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RESEARCH PAPER

# Vegetation Classification Exercise for the Pawnee National Grasslands, USA

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## Abstract

**Aims:** Vegetation classifications are useful for a variety of management purposes as well as scientific exploration. Local classifications are common throughout the United States but only recently have been integrated into a national classification system, which is now expected for local classifications. **Study Area:** The Pawnee National Grasslands (PNG) in northeastern Colorado, USA, has not been classified using plot data, and is thus a gap on the baseline knowledge of the PNG plant communities that hinders impact assessment of various anthropogenic activities. **Methods:** Here, we use 128 plots to classify the vegetation of the PNG using a two-step process: first, classifying the PNG plots alone to characterize local uniqueness, and then employing a semi-supervised classification with an additional 64 plots from areas to the north and east of the PNG, using standard classification procedures. **Results:** We document on the PNG the occurrence of two Classes, three Subclasses, four Formations, five Divisions, six Macrogroups, seven Groups and eight Alliances and Associations already described in the USNVC. **Conclusions:** The PNG is dominated by the *Bouteloua gracilis-Buchloe dactyloides* Grassland Association, which we further subdivide and describe as three local subassociations. The mixed-grass concepts in the USNVC do not exist in the PNG.

**Taxonomic reference:** Hazlett (1998).

**Syntaxonomic reference:** USNVC (2016).

**Abbreviations:** BLM = Bureau of Land Management; CPER = Central Plains Experimental Range; ESA = Ecological Society of America; EST = Ecological Site Type; GPS UTM = Global Positioning System Universal Transverse Mercator; NEON = National Ecological Observatory Network; PNG = Pawnee National Grasslands; USNVC = United States Vegetation Classification.

## Keywords

Colorado, Pawnee, semi-supervised classification, shortgrass, steppe, USNVC, vegetation

## Introduction

Classification of vegetation provides a common language to compare communities among regions, an inventory to assess change, and a baseline for land stewardship decisions (ESA Panel 2015). Vegetation classifications are useful for: (1) documenting complex vegetation patterns, (2) developing hypotheses about processes shaping such patterns, (3) mapping vegetation and related ecosystem properties, (4) surveying, monitoring and reporting plant and animal communities, and (5) developing management and conservation strategies

(De Cáceres et al. 2015). While several initial efforts toward mapping and vegetation data collection are available for the Pawnee National Grasslands, there is no plot-based classification, despite the area including the Central Range Experiment Station of the United States Agricultural Research Service and a National Ecological Observatory Network (NEON) site. Here we present a plot-based classification that follows recent standards of the United States (Jennings et al. 2009; Faber-Langendoen et al. 2014) as well as international standards (De Cáceres and Wiser 2012; De Cáceres et al. 2015).

Baker (1984) provided a preliminary list of the natural vegetation communities for the entire state of Colorado, but gave no descriptions of the communities themselves. Johnson (1987) described 13 potential natural associations (in this case, cover types) based on previous literature. Hazlett (1998) described habitats based on vegetation occurrences integrated with site abiotic characteristics, but did not use plot data and thus performed no analyses. With the multiple uses of the PNG, from grazing to missile silos to the recent oil and natural gas boom, a consistent and standards-conforming classification of vegetation communities is needed for land stewardship decisions. The Colorado Vegetation Classification Project, an effort of the Bureau of Land Management (BLM) and the Colorado Department of Wildlife (http://www.arcgis.com/home/item.html?id=893739745fcd4e05af8168b7448cda0c), produced a classification using 1993–1997 Landsat Thematic Mapper imagery that was processed using an unsupervised classification procedure. Field-gathered GPS data were used to label and group the final classes. Based on that classification on broad-based life forms, the PNG lies in the Herbaceous Riparian (only one subclass, Sedge) or Grass/Forb Rangeland, including several subclasses pertinent to the PNG: Grass Dominated Herbaceous Rangeland, Forb Dominated Herbaceous Rangeland, Grass/Forb Mix Herbaceous Rangeland, Tall-grass Prairie, Mid-grass Prairie, Short-grass Prairie, Disturbed Rangeland and Sparse Grass/Blowouts. These are general names for large-scale vegetation communities and, thus, are likely not specific enough for local land stewards.

The Vegetation Subcommittee of the Federal Geographic Data Committee has developed a standard for vegetation classification in the United States (FGDC 2008), as well as descriptions of the approach (Jennings et al. 2009; Faber-Langendoen et al. 2009; Franklin et al. 2012; Faber-Langendoen et al. 2014), and the resulting United States National Vegetation Classification (USNVC) was released in February of 2016 (http://usnvc.org/website-launch/). The USNVC has already been successfully used to develop state-and-transition models of landscape change (Kudray and Cooper 2005) by standardizing the definition of states, develop habitat suitability maps and high-quality vegetation maps essential for biodiversity stewardship and research (Evens and Keeler-Wolf 2014), and improve the sharing of vegetation information among agencies for intra- and interagency management, such as mapping of vegetation and fuels in the LandFire program (https://my.usgs.gov/eerma/data/index/4f4e486ee4b07f02db50bea7).

Classification systems around the world are being developed and used for such purposes (Bruelheide and Chytrý 2000; Rodwell 2006), but small-scale, unconnected classifications within and among countries, and in the United States, within and among governmental units, have been the bane of developing regional classifications and the identification of community concepts over the range of their occurrence. Such is the problem in many areas of the United States and a standardized effort is needed to both corroborate USNVC concept descriptions and fill in the holes of the USNVC. Peet and Roberts (2013) define nine primary components of vegetation classification: 1) project planning, 2) data acquisition, 3) data preparation, 4) community entitation, 5) cluster assessment, 6) community characterization, 7) community determination, 8) classification integration, and 9) classification documentation. The advent of the USNVC has changed how researchers in the US approach these components; specifically, regarding classification integration recognizing that integration may also affect the iterative process of entitation and assessment. Because the USNVC concept descriptions are meant to cover the range of characteristics of a community concept, while collected data are potentially from a restricted area such as a park (as is the case in this study), documenting variations on that concept that are specific to the location may be beneficial to local stewards. However, that does not suggest the community concept itself be changed, as currently accepted concepts should only be modified after careful reflection (Jennings et al 2009; Peet and Roberts 2013).

An important element of any classification is the heterogeneity of the landscape, such that many different vegetation types may be found in a small geographic area. Further, one of the main uses of such classifications is mapping that provides information to stakeholders to make stewardship decisions (ESA Panel 2015), and this mapping level tends to be at the Macrogroup scale of the USNVC (combinations of moderate sets of diagnostic plant species and diagnostic growth forms that reflect biogeographic differences; FGDC 2008). While we fully expect the Great Plains Shortgrass Prairie to dominate the PNG landscape, we also expect to find more arid (e.g., Arid West Interior Freshwater Marsh) and more mesic types (e.g., Great Plains Flooded Forest).

The objective of this research was to develop a plot-based vegetation classification of the natural and semi-natural vegetation communities in the Pawnee National Grasslands in accordance with the USNVC. We followed standard procedures for data acquisition, used a variety of multivariate analyses for community entitation and determination, and integrated our community concepts with those of the USNVC, following the standards of Peet and Roberts (2013) and De Cáceres et al. (2015). We predicted that vegetation would be strongly affected by topography, especially slope positions that affect moisture levels, and that repeating patterns of vegetation communities would be found throughout the PNG landscape (i.e., community concepts would be recognizable).

## Study area

The Pawnee National Grasslands (PNG), administered by the USDA Forest Service, covers 79,876 ha in Weld County, Colorado, between 40°36' and 41°00' N latitude and between 103°34' and 104°48' W longitude (Figure 1). The grasslands are a mosaic pattern of private and public lands; both are used for grazing, oil and gas extraction, and house below-ground nuclear missiles. Included within the PNG are the Central Plains Experimental Range (CPER; 6057 ha), a research area administered by the Agricultural Research Service (now also part of the National Ecological Observation Network, NEON) and the Shortgrass Steppe Long-term Ecological Research site (now maintained by Colorado State University).

Climate is continental, but large air masses from maritime areas may move across the area. Crabb (1981) reported an average air temperature of -2°C during the winter with an average daily minimum temperature of -10°C; during summer months, average air temperature is 21°C with an average daily maximum temperature of 31°C.

The Pawnee National Grasslands also lie in the rainshadow of the Rocky Mountains to the west. Mean annual precipitation for the study area is 305–380 mm; average annual snowfall is 102 mm (Crabb 1981). Wind-driven snow often accumulates on leeward sides of hills (typically southeastern sides), around shrubs, and near roads; meltdown, especially in rocky or sandy soil, results in water penetration to greater depths at these locations (Hazlett 1998). The PNG lies within Kuchler's (1964) Shortgrass Steppe, dominated by $C_4$ grasses, and two of his four potential natural vegetation types may occur on the PNG: the overwhelmingly dominant *Bouteloua-Buchloe* Type and the *Artemisia-Schizachyrium* Type on deep sandy soils. The Shortgrass Steppe is typically dominated by graminoids (> 60%) with less than 20% cover of succulents, dwarf shrubs, and herbaceous dicots (Laurenroth 2008). Classifications of portions of the PNG, e.g. the Central Plains Experimental Range, suggest only a handful of vegetation community types (Moir and Trlica 1976). The PNG falls in the Loamy Plains (*Atriplex canescens/Bouteloua gracilis-Pascopyrum smithii*) Ecological Site Type (EST), part of the Central High Plains (https://esis.sc.egov.usda.gov/Welcome/pgESDWelcome.aspx). The EST classification includes discrete biological and physical factors that denote specific vegetation/soil/physical characteristics that respond similarly to management and disturbance. In addition, Hazlett (1998) differentiated six habitat types on the Pawnee: (1) open steppe (> 80% of study area), (2) sandy soils (~5%), (3) breaks and barrens

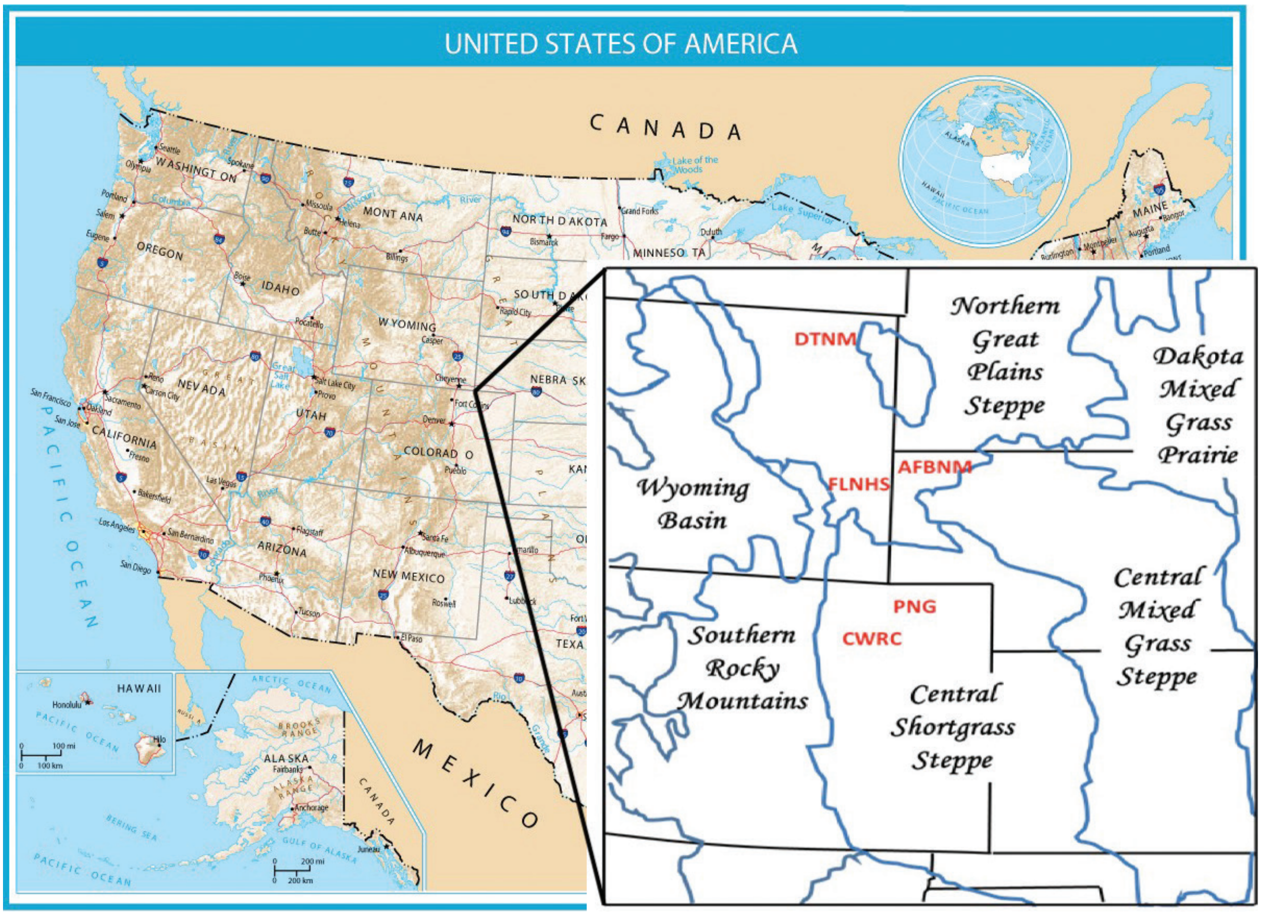


**Figure 1.** Location of Pawnee National Grasslands (PNG). Inset includes NatureServe Ecoregions of study area and additional plot data locations and studies: Classification of Natural Riparian/Wetland Plant Associations for Colorado (CWRC, throughout CO), Fort Laramie National Historic Site (FLNHS), Agate Fossil Beds National Monument (AFBNM), and Devil's Tower national Monument (DTNM).

(<2%), (4) cliffs and ravines (<2%), (5) riparian (~5%), and (6) roadsides and disturbed soils (< 5 %).

In general, the elevation of the Colorado Piedmont, an uplifted Cretaceous shale physiography that includes the PNG, declines from the mountain foothills toward the east at a rate of about 2 m $km^{-1}$; the highest elevation is 1,935 m in the northwestern portion near the "Chalk Bluffs" and the lowest elevation is 1,310 m in the southeastern portion around South Pawnee Creek. Most of the soils on the Pawnee National Grassland are shallow to deep loams that are well drained (Crabb 1981). Over most of the area is a loamy, wind-mixed veneer layer of soil of varying depths. These soils are underlain by a variable pattern of shale and sandstone bedrock materials. Barren rock or gravel areas of shale and sandstone can be exposed when erosive wind removes upper layers of soil. In addition, past tectonics and water erosion have exposed ravine "break" areas with rock exposed on the sides of the ravine. Sandy soils occur along stream terraces and on leeward sides of some hills (Hazlett 1998).

Swale areas often have finer textured soils than ridgetops, as mobile soil particles, such as silt and clay, have eroded from higher topographic positions and have been deposited in lower areas. This difference in soil texture is sometimes reflected by a greater abundance of *Buchloe dactyloides* in swales. In addition, some drainages, playas, and riparian areas have an accumulation of salts on or near the surface and thus host alkaline-tolerant plant species. Maps and detailed descriptions of the soil series types that occur in this study area can be found in Crabb (1981).

GIS techniques have been shown to be useful in determining distribution of plant and animal communities (Rotenberry et al 2006; Sangermano and Eastman 2006). The initial phase of this project used GIS map layers to develop an ecological land type classification that was subsequently used to stratify field plots (Kupfer and Franklin 2000). Map layers included elevation, bedrock geology, and soil classification obtained from the State of Colorado (http://coloradogeologicalsurvey.org/geologic-mapping/gis-data/). Plots (see below) were positioned within all 100 m elevation zones (1300–1800 m, which also was essentially an east to west gradient) and on all major parent materials (dune sand, gravel, sandstone, shale). We examined geology, soils, and topographic factors in an attempt to place plots in all environments (i.e., land types) of the Pawnee National Grasslands. Some noticeable trends are important (Figure 2). The western portion of the Pawnee is dominated by Cretaceous shales and the eastern portion by Tertiary sandstone; the eastern portion also contains some quaternary gravel and sand. There is also a general gradient in elevation, decreasing from west to east.

# Methods

## Field Data Collection

We obtained plots from all respective land types, but we purposefully did not set plots near roads, and the number of plots was fewer from habitats of lesser extent (e.g., riparian areas). Finally, discussion with Vernon Kohler (USFS, pers. comm.) and Don Hazlett (Denver Botanic Garden, pers. comm.) suggested vegetatively unique areas for plot locations. A posi-plot (positioned plot; Weaver and Robertson 1981) method was used to locate plots, first based on ecological land types and habitat types, and subsequently on visual vegetation communities. The GPS points for each of the community types were imported into ArcGIS and physical characteristics for each of these points were identified. In ArcGIS, plot locations were used to determine topographic characteristics (slope, aspect, elevation), soil type and rock type. Aspect was transformed following Beers et al. (1966).

101 plots were located based on visual homogeneity of vegetation (both dominant taxa and structure) and site characteristics, then randomly located within that area. Plot sampling followed the Carolina Vegetation Survey method (Peet et al. 1998). Plots were 0.1 ha; 20 m × 50 m made up of ten 10 m × 10 m modules unless vegetation heterogeneity constricted the size. If the area was small, modules were essentially 'fit' to the area to maintain homogenous vegetation within the plot. Within four intensive modules, subplots of 5 m × 5 m, 2 m × 2 m, 1 m × 1 m, and 0.3 m × 0.3 m were established in two corners (these corners were marked with GPS UTM coordinates; Peet et al. 1998). Presence of all taxa was described for each plot scale; cover of taxa was recorded for the 1 m × 1 m plots using the following cover scale (0–1%, 1–2%, 2–5%, 5–10%, 10–15%, 15–25%, 25–50%, 50–75%, 75–90%, >90%). Cover data were transformed to median values and averaged for all intensive modules for each plot prior to analyses. Both cover (estimated by module and averaged for the plot) and diameter at breast height (dbh) were recorded by species for all individual woody stems > 2.5 cm dbh. Cover values were used in all analyses.

In addition to the above data set, plots taken for a mountain plover study (Derner et al. 2009) with areas under heavy grazing were included in the analysis to determine the extent of differences among those communities and other steppe communities. These data were acquired with the permission of Paul Stapp, who had produced that canopy cover data in 27 fields; cover values for each field were derived from 30 1 $m^2$ quadrats spaced every 10 m along three 100 m transects. Data were transformed to median cover class values (Scale used for data collection: 0–5%, 6–15%, 16–25%, 26–40%, 41–60%, >60%) and averaged by pasture. These 27 plots along with the 101 plots make up the Pawnee-only data set (n=128).

## Classification Protocol

### *Pawnee-Only Community Classification Analyses*

We classified the data into 'plot-groups' using a hierarchical cluster analysis using the Sorenson dissimilarity measure and the Flexible Beta group linkage method

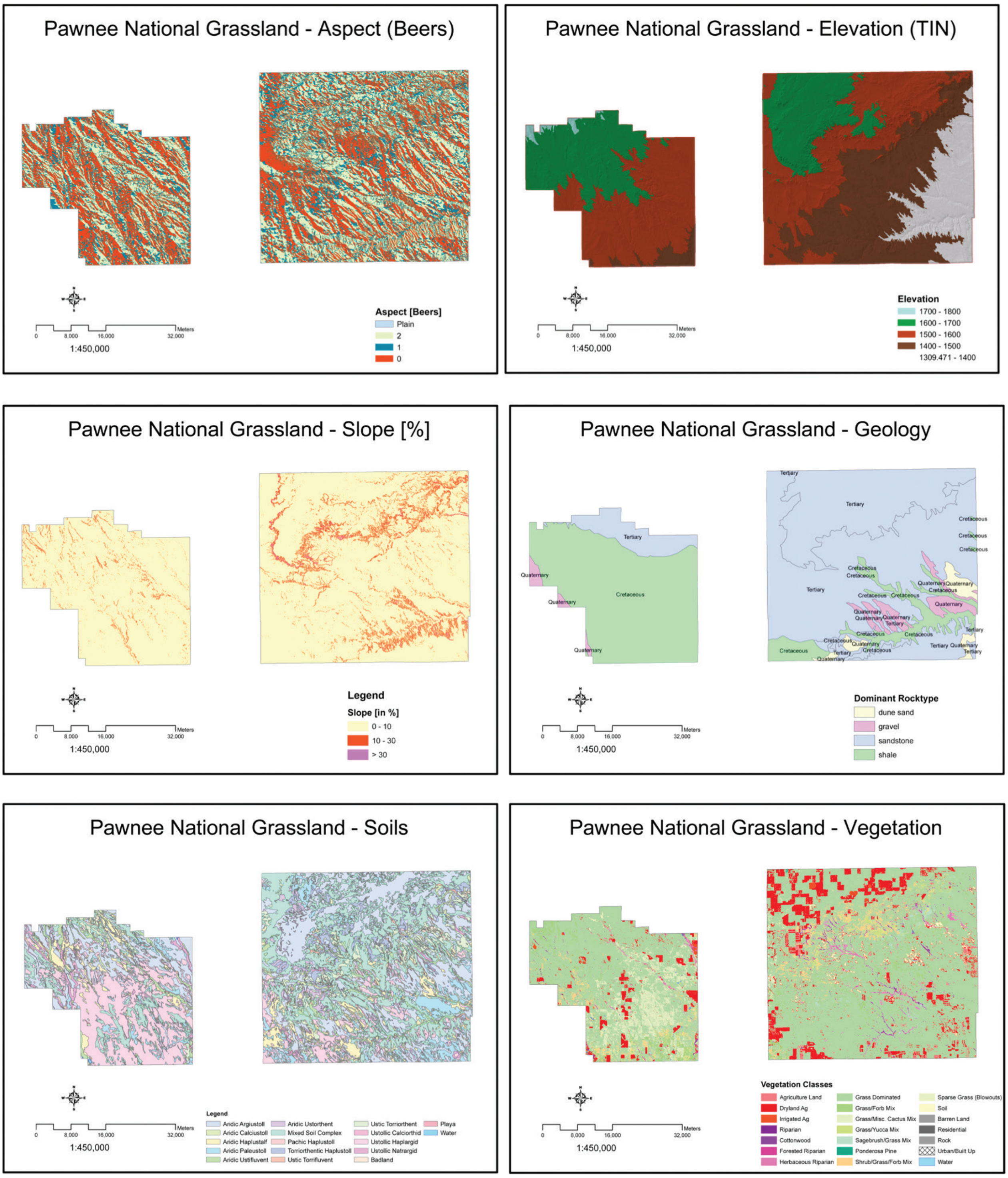


**Figure 2.** GIS maps of aspect, elevation, slope, soil type and vegetation type of the Pawnee National Grasslands (PNG). The two polygons represent the east and west sections of the PNG. Beers et al. (1966) transformation was used for aspect, ranging from 0 (SW) to 2 (NE); elevation ranges from 1309–1800 in 100 m intervals; slope ranges from low (0–10%) to medium (10–30%) to steep (>30%); vegetation and soild are based on previous classifications (see text).

(Beta = -0.25): data were square-root transformed prior to analysis using PCORD (McCune and Mefford 1999). We determined the number of plot-groups using OptimClass Type 1 (Tichý et al. 2009) using the Juice 7.0.102 Program (http://www.sci.muni.cz/botany/juice/); the method compares clustering results obtained with different methods and numbers of clusters to determine which solution is optimal in terms of the number of diagnostic species. Given an optimal number of clusters we determined diagnostic species by analysis of frequency and fidelity (phi coefficient) using the Juice program. The phi coefficient is a measure of fidelity independent of sample size. Values range from -1 to 1 and positive values indicate species occur within groups more often than expected by chance; higher values mean a greater degree of joint fidelity (Chytrý et al. 2002). Diagnostic species were those one to six species with the highest frequency and phi coefficient, chosen subjectively as meaningful.

We expected a gradient-driven distribution of vegetation related to a complex of environmental factors, including geological characteristics (soil type, rock type, % bare ground) and topographic characteristics (latitude, longitude, slope position, aspect). We promoted an ordinal scale to an interval scale for soil type, rock type, slope position, and site type, essentially from poor to less poor environmental conditions based on our knowledge of the area. We did not have data to assess scale so chose a simple linear scale and interpret the results conservatively. Soil Type included badland (1), Aridisol (2), Mollisol (3), mixed soil (4), Alfisol (5), and Entisol (6). Rock type included dune sand (1), sandstone (2), gravel (3) and shale (4). Slope position was coded 1 for convex ridgetop, 2 for flat slope, and 3 for concave ravine. Site Types were numbered from driest to most mesic: (1) blowout, (2) steppe hilltop, (3) steppe, (4) steppe buffalo wallow, (5) rock outcrop, (6) ridgetop, (7) draw slope, (8) ravine, (9) playa, and (10) riparian. Environmental data were related to vegetation groups through Canonical Correspondence Analysis and Nonmetric Multidimensional Scaling (using the Sorenson Index), species-environment correlations using 999 Monte-Carlo simulations, and descriptive statistics; all in PCORD. As a check on how strongly classified groups were tied to particular environments, we used a forward stepwise discriminant analysis (using SAS) to test if classified plot-groups could be predicted with site data, using the same promoted interval scale.

#### *Semi-supervised Classification Analysis*

Initial classification analyses showed eight plot-groups with four very small ones (including less than four plots), albeit these groupings were very different from other classified groups. After initial interpretation, we concluded these plots were all from rare mesic areas of the Pawnee National Grasslands. Accordingly, we compared PNG plots that made up the four small plot-groups with plots that had been previously classified elsewhere, a sort of semi-supervised classification (Tichý et al. 2014). For this, we retrieved an additional 64 plots from four other research projects within VegBank (Peet et al. 2013) with a query for plots containing the dominant and potentially diagnostic species of our small groups *Pascopyrum smithii*, *Carex nebrascensis*, *Eleocharis* species, and restricted to plots in the Great Plains (not foothills or mountains). These included the Agate Fossil Beds National Monument (AGFO; n=3) National Park Service Mapping Project in Nebraska (Project Contributer Jim Drake) and Devils Tower National Monument (DETO; n=6) National Park Service Mapping Project in Wyoming (Project Contributer Jim Drake), Fort Laramie National Historic Site (FOLA; n=34) National Park Service Mapping Project in Wyoming (Project Contributer Jim Drake), and the Classification of Natural Riparian/Wetland Plant Associations for Colorado (CWRC; n=21; Project Contributer Anonymous; Kittel et al. 1999).

Because all data were in VegBank there were relatively few taxonomy issues and these were vetted accordingly (e.g., *Arabis* = *Boechera, Agropyron smithii* = *Pascopyrum smithii*). However, several taxa were merged or deleted either due to questionable identification (unknown species) or too few individuals from the different study locations. For *Carex* or *Juncus* only, if species were unknown, those individual species observations were deleted, leaving only identified species data. We chose to merge taxa which were ecologically similar in their environment and when several plots did not identify them to species level (Suppl. material 1); most of these species also had very few individuals of one or more of the merged taxa. Such groupings of species make the results more conservative by increasing similarity among locations.

As with the Pawnee-only data set, we classified the full data set (all 128 Pawnee plots and 64 additional plots; n=192) using a hierarchical cluster analysis using the Sorenson distance measure and Flexible Beta (Beta = -0.25) group linkage method: data were square-root transformed prior to analysis. We determined the number of groups using OptimClass Type 1 (Tichý et al. 2009). Although we lacked sufficient data for a true semi-supervised analysis, we used the previously classified plot data (already published and in VegBank) to compare to our data within the cluster analysis.

### Classification Integration with the USNVC Classification System

Classification integration was mostly a comparison of our plot-groups with those described in the USNVC version 2.01 and known to occur in Colorado. The regional analysis provided several previously-classified plots and those concepts were compared to the plots from the PNG and integrated when possible. For those plots not clearly linked with previously classified plots, i.e., most of the steppe plots, our classified plot-group characteristic species were compared with described concepts and integrated; that is, we used characteristic species to compare our plot-groups to the USNVC classification and placed our plot-groups into the USNVC entities to which they matched most closely. Thus, the integration was non-quantitative.

## Results

### Pawnee National Grasslands Analysis

Analysis identified either 4 (Figure 3A) or 10 (Figure 3B) plot-groups (based on top two results that were not very different in their species fidelities) for the Pawnee-only plots. The main division was between the *Bouteloua gracilis-Buchloe dactyloides* Grassland Association (Groups 2, 3 and 4; Figure 3A) and mesic vegetation communi-

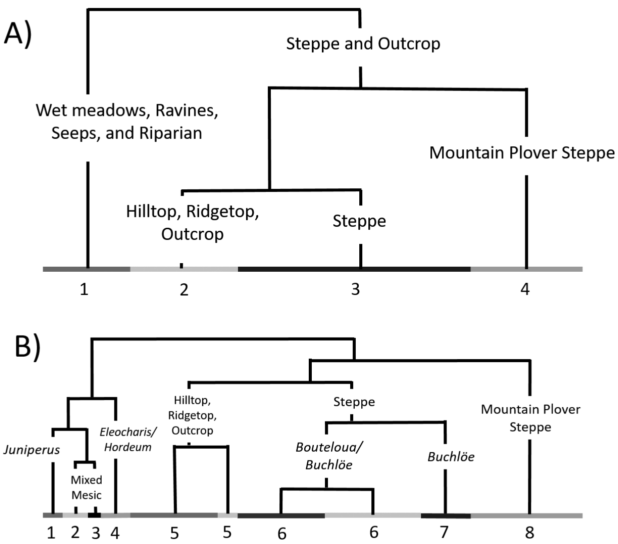


**Figure 3.** Dendrogram of Pawnee National Grassland plots showing the two peaks suggested by OptimClass. A) four groups suggested by OptimClass; B) 10 groups suggested by OptimClass with coalition of two sets based on the lack of indicator species.

ties (Group 1; Figure 3A). The initial interpretation of the 10-group dendrogram yielded two plot-groups that completely lacked indicator flora. Thus, we merged two sets of plot-groups (5 and 6) as shown in Figure 3B. Interpretation is thus based on these eight plot-groups with clear indicator species. The eight-group dendrogram essentially splits those two major groups into four plot-groups each (Figure 3B), but there is some difficulty in that there were so few plots of the mesic plot-groups; total plots = 20, each plot-group ranged from 3 to 7 plots. Thus, we discuss the mesic plot-groups only briefly here and more substantially in the regional analysis section. The eight plot-groups were also distinguished in an NMDS analysis (two dimensions, stress=20.517, p = 0.001; Figure 4A). Mesic sites were scattered throughout the bottom and left of the ordination plot and steppe sites were at the top and to the right, generally.

Albeit small in numbers of plots, and indeed limited in geographic distribution in the Pawnee National Grasslands (PNG), the diversity of vegetation in more mesic areas is high. Group 1, which contains mesic sites in scarp areas, had the second highest number of species despite having only three plots (Table 1). The highest diversity occurred in the other group that included scarp and outcrop plots, suggesting these sites have high heterogeneity and high diversity. The lowest diversity was found in the plots from the mountain plover studies (Table 1), typically prairie dog colonies, although one of our plots taken in a prairie dog colony was associated with Group 6, and we ended up combining plot-groups 6 and 8 based on their similarity of dominant and diagnostic species (especially *Bouteloua gracilis* and *Opuntia polyacantha*, Tables 1, 2). We attribute the lower diversity in the plover plots to smaller plot sizes from that study (30 m$^2$ compared to 100 m$^2$ for our plots).

Because the USNVC nomenclature is based on both dominant and diagnostic species, we examined dominance based on cover and fidelity of species in relation to the eight plot-groups (Table 2). However, the first four mesic plot-groups are heterogeneous in their dominant species; for example, Plot-Group 1 has *Juniperus scopulorum* and *Carex nebrascensis* dominating, but *J. scopulorum* was only found in one of the three plots. Thus, we do not suggest the average values or indicator species are correct for these plot-groups and instead discuss them further in the regional analysis section below.

## Species- and Community-Environment Relationships

Canonical Correspondence Analysis showed a significant species-environment correlation (0.839; p=0.001) for axis 1 only (the first axis had the only significant relationship with environment as well, 0.533, p=0.001; axis 2 = 0.352; Figure 4B). The first axis was correlated with site types,

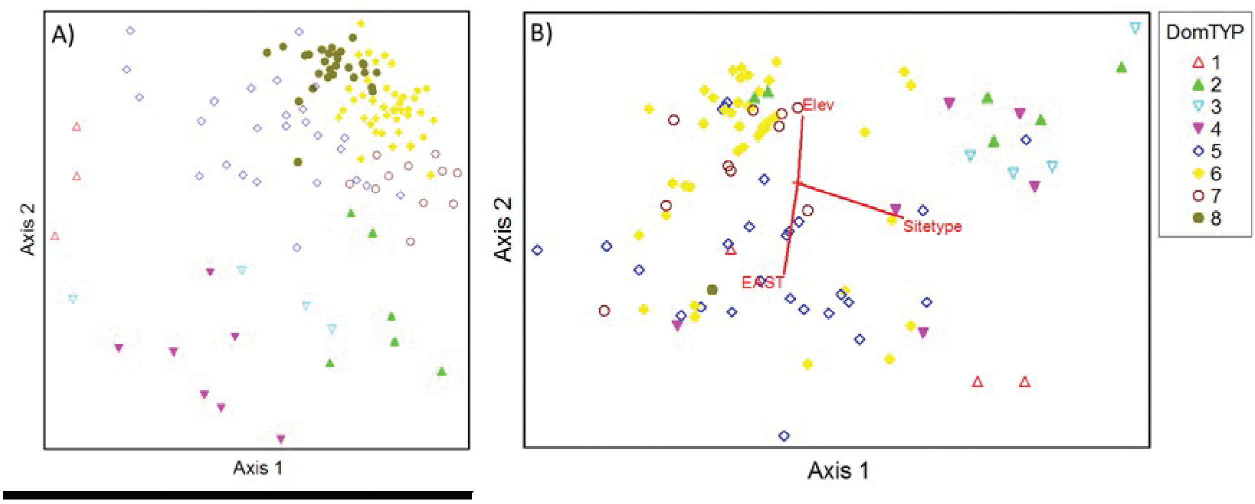


**Figure 4.** Non-metric multidimensional scaling (A) and canonical correspondence (B) analyses of 128 plots from Pawnee National Grasslands, CO. DomTyp refers to the plot-groups delineated from the analyses.

**Table 1.** Dominant species (average cover values > 1%) of the eight plot-groups found in the Pawnee National Grasslands, CO. Bold indicates highest average cover values.

| | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
|---|---|---|---|---|---|---|---|---|
| **Taxa** | **n = 3** | **n = 6** | **n = 4** | **n = 7** | **n = 26** | **n = 43** | **n = 11** | **n = 28** |
| *Carex nebrascensis* | **20.7** | | | | | | | |
| *Junipurus scopulorum* | **12.7** | | | | 0.8 | | | |
| *Rhus trilobata* | 8.0 | | | | 2.3 | | | |
| *Toxicodendron rydbergii* | 7.4 | | | | 0.1 | | | |
| *Nassella viridula* | 6.2 | | | | 1.0 | | | |
| *Agropyron cristatum* | 6.0 | | 0.1 | | 1.5 | 0.7 | 0.1 | |
| *Symphoricarpus occidentalis* | 2.7 | | | | | | | |
| *Rosa woodsii* | 1.5 | 0.7 | | | | | | |
| *Prunus virginiana* | 1.4 | | | | 0.1 | | | |
| *Solidago canadensis* | 1.3 | | | | | | | |
| *Sporobolus airoides* | | **19.8** | 1.0 | | 0.2 | | | |
| *Poa* sp. | 0.3 | 7.7 | 2.3 | 0.1 | 0.2 | | | |
| *Glycyrrhiza lepidota* | 0.8 | 6.4 | | | | | | |
| *Populus deltoides* | | 6.3 | | | | | | |
| *Distichlis spicata* | | 5.0 | 0.4 | | 0.3 | | | |
| *Rosa woodsii* | | 4.0 | | | | | | |
| *Elymus canadensis* | 0.2 | 3.7 | | | | | | |
| *Juncus balticus* | | 3.3 | | | | | | |
| *Thermopsis rhombifolia* | | 1.3 | | | | | | |
| *Eleocharis acicularis* | | | **4.5** | | | | | |
| *Erigeron* sp. | | | 4.0 | | | | | |
| *Schoenoplectus pungens* | | | 2.3 | | | | | |
| *Phalaris canariensis* | | | 2.0 | | | | | |
| *Lemna minor* | | | 2.0 | | | | | |
| *Eleocharis palustris* | | | **5.1** | **8.6** | | | 0.9 | |
| *Polygonum* sp. | | | 0.2 | **5.7** | | | | |
| *Thlaspi arvense* | | | | **5.4** | | | | |
| *Hordeum jubatum* | | | | **5.2** | | 1.0 | 0.2 | |
| *Rorippa curvipes* | | | 0.3 | 4.0 | | | 0.6 | |
| *Rumex crispis* | | | | 4.0 | | | | |
| *Ambrosia psilostachya* | 0.2 | 0.1 | | 3.3 | 0.1 | | | |
| *Bassia scoparium* | | | | 2.8 | 0.1 | | | |
| *Potentilla* sp. | | | | 1.2 | | | | |
| *Heliantus annuus* | | | | 1.2 | | | | |
| *Ribes aurea* | 0.7 | | | | 3.0 | | | |
| *Schizachyrium scoparium* | 0.2 | | | | 1.8 | | | |
| *Cercocarpus montanus* | | | | | 1.5 | | | |
| *Hesperostipa comata* | | | 0.3 | | 1.3 | 0.9 | 0.2 | 2.0 |
| *Bouteloua gracilis* | 0.1 | 1.9 | 0.3 | 0.1 | **6.8** | **23.4** | 2.3 | **17.5** |
| *Buchloe dacyloides* | | 0.7 | | | 4.3 | **21.6** | **28.7** | 1.6 |
| *Opuntia polyacantha* | | | | | 0.7 | 8.3 | 4.8 | 0.8 |
| *Atriplex canescens* | | | | | | 3.5 | | |
| *Yucca glauca* | 0.9 | | | | 2.9 | 3.3 | | |
| *Aristida purpurea* | | | | | 0.6 | 2.7 | 0.4 | 0.4 |
| *Atriplex canescens* | | | | | 0.1 | 2.2 | | |
| *Pascopyrum smithii* | 0.1 | 6.1 | 3.1 | 0.2 | 4.4 | 2.7 | **10.4** | 0.9 |
| *Sporobolus cryptandrus* | | | | | 0.3 | 0.9 | 1.9 | 0.2 |
| *Carex duriuscula* | | 0.7 | | 0.8 | 0.1 | 0.4 | 1.9 | |
| *Artemisia frigida* | 0.1 | | | | 0.7 | 0.2 | 1.8 | 0.5 |
| **Community Diversity** | | | | | | | | |
| Richness | 32 | 25 | 19 | 13 | **40** | 24 | 16 | 11 |
| Pielou Evenness | 0.47 | 0.49 | 0.71 | 0.60 | **0.72** | 0.53 | 0.55 | 0.45 |
| Shannon Diversity | 1.56 | 1.56 | 2.07 | 1.45 | **2.58** | 1.64 | 1.44 | 1.06 |
| Simpson Diversity | 0.64 | 0.66 | 0.77 | 0.65 | **0.82** | 0.69 | 0.63 | 0.47 |

suggesting vegetation was structured by a moisture gradient. Averages by plot-group also show a clear pattern in site type for the mesic communities compared to the steppe communities (Table 3). Axis 2 was correlated (albeit insignificantly) positively with elevation and negatively with easterly longitude since the Pawnee decreases in elevation from west to east; however, the gradient was not so evident by plot-group since many of these plot-groups are found throughout the PNG. There are apparently subtle changes in the flora from west to east. Since there is also a general increase in moisture from west to east, we examined floral changes along this longitudinal gradient. Of 213 species, 42 showed a significant positive correlation with easting and two showed a negative correlation. Correspondingly,

**Table 2.** Diagnostic species frequencies and fidelity values (phi coefficient × 100 superscripted) for the eight plot-groups found in the Pawnee National Grasslands, CO.

| Plot-group | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| Number of plots | n = 3 | n = 6 | n = 4 | n = 7 | n = 26 | n = 43 | n = 11 | n = 28 |
| *Carex nebrascensis* | $67^{49}$ | 17 | | 14 | | | | |
| *Toxicodendron rydbergii* | $100^{38}$ | | | | $19^{3}$ | | | |
| *Solidago canadensis* | $33^{25}$ | | | 14 | | | | |
| *Prunus virginiana* | $100^{23}$ | | | | 15 | 5 | | |
| *Rosa woodsii* | $100^{22}$ | 17 | | | 8 | | | |
| *Rhus trilobata* | $100^{23}$ | 17 | | | $54^{21}$ | 5 | | |
| *Nassella viridula* | $67^{20}$ | | | | $38^{14}$ | 2 | 9 | |
| *Parthenocissus quinquefolia* | $67^{19}$ | | | | 4 | | | |
| *Celtis laevigata* | $67^{18}$ | | | | | | | |
| *Sporobolus airoides* | 33 | $83^{47}$ | 25 | | 8 | 9 | | |
| *Distichlis spicata* | | $83^{30}$ | $75^{5}$ | | 4 | 5 | | |
| *Juncus balticus* | | $33^{30}$ | | | | | | |
| *Elymus canadensis* | $67^{0.0}$ | $33^{28}$ | | | 4 | | | |
| *Glycyrrhiza lepidota* | $67^{11}$ | $33^{24}$ | | | 4 | | | |
| *Thermopsis rhombifolia* | | $17^{21}$ | | | | | | |
| *Equisetum laevigata* | | $50^{17}$ | 25 | 14 | 4 | | | |
| *Eleocharis acicularis* | | | $25^{32}$ | | | | | |
| *Lemna minor* | | | $50^{28}$ | | | | | |
| *Schoenoplectus pungens* | | | $75^{27}$ | | | 10 | | |
| *Ranunculus cymbalaria* | | | $75^{27}$ | | | | | |
| *Phalaris canariensis* | | | $25^{24}$ | | | | | |
| *Circium floodmanii* | | | $100^{20}$ | | | | | |
| *Polygonum* sp. | | | $50^{4}$ | $100^{30}$ | 8 | | | |
| *Eleocharis palustris* | | 17 | $75^{18}$ | $57^{29}$ | | | 27 | 4 |
| *Rorippa curvipes* | | 17 | 50 | $71^{28}$ | 4 | | 27 | |
| *Bassia scoparia* | | | | $86^{25}$ | 8 | 5 | 4 | |
| *Ambrosia psilostachya* | $67^{3}$ | 50 | | $86^{25}$ | 23 | | | |
| *Hordeum jubatum* | | | | $86^{20}$ | 8 | 5 | | |
| *Schizachyrium scoparium* | 33 | 17 | | | $54^{25}$ | 5 | | |
| *Buchloe dactyloides* | | 50 | | | 65 | $100^{34}$ | $100^{19}$ | 57 |
| *Opuntia polyacantha* | 33 | 17 | | | 73 | $100^{25}$ | 55 | 100 |
| *Bouteloua gracilis* | 67 | 83 | 50 | 29 | 96 | $100^{24}$ | 91 | 100 |
| Lichen | | | | | 19 | 58 | 45 | $89^{14}$ |

**Table 3.** Average (and standard deviations) environmental values by plot-group: bold values are the highest and lowest values among plot-groups. Plot-group 8 is not shown as only one plot had environmental data. We developed ordinal scales for soil type, rock type, slope position, and site type, essentially from poor to less poor environmental conditions. Soil Type included badland (1), Aridisol (2), Mollisol (3), mixed soil (4), Alfisol (5), and Entisol (6). Rock type included dune sand (1), sandstone (2), gravel (3) and shale (4). Slope position included 1 for convex ridgetop, 2 for flat slope, and 3 for concave ravine. Site Types were numbered from driest to most mesic: (1) blowout, (2) steppe hilltop, (3) steppe, (4) steppe buffalo wallow, (5) rock outcrop, (6) ridgetop, (7) draw slope, (8) ravine, (9) playa, and (10) riparian.

| Plot-group | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| Number of plots | n = 3 | n = 6 | n = 4 | n = 7 | n = 26 | n = 43 | n = 11 |
| Easting | **604978** | **527119** | 535261 | 566184 | 585591 | 556341 | 559331 |
| | **(20316)** | **(6260)** | (14063) | (25462) | (28906) | (28821) | (28001) |
| Northing | **4521855** | 4516970 | 4520876 | 4519157 | **4512413** | 4515685 | 4516816 |
| | **(14049)** | (6867) | (2379) | (12819) | **(11184)** | (9643) | (9601) |
| Elevation (m) | **1483** | **1633** | 1600 | 1533 | 1514 | 1573 | 1565 |
| | **(58)** | **(41)** | (58) | (41) | (112) | (87) | (116) |
| Soil | 4.0 | 3.5 | **4.3** | 4.2 | 3.8 | 3.4 | **2.9** |
| | (0) | (1.4) | **(2.1)** | (1.5) | (0.9) | (1.1) | **(0.3)** |
| Rock | **2.0** | **1.0** | 1.5 | 1.8 | 1.9 | 1.5 | 1.6 |
| | **(0)** | **(0)** | (0.6) | (0.8) | (0.6) | (0.6) | (0.5) |
| Aspect | **1.3** | **0.5** | 1.0 | 0.7 | 0.9 | **1.3** | **0.4** |
| | **(1.2)** | **(0.8)** | (1.2) | (1.0) | (0.9) | **(0.9)** | **(0.7)** |
| Slope | **2.0** | 1.0 | 1.0 | 1.0 | 1.3 | 1.1 | 1.0 |
| | **(1.0)** | (0) | (0) | (0) | (0.5) | (0.3) | (0) |
| % Bare Ground | 18 | 9.2 | 24.3 | **47.5** | 35.2 | 19.2 | **43.0** |
| | (31.8) | (11.0) | (35.0) | **(37.1)** | (24.1) | (9.8) | **(33.0)** |
| Site Type | 8.7 | 7.3 | **9.5** | 7.8 | 5.4 | 3.6 | **3.1** |
| | (3.2) | (3.4) | **(1.0)** | (2.6) | (2.5) | (1.8) | **(0.9)** |

38 showed a negative correlation with elevation and one showed a positive correlation. A total of 19 species showed a negative correlation with northing and only two a positive relationship. Taken together, there is a strong suggestion of a longitudinal gradient (most likely moisture-driven) to which species are responding, but the gradient does not render distinct vegetation types.

We examined the ability to classify plot-groups with environmental data through stepwise discriminant analysis (Table 4); sitetype, longitude, percent bare ground and slope together significantly discriminated vegetation types. While some plot-groups seem to have distinct abiotic requirements (e.g., Groups 1, 3, 6 and 7), others were much less distinct.

**Table 4.** Number of observations and percent of plots (in parentheses) classified correctly based on environmental data. Model results from discriminant analysis given at the bottom of table. Group 8 was excluded due to low numbers and variability within group.

| Plot-group | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| 1 | **2** **(66.7)** | | | | 1 (33.3) | | |
| 2 | | 1 (16.7) | **3** **(50.0)** | | | 2 (33.3) | |
| 3 | | 1 (25.0) | **3** **(75.0)** | | | | |
| 4 | | 1 (16.7) | **2** **(33.3)** | **2** **(33.3)** | | | 1 (16.7) |
| 5 | 7 (26.9) | | 1 (3.9) | 2 (7.7) | **9** **(34.6)** | 3 (11.5) | 4 (15.4) |
| 6 | 3 (7.3) | 1 (2.4) | | 1 (2.4) | 3 (7.3) | **29** **(70.7)** | 4 (9.8) |
| 7 | | | | | | **6** **(60.0)** | 4 (40.0) |

**Discriminant Analysis Results**

| Variable | Partial $R^2$ | F | $p$>F |
|---|---|---|---|
| Sitetype | 0.44 | 10.13 | <0.0001 |
| Easting | 0.36 | 6.93 | <0.0001 |
| % Bare Ground | 0.25 | 4.17 | 0.0005 |
| Slope | 0.18 | 2.73 | 0.0132 |

## Semi-supervised Regional Analysis

The regional analysis clearly separated more mesic communities from mixed grass and short grass steppe (Figure 5). The rather striking difference of flora affirms the classification on the Pawnee sites as shortgrass steppe and generally negates the occurrence of mixed grass communities in the Pawnee National Grasslands; only two plots from outside of the Pawnee were classified with Pawnee plots (Groups 3 and 4; Figure 5) and only one Pawnee plot was classified with the mixed grass macrogroup (Groups 1 and 2; Figure 5). The bottom line is that while elements of the mixed grass are present in PNG (e.g., *Hesperostipa comata and Pascopyrum smithii*), they never reach sufficient cover to be called mixed grass. The one plot from the Pawnee situated with Plot-Group 1 of the regional analysis (Figure 5) and Plot-Group 5 of the Pawnee analysis (Figure 3) was closely related to the *Hesperostipa comata-Bouteloua gracilis-Carex filifolia* Grassland Association, but it is evident how different this association is from those typical of the Pawnee. In addition, the *Bouteloua gracilis-Buchloe dactyloides* Great Plains Shortgrass Prairie Macrogroup was separated from the *Hesperostipa comata-Pascopyrum smithii-Festuca hallii* Grassland Macrogroup to the north and east.

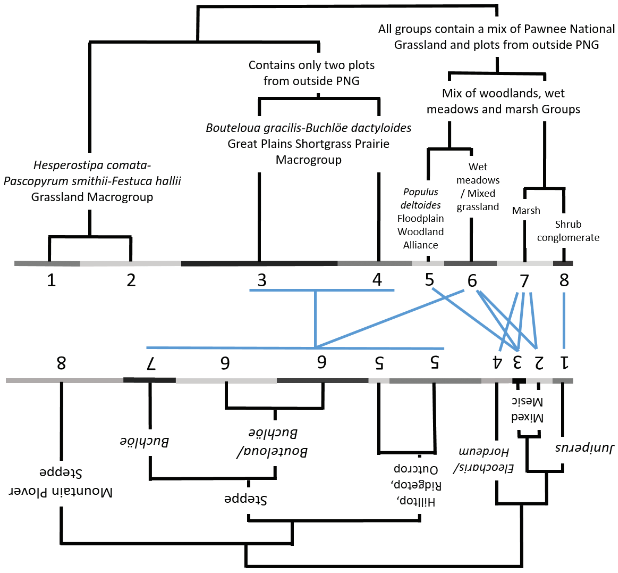


**Figure 5.** Regional analysis (right-side up) including all Pawnee National Grassland plots and plots from other local studies. The figure also depicts the relationship of plots in the Regional analysis to the Pawnee-only dendrogram (upside down).

This semi-supervised classification allowed us to characterize our few plots of mesic sites with known classified plots of similar flora from outside the PNG because mesic sites tend to be less zonal than drier sites. For example, the one plot from the Pawnee situated with Plot-Group 5 of the regional analysis linked that plot to the *Populus deltoides/Panicum virgatum-Schizachyrium scoparium* Floodplain Woodland Association.

Seven PNG plots were located in Group 6 of the regional analysis, which included a mix of *Pascopyrum smithii* and *Hesperastipa comata* USNVC associations, but also included the *Carex nebrascensis* Wet Meadow Association and the *Juncus balticus* Wet Meadow Association. We interpret this as an ‘in-between’ concept, with more mesic than usual mixed grass associations and drier than usual wet meadow associations. Supporting this conjecture, four of the seven plots, including three relic buffalo wallows, were classified with other shortgrass steppe plots (Group 6) in the Pawnee-only classification. In addition, one plot was situated in Plot-Group 5 with other scarp plots, and only two plots in Plot-Group 2 with other riparian sites (see below).

All three plots from PNG in Plot-Group 8 of the regional analysis resulted in their own Plot-Group 1 of the Pawnee-only analysis. The three plots previously classified included the *Populus deltoides/Panicum virgatum-Schizachyrium scoparium* Woodland Association, the *Juniperus scopulorum/Cornus sericea* Woodland Association, and the *Rhus trilobata/Pascopyrum smithii* Shrub Association. However, perhaps the closest USNVC concept is the *Juniperus scopulorum/Cornus sericea* Woodland Association that is supposed to occur here, except that none of our plots had >40% *Juniperus* cover. The plot-group actually shows the heterogeneity of scarp locations (although the plots were not located together), with one plot a seep dominated by *Carex nebrascensis* (and seems to fit the *Carex nebrascensis* Wet Meadow concept), another a riparian zone dominated by *Juniperus scopulorum* and *Rhus trilobata*, and the third near the scarp itself dominated by *Rhus trilobata* and *Rosa woodsii*. We suggest these belong to a new *Rhus trilobata* Alliance, but more data are needed for description of the concept. The difference between this concept and Plot-Group 5 of the Pawnee-only analysis is the presence of *Bouteloua gracilis* and *Buchloe dactyloides* in Plot-Group 5, while they are essentially absent from Plot-Group 1 of the regional analysis.

Plot-Group 7 of the regional analysis was also a mix of mesic communities based on previous designations. Indeed, PNG plots from this regional plot-group were split into Plot-Groups 2, 3, and 4 in the Pawnee-only analysis. Plot-Group 4 of the Pawnee-only analysis was most closely associated with the *Eleocharis palustris* Marsh Association and the *Hordeum jubatum* Marsh Association, with a couple of plots fitting each of those descriptions.

Plot-Groups 2 and 3 of the Pawnee-only analysis were not closely associated with any previously-classified plots. Plot-Group 2 occurs in riparian, ravine, and mesic steppe areas that, based on the dominance and fidelity of *Sporobolus airoides* and *Distichilis spicata*, have finer-textured, saline soils. This plot-group is most similar to the *Sporobolus airoides-Distichilis spicata* Wet Meadow Association, but the current USNVC description is mainly from New Mexico and should be updated to include the larger geographic area to which the type is found. Plot-Group 3 may indeed be from the mixed grass area, as it seems to fit best the *Pascopyrum smithii-Eleocharis* species Wet Meadow Association, typical of playa and periodically flooded grasslands mainly north of PNG. However, since this association does not generally have *Schoenoplectus pungens*, we suggest that at least one of the plots within this plot-group belongs to the *Schoenoplectus pungens* Marsh Association; plots more typical of permanent rather than periodic wetlands such as margins of ponds.

## USNVC Concepts in the Pawnee National Grasslands

While we do not have enough plot data to characterize all of these concepts, we provide a list of those USNVC concepts that we have evidence for in the Pawnee National Grasslands (Table 5). We document plots from two Classes, three Subclasses, four Formations, five Divisions, six Macrogroups, seven Groups and eight Alliances and

**Table 5.** USNVC concepts evidenced by plots within the Pawnee National Grasslands, CO.

| **Class** | **Mesomorphic Shrub and Herb Vegetation** | | | | | | | **Mesomorphic Tree Vegetation** |
|---|---|---|---|---|---|---|---|---|
| **Subclass** | Shrub & Herb Wetland | | | | | Temperate & Boreal Grassland & Shrubland | | Temperate & Boreal Forest & Woodland |
| **Formation** | Temperate to Polar Freshwater Marsh, Wet Meadows & Shrubland | | | Salt Marsh | | Temperate Grassland & Shrubland | | Temperate Flooded & Swamp Forest |
| **Division** | Western North American Temperate and Freshwater Marsh, Wet Meadows & Shrubland | | | Great Plains Saline Marsh | | Central North American Grassland & Shrubland | Western North American Grassland & Shrubland | Eastern North American – Great Plains Flooded & Swamp Forest |
| **Macrogroup** | Arid West Interior Freshwater Marsh | Western North American Montane-Subalpine-Boreal Marsh, Wet Meadow and Shrubland | | Great Plains Saline Wet Meadow & Marsh | | Great Plains Shortgrass Prairie | Southern Rocky Mountain Montane Shrubland | Great Plains Flooded Forest |
| **Group** | Arid West Interior Freshwater Marsh | Vacouverian-Rocky Mountain Montane Wet Meadow & Marsh | | Great Plains Saline Wet Meadow & Marsh | Western Great Plains Saline Meadow | *Bouteloua gracilis-Buchloe dactyloides-Pleuraphis jamsii* Great Plains Prairie | Southern Rocky Mountain Mountain-mahogany – *Mixed* Foothill Shrubland | Great Plains Cottonwood – Green Ash Floodplain Forest |
| **Alliance** | *Schoenoplectus americanus-Schoenoplectus acutus-Schoenoplectus californicus* Marsh | *Carex nebrascensis-Carex vesicaria-Carex pellita* Wet Meadow | *Juncus balticus-Juncus mexicanus* Wet Meadow | *Pascopyrum smithii – Distichlis spicata – Hordeum jubatum* Wet Meadow | *Sporobolus airoides* Great Plains Marsh | *Bouteloua gracilis-Buchloe dactyloides* Shortgrass Prairie | *Fallugia paradoxa-Rhus trilobata* Shrubland | *Populus deltoides* Floodplain Woodland |
| **Association** | *Schoenoplectus pungens* Marsh n=1 | *Carex nebrascensis* Wet Meadow n=1 | *Juncus balticus* Wet Meadow n=1 | *Pascopyrum smithii – Eleocharis spp.* Wet Meadow N=3 | *Sporobolus airoides* Northern Plains Marsh n=6 | *Bouteloua gracilis-Buchloe dactyloides* Grassland N=54 | *Rhus trilobata-Ribes cerneum* Shrubland n=26 | *Populus deltoides/Panicum virgatum-Schizachyrium scoparium* Floodplain Woodland n=1 |
| **Pawnee Plot-Group** | 2/3/4 | 5/6/7 | 5/6/7 | 3 | 2 | 5/6/7 | 1 | 2 |
| **Regional Plot-Group** | 7 | 6 | 6 | 6 | 6 | 3/4 | 8 | 5 |

**Table 6.** Local subassociations of the *Bouteloua gracilis-Buchloe dactyloides* Grassland Association of the Pawnee National Grasslands, CO.

| ***Bouteloua gracilis-Buchloe dactyloides* Grassland Association** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Local Subassociation Name | | | | | | | | |
| *Pawnee-Only Plot-Group 5* | | | *Pawnee-Only Plot-Groups 6,8* | | | *Pawnee-Only Plot-Group 7* | | |
| *Rhus trilobata/Schizachirium scoparium-Bouteloua* spp. Outcrop | | | *Bouteloua gracilis-Buchloe dactyloides* Steppe | | | *Buchloe dactyloides-Pascopyrum smithii* Steppe | | |
| Local Subassociation Diagnostic Species | | | | | | | | |
| **Diagnostic** | **Constant** | **Dominant** | **Diagnostic** | **Constant** | **Dominant** | **Diagnostic** | **Constant** | **Dominant** |
| *Schizachirium Scoparium*; | | *Pascopyrum smithii*; | *Bouteloua gracilis*; | | *Buchloe dactyloides*; | | *Buchloe dactyloides* | *Buchloe dactyloides*; |
| *Rhus trilobata* | | *Yucca glauca*; | *Opuntia polyacantha*; | | *Bouteloua gracilis*; | | | *Pascopyrum smithii* |
| | | *Schizachyrium scoparium*; | *Buchloe dactyloides*; | | *Opuntia polyacantha*; | | | |
| | | *Cercocarpus montanus*; | | | *Hordeum jubatum* | | | |
| | | *Bouteloua gracilis*; | | | | | | |
| | | *Buchloe dactyloides*; | | | | | | |
| | | *Agropyron cristatum* | | | | | | |
| Local Subassociation Environmental Description | | | | | | | | |
| Rock outcrops on ridgetops, scarps and draws resulting in heterogeneously-mesic conditions | | | Typical steppe concept | | | Swales and lower areas with finer-textured soils | | |

Associations. Abridged descriptions of these USNVC associations are in Suppl. material 2.

We have substantial data to characterize the *Bouteloua gracilis-Buchloe dactyloides* Grassland Association dominating the PNG. Because these data are from a limited area within the entire range of the Association, we simply document here the characteristics typical for the PNG. In addition, we present characteristics of three local subassociations that may be helpful for local management (Table 6; Suppl. material 3). One subassociation occurs on rocky outcrops that harbor more moisture at least heterogeneously. Thus, species such as *Rhus trilobata* and *Schizachirium scoparium* are common, while *Pascopyrum smithii* maintains more cover in this type than other types we describe here. These areas are quite diverse and probably deserve some attention for conservation. Another local subassociation appears to be dominated by *Buchloe dactyloides* while *Pascopyrum smithii* is again higher in cover, at least compared to other types. These communities appear to be related to shallow swales and likely finer-textured soils within the steppe complex. While we did not find a diagnostic species for the plots from the mountain plover study, except perhaps lichen, the dominance of *Bouteloua gracilis* and the lack of diversity, along with overall low total vegetation cover (averaged 27.8% cover; 72.2% bare ground) suggests these sites differ due to grazing. However, we consider these disturbed communities simply a subset of the *Bouteloua gracilis-Buchloe dactyloides* Steppe local subassociation (Suppl. material 3).

# Discussion

We used plot data to document the occurrence of two USNVC Classes, three Subclasses, four Formations, five Divisions, six Macrogroups, seven Groups and eight Alliances and Associations on the PNG, ranging from mesomorphic tree vegetation (i.e., *Populus* woodlands along riparian zones) to mesomorphic shrub and herb vegetation dominated by the wide-ranging shortgrass steppe species *Bouteloua gracilis* and *Buchloe dactyloides*. The latter is the matrix of the landscape with fragments of more mesic conditions nested within, ranging from standing water locations (e.g.. farm ponds) dominated by *Schoenoplectus pungens* or *Sporobolus airoides* under greater salinity, to *Carex*, *Juncus*, *Eleocharis*, and *Pascopyrum smithii* dominance in swales with varying levels of periodic moisture during the growing season.

Our plot-groups relate to those outlined by Hazlett (1998). Our *Buchloe dactyloides-Pascopyrum smithii* Steppe and *Bouteloua gracilis-Buchloe dactyloides* Steppe local subassociations together match his Open Steppe and Sandy Soils habitats, and our *Rhus trilobata-Ribes cernuum* Shrubland association matches his Cliffs and Ravines habitat. We suggest that his Breaks and Barrens habitat relates to our *Rhus trilobata/Schizachirium scoparium-Bouteloua* spp. Outcrop local subassociation, and that the remainder of our vegetation concepts relate to his Riparian habitat. For the latter, we clearly defined a number of different vegetation types within his one habitat, which is not surprising due to the azonal nature of more mesic locations (Faber-Langendoen et al. 2014). Baker (1984) appeared to take a strong splitter approach with grasslands and developed several associations from the many possible dominants at small scales (< 10 $m^2$). For *Bouteloua*-dominated types, he recognizes two, similar to our two local subassociations; *Bouteloua gracilis* Shortgrass Prairie and *Bouteloua gracilis-Buchloe dactyloides* Shortgrass Prairie, but also types like the *Hordeum jubatum* Plains Grassland. The unique barrens and outctrops are noted by associations such as the *Arenaria hookeri* Barrens and *Rhus trilobata-Ribes cereum /Schizachyrium scoparium* Shrub Association, but also at least two mixed prairie associations; *Stipa comata* Mixed Prairie and *Schizachyrium scoparium* Mixed Prairie. As did we, he also recognized several mesic types, including *Juncus balticus* Wetland, *Carex nebrascensis-Juncus balticus* Wetland, *Carex nebrascensis-Catabrosa aquatica-Juncus balticus* Spring Wetland, *Eleocharis palustris* Wetland, *Sporobolus airoides* Salt Meadow, and *Distichlis spicata* var. *stricta* Salt Meadow, as well as several *Populus deltoides* Forest/Woodland associations that are not clearly related to those on the PNG. There are two considerations with these comparisons. First, the previous studies are expert-based classifications and not plot-based. Further, at least for Baker (1984), that classification was for the entire state of Colorado, although we still believe he split concepts too finely compared to the current USNVC. Regardless, direct comparisons are difficult.

We propose local subassociations that may be helpful for land stewardship, but not as a change to the *Bouteloua gracilis-Buchloe dactyloides* Grassland Association concept. Our limited geographic reference for this concept does not allow any major changes, but that same geographic size suggests local subassociations may exist (Jennings et al. 2009). These groups have clear characteristic species and environments that may be of interest for conservation management.

Our 'semi-supervised' classification was successful in that it let us classify several rarer (in our dataset) plots. The ability to compare previously-classified plots with unknown plots (Tichý et al. 2014) in the same analysis allowed for a much better entitation and cleared up nearly all of our questions from the Pawnee-only analysis, and such analyses are needed to improve all future local classification efforts. One major conclusion from this analysis is that the mixed-grass concepts in the USNVC do not exist in the PNG. While the Colorado vegetation map suggests these communities are part of the PNG landscape, we argue that the vegetation composition and structure as a whole are different and should be considered so as the lines demarking the Shortgrass Steppe Ecoregion suggest (Sayre et al. 2009).

There are of course limitations to our study and this classification exercise. First, while the plot data are solid, the low number of plots (n=101+27) for the area of the PNG is a concern. Especially for the types where we have little data, additional plots are warranted. Further, while we thoroughly traversed the PNG looking for different vegetation associations, we may have missed certain associations that occur in the PNG, notably the four-wing saltbush (*Atriplex canescens*) lowlands as well as purposefully ignoring ruderal communities that are generally restricted to roadsides and highly disturbed sites in the PNG (Kotanen et al. 1998). The occurrence of the four-wing saltbush type seems to be rare, mainly on low-lying areas of private lands in the northeastern corner of the PNG (pers. obs.) and perhaps due to coarser soils (Dodd et al. 2002) or grazing intensity (Cibils et al. 2000; Hart 2001), or simply previous disturbance (Coffin et al. 1996; Augustine et al. 2017).

Finally, a thorough assessment of the abiotic characteristics of these sites is warranted, since soil texture (Dodd and Lauenroth 1997; Dodd et al. 2002) and moisture (Boutton et al. 1980) are known to affect vegetation community composition and structure on the PNG but were not examined on a site-specific basis here. While abiotic factors would not affect our plot-based vegetation classification, environmental data would be useful for interpreting the vegetation patterns.

Finally, we make a plea here that all vegetation scientists with full-species plot data place those data into VegBank or another public database. While we were able to relate some of our more mesic concepts to plots from other studies, little plot data existed for the typical shortgrass steppe communities dominated by *Bouteloua* species. Our data represent a small geographic fraction of the area this concept covers and a regional analysis would be beneficial for the PNG and the USNVC (Palmquist et al. 2016).

## Data availability

All data are in VegBank (http://www.vegbank.org).

## Author contributions

SBF collected and analyzed data and wrote initial paper; MS collected and analyzed data and edited paper; JS helped with analyses and edited paper.

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## Supplementary material

**Supplementary material 1**
**List of taxa used in the classification of the Pawnee National Grasslands, CO**
Link: https://doi.org/10.3897/VCS/2020/38629.suppl1

**Supplementary material 2**
**Abridged USNVC concept descriptions**
Link: https://doi.org/10.3897/VCS/2020/38629.suppl2

**Supplementary material 3**
**Subassociation descriptions based on plot data from current study in Pawnee National Grasslands**
Link: https://doi.org/10.3897/VCS/2020/38629.suppl3