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CLASSIFICATION AND ORDINATION  
OF  
TALL-GRASS PRAIRIE VEGETATION,  
CITY OF BOULDER OPEN SPACE PARCEL 7,  
BOULDER, COLORADO

by

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## ABSTRACT

The tall-grass prairie in Parcel 7 of the City of Boulder, Colorado Open Space Program was sampled and analyzed using Braun-Blanquet phytosociological techniques. Sampled vegetation was classified by Braun-Blanquet table analysis techniques. Nine Community Types and four Groups were defined. The site is dominated by *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Panicum virgatum*. *Spartina pectinata* forms almost monotypic stands in the wettest sites. The data were ordinated using Detrended Correspondence Analysis (DCA). Interpretation of community gradients with the DCA ordination agrees with the Braun-Blanquet classification. Interpretation of the ordination suggests that soil moisture is the controlling environmental gradient of the vegetation. Alpha diversity appears to be inversely correlated to the moisture gradient. Species identified show an affinity to taxa native to the tall-grass prairie (45%) and mountain steppe (32%), as well as adventive species (23%).

## INTRODUCTION

This study is the product of a research project carried out in the autumn of 1988 by a University of Colorado class in Plant Community Ecology. The study site is a remnant stand of tall-grass prairie south of the city of Boulder. Our objectives are fourfold: 1) characterize the vegetation, 2) delineate environmental gradients, 3) examine species diversity trends, and 4) examine geographic affinities of the flora.

### *Grasslands*

Grasslands are the largest of the North American vegetation formations, originally covering almost 300 million of the 700 million ha in the United States. Despite widespread transformation of native grasslands into agricultural lands, grasslands remain the largest of the natural biomes in the United States, covering more than 125 million ha (Sims 1988). Although graminoid species (Poaceae, Cyperaceae, and Juncaceae) physiognomically define this vegetation type, forbs typically exceed graminoids by three to four times. Important forb families are the Asteraceae and Fabaceae. While grasslands are the product of myriad factors, seasonal drought, fire, and grazing are most important.

Despite <sup>its</sup> ~~their~~ present expanse in central North America, the North American grassland is a relatively young biome, being chiefly of post-glacial origin in this region (Axelrod 1985). Fossil floras from the middle Miocene (12-10 myBP) indicate that valleys of the Great Plains were largely forested and wooded, with interfluves probably covered with scattered savannas and parklands.

During the arid Miocene-Pleistocene transition (7-5 myBP) grasses experienced an evolutionary expansion as forests and woodlands were restricted to moister valleys and grasslands spread across the interfluves.

With the onset of a cooler, moister climate in the Pleistocene (2 myBP) grasslands once again were restricted as forests and woodlands covered what are now treeless plains. Nevertheless, grasses and other grassland species persisted in the parklands and savannas, which were common in the Pleistocene. With the emergence of the warm, dry Altithermal climate ca 5000 BP, these species expanded at the expense of the wooded tracts. Concomitant with the increasing aridity was the increased occurrence of natural and man-made fires and increased pressure from large browsing mammals. These three factors - aridity, fire, and severe browsing pressure - brought the grassland biome to its present day prominence. Evidence for the grasslands youthfulness is found in its lack of endemics, the occurrence of most of its species in neighboring forests, and the relictual occurrence of diverse trees over the region (Axelrod 1985).

The tall-grass prairie is the most mesic of the grasslands associated with the central plains. It is dominated by bunchgrasses and sod-forming grasses (Risser 1985). Important species are *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Panicum virgatum*. On drier sites, or in those areas subject to grazing pressure, *Bouteloua gracilis*, *B. hirsuta*, *B. curtipendula*, and *Buchloe dactyloides* may assume a greater role. *Spartina pectinata* often forms homogeneous stands

in wet swales.

The most extensive development of tall-grass prairie is in the eastern Great Plains where it forms an ecotone with the eastern deciduous forests. The presence of this vegetation type in Boulder County probably represents the type of grassland that was common here during the Pleistocene. The survival of these grasslands and other relictual communities in the Boulder area has been attributed to the moderating effect of the mountain front. Vestal (1914) was one of the first botanists to describe the tall-grass prairie remnants in Boulder County. In a later paper he wrote:

"...the mountain front has the longest frostless season, the highest mean temperature, the mildest winters, and the least range in temperature extremes. Mountain front localities are comparatively sheltered and temperature inversion is common. Early spring plants flower several weeks earlier at the mountain front than in either the plains or foothills." (Vestal 1919)

While Boulder lies outside the "normal" climatic range of tall-grass prairie, factors such as its relictual establishment and specific site characters may explain its presence as a narrow band along the mountain front. Boulder is in a unique position at the western end of an arc the Front Range forms which opens up toward the plains. Upslope storms are funneled into the area and precipitation is significantly greater than in the surrounding areas. A cloud veil often forms on the mountains above town creating locally humid conditions (Cooper 1984).

#### *Study Site*

With the urging of Moir (1971,1982), who recognized their unique value, the City of Boulder has acquired the surviving tall-

grass remnants under the auspices of the Open Space Program. The city joined with the Colorado Natural Areas Program in the early 1980's in conducting a systematic inventory of tall-grass prairies in Boulder County. The inventory determined that the Boulder tall-grass prairies are the most extensive and highest quality remnants in Colorado. They were designated a State Natural Area in 1984. Since that time a management program incorporating grazing, fire, exclosures, and vegetation surveys have been in effect (Baker and Galatowitsch 1985).

Parcel 7, located northwest of South Boulder Creek near its junction with State Highway 93 (Figure 1), is part of the City of Boulder Open Space lands and contains some of the best examples of tall-grass remnants in Boulder County. The 245 ha parcel extends from the South Boulder Creek floodplain up onto the adjacent Pleistocene river terraces. This represents a relief of approximately 3 m. Occasional stands of cottonwood are found along the creek while scattered Ponderosa pine occur on the terraces. The elevation is 1646 m.

Baker and Galatowitsch (1985) noted that most tall-grass prairie sites in Boulder County have either high water tables or are covered with coarse gravel deposits. The former situation is represented along the South Boulder Creek floodplain while the latter condition is evident on the terraces. Coarse gravels may serve as a mulch by allowing rapid infiltration of water and decreasing loss through evaporation (Branson et. al. 1965). Moisture seems to be the primary factor affecting the type of grassland that develops in a prairie locale (Vestal 1914).

## *Climate*

Boulder has an annual precipitation of 457 mm with the maximum moisture coming in April and May. Rain and snow result when moist air is forced upward by the mountains, condenses, and falls. Upslope storms occur in the spring and autumn when air masses from the Gulf of Mexico are forced up against the mountains and create the orographic effect. Convective storms are common on late summer afternoons.

The average temperature is 10.5° C with 152 frost free days. Winds are predominantly from the west. Strong, warm, dry winds occur in the winter months and act to desiccate the landscape (Baker and Galatowitsch 1985).

## *Geomorphology*

Surficial deposits in Parcel 7 region are divisible into three main groups: pre-Wisconsin, Wisconsin, and Recent (Malde 1955). They indicate early Pleistocene valley incision below pediments, late Pleistocene valley filling, and upland eolian deposition. While events recorded by recent deposits have little modified the land, they serve to indicate minor climatic fluctuations. Buried soils and the physical geology <sup>of</sup> the region suggests the valleys were incised to near present depth during the Pleistocene (Malde 1955).

Hoffman (1986) used Malde's mapping to identify three units in Parcel 7 in an attempt to relate vegetation to surficial deposits: 1) Undifferentiated upland deposits, 2) Cobble gravel,

and 3) Post-Piney Creek alluvium. Undifferentiated upland deposits consist of strongly weathered alluvial, colluvial, and eolian deposits. They are impregnated with calcium carbonate below a red-brown clayey layer that is only locally preserved. Cobble gravel occurs with the Undifferentiated upland deposits on the terraces but is also found on the South Boulder Creek floodplain. This unit consists of coarse gravels, rich in red sandstone from the nearby foothills. Below a depth of about 30 to 45 cm it is encrusted and partly cemented by calcium carbonate. Both of these units are of Pleistocene age. The Post-Piney Creek alluvium is found along the floodplain. Of recent origin, it is a reworked gravel locally overlain by 0.3 to 0.9 m of non-calcareous sand and silt.

### *Soils*

Two soil series, both Mollisols, are found in Parcel 7 (Soil Conservation Service 1975). Mollisols are typical of tall-grass prairies, and their dominant soil-forming process is melanization, a darkening of the surficial horizons (mollic epipedons) by addition of organic matter. Melanization results from root penetration into the developing soil and the breakdown of this root material by soil fauna. The depth of mollic horizons depends on the amount of rainfall and temperature (Sims 1988).

The Nederland series, an Aridic Argiustoll, is found on the upland terraces of Parcel 7, and the Niwot series, a Typic Haploquoll, is in the floodplain. Aridic Argiustolls are well drained soils associated with old terraces and alluvial fans. They are formed in loamy alluvium containing many cobbles. Native



vegetation is mainly tall- and mid-grass prairie. They are "...moderately coarse-textured to fine-textured, well drained, grassland soils...[with]...a dark colored A horizon, a B2t horizon, and a C horizon that contains sub-horizons of secondary carbonate accumulation" (Soil Conservation Service 1975).

Typic Haplaquolls are "...medium textured to moderately fine-textured, poorly drained meadow soils that overlie beds of sand and gravel. They are characterized by a dark colored, calcareous to non-calcareous A horizon and a strongly mottled C horizon" (Soil Conservation Service 1975). These soils occur on low terraces and bottom lands in which the native vegetation is mainly water-tolerant graminoids.

## METHODS

### *Data Collection*

Results from a previous study of the area (Fisher 1987) and prior reconnaissance of the study site by the instructors, Skip and Marilyn Walker, were used to delineate the entities to be sampled. Thirteen entities were recognized, of which nine were sampled at four sites each, resulting in 36 samples. A range of xeric to hydromesic environments were represented. Sampling followed a centralized replicate method. The center of a homogeneous stand was identified and numbered, and a circle with a 2 m radius was outlined and flagged. Visual estimates of percent cover for each species and general site characteristics were recorded for each

## DISCUSSION

Classification and ordination techniques provided complimentary results which supported the initial entitation units and delineated soil moisture as the primary environmental gradient. When relevés were arranged along a soil moisture gradient from dry to wet, Braun-Blanquet analysis resulted in a two-tiered hierarchy composed of nine community types within four groups. Additionally, four broad groups outside the hierarchy were recognized which included taxa associated with two or more of the four groups. Table analysis also revealed rock cover to be an important gradient inversely related to the soil moisture gradient.

Ordination results show the community types and groups clustered along axis one which represents soil moisture. The inverse relationship of rock cover to soil moisture was also delineated by ordination. Stratified ordination of the data confirms environmental data collected as well as observations made in the field. Xeric sites had the <sup>mesic</sup> yellow  $\leftarrow$  dry hue values of the soils sampled. In the xeromesic group, the two Schizachyrium scoparium communities displayed greater microrelief than the Poa compressa-Sporobolus asper community. The two Schizachyrium scoparium communities are differentiated by the percentage of shrub cover. When mesic communities were stratified, community type Andropogon gerardii-Lupinus argentea showed greater gramminoid cover, greater forb cover, higher dry hue values, and lesser litter cover than the Panicum virgatum-Juncus interior community. The stratification of the hydromesic group did not show any correlation with environmental data collected, however, alpha diversity may be used to differentiate Spartina pectinata communities from the other two community types of this group.

Determination of alpha and beta diversity for each community type revealed a general inverse trend along the soil moisture gradient. Alpha diversity values showed this trend best while beta diversity correlated

less closely to this trend. Xeromesic communities displayed the greatest alpha diversity and hydromesic communities the least, while the greatest beta diversity found in community type Agrostis gigantea-Phleum pratense and the smallest beta diversity found in community type Panicum virgatum-Juncus interior.

Geographical affinities revealed the dominant species of Parcel 7 are associated with plains species and secondary species found in Parcel 7 are associated with mountain-steppe vegetation. Overall, 45% of the species found in Parcel 7 are associated with plains species, 32% are associated with mountain-steppe species, and the remaining 23% are adventive species.

After characterizing the vegetation of Parcel 7, delineating the primary environmental gradients, and examining trends of diversity and geographical affinity, it was concluded that Parcel 7, while considered a tall-grass remnant, is not a true tall-grass prairie when the prairie is considered as an entire <sup>community</sup> species complex. Parcel 7 may best be considered a unique assemblage of prairie species mixed with mountain-steppe species and weeds.

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It was noted that many of the weedy species occurring in Parcel 7 were associated with those community types most closely resembling the communities of the true tall-grass prairie, i.e. those containing the greatest percentage cover of the tall-grass dominants. Dominant species of any vegetation type tend to have broader amplitudes across environmental gradients. This is true of the dominant species of Parcel 7 and of the weedy species associated with the dominants. Dominant species Andropogon gerardii, Schizachyrium scoparium, Panicum virgatum, Sorghastrum nutans, and weedy species Bromus japonicus, and Dianthus deltoides are all found in two broad groups of taxa outside the hierarchy which include all but the most extreme groups.

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It is possible that in Parcel 7 weeds are replacing the secondary associated species normally found in true prairie complexes.

An alternative hypothesis is that there are still secondary associated species of the true prairie complex present, but that the prevalence of weedy species also associated with the dominant prairie species prevents the association from being clearly seen. Of the 60 species which have affinities to plains species, less than 10 species are accounted for as dominant species. Comparisons of presence, frequency, and percentage cover of the secondary associated true prairie species with species in Parcel 7 having affinities for plains species could provide support for these hypotheses.

Tall-grass vegetation <sup>Conclusion?</sup> <sup>Summary?</sup> sampled in Parcel 7 reflects the influence of the area's geographic and environmental factors. Larger groupings of species agree with those described at other tall-grass sites, yet plant communities in Parcel 7 are unique with species having a higher geographic affinity to mountain-steppe species than those typical of other tall-grass prairie regions. Hierarchical classification of thirty-six relevés and ordination analysis confirm that the controlling environmental gradient responsible for floristic patterns and diversity in the landscape is soil moisture.

## LITERATURE CITED

- Axelrod, K.E. 1985. Rise of the Grassland Biome, Central North America. *The Botanical Review*, 51(2):164-201.
- Baker, W.L. and S.M. Galatowitsch. 1985. The Boulder Tall-grass Prairies. M. Figgs and N. Lederer (eds.), Boulder County Nature Association Publication No. 3: Boulder, Colorado. 25 pp.
- Branson, F.A., R.F. Miller, and I.S. McQueen. 1965. Plant Communities and Soil Moisture Relationships Near Denver, Colorado. *Ecology* 46(3):311-319.
- Cooper, D.J. 1984. Ecological Survey of the City of Boulder, Colorado Mountain Parks (unpubl. ms.).
- Fisher, D.M., et al. 1987. Classification and Ordination of Tall-grass Prairie Vegetation, Parcel 7 Natural Area, Boulder County, Colorado. Unpubl. Report. 52 pp.
- Guach, H.G., Jr. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press: Cambridge, England. 298 pp.
- Hill, M.O. 1979. DECORANA, a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Department of Ecology and Systematics, Cornell University: Ithaca New York. 52 pp.
- Malde, H.E. 1955. Surficial geology of the Louisville Quadrangle, Colorado. U.S. Geol. Surv. Bull. 996-E:217-257.
- McGregor, R.L. 1986. Flora of the Great Plains. University of Kansas Press: Kansas. 1392 pp.
- Moir, W.H. 1971. Tall-grass prairies in remnant locations in Boulder and Jefferson Counties, Colorado. Unpublished Report.
- Moir, W.H. 1972. Tall-grass prairie in Colorado and its aesthetic value. In: J.H. Zimmerman (ed.) *The Second Midwest Prairie Conference*, Univ. of Wisconsin Arboretum, Madison.
- Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons: New York. 547 pp.
- Risser, P.G. 1985. Grasslands. pp. 232-256 in B.F. Chabot and H.A. Mooney (eds.), *Physiological Ecology of North American Plant Communities*. Chapman and Hall, New York.
- Sims, P.L. 1988. Grasslands. pp. 266-286 in M. Barbour and D.W. Billings (eds.), *Terrestrial Vegetation of North America*. Cambridge University Press.

- Soil Conservation Service. 1975. Soil Survey of Boulder County Area, Colorado. Cartographic Division, Soil Conservation Service. U.S.D.A.: Washington, D.C. 86pp. + 31 maps.
- Vestal, A.G. 1914. Prairie Vegetation of a Mountain Front Area in Colorado. Bot. Gazette, 58:377-340.
- Vestal, A.G. 1919. Phytogeography of an Eastern Mountain Front in Colorado. Bot Gazette, 68:153-193.
- Walker, M.D. 1988. EPOB 4120/5120 Plant Community Ecology Computer User Guide. Unpublished manuscript.
- Walker, M.D. 1988. Personal Communication.
- Weber, W.A. 1988. Personal Communication.
- Westhoff, V. and E. van der Maarel. 1978. The Braun-Blanquet Approach. In: R.H. Whittaker (ed.), Classification of Plant Communities. 2nd edition. Dr. W. Junk: Den Haag.

## DISCUSSION

Remnant stands of tall-grass prairie at the eastern edge of the Front Range of the Rocky Mountains were studied in order to characterize the vegetation and to examine its geographic affinities, establish controlling environmental factors, and examine species diversity. This classification of Parcel 7 shows some agreement with classification of tall-grass prairie sites in Oklahoma by Rice(1952), Kelting(1954), and Ray(1959). Panicum virgatum, Andropogon gerardii, Sorghastrum nutans(Sorghastrum avenaceum), and Andropogon scoparius (Schizachyrium scoparium) were all listed as dominants in Oklahoma, as they are listed as group indicators in the present classification. Moir(1969) recognized three grass communities in Colorado that are similar to the the Parcel 7 tall-grass communities identified in this classification. Indicator species in Moir's communities are also differentiating species in broad groupings-xeric, xeromesic, and mesic to hydromesic taxa- of this classification, suggesting that these latter groups may be approximately equal to Moir's communities. Two major differences occur. Table analysis classification allowed designation of a hydromesic group and three community types within that group that are not similar to groups recognized by any of the above authors. In these <sup>xr</sup> taxa tall-grass species are not dominant. Further, Bouteloua gracilis is a group indicator of the xeric group at Parcel 7, while Bouteloua curtipendula appears to be

a more common indicator of xeric sites in the other studies of tall-grass prairies mentioned. <sup>6</sup> Bouteloua gracilis's presence in the xeric sites in Parcel 7 <sup>?</sup> influences the influence of short-grass prairie and the abundance of this element in Boulder.

In fact, the tall-grass prairie at Parcel <sup>7</sup> is not typical tall-grass prairie, if this is defined by the stands that have been characterized at the eastern edge of the Great Plains where the tall-grass prairie had its most extensive development. Boulder tall-grass prairie is a mixture of tall-grass species, mid-grass and species (Hanson, 1931), <sup>^</sup> a short grass prairie (Weaver and Albertson, 1956) with a good proportion of mountain steppe species and adventive species. Nearly half (45%) of the species in Parcel 7 are prairie species, with the remainder being either adventive or associated with mountain steppe vegetation. Prairie species dominate in the mesic groups, with mountain steppe species becoming more common in the xeric plots and adventive species more common in the hydromesic plots. The prairie species physiognomically define the vegetation in Parcel 7, while the mountain steppe species provide a unique element which separates the site from tall-grass prairie found in the eastern Great Plains, <sup>7</sup> this aspect could serve to place the tall-grass prairie remnant found in Parcel 7 into a different syntaxonomical group in a Braun-Blanquet hierarchy.

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Initial entitation of plots recognized a soil moisture gradient. Table analysis and the detrended correspondence analysis confirmed that a complex moisture gradient is the overriding factor in determining the flora present. Data on specie's presence and abundance in the table analysis agrees <sup>5</sup> partially agrees with species amplitudes along a moisture gradient as suggested by Bazzaz and Parish (1982) for six major grass species present at the Boulder



study site (Fig. 16). All six species were present at the site. Relative abundance of Schizachyrium scoparium (Andropogon scoparius of Fig. 16), Sorghastrum avenaceum (Sorghastrum nutans of Fig. 16), Andropogon gerardii, and Spartina pectinata basically agree with Bazzaz and Parish. As noted earlier, Bouteloua curtipendula is not common on xeric sites at Parcel 7. Instead, Bouteloua gracilis exhibits a distribution similar to that suggested by Bazzaz and Parish for Bouteloua curtipendula.

Further, broad groups of species divide their occurrence in the table along a soil moisture gradient. Species associated with the xeric to xeromesic <sup>sites</sup> taxa are rare in the area of the table where species in the mesic to hydromesic taxa occur. Similarly, species in the mesic to hydromesic group are rare in the part of the table where the xeric to xeromesic group occurs. They are almost mutually exclusive in their presence. Interestingly, these groups are also divided floristically. The species associated with the Xeric to Xeromesic group are composed primarily of prairie and mountain steppe species, almost evenly divided. Species associated with the Hydromesic group are composed almost entirely of adventive species.

The first vector of the detrended correspondence analysis sample ordination appears to be primarily a moisture gradient with the driest sites to the left and the wettest sites to the right. Plots on the flood plain tended to have higher soil moisture than upland sites.

Interestingly, species diversity is highest in the plots with the least soil moisture and lowest in those with the highest soil moisture. Spartina pectinata community type averages 10 species per plot, while the xeric Bouteloua gracilis community type averages 19 species per plot. Rock cover is also positively associated with a decreasing moisture gradient. The presence of cobbles in 1.

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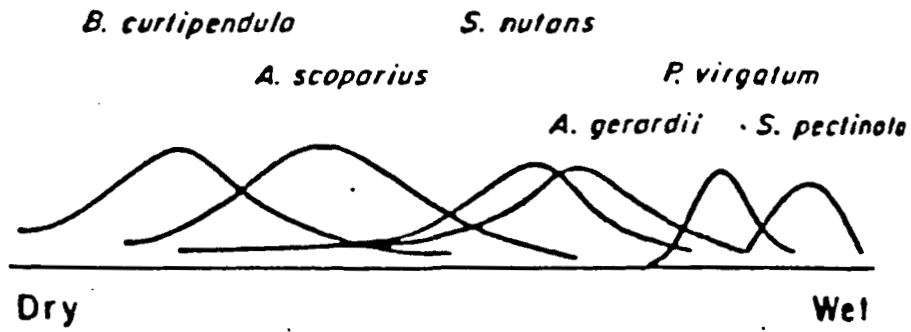


Figure 16. Idealized distributions of tall-grass-prairie grass species in relation to soil moisture (Bazzaz and Parrish 1982).

the soil of drier sites could provide locally moist microsites that could support species that might otherwise be excluded from the site by lack of moisture. Moss(1944) found that even small variations in microrelief is accompanied by pronounced differences in grass flora.

Tall-grass vegetation sampled on Parcel 7 reflects influences of the areas geographic and environmental factors. Larger groupings of species agree fairly well with those already described in the tall-grass prairie literature, but plant communities at Parcel 7 are unique with various associated species having a higher floristic affinity to species of the mountain steppe than those typical of the same groups of species in other parts of the prairie region. Hierarchical classification of thirty six plots and detrended correspondence analysis confirm that the controlling environmental variable in determininig the flora present and its pattern in the landscape is soil moisture.

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