

Multivariate analysis of grassland communities on the eastern boundary of Glacier National Park, Montana, USA

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Abstract. The east-side grassland communities in Glacier National Park (GNP) are divided into nine distinct groups using cluster analysis. These groups are characterized by the relative dominance of several key species, including *Arctostaphylos uva-ursi*, *Phleum pratense*, *Festuca scabrella*, and *Poa pratensis*. Detrended correspondence analysis (DCA) indicates that the most important mechanism affecting these groups is their disturbance history. DCA axis 1 (eigenvalue 0.64) shows that GNP plots are spread along a gradient that ranges from plots with very few non-native species (<4%) to groups that have fairly high non-native species (over 10%). DCA axes 2 and 3 are less influential in DCA (eigenvalues 0.48 and 0.28, respectively), but they indicate that other factors also affect the composition of GNP plots. These factors include moisture and/or soil drainage and temperature (as a function of aspect and elevation). Using canonical correspondence analysis to compare the correlation of the species matrix with 1) a matrix of topographic variables (i.e. elevation, slope and aspect) and 2) a matrix of abiotic variables supports the results and interpretation of mechanisms obtained using DCA. Like other western Montana grasslands, GNP plots are very diverse. Unlike other western Montana grasslands, however, they seem to occur in moister and cooler environments, which makes their conservation and management strategies different than grasslands typically associated with this region.

Keywords: Biodiversity, bunchgrass, community analysis, detrended correspondence analysis, *Festuca*, Glacier National Park, mid-elevation grasslands, non-native species, *Phleum*, Rocky Mountains, vegetation communities

Nomenclature: Biota of North America Program (Kartesz 1998)

Introduction:

Festuca grasslands are currently considered one of the most sensitive community types in Glacier National Park (GNP). Located on the eastern boundary of the park, these ecosystems reside within a permeable landscape that is affected both by wildlife and visitor use inside the park and land-use activities outside park borders. While invasion by exotics is thought to be the biggest threat to their continued existence, little is known about the current vegetation communities in this grassland type. Without baseline knowledge of their present ecological condition, it is impossible to assess if their composition is unique compared to other fescue grasslands or if they are particularly sensitive to disturbance or environmental factors. It is also impossible to effectively plan future restoration efforts. This study provides baseline data on the characteristics of vegetation communities in these grasslands using tabular classification techniques and multivariate analysis. It compares characteristics of Glacier's east-side grasslands with other grasslands in western Montana that currently face similar threats to their composition. It also compares

current grassland characteristics in Glacier National Park to conditions in the park in the recent past and to grassland habitat types established in western Montana for *Festuca* grasslands.

Three main studies have been conducted in grassland ecosystems in Glacier National Park that span both sides of the continental divide (Koterba and Habeck 1971; Tyser 1992; Tyser and Worley 1992). Koterba and Habeck (1971) found that the grasslands of the North Fork valley near Polebridge, Montana, had compositional characteristics similar to two distinctly different grassland types on each side of the continental divide. They had some species that were common in the Palouse prairie to the west in Washington state and other species that were more common in the mixed-grass prairie to the east. The four dominant grasses in the North Fork Valley plots included *Agropyron spicatum*, *Festuca idahoensis*, *Festuca scabrella*, and *Danthonia intermedia*. Coverage of *Danthonia intermedia* was unusual in their plots because (a) it is not usually dominant in western Montana grasslands and (b) coverage was ubiquitous and high enough to be unique to the area (Koterba and Habeck 1971). Canopy coverage of a few non-native species were also fairly high in the Koterba and Habeck (1971) study and coverage of each varied across a compositional gradient. The non-native species included only three grasses: *Phleum pratense* (0-25%), *Poa pratensis* (0-28%) and *Poa compressa* (trace-17%). Koterba and Habeck (1971) suggested that the west-side grasslands of the North Fork Valley were developed and maintained by local climate, soils texture and fire history.

Tyser (1992) and Tyser and Worley (1992) focused on the threat to *Festuca* grasslands from non-native species that were invading Glacier National Park. They studied plots invaded with *Centaurea maculosa*, plots dominated by *Festuca* and plots dominated by *Phleum* for characteristic composition. Like the Koterba and Habeck study, Tyser (1992) reported only a few non-native species from the study area, which was located in the St. Mary drainage on Glacier's eastern boundary. These included *Phleum pratense*, *Poa pratensis*, *Centaurea maculosa*, *Taraxacum officinale*, and *Tragopogon dubius*. Only three non-native species were sampled within the *Festuca*-dominant stand and total canopy coverage of all three was <1.0%. The *Phleum*- and *Centaurea*-dominated plots contained much higher coverage of the non-native species. In contrast, Tyser and Worley (1992) recorded fifteen alien species along transportation corridors of different sizes in Glacier National Park. They also found both *Phleum pratense* and *Poa pratensis* were particularly common in most of the study sites. Tyser (1992) suggests that the most important factors controlling vegetation characteristics and the invasion of non-native species in these grasslands may be the cryptogam layer and the amount of disturbance by native herbivores and disturbance. Tyser

and Worley (1992), on the other hand, suggest that these species are successfully invading grasslands from the roadside areas and trails in the backcountry.

In the early 1970's, many types of grasslands were sampled throughout western Montana to create a habitat-type classification system for grasslands of this region (Mueggler and Stewart 1980). Over 350 locations were sampled for the study – nine of these on the eastern boundary of Glacier National Park. The sampling scheme consisted of 40 microplots using Daubenmire frames (20 x 50 cm) that were randomly placed within a 20m x 20m macroplot at each location. Mueggler and Stewart (1980) developed their classification by analyzing the field data using ordination and association techniques developed by (Bray and Curtis 1957) and (Mueller-Dombois and Ellenburg 1974), which are the same techniques that form the basis of modern computer programs for vegetation analysis. The habitat type classification that Mueggler and Stewart (1980) created for Montana grasslands from the data collected in the 1970s has long been considered the standard for classifying these ecosystems in Montana. With the invasion of non-native species into these grasslands in the past 30 years, however, the classification system does not work well in some areas. This study examines the current vegetation conditions in the grasslands on the eastern side of Glacier National Park and how they fit into the standard habitat-type classification.

Study area

The study area is located on the eastern boundary of Glacier National Park (Figure 1).

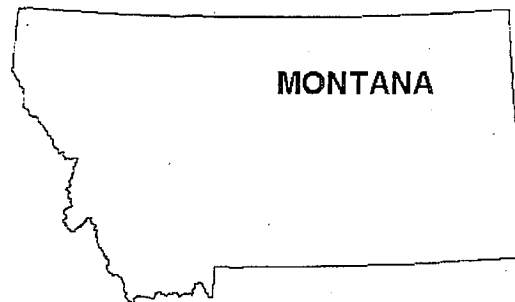


Figure 1: Location of study plots, east-side grasslands, Glacier National Park, USA
(**Need complete map of these plots in the park)

Methods

Field methods

Field work for this study was conducted from 1999-2001 for an ecological assessment of current vegetation conditions on the eastern boundary of Glacier National Park (Asebrook 2002). 155 plot locations in approximately 40 different meadows were sampled in three-year time frame. Plot locations within each meadow are permanently marked with pins and tags. At each plot, technicians trained by Glacier National Park personnel collected data on location, topographic, soil, and canopy coverage for all species and abiotic variables. ~~A modified Whittaker~~ ^{not used} ~~sampling scheme was used~~, which consisted of 14 microplots (⁵⁰20 cm x 50 cm) randomly placed within a 5mx20m macroplot location. Canopy coverage of species and abiotic variables was visually estimated to the nearest 1% using visual card keys.

Statistical analysis

Glacier National Park supplied the data for this study in Microsoft Access format. Minor changes were made to the original relational tables so the data could be used in statistical analyses. First, some species abbreviations were changed, especially those with variety names, so that multiple varieties were standardized to a single species abbreviation and richness differences were minimized. Second, a DateId code is used in this study instead of the original plot numbers so that a single number represents each plot in the analyses. Plot numbers in the original file consisted of an identification number and the year that the plot was measured. Data from DateId codes 1-60, 61-107, and 108-159 were collected in 1999, 2000, and 2001 respectively. Four numbers are missing from the DateID sequence (nos. 3, 18, 125 and 127). Finally, three distinct matrices were created from the original data.

The first matrix is composed of only vegetation. It includes 325 species. *Selaginella* sp. and some mosses and lichens with distinct species names were also left in this matrix. All original summed entries (e.g. "Native Grass", "Exotic Forb" or "Shrub") were removed for the vegetation matrix. Since these entries are covered in the plot data both as an individual species of native grass and as a group total of "Native Grass", the two are redundant for multivariate analysis. Mean coverage values from the 14 microplots were exported directly from an Access query for each species and each plot. They were exported in comma-delimited format so they could be used directly in all of the statistical analyses. Similarly, mean coverage of abiotic variables was exported into a second, or abiotic, matrix that consists of 10 attributes. These include canopy coverage of soil, gravel, litter, other (i.e. wildlife scat),

consistency
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rock, tree, wood, and moss and/or lichen as a general group (or designated as M/L). Entries for elevation, slope and aspect at each location were moved from the original files into a third, or topographic, matrix. Aspect was recorded from the original data into categories. These categories include (1) 0-60°; (2) 61-120°; (3) 121-180°; (4) 181-240°; (5) 241-300°; (6) 301-360°.

PCOrd Version 4.21 (McCune and Mefford 1999) was used for most statistical analyses, including outlier analysis, cluster analysis, indicator species analysis, diversity values, detrended correspondence analysis, and canonical correspondence analysis. **Outlier analysis** was used to determine the total variation between the plots. Plots are flagged as outliers if they were greater than two standard deviations from the mean of all plots. Outliers were not removed from subsequent analyses in this study, however, because they are important to describing the total variation of vegetation communities in Glacier National Park and to creating a classification that encompasses that variation. Outliers are specified in the descriptions of each vegetation type. **Cluster analysis** was used to explore the similarity of overall composition between plots and create groups that have similar species and canopy coverage of those species. Ward's method linkage and Euclidean distance measures were used. Tabular summaries of the most important species in each cluster group were created to determine which species created divisions both between and within groups in cluster analysis. Tabular results explained small divisions within the dendrogram. Overall indicator species for the larger groups, however, was determined using **indicator species analysis** in PCOrd. A grouping variable (based on cluster group number) was added to both the abiotic and topographic matrix after cluster analysis and used to compare groups in all subsequent multivariate analyses. Significance values for groups created in cluster analysis were generated using Multi-Response Permutation Procedures (MRPP), which is a nonparametric method for testing multivariate differences among pre-defined groups. MRPP used Sorenson's (Bray-Curtis) distance measures with a weighting option standard for vegetation analysis ($C(I)=n(I)/\sum(n(I))$). Differences were considered significant for this study if $p \leq 0.05$.

Diversity measures for the Glacier plots were generated using both PCOrd and Microsoft Access. PCOrd generates Shannon-Weaver diversity (H') and evenness for each plot, which were exported to an outside application for graphing. Richness and classification of species by origin were computed directly within Access queries. The origin codes within Access include: (1) endemic to Glacier National Park and immediate environs; (2) native to the park; (3) non-native to the park but native to North America, Hawaii, or the Caribbean; (4) non-native to North

America, Hawaii, or Caribbean; (5) other; and (6) origin unknown. Differences in richness, Shannon-Weaver diversity and evenness between groups was tested using MRPP and were significant if $p < 0.05$.

Detrended correspondence analysis (DCA) explored the similarity of both plots and cluster groups in three-dimensional ordination space. It was also used to generate hypotheses on possible mechanisms to explain that distribution. The analysis used default values standard in PCOrd for vegetation analysis (i.e. 30 segments, no downweighting of rare species, and rescaled axes). The amount of variation explained by each axis is given by the eigenvalues.

Canonical correspondence analysis (CCA) tests the relationship of the abiotic and topographic matrices to the vegetation matrix. The strength and direction of the relationship is given by vector characteristics for each variable, including the vector length, its angle with the matrix, and its arrow direction compared to the matrix. Not all vectors for abiotic attributes are significant enough to plot on the CCA diagrams. CCA specifications for this study are default values within PCOrd, including a 0.200 minimum to plot the vector, axis scores centered and standardized to unit variance, and axes scaled to optimize stands. "R" values generated within CCA test the significance of each variable on the individual axis. A Monte Carlo test (MCT) indicates the significance of the relationships between matrices in all CCA analysis conducted for this study. MCT tests the null hypothesis that there is no relationship between the matrices being examined.

Results

Characteristics of vegetation communities based on cluster analysis

Grasslands along the eastern border of Glacier National Park fall into nine distinct groups using cluster analysis (Appendix A). These groups are statistically significant ($p < 0.01$) using Multi-Response Permutation Procedures (MRPP), which is a nonparametric method for testing multivariate differences among pre-defined groups. Figure 2 highlights the major characteristics for each of these vegetation groups as they are defined by cluster analysis and tabular classification procedures.

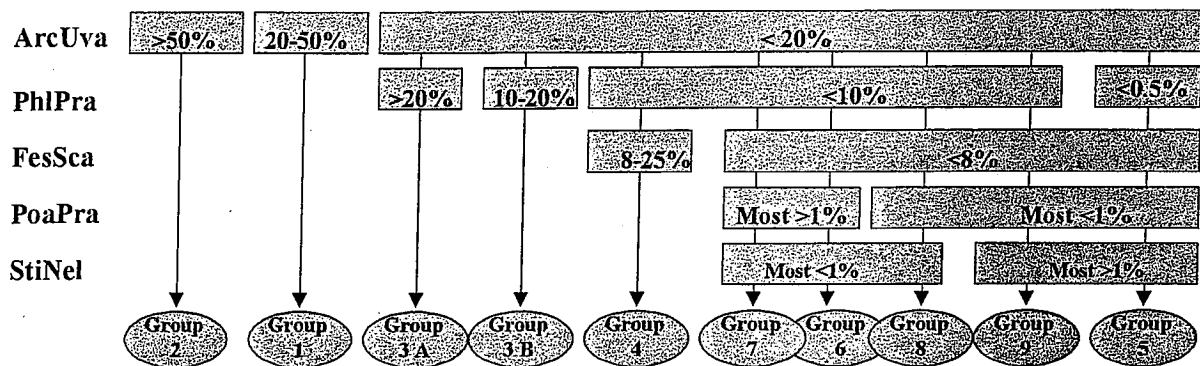


Figure 2: Major species characteristics for each group using cluster analysis on east-side grassland plots, Glacier National Park, Montana, USA. Constructed using Ward's method and Euclidean distance measures. ArcUva= *Arctostaphylos uva-ursi*; PhlPra= *Phleum pratensis*; FesSca= *Festuca scabrella*; PoaPra= *Poa pratensis*; StiNel= *Stipa nelsonii*.

Group 1 (13 plots): *Arctostaphylos uva-ursi* / *Juniperus communis*

Arctostaphylos uva-ursi comprises 20-50% of the canopy coverage in this group. The two main divisions within group 1 are based on whether the dominant shrub is *Juniperus communis* with *Rosa* sp. or whether it is *Juniperus communis* with *Spiraea betulifolia* / *Vaccinium caespitosum*. *Juniperus communis* is an indicator species for the group in PCOrd ($p < 0.009$), although it is not found in each and every one of the 13 plots. The dominant sedge is *Carex obtusata*. Other important species include *Festuca scabrella* (0.5 – 20%), *Festuca idahoensis* (1-6%), *Elymus spicatus* (0.5-4%), *Penstemon confertus* (0.5-5%), and *Lupinus sericeus* (1-5%).

Group 2 (8 plots): *Arctostaphylos uva-ursi* / *Carex* sp.

This group consists entirely of outliers from the cluster analysis that are more than two standard deviations outside the mean of all plots analyzed in this study. It is distinguished by a very high canopy coverage of *Arctostaphylos uva-ursi* (> 50%). The two main divisions within group 2 are based on the species of *Carex* present. In some of the plots, *Carex obtusata* is the dominant sedge. In others, *Carex geyeri* or *Carex* sp. are dominant.

Rosa sp. is the dominant shrub, but *Spiraea betulifolia* and *Juniperus communis* comprise a small portion of some plots. *Festuca scabrella* coverage is about the same as group 1 (5 – 22%, except for plot 102 where it is absent). *Festuca idahoensis*, when present, is approximately 1%. *Penstemon confertus* is almost always < 0.5%, and *Lupinus sericeus* varies from 0.1 to 3%. *Pentaphylloides fruticosa* is always 1-5%. Indicator species for this group include *Hedysarum sulphurescens* ($p=0.013$), *Trisetum spicatum* ($p=0.014$), *Senecio canus* ($p=0.011$), and *Shepherdia canadensis* ($p=0.002$), but each of these indicator species are also present in some group 1 plots, so none of them would make good classifiers for group 2 by themselves.

Group 3 (22 plots): *Phleum pratense* / *Vicia americana* or *Phleum pratense* / *Bromus carinatus*

Canopy coverage of *Phleum pratense* is quite high in this group compared to all other groups formed during cluster analysis. It ranges from 10 to 30% with only one exception (Plot 90). *Vicia americana* and *Aster laevis* are also notably more abundant than in the previous two groups (both are mostly >1% in this group). The dominant sedges are *Carex petasata* and *Carex raynoldsii*. Indicator species for group 3 include *Phleum pratense*, *Taraxacum officinale*, *Vicia americana*, *Geranium viscosissimum*, and *Bromus carinatus* (all $p<0.01$). Group 3 has two distinct subgroups based on the percentage of *Phleum pratense*.

In plots where *Phleum pratense* is greater than 20%, the canopy coverage of *Festuca scabrella* or *Bromus carinatus* can be used to further subdivide the communities in group 3 because *Festuca scabrella* has a negative relationship to *Bromus carinatus*, *Taraxacum officinale*, and *Poa pratensis*. Where the coverage of these disturbance or non-native species is relatively low, coverage of *Festuca scabrella* (12-27%) and *Penstemon confertus* (3-11%) are relatively high. When *Bromus carinatus* is higher, the percentage of *Festuca scabrella*, *Festuca idahoensis*, and *Poa pratensis* are all <1%. Alternately, in plots where *Phleum pratense* is 10-20%, the percentage of *Poa pratensis* works well to further subdivide the communities. If *Poa pratensis* is high (>15%), native grasses such as *Festuca scabrella*, *Festuca idahoensis*, *Stipa nelsonii*, or *Danthonia intermedia* are usually absent. If coverage of *Poa pratensis* is relatively low (<5%), these grasses are present and coverage of *Fragaria virginiana*, *Geranium viscosissimum* and *Rosa* sp. are more useful to differentiate differences in communities.

Group 4 (28 plots): *Festuca scabrella* / *Festuca idahoensis* - *Penstemon confertus*

High canopy coverage of *Festuca scabrella* distinguishes group 4 (8-25% with one exception at 5%). In addition, *Festuca idahoensis* is consistently between 1 and 5%. Compared to group 3, the percentages of *Phleum pratense* and *Poa pratensis* are much reduced (<5% and <1%, respectively), *Bromus carinatus* is notably absent, and *Vicia americana* is mainly present in plots where *Festuca scabrella* is <20%. There are also a wide variety of sedges in this group compared to the previous groups including *C. raynoldsii*, *C. geyeri*, *C. petasata* and *C. filifolia*. Other important species include *Penstemon confertus* (1-5% in most plots but several plots have more than 5%), *Potentilla gracilis* (<5%), and *Lupinus sericeus* (1-5% in most). The indicator species for this group is *Festuca scabrella* ($p < 0.002$).

The grass communities in this group can be first divided on the amount of *Festuca scabrella* (i.e. greater than 20% or less than 20%). The plots that have less than 20% *Festuca scabrella* are further subdivided based first on the percentage of *Penstemon confertus* (<10% or >10%) and moss, and then plots with lower percentages of *Penstemon confertus* are further subdivided based on percentages of *Pentaphylloides fruticosa* (<0.5 or >0.5). The main difference in plots containing greater than 20% *Festuca scabrella* is the coverage of moss (*Tortula ruralis*).

Group 5 (12 plots): *Festuca idahoensis* / *Festuca scabrella* - *Selaginella* sp.

Plots in group 5 contain much higher percentages of *Selaginella* sp. than any other group (5-28%), with the single exception of plot 144. Plot 144 is flagged as an outlier in PCOrd because it has exceptionally low coverage of *Selaginella* sp. (<1) compared to other plots within this group. It also has exceptionally high coverage of *Tortula ruralis* (49.5%) and *Lupinus sericeus* (10%) compared to all of the plots sampled in this study.

Compared to the previous groups, the relative percentages of *Festuca scabrella* and *Festuca idahoensis* are quite different. With only one exception, the coverage of *Festuca idahoensis* is greater than or equal to *Festuca scabrella*. *Phleum pratense*, *Poa pratensis*, and *Pedicularis contorta* are all <0.5%. The dominant sedge is *C. obtusata*. A combination of native grasses including *Stipa nelsonii*, *Danthonia intermedia*, *Koeleria macrantha* and *Elymus spicatus* are present in almost every plot along with the fescues and the percentages of each are significantly greater than they are in any of the previous groups. The indicator species for this group are *Selaginella* sp., *Comandra umbellata* and *Orthocarpus tenuifolius* ($p = 0.001$, 0.014, and 0.012, respectively). Like group 2, these

indicator species are not indicative of group 5 placement by themselves, but used in combination with the relative percentages of the different grasses should be useful to this classification.

Group 6 (3 plots): No Species Designation

The three plots that comprise this group are outliers. They share several species and abiotic characteristics in common so they group in close proximity on the dendrogram. For example, all three have litter coverage around 80% and very little moss coverage. However, the dominance of certain unusual species in these outliers makes them quite different from each other and from all other plots analyzed in this study. Plot 100 is dominantly *Dryas octopetala* (32%) and *Pentaphylloides fruticosa* (6%). *Elymus repens* (39%) dominates plot 129. Plot 78 consists of a unique combination of species including *Vaccinium caespitosum* (24%), *Calamagrostis canadensis* (19%), *Fragaria virginiana* (19%), *Festuca saximontana* (12%), *Juncus balticus* (9%) and *Penstemon confertus* (7%). The indicator species for this group are *Elymus repens* ($p=0.008$), *Vaccinium caespitosum* ($p=0.004$), *Valeriana sitchensis* ($p=0.01$), *Stellaria longifolia* and *Poa palustris* ($p=0.014$). The indicator species reflect the unique combination of species and extremely high canopy coverage of the indicator species in their respective plots rather than a unique occurrence of these species only to group 6.

Group 7 (28 plots): *Phleum pratense* / *Poa pratensis* - *Pentaphylloides fruticosa*

Two subgroups can be distinguished within this group based on coverage of the moss *Tortula ruralis*. One group has *Tortula ruralis* >10% and the abundance of other species is quite variable. *Pentaphylloides fruticosa* is usually quite low (<2%) in these plots. The second subgroup has <10% *Tortula ruralis*. In these plots, differences in the coverage of *Pentaphylloides fruticosa* become important to further divide the group. Depending on whether *Pentaphylloides fruticosa* is >5% or <5%, *Aster laevis*, *Fragaria virginiana*, *Festuca idahoensis* or *Poa pratensis* are critical species to further subdivide them.

For group 7, no species met the $p=0.01$ cutoff to be considered an indicator species. The closest species are *Poa compressa* ($p=0.055$) and *Bromus inermis* ($p=0.086$). *Bromus inermis* is found mainly in group 7 but does occur in one plot in group 3. *Poa compressa* also occurs mainly in group 7, but also has occurrences in plots within all of the other groups.

Group 8 (30 plots): *Festuca scabrella* / *Festuca idahoensis*

Group 8 is very similar to group 4 in grass composition and species dominance but there are some important differences between the two groups. *Festuca scabrella* is much less abundant (<8%) in this group than group 4. With the reduction in *Festuca scabrella*, the coverage of *Penstemon confertus* and *Vicia americana* are also much reduced and less consistent than group 4. *Penstemon confertus* composition is mostly less than 2%, while *Vicia americana* is absent from most samples in this group. Alternately, *Pentaphylloides fruticosa* (0-20%) and *Danthonia intermedia* (0-5%) are more abundant and occur more consistently in this group than group 4. Sedges, which consist of many species in group 4, are mainly *C. obtusata* and *C. petasata* in Group 8.

The most important criteria used in cluster analysis to subdivide group 8 are the coverage of *Pentaphylloides fruticosa*, *Danthonia intermedia*, *Arctostaphylos uva-ursi*, *Lupinus sericeus* and *Stipa nelsonii*, which result in four or five distinct subgroups. The subgroups range from those that have high *Arctostaphylos uva-ursi* (>8%) and *Muhlenbergia richardsonis* (<2%) to those with lower *Arctostaphylos uva-ursi* (<8%), but varying amounts of *Lupinus sericeus* (0-20%), *Danthonia intermedia* (0-5%), and *Stipa nelsonii* or *Stipa richardsonii*.

Group 9 (11 Plots): *Festuca scabrella* / *Festuca idahoensis* / *Danthonia intermedia* / *Stipa nelsonii*

Although technically group 9 should probably be included with group 8 based on the major breakpoints in the dendrogram, it is subdivided here to describe the full range of plot variation in the Glacier National Park plots. It is also distinct from group 8 because the dominance of the main grass species is different than in the groups described above. In most plots of this group, *Festuca scabrella*, *Festuca idahoensis*, *Danthonia intermedia*, and *Phleum pratense* are all about equally abundant, although coverage of each is generally low (<5%). *Stipa nelsonii* is more common in this group than in any of the previous groups, although its coverage is also generally less than 5%. Two exceptions include plots 5 and 20, which have relatively high *Stipa nelsonii* (10 and 12%, respectively). In addition, about one-half of the plots have very high moss coverage (>25%). However, this coverage does not adversely affect species richness. Richness ranges from 50 to 60 species in the plots with high moss (mean = 53) while plots with low moss coverage have a mean richness of 45 species. *Stipa nelsonii* is an indicator species for this group ($p=0.006$).

Diversity of vegetation communities

Grasslands on the eastern side of Glacier National Park have a mean richness of 43.1 species (± 8.9) per 0.1 ha for all 155 plots. Richness of the vegetation communities delineated in cluster analysis varies from a mean of 37 species within Group 2 to a mean of 56 species within Group 6 (Figure 3). Group 6 consists of only three plots that have from 49 to 61 species and the vegetation composition of each one is very different from others in the group. The differences in numbers of species between groups are significant using MRPP ($p=0.000$).

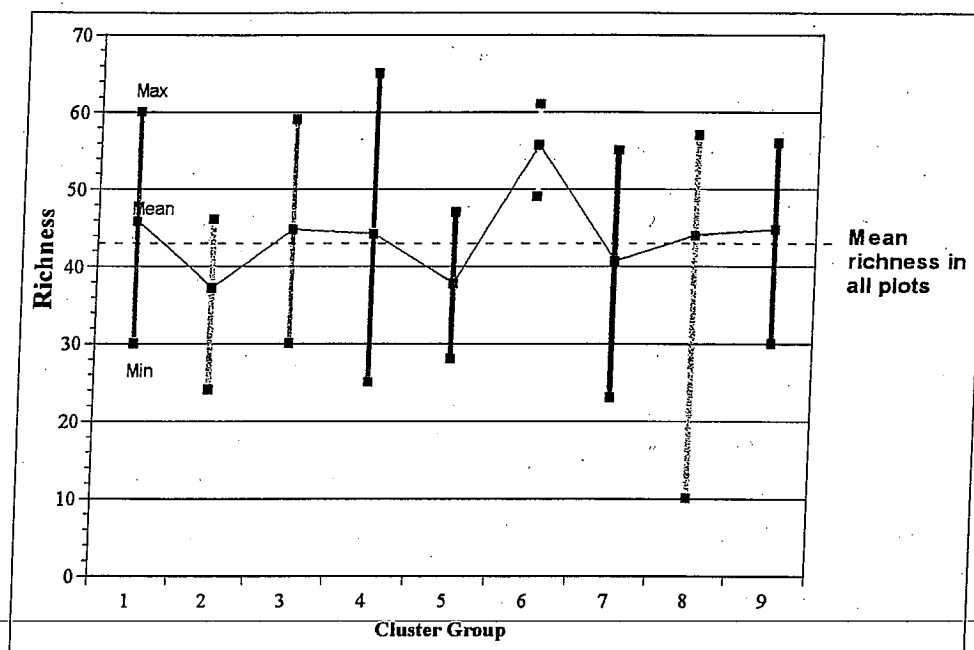


Figure 3: Species richness of vegetation groups delineated by cluster analysis. Maximum-Minimum bars show range of richness within each group. **Mean** = mean value, **Max**=Maximum value, **Min**=Minimum value.

Comparison of cluster groups using Shannon Weaver diversity index (H') and evenness (E) also shows a significant difference between groups in the east-side grassland plots ($p=0.000$). The groups with the lowest mean values for H' diversity are two and six (Figure 4). Both of these groups have low species counts in both the native and non-native origin categories (Table 1) and they also have the lowest evenness values (E) of all groups at $E=0.478$ and 0.529 , respectively ($p=0.000$).

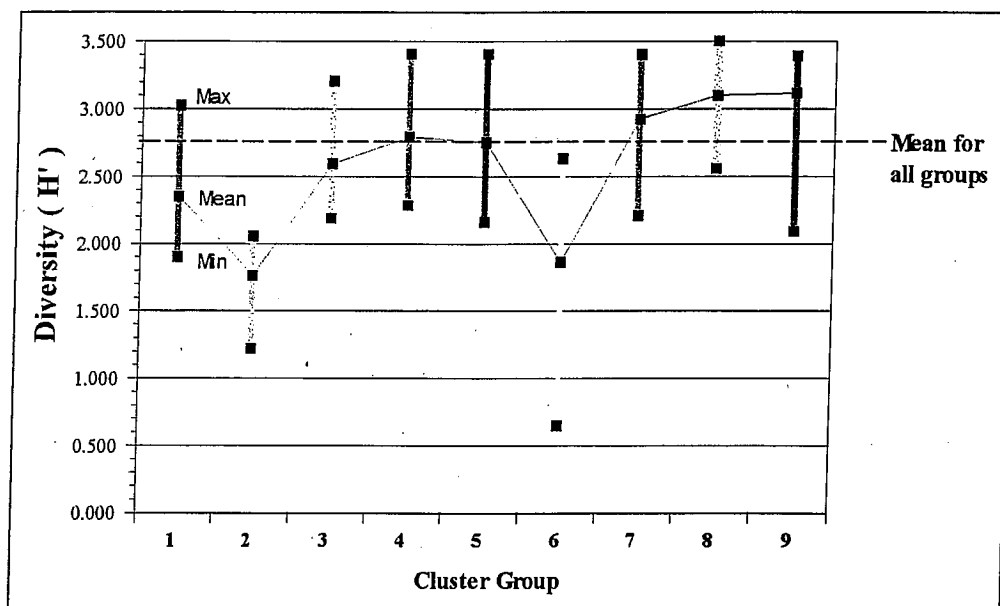


Figure 4: Comparison of Shannon Weaver Diversity Index (H') values between cluster analysis groups. Maximum-minimum bars show the range of H' values.

Table 1 shows the total number of species within each of the different origins classified for this study. The "6" or "Origin unknown" class consists mainly of plants that were designated as "unknown forb" or "unknown grass" or "unknown legume", etc., in the field data (Table 1). Table 1 shows that groups 3 and 7 have a high representation of species that are non-native to North America, Hawaii or the Caribbean compared to other groups (9.9 and 10.2% of total, respectively). These species are a major factor for cluster analysis to separate these plots

Table 1: Number of native and non-native species within each cluster group.

Origin	Group #								
	1	2	3	4	5	6	7	8	9
1- Indigenous to GNP	5	2	4	2	2	2	2	5	2
2- Native to N.Am, Hawaii, Caribbean	146	97	146	161	119	81	172	182	113
3- Non-native to GNP, Native to N.Am, Hawaii, Caribbean	0	0	1	0	0	0	1	0	0
4 - Non-native to N.Am., Hawaii, Caribbean	6	4	17	10	9	6	20	9	10
5 - Other	0	0	0	0	0	0	0	0	0
6 - Origin Unknown	1	0	3	2	2	0	1	2	1
Total species per group	158	103	171	175	132	89	196	198	126

from others in the east-side grasslands. Appendix B gives details on the non-native species that characterize each of the groups and shows how individual non-native species differ between groups.

Indirect ordination: Detrended correspondence analysis results

Because species composition at any one place reflects highly integrated environmental, biological, and historical factors, indirect ordination is used to assess patterns in composition within the east-side grassland plots. Detrended correspondence analysis (DCA) within PCOrd (McCune and Mefford 1999) is used to assess the similarity of each plot to each other, the similarity of individual plots within the pre-defined groups, and the complexity of composition within 3-dimensional space. It is also used to create hypotheses on possible underlying environmental mechanisms that may cause the ordination patterns by analyzing the compositional gradient along each ordination axis.

The DCA ordination results on the Glacier National Park plots are shown in Figures 5 and 6. The eigenvalues for axes 1 and 2 are 0.64 and 0.48, respectively. DCA axis 1 shows that cluster groups 1 and 2 are located on the lowest portion of axis 1 (Figure 5); and that they are oriented closest to each other in ordination space, which means they are more similar to each other in composition than to other groups. Groups 1 and 2 contain the fewest non-native species and are comprised mainly of species that thrive in drier environments, such as *Arc-Uva*, *Festuca scabrella*, and *Carex obtusata*. At the upper end of axis 1, groups 3 and 7 are the most similar to each other. However, the spread of the plots within these two groups is quite a bit greater than groups on the lower part of the axis and indicates less similarity in composition within these two groups themselves. Both group 3 and group 7 plots contain a number of non-native species (Table 1, Appendix B), which vary in frequency and occurrence. Most common are *Phleum pratense*, *Poa pratensis*, *Taraxacum officinale*, and *Centaurea maculosa* but other species do occur in both groups. At the extreme ends of axis 1 are plots 102 and 129. Plot 102 consists mainly of *Arctostaphylos uva-ursi* (61.4%) with some *Pinus contorta* and *Dryas octopetala*. It is an outlier plot with no fescues or exotics. Plot 129 is an outlier plot that historically has been highly disturbed. It is inundated yearly with water from Sherburne reservoir, has little remaining topsoil, and is grazed by cattle. It consists mainly of *Elymus repens* and litter. Species that rank highest on DCA axis 1 are *Barbarea orthoceras* (594), *Poa palustris* (584), *Elymus repens* (573), and *Tanacetum vulgare* and *Camelina microcarpa* (both 557).

84, 89, 30, 31). Several species rank at the same position on DCA axis 2. These include *Calamagrostis canadensis*, *Carex epappilosa*, *Carex microptera*, *Carex presleyii*, *Rumex acetosa*, *Stellaria borealis*, *Veratrum viride*, *Veronica serpyllifolia*, *Veronica wormskjoldii*, and *Festuca saximontana* (all at 444).

DCA axis 3 is marked by a gradient from plots in groups 1 and 2 to plots in groups 8 and 9 (Figure 6). Plots within groups 1 and 2 are located mainly on southern exposures of sedimentary rock or on eastern exposures on glacial deposits between 4500 and 6700 ft. They are comprised of plants that are adapted to hot, dry environments of southern slopes, such as *Arctostaphylos uva-ursi*, *Juniperus communis*, *Pinus contorta*, *Senecio canus* and *Bupleurum americanum*. Groups 8 and 9 are located within the same elevations but are mainly on northern to southeastern slopes on a variety of substrates.

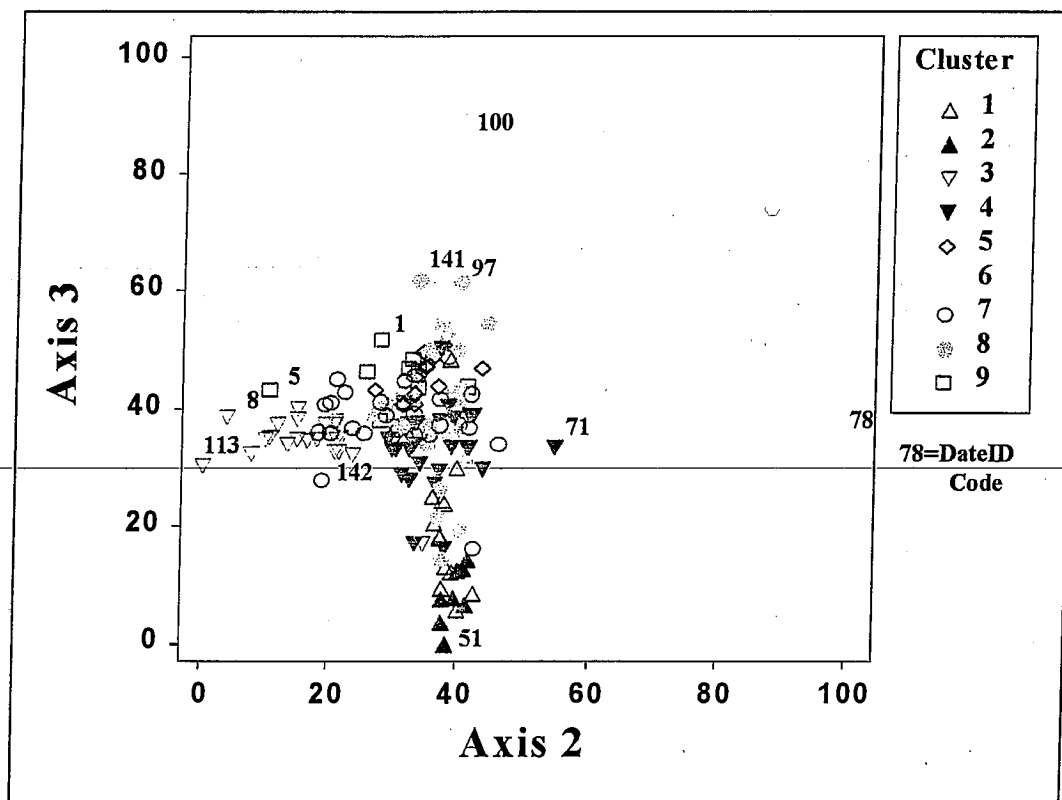


Figure 6: DCA results for axis 2 and 3.

These groups have more *Carex petasata*, *Danthonia intermedia*, *Stipa nelsonii*, *Bromus carinatus*, *Potentilla gracilis* and moss cover than groups 1 and 2. Plots 51 and 100 mark the extreme compositions on DCA axis 3. Plot 51 is an outlier that consists of *Arctostaphylos uva-ursi* (66%), *Festuca scabrella* (6%), and *Senecio canus* (1%). It shows evidence of recent wildlife and domestic livestock use, but has 43 species that are all native in origin. Plot

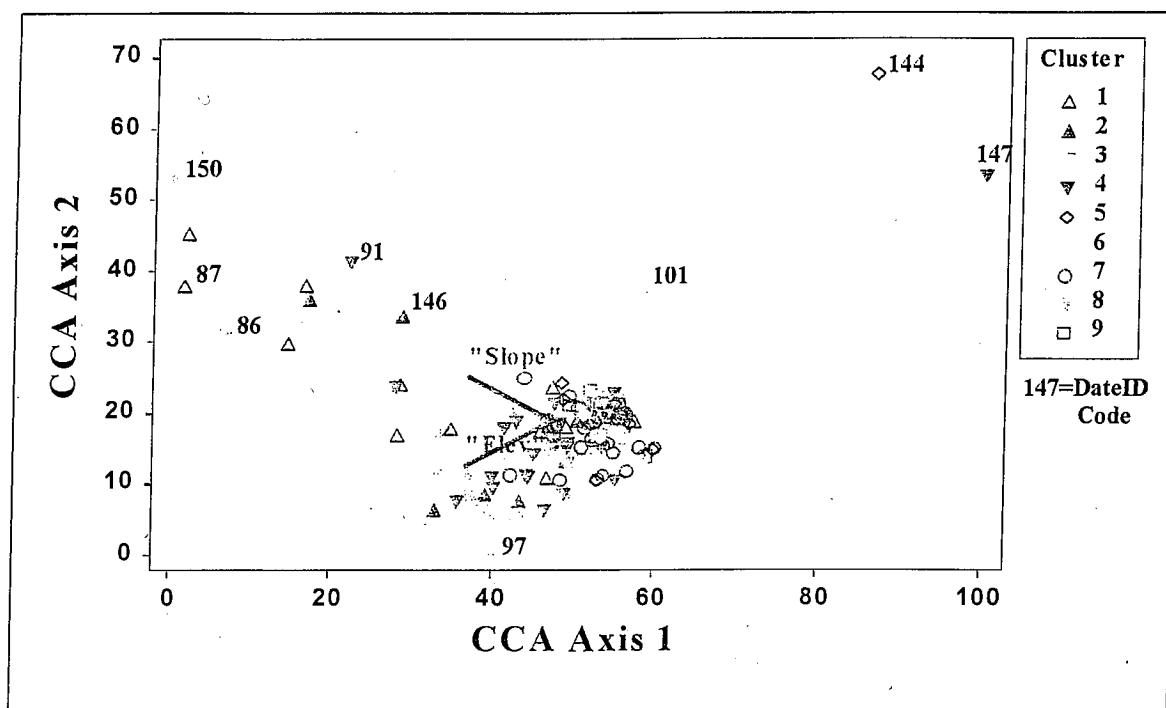
100 is located on a northeast slope at 6660 ft. It is composed dominantly of *Dryas octopetala* (32%), *Pentaphylloides fruticosa* (5%), and *Arctostaphylos uva-ursi* (3%), but total richness is 46. All species are native in origin. Plots 141 and 97, which are lower on axis 3 than plot 100 but still on the high end (Figure 6), are also above 6500 ft. They are on eastern slopes and, compared to plot 100, they have more moss, *Festuca idahoensis*, and *Bupleurum americanum*. They have richness that is similar to plot 100 and also consist of only native species. Ordination on DCA axis 3 apparently is not along elevation or substrate gradients. Both ends of the axis contain plots above 5500 and both have plots on sedimentary and glacial deposits.

Indirect ordination: Canonical Correspondence Analysis results

The relationship of topographic and abiotic variables to plot composition is explored using canonical correspondence analysis within PC-Ord (McCune and Mefford 1999). The analyses were conducted with a Monte Carlo test to determine the significance of the species-environment correlation and the eigenvalues for each axis compared to randomized data. The null hypothesis for the Monte Carlo test is that there is no relationship between the species matrix and the second (topographic or abiotic) matrix.

The topographic variables include elevation, slope and aspect. Results of CCA are shown in Figures 7a and 7b. Eigenvalues for axes 1, 2, and 3 are 0.203, 0.114 and 0.085, respectively. Pearson correlation coefficient values (species-environment correlation) are 0.692, 0.703, and 0.598, respectively for each axis. The total variance in the species data is 8.6556. "R" correlation values for all axes are shown in Appendix C. The length of the biplot line represents the strength of the correlation between plot composition and the topographic variable (Figure 7). The angle of the line with each axis represents the correlation with the particular axis. Axis 1 shows a slight negative relationship with slope ($r=-0.808$) and elevation ($r=-0.780$). Axis 2 shows a slightly positive relationship with slope and a negative with elevation ($r=0.616$, $r=-0.567$ respectively). Axis 3 shows a greater (i.e. longer line length than the other axes) positive relationship with aspect ($r=0.990$). The Monte Carlo results for significance on axes 1, 2, and 3 are $p=0.09$, 0.01, and 0.04 respectively. Therefore, only axes 2 and 3 have significant correlation between

A.



B.

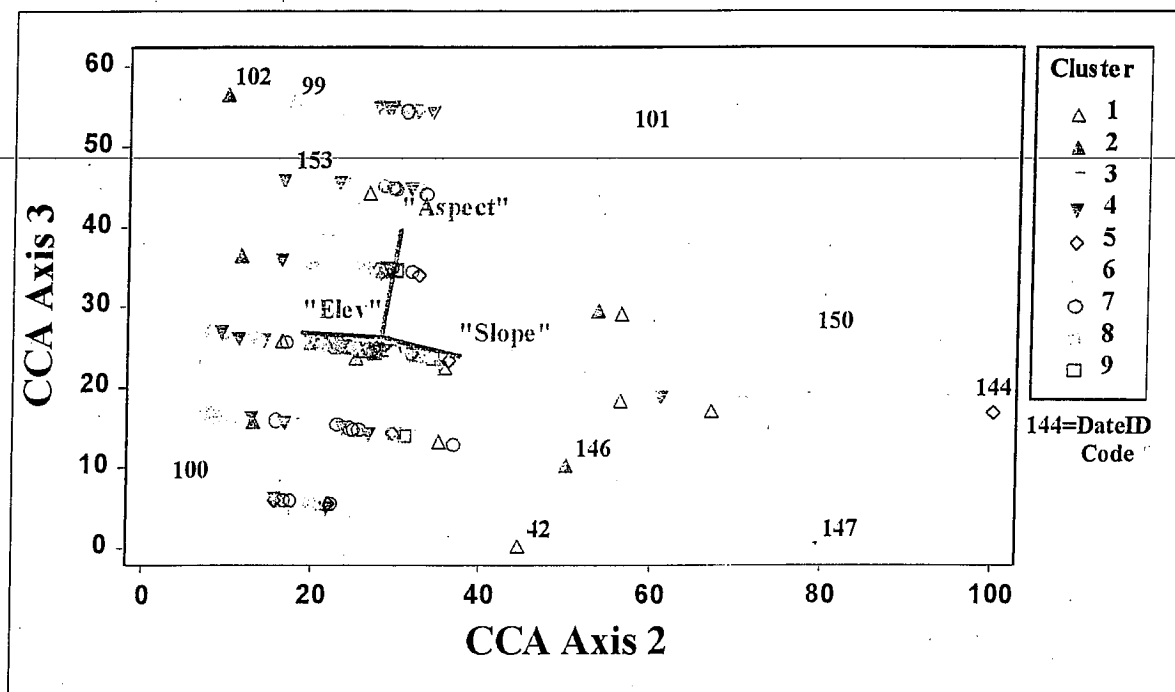


Figure 7: Correlation of topographic variables with plot composition using canonical correspondence analysis. A: Axis 1 and 2; B: Axis 2 and 3. Eigenvalues for Axis 1, 2, and 3 are 0.203, 0.114 and 0.085, respectively

plot vegetation and the topographic variables within the confidence limits set for this study. Visual analysis of Figure 7 does not show any cluster group members obviously align along an axis in either graph (e.g. Group 1 members do not all align along slope line or elevation line).

Abiotic variables include canopy coverage of soil, gravel, lichen, litter, moss, rock, tree, wood, M/L (Moss/Lichen), and other. Figures 8a and 8b show the biplot results for these variables. Most of the vectors are not significant enough to show on the graph. Figure 8a shows that Axis 1 does have a positive correlation with lichen ($r=0.792$), rock ($r=0.592$) and wood ($r=0.425$) and a negative relationship to soil ($r=-0.561$) and litter ($r=-0.427$). However, this axis is not highly significant in the species-environment correlation with the Monte Carlo test ($p=0.17$). Axis 2 is highly significant ($p=0.01$) with a positive association for moss ($r=0.734$) and Moss/L ($r=0.781$). It is negatively correlated with most of the other abiotic variables. Similarly, axis 3 is significant ($p=0.04$) for correlation of vegetation species with a category simply lumped as "other" ($r=0.557$), which consists mainly of wildlife scat from a number of different animals (Figure 8b). It also has a negative correlation with most other variables.

Discussion

Diversity in the grasslands on the east side of Glacier National Park is higher than many other vegetation types in the region and than other western North American grasslands. Both (Alaback et al. 2000) and (Latham 1996) reported no more than 30 species per 0.1 ha in temperate coniferous forests of the northwestern United States, which is much less than the mean richness of 43 species found in the Glacier plots (Figure 3). Similarly, (Sims et al. 1978) reported less than 30 species in each of three grassland sites of the US/IBP Grassland Biome Program in eastern Washington and Montana. In a comparative sample area west of the continental divide, Koterba and Habeck (1971) had a mean of approximately 20 species per plot with a total of about 50 species encountered in their study area compared to the 325 species found in the 155 plots at Glacier. East of the divide, however, Tyser (1992) found mean richnesses of 51 and 59 in *Festuca* and *Phleum* stands, respectively, within the park. Recently, vegetation studies in the intermountain region of western Montana have found a comparable richness in grasslands west of the continental divide. Sikkink and Alaback (in preparation) found a mean richness' of 40 (+/- 9) and 47 (+/- 7) species of vascular plants per 0.1-hectare plot in a natural area and city preserve dominated by *Festuca* and *Pseudroegneria spicata*, respectively. An earlier study in the same natural area (Sikkink 1997) had considerably higher values for

Shannon-Weaver diversity ($H' = 3.3$) for the fescue-dominated grassland than are shown in Figure 4 for the Glacier study plots (mean = 2.75).

Cluster analysis shows the wide range of compositions in the park. Group 1 (Appendix 1) plots have some hot, dry species, such as *Juniper communis*, *Carex obtusata*, and *Carex filifolia*, and an abundance of the woody species *Arctostaphylos uva-ursi* and *Rosa sp.* Groups 3 to 9 have mixture of mesic species (i.e. *Juncus balticus*, *Valeriana sitchensis*, *Carex petasata*, ferns and moss) and dry species (i.e. *Festuca scabrella* and *Carex filifolia*). *Phleum pratense* and *Poa pratensis* are dominant species in Groups 3-9, but these species have dominated grassland communities in Glacier National Park grasslands for at least 30 years (Koterba and Habeck 1971; Tyser 1992). Some of these groups are subdivided based on canopy coverage of moss. Others are subdivided based on coverage of *Pentaphylloides fruticosa*, *Penstemon confertus*, *Fragaria virginiana*, *Bromus carinatus*, or species of *Carex*. Group 4 has abundant *Festuca scabrella*, but low coverage of *Pentaphylloides fruticosa* and woody species. Groups 3 and 7 have a high percentage of non-native species (10%) that affects their overall composition compared to other groups (Table 1, Appendix B). However, they also have more species of native grasses and sedges, which have low canopy coverage but increase the overall diversity values in conjunction with the increase in non-native species (Figure 4). Group 8 has a wide variety of richness for each plot (Figure 3), but mean evenness and Shannon-Weaver diversity (H') are high compared to other groups (Figure 4). Like group 1, group 8 contains *A. uva-ursi*, *Rosa* and *Pentaphylloides fruticosa*, but coverage is low (<10%, <5%, and 3% respectively). (Figure 2).

The current occurrence and dominance of species comprising the vegetation in the east-side grassland plots makes classification with the standard habitat type key developed by Mueggler and Stuart (1980) difficult. There are three main reasons. First, nomenclature changes since the key was created make transposing to current names difficult. Of the 26 main species comprising the key, 12 have undergone name changes. These include all of the *Agropyrons* and *Stipas* used in the key plus *Potentilla fruticosa*, *Carex stenophylla* and *Poa sandbergii*. Second, many of the species used to make the key do not occur in Glacier plots. Some are listed on the species list for the park, but do not actually occur in any of the plot data. 13 species used in the habitat type key fit this category. Third, the percentages of some key species are between coverage requirements in the key and make the decision of which part of the key to follow difficult. For the groups that meet the classification key requirements of at least 5% *Festuca scabrella*, which is the first couplet in the key, none meet the requirements of the third couplet for >5% *Potentilla fruticosa* (now *Pentaphylloides fruticosa*). Using the ancillary requirement of the third couplet that P.

fruticosa occurs as "scattered plants often hidden by tall herbaceous growth" (instead of the minimum 5% coverage) makes these groups most similar to the *Potentilla fruticosa*/ *Festuca scabrella* h.t. *Danthonia intermedia* phase. Groups that meet the 5% *Festuca scabrella* coverage are groups 1, 3b, 4, 8. All other groups are between the key canopy coverage requirements. They have *F. scabrella* that is less than 5%, which doesn't meet the "common" designation, but they have more than the <1% coverage that is considered rare. Keying these groups with the higher *Festuca* percentage results in the same classification as if they met the >5% cover to begin with. Keying with the lower percentage gives no classification because it ends in habitat types consisting of species that do not exist in the park. In all groups, *P. fruticosa* occurs in much lower percentages than described for this habitat type by Mueggler and Stewart (1980) (i.e. <5%) except for five plots within group 7 that range from 7%-13%.

The *Potentilla fruticosa*/ *Festuca scabrella* h.t. *Danthonia intermedia* phase actually fits the Glacier data moderately well. It occurs primarily east of the divide on gentle rolling slopes at moderate elevations. Soils are mostly limestone or sandstone parent materials and litter and vegetation coverage can reach up to 98%. According to Mueggler and Stuart (1980), it occurs in moderately mesic foothills where moisture availability is better than average and probably reaches between 20- to 30- inches (50-75 cm) of precipitation per year. This makes them much moister than other grasslands in the intermountain regions of western Montana (Sikkink and Alaback in preparation). The habitat type supports a wide variety of forbs including *Galium boreale*, *Gaillardia aristata*, *Achillea millefolium*, *Solidago missouriensis*, and *Campanula rotundifolia*. The *Danthonia intermedia* phase consists of *Danthonia intermedia* in combination with *Elymus caninus* (formerly *Agropyron caninum* and *Elymus trachycaulus*), *Potentilla gracilis*, *Lupinus sericeus*, and *Carex obtusata*. In total, 84 species were identified in the original habitat type (Appendix E9, Mueggler & Stuart 1980). Most of them are also currently found in Glacier National Park. However, the current coverage of *Arctostaphylos uva-ursi* and non-native grasses, such as *Phleum pratense* and *Poa pratensis*, are significantly higher today than the original descriptions for this habitat type, which had mean canopy covers of 11%, 0% and 6%, respectively (Mueggler and Stewart 1980). *Juncus balticus* and *Stipa nelsonii* were not observed in this habitat type originally, although the *Stipa* may have been called *Stipa occidentalis* var. *nelsonii* during that time. In addition, over 50% of the non-native species currently present in the cluster groups (table 1, appendix B) are not listed on the original habitat type description (e.g. *Centaurea maculosa*, *Poa compressa*, and *Thlaspi arvense*), which means that several are new invaders since 1970. These non-native species are also important in ordination analysis and affect the distribution of Glacier plots in ordination space.

Detailed analysis of vegetation composition within both plots and groups at the extreme ends of each DCA axis suggests several hypotheses for causal mechanisms driving the ordination. DCA axis 1 (Figure 5) shows a clear pattern of increasing disturbance along its gradient. Plots with few non-native species (Groups 1 and 2) are located at the lower end. Plots with the most non-native species (groups 3 and 7), or that are disturbed yearly (plot 129, Figure 5), are at the upper end. It is interesting how clear this pattern is because moisture is expected to be the strongest driving mechanism for ordering plots along the main axis in many grassland ecosystems. The strength of the DCA axis (eigenvalue 0.64) also indicates that historic disturbance on the grasslands of this area has had a large effect on current community composition. DCA axis 2 shows the expected moisture gradient (Figures 5 and 6). The axis is fairly compacted, indicating that variation is not large. However, the plots range from those containing drier species, like *Aster conspicuus* and *Rosa woodsii* (Plot 113) on the lower end, to many that contain moisture loving plants, like moss, ferns, *Juncus balticus* and *Calamagrostis canadensis* (Plots 89, 71, 84, 78, etc.) at the upper end. The eigenvalue on DCA axis 2 is also fairly strong (0.48), which indicates that moisture, although less important than disturbance, is also very important determinant to composition in these grasslands. DCA axis 3 suggests a temperature gradient, perhaps resulting from a combination of elevation and aspect differences along it. Plots from groups 1 and 2 (south facing, mid-elevation) are at the lower end of the axis. Plots from group 8 that generally exist at higher elevations (>6000 ft) on mostly north or east slopes are highest on the axis (Plots 141, 97, 100, and 136, figure 6). Canonical correspondence analyses (CCA) results also support these hypotheses for mechanisms affecting the DCA axes.

Canonical correspondence analysis was used to test correspondence between the vegetation matrix and (1) a matrix containing topographic variables, and (2) a matrix containing canopy coverage of abiotic variables. The topographic variables include elevation, slope, and aspect (Figure 7a and 7b). Only axes 2 and 3 are significant in CCA within the limits of this study. Slope is positively correlated with axis 2 ($r = 0.616$) and highly significant (Monte Carlo test = 0.01). It may, along with subsurface soil characteristics, contribute significantly to moisture loss or retention in these plots. Like DCA, CCA suggests that aspect is also very important to composition. Aspect is highly correlated with the vegetation matrix ($r = 0.990$) and is significant along CCA axis 3 (Monte Carlo test = 0.04). As described above, DCA axis 3 is not solely related to aspect along its gradient (i.e. all south-facing slopes at the lower end and north facing at the upper end). A combination of factors is hypothesized to control DCA axis 3

that can be grouped together as "temperature," and it is obvious from the CCA that aspect is a very important contributing factor to temperature.

CCA also tested how canopy coverage of 10 abiotic variables corresponded to vegetation composition in the east side grasslands. These included soil, rock, litter, lichen, moss and many more. Like the topographic variables, only axes 2 and 3 are significant in this analysis. Figure 8a shows that CCA axis 1 is highly correlated to lichen ($r=0.79$), rock ($r=0.592$) and wood ($r=0.425$), but it was not significant within the limits set for this study (Monte Carlo test $p=0.170$). CCA axis 2 is highly correlated with moss ($r=0.734$) and Moss/Lichen ($r=0.781$), and the Monte Carlo test shows that it is highly significant ($p=0.01$). These results clearly relate to the results from DCA (Figure 6) that suggest a moisture gradient along DCA axis 2 with plots containing moss, ferns and *Juncus* at the upper end. DCA axis 3 correlates most strongly with only one factor, "other" ($r=0.557$). "Other" is a general classification for different kinds of wildlife scat. The axis is significant ($p=0.04$) but it is hard to relate a physical factor that may control this axis but it is clear that wildlife also affects the vegetation in a variety of ways.

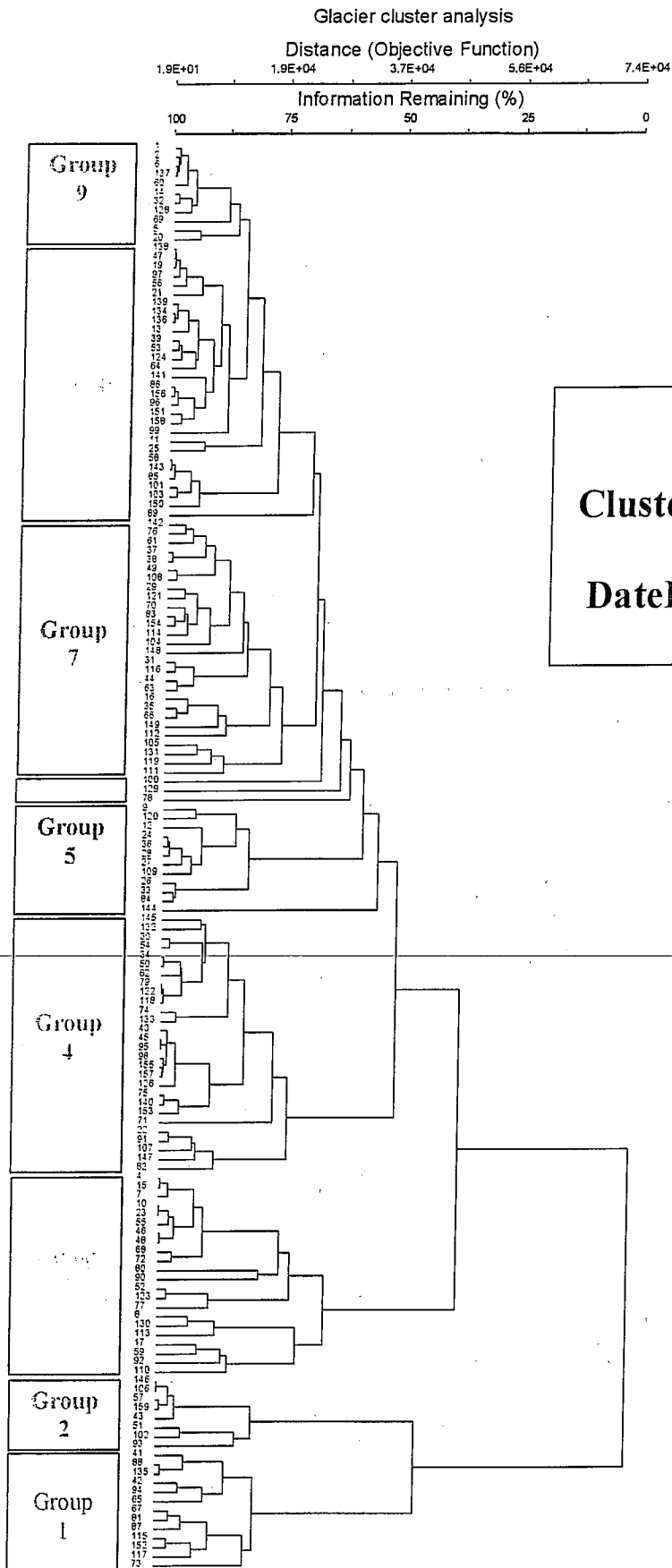
Management implications

The fescue grasslands on the eastern boundary of Glacier National Park occur in a moister, cooler environment than other grasslands in western Montana where *Festuca scabrella* is the dominant native grass. They best fit the *Potentilla fruticosa*/*Festuca scabrella* h.t. *Danthonia intermedia* phase for habitat type classification developed in the 1970s (Mueggler and Stewart 1980). However, there are several problems with the fit to this classification also. Proportions of native grasses are currently different, non-native grasses and woody shrubs are much more abundant, and several non-native species now occur in the Glacier plots that were not encountered in this habitat type when it was first described. For management, this means that the grasslands of Glacier National Park cannot be treated as "typical" dry mid-elevation fescue grasslands; but rather they must be considered as a unique ecosystem. It also means that some changes in species dominance from the original habitat type descriptions may be irreversible and that some restoration targets are impractical. For example, assuming that the most similar habitat type is even the proper target for restoration, the current high canopy cover of non-native grasses *Phleum pratense* and *Poa pratensis* is many times more than the coverage of these species in the original description of the *P. fruticosa*/*F. scabrella* h.t. for some cluster groups in this study. Because high canopy coverage of these grasses has existed for many years (see Koterba and Habeck 1971 and Tyser 1992), it may be impractical to reverse this

characteristic in any restoration efforts. Other non-native species, however, will be easier to address in restoration efforts because they are not as widespread across the area or as abundant in individual plots. The importance of controlling these non-native species is shown in the DCA analysis in this study. DCA shows that community composition in this ecosystem is affected more by non-native species and the effects of past disturbance than by moisture availability. This makes them particularly sensitive to change within a permeable landscape.

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Appendix A:

**Cluster Analysis Dendrogram
with
DateID and Group Numbers**

Appendix B: Species found in Glacier National Park (GNP) plots that are non-native to park or non-native to the region

	1	2	3	4	Group	5	6	7	8	9
3 - Non-native to Glacier National Park										
Native to N.Am, Hawaii, Caribbean			LinVul					LinVul		
4 - Non-native to N.Am, Hawaii, Caribbean										
	AraGla		AgSto	AraGla	AlyAly	ElyRep		AraGla	AlyAly	AraGla
	CenMac		AraGla	Broxxx	CenMac	PhilPra		Broxxx		
	PhilPra	PhilPra	Broxxx	CenMac	EriChe	PhilPra	PhilPra	Broxxx	AraGla	CenMac
	PoaPra	PoaPra	CenMac	DesSop	PhilPra	TarOff	PoaPra	CamMic	CenMac	PhilPra
	TarOff		CirArv	PhilPra	PoaCom	TriRep	TarOff	CenMac	MedLup	PoaCom
	TraDub	TraDub	DesSop	PoaPra	PoaCom	VerSer	PhilPra	CirArv	PhilPra	PoaPra
		PoaCom	DiaBar	PoaPra	PoaPra			ElyRep	PoaCom	TarOff
			ElyRep	RumAce	RumAce			EriChe	PoaPra	ThiArv
			EriChe	TarOff	TarOff			MedLup	TarOff	TraDub
			PhilPra	TraDub				PhilPra	TraDub	TriPri
			PoaCom					PoaCom		TriRep
			PoaPra					PoaPra		
			RumCri					RumAce		
			TarOff					TanVul		
			TraDub					TarOff		
			TriPra					ThiArv		
			TriRep					TraDub		
								TriHyb		
								TriPra		
								TriRep5		
								Trixxx		

Appendix C: R values for correlation of vegetation matrix with topographic and abiotic matrices in canonical correspondence analysis.

**Topographic
Matrix**

Variable	Axis 1	Axis 2	Axis 3
Elevation	-0.780	-0.567	0.010
Aspect	-0.036	0.187	0.990
Slope	-0.808	0.616	-0.162

**Abiotic
Matrix**

Soil	-0.561	0.034	0.003
Gravel	0.271	-0.247	-0.075
Lichen	0.792	-0.108	0.053
Litter	-0.427	-0.366	-0.324
Moss	0.160	0.734	0.078
Other	0.059	0.332	0.557
Rock	0.592	-0.366	-0.148
Tree	-0.057	-0.170	-0.136
Wood	0.425	-0.046	-0.187
M/L	0.106	0.781	-0.273

Illustrations and tables

Figure 1: Location of study plots, east-side grasslands, Glacier National Park, USA

Figure 2: Major species characteristics for each group using cluster analysis on east-side grassland plots, Glacier National Park, Montana, USA. Constructed using Ward's method and Euclidean distance measures. ArcUva= *Arctostaphylos uva-ursi*; PhlPra= *Phleum pratensis*; FesSca= *Festuca scabrella*; PoaPra= *Poa pratensis*; StiNel= *Stipa nelsonii*.

Figure 3: Species richness of vegetation groups delineated by cluster analysis. Maximum-Minimum bars show range of richness within each group. **Mean** = mean value, **Max**=Maximum value, **Min**=Minimum value.

Figure 4: Comparison of Shannon Weaver Diversity Index (H') values between cluster analysis groups. Maximum-minimum bars show the range of H' values.

Figure 5: Detrended correspondence analysis results for axis 1 and 2, east side grassland plots (includes outliers), Glacier National Park.

Figure 6: DCA results for axis 2 and 3.

Figure 7: Correlation of topographic variables with plot composition using canonical correspondence analysis. **A:** Axis 1 and 2; **B:** Axis 2 and 3. Eigenvalues for Axis 1, 2, and 3 are 0.203, 0.114 and 0.085, respectively

Figure 8: Correlation of topographic variables with plot composition using canonical correspondence analysis. **A:** Axis 1 and 2; **B:** Axis 2 and 3. Eigenvalues for Axis 1, 2, and 3 are 0.244, 0.206, and 0.166, respectively.

Appendix A: Cluster Analysis Dendrogram with DateID and Group Numbers

Appendix B: Species found in Glacier National Park (GNP) plots that are non-native to park or non-native to the region

Appendix C: R values for correlation of vegetation matrix with topographic and abiotic matrices in canonical correspondence analysis.