and fauna referred to as communities that are critical to sustaining sage-grouse.

Classifying these taxa and characterizing the environments where they occur is a key activity and essential to successful restoration. The most predominant sagebrush species across the Great Basin, Wyoming Basin, and Colorado Plateau is *A. tridentata* (full nomenclature for most species discussed in this article is found in Tables 1–4). This species has, however, clearly diverged into subspecies that occupy specific niches (Mahalovich and McArthur 2004; Shultz 2006). Two subspecies, *A. tridentata* ssp. *tridentata* (basin big sagebrush) and *A. tridentata* ssp. *wyomingensis* (Wyoming big sagebrush), co-occur in basin habitats but are differentiated based primarily on soil depth (Barker and McKell 1983; McArthur and Sander-son 1999). With increasing elevation and precipitation these subspecies transition into subspecies *A. tridentata* ssp. *vaseyana* (mountain big sagebrush). Genetic markers (Richardson and others 2012), growth rates (McArthur and Welch 1982), and phytochemicals (Stevens and McArthur 1974; Welch and McArthur 1981; Kelsey and others 1983; Wilt and others 1992) can be used to differentiate these 3 subspecies. In addition to these 3 widespread subspecies, 4 range-restricted subspecies (Table 2) occur across the Great Basin, Colorado Plateau, and southwestern US (Goodrich 2005). These subspecies have likely formed through hybridization with other subspecies or species similar to that proposed by Garrison and others (2013).

Dwarf sagebrush, *A. arbuscula* (includes 3 subspecies) and *A. nova*, are an important component to sagebrush communities (Goodrich 2005; Shultz 2006). These species are typically found in areas where soil and (or) climatic characteristics do not support *A. tridentata* (Rosentreter 2005). For example, *A. nova* can occupy ridgetops or rocky soils and form boundaries with *A. tridentata* ssp. *wyomingensis*. *Artemisia nova* can also form more continuous distributions, apparently driven by warmer and drier climates at lower elevations (Kitchen and McArthur 2007). Similarly, some subspecies of *A. arbuscula* occupy poorly drained claypan soils. Other sagebrush species have regional importance to mosaics and sage-grouse habitat. These include *A. tripartita* ssp. *tripartita* distributed across higher elevations that co-occur primarily with *A. vaseyana*, *A. rigida* distributed across basalt scablands in the Columbia Basin and Oregon, and *A. cana* ssp. *cana* found principally along the front range of the Rocky Mountains (Mahalovich and McArthur 2004; Rosentreter 2005). This robust mosaic of taxa is the foundation for sagebrush community floral diversity necessary for supporting sage-grouse. Biologists can use a pocket

Artemisia field guide (Shultz 2012) to help distinguish taxa and communities. While ample information and understanding of sagebrush taxonomy and niche specialization exists, developing the guidelines and methodologies to support a successful habitat restoration framework remains a major challenge.

SAGEBRUSH HABITAT USE

In general, GRSG use sagebrush habitat for courting, cover, and food based on sagebrush species composition and density. GRSG populations can remain resident in some areas, while other populations migrate between winter and breeding habitat or exhibit more complicated movements (Eng and Schladweiler 1972). Juvenile birds can use a wide range of habitats during autumn dispersal (Dunn and Braun 1986; Hannon and Martin 2006). Home range size varies from 125 km² to 2764 km² (30,888 ac to 683,000 ac) (Connelly and others 1988; Leonard and others 2000; Smith 2013). Leks occur where sagebrush cover is minimal (< 10%), such as open meadows, sparsely vegetated ridges, and even agricultural fields (Ellis and others 1989; Connelly and others 2004). Females can travel great distances from breeding leks to suitable nesting habitat (Braun and others 2005).

Although pre-laying hens use dwarf sagebrush communities for feeding (Figure 4), nesting occurs primarily in denser, tall sagebrush with tall native grass cover and proximity to abundant forbs (Connelly and others 2000; Thompson and others 2006; Hagen and others 2007; Ersch 2009). These sagebrush communities generally have canopy cover values that range from 12 to 43% (Connelly and others 2000). Throughout the Wyoming Basin and Great Basin, GRSG tend to utilize sagebrush communities that include *A. tridentata* ssp. *tridentata* and *A. cana* in valleys, floodplains, and lower elevations and *A. tridentata* ssp. *wyomingensis* and *A. tridentata* ssp. *vaseyana* at mid to higher elevations. *Artemisia rigida* is also used for cover and nesting in central Washington. In the northern Great Basin, nesting success is associated with dense sagebrush cover with 10 to 50% tall bunchgrass cover (Gregg and others 1994; Crawford and others 2004). While dwarf and tall sagebrush communities are most commonly used for nesting, other shrub communities in association with sagebrush can support nests, including those inhabited by *Purshia tridentata* Pursh DC (Rosaceae) and members of the Asteraceae (*Ericameria*, *Chrysothamnus*, *Tetradymia canescens* DC).

During late spring to early summer following hatch, broods move to more open sagebrush canopy cover to feed on insects and forbs. Not surprising, as canopy cover of big sagebrush decreases, the abundance of grasses and forbs increases (Olson and Whitson 2002) as does the abundance of invertebrates hosted by the herbaceous plants. Moreover, as discussed earlier, dwarf sagebrush (for example, *A. arbuscula*, *A. nova*, *A. tripartita*) inhabits soils less conducive to big sagebrush.

TABLE 2

Artemisia conservation status, range, and community types.

Species •According to Garcia and others (2011)	Global status	Range	Soils	Community ranks and types
<i>Artemisia arbuscula</i> Nutt. ssp. <i>arbuscula</i>	G5	CA, ID, MT, NV, OR, UT, WA, WY	Rocky, calcareous clays or silt loams	G2–G5 sage-steppe and grasslands
<i>A. arbuscula</i> ssp. <i>longicaulis</i> Winwood & McArthur	G4	CA, NV, OR	Alluvial silts and sands	Sage-steppe communities on alluvial fans
<i>A. arbuscula</i> ssp. <i>longiloba</i> (Osterh.) L.M. Shultz • <i>A. longiloba</i> (Osterh.) Beetle	G4	MT, WY	Fine textured, shallow clay or silt loams	G3–G4 sage-steppe and stream terraces
<i>A. arbuscula</i> ssp. <i>thermopola</i> Beetle	G5T3Q	CA, ID, OR, UT, WY	Well-drained to poorly drained clay soils above igneous or volcanic rock	G2 grasslands ID, WY
<i>A. bigelovii</i> A. Gray	G5	AZ, CA, CO, NV, NM, TX, UT	Shallow sandy to clay loams	G3 warm and cool woodlands, grasslands, desert rock vegetation, rock outcrops
<i>A. cana</i> Pursh ssp. <i>cana</i>	G4	Canada: AB, BC, MB, SK; US: CO, NE, ND, MN, MT, SD, WY	Sandy loams	G3–G4 sage-steppe, grasslands
<i>A. cana</i> ssp. <i>bolanderi</i> (A. Gray) G.H. Ward	G3G4?	CA, NV, OR	Gravelly loams	G1–G3 streams and sage-steppes mountain meadow
<i>A. cana</i> ssp. <i>viscidula</i> (Osterh.) Beetle	G3G4?	Canada: AB, MB; US: AZ, CO, ID, MT, NV, NM, UT, WY	Alluvial sandy loams to loams	G1–G5 wet meadows, streambanks, floodplains, snow beds
<i>A. filifolia</i> Torr.	G5	AZ, CO, KS, NE, NV, NM, OK, SD, UT, WY	Sandy or gravelly or clay loams with clay or caliche layers; biological crusts in Colorado Plateau	G1–G3 communities in western Great Plains G4–G5 communities dry sandy uplands washes and river floodplain terraces
<i>A. frigida</i> Willd.	G5	Throughout North America	Rocky, sands, sandy loams to clay loams	G3–G5 grasslands, woodlands, and sage-steppe
<i>A. longifolia</i> Nutt.	G5	Canada: AB, BC, MB, SK; US: ID, MT, NE, ND, SD, WA, WY	Shale derived sandy to clay loams	G3–G5 grasslands and open forests
<i>A. ludoviciana</i> Nutt.	G5	Throughout North America	Stony, sands, sandy to clay loams	G3–G5 communities, grasslands, sage-steppe, streams, river terraces, woodlands, talus slopes
<i>A. nova</i> A. Nelson	G5	CA, CO, ID, MT, NV, NM, OR, UT, WY	Shallow, gravelly, lithic, calcic	G1–G3 dry, rocky hills, open sage- steppe G4–G5 southern Great Basin and southwest US
<i>A. papposa</i> S.F. Blake & Cronquist	G4	ID, (NV), OR	Sands, sandy loams, sandy clays or poorly drained clays	G3/G4 sage-steppe and grasslands, 1 G2/G3 riparian community
<i>A. pedatifida</i> Nutt.	G4	ID, CO, southwest MT, WY	Sands, sandy loams, sandy clays derived from shales or sandstones or clays from alluvium	G2–G3 communities sage-steppe grasslands
<i>A. porteri</i> Cronquist	G2	WY	Barren, gravelly clays to clay loams	G2 barren slopes
<i>A. pygmaea</i> A. Gray	G3G4	AZ, CO, NV, NM, UT	Calcic, shale clays with gravel content, gypsum outcrops	G2 communities in some states; G3–G4 sage-steppe

TABLE 2 *continued**Artemisia conservation status, range, and community types.*

Species •According to Garcia and others (2011)	Global status	Range	Soils	Community ranks and types
<i>A. rigida</i> (Nutt.) A. Gray	G5	ID, MT, OR, WA	Stony, shallow rarely with clay subsoils	G2–G4 sage communities in dry rocky scablands, volcanic plains
<i>A. rothrockii</i> A. Gray	G3	CA	Clays to gravelly silt loams to loamy sands; often carbonate rich	G3 mountain meadows
<i>A. tridentata</i> Nutt. ssp. <i>parishii</i> (A. Gray) H.M. Hall & Clem.	G5T2T4	Central and southern CA	Dry, sandy	Desert, mountain, and coastal grasslands and shrub communities in valleys and foothills
<i>A. tridentata</i> Nutt. ssp. <i>spiciformis</i> (Osterh.) Kartesz & Gandhi • <i>A. spiciformis</i> Osterh.	G5T3T4	CA, CO, ID, MT, NV, WA, WY	Shallow loams, rocky	Subalpine, mountain sage-steppe and grasslands
<i>A. tridentata</i> Nutt. ssp. <i>tridentata</i> • <i>A. tridentata</i> ssp. <i>tridentata</i> (Osterh.) Beetle	G5	Canada: AB, BC; US: AZ, CA, CO, ID, MT, NE, NM, ND, OR, SD, WA, WY	Sandy to sandy loams, loess soils	G1–G5 warm to cool sage-steppe and grasslands
<i>A. tridentata</i> Nutt. ssp. <i>vaseyana</i> (Rydb.) Beetle	G4/G5	Canada: AB, BC; US: CA, CO, ID, MT, NE, NV, ND, OR, SD, UT, WA, WY	Loamy soils	G2–G4 cool sage-steppe, grasslands, forests and woodlands
<i>A. tridentata</i> Nutt. ssp. <i>wyomingensis</i> Beetle & A.M. Young	G5	CA, CO, ID, MT, NE, NV, ND, OR, SD, UT, WY	Loamy to clay soils	G1–G5 (WY) cool dry, sage-steppe, grasslands, forests and woodlands, rock vegetation
<i>A. tridentata</i> Nutt. ssp. <i>xericensis</i> Winward ex R. Rosentreter & R. Kelsey	G5T1T3	ID	Deep alluvial soils	G1 sage-steppe
<i>A. tridentata</i> Nutt. ssp. <i>xbonnevillensis</i> H. Garrison, L. Schultz, & E.D. McArthur	No rank	ID, UT	Sandy alluvial loams	Sage-steppe on lakeshore sediments
<i>A. tripartita</i> Rydb. ssp. <i>rupicola</i> Beetle	G5T3	MT, WY	Coarse-textured soils	G3 grassland and sage-steppe
<i>A. tripartita</i> Rydb. ssp. <i>tripartita</i>	G5T3T5	Canada: BC; US: CA, ID, MT, NV, OR, UT, WA, WY	Sandy to gravelly soils, loams, or loess over bedrock	G1–G3 grassland and sage-steppe
<i>A. tridentata</i> Nutt. ssp. <i>spiciformis</i> (Osterh.) Kartesz & Gandhi • <i>A. spiciformis</i> Osterh.	G5T3T4	CA, CO, ID, MT, NV, WA, WY	Shallow loams, rocky	Subalpine, mountain sage-steppe and grasslands
<i>A. tridentata</i> Nutt. ssp. <i>tridentata</i> • <i>A. tridentata</i> ssp. <i>tridentata</i> (Osterh.) Beetle	G5	Canada: AB, BC; US: AZ, CA, CO, ID, MT, NE, NM, ND, OR, SD, WA, WY	Sandy to sandy loams, loess soils	G1–G5 warm to cool sage-steppe and grasslands
<i>A. tridentata</i> Nutt. ssp. <i>vaseyana</i> (Rydb.) Beetle	G4/G5	Canada: AB, BC; US: CA, CO, ID, MT, NE, NV, ND, OR, SD, UT, WA, WY	Loamy soils	G2–G4 cool sage-steppe, grasslands, forests and woodlands
<i>A. tridentata</i> Nutt. ssp. <i>wyomingensis</i> Beetle & A.M. Young	G5	CA, CO, ID, MT, NE, NV, ND, OR, SD, UT, WY	Loamy to clay soils	G1–G5 (WY) cool dry, sage-steppe, grasslands, forests and woodlands, rock vegetation

continued

TABLE 2 *continued**Artemisia* conservation status, range, and community types.

Species •According to Garcia and others (2011)	Global status	Range	Soils	Community ranks and types
<i>A. tridentata</i> Nutt. ssp. <i>xericensis</i> Winward ex R. Rosentreter & R. Kelsey	G5T1T3	ID	Deep alluvial soils	G1 sage-steppe
<i>A. tridentata</i> Nutt. ssp. <i>xbonnevillensis</i> H. Garrison, L. Schultz, & E.D. McArthur	No rank	ID, UT	Sandy alluvial loams	Sage-steppe on lakeshore sediments
<i>A. tripartita</i> Rydb. ssp. <i>rupicola</i> Beetle	G5T3	MT, WY	Coarse textured soils	G3 grassland and sage-steppe
<i>A. tripartita</i> Rydb. ssp. <i>tripartita</i>	G5T3T5	Canada: BC; US: CA, ID, MT, NV, OR, UT, WA, WY	Sandy to gravelly soils, loams, or loess over bedrock	G1–G3 grassland and sage-steppe
Bud Sage and Chicken Sage				
<i>Picrothamnus desertorum</i> Nutt. • <i>Artemisia spinescens</i> DC. Eaton	G5	AZ, CA, CO, MT, NV, NM, OR, UT, WY	Sands, sandy loams, sandy clays eolian or alluvium derived or poorly drained clays from alluvium	G2/G3 (MT, WY) sage-steppe and G3–G5 (NV, OR, UT, WY)
<i>Sphaeromeria argentea</i> Nutt. • <i>A. argentea</i> S. Garcia and others	G3G4	CO, ID, MT, NV, WY	Sands, silts, clays loams, gravelly loams, often calcareous, with cobble or gravel	G2 grassland communities in WY, ID
<i>S. cana</i> (D.C. Eaton) A. Heller • <i>A. albicans</i> S. Garcia and others	G3/G4	CA, NV, OR	Rocky crevices and talus slopes	Sparsely vegetated cliffs, talus slopes
<i>S. capitata</i> Nutt. • <i>A. capitata</i> (Nutt.) S. Garcia and others	G3	CO, MT, UT, WY	Shallow, rocky sometimes calcareous soils	G3 dry, rocky hills, sage-steppe
<i>S. compacta</i> (H.M. Hall) A.H. Holmgren, L.M. Shultz & Lowrey • <i>Artemisia constricta</i> S. Garcia and others	G2	NV	Gravelly, limestone	G2 coniferous woodlands, alpine and rock, talus and scree
<i>S. diversifolia</i> (D.C. Eaton) Rydb. • <i>A. inaequifolia</i> S. Garcia and others	G3/G4	NV, UT	Shallow to moderately deep, rocky soils, rock crevices on limestone or quartzite	Sparsely vegetated cliffs, rocky slopes
<i>S. potentilloides</i> (A. Gray) A. Heller var. <i>nitrophila</i> (Cronquist) A.H. Holmgren, L.M. Shultz & Lowrey	G5T4	Snake River ID, NV	Alkaline fine-textured soils subjected to seasonal flooding	Wet meadows, springs
<i>S. potentilloides</i> (A. Gray) Rydb. var. <i>potentilloides</i>	G5TNR	CA, ID, NV, OR	Non-alkaline fine-textured soils	G2 mountain wet meadows, hot springs, seeps
<i>S. ruthiae</i> A.H. Holmgren, L.M. Shultz & Lowrey • <i>A. ruthiae</i> (A.H. Holmgren, L.M. Shultz & Lowrey) S. Garcia and others	G2	UT	Sandstone, cliffs, boulder talus and scree	G2 woodlands, chaparral, rock, talus scree sandstone crevice woodland communities
<i>S. simplex</i> (A. Nelson) A. Heller • <i>A. simplex</i> (A. Nelson) S. Garcia and others	G2	WY	Rocky limestone soils	G2 cushion communities

Notes: Conservation rankings: G1 = highly imperiled; G2 = imperiled; G3 = vulnerable; G4 = apparently secure; G5 = secure (NatureServe 2014).



Figure 4. Female Greater Sage-Grouse on the Seeskadee National Wildlife Refuge, Sweetwater County, Wyoming. Photo by Tom Koerner, US Fish & Wildlife Service

As summarized by Arkle and others (2014), in the Great Basin, GRSG occur more frequently on sites where big and dwarf sagebrush intergrade, perhaps because of the cover advantages of the tall shrubs and because the dwarf sagebrush species provide a more metabolically efficient forage for GRSG. Low elevation sagebrush communities are used for brood rearing and are preferred for forage (Connelly and others 2013). Subshrub sagebrush species, such as *A. frigida* and *A. pedatifida*, and herbaceous species, such as *A. ludoviciana* and related genera such as *Tanacetum nuttallii* Torr. & A. Gray (Asteraceae), are consumed by juvenile and adult GRSG. Other woody *Artemisia*, such as *A. filifolia*, of the west-central Great Plains and Southwest historically provided habitat, and *A. cana* of the northern Great Plains and Great Basin, provides habitat in association with major rivers.

During winter, the diet of GRSG is exclusively sagebrush (Wallestad and others 1975) and winter habitat may be the most limited because, in addition to the forage quality of different sagebrush species, topographical and stand structure features are critical (Eng and Schladweiler 1972; Remington and Braun 1985). When winter precipitation is high, birds may travel greater distances to find sagebrush blown free of snow.

Low elevation sagebrush communities are often used as winter habitat (Connelly and others 2013).

GREATER SAGE-GROUSE DIET

Life history and diet of GRSG are closely tied to the phenological development of sagebrush habitats. Brood rearing and chick productivity are highly dependent on sagebrush communities that contain a diversity and abundance of forbs and insects necessary for early GRSG development. Physiological condition of pre-laying hens may also contribute to juvenile survival and is highly dependent on understory flora from early spring to midsummer, as well as during the first few weeks post-hatch for young broods.

Barnett and Crawford (1994) found that forbs comprised 18 to 50% (by weight) of the diet of pre-nesting hens; consumption of forbs containing high calcium, crude protein, and phosphorus content can improve reproductive success. Hens are known to feed on a variety of early spring annuals and perennials including the flower buds of *Ranunculus* and *Lomatium*. Chicks have been documented to consume 41 families of invertebrates and 34 genera of forbs (Drut and others 1994b);

however, some plant taxa are preferred. Gregg and Crawford (2009) found that Lepidoptera availability and the annual *Microsteris gracilis* frequency were the only habitat variables related to brood survival, decreasing risk of total brood loss by nearly 12% and 3%, respectively (Figure 5).

Chicks less than 3 wk old need adequate quantities of insects for survival and development, whereas chicks greater than 3 wk old require insects for optimum growth (Johnson and Boyce 1990). Klebenow and Gray (1968) and Peterson (1970) found that invertebrates comprised 52 to 60% of the diet of chicks less than 7 d old, whereas forbs were the major component of chick diets 2 to 10 wk post-hatch. Greater forb and insect consumption has been positively correlated to chick survival (Barnett and Crawford 1994; Drut and others 1994a,b; Thompson and others 2006).

In Oregon, during the first week post-hatch (May to June), chicks consume ants (Hymenoptera: Formicidae), darkling beetles (Coleoptera: Tenebrionidae), scarab beetles (Coleoptera: Scarabaeidae), and various caterpillars (Lepidoptera) (Ersch 2009). Noteworthy, *Ericameria* and *Chrysothamnus* (rabbitbrush) communities contained more caterpillars throughout May and June than did *A. tridentata* ssp. *vaseyana* communities (Ersch 2009), providing optimal food sources during early brood rearing. Many other invertebrate taxa are consumed by chicks in other regions of the Great Basin and Wyoming Basin and Great Plains (Wallestad and others 1975; Thompson and others 2006).

Early spring emerging forbs are especially important for pre-laying hens and chicks during their first 3 wk of development. Research revealed that forbs comprised 50% or more of the juvenile and adult summer diets in Utah, Idaho, Montana, and Oregon (Trueblood 1954; Klebenow and Gray 1968; Wallestad and others 1975; Barnett 1992; Barnett and Crawford

1994; Connelly and others 2000; Gregg and others 2008; Ersch 2009). In particular, *Lomatium* species (Figure 6) are preferred forage by pre-laying hens and chicks in the Columbia Basin and Great Basin, comprising a significant portion of their diet (Barnett 1992; Barnett and Crawford 1994; Ersch 2009). Important forbs, including annuals, consumed by adults and chicks (for their first 10 wk) are listed in Table 3.

The suite of plants consumed reflects species availability as summer progresses and includes native species in natural communities, forage crops in agricultural fields, and weeds in disturbed sagebrush communities (Klebenow and Gray 1968). Where sagebrush has been removed, grazed, or burned, crops and weeds commonly occur (Prevéy and others 2010a,b) and have been found to be major dietary components (Wallestad and others 1975; Barnett 1992; Barnett and Crawford 1994). Throughout the late summer and fall, juveniles continue feeding on available forbs, such as *Eriogonum* (Braun and others 2005) in a variety of upland habitats, succulent forbs in riparian areas, as well as leaves and flower buds of sagebrush. GRSG



Figure 5. *Microsteris gracilis* is an important annual in chick survival of Greater Sage-Grouse. Photo by Jim Morefield

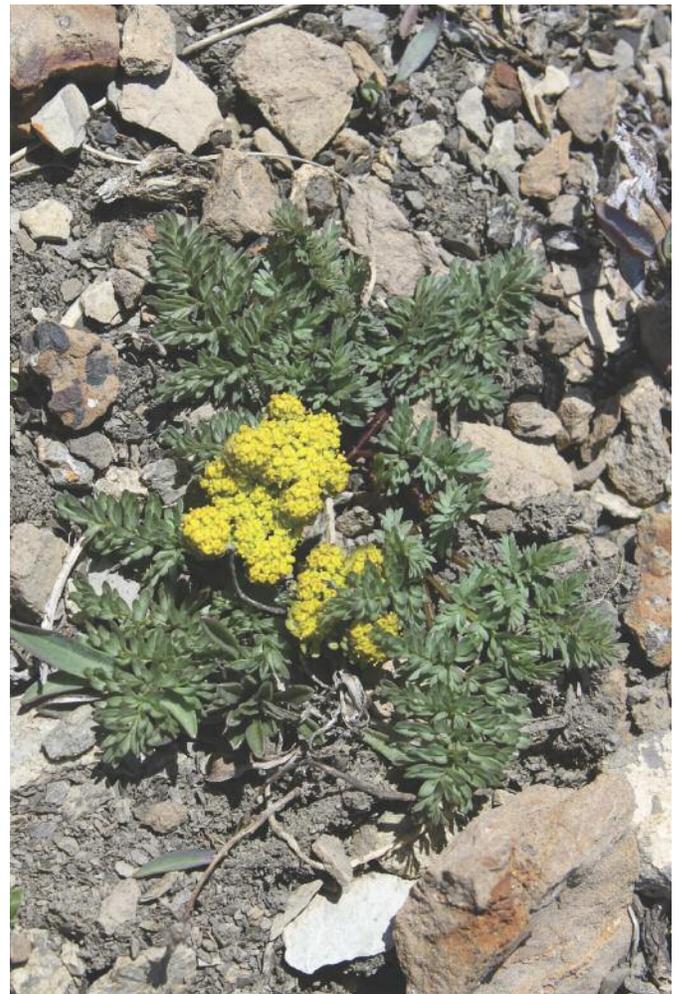


Figure 6. The lomatiums, including *Lomatium cous* (S. Watson) J.M. Coult. & Rose, are a valuable contributor to the diet of Greater Sage-Grouse. Photo by Tara Luna

TABLE 3

Native forb species documented to be in the diet of Greater Sage-Grouse.^z

Species	Source ^y	Species	Source ^y
<u>Achillea</u> L. Asteraceae	2	<u>Eriogonum</u> Michx. Polygonaceae	6,8
<i>A. millefolium</i> L.	1,3,4,5,8	<u>Fritillaria</u> atropurpurea Nutt. Liliaceae	5
<u>Agoseris</u> Raf. Asteraceae	1,6,7,8	Gayophytum A. Juss. Onagraceae	5,8
<i>A. glauca</i> (Pursh) Raf.	5	<u>Geum</u> L. Rosaceae	2
<i>A. grandiflora</i> (Nutt.) Greene	5	Grindelia squarrosa (Pursh) Dunal Asteraceae	3,4
<i>A. heterophylla</i> (Nutt.) Greene	5	<u>Lactuca tatarica</u> (L.) C.A. Mey. var. <i>pulchella</i> (Pursh)	
<u>Antennaria</u> Gaertn. Asteraceae	2,6	Breitung ^w Asteraceae	3
<i>A. dimorpha</i> (Nutt.) Torr. & A. Gray	8	<u>Lepidium</u> densiflorum Schrad.	3
<i>A. microphylla</i> Rydb.	5	Leptosiphon harknessii ^v (Curran) J.M. Porter &	1
<u>Arabis</u> L. Brassicaceae	6	L.A. Johnson Polemoniaceae	
<u>Arenaria</u> L. Caryophyllaceae	5,7	<u>Lomatium</u> Raf. Apiaceae	6,7,8
<u>Astragalus</u> L. Fabaceae	2,7	<i>L. nevadense</i> (S. Watson) J.M. Coult. & Rose	5
<i>A. convallarius</i> Greene	1	<i>L. triternatum</i> (Pursh) J.M. Coult. & Rose	5
<i>A. curvicaulis</i> (A. Heller) J.F. Macbr.	5	<u>Lupinus</u> L. Fabaceae	7
<i>A. filipes</i> Torr. ex A. Gray	5	<u>Machaeranthera</u> canescens (Pursh) A. Gray Asteraceae	5
<i>A. lentiginosus</i> Douglas ex Hook.	5	<u>Mertensia</u> Roth Boraginaceae	6
<i>A. obscurus</i> S. Watson	5,6,8	<u>Microseris</u> D. Don Asteraceae	8
<i>A. purshii</i> Douglas ex Hook.	5,6,8	Microsteris gracilis (Hook) Greene Polemoniaceae	5,7,8
<u>Balsamorhiza</u> Nutt. Asteraceae	8	<i>M. gracilis</i> (Hook.) Greene var. <i>gracilis</i> ^u	8
Blepharipappus scaber Hook. Asteraceae	7	<u>Mimulus</u> L. Scrophulariaceae	8
<u>Calochortus</u> macrocarpus Douglas	1	<i>M. nanus</i> Hook. & Arn.	5
<u>Castilleja</u> angustifolia (Nutt.) G. Don Scrophulariaceae ^x	1	<u>Monolepis</u> nuttalliana (Schult.) Greene Chenopodiaceae	1
<u>Cleome</u> platycarpa Torr. Capparaceae	5	<u>Orobancha</u> L. Orobanchaceae	7,8
Collinsia Nutt. Scrophulariaceae ^x	6	<u>Phlox</u> L. Polemoniaceae	6,7
<i>C. parviflora</i> Lindl.	5	<i>P. longifolia</i> Nutt.	1,5,6,8
<u>Crepis</u> L. Asteraceae	6,7	<u>Ranunculus</u> L. Ranunculaceae	1,6
<i>C. acuminata</i> Nutt.	1,5,8	<i>R. glaberrimus</i> Hook.	8
<i>C. modocensis</i> Greene	5	<u>Symphotrichum</u> ^t Nees Asteraceae	4,8
<u>Delphinium</u> L. Ranunculaceae	6	<i>S. spathulatum</i> (Lindl.) G.L. Nesom var. <i>spathulatum</i> ^s	5
<i>D. nuttallianum</i> Pritz. ex Walp.	8	<u>Trifolium</u> L. Fabaceae	2,6,7,8
Epilobium L. Onagraceae	5	<i>T. cyathiferum</i> Lindl.	5
<u>Eriogonum</u> L. Asteraceae	2,7,8	<i>T. gymnocarpon</i> Nutt.	5
<i>E. corymbosus</i> Nutt.	5	<i>T. macrocephalum</i> (Pursh) Poir.	8
<i>E. lonchophyllum</i> Hook.	5	<i>Vicia americana</i> Muhl. ex Willd. Fabaceae	3

Notes: Underlined *genera* are consumed by chicks during their first 14 wk of development. Bold **genera** include annual plants.^z Determined from analysis of GRSG crops; most likely this is partial list. For example, in their results, Drut and others (1994) stated that they observed GRSG consuming 34 genera of forbs, yet named only 11. In addition, most authors referenced here identified plants only to the genus. Note this list does not account for GRSG preference; some of these species are consumed in large amounts, others rarely. Consult the original sources for more information on GRSG feeding preferences. Chick diet information from sources 1, 3, 5, 7, and fide 8.^y Sources: 1 = Klebenow and Gray (1968); 2 = Martin (1970); 3 = Peterson (1970); 4 = Wallestad and others (1975); 5 = Pyle (1992); 6 = Barnett and Crawford (1994); 7 = Drut and others (1994b); 8 = Gregg (2006).^x ITIS (2015) places *Castilleja* in the Orobanchaceae and *Collinsia* in the Plantaginaceae.^w Formerly *Lactuca pulchella*.^v Formerly *Linanthus harknessii*.^u Formerly *Phlox gracilis*.^t Formerly *Aster*.^s Formerly *Aster occidentalis*.

feed exclusively on sagebrush during winter months (Wallestad and others 1975).

RESTORATION TO SUPPORT GREATER SAGE-GROUSE

Given the limited resources of management agencies, it is imperative to develop restoration strategies that yield the best success for establishing and retaining resilient sagebrush communities to support GRSG and other sagebrush-obligate species. The Great Basin Native Plant Project (GBNPP), a joint project of the USDI Bureau of Land Management (BLM) and the USDA Forest Service (USFS), is one of the primary research and development projects promoting the development of diverse native plant materials for restoration of the GRSG (Shaw and others 2012). GBNPP currently has more than 30 cooperating partners made up of universities, state and federal land management and research agencies, NGOs, private landowners, and seed producers. GBNPP continues to work with managers and botanists at BLM, USFS, and US Fish & Wildlife Service to strategically develop plant materials that are known to be important components of GRSG habitat. Past research results, information to assist land managers, and current work can be viewed at the GBNPP website (<http://www.GreatBasinNPP.org>). In addition, ongoing research by the USFS Rocky Mountain Research Station (RMRS) focuses on sagebrush genetics, seed transfer guidelines, native plant development, restoration methods, habitat loss, modeling, and monitoring (see Finch and others 2015 for a concise review). While the scientific literature concerning sagebrush restoration is rich (for example, Arkle and others 2014; Chambers and others 2014), sources of a more applied nature, such as the Sagebrush Steppe Treatment Evaluation Project (SageSTEP; <http://www.sagestep.org>) and the Sagegrouse Habitat Assessment Framework (Stiver and others 2015) provide a wealth of pragmatic restoration information. Within the scope of this paper, we will narrow the discussion to 1) using proper sagebrush seed sources now and in the future, 2) developing and outplanting forbs, and 3) control of invasive grasses and forbs to ensure restoration success.

Outplanting the Correct Sagebrush in the Correct Location

Given that sagebrush is the foundation species in GRSG habitat, and that its absence from the landscape allows the populations of invasive plants to increase and native forbs and grasses to decrease (Prevéy and others 2010a,b), returning sagebrush to the landscape is imperative. Unfortunately, for sagebrush restoration, we may be failing to meet the mantra: the right seed in the right place at the right time. In the sagebrush steppe, disturbances and invasion by weeds are most prevalent in the driest and warmest areas (Chambers and others 2007). Therefore, *A. tridentata* ssp. *wyomingensis* (hereafter

wyomingensis) is appropriate for many sagebrush restoration projects, and populations more local to the restoration site have higher first-year survival than more distant sources (Brabec and others 2015).

To obtain the sagebrush seed needed for restoration, land management agencies rely on private seed collectors and vendors. In high fire years, land management agencies may request in excess of 226,800 kg (500,000 lb) of sagebrush seeds (Krabacher 2015). Despite *wyomingensis* and *A. tridentata* ssp. *tridentata* (hereafter *tridentata*) growing in close proximity, these subspecies have vastly different moisture requirements and growth rates: *tridentata* prefers deeper soils or areas that retain winter moisture longer into the summer along dry washes and roadside ditches (Barker and McKell 1983; McArthur and others 1988) whereas *wyomingensis* favors shallower, drier soils in uplands and plateaus. The implication is clear: seeding misidentified *tridentata* on the wrong (that is, *wyomingensis*) site has the potential to reduce restoration success. In a recent study, Richardson and others (2015) found that *wyomingensis* had significantly greater seed weight than *tridentata* regardless of environment. Using this data, they determined that 83% of the certified seedlots labeled as *wyomingensis* collected in 2013 and 2014 and purchased by the BLM were largely composed of *tridentata*. Thus, we encourage seed collectors and land managers to use seed weight as a screening technique to ensure “the right seed for the right place.”

In the future, sagebrush restoration planning will have to account for the impacts of climate change to maximize successful outcomes. It is clear from research that plant communities, taxa, and populations are in flux (Menzel and others 2006; Hackett and others 2008). Overall, the desert biomes of western North America are expected to expand 25% by mid-century. This expansion is, however, largely gained by warm deserts (that is, Mojave and Chihuahuan) at the expense of the sagebrush steppe (Rehfeldt and others 2012). Bioclimatic niche modeling of *wyomingensis* supports these findings. The climate niche of *wyomingensis* predicts a reduction of 39% by mid-century (Still and Richardson 2015) (Figure 7). Losses mainly occur in the trailing edge of subspecies distribution, which are associated with aridity; recent ecohydrological models for decade 2070 found that winter and spring precipitation will not support big sagebrush at its trailing edge (Schlaepfer and others 2015). The contracting areas of *wyomingensis* (Figure 7) are in the same areas where Mojave Desert climates are predicted to expand (Rehfeldt and others 2012). Moreover, contracting areas should not be viewed as hopeless for *wyomingensis* restoration, but they are more likely to be less resilient over the next few decades.

Developing and Outplanting Forbs and Grasses

The recovery of healthy GRSG populations will require the restoration of diverse sagebrush-associated native plant

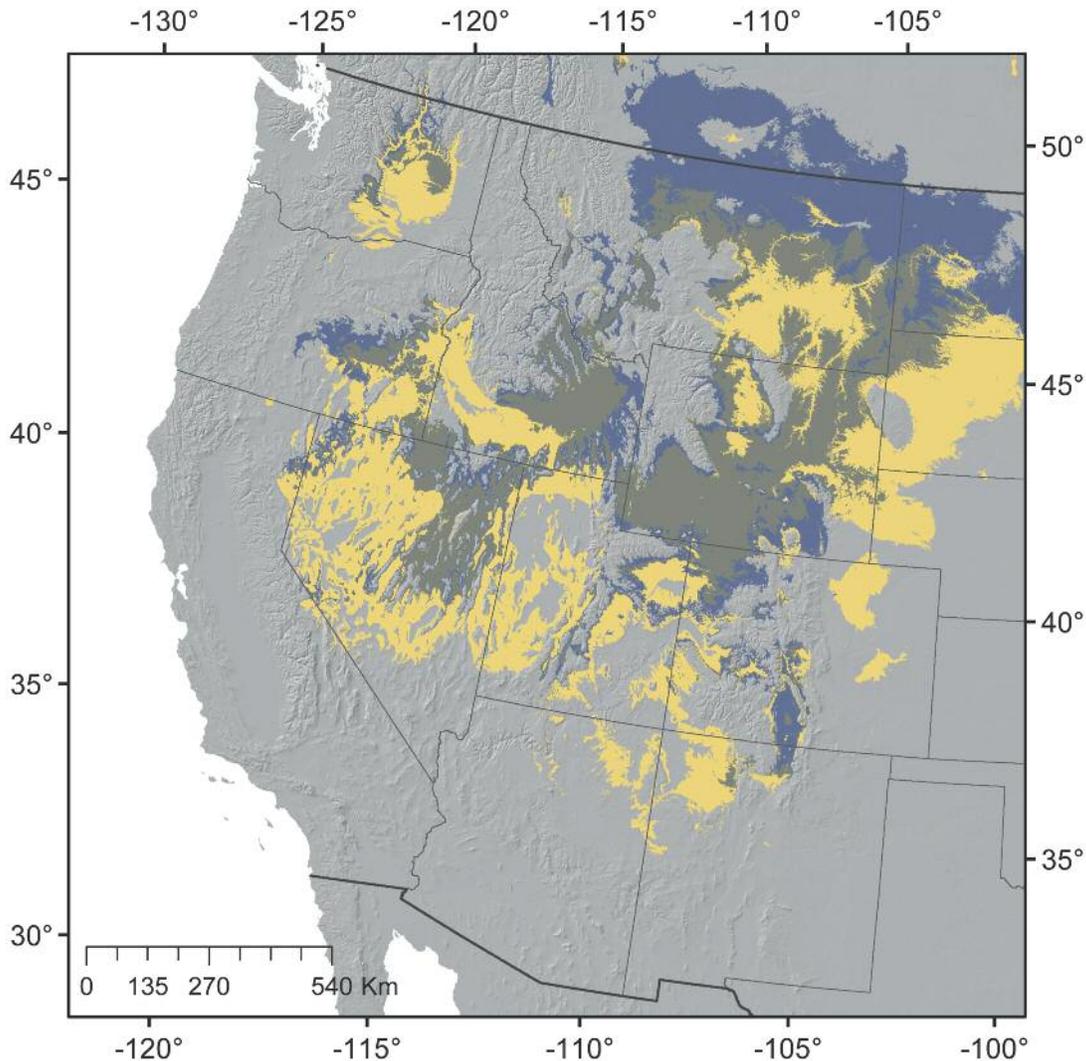


Figure 7. *Artemisia tridentata* ssp. *wyomingensis* climatic niche from present to decade 2050 (adapted from Still and Richardson 2015). Contracting niche space = yellow, stable = dark gray, and expanding = blue. Projections for 2050 are based on representative concentration pathway 6.0 of the IPCC 5th assessment report.

communities. Restoration success can hinge on selecting plant materials that “match” conditions at degraded sites (Lesica and Allendorf 1999; Hufford and Mazer 2003), and the National Seed Strategy calls for using the “right seed in the right place at the right time” (PCA 2015). Plant species exhibit intraspecific, or ecotypic, adaptive variation across multiple spatial scales, from local to regional (Linhart and Grant 1996), which needs to be taken into account in seed source selection and plant material development (McKay and others 2005). The strength, spatial scale, and trait by environment correlations that define intraspecific adaptive variation can vary substantially by species and ecosystem (Linhart and Grant 1996; McKay and others 2005). Seed zones and seed transfer guidelines are management tools, developed originally in forestry, that are currently being used to define acceptable distances to transplant germplasm that preserve ecological and evolutionary relation-

ships (Campbell 1991; Ying and Yanchuk 2006; Kilkenny 2015). Species-specific seed zones, also called empirical seed zones, are constructed by modeling the relationship between plant phenotypic traits, determined through common-garden studies, and climatic variables (St Clair and others 2013; Kilkenny 2015).

The 2 primary forms of common-garden studies include genecological studies, where many populations (often > 100) are tested in one or a few common gardens, and reciprocal transplant studies, which test populations across multiple environments and usually use only a few populations (but see Wang and others 2010). Genecological studies are best suited to characterize adaptive genetic variation across a large proportion of a species’ range and are therefore most often used for cost-effective seed zone construction, while reciprocal transplant studies are best suited for fully characterizing the adaptivity

and plasticity of specific plant materials across a range of environments (Kilkenny 2015). Data from all common-garden studies can be leveraged for use in more traditional agronomic methods of plant material selection, as well as to predict the effects of changing climates on plant populations of conservation concern (Kilkenny 2015). Plant material selection may include breeding or selection for specific traits, such as enhanced ability to establish under harsh conditions (for example, Jones and others 2009; Leger and Baughman 2015) or to compete with invasive species (for example, Leger 2008) or to just simply increase wild collections (Johnson and others 2010).

These studies are robust in the information they provide, but they require appreciable funding and time to accomplish. Despite this disadvantage, many species important to the sagebrush biome, and therefore, GRSG, have been evaluated and seed zones are now available, including grasses (for example, *Pseudoroegneria spicata*; St Clair and others 2013) and forbs (for example, *Allium acuminatum* Hool.; Johnson and others 2013). Until empirical seed zones can be developed for the full suite of grasses and forbs used by GRSG, provisional seed zones can be used to guide germplasm movement (Bower and others 2014).

With knowledge about where the plant species occurs and where seed sources can be moved, plant material production can proceed. Given that GRSG use a variety of forb species throughout the year, and their use also varies by season, it is important that species mixtures used in restoration activities be robust in their compliment of forb species—mixtures that include only a few forb species will not support the dietary needs of GRSG. Currently available materials, however, are unlikely to be adequate (in quantity and diversity) to restore sufficient sagebrush habitats for GRSG. Indeed, habitat models indicate that sage-grouse need highly diverse plant communities to thrive, and current seeding practices have fallen well short of that goal (Arkle and others 2014). Failure to meet the goal is in part because some forbs are just difficult to produce economically in quantities that allow for abundant use in projects. Notable problems include seed dormancy, indeterminate seed ripening, low stature that makes mechanical harvesting difficult, long durations between initial seed sowing and first seed harvest, and other factors (Shaw and others 2005; Meyer 2006; Boyer 2008). Thus, typical seed mixtures for sage-grouse restoration work often have limited numbers of species despite, for example, data from Wyoming documenting at least 10 genera of native forbs growing on quality GRSG habitat (Jacobs and others 2013). For example, Lambert (2005), discussing restoration of big sagebrush habitat (not specifically sage-grouse restoration), provides “generic” mixtures; these averaged 2, 6, and 4 species of shrubs (one being sagebrush), forbs, and grasses, respectively. A recommendation from North Dakota specifies 1 sagebrush species and 5 species each of forbs and grasses (USDA NRCS 2007). And, recommendations from Wyoming call for a minimum of 4, 2, 1, and 2 species of forbs,

bunchgrasses, rhizomatous grass, and shrubs, respectively (UGRB 2015). Thus, it is important that more economical methods for producing forbs are developed for commercial seed and nursery production. Not surprisingly, the recently released National Seed Strategy specifically discusses the need for additional research to develop species-specific methods for improved production (seeds and plants) of native species for restoration (PCA 2015).

A good starting point for working with native forbs is their life histories. Many native forbs important to GRSG initiate germination at temperatures at or barely above freezing, coinciding with cold to cool spring soil temperatures. Many early cold to cool temperature-requiring forbs adapted to soil moisture limitations possess thickened taproots or vertical fleshy root systems that can potentially reach greater root depth and efficiently utilize available soil moisture earlier and deeper in the soil profile and effectively compete for space and soil moisture with invasive annual grasses. For example, Parkinson and others (2013) found that early emerging and senescing forbs with vertical taproots, such as *Lomatium macrocarpum* (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose, and rapidly growing species, such as *Sphaeralcea munroana* (Douglas ex Lindl.) Spach ex Gray, showed no reduction in relative growth rate when grown with native grasses and exhibited the least reduction in relative growth rate when grown with cheatgrass.

Lomatium species, as a group, are early spring emergers, germinate at cold temperatures, and possess deep, storage taproots. Common and endemic Great Basin and Colorado Plateau spring and summer flowering Fabaceae (*Astragalus*, *Lupinus*, *Trifolium*), *Eriogonum*, and many Asteraceae provide important forage during later stages of juvenile development. Many of these same plants also possess deep taproots and occur in a wide range of Basin and Plateau sagebrush communities. *Penstemon* species (Figure 8) frequently found in sagebrush communities often possess woody caudexes surmounting fleshy branched roots, and these species may be more successfully established on moderately invaded sites. In addition to GRSG, they are important for supporting bees and migratory hummingbirds (Trochilidae). *Balsamorhiza sagittata* with its large caudex provides tall cover in association with sagebrush.

Propagation and native seed production protocols are available for many Great Basin, Wyoming Basin, and Colorado Plateau perennial forb species (Dunne and Dunne 2002; Archibald 2006; NPN 2015) and native bunchgrasses (Archibald and others 2000; Smith and Whalley 2002; NPN 2015). Researchers are gaining an understanding of critical seed germination temperatures for these forbs; *Lomatium*, *Phlox*, and some *Eriogonum*, adapted to late winter germination, germinate at cold temperatures of 3 to 6 °C (37 to 42 °F), while many basin *Castilleja*, *Penstemon*, and *Trifolium* species germinate at cool temperatures (15 °C [60 °F] or below). Asteraceae species, such as *Agoseris*, *Antennaria*, *Erigeron*, and



Figure 8. *Penstemon radicosus* A. Nelson growing with *Artemisia tridentata* ssp. *tridentata* in southwest Montana. Photo by Tara Luna



Figure 9. *Crepis acuminata* flowers (left) and growing within *Artemisia tridentata* ssp. *wyomingensis* (right) in Bingham County, Idaho. Photos by Matt Lavin

Crepis (Figure 9), as well as *Astragalus*, *Lupinus*, and some *Castilleja* and *Penstemon* species germinate at 20 °C (68 °F) (Baskin and Baskin 1998; Luna 2005). Some species have specific germination-enhancing requirements; *Balsamorhiza sagittata*, for example, germinates better when exposed to ethylene before stratification (Chambers and others 2006). And some genera, such as *Eriogonum* have species that germinate under a wide range of temperatures and during an extended period of several weeks (Meyer and Paulsen 2000).

Protocols for growing native forbs in seed production fields continue to improve (for example, Shock and others 2015). The same can be said for other shrub species important to the biome (for example, *Ericameria nauseosa* (Pall. ex Purch) G.L. Neson & Baird; Love and others 2014a,b). Techniques for long-term storage of sagebrush seeds have been developed (Karrfalt and Shaw 2013), and techniques for growing (Long and Trimmer 2004; Fleege 2010), storing (Overton and others 2013), and outplanting (Davis and others forthcoming) sagebrush nursery stock are helping ensure successful restoration. For producing seedlings of strongly tap-rooted species (for example, *Lomatium*, *Balsamorhiza*) for which it is difficult to grow a “firm plug” for outplanting, rhizomes grown in bareroot beds (Landis 2008) or “soft-walled” container seedlings grown using Jiffy pellets or stabilized media that maintain a root plug regardless of root architecture (Woodruff and others 2014; Landis and Dumroese 2015) are worthy options to consider.

From 2001 through 2014, the GBNPP program evaluated 92 genera and 225 taxa of native plants (Table 4), of which about 80% are forbs. The number of annual forbs studied by GBNPP is only about 15% of all taxa (Table 4). More use of annual native forbs may have benefit. In addition to annual forbs being an important part (up to 45%) of the diet of GRSG chicks less

TABLE 4

Genera of native shrubs (S), forbs (F; genera with annuals in **bold**), and perennial grasses (G) and the number of taxa (species and subspecies) under evaluation through the Great Basin Native Plant Project from 2001 through 2014.

Genus	Taxa	Type	Genus	Taxa	Type
<i>Achillea</i> L. Asteraceae	2	F	<i>Heterotheca</i> Cass. Asteraceae	1	F
<i>Achnatherum</i> P. Beauv. Poaceae	4	G	<i>Iliamna</i> Greene Malvaceae	1	F
<i>Agastache</i> Clayton ex Gronov. Lamiaceae	1	F	<i>Ipomopsis</i> Michx. Polemoniaceae	2	F
<i>Agoseris</i> Raf. Asteraceae	4	F	<i>Koeleria</i> Pers. Poaceae	1	G
<i>Allium</i> L. Liliaceae	1	F	<i>Krascheninnikovia</i> Guldenstaedt Chenopodiaceae	1	S
Amsinckia Lehm. Boraginaceae	3	F	Lappula Moench Boraginaceae	1	F
<i>Aquilegia</i> L. Ranunculaceae	1	F	<i>Lathyrus</i> L. Fabaceae	1	F
<i>Arenaria</i> L. Caryophyllaceae	1	F	<i>Lepidium</i> L. Brassicaceae	1	F
Argemone L. Papaveraceae	1	F	<i>Leymus</i> Hochst. Poaceae	3	G
<i>Aristida</i> L. Poaceae	1	G	<i>Ligusticum</i> L. Apiaceae	2	F
<i>Artemisia</i> L. Asteraceae	13	S	<i>Linum</i> L. Linaceae	5	F
<i>Astragalus</i> L. Fabaceae	5	F	<i>Lomatium</i> Raf. Apiaceae	12	F
<i>Atriplex</i> L. Chenopodiaceae	3	S	<i>Lotus</i> L. Fabaceae	1	F
<i>Balsamorhiza</i> Nutt. Asteraceae	3	F	Lupinus L. Fabaceae	8	F
Blepharipappus Hook. Asteraceae	1	F	<i>Machaeranthera</i> Nees Asteraceae	1	F
<i>Bromus</i> L. Poaceae	2	G	Mentzelia L. Loasaceae	3	F
<i>Castilleja</i> Mutis ex L.f. Scrophulariaceae ^z	1	F	Microsteris gracilis (Hook) Greene Polemoniaceae	1	F
<i>Chaenactis</i> D.C. Asteraceae	3	F	<i>Muhlenbergia</i> Schreb. Poaceae	1	G
<i>Chamerion</i> Raf. ex Holub Onagraceae	1	F	Nemophila Nutt. Hydrophyllaceae	1	F
<i>Chenopodium</i> L. Chenopodiaceae	1	F	Nicotiana L. Solanaceae	1	F
<i>Chrysothamnus</i> Nutt. Asteraceae	3	S	<i>Oenothera</i> L. Onagraceae	1	F
Clarkia Pursh Onagraceae	1	F	<i>Packera</i> Á. Löve & D. Löve Asteraceae	1	F
<i>Cleome</i> L. Capparaceae	2	F	<i>Pascopyrum</i> Á. Löve Poaceae	1	G
Collinsia Nutt. Scrophulariaceae	2	F	<i>Penstemon</i> Schmidel Scrophulariaceae ^z	26	F
<i>Crepis</i> L. Asteraceae	3	F	<i>Perideridia</i> Rchb. Apiaceae	1	F
Cryptantha Lehm. ex G. Don Boraginaceae	2	F	Phacelia Juss. Hydrophyllaceae	7	F
<i>Cymopterus</i> Raf. Apiaceae	2	F	<i>Phlox</i> L. Polemoniaceae	1	F
<i>Dalea</i> L. Fabaceae	3	F	Plagiobothrys Fisch. & C.A. Mey. Boraginaceae	1	F
<i>Delphinium</i> L. Ranunculaceae	2	F	<i>Poa</i> L. Poaceae	2	G
<i>Descurainia</i> Webb & Bethel. Brassicaceae	1	F	<i>Potentilla</i> L. Rosaceae	2	F
<i>Elymus</i> L. Poaceae	8	G	<i>Pseudoroegneria</i> (Nevski) Á. Löve Poaceae	1	G
<i>Enceliopsis</i> (A. Gray) A. Nelson Asteraceae	1	F	<i>Psoralidium</i> Rydb. Fabaceae	1	F
<i>Epilobium</i> L. Onagraceae	1	F	<i>Purshia</i> DC. ex Poir. Rosaceae	4	S
Eriastrum Wooton & Standl. Polemoniaceae	1	F	<i>Rudbeckia</i> L. Asteraceae	1	F
<i>Ericameria</i> Nutt. Asteraceae	1	F	<i>Scrophularia</i> L. Scrophulariaceae ^z	1	F
<i>Erigeron</i> L. Asteraceae	3	F	<i>Shepherdia</i> Nutt. Elaeagnaceae	2	S
Eriogonum Michx. Polygonaceae	9	F	<i>Sphaeralcea</i> A. St.-Hil. Malvaceae	5	F
Eriophyllum Lag. Asteraceae	1	F	<i>Sporobolus</i> R. Br. Poaceae	1	G
<i>Festuca</i> L. Poaceae	1	G	<i>Stanleya</i> Nutt. Brassicaceae	2	F
<i>Frasera</i> Walter Gentianaceae	1	F	<i>Stenotus</i> Nutt. Asteraceae	1	F
<i>Gaillardia</i> Foug. Asteraceae	1	F	<i>Thelypodium</i> Endl. Brassicaceae	1	F
Gilia Ruiz & Pav. Polemoniaceae	2	F	Townsendia Hook. Asteraceae	1	F
<i>Grayia</i> Hook. & Arn. Chenopodiaceae	1	F	<i>Veratrum</i> L. Liliaceae	1	F
<i>Hedysarum</i> L. Fabaceae	2	F	<i>Vicia</i> L. Fabaceae	1	F
<i>Heliomeris</i> Nutt. Asteraceae	3	F	<i>Vulpia</i> C.C. Gmel. Poaceae	1	G
<i>Hesperostipa</i> (Elias) Barkworth Poaceae	1	G	<i>Wyethia</i> Nutt. Asteraceae	1	F

^z ITIS (2015) places *Castilleja* in the Orobanchaceae and *Penstemon* in the Plantaginaceae.

than 6 wk old (see Table 3), they may also be an underutilized aspect to restoring degraded sites. In a California Mediterranean climate, annual native forbs seeded on sites dominated by invasive species remained abundant for several years (Seabloom and others 2003). In Oregon, a prairie restoration strategy that included multi-year sowing of natives, including annual forbs, resulted in exceptional cover of native species after 5 y; the annual forbs were thought to reduce weed establishment (Wold and others 2011). Thus, annual native forbs could be important in re-establishing sagebrush habitat and their inclusion in restoration plans deserves more attention.

Controlling Invasive Grasses and Forbs

Our best efforts to produce native plants for restoration are honorable, but successful conservation and restoration of sage-grouse habitat will, in many cases, require controlling invasive plant species (Ielmini and others 2015). One of the most important threats to the sagebrush biome and restoration of sage-grouse habitat is invasion by cheatgrass; this exotic annual grass displaces native forbs, increases fire frequency, and readily re-

establishes after fire creating a self-perpetuating cheatgrass-fire loop (D'Antonio and Vitousek 1992). Unfortunately, cheatgrass is not the only invasive plant causing problems. Many invasive forb species can also degrade sagebrush habitat by outcompeting and displacing desirable native plants (Ielmini and others 2015). Nonnative forbs known to invade sagebrush habitats include several members of the Asteraceae (rush skeletonweed, *Chondrilla juncea* L. [Figure 10]; spotted knapweed, *Centaurea stoebe* L.; diffuse knapweed, *C. diffusa* Lam.; Russian knapweed, *Acroptilon repens* (L.) DC.; Canada thistle, *Cirsium arvense* (L.) Scop.; yellow starthistle, *Centaurea solstitialis* L.), 2 members of the Brassicaceae (whitetop, *Cardaria* Desv. spp.; Dyer's woad, *Isatis tinctoria* L.), and leafy spurge (*Euphorbia esula* L. [Euphorbiaceae]) (Miller and others 2011; Ielmini and others 2015).

Chemical herbicides are commonly used to suppress exotic weeds, but effectiveness is usually short-term; herbicides must be re-applied to maintain control and it is often economically unfeasible to apply on a landscape scale. Moreover, herbicides can, as discussed earlier, have long-lasting non-target effects on



Figure 10. Nonnative rush skeletonweed (green with small, yellow flowers), invading and overrunning sagebrush habitat in Craters of the Moon National Preserve in southern Idaho. Photo by Justin B Runyon

native plants (Crone and others 2009), including those important to sage-grouse (Baker and others 2009; Rinella and others 2009). This underscores the need to develop other weed control tactics to minimize use of herbicides and lower non-target impacts.

Biological control, the deliberate use of a weed's natural enemies to suppress its abundance, is a crucial management tool because it is one of the few methods that can provide cost-effective, host-specific, long-term control of widespread invasive plants. Ongoing biological control research at the USFS RMRS is targeting the invasive plants most threatening to sage-grouse habitat. For example, evaluation of seed pathogens, including "black fingers of death" (*Pyrenophora semeniperda* (Brittleb. & D.B. Adam) Shoemaker), to control cheatgrass continues (Meyer and others 2008; Masi and others 2014; Soliai and others 2014), as does the search for, and testing of, new potential bio-control herbivores of several invasive forb species, including rush skeletonweed (Littlefield and others 2013). RMRS scientists are also evaluating how climate change will affect invasive species and the use of biological control to manage them (Runyon and others 2012). Biological control holds great potential to safely and effectively manage invasive plants in sagebrush habitats and to serve a critical role in sage-grouse conservation.

SUMMARY

The sagebrush-dominated landscape of the western US is a rich mosaic of *Artemisia* species, subspecies, and hybrids foundational to a robust understory of grasses and forbs. This floral understory in turn supports diverse invertebrate communities. Together, these invertebrates and understory species are critical to the diet of GRS; indeed, GRS are known to consume nearly 40 genera. Thus, when an objective of restoration in the western US is to provide suitable GRS habitat, land management protocols that incorporate a broad diversity of forb and grass species will provide more resources for GRS and other sagebrush-steppe-dependent wildlife than management strategies that do not. To ensure restoration success, control of invasive plants is required, and biological control offers opportunity to accomplish this in a sustainable way.

ACKNOWLEDGMENTS

We thank Steven Schwarzbach, Brian Perkes, Jim Morefield, Matt Lavin, Tom Koerner, Steve Fairbairn, and Bebe Crouse for allowing us to use their photos; and Candace Akins, Deborah Finch, Steve Love, Mary I Williams, and 2 anonymous reviewers for insightful comments and suggestions. This work was supported by the USFS Rocky Mountain Research Station and the National Center for Reforestation, Nurseries, and Genetics Research, and the USFS-BLM Great Basin Native Plant Project.

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