

# Native Perennial Forb Variation Between Mountain Big Sagebrush and Wyoming Big Sagebrush Plant Communities

Kirk W. Davies · Jon D. Bates

Received: 10 December 2009 / Accepted: 30 June 2010 / Published online: 23 July 2010  
© US Government 2010

**Abstract** Big sagebrush (*Artemisia tridentata* Nutt.) occupies large portions of the western United States and provides valuable wildlife habitat. However, information is lacking quantifying differences in native perennial forb characteristics between mountain big sagebrush [*A. tridentata* spp. *vaseyana* (Rydb.) Beetle] and Wyoming big sagebrush [*A. tridentata* spp. *wyomingensis* (Beetle & A. Young) S.L. Welsh] plant communities. This information is critical to accurately evaluate the quality of habitat and forage that these communities can produce because many wildlife species consume large quantities of native perennial forbs and depend on them for hiding cover. To compare native perennial forb characteristics on sites dominated by these two subspecies of big sagebrush, we sampled 106 intact big sagebrush plant communities. Mountain big sagebrush plant communities produced almost 4.5-fold more native perennial forb biomass and had greater native perennial forb species richness and diversity compared to Wyoming big sagebrush plant communities ( $P < 0.001$ ). Nonmetric multidimensional scaling (NMS) and the multiple-response permutation procedure (MRPP) demonstrated that native perennial forb composition varied between these plant communities ( $P < 0.001$ ). Native perennial forb composition was more similar within plant communities grouped by big sagebrush subspecies than expected by chance ( $A = 0.112$ ) and composition varied between community groups ( $P < 0.001$ ). Indicator analysis did not identify any perennial forbs that were completely exclusive and faithful, but did identify several perennial

forbs that were relatively good indicators of either mountain big sagebrush or Wyoming big sagebrush plant communities. Our results suggest that management plans and habitat guidelines should recognize differences in native perennial forb characteristics between mountain and Wyoming big sagebrush plant communities.

**Keywords** *Artemisia tridentata* · Composition · Diversity · Habitat · Indicator species analysis · Ordination

## Introduction

Sagebrush (*Artemisia* L.) occupies ~62 million hectares in the western United States (Küchler 1970; Miller and others 1994; West and Young 2000). The most widely distributed and abundant genus of sagebrush is big sagebrush (*Artemisia tridentata* Nutt.) (Miller and Eddleman 2000). Big sagebrush plant communities provide critical habitat for sagebrush obligate wildlife species (Connelly and others 2000; Shipley and others 2006; Wallestad and others 1975) and are an important forage base for livestock production (Davies and others 2006). However, information is limited comparing important habitat components among plant communities inhabited by the different subspecies of big sagebrush. Because perennial forb characteristics (composition, diversity, and biomass production) are key habitat elements (Gregg and others 2008; Kufeld 1973; Wallestad and others 1975; Willms and others 1979), at several tropic levels, the recognition of these facets will foster more refined management. Identification of potential indicator species might also facilitate plant community classification.

Native perennial forb composition, diversity, and production may differ between plant communities dominated

---

K. W. Davies (✉) · J. D. Bates  
United States Department of Agriculture—Agricultural  
Research Service, Eastern Oregon Agricultural Research Center,  
67826-A Hwy 205, Burns, OR 97720, USA  
e-mail: kirk.davies@oregonstate.edu

by the two most abundant subspecies of big sagebrush, Wyoming big sagebrush [*Artemisia tridentata* spp. *wyomingensis* (Beetle & A. Young) S.L. Welsh] and mountain big sagebrush [*Artemisia tridentata* spp. *vaseyana* (Rydb.) Beetle], as a result of differences in site-specific conditions. Mountain big sagebrush plant communities are generally on cooler, more mesic sites at higher elevations than Wyoming big sagebrush plant communities (Blaisdell and others 1982; Hironaka and others 1983; West and others 1978; Winward 1980; Winward and Tisdale 1977). Conversely, Wyoming big sagebrush plant communities usually occupy xeric foothills and valleys (Blaisdell and others 1982; Hironaka 1978; McArthur and Plummer 1978; Morris and others 1976; Tisdale 1994; Winward and Tisdale 1977). The differences in environmental and site conditions suggest that substantial variation in native perennial forb composition, biomass production, and diversity might exist between mountain big sagebrush and Wyoming big sagebrush plant communities. In Wyoming big sagebrush plant communities, perennial forb abundance increased as sites become more mesic (Davies and others 2007). This implies that mountain big sagebrush plant communities, because they are more mesic than Wyoming big sagebrush plant communities, might produce a greater amount and variety of perennial forbs than Wyoming big sagebrush plant communities.

Identifying potential differences in perennial forb diversity and biomass production between big sagebrush plant communities are critical to successful management of sagebrush plant communities and sagebrush obligate wildlife species. Guidelines for sagebrush obligate and facultative wildlife species habitat, livestock grazing, and other uses need to be based, in part, on the potential perennial forb component of different big sagebrush plant communities to ensure that objective and goals for management are realistic. However, relatively little is known about the potential differences in native perennial forb components between mountain big sagebrush and Wyoming big sagebrush communities. Winward (1980) reported observing many perennial forbs in mountain big sagebrush plant communities and few in Wyoming big sagebrush plant communities but did not compare between the two subspecies. Thus, information quantifying differences in native perennial forb production, diversity, and composition between mountain big sagebrush and Wyoming big sagebrush plant communities is generally lacking but needed to effectively manage these ecosystems for a diversity of needs.

Determining the native perennial forb composition of mountain big sagebrush and Wyoming big sagebrush plant communities could also improve efforts to distinguish between these two subspecies. Although taxonomical keys have been developed to identify species and subspecies of

sagebrush (e.g., Winward 1980), misidentification of subspecies of big sagebrush can easily occur when rapid identification is attempted. A few native perennial forbs that could be used to assist in distinguishing between mountain big sagebrush and Wyoming big sagebrush plant communities could improve management efficiency by decreasing the amount of time required to indentify these big sagebrush subspecies. Indicator species could be especially useful at identifying what big sagebrush subspecies should occupy a site where big sagebrush has been removed by disturbance. For example, fire often removes all of the big sagebrush but has limited influence on the native perennial forbs (Davies and others 2009; Rhodes and others 2010).

The objectives of this study were to determine if native perennial forb composition, biomass production, and diversity varied between mountain big sagebrush and Wyoming big sagebrush plant communities and to ascertain if any native perennial forb species might be used as indicator species to distinguish between mountain big sagebrush and Wyoming big sagebrush plant communities. We hypothesized that (1) native forb biomass production and diversity would be greater in mountain big sagebrush plant communities compared to Wyoming big sagebrush plant communities and (2) native perennial forb species composition would vary between mountain big sagebrush and Wyoming big sagebrush plant communities.

## Methods

### Study Area

The study area comprises over 1,500,000 ha in southeastern Oregon. Dominant shrubs were either Wyoming big sagebrush or mountain big sagebrush at all plant communities sampled. Climate across the study area is characterized by hot, dry summers and cool, wet winters. Regional precipitation was 80% and 66% of the long-term (40-year) average annual precipitation in 2007 and 2008, respectively. Common perennial bunchgrasses are Sandberg bluegrass (*Poa secunda* J. Presl), Idaho fescue (*Festuca idahoensis* Elmer), prairie junegrass [*Koeleria macrantha* (Ledeb.) J.A. Schultes], Thurber's needlegrass [*Achnatherum thurberianum* (Piper) Barkworth], bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve], Columbia needlegrass [*Achnatherum nelsonii* (Scribn.) Barkworth], and needle and thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth]. Study sites were considered intact big sagebrush plant communities using criteria described by Davies and others (2006). Intact sagebrush plant communities had not burned in the last 50 years nor had sagebrush control treatments been applied

at the site. The understory was dominated by native perennial herbaceous vegetation and the overstory was dominated by sagebrush in intact sagebrush plant communities. Soils were variable across the study area and included Aridisols, Mollisols, and Andisols. Slope and aspect varied among the study sites. Elevation at the mountain big sagebrush plant communities was, on average, 1863 m above sea level and ranged from 1601 to 2164 m. Among Wyoming big sagebrush plant communities sampled, the average elevation was 1537 m above sea level and ranged from 1307 to 1796 m.

### Experimental Design and Measurements

One hundred six big sagebrush plant communities were sampled that met the criteria described by Davies and others (2006) for intact big sagebrush plant communities. Half of the sites sampled were mountain big sagebrush plant communities and the other half were Wyoming big sagebrush plant communities. Sampling spanned 2 years, and in 2007 and 2008, 46 and 60 big sagebrush plant communities were sampled, respectively. Response variables included native perennial forb composition, biomass production, and species richness and diversity.

One randomly located 80 × 50-m plot (0.4 ha) was used to sample each plant community. Five 50-m transects, spaced at 20-m intervals, were deployed perpendicular to an 80-m baseline transect. Native perennial forb density was measured by species by counting individuals rooted inside 40 × 50-cm frames (0.2 m<sup>2</sup>) located at 3-m intervals on each 50-m transect line (starting at 3 m and ending at 45 m), resulting in 15 frames per transect and 75 frames per site. No invasive perennial forbs were observed in any of the plant communities sampled. Native perennial forb diversity was calculated from species density measurements using the Shannon diversity index (Krebs 1998). Species richness was determined by recording all native perennial forb species found in the 75, 40 × 50-cm frames at each site. Native perennial forb biomass production was determined by clipping, oven-drying, and then weighing the current year's growth from 25 randomly located 1-m<sup>2</sup> frames per site. All native perennial forbs were combined for biomass production measurements.

### Statistical Analysis

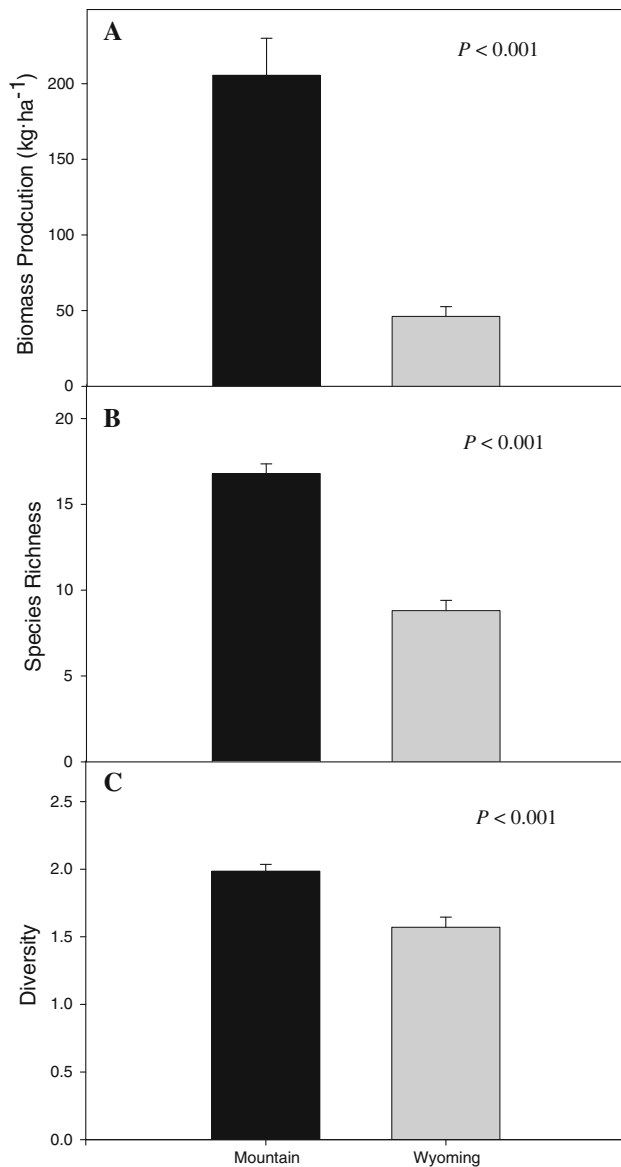
Analysis of variance (ANOVA) (S-Plus v. 8.0 2007; Insight Corp., Seattle, WA) was used to test for perennial forb biomass production, species richness, and diversity differences between mountain big sagebrush and Wyoming big sagebrush plant communities. Subspecies of big sagebrush (mountain big sagebrush or Wyoming big sagebrush) inhabiting the plant community and year were used as

explanatory factors. Year was used as a covariate but was not an effect of interest. Differences between means were considered significant if *P*-values were ≤0.05. Means were reported with standard errors (mean + SE). A multiple-response permutation procedure (MRPP) was used to test for homogeneity of native perennial forb species composition, based on density, within mountain big sagebrush and Wyoming big sagebrush plant communities (PC-ORD v. 4.25 1999; MjM Software, Gleneden Beach, OR). A Euclidean distance measurement was used in the MRPP. In MRPP, the *A*-statistic (chance-correct within-group agreement) was used to determine if groups were more homogeneous than expected by chance. If *A* > 0, then groups are more homogeneous than expected by chance. If groups are more heterogeneous than expected by chance, then *A* < 0. Indicator species analysis (Dufrêne and Legendre 1997) was used to determine indicator values of native perennial forb species for mountain big sagebrush and Wyoming big sagebrush communities (PC-ORD v. 4.25 1999; MjM Software). Indicator species analysis was performed with a Monte Carlo test with 1000 runs and random number seed. Indicator values range from 0 (no indication) to 100 (perfect indication). Perfect indication means that the species occurred in all samples of that group (faithful) but did not occur in any other group (exclusive). Nonmetric multidimensional scaling (NMS) was used to plot mountain big sagebrush and Wyoming big sagebrush plant communities sampled in native perennial forb species space (PC-ORD v. 4.25 1999; MjM Software). Perennial forb species density values were log-transformed to improve the amount of variation explained by the NMS ordination. To log-transform zeros, a small number (0.001) was added to all data points prior to transformation, and after transformation its log was subtracted from all data points (McCune and Grace 2002). The NMS ordination was operated with a random starting location and Sorensen's distance measurement was used with the slow and thorough autopilot method. A Monte Carlo test was used to determine if the NMS solution was extracting stronger axes than expected by chance.

## Results

### Production and Diversity

Native perennial forb biomass production was ~ 4.5-fold greater in mountain big sagebrush compared to Wyoming big sagebrush plant communities (*P* < 0.001; Fig. 1a). Perennial forb biomass production also varied between years (*P* < 0.001). Both mountain big sagebrush and Wyoming big sagebrush plant communities sampled in 2008 had more perennial forb biomass production compared to those sampled in 2007. Native perennial forb species richness was



**Fig. 1** Native perennial forb biomass production (a), species richness (b), and diversity (c) (mean + SE) in mountain big sagebrush and Wyoming big sagebrush communities in the northern Great Basin in 2007 and 2008. Data were combined for 2007 and 2008. Mountain = mountain big sagebrush plant communities; Wyoming = Wyoming big sagebrush plant communities. Diversity was calculated as Shannon diversity index (Krebs 1998). Reported  $P$ -values were comparisons between mountain big sagebrush and Wyoming big sagebrush plant communities

1.9-fold greater in mountain big sagebrush than Wyoming big sagebrush plant communities ( $P < 0.001$ ; Fig. 1b). Mountain big sagebrush plant communities had greater native perennial forb diversity than Wyoming big sagebrush plant communities (Fig. 1c). Native perennial forb diversity (Shannon diversity index) was about 1.3-fold higher in mountain big sagebrush plant communities compared to Wyoming big sagebrush plant communities ( $P < 0.001$ ).

Native perennial forb diversity and species richness did not vary between years ( $P = 0.541$  and  $0.212$ , respectively).

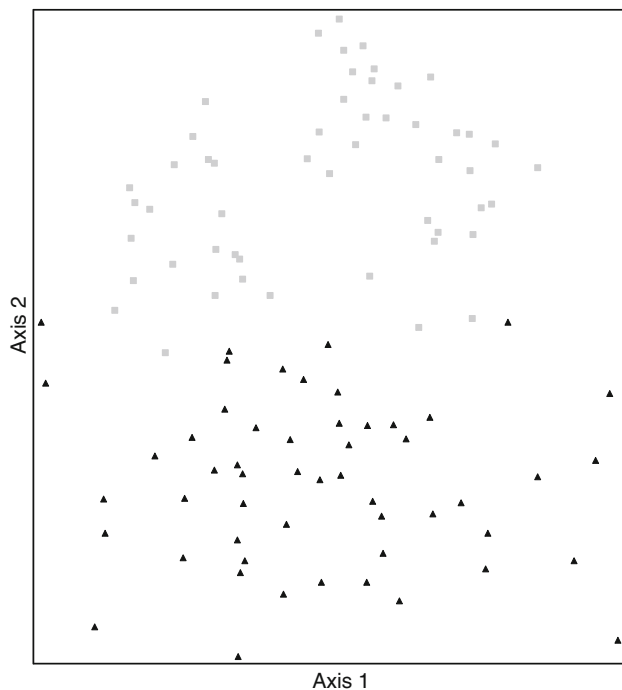
### Composition

Native perennial forb composition within groups delineated by subspecies of big sagebrush were more homogeneous than expected by chance ( $A = 0.112$ ). In community ecology, meaningful values for  $A$  are commonly  $<0.1$  (McCune and Grace 2002). The MRPP determined that the perennial forb composition differed between mountain big sagebrush and Wyoming big sagebrush plant communities ( $P < 0.001$ ). Indicator species analyses determined that no perennial forbs were completely exclusive or faithful to either mountain big sagebrush or Wyoming big sagebrush communities. However, some species were strong indicators of one or the other. False agoseris [*Agoseris glauca* (Pursh) Raf.], Columbia ragwort [*Senecio integerrimus* Nutt.], and woolly groundsel [*Packera cana* (Hook.) W.A. Weber & A. Löve] were 85%, 75%, and 67% indicators (% of perfect indication) of mountain big sagebrush plant communities, respectively ( $P = 0.001$ ). Longleaf phlox (*Phlox longifolia* Nutt.) and cushion buckwheat (*Eriogonum ovalifolium* Nutt.) were the best indicators (64% and 43%, respectively) of Wyoming big sagebrush plant communities ( $P = 0.001$  and  $0.003$ , respectively). Some perennial forb species were only recorded in one of the subspecies of big sagebrush communities: 36 and 12 species in mountain big sagebrush and Wyoming big sagebrush plant communities, respectively. However, these species were not “faithful” enough to that subspecies of big sagebrush to be useful indicators.

The final NMS solution was three dimensional, explained 77% of the variation in perennial forb species composition ( $R^2 = 0.77$ ), and explained more variation than expected by chance ( $P < 0.001$ ). Axis 1, 2, and 3 explained 32%, 19%, and 26% of the variation in perennial forb composition, respectively ( $R^2 = 0.32$ ,  $0.19$ , and  $0.26$ , respectively). Stress and instability for the final solution were 17.75 and 0.00001, respectively. For the solution to be useful, final stress and instability should be  $<20$  and  $<0.0001$ , respectively (McCune and Grace 2002). The final NMS solution illustrates that mountain big sagebrush and Wyoming big sagebrush plant communities differ in their locations in native perennial forb species space (Figs. 2 and 3).

### Discussion

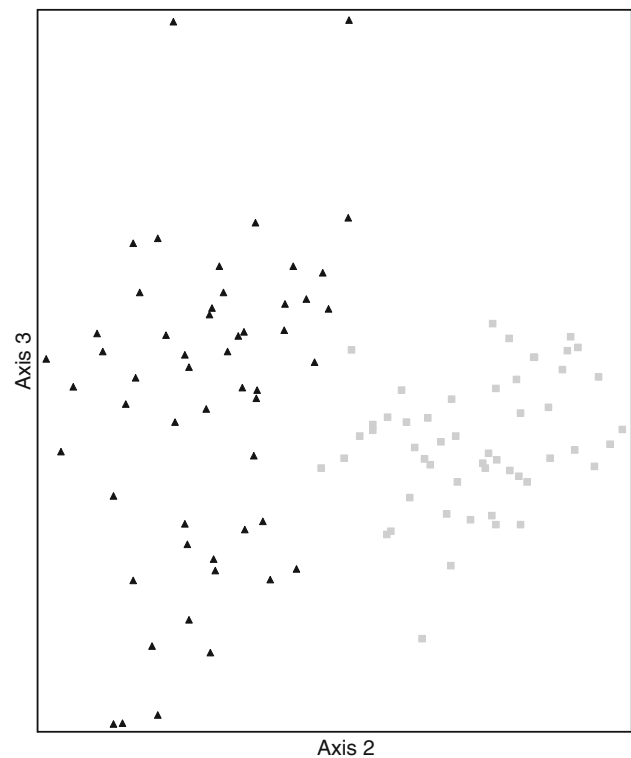
Native perennial forb biomass production, diversity, and composition varied between mountain big sagebrush and Wyoming big sagebrush plant communities across our



**Fig. 2** NMS of mountain big sagebrush communities (*gray squares*) and Wyoming big sagebrush communities (*black triangle*) in native perennial forb species space (i.e., communities are arranged by similarity in composition) along Axes 1 and 2. The final NMS solution explained 77% of the variation in perennial forb species composition ( $R^2 = 0.77$ ,  $P < 0.001$ ). Axis 1 and 2 explained 32% and 19% of the variation in perennial forb species composition, respectively

study area in southeastern Oregon. These differences in native perennial forbs are important distinctions that need to be recognized for informed land and wildlife management. Some native perennial forbs have the potential to be used as indicator species that can assist in efforts to more rapidly and accurately distinguish between mountain big sagebrush and Wyoming big sagebrush plant communities. Although the results of this study are specific to southeastern Oregon, we hypothesize that native perennial forb differences between mountain and Wyoming big sagebrush plant communities can be generally applied across the sagebrush biome.

The differences in native perennial forb production between mountain big sagebrush and Wyoming big sagebrush plant communities suggest that ecologists and biologists need to be cognizant of the potential differences when developing management guidelines for wildlife, livestock grazing, vegetation manipulations, or other uses. Unrealistic expectations or guideline requirements could result in wasted resources. For example, Wyoming big sagebrush plant communities do not produce the same amounts of perennial forbs as mountain big sagebrush plant communities, thus management should not try to increase



**Fig. 3** NMS of mountain big sagebrush communities (*gray squares*) and Wyoming big sagebrush communities (*black triangles*) in native perennial forb species space (i.e., communities are arranged by similarity in composition) along Axes 2 and 3. The final NMS solution explained 77% of the variation in perennial forb species composition ( $R^2 = 0.77$ ,  $P < 0.001$ ). Axis 2 and 3 explained 19% and 26% of the variation in perennial forb species composition, respectively

native perennial forbs in Wyoming big sagebrush plant communities to similar levels as found in mountain big sagebrush plant communities. Although we only measured mountain and Wyoming big sagebrush plant communities in southeastern Oregon, we expect that relatively similar differences in perennial forb production between mountain and Wyoming big sagebrush plant communities exist across the sagebrush biome.

The greater production of native perennial forbs in mountain big sagebrush plant communities suggest that they provide higher-quality spring and summer habitat, compared to Wyoming big sagebrush plant communities, for a variety of wildlife species. Many wildlife species native to the sagebrush steppe consume large quantities of native perennial forbs during the spring and summer. For example, sage-grouse (Barnett and Crawford 1994; Gregg and others 2008), mule deer (Collins and Urness 1983; Willms and others 1979), and elk (Kufeld 1973) all consume considerable amounts of native forbs. Gregg and others (2008) surmised that greater availability and subsequently consumption of forbs by female sage-grouse partially explained greater reproductive success. Native



perennial forbs in sagebrush plant communities are highly nutritious and their consumption increases sage-grouse dietary intake of crude protein, calcium, and phosphorus (Barnett and Crawford 1994; Gregg and others 2008). Similarly, mule deer production was higher on summer ranges with greater forb production than less productive ranges (Julander and others 1961). Thus, differences in perennial forb biomass production between mountain big sagebrush and Wyoming big sagebrush plant communities have significant implications to sagebrush obligate and facultative wildlife species. This suggests that if management goals are to improve spring and summer habitat, the greater productivity of mountain big sagebrush compared to Wyoming big sagebrush plant communities should be taken into consideration.

Differences in native perennial forb species diversity and richness between plant communities might also have implications to other higher trophic levels. Increasing plant diversity positively influences higher trophic-level diversity and abundance (Haddad and others 2001). This suggests that mountain big sagebrush plant communities are probably more diverse at higher trophic levels than Wyoming big sagebrush plant communities. Insect abundance is positively correlated with increasing plant species richness (Haddad and others 2001; Knops and others 1999). Therefore, mountain big sagebrush plant communities probably provide higher-quality sage-grouse breeding and brood rearing habitat compared to Wyoming big sagebrush plant communities because of an increased abundance of native perennial forbs and probably insects. Similar to forbs, insects are a critical component of sage-grouse diets. Sage-grouse chick survival and growth were restricted when they were deprived of insects for the first 10 days post-hatching (Johnson and Boyce 1990). Clearly, differences in native perennial forb diversity and richness in big sagebrush plant communities have the potential to influence higher trophic levels.

Our results indicate that the composition of native perennial forbs differed between mountain big sagebrush and Wyoming big sagebrush communities. The MRPP analysis demonstrated that native perennial forb composition of mountain big sagebrush and Wyoming big sagebrush plant communities were different from one another. The MRPP analysis also demonstrated that similarities in native perennial forb composition were greater than expected by chance within plant communities grouped by big sagebrush subspecies. In agreement with the MRPP analysis, the NMS solution indicated that mountain big sagebrush and Wyoming big sagebrush plant communities differ in their native perennial forb composition. Mountain big sagebrush and Wyoming big sagebrush plant communities occupied distinct locations in native perennial forb space (Figs. 2 and 3). The limited overlap in native perennial forb species space

between mountain and Wyoming big sagebrush plant communities indicates that the differences in perennial forb composition were substantial.

The indicator species analysis suggested that some native perennial forbs might be used to increase the efficiency and accuracy of distinguishing between mountain big sagebrush and Wyoming big sagebrush plant communities. Although no native perennial forb species were completely faithful and exclusive to either mountain big sagebrush or Wyoming big sagebrush plant communities, they provided useful information for distinguishing between big sagebrush plant communities. Using several of the indicator species identified in this analysis could improve the probability of accurately distinguishing between mountain big sagebrush and Wyoming big sagebrush plant communities. The presence of false agoseris, Columbia ragwort, or wooly groundsel were strong indicators of mountain big sagebrush plant communities, whereas long-leaf phlox was a strong indicator of Wyoming big sagebrush plant communities. Further refinement by geographic regions might also improve native perennial forb species indicators use and accuracy in identifying mountain big sagebrush and Wyoming big sagebrush plant communities. However, the current perennial forb species indicator analysis was strong enough to improve efforts to accurately and rapidly distinguish between mountain big sagebrush and Wyoming big sagebrush plant communities in the northern Great Basin.

## Conclusions

Native perennial forb biomass production, diversity, and composition varied considerably between mountain big sagebrush and Wyoming big sagebrush plant communities. Mountain big sagebrush and Wyoming big sagebrush plant communities had distinctly different native perennial forb composition. Delineating plant communities by subspecies of big sagebrush grouped communities with similar native perennial forb composition together. Mountain big sagebrush plant communities produced more native perennial forb biomass and diversity compared to Wyoming big sagebrush plant communities; thus, the potential of these plant communities to provide quality habitat for higher trophic levels differs. The difference in native perennial forb diversity and richness also suggests that higher-trophic-level diversity would also vary between mountain big sagebrush and Wyoming big sagebrush plant communities. These differences need to be considered in management plans and habitat guidelines to develop realistic expectations for these plant communities. Our results suggest that native perennial forbs can be used to assist in rapid and accurate identification of mountain big sagebrush and Wyoming big sagebrush plant communities. Indicator forbs

would be especially useful when land managers want to restore the appropriate big sagebrush subspecies on sites where the shrub component has been lost. Our results also suggest that the greater perennial forb diversity and productivity of mountain big sagebrush plant communities compared to Wyoming big sagebrush plant communities should be considered when prioritizing restoration and protection efforts.

**Acknowledgments** The authors thank the summer field crews for assisting with data collection. The authors were also grateful for data management by Aleta Nafus and Georjanna Pokorney. Reviews of earlier versions of this manuscript by Ed Vasquez and Dave Ganskopp were greatly appreciated. The authors also thank the anonymous reviewers for providing constructive criticism and useful suggestions on this manuscript. The authors also thank Burns- and Lakeview-District Bureau of Land Management and the Hart Mountain National Antelope Refuge for providing land for this research project. Mike Gregg, Gail Collins, and Paul Steblein assistance in accessing intact big sagebrush on Hart Mountain National Antelope Refuge was greatly appreciated. This research was funded by the USDA–Agricultural Research Service at the Eastern Oregon Agricultural Research Center.

## References

- Barnett JK, Crawford JA (1994) Pre-laying nutrition of sage grouse hens in Oregon. *Journal of Range Management* 47:114–118
- Blaissdell JP, Murry RB, McArthur ED (1982) Managing intermountain rangelands: sagebrush-grass ranges. General Technical Report INT-134. USDA Intermountain Forest and Range Experiment Station, Ogden, UT
- Collins WB, Urness PJ (1983) Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. *Journal of Wildlife Management* 47:646–663
- Connelly JW, Schroeder MA, Sands AR, Braun CE (2000) Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin* 28:967–985
- Davies KW, Bates JD, Miller RF (2006) Vegetation characteristics across part of the Wyoming big sagebrush alliance. *Rangeland Ecology & Management* 59:567–575
- Davies KW, Bates JD, Miller RF (2007) Environmental and vegetation characteristics of the *Artemisia tridentata* spp. *wyomingensis* alliance. *Journal of Arid Environments* 70:478–494
- Davies KW, Svejcar TJ, Bates JD (2009) Interaction of historical and non-historical disturbances maintains native plant communities. *Ecological Applications* 19:1536–1545
- Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366
- Gregg MA, Barnett JK, Crawford JA (2008) Temporal variation in diet and nutrition of preincubating greater sage-grouse. *Rangeland Ecology & Management* 61:535–542
- Haddad NM, Tilman D, Haarstad J, Ritchie M, Knops JMH (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist* 158:17–35
- Hironaka M (1978) Basic synecological relationships of the Columbia River sagebrush type. In: Gifford GF, Busby FE, Shaw JD (eds) Sagebrush ecosystem symposium. Utah State University Press, Logan, pp 27–32
- Hironaka MM, Fosberg M, Winward AH (1983) Sagebrush-grass habitat types of southern Idaho. *Bulletin* 35. University of Idaho, Moscow
- Johnson GD, Boyce MS (1990) Feeding trials with insects in the diet of sage grouse chicks. *Journal of Wildlife Management* 54:89–91
- Julander O, Robinette WL, Jones DA (1961) Relation of summer range condition to mule deer herd productivity. *Journal of Wildlife Management* 25:54–60
- Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreak, insect abundance and diversity. *Ecological Letters* 2:286–293
- Krebs CJ (1998) *Ecological methodology*, 2nd edn. Benjamin Cummings, Menlo Park, CA
- Küchler AW (1970) Potential natural vegetation. In: Gerlach AC (ed) The national atlas of U.S.A. US Government Printing Office, Washington, DC, pp 90–91
- Kufeld RC (1973) Foods eaten by the Rocky Mountain elk. *Journal of Range Management* 26:106–113
- McArthur ED, Plummer AP (1978) Biogeography and management of western native shrubs: a case study, section *Tridentatae* of *Artemisia*. *Great Basin Naturalist Memoirs* 2:229–243
- McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR
- Miller RF, Eddleman LL (2000) Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Technical Bulletin 151. Oregon State University, Corvallis
- Miller RF, Svejcar TJ, West NE (1994) Implications of livestock grazing in the Intermountain sagebrush region: plant composition. In: Vavra M, Laycock WA, Pieper RD (eds) Ecological implications of livestock herbivory in the West. Society of Range Management, Denver, CO, pp 101–146
- Morris MS, Kelsey RG, Griggs D (1976) The geographic and ecological distribution of big sagebrush and other woody *Artemisia* in Montana. *Proceeding of the Montana Academy of Science* 36:56–79
- Rhodes EC, Bates JD, Sharp RN, Davies KW (2010) Fire effects on cover and dietary resources of sage-grouse habitat. *Journal of Wildlife Management* 74:755–764
- Shiple LA, Davila TB, Thines NJ, Elias BA (2006) Nutritional requirements and diet choices of the pygmy rabbit (*Bachylagus idahoensis*): a sagebrush specialist. *Journal of Chemical Ecology* 32:2455–2474
- Tisdale EW (1994) Wyoming big sagebrush SRM 403. In: Shiftlet TN (ed) Rangelands cover types of the United States. Society for Range Management, Denver, CO, pp 42–43
- Wallestad RO, Peterson JG, Eng RL (1975) Foods of adult sage grouse in central Montana. *Journal of Wildlife Management* 39:628–630
- West NE, Young JA (2000) Intermountain valleys and lower mountain slopes. In: Barbour MG, Billings WD (eds) North American terrestrial vegetation. Cambridge University Press, Cambridge, pp 255–284
- West NE, Tausch RJ, Rea KH, Tueller PT (1978) Taxonomic determination, distribution, and ecological indicator values of sagebrush within the pinyon-juniper woodlands of the Great Basin. *Journal of Range Management* 31:87–92
- Willms W, McLean A, Tucker R, Ritcey R (1979) Interactions between mule deer and cattle on big sagebrush range in British Columbia. *Journal of Range Management* 32:299–304
- Winward AH (1980) Taxonomy and ecology of sagebrush in Oregon. Oregon Agricultural Experiment Station Bulletin 642. Oregon State University, Corvallis
- Winward AH, Tisdale EW (1977) Taxonomy of the *Artemisia tridentata* complex in Idaho. Forest, Wildlife, and Range Experiment Station Bulletin 15. University of Idaho, Moscow