Environmental and vegetation relationships of the *Artemisia tridentata* spp. *wyomingensis* alliance ☆

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Abstract

The *Artemisia tridentata* spp. *wyomingensis* (Beetle & A. Young) S.L. Welsh alliance is the most extensive of the big sagebrush complex in the Intermountain West and is characterized by a wide range of environments and vegetation heterogeneity. The purpose of this study was to identify environmental factors driving variation in plant species composition and determine the potential for using environmental factors to explain vegetation characteristics of the *A. tridentata* spp. *wyomingensis* alliance. Seventeen environmental factors and seven vegetation response variables were measured on 107 relatively undisturbed, late seral *A. tridentata* spp. *wyomingensis* sites across southeastern Oregon and northern Nevada. Non-metric multidimensional scaling (NMS) was used to identify environmental factors correlated with plant species composition as indexed by canopy cover. Stepwise multiple linear regressions were used to develop models correlating plant cover and structural characteristics with environmental factors. Vegetation composition variation appears to be driven by soil characteristics. Canopy cover of perennial grasses and forbs was moderately correlated with direct incident radiation and soil characteristics, particularly soil texture in the upper 15 cm of the profile. Total herbaceous cover variation was better explained by environmental factors (soil water-holding capacity, incident radiation, depth to Bt horizon, and percent sand in the upper 15 cm of the soil profile) ($P < 0.0001$, $R^2 = 0.52$) than any other vegetation characteristic. Vegetation structural characteristics (e.g. sagebrush height, canopy volume and canopy cover, density, and plant visual obstruction) exhibited weak or no relationships with measured environmental variables. Limited correlation among environmental factors and some vegetation characteristics was likely due to the large ecological amplitudes and ecotypic variations expressed by many of the plant species in

the sagebrush steppe. This study expands our understanding of the *A. tridentata* spp. *wyomingensis* alliance and elucidates the complexity of environmental–vegetation relationships.
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1. Introduction

A better understanding of environmental–vegetation relationships in *Artemisia tridentata* spp. *wyomingensis* (Beetle & A. Young) S.L. Welsh (Wyoming big sagebrush) alliance is needed for determining vegetative potentials, integrating wildlife habitat requirements with site potential, and quantifying the natural range of variation. The influence of environmental attributes on vegetation characteristics is large unexplored in the *A. tridentata* spp. *wyomingensis* alliance. Previous efforts have focused on identifying environmental differences among *Artemisia* alliances, associations, community types, or habitat types to explain environmental attributes relationships with *Artemisia* community classification systems.

These past classification systems have described the major *Artemisia* alliances and have provided broad underlying environmental factors (e.g. soils characteristics, topography) to explain vegetation characteristics (Hironaka et al., 1983; Swanson et al., 1986; Tisdale and Hironaka, 1981; Winward, 1980). However, these studies have not provided information on the environmental–vegetation relationships in the *A. tridentata* spp. *wyomingensis* alliance. Furthermore, efforts to quantify environmental–vegetation relationships with *Artemisia* plant associations, community types, and habitat types have met with varying success (Daubenmire, 1970; Jensen et al., 1990; Lentz and Simonson, 1987a, b; Munn et al., 1978; Passey et al., 1982). Daubenmire (1970) and Munn et al. (1978) suggested that definitive relationships among soil characteristics and habitat types do not exist. Other authors have observed some limited environmental–vegetation relationships that discriminate among *Artemisia* community types and/or plant associations, but concluded these relationships are too complex to consistently identify plant community types or associations (Jensen et al., 1990; Lentz and Simonson, 1987a, b; Passey et al., 1982). Thus, information describing environmental–vegetation relationships in *Artemisia* alliances, especially the *A. tridentata* spp. *wyomingensis* alliance, are generally lacking.

Difficulties in identifying relationships among environmental and vegetation characteristics in *Artemisia* systems have arisen because: (1) plant species exhibit wide ecological amplitudes and ecotypic variability (Doescher et al., 1985; Jensen et al., 1990; Passey et al., 1982; West, 1988), (2) detailed climate data are usually lacking, thus important site information is missing in analyses (Jensen et al., 1990), (3) a lack of precision in field observations, especially soil characteristics (Lentz and Simonson, 1987a), and (4) limited detail in vegetation and soils descriptions (Lentz and Simonson, 1987a). Improving measurement detail may provide greater insight into environmental–vegetation relationships in *A. tridentata* spp. *wyomingensis* alliance.

The purpose of our study was to determine the potential for using environmental attributes to explain variation in vegetation characteristics of the *A. tridentata* spp. *wyomingensis* alliance in the northern Great Basin. The *A. tridentata* spp. *wyomingensis*

alliance was selected because it is the most extensive, least resilient to disturbance, most endangered of the *A. tridentata* Nutt. (big sagebrush) complex in the Intermountain West (Barker and McKell, 1983; Beetle and Young, 1965; McArthur and Plummer, 1978; Miller and Eddleman, 2000; Morris et al., 1976; Tisdale, 1994; West et al., 1978), and the alliance occurs within a relatively narrow band (180–300 mm) of precipitation (Goodrich et al., 1999; Tisdale, 1994). By focusing on the *A. tridentata* spp. *wyomingensis* alliance and limiting the study to a geographical area (southeastern Oregon and northern Nevada) with similar climate patterns, we expected that underlying environmental attributes would be better correlated with vegetation characteristics. The objectives of the study were to: (1) identify environmental attributes related to variation in plant species composition; and (2) derive models to correlate potential vegetation cover and structure with underlying environmental attributes in the *A. tridentata* spp. *wyomingensis* alliance.

2. Methods

2.1. Study area description

The study sites were selected across a 50 000 km^2 area in southeastern Oregon and the northern most portion of Nevada. Study sites were in relatively undisturbed, late seral *A. tridentata* spp. *wyomingensis*-bunchgrass communities. Most sites were in the High Desert and Humboldt Ecological Provinces with a few located in the western edge of the Snake River Ecological Province (Fig. 1). Long-term precipitation for the study locations averaged between 200 and 300 mm annually (Natural Resources Conservation Service, 1998). Annual precipitation amounts (from 1 October to 30 September) at weather stations within the study area were between 127% and 76% of the long-term average (30 years) in 2000–2001 and between 80% and 58% of the long-term average in 2001–2002 (Oregon Climatic Service, 2006). Precipitation mainly comes in the fall, winter, and spring. Summers are typically hot and dry. Topography and soils were variable across the study area.

2.2. Site selection

Bureau of Land Management (BLM) wildlife and rangeland experts from Lakeview, Vale, and Burns, OR, and Winnemucca, NV, and ecological site inventory maps, were consulted to expedite locating relatively undisturbed, late seral *A. tridentata* spp. *wyomingensis* sites.[1] Sites were included in the study if they met the following criteria: (1) the understory was dominated by tall tussock native perennial bunchgrasses and native forbs, (2) exotic species were a minor to non-existent component, (3) there was evidence of limited livestock use based on criteria developed by Passey et al. (1982), and (4) sites were dominated by mature stands of *A. tridentata* spp. *wyomingensis* with limited recruitment of new shrubs (no recorded fire at sites for >50 years) (Davies et al., 2006). Ecological Site (Natural Resources Conservation Service, 1997) was determined at each site by performing a soil profile description. Vegetation characteristics were compared to ecological site descriptions to ascertain that the sites were at the historic "climax" state. All sites included in the analysis also met the criteria used to select reference sites in rangeland health

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[1]*Site*—A location of variable size with uniform soil, slope, aspect, and vegetation.
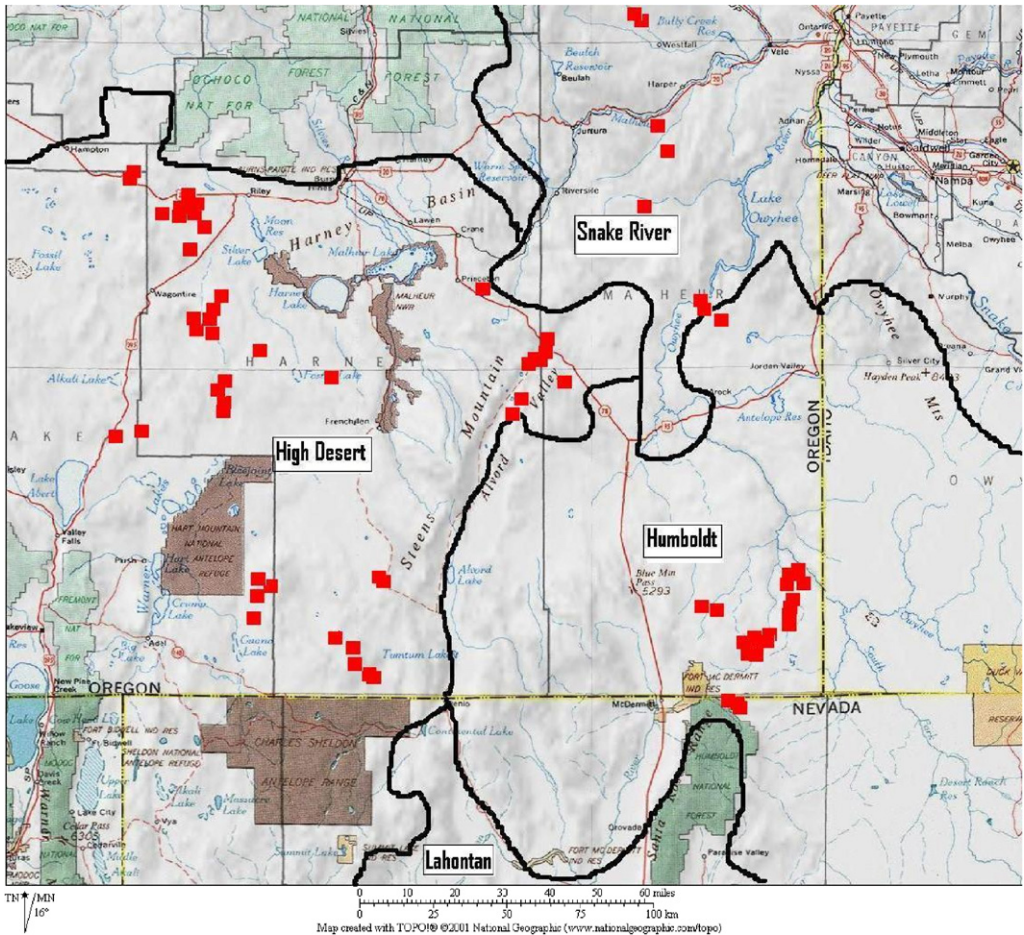
Fig. 1. Study site locations ($n = 107$). Red squares represent areas where *A. tridentata* spp. *wyomingensis* vegetation and environmental characteristics were sampled. The Snake River, High Desert, Humboldt, and Lahontan Ecological Province boundaries (bold black lines) were derived from Bailey (1994) and Anderson et al. (1998).

assessments (Pellant et al., 2005). We also evaluated the range health of each site to ensure that departures of soil/site stability, hydrologic function, and biotic integrity were none to slight based on the criteria in Pellant et al. (2005). A total of 107 sites were sampled that met our criteria.

2.3. Field sampling

To provide greater insight into environmental–vegetation relationships, detailed environmental measurements and plant community descriptions were performed. Sampling of vegetation characteristics and soil texture, total carbon and total nitrogen was conducted between late May and early July 2001 and 2002. Vegetation sampling occurred just prior to or coincided with herbaceous peak standing crop (late May–early

July depending on the site). Sites were revisited in late July through September to describe soil profiles.

2.3.1. Vegetation characteristics

Seven vegetation characteristics (Table 1) were measured at each site along five parallel 50-m transects laid out at 20-m intervals. Shrub canopy cover was measured by species using the line intercept method (Canfield, 1941). Shrub densities were measured inside five 2×50-m belt transects. *A. tridentata* spp. *wyomingensis* canopy volume was determined by measuring the height and two intersecting diameters of 50 randomly selected *A. tridentata* spp. *wyomingensis* plants at each site (Rittenhouse and Sneva, 1977).

Herbaceous canopy cover was visually estimated by species using 0.2-m^2 (40×50-cm) frames located at 3-m intervals along the transect lines (starting at 3 m and ending at 45 m) resulting in 15 frames per transect and 75 frames per site. Herbaceous composition was based on species canopy cover.

Horizontal visual obstruction, an estimate of horizontal concealment for wildlife, was estimated using a 1-m^2 board (Griffith and Youtie, 1988; Nudds, 1977). The board was vertically stratified into thirds (lower = 0–33.3 cm, middle = 33.3–66.6 cm, and upper = 66.6–100 cm) with each stratum divided into 12 equal size squares (16.7 cm $\times$ 16.7 cm). Squares were alternately colored white and black. Visual obstruction was determined by counting, from a location 5 m from the 1-m^2 board and at a 30-cm eye-height, the alternating black and white squares that were visually obscured by vegetation. Measurements were taken every 10 m on both sides of established transect lines, starting at the 5-m point. This resulted in 10 measurement locations (5 per side) per transect, yielding a total of 50 per plot.

2.3.2. Environmental factors

A total of 17 environmental explanatory variables were measured or estimated for each site (Table 1). Precipitation (long-term estimated average) for each site was determined

Table 1
Environmental factors and vegetation characteristics measured at each site

Vegetation characteristics	Environmental factors
Shrub cover	Precipitation
Shrub density	Elevation
A. tridentata spp. *wyomingensis* canopy volume	Soil water-holding capacity
A. tridentate spp. *wyomingensis* height	Soil texture
Herbaceous cover	Effective rooting depth
Herbaceous composition	Depth to Bt horizon
Horizontal visual obstruction	Soil total carbon and nitrogen
	Carbon:nitrogen ratio
	Soil pH
	Soil depth
	Slope
	Aspect
	Landscape position
	Direct incident radiation
	Universal transverse mercator
	Latitude

from climate maps (Natural Resources Conservation Service, 1998). Precipitation data was estimated at a coarse scale (50 mm precision) within a relatively narrow band of precipitation (200 and 300 mm). Elevation was recorded from US Geological Survey (1967) maps. Slope and aspect were determined in the field using a clinometer and compass. Each site's Universal Transverse Mercator (UTM) coordinates and landscape position were recorded. Direct incident radiation was estimated using an equation developed by McCune and Keon (2002).[2] A soil pit was dug to a restrictive layer (e.g. bedrock, hardpan) or 2 m depth, whichever was reached first, at each site. For each horizon, soil color, texture, thickness, structure, carbonates, and rock fragment percentage was described in the field. Water-holding capacity was estimated using the texture and thickness of each horizon minus the rock fragment (Brady and Weil, 2002). Effective rooting depth was measured in each soil pit. Depth to Bt horizon (clay accumulation layer) was measured on all sites where present. When a Bt horizon was not present, depth of the soil was its substitute in analyses. Depth of the soil is not a perfect substitute for depth to Bt horizon, however, soil water and root downward movement are restricted by both (Brady and Weil, 2002). Three soil samples from the surface to a depth of 15 cm were collected at randomly selected locations between shrubs. The three soil samples were measured for soil texture, total carbon, total nitrogen content, and pH. Soil texture was determined using the hydrometer method (Gee and Bauder, 1986). Soil total carbon and nitrogen was determined using a LECO CN 2000 (LECO Corp., St. Joseph, MI).

2.4. Statistical analysis

Non-metric multidimensional scaling (NMS) (PC-ORD v. 4.25, 1999) was used to identify environmental variables correlated with plant species composition. Prior to employing NMS, rare species (species occurring in less than 3 sites) were removed from the analysis. Deleting rare species reduces noise in large data sets and often enhances detection of relationships between environmental factors and community composition (McCune and Grace, 2002). Species cover 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 and then its log was subtracted from all data points after transformation (McCune and Grace, 2002). A random starting location and Sorensen's distance measurement were used with the NMS autopilot slow and thorough method.

Stepwise multiple linear regression (S-PLUS, 2000) was used to select models correlating vegetation cover and structure with environmental factors. Environmental explanatory factors that were not significant contributors (as determined from using stepwise selection at $\alpha = 0.05$) were excluded from the final model. For these analyses, herbaceous cover was grouped into four functional groups: tall tussock perennial grasses, annual grasses, perennial forbs, and annual forbs. The purpose of using functional groups is to combine species that respond similarly to environmental perturbation and to reduce data to a simpler form for analysis and presentation (Boyd and Bidwell, 2002). Functional groups also permit comparisons among sites with different species composition. *Poa sandbergii*

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[2]Direct incident radiation $(\mathrm{MJ\,cm}^{-2}\ \mathrm{year}^{-1}) = 0.339 + 0.808(\cos(L) \times \cos(S)) - 0.196(\sin(L) \times \sin(S)) - 0.482(\cos(A) \times \sin(S))$, where A = folded slope in radians east of north, S = slope in radians, L = latitude radians north.

Vasey (Sandberg bluegrass), *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass), *Elymus elymoides* (Raf.) Swezey (squirreltail), *Achnatherum thurberianum* (Piper) Barkworth (Thurber's needlegrass), *Hesperostipa comata* (Trin. & Rupr.) Barkworth (needle-and-thread), and *Festuca idahoensis* Elmer (Idaho fescue) were also analyzed separately because of their importance across this alliance. Total herbaceous cover was the sum of all herbaceous species and total vegetation cover was the summation of the total herbaceous and shrub cover.

3. Results

3.1. Environmental factors correlation to plant species composition

The NMS final solution was three dimensional and explained 81% (cumulative $R^2 = 0.814$, Axis 1 $R^2 = 0.218$, Axis 2 $R^2 = 0.289$, and Axis 3 $R^2 = 0.308$) of the variation in species composition and explained more variation than expected by chance (Monte Carlo test, $P < 0.0001$). Final stress for the three-dimensional solution was 16.978 and final instability was 0.00001 with 151 iterations. For ecological data to be useful, NMS final stress and final instability should not exceed 20 and 0.0001, respectively (McCune and Grace, 2002). Number of iterations is the number of steps that NMS performed to find the final solution (McCune and Grace, 2002).

Variation in plant species composition was related mainly to soil characteristics as shown by the axes' correlations with soil texture, soil nutrients, and depth to a Bt horizon. Percent clay in the upper 15 cm of soil was positively correlated, while sand was negatively correlated with Axis 1 ($R^2 = 0.340$ and 0.333, respectively) (Fig. 2). Slope was positively correlated with Axis 2 ($R^2 = 0.281$) (Fig. 3). Depth to a Bt horizon and percent sand in the upper 15 cm of soil were positively correlated ($R^2 = 0.188$ and 0.154, respectively), while percent nitrogen, carbon, and silt in the upper 15 cm of soil were negatively correlated with Axis 3 ($R^2 = 0.245$, 0.217, and 0.153, respectively). Aspect, precipitation, landscape position, elevation, incident radiation, soil pH in the upper 15 cm, effective rooting depth, and latitude had limited correlations with any axes ($R^2 < 0.141$).

Individual tall tussock perennial grass species were significantly correlated ($R^2 \geqslant 0.125$) with one or more axis(es) (Table 2). Soil surface texture was one of the more important variables in determining perennial grass species composition on a site. As clay increased and sand decreased in the upper 15 cm along Axis 1, *P. sandbergii* and *P. spicata* cover increased, while *Koeleria macrantha* (Ledeb.) J.A. Schultes (prairie junegrass) and *H. comata* cover decreased. On sites with more sand and less silt or clay in upper horizons, *H. comata* increased. *F. idahoensis* also appeared to decrease and *Achnatherum hymenoides* (Roemer & J.A. Schultes) Barkworth (Indian ricegrass) increased as soil surface texture became sandier and less silty. *P. spicata* and *F. idahoensis* cover increased as degree of slope increased along Axis 2, while *E. elymoides*, *H. comata*, and *A. thurberianum* cover decreased. As the percent of sand increased and nitrogen, silt, and carbon decreased in the upper 15 cm of the soil profile, and depth to the Bt horizon increased along Axis 3, *P. sandbergii*, *P. spicata*, and *F. idahoensis* cover decreased, while *H. comata*, *A. hymenoides*, and *Bromus tectorum* L. (cheatgrass) cover increased.

More perennial forb species were correlated with Axis 1 than both the other axes combined (Table 2), suggesting that percentages of sand and clay in the upper 15 cm of the soil profile were the most important factors influencing perennial forb composition.
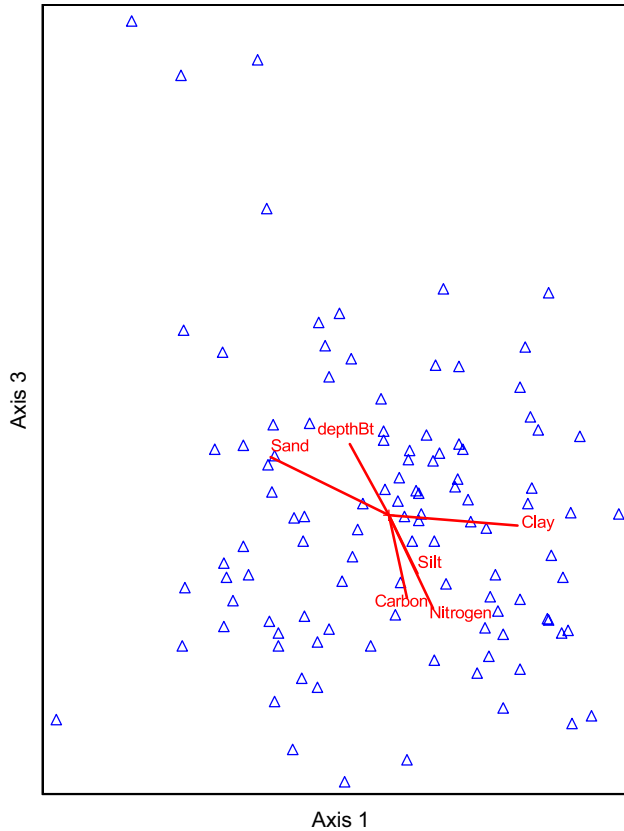
Fig. 2. Non-metric multidimensional scaling of sites (blue triangles) in species space (i.e. plots are arranged by their similarity in species composition) along Axes 1 and 3 with some of the correlated environmental factors. Direction of red lines indicates positive or negative correlation and length traversed along an individual axis depends on the strength of the correlation to that axis. Sand in the upper 15 cm of the soil profile was positively correlated with Axis 3 and negatively correlated with Axis 1. Clay in the upper 15 cm of the soil profile was positively correlated with Axis 1 and had almost no correlation with Axis 3. Nitrogen, carbon, and silt in the upper 15 cm of the soil profile were negatively correlated with Axis 3 and had little correlation with Axis 1. Depth to Bt horizon was positively correlated with Axis 3 and had little correlation with Axis 1.

No perennial forb species were well correlated with Axis 2. *Lupinus leucophyllus* Dougl. ex Lindl. (velvet lupine), *Phlox hoodii* Richards. (Hood's phlox) and *Phlox longifolia* Nutt. (long-leaf phlox) were negatively correlated with Axis 3. Only four annual forbs species had strong correlations with any of the axes (Table 2). Three species were positively correlated with Axis 2 and one with Axis 1.

3.2. Multiple linear regression solutions: vegetation cover

Several environmental factors were correlated with vegetation cover characteristics ($P < 0.05$). Functional group, *A. tridentata* spp. *wyomingensis*, and individual species of common perennial bunchgrasses cover values were generally weakly to moderately correlated ($R^2 = 0.12$–0.30) with environmental factors (Table 3). However, about half the
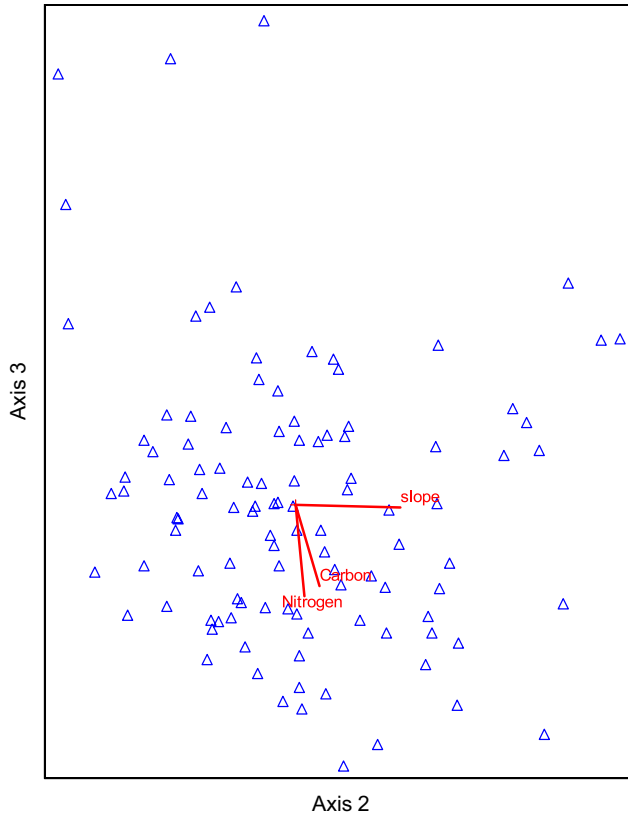
Fig. 3. Non-metric multidimensional scaling of sites (blue triangles) in species space (i.e. plots are arranged by their similarity in species composition) along Axes 2 and 3 with some of the correlated environmental factors. Direction of red lines indicates positive or negative correlation and length traversed along an individual axis depends on the strength of the correlation to that axis. Slope was positively correlated with Axis 2 and had almost no correlation with Axis 3. Nitrogen and carbon in the upper 15 cm of the soil profile were both negatively correlated with Axis 3 and had little or no correlation with Axis 2. Nitrogen was more negatively correlated with Axis 3 than carbon.

variation in canopy cover of total herbaceous, total vegetation, and *H. comata* was explained by environmental factors ($R^2 = 0.52$, 0.45, and 0.46, respectively). Annual forb and annual grass cover were not associated with any measured environmental variables ($P > 0.05$).

   Direct incident radiation was correlated with more vegetation cover characteristics than other environmental factors (Table 3). Percent sand in the upper 15 cm of the soil profile and depth to a Bt horizon were also correlated with many vegetation cover characteristics. Soil water-holding capacity, percent silt and nitrogen in the upper 15 cm of the soil profile, and slope were each correlated with at least two vegetation cover characteristics.

3.3. Multiple linear regression solutions: vegetation structure

   Correlations between measured environmental factors and vegetation structure were weak or not significant. Variation in *A. tridentata* spp. *wyomingensis* density (number/ha),

Table 2
Plant species moderately correlated ($R^2 \geqslant 0.125$) with at least one of nonmetric multidimensional scaling solution's axes

Species	Axis 1 (R^2)	Axis 2 (R^2)	Axis 3 (R^2)
Perennial grass			
Poa sandbergii	0.133	*	0.374 (—)
Pseudoroegneria spicata	0.147	0.281	0.150 (—)
Festuca idahoensis	*	0.137	0.212 (—)
Koeleria macrantha	0.186 (—)	*	*
Achnatherum hymenoides	*	*	0.210
Elymus elymoides	*	0.634 (—)	*
Hesperostipa comata	0.125 (—)	0.126 (—)	0.365
Achnatherum thurberianum	*	0.343 (—)	*
Annual grass			
Bromus tectorum	*	0.155	0.440
Perennial forb			
Agoseris grandiflora	0.226	*	*
Astragalus obscurus	0.205	*	*
Crepis acuminata	0.286 (—)	*	*
Crepis occidentalis	0.376	*	*
Leptodactylon pungens	0.165 (—)	*	*
Lomatium macrocarpum	0.144	*	*
Lupinus leucophyllus	*	*	0.165 (—)
Phlox hoodii	0.258 (—)	*	0.140 (—)
Phlox longifolia	0.425	*	0.158 (—)
Annual forb			
Blepharipappus scaber	*	0.172	*
Collomia linearis	0.167	*	*
Draba verna	*	0.265	*
Epilobium paniculatum	*	0.153	*
Shrub			
Chrysothamnus nauseosus	*	0.202	*
Chrysothamnus viscidiflorus	0.155 (—)	*	*

Asterisk (*) indicates species not moderately correlated with that axis ($R^2 < 0.125$).

A. tridentata spp. *wyomingensis* canopy volume (m^3), total visual obstruction (average of the strata), and individual stratum of visual obstruction (# of squares blocked per transect side) explained by environmental variables did not exceed 10% ($R^2 \leqslant 0.10$) (Table 4). Average mature *A. tridentata* spp. *wyomingensis* height (cm) was not correlated with any of the environmental factors measured ($P > 0.05$).

4. Discussion

Our study has expanded our understanding of environmental–vegetation relationship in the *A. tridentata* spp. *wyomingensis* alliance. Our results demonstrated that soil characteristics, direct incident radiation, and other environmental factors measured in this study explain some of the variation in vegetation characteristics across the

Table 3
Regression models for vegetation cover

Regression model, w/ standard errors in parentheses below coefficients	Residual standard error	*P*-value	R^2
$PG = 30.55 + 0.32(SWHC) - 18.92(IR) - 0.09(S)$ (5.23) (0.10) (5.37) (0.04)	3.97	< 0.0001	0.20
$PF = 17.16 - 13.19(IR) - 0.04(Bt)$ (2.82) (3.14) (0.01)	2.45	< 0.0001	0.25
$THerb = 63.34 + 0.49(SWHC) - 38.25(IR) - 0.08(Bt) - 0.17(S)$ (6.13) (0.12) (6.27) (0.02) (0.05)	4.73	< 0.0001	0.52
$TVeg = 34.01 + 60.30(N) + 0.31(Si) + 0.68(SWHC) - 22.36(IR)$ (9.07) (23.09) (0.08) (0.16) (8.40)	6.17	< 0.0001	0.45
$ARTRW8 = 15.50 + 0.04(ERD) - 0.12(S)$ (1.84) (0.01) (0.04)	7.54	0.0009	0.12
$POSA = 10.74 + 0.08(Si) - 8.89(IR) - 0.2(Bt)$ (3.01) (0.03) (2.73) (0.02)	2.06	< 0.0001	0.26
$PSSP6 = 5.00 - 0.18(S) + 0.88(C:N)$ (3.71) (0.04) (0.29)	4.45	< 0.0001	0.19
$FEID = -33.15 + 631.48(N) + 36.81(IR) - 675.85(N \times IR)$ (13.82) (155.45) (15.53) (176.88)	4.32	< 0.0001	0.26
$ELEL5 = -0.41 + 0.0009(Elev) - 0.04(Slope)$ (0.67) (0.0004) (0.01)	0.75	< 0.0001	0.15
$HECO26 = 0.98 - 0.03(S) - 0.06(Bt) + 0.002(S \times Bt)$ (1.09) (0.02) (0.02) (0.001)	1.32	< 0.0001	0.46
$ACTH7 = 2.97 - 0.13(Slope)$ (0.33) (0.03)	2.20	0.0002	0.12

PG = tall tussock perennial bunchgrasses, PF = perennial forbs, THerb = total herbaceous, TVeg = total vegetation, ARTRW8 = *A. tridentata* spp. *wyomingensis*, POSA = *P. sandbergii*, PSSP6 = *P. spicata*, FEID = *F. idahoensis*, ELEL5 = *E. elymoides*, HECO26 = *H. comata*, ACTH7 = *A. thurberianum*, SWHC = soil water holding capacity (cm), IR = direct incident radiation, S = percent sand in upper 15 cm of the soil profile, Bt = depth to Bt horizon (cm), N = percent total nitrogen in the upper 15 cm of the soil profile, ERD = effective rooting depth (cm), Si = percent silt in the upper 15 cm of the soil profile, C:N = carbon:nitrogen ratio, Elev = elevation (m).

Table 4
Regression models for vegetation structure

Regression model, w/ standard errors in parentheses below coefficients	Residual standard error	*P*-value	R^2
$ARTRW8\ density = 3090.78 + 2.23(Elev) - 39.87(S)$ (1600) (0.96) (15.68)	1647	0.0038	0.10
$ARTRW8\ volume = 1.27 - 0.12(pH)$ (0.29) (0.04)	0.13	0.0070	0.07
Total visual obstr. $= 52.04 - 0.009(Elev) + 0.03(Depth)$ (5.65) (0.004) (0.02)	6.01	0.0070	0.10
Lower visual obstr. $= 71.80 - 1.968(pH)$ (5.09) (0.75)	2.34	0.0101	0.06
Middle visual obstr. $= 63.19 - 0.013(Elev)$ (7.30) (0.005)	8.26	0.0099	0.07
Upper visual obstr. $= 44.32 - 2.36(ppt) + 0.05(Depth)$ (9.79) (0.93) (0.03)	9.35	0.0061	0.10

ARTRW8 = *A. tridentata* spp. *wyomingensis*, Obstr. = obstruction, Elev = elevation (m), S = percent sand in upper 15 cm of the soil profile, Depth = soil depth (cm), and ppt = precipitation (cm).

A. tridentata spp. *wyomingensis* alliance. The amount of variation in vegetation characteristics not explained by measured environmental attributes suggests other factors or interactions not taken into account in this study also influence vegetation characteristics in this alliance. Other studies in the *Artemisia* steppe (Jensen et al., 1990; Passey et al., 1982) also found limited direct relationships among environmental factors and vegetation characteristics. Inconsistent with Hironaka et al. (1991) suggestion that soil–vegetation relationships do not exist beyond a small geographic area, we found soil characteristics were correlated with vegetation characteristics in the *A. tridentata* spp. *wyomingensis* alliance. Several environmental–vegetation relationships we reported provide new information or were consistent with earlier observations.

4.1. Plant composition

Soil characteristics have the most potential of the environmental variables measured for explaining variation in plant species composition within individual *Artemisia* alliances. Variation in plant species composition was correlated mainly with soil characteristics, indicating edaphic characteristics are some of the more important factors driving plant species composition in this portion of the *A. tridentata* spp. *wyomingensis* alliance. Other studies have also reported that soil characteristics affected species composition in the *Artemisia* steppe (Anderson, 1956; Barker and McKell, 1983; Jensen et al., 1990; Lentz and Simonson, 1987a, b; Passey et al., 1982; Shumar and Anderson, 1986; Swanson et al., 1986). Similar to our findings, several studies reported that soil texture (Jensen et al., 1990; Shumar and Anderson, 1986; Swanson et al., 1986) and soil nitrogen (Barker and McKell, 1983; Jensen et al., 1990) influenced plant species composition in the *Artemisia* steppe. Unlike our study, these previous efforts did not report total soil carbon or depth to a Bt horizon as associated with plant species composition. Also in contrast to our results, previous studies reported that numerous other soil characteristics were associated with variation in plant species composition. However, the discrepancies in findings are due to previous studies investigating the influence of soil factors on only dominant species (Anderson, 1956; Barker and McKell, 1983; Jensen et al., 1990; Lentz and Simonson, 1987a, b; Passey et al., 1982; Shumar and Anderson, 1986; Swanson et al., 1986), whereas our research investigated soil factors influence on community composition. Slope was the only non-soil factor we found to be at least moderately correlated with plant species composition. Similar to our results, Anderson (1956) observed slope was an important factor influencing bunchgrass composition in eastern Oregon.

4.2. Vegetation cover and structure

We were able to identify some useful relationships between vegetation cover and environmental factors. Being able to explain about half of the variation in total herbaceous, total vegetation, and *H. comata* cover using environmental factors will help land managers determine site potentials in the *A. tridentata* spp. *wyomingensis* alliance. However, the descriptive powers of our regression models were variable, with some being too weak for management purposes. Relationships between environmental factors and vegetation structure were limited and had weak descriptive power. The lack of or weak relationships among environmental factors and vegetation structure and *A. tridentata* spp.

wyomingensis cover indicate that the relationships are too complex to be used for management purposes. However, these relationships expand the current knowledge of how these systems function.

Texture-related soil characteristics (percent sand and silt in the upper 15 cm, and soil water-holding capacity), direct incident radiation, and depth to a Bt horizon were the most consistently correlated explanatory factors with vegetation cover values. The relative importance of soil characteristics to vegetation cover is probably related to the amount, length of time, and location where soil water is available for plant use, because soil characteristics (texture, Bt horizon depth, etc.) exert a major influence over infiltration rates and soil water retention characteristics (Brady and Weil, 2002). When the Bt horizon is deeper in the soil profile (i.e. beneath the roots of shallow-rooted plants), shallow-rooted species would be less able to exploit this soil water. For example, we found *P. sandbergii* cover was inversely related to depth to a Bt horizon. Shallow-rooted plants, including *P. sandbergii*, may have a competitive advantage over deeper rooted species when the Bt horizon results in shallow root penetration (Passey et al., 1982). Perennial forb and total herbaceous canopy cover were also negatively correlated with increased depth of Bt horizon. Distinct soil textural changes within a soil profile result in soil water held above the textural change until the upper horizon is saturated (Miller and Gardener, 1962), thus soil water could be more available to herbaceous vegetation for longer periods of time above a Bt horizon.

The negative correlation of direct incident radiation to perennial functional groups, total herbaceous vegetation, and total vegetation canopy cover is related partially to the influence of direct incident radiation on temperature. Higher direct incident radiation results in warmer temperatures (McCune and Keon, 2002) that may increase plant water stress, thereby limiting plant growth and cover potential. Direct incident radiation appears to be an important factor influencing vegetation characteristics across the *A. tridentata* spp. *wyomingensis* alliance. Though previous studies have not directly tested the importance of direct incident radiation to vegetation characteristics, several have alluded to its importance. For example, Passey et al. (1982) reported that total vegetation production was greater on a north- than south-facing slope over a 10-year period. The south-facing aspect would have had greater direct incident radiation than the north-facing slope, thus agreeing with our results. Passey et al. (1982) also mentioned that the influence of degree and direction of slope on vegetation characteristics are difficult to evaluate because the influence of these factors are interrelated. Using direct incident radiation resolves this problem by incorporating both degree and direction of slope into one explanatory factor (McCune and Keon, 2002).

The negative associations of sand content in the upper 15 cm of the soil profile with perennial grass, sagebrush, and total herbaceous vegetation canopy cover were likely related to the availability of soil water. Similarly, the positive correlation between silt content in the upper 15 cm of the soil profile and total vegetation canopy cover, and the positive correlations of soil water-holding capacity with total herbaceous vegetation, perennial grass, and total vegetation canopy cover were the result of the influence of soil texture on the availability of soil water for plant growth. Sandy soils often support less vegetation than finer-textured soils in areas that receive moderate levels of precipitation because less water is held for vegetation uptake (Comstock and Ehleringer, 1992). This is especially true in areas that receive most of their precipitation in the cool season (Comstock and Ehleringer, 1992).

The lack of correlation between annual forb or grass canopy cover and measured environmental factors may be the result of annuals being opportunistic and highly responsive to current year's climatic conditions. Bates et al. (1998) and Bates (2004) found annual forbs were the most responsive functional group to different precipitation patterns. The winter and spring were generally dry across our study area during both years of our study and precipitation was variable across the study area (Oregon Climatic Service, 2006). Annuals typically decline in productivity and abundance in years with a dry winter and spring in comparison to years receiving average to above average winter or spring precipitation (Bates et al., 2006; Passey et al., 1982; West and Yorks, 2002).

More variation in total herbaceous and total vegetation than functional groups cover was explained by environmental factors. Interactions between functional groups could confound the relationships between environmental factors and vegetation characteristics. By focusing on the sum of functional groups cover (total herbaceous or total vegetation cover), these confounding effects were removed. Our results indicate environments with favorable soil characteristics (loamy surface texture, greater soil water-holding capacity, etc.) and lower direct incident radiation can be expected to produce more total herbaceous and total vegetation canopy cover than environments with higher direct incident radiation and less favorable soil characteristics in the *A. tridentata* spp. *wyomingensis* alliance.

Cover of bunchgrass species were mainly correlated with soil characteristics, especially texture related characteristics, and direct incident radiation. Sand content in the upper 15 cm was positively correlated with *H. comata* cover and negatively correlated with *P. spicata* cover. Hironaka et al. (1983) observed *P. spicata* and *A. thurberianum* did not occupy sandy soils, while *H. comata* commonly occurred on sandy soils. *H. comata* cover increased as the depth to a Bt horizon increased, indicating that *H. comata* is more common on deep, well-drained soils. All the sites that were dominated by *H. comata* did not have a Bt horizon, and generally had soils deeper than sites dominated by other bunchgrasses. Environmental factors explained more of the variation in *H. comata* cover than other common perennial bunchgrasses, which is probably the result of *H. comata* having more specific site requirements than the other perennial bunchgrasses. *A. thurberianum* and *E. elymoides* decreased with increasing slope, which has not been previously reported. *F. idahoensis* cover appears to increase with soil fertility, because *F. idahoensis* cover was positively correlated with N content.

The lack of strong correlations among environmental factors and vegetation characteristics are potentially related to several factors. First, various combinations of environmental factors can produce relatively equivalent environments for plant growth (Daubenmire, 1968; Jensen et al., 1990). Second, many plant species common to the *Artemisia* steppe possess wide ecological amplitudes and large ecotypic variation (Jensen et al., 1990; Passey et al., 1982; West, 1988). Third, interactions between plant species or functional groups can mask the relationships among environmental factors and vegetation characteristics. For example, Rittenhouse and Sneva (1976) documented a 1% increase in *A. tridentata* spp. *wyomingensis* cover resulted in a production decrease of between 37 and 61 kg/ha in *Agropyron desertorum* (Fisch. ex Link) J.A. Schultes (desert wheatgrass) in southeastern Oregon. Lastly, our study was lacking detailed climate data, which might have improved our ability to predict vegetation characteristics with environmental factors.

5. Conclusions

This study suggests soil characteristics are important factors driving variation in species composition in the *A. tridentata* spp. *wyomingensis* alliance and elucidated the complexity of describing relationships between environmental attributes and vegetation cover and structure. We also demonstrated the influence of direct incident radiation on vegetation cover and reaffirmed soil as an important factor influencing variation in vegetation cover in the *A. tridentata* spp. *wyomingensis* alliance. The influence of direct incident radiation on vegetation characteristics of other *Artemisia* alliances should be investigated because its correlation with many of the vegetation characteristics in our study suggests it has potential for explaining vegetation variation in other *Artemisia* alliances. The environmental–vegetation relationships in the *A. tridentata* spp. *wyomingensis* alliance are complex, however, this study has advance our understanding of the influence of environmental attributes on vegetation cover and structure. The information provided by this study could be used to develop stronger models by accounting for factors (i.e. detailed climatic data) or interactions not included in this study.

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