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The nature of change in Western Montana's bunchgrass communities

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THE NATURE OF CHANGE IN WESTERN MONTANA'S BUNCHGRASS COMMUNITIES

by

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The Nature of Change in Western Montana's Bunchgrass Communities

Director: Dr. Paul B. Alaback PA

Grasslands are particularly sensitive to environmental change, including fluctuations in climate, grazing intensity, and invasive species. Understanding how individual grasslands respond to each of these external factors across a broad environmental gradient is essential to developing realistic successional models and appropriate management and conservation strategies.

This study examined compositional changes in western Montana's *Pseudoroegneria* and *Festuca* bunchgrass communities at several spatial and temporal scales. General trends in community composition were first compared between two points in time and at three spatial scales, including the western Montana landscape, four regional areas, and eleven locally paired plots. I found that spatial scale affected perceptions of change after 30 years and that the change patterns at each spatial scale correlated with different environmental and disturbance factors. Changes in community composition were also examined at permanent monitoring plots that were re-sampled at more frequent intervals. Species fluctuations during 20-50 years at these sites were explored using facies diagrams and indirect ordinations. Like the two-points-in-time perspective, compositional change at the monitoring sites was examined at several spatial scales. At individual sites, the bunchgrass communities were extremely dynamic and compositional history was unique. Within each ecoregion, long-term trends differed for each area. Community change correlated most significantly with climatic variables, particularly fall and winter precipitation and winter and spring mean temperatures. The stability and change patterns exhibited by these communities over multiple decades was most similar to patterns predicted by current non-equilibrium successional models, especially state-and-transition and persistent non-equilibrium.

The value of using indicator species and habitat-typing to classify these communities was tested using several methods. Indicator species fluctuated so significantly at many locations that classifications changed in as little as five years. Classification systems and successional models based on assumptions about community stability and equilibrium were not supported by these long-term data. Classification and management of grasslands must consider their dynamic nature and the unique combinations of change drivers at each spatial scale.

This study shows the importance of long-term data sets and an historical perspective to community studies. Both provide unique insights for clarifying ecological theory and proposing more realistic tools for management.

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Preface

"To look backward for a while is to refresh the eye, to restore it,

and to render it more fit for its prime function of looking forward."

- Margaret Fairless Barber (1869-1901) *in* Andrews *et al.*(1996) -

Although some people do not like to dwell on the past, historical studies play a very important role in ecology. My interest in the historical perspective, and particularly the process of change, stems from working as a research geologist. Geologists have a keen awareness of the transient nature of ecosystems. No community remains the same for long; no landform is permanent. The evidence is in the rocks. In ecology, the evidence for change resides in historical records. Collecting such evidence requires the dedication of some person(s) to conduct long-term monitoring and an obsession to save.

The process of piecing together many decades of disjointed time passages (technically called monitoring records) for this study alternated between tedious, challenging, exhilarating, and extremely rewarding. Forgotten files and dusty attics were scoured to find passages that were complete enough to reconstruct the successional history of these northern grasslands. Resampling so many important sites in one field season to update the old records was also an adventure. Taken together, however, the old and new records have produced a unique story that hints at how these grasslands have been affected by environmental stresses and will, I hope, guide the process of "looking forward."

Very little is known about how these northern Rocky Mountain grasslands will change in response to predicted climate warming, further invasion by non-native species, and changes in disturbance regimes. By examining what has affected these bunchgrass communities in the past, we can better predict how changes in these environmental conditions will affect them in the future. Reconstructing the historical trends is also important because Montana rangeland management policies need to reflect the natural change patterns and successional trends that are peculiar to these cool-season bunchgrass communities - not be guided by grassland policies developed in other areas of the United States.

This work is composed of three chapters that investigate change in Montana's grasslands from many different perspectives. From short- to long- time scales and small- to large- spatial areas, this look backward puts change in limited context and hints at what may be in store for these communities in the future.

Description of Chapter 1

This chapter analyzes change from a very common perspective: the difference between two points in time. In the early 1970, plant communities on the western Montana landscape were sampled in detail to create a classification system for the grasslands. As with much historical data, the study cannot be replicated. Sites were not permanently marked to remeasure. The historical data are extremely valuable, however, because they give a detailed picture of plant community membership in the 1970s to compare with data from bunchgrass communities that were sampled in 2002. Used together, the data address the central question of whether typical 2002 communities differ in significant ways from typical bunchgrass communities that existed 30 years ago. If so, at what scale do differences become apparent?

Description of Chapter 2

The search for community change in the bunchgrass communities is ultimately a search for context - an analysis of the larger forces that produced the community that we see on the landscape before us today (Potyondi 1995). The search in the western Montana grasslands brings us to such questions as the following: "How have these communities responded to changes in their environment? Do the bunchgrass communities exhibit long-term trends that we can consider 'succession'? At what time or spatial scales is change apparent? Do the change patterns within these communities really fit currently accepted successional models?"

Chapter 2 examines bunchgrass community dynamics using detailed time-series data from over 50 permanent plots, which have been sampled repeatedly over 20-50 years. The multiple sampling intervals provide insight on species' turnover, community trends and community stability on a time scale that is difficult to investigate first-hand. Change patterns are explored for 1) the bunchgrass community and 2) lifeforms within the community at the site and ecoregion scales. The amount and direction of community change between samplings are quantified using vectors in species space. Community change is examined within the context of fluctuating temperature and precipitation, increasing proportions of non-native species, and varying populations of livestock and wildlife. The nature of change in the bunchgrass communities is also compared to the pathways, change drivers, and directionality of equilibrium and non-equilibrium successional models to assess how appropriately these models depict decadal change in the western Montana grasslands. Fitting the models to this long-term data, not vice versa, is especially important to developing realistic and appropriate management goals for these grasslands.

Description of Chapter 3

As humans, we have a need to classify items so we can organize efficiently, communicate easily and manage like items similarly. Throughout the United States, classification systems have been created during the past 30 years for grassland communities using the habitat-type system. In Europe, grasslands have been classified using similar philosophies based on indicator species. Management of grasslands has relied on assumptions of stability and potential vegetation inherent within these classification systems. One of the problems with these classification systems, however, is that they are usually static, i.e. made at one point in time. Rarely do we revisit the classifications after several decades to determine whether the assumptions used to create them were correct or whether the classification worked as it was intended in its ecosystem.

The third chapter revisits Mueggler and Stewart's (1980) habitat-type classification, which was developed specifically for western Montana, and looks in-depth at how decades of species fluctuations in these ecosystems affect traditional classifications. It examines the stability of indicator species within the bunchgrass communities and assesses their reliability as predictors of future community change. The implications for management are clear – if the indicator species do not truly represent community stability or potential vegetation in these grasslands, then management policies based on these classifications are flawed.

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CHAPTER 1

The changing face of mountain grasslands: 30 years of succession in western Montana's bunchgrass communities

Abstract:

Pseudoroegneria spicata and *Festuca spp.* bunchgrass communities in western Montana have changed both compositionally and structurally in the past 30 years. I used similarity analysis, two-sample non-parametric tests, and non-metric multidimensional scaling (NMS) to compare the composition of typical bunchgrass communities sampled in the 1970s with typical bunchgrass communities sampled from the same regions between 1999 and 2002. Comparisons were made at several spatial scales, including the western Montana landscape, four ecoregions, and paired plots within the landscape. At most scales, current compositions differed significantly from historic composition. At the broadest landscape scale, the distribution of plots in ordination space correlated most closely with topographic variables. Differences between historic and current conditions were masked by strong latitudal and elevational differences that affected microclimate across the large geographic region. At the ecoregion scale, however, differences between historic and current compositions were apparent on at least one dimension of ordination space. At the paired-plot scale, plots gained and lost many different species over time, but 19 to 55% of the original species still persisted in the communities after 30 years.

Throughout the West, introduced species, grazing and other disturbance factors are known to cause compositional change in plant communities. This study showed that, even within much smaller spatial areas, each of these factors varied in relative importance to affect perceptions of why these communities might have changed over time. Unique combinations of disturbance and environmental factors correlated with the compositional changes within each region. In the south, xeric species and shrubs increased in dominance and the changes correlated with general climate warming. In the southwest, changes in diversity measures correlated with increases in bare soil, introduced species, and annual species over time ($Z= 3.49$-6.62, $p<0.001$). In the north and northwest, both introduced species and grazing affected diversity and vegetation change patterns.

The two-points-in-time perspective over ecoregion scales showed general trends in compositional change that gave the impression that these bunchgrass communities changed significantly in 30 years. In contrast, comparisons of closely-spaced paired plots showed persistent, core groups of species after thirty years that gave the impression of more constancy and interrelatedness in the community.

Keywords: *Festuca idahoensis*, historical data, non-metric multidimensional scaling, grassland communities, *Pseudoroegneria spicata*, similarity analysis, temporal change

Introduction

Even after a century of ecological research, we still have little consensus on how temperate grasslands change or what mechanisms are most important to the process (Briske *et al.* 2003). At one extreme, Clements (1916) proposed that species follow a predictable, linear pathway of change. Each species is part of a highly integrated, tight-knit, and interrelated biological group with such strong biological interactions that what affects one member affects the functioning and identity of the entire group to some degree. At the other extreme, Gleason (1917) proposed the individualistic model of community change in which individuals come and go in random fashion and have minimal effects on community functions or the fate of other individuals. In between these two endpoints, lie more current theories that suggest that the existence of plant species within the communities is not random, but that each species has a tolerance threshold for certain environmental conditions and/or disturbance regimes (Friedel 1991, May 1977, Westoby 1989). Succession is driven by whether an individual's tolerance for changing environmental conditions is exceeded and whether the environmental alterations affect the dominance or persistence of enough species to change plant relationships, such as competition or facilitation, within the community. Developing realistic models for community change requires historical evidence that does not exist for many communities. Even data from two points in time, however, can suggest general directions of change and provide indications of how fast change can occur in specific plant communities.

The mechanisms that ultimately drive temperate grassland communities to change composition are just as controversial as successional models. Climatic fluctuations have been shown to particularly affect individual species in grassland communities. Fluctuations in temperature and seasonal precipitation affect competition, biomass production and plant survival (Alward *et al.* 1999, Briggs & Knapp 1995, Coffin & Lauenroth 1996, De Valpine & Harte 2001, Herben *et al.* 1995, Knapp & Smith 2001, Lauenroth & Sala 1992). Grassland ecosystems have been shown to be so sensitive to variation in precipitation and temperature that Kaiser (2001) dubbed them "early warning systems for climatic change." Other factors that drive change in plant communities over multiple decades include substrate conditions, invasive species, and grazing. Changes in substrate conditions drive compositional change through chemical or faunal variations (Callaway *et al.* 2003, Horn & Redente 1998, Jackson *et al.* 1998, Shaw *et al.* 2002, Tilman & Wedin 1991, Wilsey *et al.* 1997). Invasive species affect plant interactions, water availability, soil chemistry and faunal assemblages, and growing space (Bais *et al.* 2003, Burke 1996, Mack 1989, Mack & Lonsdale 2001, Marler *et al.* 1999, Ridenour & Callaway 2001, Schenk *et al.* 1999, Zabinski *et al.* 2002). Grazing affects community composition in either negative or positive ways depending on how grasslands are managed. Animal species, grazing intensity and duration, and seasonality of use all affect how individual plant species survive within a community (Fleischner 1994). Grazing is considered detrimental to grassland communities when palatable species are preferentially removed, ecosystem structure is altered, or species diversity is lowered over time (Fleischner 1994, Singer *et al.* 1998, Willms & Quinton 1995). Ecological functions in some native grassland, however, benefit from grazing when it works to control shrub cover (Anderson & Holte 1981, Floyd *et al.* 2003, Van Auken 2000), maintain biological diversity (Collins *et al.* 1998, Hayes & Holl 2003, Stohlgren *et al.* 1999), and stimulate production and quality of individual grass species (Frank & McNaughton 1993, Merrill *et al.* 1994, Savory 1988, Wallace & Macko 1993). Historical data contain species-specific responses to grazing intensity, invasion of the community, and variations in environmental conditions within these temperate grasslands.

The *Pseudoroegneria spicata* (Pursh) A. Love, *Festuca idahoensis* Elmer, and *F. altaica* Trin. communities of western Montana (hereafter referred to as bunchgrass communities) provide a unique perspective on how temperate grasslands change over time. They exist within relatively natural settings that have not been highly fragmented by increases in human population during the past 30 years, and they have been affected to varying degrees by all of the mechanisms known to affect grassland change - including climatic fluctuations, grazing and invasive species. Because these communities exist within such a large landscape area, they are also well suited for examining how spatial scale affects perceptions of overall change and how environmental and disturbance factors correlate with change over a variety of spatial scales. Three studies have previously focused on how bunchgrass communities change in the northern Rockies over two decades (Anderson & Holte 1981, Mueggler 1992, Schirokauer 1996). All were limited to local sites. The successional changes found in these studies ranged from shrub invasion after release from grazing to compositional change that was attributed to weather 'peculiarities' in the prior year.

This study focuses on how the characteristics of the western Montana bunchgrasses, as a general class, have changed over time. It explores compositional data from these communities, which were taken at two points in time and from the same general spatial areas, to determine if (1) significant changes have occurred in the composition of western Montana grasslands during the past 30 years; (2) spatial scale affects impressions of change; and (3) disturbance or environmental factors correspond with vegetation change in these northern ecosystems over time.

Methods

Study area

Western Montana bunchgrass communities are located between 44.5° and 49.9° N latitude and 108.4° and 114.8° W longitude (Fig. 1-1). They generally occupy valley bottoms and foothills at elevations of 750 to 2800 meters and occur across a full spectrum of aspects. They exist in areas that have a unique geologic history, physiography, climate, soil characteristics, and grazing history compared to other grassland ecosystems. Geologically, the vegetation began as a combination of tropical-coastal and northern-temperate flora during the Tertiary Period (Daubenmire 1970, 1975). Today, the grasslands are located adjacent to three distinct ecosystems - the Palouse prairie, mixed-grass prairie, and forest ecotones – so they consist of combinations of species not found together elsewhere (Koterba & Habeck 1971, Morris & Brunner 1971, Stringer 1973). The climate of western Montana is semi-arid and cooler than most other western U.S. grasslands (Sims *et al.* 1978). The soils are varied throughout the region but most have minimal water-holding capacity during drought because of their coarse, skeletal texture (USDA Natural Resources Conservation Service National Soil Survey Center 2004). Most are derived from the PreCambrian Belt Series, the Boulder Batholith, and Tertiary volcanic rocks (Veseth & Montagne 1980). Bare ground (or spring ephemeral habitat, including cryptograms) is significant within the bunchgrass communities so that the soils are particularly susceptible to erosion when disturbed (Kaiser 1961). The bunchgrasses are also especially sensitive to depletion and/or reduced vigor from livestock grazing (Bedunah 1992). Intense grazing reduces their forage production and reproduction instead of triggering increased production (Mack & Thompson 1982). Unlike grasses of the Great Plains, the grasses in the northern Rocky Mountains did not historically develop under heavy grazing pressure from bison (*Bison bison*) or other ungulates, which may explain their current sensitivity (Bamforth 1987).

Data sources

The data sets used to compare the compositional characteristics of historic bunchgrass communities with current communities came from three sources. The historical data were from a regional study that created a classification for these grasslands in the early 1970s (Fig.1). The current data came from a study in Glacier National Park (GNP) and a second study that sampled select locations across western Montana. All three studies yielded detailed field data that quantified the canopy coverage of each plant species within microplots (0.1 m^2/microplot); estimated the coverage of bare soil, rock, moss and lichen by microplot; and described any disturbances observed during sampling within auxiliary field notes. At each location, a specific number of microplots were aligned along a line transect at predetermined intervals. The collection of microplots forms the site description. Plot and site are used interchangeably in this paper to designate a location with a collection of microplots.

The data for the historical perspective were collected between 1971 and 1973. The three-year regional project described the state of grassland vegetation in western Montana in the early 1970s and provided detailed compositional data to develop a grassland habitat-type classification (Mueggler & Stewart 1980). During the duration of the study, four field crews collected canopy-coverage data from over 350 locations throughout western Montana (Fig. 1-1). Each site consisted of 40 microplots and was

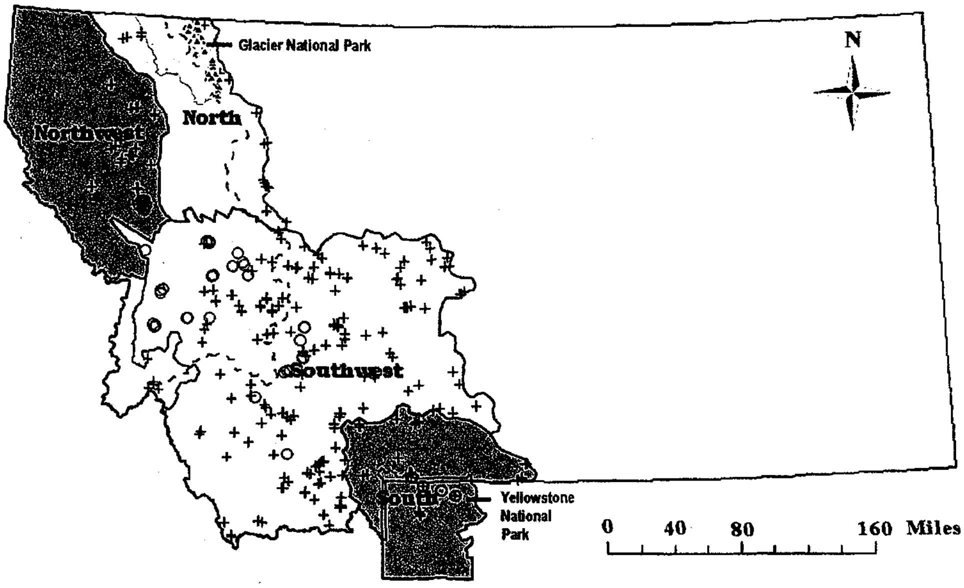


Figure 1-1: Location of Glacier National Park 1999-2001 study plots (triangle), Sikkink 2002 plots (circle), and Mueggler and Stewart 1971-1973 historic plots (+). Regional divisions based mainly on Level 3 Ecoregions of Woods et al. (1999).

sampled only once. None of the historical sites were marked with permanent stakes or global positioning records so they could be relocated decades after the completion of the original study. In 2000, W.F. Mueggler sent his original data forms to the University of Montana to be entered into a modern database. The retyped database, which contains all raw microplot data, original location data, and original field notes on animal use and grazing history, composes the historical perspective in this paper.

The Glacier National Park data set consisted of samples from the east-side grasslands of the park. Fourteen microplots were sampled at each of 155 permanently marked sites that span the entire length of GNP's eastern boundary (Fig. 1-1). Each site was sampled only once during the duration of the study, which lasted from 1999 to 2001.

Canopy coverage was estimated in the field using standardized cue-cards that contained visual depictions representing various cover percentages. The cards increased consistency of visual estimates as research personnel changed during the three-year study.

The western Montana data set was collected in the summer of 2002 to investigate regional differences in the current composition and plant diversity of the intermountain grasslands in western Montana. Thirty microplots were sampled along a 33.3 m transect at most of the 50 permanently marked grassland monitoring sites. The sites extended from the National Bison Range (NBR) in the north to Yellowstone National Park (YNP) in the south (Fig. 1-1). All sites had good historical descriptions at several intervals during the past 30 years. Each was revisited once in 2002 to describe the current diversity of vascular plants and to quantify species coverage. Percent canopy cover of all species and several abiotic and non-vascular plant variables were visually estimated to six categories in each microplot (1=<1%, 2=1-5%, 3=6-25%, 4=26-50%, 5=51-75%; 6=76-100%) and recorded as field observations. Site disturbance was qualitatively described and soil samples from the upper root zone were collected at each location.

Only historic and recent plots that were dominated by *Festuca idahoensis*, *Festuca scabrella*, or *Pseudoroegneria spicata* bunchgrass were included in this study. Other potential vegetation types existed within the regions, but their composition differed significantly from these target bunchgrass communities and would have confounded the analyses. To equalize comparisons with the historic plots, no current sites were included in any statistical analysis if they showed obvious recent treatment for brush removal, ecotonal change (e.g., tree/grass interface), or were located across fence-lines with obvious grazing differences.

Nomenclature

Change in nomenclature is an ongoing and often controversial process. For this project, nomenclature was standardized to the currently accepted genus and species listed on the Biology of North America Program web site (Kartesz 1998). Because this site is regularly updated and also lists all old nomenclature equivalents for each species, obsolete names were easily located and their currently-accepted modern equivalent determined. Appendix A lists the species cited in this paper, the current names as defined by the web site, and the historic equivalents.

In all analyses, origin designations for introduced species in Montana follow Rice (2004). Life form and life history designations follow Hitchcock and Cronquist (1973). Response to grazing by species is designated according to the American Society of Range Management (Willard 2003a) and Wroe et al. (2000).

Spatial perspectives

All three data sets were analyzed together for the landscape perspective in this paper. The data sets were subdivided into five ecoregions, however, to determine if the changes in community composition were isolated to certain parts of the state or if the processes driving change differed across the study area (Fig. 1-1). The divisions are based on the Level 3 ecoregions boundaries of Woods et al. (1999) with one exception. Technically, the Yellowstone National Park (YNP) area is within the same Level 3 ecoregion as the southwest part of Montana (i.e. ecoregion 17 – Middle Rockies). However, it was separated within this study to facilitate comparison with similar vegetation-change studies that were conducted in YNP over a decade ago (Coughenour *et al.* 1991).

Ecoregions were used because they have similar geology, soils, topography, vegetation, macroclimate, and land use (Woods *et al.* 1999). By subdividing the landscape into ecoregions, the variation among in these factors was minimized within each ecoregion and the variation in community composition due to time was accentuated.

Because it could be argued that plots located in close spatial proximity may be much more similar to each other in the bunchgrass habitats than plots compared at regional scales, the data sets were also sub-divided into paired plots for a local perspective on how communities changed. Seventeen pairs of current plots were matched with the nearest historical plot on the landscape. Compositional changes were compared between the historic site (40 microplots/site) and current site (14 in GNP or 30 in southwest Montana). The paired-plots were a maximum of five kilometers from each other, were located within the same general topographic settings (i.e. similar elevation, aspect, and slope), and were almost equally distributed among the four ecoregions.

Statistical analysis

Three types of analyses were used to test whether historic and current compositions in these communities differed significantly after 30 years of exposure to grazing, invasive species, and climatic change. Each analysis measured different aspects of the multi-decade changes. Percentage similarity simply tested whether historic and current sites differed in composition. Wilcoxon rank sum tests tested for differences among individual components of the sites, such as diversity indices and life forms. Non-metric multidimensional scaling tested the differences between historic and current communities and how they aligned along interpreted environmental and disturbance gradients.

Analysis of all data used mean percent frequency of occurrence as the dependent variable to investigate compositional trends. Percent frequency was calculated for each species and each abiotic variable based on the number of microplots at each site. Percent frequency, rather than percent canopy cover, was used for a number of reasons. First, all three vegetation studies used in this analysis had a different number of microplots, so percent frequency standardized the data into proportions that are comparable between sites with different sample sizes. Second, the frequency that certain species occurred in each area was more objective and more readily comparable than the original percent-cover values because the exact site locations from the 1970s couldn't be relocated. Third, several studies have shown that percent frequency is a more reliable indicator of compositional change than cover for long-term studies (Elzinga *et al.* 1998, Greig-Smith 1983, Lesica & Hanna 2002, Smith *et al.* 1986).

To determine if historic and current plots were significantly different, the compositions of each historic and current plot within an ecoregion were compared using percentage similarity. The percentage similarity (Sorensen 1948) was calculated as $D_{ih} = 100 - 200 * (\text{sum min} (Y_{ij}, Y_{hj}))/ (\text{sum } Y_{ij} + \text{sum } Y_{h})$, as described in McCune (2002). Distance relationships between the samples obtained from the similarity analyses were subjected to multidimensional scaling (MDS) to diagram how similar they were. All similarity and distances relationships were calculated within the Brodgar statistical package (Zuur 2000).

Wilcoxon rank sum tests (van der Waerden 1969), which are equivalent to Mann-Whitney non-parametric tests, were used to test whether the plots from the current and historic sample sets could have come from the same sample distribution at the landscape or ecoregion scales. Differences in life-form dominance, life history, species origin, family proportions, abiotic (bare soil, rock) coverage, and moss and lichen coverage were tested between the two time periods. Topographic characteristics were also tested to determine if historic and current plots fell within the same general variations in physiography within each ecoregion. The Wilcoxon tests were run within S-Plus statistical software (Insightful Corporation 2001) and differences between the historic and current sample sets were considered significant if $p<0.05$. Most comparisons, however, had much higher significance values than this minimum (i.e. $p<0.01$). VTAB Ecosystem Reporter (Emanuel 1999) was used to summarize total coverage for each of the plant-related variables by plot. Non-standardized, calculated mean frequencies from the raw data were input into VTAB to compute these totals. The tallies of total plant coverage in a plot for each characteristic were then converted to proportion of total plot coverage, which was then used in the Wilcoxon comparisons. (Note: VTAB's original plant look-up file and parameter file for categorizing plant characteristics has been extensively modified and expanded to fit the output needs of this particular study.)

Differences in total diversity between the 1970s and current communities were also tested for each ecoregion. Richness comprised one variable. Shannon diversity, a common index that measures both richness and evenness, was computed within VTAB as

H'= (N log N – sum (n log n))/N, where n is % mean frequency for each species in a sample multiplied by 10 and N is total % mean frequency for all species multiplied by 10. Simpson's dominance was calculated because it emphasizes evenness and is relatively stable with sample size. It is calculated as I=(sum (n*(n-1)))/N*(N-1)). Mean values for the three diversity measures were compared between the historic and current plots using S-Plus Wilcoxon tests as described above.

While Wilcoxon tests were used to determine if the set of historic plots differed significantly from the set of current plots in general terms, non-metric multi-dimensional scaling (NMS) compared the plots as individual entities with their own characteristic compositions, structures, and distributions along disturbance and environmental gradients. As with similarity analysis, the effect of time was minimized within NMS. The analyses focused solely on the relative similarities of each site's composition, no matter when it was measured, compared to all other sites within the ecoregion. NMS was calculated within PCOrd V4.27 (McCune & Mefford 1999) using a Bray-Curtis distance measure and the autopilot function (step-down dimensionality starting in 6-D space, stability criterion=0.005, random number start). Each NMS analysis was run several times with random start numbers to ensure the best configuration was achieved (i.e. solution with least stress). The calculated stress value for each ordination represents how well the sequence of ordination distances fit the sequence of original distances in the actual compositional data in each data set. The better the fit, the lower the stress values were. Prior to data transformation, the main matrix for NMS consisted only of percent frequency values for vascular plant species. No species was omitted from the ordination if it occurred in the original microplot data. A separate, secondary matrix consisted only of frequency values for abiotic and non-vascular variables, including bare soil, rock, lichens, moss, and litter.

Raw data were transformed in PCOrd with a Beal's smoothing algorithm prior to running NMS analyses only. Beal's smoothing was used in this study, rather than data standardizations or relativization, to address three main problems with the data sets. First, it smoothed out differences due to varying sampling intensity or sampling quality (McCune 1994). In long-term studies, uneven sampling quality is common because investigators with different abilities and priorities change over the lifetime of the project. Sample intensity also varies considerably with study objectives and project scale. In this study, both problems affected the raw data. Several different crews collected the historic data. The historic crews are different from the crews collecting more recent data. Data were collected for a different purpose in each study, even though all three data sets used the same general collection techniques (i.e. Daubenmire microplots). Second, Beals smoothing removed the excessive number of zeros in the vegetation matrix caused by a small number of species in each sample compared to the large number of species in the overall study. The grassland plots typically consisted of fewer than 40 species, but over 400 species occurred across the landscape and within the 30-year time. Finally, the Beals smoothing function addressed the classic "zero-truncation" problem common to all plant community data. The "zero-truncation" problem refers to the zero values in the vegetation data that reveal nothing about how unfavorable a particular site is for a particular species (i.e. whether a plant can not grow in a community or whether it just is not found at a particular sampled location). Although the Beals transformation eliminated some quantitative variability from the original grassland matrix, smoothing was only a problem with the NMS for the north region. In the north, so much variability was lost smoothing that the NMS was 1-dimensional (i.e. ranked data in a single line). Therefore, the ordination for the north region presented in this paper was created using raw frequency data values in the vegetation matrix instead of transformed values.

For a complete discussion of the mathematical procedures used by NMS and the advantages and disadvantages of using this technique see McCune (2002), Kruskal and Wish (1978), Young (1987) and Clarke (1993). See McCune (1994, p.83) for a description of Beal's smoothing and its advantages when analyzing long-term data.

Statistical procedures for analyzing compositional change among the paired-plots included tallying the number and types of species lost or gained between the historic and current samples, analyzing the functional groups that were lost or retained over time, and comparing compositional similarities among the pairs using NMS as described above.

Relating environmental and indicator variables to NMS plot distribution

Climate summaries from 38 climate stations distributed across western Montana were used to correlate variations in temperature and seasonal precipitation between 1971 and 2002 with compositional change in the bunchgrass communities (Western Regional Climatic Center 2002). For each climate station, monthly mean temperatures were averaged by season and monthly precipitation values were totaled by season. The seasonal categories included: **fall prior to sampling** (September-October), **winter** (November – March), **spring** (April-May) and **summer** (June-August). The stations were divided into categories based on ecoregion and elevation within the ecoregion to make the climate data more applicable to the range of elevations covered by Montana's grassland sites. High elevation stations were above 1800 m; low elevation stations were below 1800 m.

For each ecoregion and elevation range, the individual seasonal values from each climate station were, in turn, averaged to obtain a mean temperature and mean precipitation total by season for each of three time periods. The time periods included: (1) the sample years of the historical study; (2) the sample years of current studies; and (3) a 30-year mean. The means for the sample years were calculated in two ways- as a seasonal for the three years prior to each sampling year and as a straight average by season for the year of sampling. The three-year seasonal averages are presented in this paper, but there was virtually no difference to trend interpretations if the prior-year seasonal values would have been used. Thirty-year means were computed for each climate station using mean annual values from 1971 to 2002 and then stations were aggregated by region and elevation to create a single number representing the thirty-year mean for high and/or low elevations within each ecoregion.

To examine how individual variables, such as coverage of annual species or diversity indices, correlated with plot distribution in each NMS, the dependent variables were tested against each NMS axis score using linear regression within S-Plus statistical software. In statistical terms, each variable is regressed over the coordinates of the configuration (Kruskal & Wish 1978). Results of linear regression on NMS axis scores were considered significant if $p<=0.05$. The substrate index variables included the frequency of bare soil, rock, litter and other (animal droppings). The non-vascular plant variables included mosses and/or lichens. Other variables represent totals of certain types of species assigned to certain plant categories in VTAB. The "introduced species" variable was a total of all introduced species by plot converted to a proportion of the total plot vegetation. Plot totals were then averaged by ecoregion. Grazing effects were quantified using tallies of indicator plants. Ideally, the direct effects of grazing would be quantified and correlated with results using specific information on stocking rates, grazing rotational method and the type of animal eating from each plot location in each sample year. However, this information was not available for the historic and current plots used in this study for a variety of reasons. Compounding the issue, wildlife grazing was more common in some areas than livestock grazing and forage preferences differed between wildlife and livestock. Estimating when, where and how much elk, bison, bighorn sheep and deer ate and how herds congregated in a certain area to forage was difficult and highly speculative at best. To counteract these problems, I used indicator plants that are accepted by range managers as a measure of how certain plants are known to respond to cattle grazing (Willard 2003a, Wroe *et al.* 2000). Individual species were classified according to their response to foraging, then summed and converted to a proportion of plot coverage. These values formed the increaser, decreaser, and invader variables (Dyksterhuis 1949). *Increasers* are plants that are known to increase cover with grazing. *Decreasers* decrease in cover with grazing. *Invaders* increase in communities and replace other community members over time. The effects due to wildlife grazing were captured only if a plant responds in the same way to both foragers.

Interpreting how and why plots were distributed along each NMS axis and labeling the most important factors driving the distribution were done using several lines of evidence including: (a) the physiologic requirements of key species in plots along the axes; (b) the differences in substate, non-vascular, or composite variables in plots at axis extremes; (c) high significance values for correlation of a variable with NMS axes scores; and (d) the importance of topographic variables to each analysis. Many of the axes had more than one distinct gradient along their length. Other axes, however, had gradients that represented a combination of many individual factors, which couldn't be distinguished as individually controlling distribution. For example, plots along some axes showed strong correlations with elevation, aspect, surface litter, shrub overstory, and plant growth requirements when regressed on the NMS axis scores, but no one factor was more significant than any others. These axes were best represented by combining the factors under a single label (e.g., "evapo-transpiration"). Similarly, "surface soil temp" was assigned to plots that had only factors insulating the soil surface and no evidence of shading from overstory shrubs or trees.

Results

Montana regional patterns

The western Montana region is a composite of so many different ecoregions within such a large geographic area that distinguishing compositional differences between historic and current plots within the landscape was confounded by differences in topography and latitude. Virtually every variable compared for differences between historic and current community structure with Wilcoxon tests was highly significant and, therefore, changes between the two time periods appeared quite dramatic (Table 1-1). Dominance shifts in 38 families over time also contributed to the appearance of significant compositional change (Fig. 1-2). At this scale of analysis, the dominance shifts over the past three decades appeared quite significant, especially in decreases in the *Poaceae* and *Polemoniaceae* and increases in *Rosaceae*, and *Rubiaceae* (Fig. 1-2). However, these

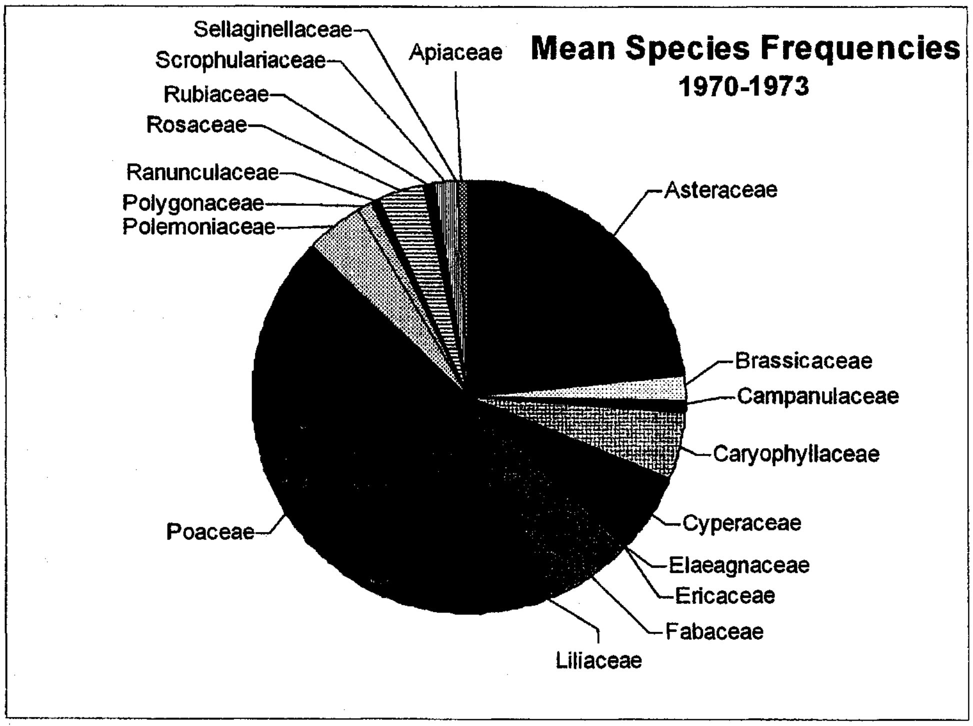
Table 1-1: Comparison of mean frequencies of occurrence of historic and current topographic and vegetation variables for each region and the western Montana landscape

	South Region			Southwest Region			Northwest Region			North Region			Western Montana		
	Current	*Historic*	*Signif. Level*	*Current*	*Historic*	*Signif. Level*	*Current*	*Historic*	*Signif. Level*	*Current*	*Historic*	*Signif. Level*	*Current*	*Historic*	*Signif. Level*
Topographic Variables															
Elevation						**[1]									**
Slope						**						**			**
Latitude			*[2]			**			**			**			**
	Mean Freq Current	*Mean Freq Historic*	*Signif. Level*	*Mean Freq Current*	*Mean Freq Historic*	*Signif. Level*	*Mean Freq Current*	*Mean Freq Historic*	*Signif. Level*	*Mean Freq Current*	*Mean Freq Historic*	*Signif. Level*	*Mean Freq Current*	*Mean Freq Historic*	*Signif. Level*
Surface Characteristics															
Bare soil	19.17	8.48	**	18.78	7.01	**	19.20	2.24	**	1.54	1.44		5.89	8.15	**
Surface rock	27.52	11.72	*	9.14	8.73		5.67	5.73		0.76	4.49	**	0.29	0.00	**
Surface Litter	12.10	51.93	**	28.50	47.31	**	47.88	74.68	**	82.22	78.51		89.37	52.38	**
Composite Variables															
Annuals	1.73	1.19		11.45	2.00	**	29.88	14.86	**	3.77	0.21	**	5.85	3.02	**
Perennials	92.80	93.22		78.86	94.33	**	60.47	80.37	**	94.97	97.70	**	91.08	93.04	+
Introduced species	1.18	3.86	+[3]	9.42	2.75	**	19.43	11.13	+	6.87	0.71	**	7.46	3.56	**
Lifeform Variables															
Graminoids	46.30	47.17		47.27	46.31		45.77	44.28		32.17	47.61	**	35.85	48.28	**
Deciduous shrubs	14.85	8.00	*	8.18	5.87		1.43	2.47		5.18	4.13		5.85	5.59	+
Ferns										2.11	0.00	**	1.80	0.00	**
Evergreen shrubs				0.06	0.05					2.03	1.97		1.55	0.15	**
Herbs	37.80	44.82	**	43.32	47.78		49.04	53.25		57.48	46.29	**	54.05	47.96	**
Surface Moss/Lichen	14.71	18.92		9.14	10.04		7.65	32.78	**	3.24	16.12	**	4.88	13.65	**
Mosses	1.05	0.00	*	10.14	0.00	**	3.76	0.00	**	0.97	0.00		1.39	0.00	**
Diversity Variables															
Shannon Index	1.08	1.18		1.17	1.20		1.24	1.20		1.38	1.31	*	NA		
Simpson's Index	0.11	0.09		0.08	0.09	+	0.07	0.08		0.05	0.06	**	NA		
Richness	19.00	25.00		24.00	27.00		27.00	26.00		43.00	34.00		NA		
Grazing Variables															
Invader grass	1.25	1.41		3.42	0.89	**	18.68	6.48	*	6.29	0.53	**	1.55	1.12	+
Invader forb	9.85	1.75		20.98	12.31	**	19.54	21.24		18.48	13.41	*	28.83	22.92	**
Invader shrub	7.57	4.84	+	2.38	2.58		0.00	0.28		0.24	0.04		1.85	5.69	**
Decreaser grass	14.90	11.81		14.25	12.73		10.08	14.38	+	9.48	14.32	**	16.35	20.77	**
Decreaser forb	0.00	1.39	*	1.82	1.22		0.15	1.00	+	1.04	2.11		0.41	0.48	
Decreaser shrub	2.58	0.57		0.19	0.15		0.03	0.67		1.01	0.28	+	0.85	0.23	**
Increaser grass	28.33	28.39		26.43	26.04		16.87	22.42		11.75	25.10	**	6.60	3.02	**
Increaser forb	20.81	22.41		18.63	26.71	**	25.31	23.56		30.83	23.22	**	4.66	2.29	**
Increaser shrub	6.27	2.91		3.14	3.44		1.40	1.52		4.69	4.83		NA		

[1] ** $p < 0.001$

[2] * $0.001 < p < 0.01$

[3] + $0.01 < p < 0.05$



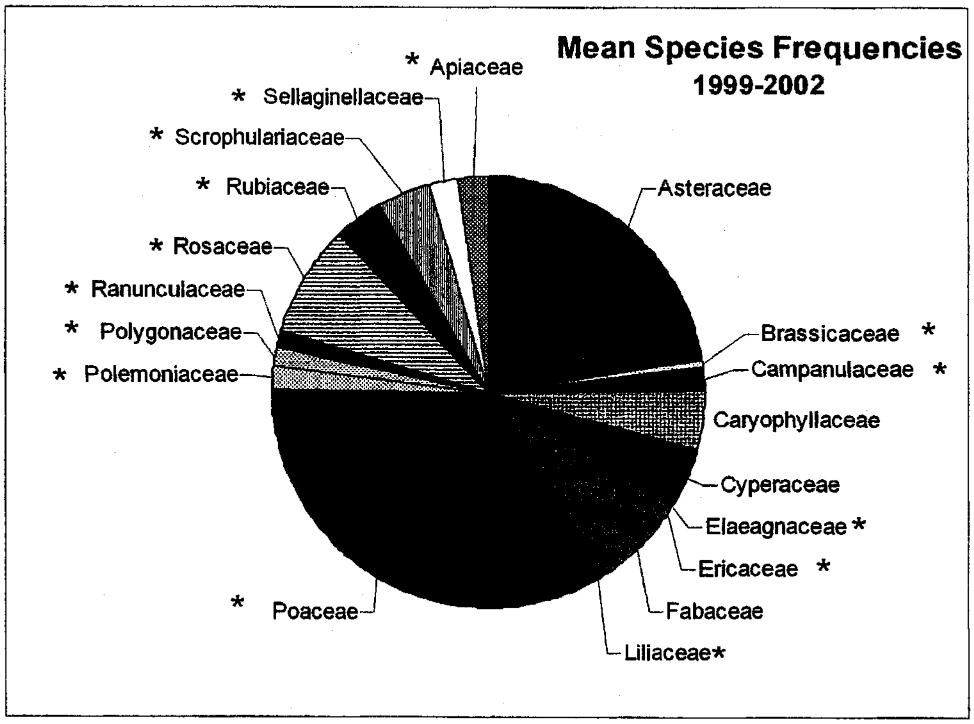


Figure 1-2: Mean frequencies of species by plot, summarized by family, for western Montana landscape. Only top 18 families with frequency greater than 1% are shown. 38 total families have statistically significant changes between the two sampling periods (*=differences significant at p<0.01).

trends were not ubiquitous across the landscape. If members of *Poaceae*, for example, are tallied by region, they actually increased slightly in frequency (<5%) in all regions except the north. In the north, Poaceae decreased by 12%, which dominates the western Montana analysis. The only species that varied uniformly across all regions were members of the *Cyperaceae* (decreased), and *Sellaginellaceae* (increased).

A distinctly different perspective of compositional change over the entire region was given by the NMS where both historic and current plots were well distributed in ordination space and neither sample set was distinctly separated from the other based on composition (Fig. 1-3). Plots were arranged mainly by latitude and moisture gradients that range from moist conditions in the north to extremely dry conditions in the south and southwest. At the extreme negative end of axis 1 in Fig. 1-3, plots averaged over 40 species per plot, were coincident with moist conditions, and were located at the highest latitudes in Glacier National Park. They included communities containing *Calamagrostis canadensis* (Michx.) Beauv., *Juncus balticus* Willd., and *Equisetum arvense* L. On the positive end of the axis, plots averaged fewer than 10 species, were well-drained and dry, and were mostly from southwestern Montana. Compositions contained *Kraschenninnikovia lanata* (Pursh) A.D.J Meeuse & Smit, *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, and *Opuntia polyacantha* Haw. Introduced species, in general, correlated significantly only with axis 1 (R^2=0.03, p<0.01). Because of the low orthogonality of the graph, which indicates high correlation among the axes, plots from disturbed communities with an abundant cover of introduced species created a scattered distribution on diagonals out from the main axis of the western Montana plots (see vectors in Fig. 1-3).

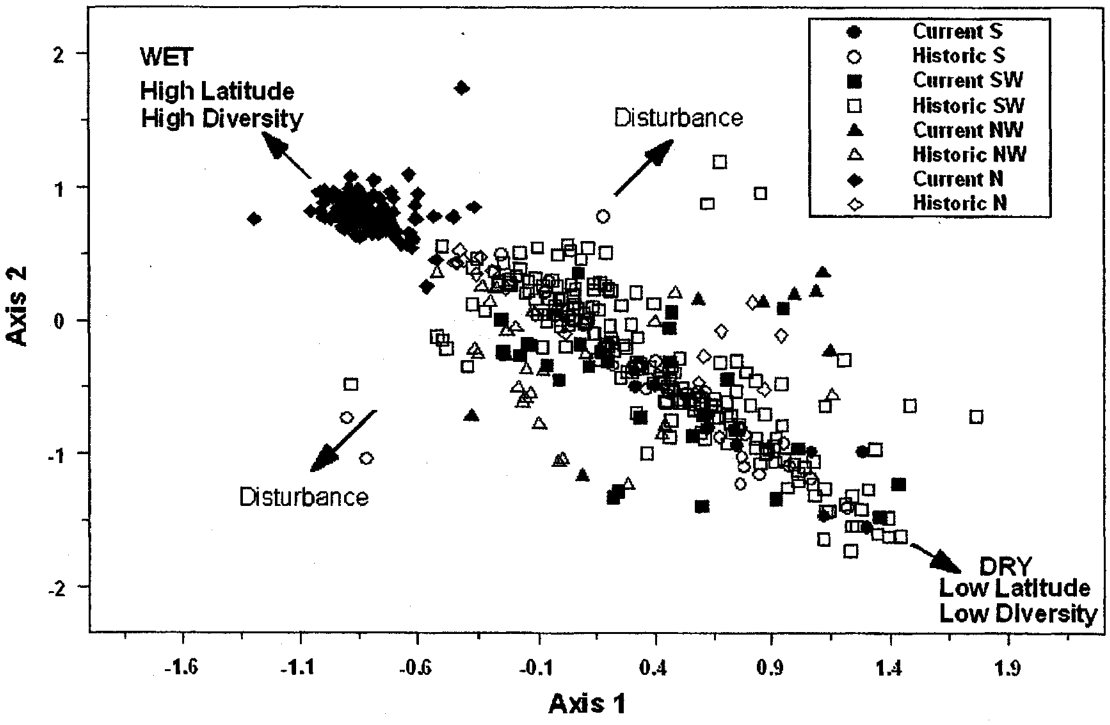


Figure 1-3: Non-metric multidimensional scaling of species frequency matrix for western Montana grasslands (S=south region; SW=southwest region; NW=northwest region; N=north region). n=460. # species=622. Axis 1 R^2=0.82; axis 2 R^2=0.16. Orthogonality=48.5%. Stress=7.491.

Ecoregion patterns

Differences in composition among typical historic bunchgrass communities and typical contemporary bunchgrass communities were best distinguished at the ecoregion scale. In general, the ecoregion divisions made climatic, geologic, and topographic conditions much less dominant than at the larger western Montana scale so differences in vegetation pattern over time were more prominent. Historic and current plots separated quite distinctly in most ecoregions using percentage similarity (Fig. 1-4). As in the western Montana landscape, however, the strongest influences on the distribution of most historic and current plots in the NMS for most of the ecoregions were combinations of environmental and topographic factors that control moisture and temperature. Climatic variations between ecoregions and the mean differences in precipitation and temperature for the growing season over time are shown in Fig. 1-5. In all ecoregions except the northwest, the climatic influences - whether they were ultimately driven by differences in elevation, latitude, slope and aspect, or climate warming - controlled plot distributions along the NMS axes that explained the most variability (i.e. had the highest R^2).

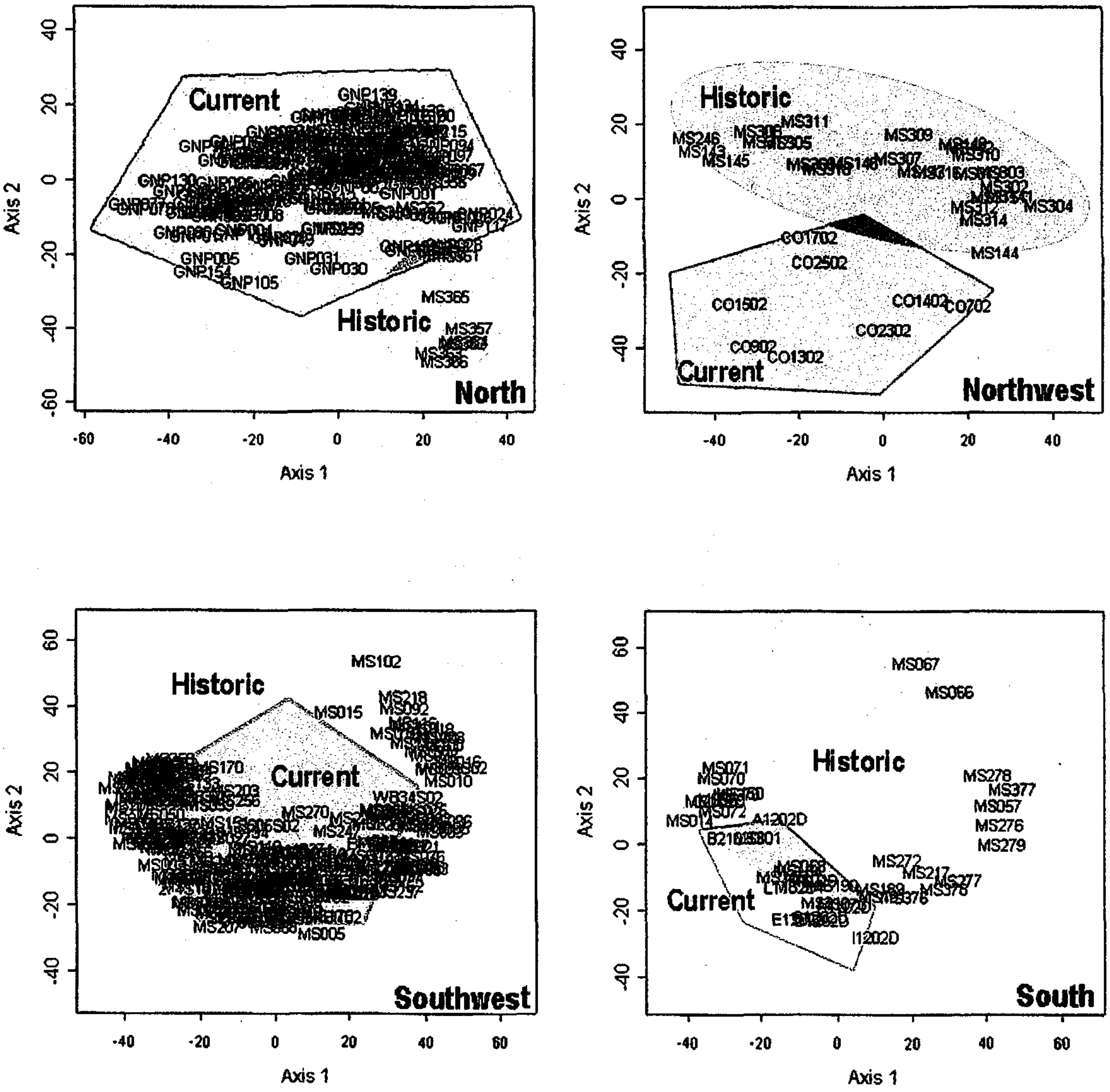


Figure 1-4: Comparisons between historic (ellipse) and current (polygon) plots by ecoregion as measured by percentage similarity in composition.

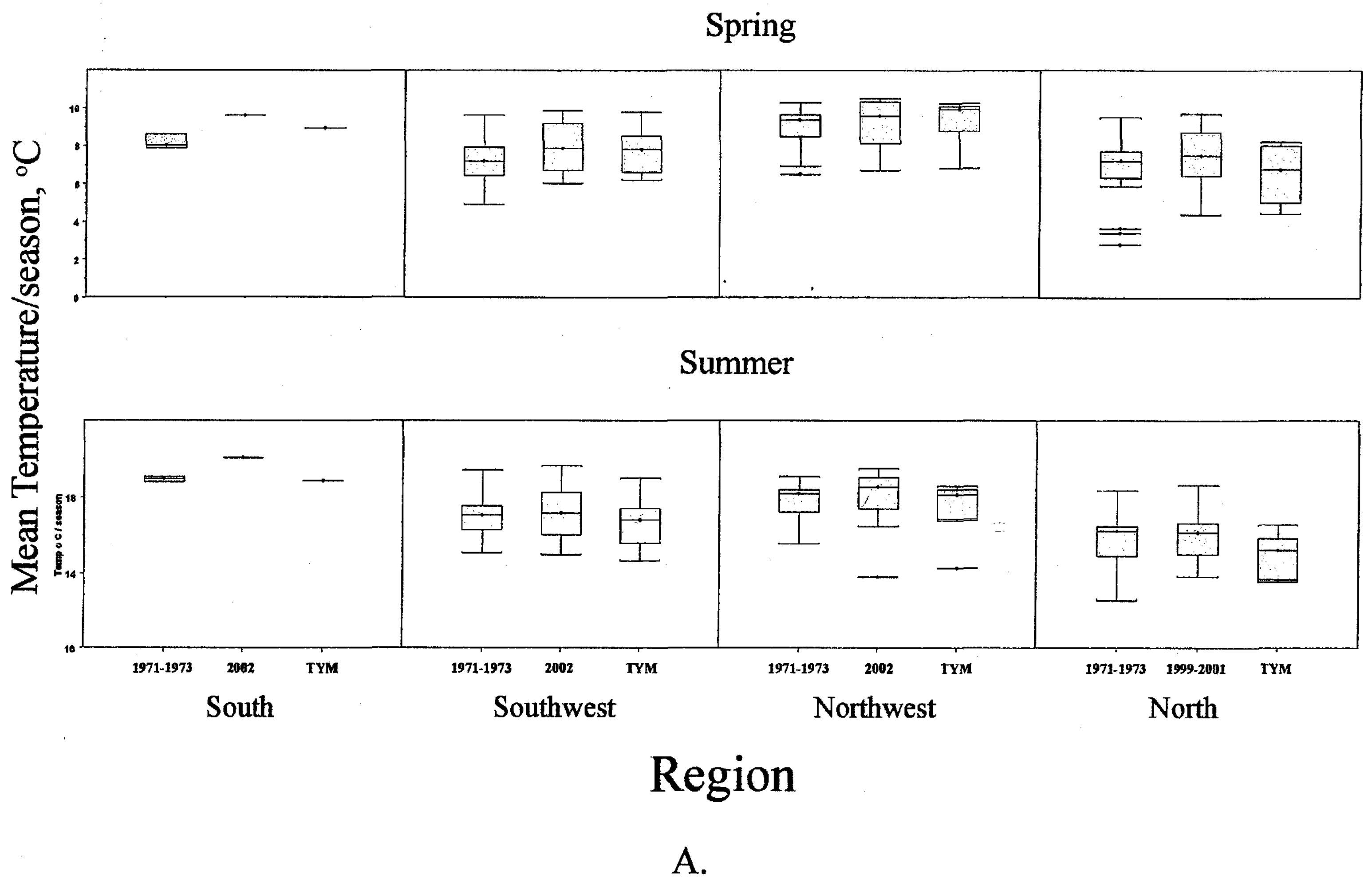
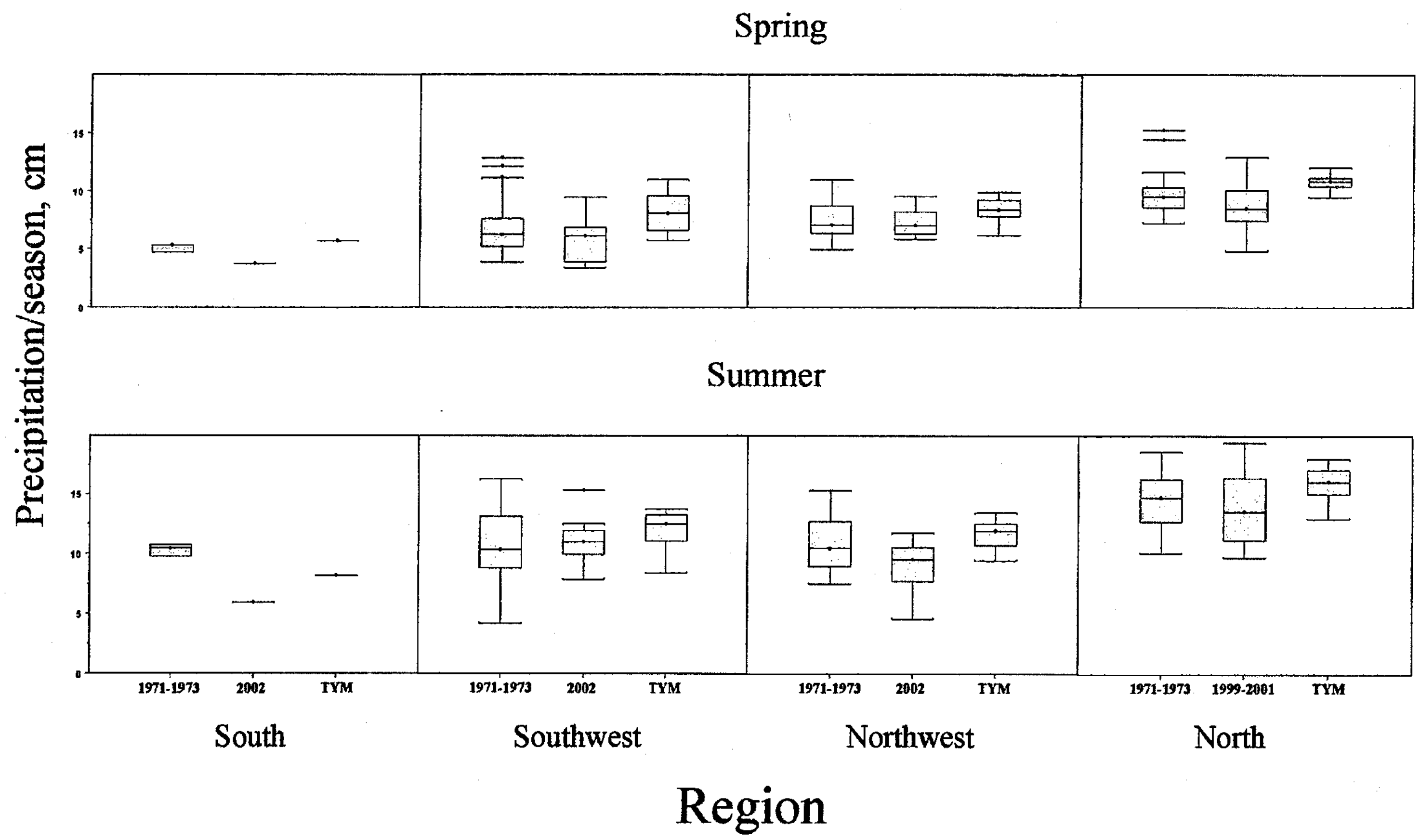


Figure 1-5a: Regional variations in mean temperature (A) and precipitation (B) during growing season for historic and current sampling period. TYM=thirty year mean for the region.



B.

Figure 1-5b: Regional variations in mean precipitation (B) during growing season for historic and current sampling period. TYM=thirty year mean for the region.

South ecoregion change patterns

The NMS graph for the south region has three distinct clusters, or group spaces, along its dominant axis, which consist of communities that increase in moisture requirements along the length of the axis (Fig. 1-6). Group space one was comprised of plots dominated by *Pseudoroegneria spicata*, *Opuntia polyacantha*, and *Gutierrezia sarothrae* (Pursh) Britt. & Rusby that thrive in hot, dry environments. Group three consisted of historic plots with combinations of species that grow in moist or very wet environments, including *Deschampsia caespitosa* (L.) Beauv., *Juncus balticus*, and *Galium boreale* L. Group two consisted of plots with *F. idahoensis* and *P. spicata* as co-dominants combined with several shrub and succulent species. Although the historic sampling

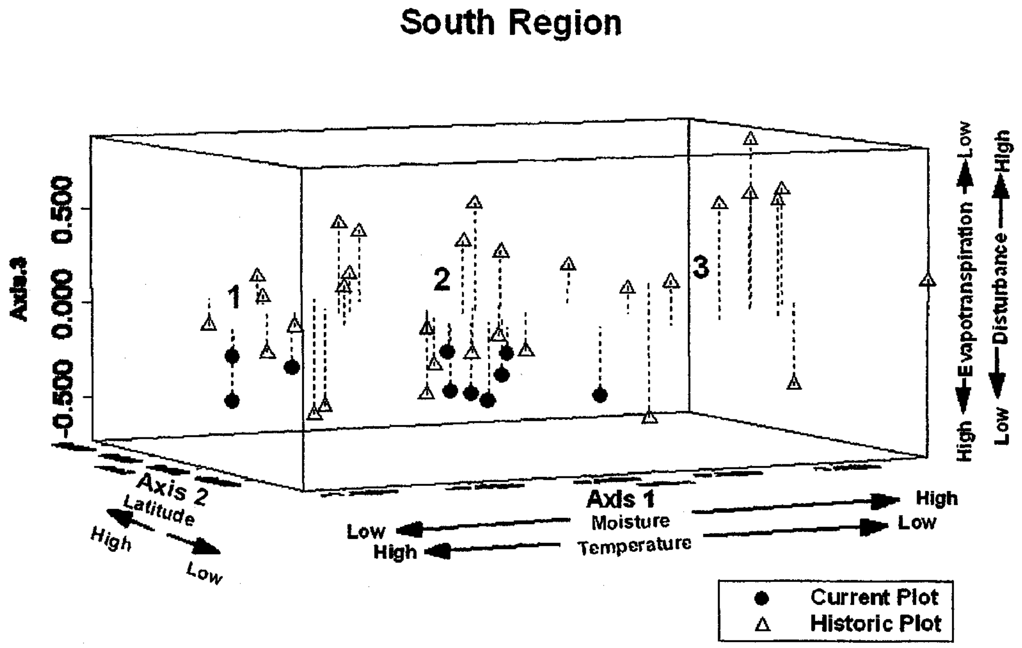


Figure 1-6: Non-metric multidimensional scaling of species frequency matrix for south region. n=41. #species=205. Axis 1: R^2=0.62; Axis 2: R^2=0.14; Axis 3: R^2=0.10. Orthogonality: NMS axis 1 vs. 2=89.2; 1 vs. 3=91.2; 2 vs. 3=88.5. Stress=13.085. Numbers refer to group-space descriptions in text.

spanned a wider range of moisture regimes than contemporary sampling to contribute to differences along NMS axis 1, the differences in composition due mainly to time were most apparent along NMS axis 3 (Fig. 1-6). Historic plots at the low end of axis 3 showed little evidence of disturbance factors; recent plots at the high end had more invader forbs and shrubs (Appendix B).

In 2002, the south ecoregion was warmer and drier than either the 1970 sampling seasons or the 30-year mean conditions (Fig. 1-5). The Gardiner climate station near Yellowstone National Park (south, low elevation) had the most warming over the 30 years of any location. It experienced increases of 0.5 to 2.5° C for each season.

Several compositional trends in the community data suggest that the plant communities may have experienced enough warming and drying during the past 30 years to cause significant change over the three decades. The dominant trends in the south include:

1. Bare soil and exposed rock increased three-fold from 6% to 19% and 11% to 27%, respectively (Table 1-1).
2. Surface litter decreased from 51% to 12% between sample periods.
3. Diversity indices remained stable, although the mean number of species per plot actually declined (Table 1-1). Diversity is strongly correlated with the moisture gradient along NMS axis 1 (Shannon index R^2=0.50 and Simpson's index R^2 =0.46), but it is also correlated with the difference between historic and current plots on NMS axis 3 (R^2=0.16 and R^2 =0.11). Some diversity loss was attributed to a significant reduction in the frequency of non-native species (Table 1-1), which also correlates with plot distribution along axis 3

($R^2=0.237$) in the NMS. The south region is the only region in this study where non-native species declined during the 30 years, although introduced species were not a significant problem in the region during either time period.

4. Species with drought-resistant physiology, like cacti and sedum, more than doubled in frequency.
5. Species with deeper root systems (i.e. several species of shrubs) increased significantly during the drought conditions. In general comparisons, all invader, decreaser, and increaser shrubs more than doubled in the past 30 years, although most of the increases were not significant within the limits of this study (Table 1-1). Within ordination space, shrub increases and/or invasion were second only to differences in the abiotic variables and introduced species as important factors for separating historic and contemporary plots along NMS axis 3 ($R^2=0.19$).
6. All non-shrub grazing indicators showed only minimal differences with past conditions.

Southwest ecoregion change patterns

Like the landscape-scale analysis (Fig. 1-3), the ordination for the southwest region showed strong moisture and topographic gradients along its dominant axis (Fig. 1-7). The southwest had so many more historic plots in proportion to contemporary plots and they existed in such a varied topography, that all correlations of these plots with latitude, slope and elevation were highly significant ($p<0.001$). As a result of this topographic

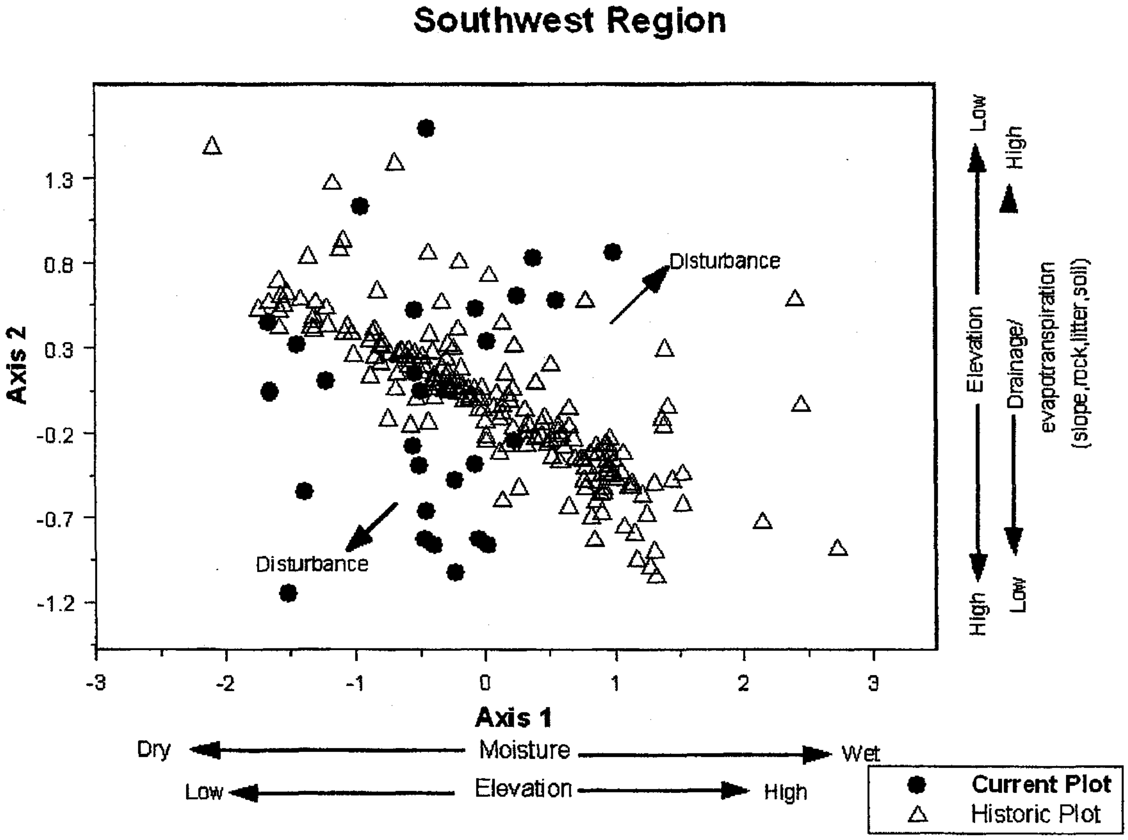


Figure 1-7: Non-metric multidimensional scaling of species frequency matrix for southwest region. n=222. # species=440. Axis 1: R^2=0.85; Axis 2: R^2=0.10. Orthogonality=63.8%. Stress=10.716.

bias, composition changes associated with moisture variables may be slightly skewed in the southwest NMS.

Like the south region, this region was drier than normal for most of the current sampling year. However, it did receive almost normal precipitation in the summer of 2002 at low elevations. Mean temperatures were comparable to the historic sampling period and the 30-year mean for all seasons except the fall.

Of all the ecoregion analyses, the southwest region had the least separation between historic and current plots in both the similarity analysis and in the NMS. Covariance among the axes of the NMS was also highest among the ecoregions (orthogonality=64%). The high degree of covariance and the low explanatory power of axis 2 (R^2=0.10) made it difficult to determine why current plots were distributed on the fringes of the main historical distributions in Fig. 1-7. No specific mechanism for the separation was apparent from linear regression, but both current and historic plots located out from each side of the main diagonal axis of historic plots seemed to have proportionally higher combinations of introduced and annual species that were characteristic of disturbance, including *Centaurea biebersteinii* DC *(C. maculosa)*, *Bromus tectorum* L., *Cirsium undulatum* (Nutt.) Spreng., *Polygonum douglasii* Greene and *Melilotus officinalis* (L.) Lam.

The compositional trends for this region include:

1. A significant increase in introduced species from 3% to 9% in 30 years (Table 1-1).
2. A significant increase in annual species at the expense of perennials (from 2% to 11%).

3. An increase in moss and lichen coverage from 0% to 10%. (note: this may be an artifact of increased awareness on the importance of cryptogamic crusts in these communities now so they were measured separately during recent sampling).
4. An increase in bare soil and decrease in litter (Table 1-1), but no significant changes in cacti or other succulents.
5. An increase in most grazing indicators (Table 1-1). Few of the increases are significant within the limits of this study, however. Decreasers, which should decline under grazing, have also increased in frequency.
6. Members of *Poaceae*, in general, increased 5% over time.
7. Overall richness and diversity indices have remained the same over the 30 years.

The most important change factors in this region appear to be the dry conditions, the compounding effects of five years of drought, and the increases in introduced species. At this spatial scale, neither Wilcoxon comparisons nor correlations with NMS axes suggest that grazing has had detrimental effects on bunchgrass communities since 1971; but it is unclear how much the grazing effects are masked by the dominant climatic and soil factors along axis 1 like they were in the western Montana NMS.

Northwest ecoregion change patterns

Although many of the historic plots in the northwest region were located in relatively close spatial proximity to the current plots that were sampled in the National Bison Range, current and historic plots were completely separated in ordination space along both axes (Fig. 1-8). The climatic differences between the two time periods were also distinctly different. During 2002 sampling, the region was warmer and drier than historic conditions for all seasons. Temperatures were also higher than historic sampling and normal means during the growing season (Fig. 1-5).

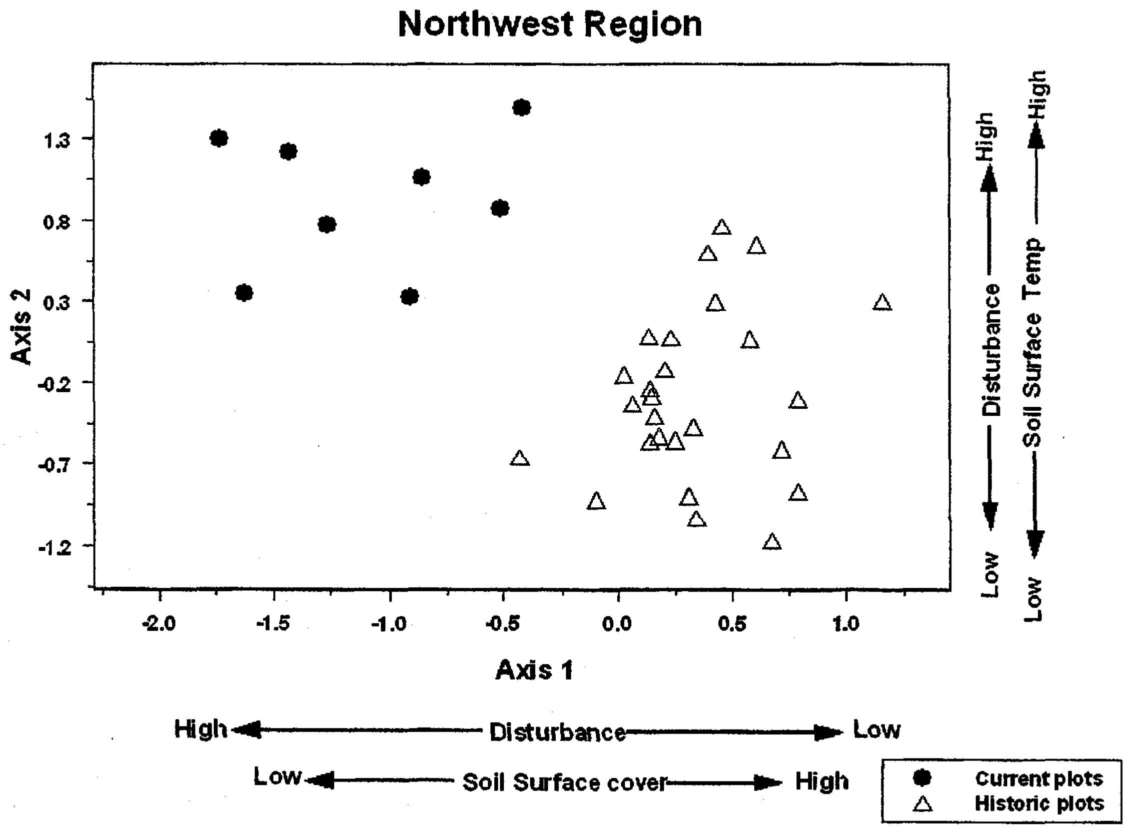


Figure 1-8: Non-metric multidimensional scaling of species frequency matrix for northwest region. n=34. # species=151. Axis 1: R^2=0.63; Axis 2: R^2=0.29. Orthogonality=69.3%. Stress=10.376.

The trends within these communities over the past 30 years include:

1. An overall increase in bare ground from 2% to 19% correlated with a decrease in vegetation cover and litter production (Table 1-1). These surface characteristics were highly correlated with differences along NMS axes 1 (bare ground R2=.32 on NMS axis 1) and NMS axis 2 (bare ground R2=0.35 and litter R2=0.68).
2. An increase in the frequency of annuals to comprise up to one-third of plot species. Linear regression showed that annual species correlated significantly with plot distribution along both NMS axis 1 (R^2= 0.23) and NMS axis 2 (R^2= 0.50).
3. A significant decline in perennial species, especially bunchgrasses, from 80% to 60% (Table 1-1).
4. An increase in non-native species from 11% to 19%. This region has higher proportions of introduced species than any other ecoregion in western Montana.
5. A decrease in grazing indicators with time, but most of the declines were not significant within the criteria of this study. Annual invader grasses increased the most, including *Bromus tectorum*, *Aristida purpurea* Nutt., *Apera interrupta* L., and *Poa compressa* L..
6. Overall, the members of *Poaceae* increased significantly over time because of invader grasses; but the increase has been at the expense of more palatable native perennial grasses and perennial forbs in the

Asteraceae and *Brassicaceae* families, which have each declined about 5%.

7. Diversity measures were unchanged. The mean number of species per plot is essentially the same after 30 years even with the increase in non-native species.

The differences in plot distributions in this ecoregion correlated almost exclusively with disturbance factors, not with climatic variation. Individually, many of the trends listed above would be consistent with climate warming, prolonged drought, or grazing. However, the correlations with grazing variables, the decline in perennial bunchgrasses, and the dramatic increase in introduced species suggested that disturbance or grazing may have been the most important driver of change in this ecoregion (Appendix B).

North ecoregion change patterns

Interpretations of change patterns for the northern ecoregion were complicated by a shift in the dominant NMS axis to axis 3 instead of axis 1 (Fig. 1-9), latitudinal effects (R^2=0.26, $p<0.001$) that could mask some changes due to time, and a disproportionate number of current plots compared to historic plots that could bias the Wilcoxon tests. Current plots covered the full extent of the eastern portion of the park, but the majority of historic plots were concentrated in the southern portion (Fig. 1-1). Several of the historic plots at the extreme upper range of NMS axis three were actually sampled just outside the park boundary in 1970, which probably have skewed the composition comparisons slightly toward more disturbed conditions than would have been present in Glacier

National Park alone; but field notes for the plots did not highlight any unusual disturbance patterns that were not also present in other sample locations within the park. Climatically, the area experienced less precipitation and higher temperatures than normal for the growing season, but conditions were comparable to those in the 1970s (Fig. 1-5).

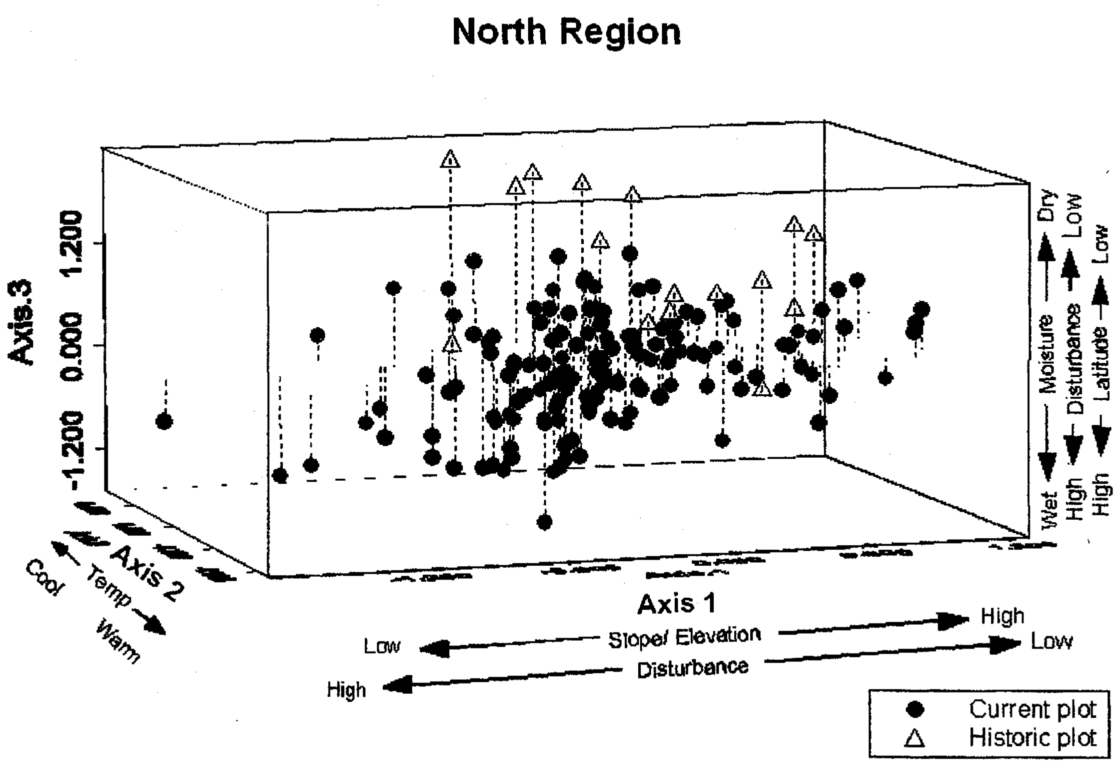


Figure 1-9: Non-metric multidimensional scaling of species frequency matrix for north region. n=163. # species=364. Axis 1: R^2=0.19; Axis 2: R^2=0.16; Axis 3: R^2=0.47. Orthogonality: NMS axis 1 vs. 2=99.8%; 1 vs. 3=94.4%; 2 vs. 3=99.9%. Stress=16.94.

The dominant trends for the species-rich north include:

1. A decrease in exposed rock and an increase in surface litter over time (Table 1-1).

2. An increase in diversity. Of the three diversity measures tested, those sensitive to richness increased significantly over time and those sensitive to evenness decreased (Table 1-1).
3. An increase in non-native species over thirty years. Correlations with introduced species were highly significant along NMS axis one (R^2=0.50) and axis three (R^2=0.31). Invader grasses were also highly correlated on the same axis (R^2=0.39 and 0.29, respectively).
4. An increase in shrubs and forbs, including significant increases in *Rosaceae* (+5%) and *Asteraceae* (+3.8%). Shrubs that are grazing indicators have not changed significantly, but general shrub frequency has increased in the area (Table 1-1).
5. A decrease in species of *Poaceae* of 12%.
6. A reduction in decreaser grasses that correlated with plot distribution along NMS axis 3 (R^2=0.19), suggesting that grazing has had an effect on bunchgrass communities in Glacier National Park over 30 years.

The change patterns and their correlations with plot distributions in ordination space suggest that an influx of non-native species and the effects of grazing were the two dominant factors driving community change in this region (Fig. 1-9, Appendix B). In contrast to the south, the north region shows little evidence of composition change due to climate fluctuation. Although total precipitation declined for all seasons since 1970, the historic plots were actually distributed in the NMS counter to the locations where they would be expected if climate alone were controlling their distribution. Historic plots are located at the driest end of the moisture gradient instead of in a wetter portion (Fig. 1-9). They do, however, fall at the cooler end of the temperature gradient on NMS axis 2 where they would be expected if warming alone were determining their position. If climate warming is affecting western Montana vegetation, it is not affecting all regions to the same degree and the effects of climate change in the north lag behind other regions.

Paired – plot change patterns

For sites that were located within five kilometers of each other and analyzed as paired plots, the comparisons show many of the same compositional trends that were present within the individual ecoregions. Introduced species and shrubs (if present) generally increased in frequency with time. Depending on where the paired-plots were located, some species of grasses decreased or disappeared while others (mainly invader grasses) increased considerably in frequency. Of the many species investigated in this study, there was no one species that did not move in or out of a community in at least one of the regions, including *P. spicata* or the fescues that were the study's focus. At each of the paired-plot sites, the gains and losses of different species over time were numerous, but each location also had a core group of grass and forb species that persisted even after 30 years. These persistent species differed at each location, and not all were native species.

Discussion

Change is inevitable in any plant community. Both Clements (1916) and Gleason (Gleason 1926) recognized the inevitability of change even if they could not agree on its form or direction. Over the past century, scientists have come to realize that many factors contribute to plant-community change, and that these factors may be unique to a particular region or even a particular ecosystem (Bartlein *et al.* 1997, Weltzin *et al.* 2003). Deciphering change patterns and the factors driving change in the bunchgrass communities also depends on spatial perspective.

When communities are examined at the western Montana scale, they project contrasting perspectives of change – from dramatic to undistinguishable. Significant changes in family dominance on the landscape scale has changed not only composition, but structure within these communities (Fig. 1-2). The changes are not uniform across the entire landscape, however, and impressions of trends in family dominance can be misleading if they are not examined at smaller spatial scales, such as the trends in *Poaceae* in this study. Alternately, differences in the community composition that can be attributed specifically to time are virtually masked in both the Wilcoxon tests (Table 1-1) and the NMS (Fig. 1-3) by topographic and climatic differences over the large geographic area.

At the ecoregion scale, the effects of topography and climatic variations are mitigated and changes due to time are more pronounced. Each region shows unique change patterns and varying degrees of change in the proportions of lifeforms, plant origin, dominant life cycles and trends in diversity after 30 years (Table 1-1). From the ecosystem perspective, communities have not changed in a clear, singular trend across the state. The south has patterns showing decreased diversity, but increased frequencies of xeric species and shrubs. The southwest has significant increases in annual and non-native species but little change in overall diversity measures. The northwest has experienced an influx of annual, non-native species and a decrease in desirable species for grazers. The north has gained non-native species, decreased desirable grazing indicators, increased shrub cover, and increased in diversity over time. These changes all suggest that bunchgrass communities are very dynamic ecosystems that have been affected by several different change processes during three decades.

At the smallest spatial scale examined in this study (i.e. paired-plots), the bunchgrasses communities appear even more dynamic than at the ecoregion scale. Each community has a small stable core group of species that persist after three decades, but up to 55% of its members have moved in or out of the community at some time during the interval. Fuhlendorf and Smeins (1996) found similar trends toward increased variation and decreased stability at the local scale in the semi-arid grasslands of Texas.

Inferring process from pattern in ecological communities has sparked debate since successional theories were first proposed. Clements (1916) and Gleason (1926) each explained the patterns they observed differently; and both based their explanations on natural biotic and abiotic processes (Cale 1989). During the past 30 years, a variety of natural processes have affected these bunchgrass communities and each one's importance to compositional change has varied across the landscape. As suggested by Knapp (2001), these grasslands are sensitive to climatic change - and climate warming appears to directly correlate with change in the south region. Not only has the temperature increased and precipitation declined, but the shrub invasion in this region can also be tied to climate warming (Van Auken 2000). Compositional patterns may reflect the influence of climate because moisture and temperature factors control distribution of plots along the dominant axis (Figs. 5, 6, and 8). Only in the northwest, where the effects of grazing and introduced species dominate change, is the NMS not obviously controlled by climate (Fig. 1-8). The importance of non-native species to driving vegetation change is also well known (LeJeune & Seastedt 2001, Mack 1989, Stohlgren *et al.* 2003); and introduced species are very important to explaining the change patterns in the Montana bunchgrass communities. All regions have a disturbance gradient in NMS that reflects increases in the proportion of introduced species, or a combination of grazing and introduced species effects (Figs. 5-8). Introduction of non-native species does seem to be consistent with the diversity of each community. The species-rich north has had a significant increase in non-native species over time while introduced species are not as significant to change patterns in the comparatively species-poor south, which supports work by Lonsdale (1999) and Stohlgren (2003).

Grazing has had mixed effects on the ecoregions even though overall grazing pressure has increased in most areas of Montana during the past 30 years. In the south, which includes Yellowstone National Park, bison herds in the park have increased from 713 in 1971 to 3,899 in 2002 (Wallen 2004) and actual observed elk in the northern winter range have increased from 8,215 in 1971-72 to 11,969 in 2001-02 (White 2004); but grazing indicators show minimal differences from past conditions (Table 1-1). Trends are the same for the southwest region, which has had three- and four-fold increases in ungulate populations over the same time interval (Montana Department of Fish Wildlife and Parks 2003) without much effect on grazing indicators. However, in the northwest region, which includes the National Bison Range, grazing indicators suggest bison and ungulate populations have preferentially changed community composition and diversity. Changes in management of the bison herd to a less frequent herd rotation (Willard 2003b), along with increases in herd size, are probably responsible for the diversity changes and for the striking differences between historic and current plots shown in Fig. 1-8. The north region has the widest array of significant grazing indicators found in any of the ecoregions (Table 1-1, Appendix B). Although Glacier National Park currently does not allow domestic grazing, the park has a long history of domestic livestock use on its east-side grasslands both before and after the park was created (Shea *et al.* 2003). Today, the park sustains deer, elk, and bighorn sheep populations; but livestock trespass over park boundaries into the park is still a serious problem (Shea *et al.* 2003). These factors all contribute to the highly significant differences in grazing indicators over time (Table 1-1 and Appendix B) and the strong disturbance gradient along NMS axis 3 in Fig. 1-9. Harding (1998) and Leach & Givnish (1996) proposed that, in some ecosystems, historic land-use practices may be better predictors of current biodiversity and ecosystem dynamics than current management practices. In the north region, the residual effects of historic grazing are still evident on the landscape and may partially explain why historic plots are not as separated from current plots in the NMS as they are in the other regions.

While the comparisons between the historic and current plots do indicate general trends in species abundance over the past 30 years, the two-points-in-time approach has several limitations. The species changes between the 1970s and 2002 are relative changes; not absolute trends. Some species obviously increase overall more than others but each may differ in their change rates; thus, making absolute increases appear as decreases in the analyses. This limitation can be overcome with more analyses on the absolute changes in species and families at the different spatial scales. The comparison of the historic class of bunchgrasses with the current class of bunchgrasses also suffers from the inability to go back to exact sites to measure change (this approach will be covered in chapter 2). There are differences on the landscape in community composition that can not be overcome by limiting analyses to ecoregions with similar climate, vegetation, and land-use history. The class comparisons in this study, however, indicate several types of changes that have occurred within the same general areas in the past 30 years. More detailed analyses at the local scales are needed to determine how well the two-points-in-time approach assesses the long-term trends.

Clearly, the sensitivity of certain ecosystems, like grasslands, to climatic variation and the substantial effects of increased non-native species and grazing demands on plant communities over the past century could not have been envisioned in the early 1900s when succession theory was born. Ecologists also could not have predicted the impact of human activity on climate when they were developing models of succession that required stable climates for simplicity. With only two points in time, it is impossible to determine if some species have reached levels of environmental or biotic stress that make their trends irreversible (thresholds), if some communities react in different ways to the same external stimuli in the different regions (multiple pathways), or if the communities have existed in several different stable states during the 30 years (state and transition). The perspectives examined in this study do show, however, how important spatial scale is to interpreting change patterns. The patterns may vary with area, but the bunchgrass communities of western Montana show how important contemporary processes like invasion and climate fluctuations are to compositional trends and how rapidly community change has occurred in this northern ecosystem.

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Appendix A: Nomenclature information for species cited

Code	**Current Name** [1]	**Synonyms**
ApeInt	*Apera interrupta* (L.) Beauv.	*Agrostis interrupta* L.
AraTha	*Arabidopsis thaliana* (L.) Heynh.	
AriPur	*Aristida purpurea* Nutt.	*A. longiseta* Steud
BouGra	*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths	
BroTec	*Bromus tectorum* L.	
CalCan	*Calamagrostis canadensis* (Michx.) Beauv.	
CenBie	*Centaurea biebersteinii* DC.	*C. maculosa* auct.non Lam
CirUnd	*Cirsium undulatum* (Nutt.) Spreng.	
DesCae	*Deschampsia caespitosa* (L.) Beauv.	
EquArv	*Equisetum arvense* L.	
FesAlt	*Festuca altaica* Trin.	*F. scabrella* Torr.ex Hook.
FesIda	*Festuca idahoensis* Elmer	
GalBor	*Galium boreale* L.	
GutSar	*Gutierrezia sarothrae* (Pursh) Britt. & Rusby	
JunBal	*Juncus balticus* Willd.	
KraLan	*Krascheninnikovia lanata* (Pursh) A.D.J Meeuse & Smit	*Ceratoides lanata*
KraLan	*Krascheninnikovia lanata* (Pursh) A.D.J Meeuse & Smit	*Eurotia lanata* Pursh Moq.
MelOff	*Melilotus officinalis* (L.) Lam.	
OpuPol	*Opuntia polyacantha* Haw.	
PoaCom	*Poa compressa* L.	
PolDou	*Polygonum douglasii* Greene	
PseSpi	*Pseudoroegneria spicata* (Pursh) A. Love	*Agropyron spicatum* Pursh

1 Current nomenclature standardized to Kartesz 1998.

Appendix B: Linear regression R^2 and significance values on all NMS axis scores

	South Region						Southwest Region				Northwest Region			
	Axis 1	p	Axis 2	p	Axis 3	p	Axis 1	p	Axis 2	p	Axis 1	p	Axis 2	p
NMS axis R^2	0.62		0.14		0.10		0.85		0.10		0.63		0.29	
Topographic Variables														
Elevation	0.54	**[1]	0.05		0.00		0.41	**	0.23	**	0.00		0.04	
Slope %	0.04		0.13	[3]+	0.00		0.02	+ m	0.06	** m	0.03		0.01	
Latitude	0.13	+	0.36	**	0.01		0.01		0.01		0.26	**	0.33	**
Surface Characteristics														
Bare Soil	0.45	**	0.01		0.13	+	0.32	**	0.15	**	0.32	**	0.04	**
Surface Rock	0.30	**	0.05		0.25	**	0.12	**	0.21	**	0.01		0.14	+
Surface Litter	0.28	**	0.13	+	0.41	**	0.12	**	0.03	+	0.35	**	0.68	**
Surface Moss/Lichen	0.03		0.07		0.14	+	0.02	+	0.00		0.07		0.15	+
Composite Variables														
Annuals in stand	0.00		0.02		0.03		0.02	+	0.01		0.23	**	0.50	**
Perennials in stand	0.01		0.00		0.09		0.03	*	0.00		0.14	+	0.57	**
Introduced species	0.00		0.00		0.24	**	0.02		0.01		0.12	+	0.20	*
Diversity Variables														
Shannon Index	0.50	**	0.00		0.16	*[2]	0.39	**	0.30	**	0.06		0.02	
Simpson's Index	0.46	**	0.00		0.11	+	0.31	**	0.28	**	0.07		0.00	
Lifeform Variables														
Graminoids	0.05		0.06		0.06		0.19	**	0.09	**	0.00		0.09	
Deciduous shrubs	0.26	**	0.02		0.24	*	0.38	**	0.27	**	0.10		0.00	
Grazing Variables														
Invader grass	0.02		0.00		0.15	*	0.01		0.02	+	0.14	+	0.43	**
Invader forb	0.01		0.00		0.05		0.13	**	0.10	**	0.00		0.01	
Invader shrub	0.07		0.00		0.19	**	0.16	**	0.07	**	0.00		0.01	
Decreaser grass	0.01		0.04		0.12	+	0.05	**	0.11	**	0.01		0.08	
Decreaser forb	0.18	*	0.09		0.15	*	0.02		0.01		0.04		0.21	*
Decreaser shrub	0.10	+	0.00		0.04		0.02		0.02	+	0.01		0.00	
Increaser grass	0.22	**	0.01		0.02		0.08	**	0.00		0.11		0.06	
Increaser forb	0.35	**	0.01		0.01		0.23	**	0.12	**	0.02		0.11	
Increaser shrub	0.20	**	0.04		0.07		0.29	**	0.25	**	0.10		0.00	

F-stat p values:

[1] ** $p < 0.001$

[2] * $0.001 < p < 0.01$

[3] + $0.01 < p < 0.05$

[m] missing values

Appendix B: Linear regression R^2 and significance values on all NMS axis scores (continued)

	North Region						Western Montana			
	Axis 1	p	Axis 2	p	Axis 3	p	Axis 1	p	Axis 2	p
NMS axis R^2	0.19		0.16		0.47		0.82		0.16	
Topographic Variables										
Elevation	0.16	**	0.03	+	0.00		0.01		0.00	
Slope %	0.12	**	0.02	+	0.05	*	0.12	** m	0.15	** m
Latitude	0.00		0.03	+	0.26	**	0.55	**	0.48	**
Surface Characteristics										
Bare Soil	0.07	**	0.02		0.02		0.32	**	0.34	**
Surface Rock	0.01		0.07	**	0.17	**	0.20	**	0.22	**
Surface Litter	0.01		0.09	**	0.17	**	0.45	**	0.44	**
Surface Moss/Lichen	0.01		0.01		0.10	**	0.05	**	0.09	**
Composite Variables										
Annuals in stand	0.01		0.03	+	0.03	+	0.00		0.01	
Perennials in stand	0.01		0.04	+	0.04	+	0.02	**	0.05	**
Introduced species	0.50	**	0.03	+	0.31	**	0.03	**	0.01	*
Diversity Variables										
Shannon Index	0.04	*	0.30	**	0.01		0.45	**	0.47	**
Simpson's Index	0.04	*	0.32	**	0.02		0.36	**	0.37	**
Lifeform Variables										
Graminoids	0.10	**	0.16	**	0.19	**	0.31	**	0.34	**
Deciduous shrubs	0.19	**	0.04	*	0.00		0.12	**	0.15	**
Grazing Variables										
Invader grass	0.39	**	0.05	**	0.29	**	0.02	**	0.01	*
Invader forb	0.00		0.06	**	0.01		0.08	**	0.08	**
Invader shrub	0.03	**	0.01		0.00		0.41	**	0.41	**
Decreaser grass	0.07	**	0.06	**	0.19	**	0.03	**	0.03	**
Decreaser forb	0.05	*	0.02		0.00		0.00		0.00	
Decreaser shrub	0.03	+	0.01		0.02		0.01	+	0.01	
Increaser grass	0.00		0.01		0.47		0.29	**	0.30	**
Increaser forb	0.00		0.12	**	0.33	**	0.25	**	0.32	**
Increaser shrub	0.27	**	0.07	**	0.01		NA		NA	

F-stat p values:

'**' $p < 0.001$

'+' $0.01 < p < 0.05$

'*' $0.001 < p < 0.01$

'm' missing values

CHAPTER 2

Communities in motion: The nature of change within intermountain bunchgrass communities at site and regional scales

Abstract:

For over two decades, *Pseudoroegneria* and *Festuca* bunchgrass communities across western Montana have been part of a natural experiment that has quietly recorded their responses to disturbance and fluctuating climate. In this study, I focus on how these communities have changed during the past 20 to 50 years under these non-experimental conditions. I use time-series data from historical monitoring records to examine species stability within them and how their change patterns correlate with fire, grazing, non-native species, and climatic fluctuation. Patterns are examined at the site and ecoregion spatial scales.

At the site scale, each community had a unique compositional history. Forb and grass species moved into and out of the communities often. Even the frequency of focal grasses varied significantly between sample periods. The transient nature of the species at this scale gave the impression that the communities were in a constant state of flux. At the ecoregion scale, each area had different long-term trends in diversity and lifeform proportions. Richness decreased in most ecoregions since the 1970s. Grass coverage decreased since 1958 in the south ecoregion, but shrub and forb coverage increased. Alternately, the northwest area increased grass coverage significantly, but forb frequency decreased. The southwest decreased in forbs and shrubs, but trends in grass frequency were mixed.

I tested all measured disturbance and environmental variables concurrently and found that climatic variables correlated most significantly with community change at all spatial scales. The relative importance of temperature and precipitation, however, differed among ecoregions. Fall and winter precipitation and winter and spring mean temperatures correlated best with community change. Non-native species correlated significantly only in the southwest ecoregion (t=2.0 to 3.3).

The effects of grazing on community change were assessed in a case study area with big-game exclosures. No lifeforms trends were attributed strictly to grazing. The trends inside and outside the exclosures were in the same directions and differed only in relative amounts.

The stability and change patterns in these communities were consistent with successional models based on non-equilibrium, but near-linear patterns did exist. The most common change patterns fit those expected in the state-and-transition and persistent non-equilibrium models.

Keywords: community dynamics, difference matrix, *Festuca spp.*, facies diagram, historic vegetation, path analysis, plant functional type (PFT), *Pseudoroegneria*, successional models, temporal change, time series

Introduction

> ***"What endures on the grassland is motion. In the long view, in the short view, on micro and macro site, the grassland is a place of motion."***
>
> -Richard Manning (1995:47)

The ebb and flow of plant species on the landscape creates many unique communities in space and time. Each of these communities experiences its own history, which is shaped by the interrelationships of species within it and by the effects of environmental stresses upon it. Modeling how these communities respond to internal and external stresses over time has been the topic for passionate debates and on-going arguments about the nature of plant community change for almost a century. At the heart of the problem is the lack of sufficient long-term historic data to define and compare actual change patterns from these communities with the change patterns predicted by theoretical succession models.

Successional models built upon grassland research have been particularly controversial. From his work in Great Plains grasslands, Clements (1916) first proposed that plant communities changed in predictable, linear directions because the species that comprised them were so highly integrated, tight-knit, and interrelated that they acted together through time as one biological unit. At the other extreme, communities were envisioned as totally random occurrences of species that change in unpredictable ways solely in response to environmental stresses (Gleason 1926). Today, the search for the nature of change in different types of plant communities is even more relevant because western ecosystems are experiencing unprecedented environmental stress and changes in competitive interactions that affect both community membership and function. Exotic species invasions, global climate change, fragmentation of the landscape, and rapid increases in human population are affecting the physical environment and the biotic relationships among native grassland species at unprecedented rates. Grassland communities react to each of these pressures in different degrees depending on their history, diversity, and spatial location.

Worldwide, the drivers for grassland change are quite diverse because these ecosystems are sensitive to the interactions of so many environmental and biological factors (Copeland 1992, Heady & Child 1994). Species compositions of grasslands are now known to vary with both the timing and amount of precipitation and temperature (Alward *et al.* 1999, Coffin & Lauenroth 1996, Fay *et al.* 2002, Kaiser 2001). Temperate grasslands are also sensitive to the timing and intensity of grazing (Collins *et al.* 1998, Fuhlendorf *et al.* 2001, Heady & Child 1994). The ultimate effects of grazing in each community depend as much on the evolutionary history of each community (i.e. whether they developed under conditions of heavy herbivory) as it does on the fluctuations within current grazing regimes (Mack & Thompson 1982). The timing and intensity of burning also dramatically affect grassland composition and species' dominance. Like grazing, the response of grassland to burning is dependent on its historical fire regime and the timing of the disturbance (Bailey & Anderson 1978, Jacobs & Schloeder 2002, Redmann *et al.* 1993). Because the relative effects of each of these environmental factors differs by community, determining whether any grassland is undergoing directional change or responding to short-term fluctuations in environmental factor(s) requires long-term monitoring records that put the short-term variations due to all these sensitivities into wider temporal perspectives.

In this paper, I examine the nature of change in dynamic temperate grasslands in the northern Rocky Mountains, USA. These grasslands are unique because they exist in cool, semi-arid northern latitudes within relatively natural settings that have not been highly fragmented by increases in human population nor manipulated in experimental studies. I used long-term monitoring records to examine the patterns of species dynamics over multiple decades within the *Pseudoroegneria spicata* (Pursh) A. Love, *Festuca idahoensis* Elmer, and *Festuca altaica* Trin bunchgrass communities of the intermountain regions of western Montana. Several governmental agencies have monitored these grasslands on permanent study plots for at least two decades. Originally, the data were collected to monitor the trends in vascular and non-vascular plant species in habitats used by wildlife or domestic livestock. The historic data sets now present a detailed picture of the temporal change that has occurred in the grassland communities of this northern ecosystem over several decades in the absence of experimental manipulation. They record changes within communities that have been affected to varying degrees by all of the mechanisms known to affect grassland change, including climatic fluctuations, grazing, burning, and invasive species, so the relationship of these factors to change in this specific community can be correlated. The Montana data sets also span an area large enough to examine the trends in community composition across environmental gradients at a variety of spatial scales over time.

Within this analysis, I address the following questions: What is the general form of change within the bunchgrass communities? Is there directionality to the fluctuations in community composition of the western Montana grasslands in response to environmental change? Do lifeforms within the community have distinctive responses to environmental change? If so, do the fluctuations fit any change patterns that would be predicted by current successional models? Does the pattern of change differ between the plot and regional scales? What are the principle drivers of compositional change in western Montana's bunchgrass communities?

Methods

Study area

The study area is located in the northern Rocky Mountains between 44.8° and 47.4° N latitude and 110.2° and 114.2° W longitude. The grasslands occupy valley bottoms and foothills at elevations of 825 to 2250 meters and occur across a full spectrum of aspects. The study area receives an average of 550 mm precipitation annually. West of the continental divide, the climate is a modified north Pacific coastal type; east of the divide, the climatic characteristics are continental (Western Regional Climatic Center 2002).

The study sites are located in relatively intact landscapes that have not been highly fragmented by urban expansion. The sites have never been cultivated like prairies in other parts of the United States, but they have been quite heavily grazed during certain periods of Montana history. They are not subjected to extensive fertilization or other chemicals, except for minor weed control. Most are now located within protected areas or are parts of grazing allotments that are strictly regulated by federal agencies.

Data sets

The data sets consist of monitoring data from four different agencies that manage Montana's grasslands. During the past 50 years, the four agencies have monitored their acreage using several different sampling protocols. In Yellowstone National Park and on the U.S. Fish and Wildlife Service's National Bison Range, sites have been monitored since the late 1950s and 1960s using 30 m (100 ft) permanent line-intercept transects. Every species or abiotic variable (e.g. soil, rock, litter, etc.) encountered along the line at 0.33 m (1 ft) intervals was tallied to obtain a data set with 100 elements. The Bureau of Land Management (BLM) and the Montana Department of Fish, Wildlife and Parks (FWP), however, monitored their plots using methods developed by Daubenmire (1959). For each species or abiotic variable within a 20 x 50 cm microplot, the percent coverage was visually estimated. Multiple microplots were arranged along a permanently marked 30 m (100 ft) or 66 m (200 ft) transect. The arrangement of the microplots along each transect varied by agency. The total number of microplots also varied from 20 to 30, depending on the agency.

All repeat sampling for each site followed the same sampling protocol for the entire monitoring period, which was specified in each agency's files. Sample timing was matched as closely as possible to the previous sampling, although many sites varied within two weeks on either side of a mean sampling time. The number of repeat samples at each site varies with location. Many of the sites were measured by the same person several years in a row. Although every attempt was made to duplicate sampling protocol and accurately capture all species at each site, changes in sampling personnel over the years could have affected impressions of change. Experience in forb and grass identification varied among personnel, as well as over the course of a career. Even with each end of a transect marked by stakes, slight variations in the position of the tape between the markers or in the positions of the microplots along the line could also affect impressions of change, especially random change patterns among sample periods.

Only 50 sites were selected to test for compositional change (Fig. 2-1). First priority in site selection was given to sites that had the most repeat sampling over time. Minimum sampling was three times in 30 years. The data sets had to include detailed information on grass, forb, and shrub species and cover; and estimates of substrates (i.e. rock, bare soil, moss, lichen) for all sample periods. Site selection was further refined to ensure that the sites were well-spaced on the landscape and covered as much of the study area as possible. Sites with any irregularities in the sampling data, such as discrepancies between sampling directions on site maps and transect descriptions, were discarded. Sites that had fluctuations in sample timing of more than a month were also eliminated. Sites at two areas required choosing which transect according to random selections. At the National Bison Range, three to five line-intercepts were clustered at each location and all were potentially available to use in this study. A randomly selected transect number was used to select the representative transect for each location. In Yellowstone National Park, one transect was randomly chosen to represent communities inside big-game exclosures for a total of six replicates. One transect was chosen to represent the communities outside of each enclosure for a total of four replicates. Together the paired transects were used to test the effects of grazing on community change over time.

To evaluate the effect of scale on impressions of change, the data sets were separated into four geographic regions (Fig. 2-1). The regions were based on the ecoregion designations of Woods et al. (1999). Each ecoregion has similar climatic, geologic and soil conditions, so variations due to these factors are minimized within the subdivisions, making temporal changes more evident in each region (see chapter 1). Ecoregion subdivisions also kept all data collected within the respective region under the same sampling protocol. For the south and northwest regions, the data were collected along line intercepts; in the west and southwest, communities were described from microplots.

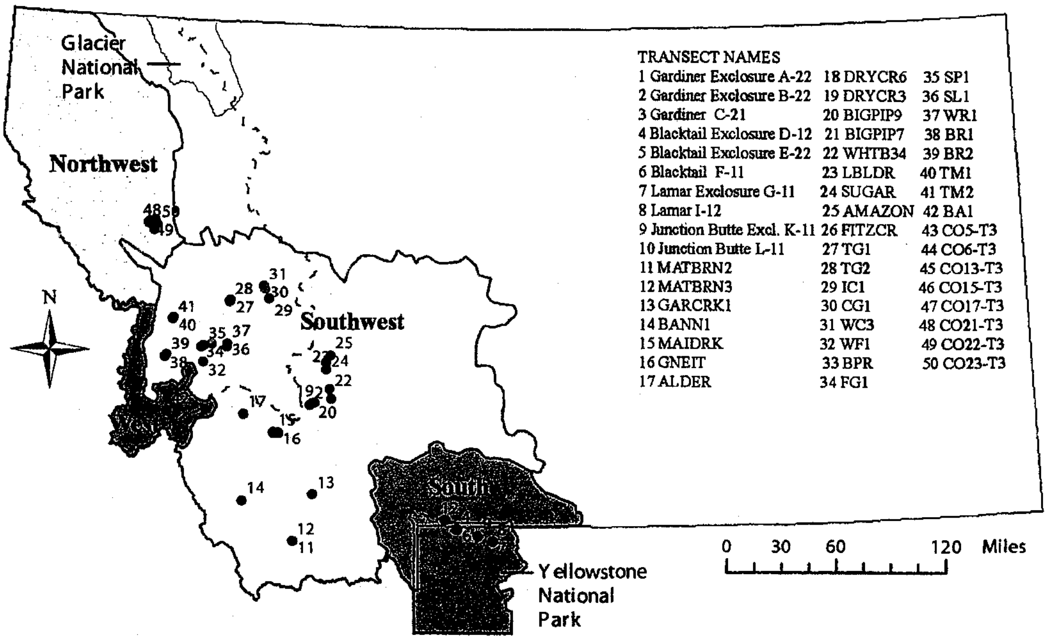


Figure 2-1: Location of sites used in site-level analyses and their ecoregions (based on Woods et al. 1999) within the landscape. Dashed line is continental divide.

Nomenclature

During the 30 years covered by this study, nomenclature changed dramatically. All nomenclature was standardized to the currently accepted genus and species listed on the

Biology of North America Program web site (Kartesz 1998). Origin designations for introduced species in Montana followed Rice (2004). Lifeform and life history designations followed Hitchcock and Cronquist (1973).

Data analysis

All species and substrate variables were standardized to percent frequency of occurrence to make them comparable between the different sampling protocols in each ecoregion. For line transects, the tallies of species and substrate variables were already in frequency percent format from the collection method. For the microplot data, frequency percent was calculated by counting the number of times a species occurred within the microplots and dividing by the total number of microplots used at the site. The southwest region was the only area where two agencies used different numbers of microplots to sample their management areas. Because sample size may affect data analysis in these types of plots (Krebs 1999), a separate analysis was conducted with a test group of sites to determine if frequency percentages differed significantly when 30-microplot data was converted to 20-microplot data. In the 30-microplot data, the last 10 microplots were eliminated for calculations. Eliminating these 10 microplots insured that the entire line was represented in frequency calculations as per the 20-microplot samples. The test group showed the same ebb and flow change patterns as in the 30-microplot data. Some species increased frequency, some decreased, and some remained unchanged. The relative change between years, however, did not change significantly. Minor species loss occurred in some years, including focal grass species. The total cumulative frequency of species within each lifeform changed very little. Because the change-over-time comparisons in this study focus on the site, which were sampled with the same protocols each year, the only analyses where the differences in microplot totals along the transect may affect results are in the full ordinations of the southwest region.

Species fluctuations at site and ecoregion scales

Variations in community composition over time were explored both diagrammatically and statistically. At the site scale, the frequency of each species was diagrammed to scale using facies diagrams like those used in geologic studies. Facies diagrams visually show the actual observed changes in the proportions grass, forb, and shrub species at each site during each sample period, the constancy of individual species, and relative speed of species turnover within these communities. Within each diagram, a single species was considered a facie.. The community was considered composed of all of the species (facies) observed during a sampling.

Statistical changes in diversity, species dominance, and turnover percentages were calculated from queries of the raw data within Access (Microsoft Corporation 2001). Richness was tallied by site and year. Although richness varies with sample area, no rarefaction adjustments were made to the data, because all sites within an ecoregion were sampled by the same method. However, comparisons of richness values between ecoregions should be used with caution because the sampling techniques are so different. Turnover was calculated using richness values between two periods of sampling and by tabulating how often specific species occurred in the historic record. Common species were ranked by (1) the number of times they were present during the sample history and

(2) the total of all frequency percentages of each species. A rank of "1" was given to the most common species by each measure.

Lifeform fluctuations at site and ecoregion scales

The species from the south ecoregion were used in a case study to test whether change patterns that were characteristic of the whole community differed from the change patterns of separate lifeform groups. Each species was classified into the following lifeform types using VTAB Ecosystem Reporter (Emanuel 1999): (a) annual/biennial forbs, (b) perennial forbs, (c) perennial shrubs and sub-shrubs and d) perennial graminoids. The species from the total community and the species of each lifeform group were imported separately into PCOrd (McCune & Mefford 1999) and analyzed for changes through time using non-metric multidimensional scaling (NMS). Raw data frequencies for each species were relativized on row (stand) totals before running NMS. NMS was run using Sorensen's (Bray-Curtis) distance. The ordinations started at six dimensions and iteratively stepped down one dimension per cycle with a step length of 0.20. NMS used 40 runs on raw data for the analyses and 50 runs on randomized data for Monte Carlo significance tests. Multiple tests were run on each ecoregion to assure that a local minimum did not bias the results. In the NMS, no species, whether it was considered rare or common, was eliminated from any analysis based on a set minimum percent coverage as is common practice in many vegetation studies (Rodriguez *et al.* 2003). This ensured that all members of the lifeform "community" were represented through time, no matter how much they varied in frequency, and that the comparisons between the same sites were valid for all intervals. NMS integrated all of the species into a "community" value, which was depicted by a point in the species space of the ordination. The perception of change between any two points in time in the NMS depends on the size and direction of the vectors between each of the plot locations. The connection of consecutive samples with directional vectors indicates how these plots change compositionally during their sampling history compared to others in their ecoregion. In the south ecoregion, lifeform groups from both grazed and ungrazed sites had to be analyzed together to get a meaningful NMS, but the groups were graphed separately to highlight any pattern differences due to grazing. The data structure of the annual/ biennial grouping was too weak to create a meaningful NMS so its NMS is not included in this paper.

Correlation of community change with climate and disturbance factors

Four difference matrices were created for each ecoregion to test whether fluctuations in composition correlated with environmental variables over time. These included a species, climatic, substrate, and origin difference matrix. The **species difference matrix** focused only on the species that changed at each site between sampling periods. A first-difference matrix was created by subtracting the frequency of each species in the initial sampling period **t** from its frequency in sampling period **t+1.** Original (non-transformed) sample data were used in the difference calculations. A second-difference matrix was calculated as the differences in each species between **t+1** and **t+2.** Subsequent difference matrices between sample periods were constructed in a similar manner. If a species did not change between time periods, its value in the species difference matrix was zero. The time series within this study were well-suited to using difference matrices instead of other time-series techniques, such as minimum/maximum autocorrelation factor analysis (Solow 1994), because there were (a) few sampling units compared to other time-series studies (mean for all regions was less than five sampling units within the 30-50 year time frame); (b) highly irregular sampling intervals between sites; and (c) some species that varied collinearly over time.

Because the focus of this study was not on how individual species correlated with climate or disturbance factors but on how the community as a whole was affected by them, NMS was used to integrate all species changes from the difference matrix into a single value that represented a "community" during each sample year. The single value was a point in dimensional space depicted by the NMS axis scores, which identify each community's unique position dimensional space for each sample period. NMS was run within PCOrd using a non-relativized difference matrix analyzed with Sorensen's distance measures starting with six dimensions and stepped down at each cycle as described above. In each NMS diagram, communities with similar changes in frequency and direction of species loss or gain plotted close to each other in ordination space. Only the difference matrix from the northwest ecoregion failed to provide a useful NMS to represent community change. Even though outliers were removed from the difference matrix and the stability criterion for convergence was lowered, the northwest data did not have enough difference in structure to give a meaningful NMS result that could be used to test correlations with either substrate or climatic variables.

One of the challenges of long-term studies is assigning reasonably accurate temperature and precipitation values to monitoring sites that have never had climate monitoring equipment nearby. In this study, I began by collecting historic data from 35 climate stations across western Montana. Maximum (Tmax) and minimum (Tmin) monthly temperatures were aggregated into seasons then averaged to obtain a mean seasonal value for each year from 1958 to 2002. Mean monthly precipitation values were totaled by season for the same years. The seasonal divisions included fall (September - October prior to sampling year), winter (November - March), spring (April - May), and summer (June - August). The resulting climate variables included FallTmin (fall mean minimum temperature), WinTmin, SprTmin, SumTmin, FallTmax (fall mean maximum temperature), WinTmax, SprTmax, SumTmax, FallPrec (fall total precipitation), WinPrec, SprPrec, and SumPrec.

When each year's seasonal climate values were assigned to the 35 climate stations, the values were interpolated to the monitoring plot locations using a new technique developed by Jolly *et al.* (2004) known as the surface observation gridding system (SOGS). In the SOGS process, each of the monitoring sites received interpolated seasonal climate values that were adjusted for each site's unique elevation, slope, aspect and location on the landscape. The resulting SOGS climate values were stored in a database by site and year; which in turn was related to the database storing each site's compositional and substrate data. For a complete description of the SOGS process, its error matrix, and its output format see Jolly *et al.* (2004).

The environmental differences between monitoring samples were summarized within three matrices that were constructed as described above for the species matrix. A **climatic difference matrix** was constructed from the SOGS values by calculating the absolute differences in each temperature and precipitation variable between monitoring periods. After the difference matrix was created, however, Tmax and Tmin were further averaged to create Tave and reduce the number of independent variables for regression analysis. A **substrate difference matrix** focused on the differences in frequency of bare soil, rock, and litter coverage between samplings at each site. An **origin difference matrix** focused on the differences between the total frequencies of non-native species. For each sample year, frequencies of non-native species were totaled within VTAB Ecosystem Reporter (Emanuel 1999).

Path analysis was used to test the strength of correlations between the changes in community composition and the environmental variables. The advantage of using path analysis to test the causal relationships among this specific set of traits as a unit, rather than using multiple regression to test single traits in separate analyses, has been well documented (Li 1975, McCune & Grace 2002, Scheiner *et al.* 2000). In the path models constructed for this study, the changes in community composition were represented by changes in the NMS axes (designated y-variables). The covariance of each y-variable was tested against the absolute changes in bare soil, rock, litter, FallTave, WinTave, SprTave, SumTave, FallPrec, WinPrec, SprPrec, SumPrec, and origin (x variables). Tests were run within LISREL 8.54 (Jöreskog & Sörbom 2003) using maximum likelihood estimations, 250 iterations, and a 0.000001 convergence criterion. Some paths in each model were eliminated if their deletion did not affect the overall R^2 values on each axis but did reduce the degrees of freedom tested within the model. In path analysis, the R^2 value represents the fit of the model as a whole, not the fit of each separate factor to the changes in positions the NMS axes. Path models with good fits to the measurement (raw) data from each ecoregion should have the following characteristics: (a) non-significant chi-square values (i.e. high p values); (b) ratios of chi-square values to degrees of freedom of less than 2.0; and (c) root mean square error of approximation (RMSEA) values of <0.09 (Grace 2003). A non-significant Chi-square value indicates that expected covariance matrix from the hypothesized model does not differ significantly from the covariance matrix created using the actual measured variables.

The covariance of grazing and fire with community change was not quantifiable like the climate and origin variables. For most sites, actual data on grazing regimes and intensity either did not exist or they were extremely difficult to extract from historic records for the time periods required. Qualitative comparisons between grazed and ungrazed sites in the south ecoregion, and burned and unburned sites in the southwest region, were made using the facies diagrams, tabular summaries, and NMS results for lifeform trends.

Comparison of change patterns with current successional models

Many conceptual diagrams exist to describe successional models for plant communities (Ellis & Swift 1988, Laycock 1991, Westoby 1989). However, the way vegetation change manifests itself in n-dimensional ordination space under each model type is not well documented so conceptual diagrams for equilibrium and non-equilibrium models were developed for how each might behave in ordination space (Fig. 2-2a and 2b). The change pathways from the Montana bunchgrass communities were categorized by comparing their pathways to the conceptualized pathways of the models using the following criteria. For linear models, trends had to follow nearly straight lines (Fig. 2-2a); no reverse directions were permitted. For persistent non-equilibrium models (Fig.2-2b:3), the vectors had to cross each other at many different angles, or they had to trend off a previously regular pattern at obtuse angles sometime during the time series. If vectors oscillated around a point in (or area of) species space, the patterns were considered to fall into the state-and-transition pattern or the threshold pattern. For the threshold model (Fig. 2-2b:1), no reversals in direction were allowed after the vectors veered off the oscillation area. Zig-zag patterns could represent either (a) the state-and-transition model (Fig. 2-2b:3) if they oscillated around an area of species space or (b) the deterministic chaos model (Fig. 2-2b:4) if additional information showed that key species reached density limits. Zig-zag vectors, by definition, reversed directions but they had to remain linear and not cross over previous vectors or oscillate around any point. Patterns that did not fit any of these criteria were classified as "other." The "other" classification included patterns that either had too few samples to establish a pattern within the sample history or the patterns were combinations of the above types so they were difficult to classify.

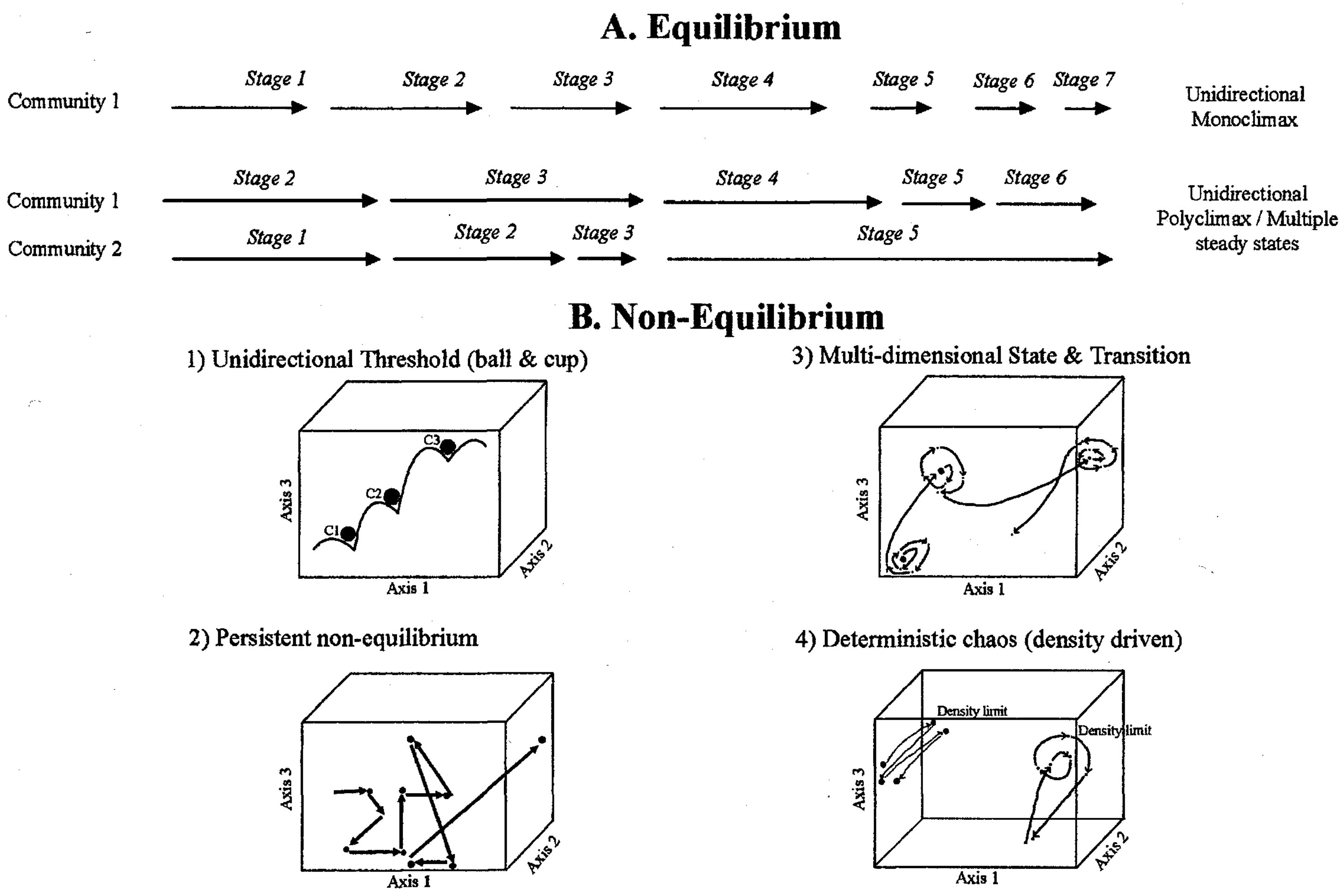


Figure 2-2: Conceptual models of vector movements and directions in ordination space under (a) equilibrium and (b) non-equilibrium successional models.

Results

Historical context for change patterns

During the temporal span of this study, western Montana has undergone significant changes in population and land use, invasion of exotic species, and climatic fluctuation. Population has increased since 1950 in all ecoregions from a low of 0.8 person per km^2 (2.0 per mi^2) in the northwest ecoregion to 3.5 persons per km^2 (9.0 per mi^2) in the west (Fig. 2-3a) (U.S. Bureau of the Census 2000). The same linear increase is apparent in exotic species with 75 to 170 new exotic species documented in the same time period (Fig. 2-3b) (Rice 2004). Total livestock inventory has declined significantly since 1950 (Fig. 2-3c) (U.S. Dept. of Agriculture 2002, U.S. Dept. of Commerce 1952). Sheep inventories have declined the most dramatically from 455,000 animals in 1950 to under 50,000 in 2002. Cattle inventories increased until 1982 then declined to numbers equal to or just slightly greater than the 1950 levels by 2002. Horse inventories declined until 1969, stabilized through the 1990s, but increased significantly in all ecoregions in 2002. Where agencies have tracked wildlife population growth (in Yellowstone National Park and the major game management areas), elk and bison have increased three- to four- fold since 1970 (Montana Department of Fish Wildlife and Parks 2003, Wallen 2004, White 2004). Land committed to farms has remained essentially the same in all ecoregions except for a slight decline in pastureland and woodland in the southwest since 1992 (Fig. 2-3d). Temperature and precipitation have fluctuated considerably since 1950, but mean temperatures appear to have risen slightly since 1980 (Figs. 2.4 and 2.5) (Western Regional Climatic Center 2002). In spite of all of these changes, however, the monitoring sites in this study exist in relatively natural settings compared

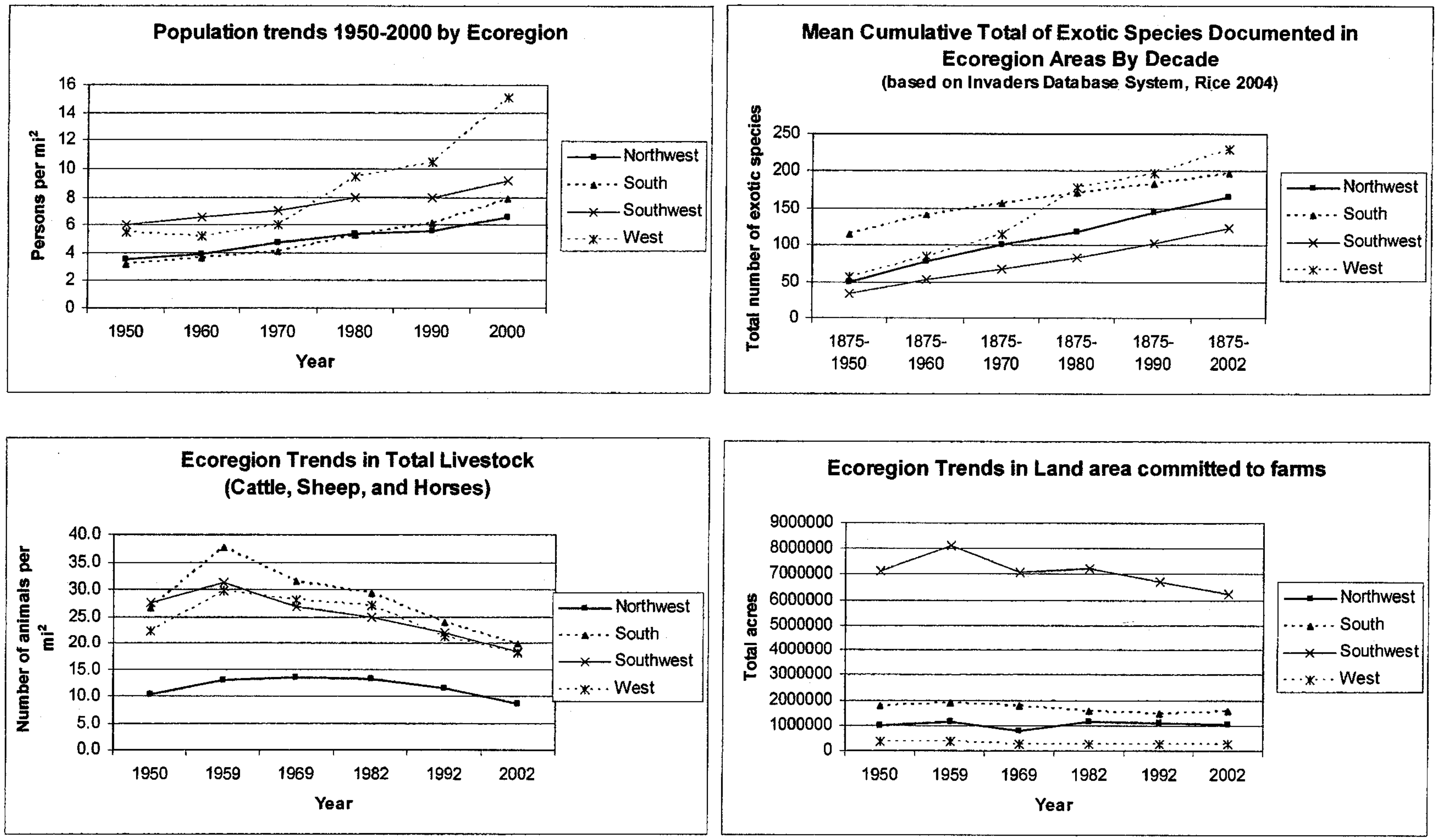


Figure 2-3: Historical trends in western Montana from 1950 to 2002 for (a) Population; (b) Exotic species; (c) Livestock; and (d) Farms.

Sources: U.S. Bureau of the Census 2000, U.S. Dept. of Agriculture 2002, U.S. Dept. of Commerce 1952.

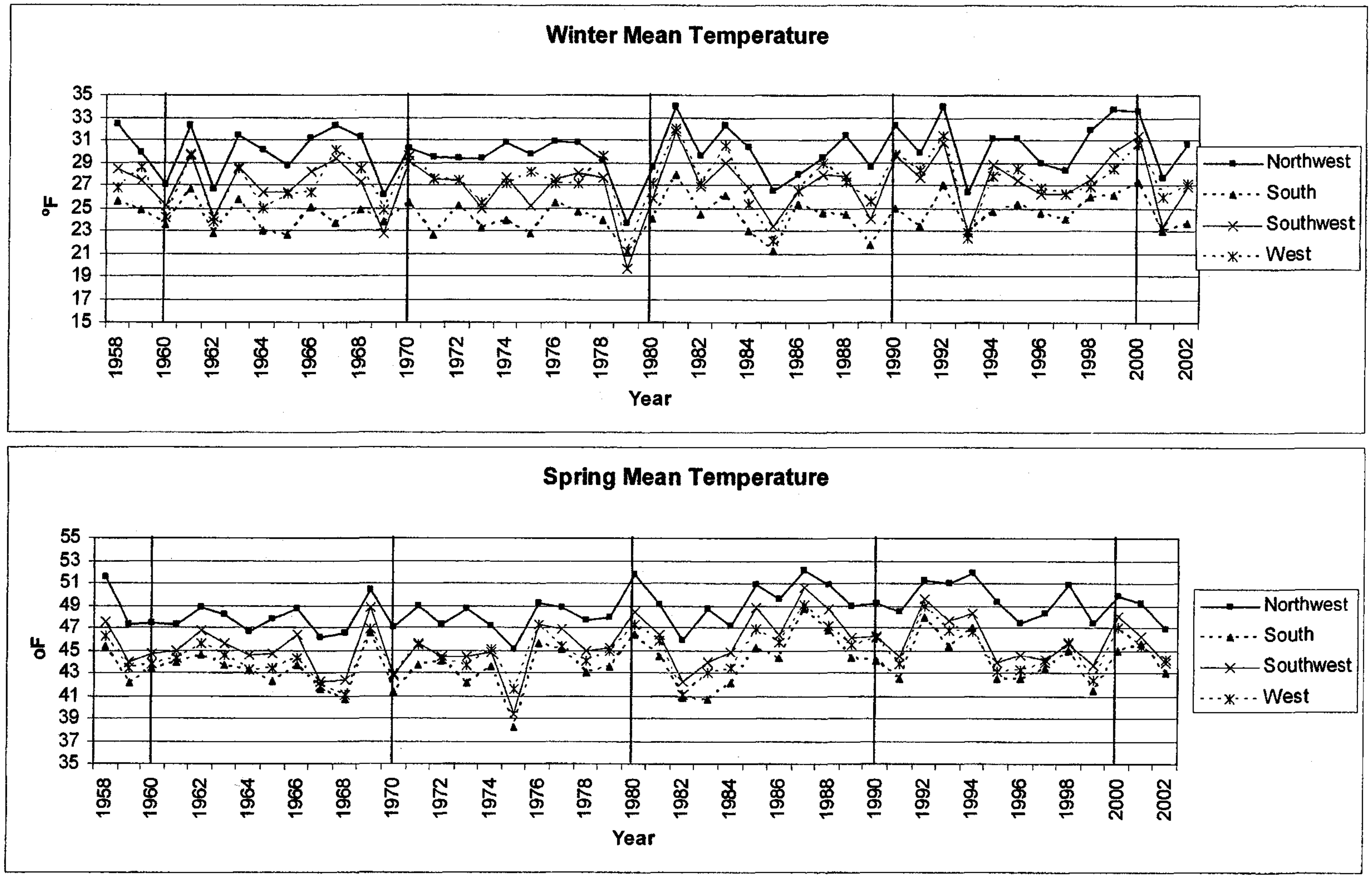


Figure 2-4: Temperature fluctuations since 1958 for the seasons with significant correlations to community change (a) Winter; (b) Spring.

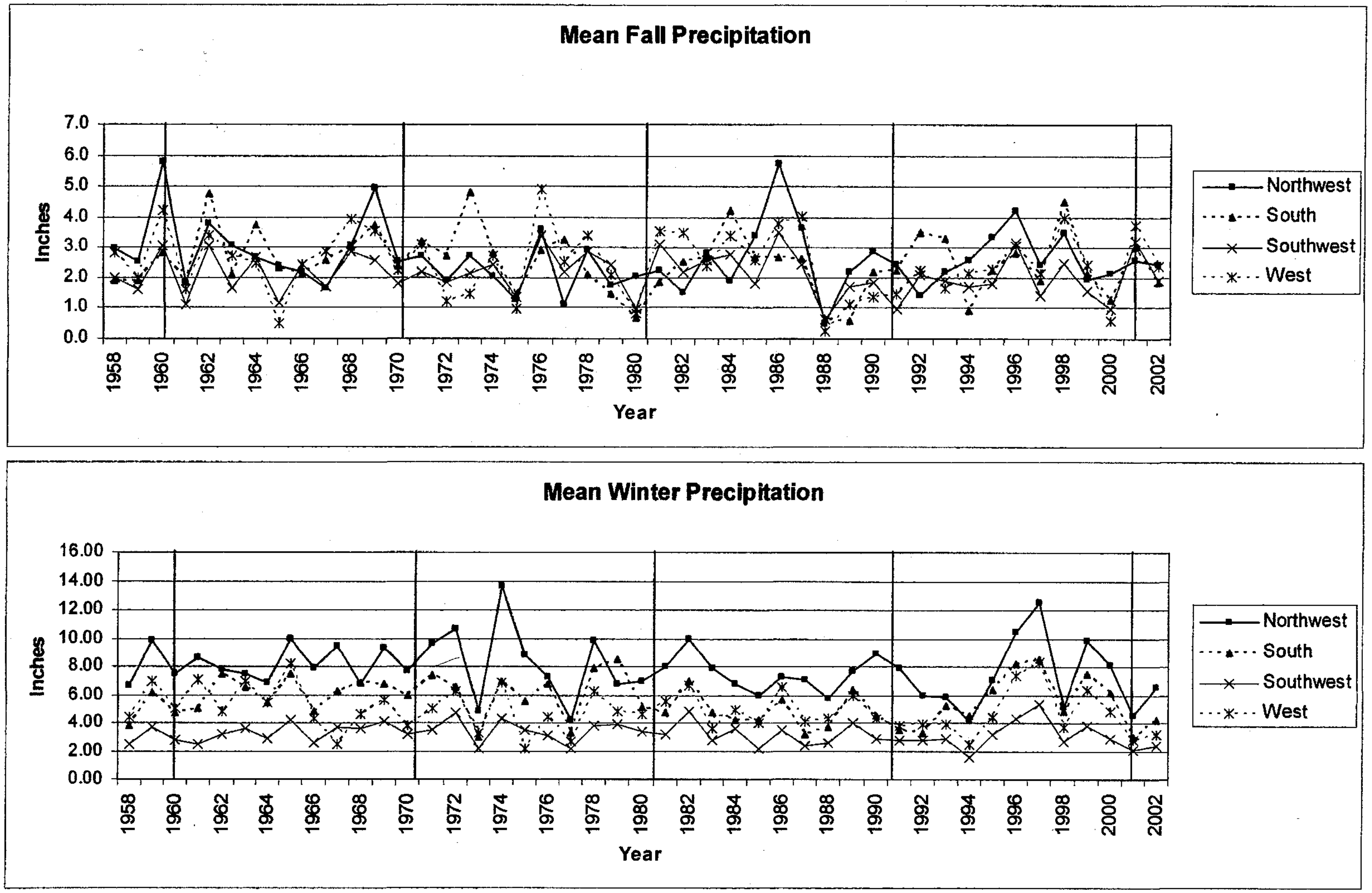


Figure 2-5: Precipitation fluctuations since 1958 for the seasons with significant correlations to community change (a) Fall; (b) Winter.

to other grassland systems. Their locations in protected and regulated areas have insulated most of them from agricultural (crop) effects and widespread fragmentation. However, the entire area was subjected to heavy grazing during the late-1800s to early 1900s when Montana's cattle inventories were particularly high and its rangeland limited (Potyondi 1995). Some of the sampled areas are still under light to moderate grazing today as part of BLM grazing leases.

Form of change at site and ecoregion scales

The most striking feature of change at the site scale was the dynamic nature of all species in the community, whether they were focal species, less important forbs, common, rare, or non-natives. Many species came and went from the sites during the past 50 years. Over 270 species were members of the bunchgrass communities at some time during the study. Over 70% occurred less than ten times in the monitoring history (Table 2-1). Approximately 30% of species occurred only once.

Determining whether common or rare species affected perceptions of change the most depended on spatial scale and whether frequency or dominance was used to classify it (Table 2-2). By far, the majority of the plant species in these communities was considered rare because they occurred so infrequently over the time period. However, rare species were so numerous, and varied so much in frequency during their relatively short tenures on the landscape, that they had significant effects on multivariate analyses and perceptions of the amount of compositional change over time. For example, between 1981 and 1989, several forb species were added to the Lamar I-12 community (Fig. 2-6)

Table 2-1: Percent of times an individual species were detected during 15 to 44 years of monitoring

	Total Species	Mean number of years monitoried	Detected 1 time	Species Detected 1-5 times	Detected 1-10 times
Landscape	272	30	20%	54%	69%[1]
South	69	44	30%	51%	70%
Southwest	236	20	20%	55%	70%
West[2]	32	23	40%	100%	-
Northwest	68	32	35%	62%	74%

[1] 186 species out of 272 total were detected in landscape analysis < 10 times during the monitoring history = 69%

[2] West region has only one site with 3 repeat samples

Table 2-2: Most commonly occurring species in bunchgrass communities of western Montana and their rankings in each ecoregion

		Rankings by frequency within ecoregions[1,2,3]					Rankings by dominance within ecoregions[1,2,3]				
Species	Lifeform[4]	West. MT	South	Southwest	West	Northwest	West. MT	South	Southwest	West	Northwest
Pseudoroegneria spicata	PG	1	1	1	6	1	1	2	1	7	3
Koeleria macrantha	PG	2	2	2	5	3	3	4	3	1	5
Festuca idahoensis	PG	3	3	5	8	5	2	1	2	19	1
Achillea millefolium	PF	4	31	6	12	2	8	36	9	3	6
Artemisia frigida	PS	5	7	7	-	16	7	11	7	-	13
Unknown perennial forb	PF	6	40	4	9	15	9	54	8	5	42
Poa secunda	PG	7	-	3	-	-	4	-	4	-	-
Poa spp. [5]		8	4	55	7	4	20	5	35	2	2
Artemisia tridentata	PS	9	5	15	-	-	11	3	12	-	-
Hesperostipa comata	PG	10	9	10	-	25	15	8	15	-	20
Carex spp.	PG	11	13	9	-	-	10	13	10	-	-
Antennaria microphylla	PF	12	6	32	-	7	34	6	38	-	16
Festuca altaica	PG	14	51	13	27	9	5	45	5	30	8
Lupinus spp.	PF	13	-	8	2	19	6	-	6	4	26
Antennaria rosea	PF	19	-	12	-	-	12	-	11	-	-

[1] All rankings scaled from low (most common) to high numbers (least common)

[2] All rankings based on queries of raw data from historic records

[3] Rankings by frequency = each species counted as present or absent in each sample unit then ranked by abundance; Rankings by dominance = frequencies in each sample unit summed, totalled for all sample units, then ranked in ecoregion

[4] PG= Perennial graminoid; PF = perennial forb; PS = perennial shrub or subshrub

[5] Historic records did not specify whether *Poa spp* was annual or perennial

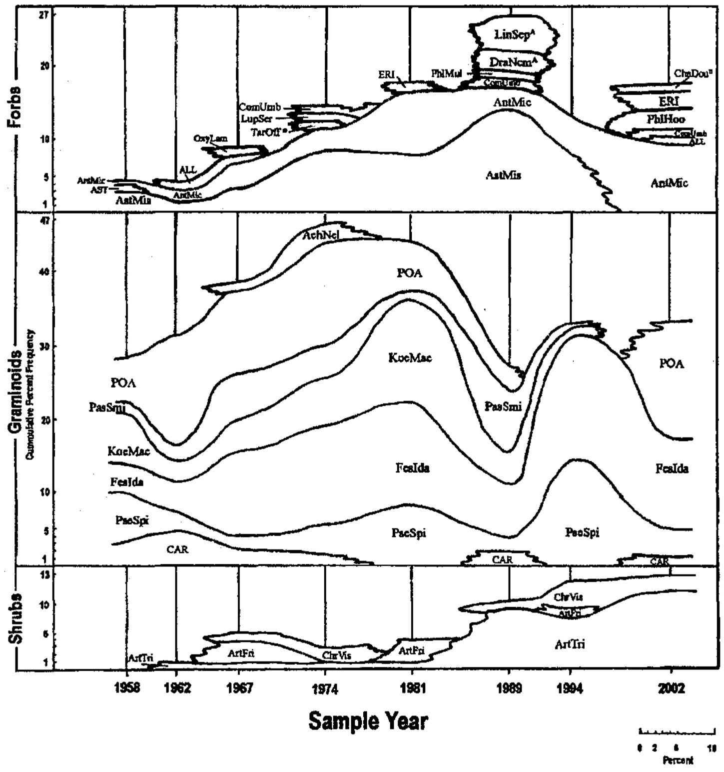


Figure 2-6: Representative facies diagram from grazed area of south ecoregion (Lamar I-12) showing increase in shrub cover, change in graminoid diversity, and variation in both the rare and common species over 50 years. All species frequencies are plotted to scale. Superscripts: *=non-native species; **A**=annual; **B**=biennial.

Graminoids: CAR – *Carex spp.*; PseSpi - *Pseudoroegneria spicata*; FesIda - *Festuca idahoensis*; KoeMac -*Koeleria macrantha*; PasSmi - *Pascopyrum smithii*; POA – *Poa spp.*; AchNel - *Achnatherum nelsonii*; **Forbs:** AstMis - *Astragalus miser*; AntMic - *Antennaria microphylla*; AST - *Aster spp.*; ALL – *Allium spp.*; OxyLam - *Oxytropis lambertii*; TarOff - *Taraxacum officinale*; LupSer - *Lupinus sericeus*; ComUmb - *Comandra umbellata*; ERI – *Erigeron spp.*; PhlMul - *Phlox multiflora*; DraNem - *Draba nemorosa*; LinSep - *Linanthus septentrionalis*; PhlHoo - *Phlox hoodii*; ChaDou - *Chaenactis douglasii*; **Shrubs:** ArtTri - *Artemisia tridentata*; ArtFri - *Artemisia frigida*; ChrVis - *Chrysothamnus viscidiflorus.* See Appendix B for more information on individual species.

in minor amounts (<5% frequency each). *Artemisia tridentata* increased at the location from less than 1% to almost 10%, and some grasses were reduced by 5% or less. These seemingly small changes contributed to impressions of significant change, however, because Lamar I-12 moved the most in species ordination space during this interval.

Another striking result from the facies diagrams was how quickly the proportions of common species (if measured at >10%) changed to rare or vice versa (see *FesIda* in Fig. 2-6). Although some studies eliminate species that do not show constancy in the short term, the deletion of any species, simply because it fell below an arbitrary minimum in the sample year, was difficult to justify because of their quick reversals in dominance through time. Normally common species fell below arbitrary minimums of 5 or 10% to be considered "rare" in one year, and "rare" species reached frequencies of 10 or 20% to be considered important members of the community in good-growth years. This study exemplifies this phenomenon. Even the focal grasses, including *Pseudoroegneria spicata*, fluctuated widely. Annual and biennial species appeared very common in the community if sampling was done in years that were favorable for their growth (see *OrtTen* in Appendix A: Fig.1), although shrub species and non-natives were just as vulnerable to changes in dominance as the shorter-lived species were. Total frequency within lifeform groups (grass, forbs, and shrubs) followed the same fluctuation patterns through time (Fig. 2-6; see also Appendix A).

At the local scale, each site had a completely different compositional history and different patterns of short-term change (Fig. 2-6; see also Appendix A). Even sites that were located adjacent to each other on the ground (e.g. Matbrn2 and Matbrn3) had different species at the same points in time and different variations in those species over time, which F. W. Preston (Preston 1948) dubbed a characteristic of landscape richness over 50 years ago. The continual variations in species dominance and rapid turnover in species membership at each site gave the impression that change occurred as a continuum - not discrete stages that each bunchgrass community passed through.

At the ecoregion scale, the transient nature of species was also apparent. In all ecoregions, richness varied significantly depending on sample year (Fig. 2-6; Appendix A). The total number of species found in each plot in all the monitoring years was double or triple the mean richness at any single point in time (Mean Cumulative Diversity, Table 2-3). The mean amount of species turnover from all ecoregions combined was 48% from the time of the region's first sampling to the sampling in 2002. The highest species turnover was in the northwest ecoregion at the National Bison Range (59% between the early 1970s and 2002). Higher elevations tended to have more species that carried over into consecutive sampling periods than lower elevations did, although the proportions were generally still quite low (<10%). In general, the carry-over species for all elevations were deciduous shrubs.

Directionality at the site and ecoregion scales

Although the facies diagrams showed that individual sites experienced their own unique history, ecoregion groupings of the sites showed distinct trends in both richness and lifeform characteristics during the decades of monitoring.

- In the **northwest,** mean species richness decreased from the first sampling of the sites in the 1970s (Table 2-3). Richness was highest between the mid-1970s and early-1980s and, in several sites, peaked

Table 2-3: Diversity trends within each ecoregion from 1958-2002

Ecoregion	Excl.[1]	Number of sites	Mean number of years monitored	Monitoring method[2]	Mean No. species 1st sample yr.	Mean No. species last sample yr.	Mean No. species all sample years	Mean Cumulative diversity[3]
South	U	6	44	Line intercept	9 (2.9)[4]	10 (2.5)	10 (3.1)	23 (6.2)
South	G	4	44	Line intercept	8 (1.9)	9 (4.9)	10 (3.2)	20 (2.9)
Southwest		31	20	Microplots	18 (6.2)	22 (6.6)	19 (6.6)	39 (11.1)
West		1	23	Microplots	22 (0)	16 (0)	20 (3.8)	32 (0)
Northwest		8	32	Line intercept	10 (3.2)	6 (1.7)	8 (2.5)	25 (3.8)

[1] Position of transect in relation to Yellowstone NP exclosure (U = ungrazed; G = grazed)

[2] Line intercepts = 100 points per site; microplots 20-30 sample frames per site

[3] Total number of species observed at each site (includes all monitoring years); then averaged for ecoregion

[4] Standard deviation follows mean in parentheses

- again in the mid-1990s (e.g. Appendix A: Fig.1). The increases in richness were due mainly to annual species, although non-native species also minimally contributed. At these intervals, spring temperatures and precipitation were lower than the 30-year average; winter precipitation was higher than average. Over the entire 25+ years of monitoring, forbs decreased 20%. Total grass increased 20%. At half of the sites, however, perennial grasses decreased without the accompanying increase in annual grasses that occurred at other sites. Shrub presence was intermittent over time but its total frequency remained unchanged when only the first and last sample years were compared to each other.
- In the only site in the **west**, mean richness was highest in the mid-1970s and 1980 (Appendix A: Fig.2) and declined significantly over the sample period (Table 2-3). As with the northwest sites, the high richness corresponded to lower spring temperatures but higher precipitation than the 30-year mean; winter temperatures were highly variable. Forbs decreased significantly in the late 1990s compared with early records. Overall, forbs decreased 15% in 23 years; graminoids increased 15%.
- In the **southwest**, the sampling intervals were not as consistent as in other regions, and the sites were spread over a much greater spatial area. As a result, trends were more difficult to discern. Unlike the previous ecoregions, richness increased between the first and last monitoring years (Table 2-3). In the sites that had sampling records from the 1970s,

species richness was higher than it was in the mid-1980s. The highest diversity for the southwest sites in general, however, was between 1995 and 2002 (Appendix A: Fig. 3). Richness increased in 90% of the sites during this period. Of these sites, over 60% also increased in the proportion of non-native species. Between 1995 and 2002, spring temperatures were generally lower than the 30-year mean; and spring and winter precipitation were higher than normal. For the entire monitoring period, 50% of the sites increased in grass coverage. Overall, graminoids increased an average of 4% in 24 years; forbs and shrubs each decreased an average of 3%.

  - In the burned areas of the southwest, shrubs declined after the burn year (approx. 25%). By three years after the burn, non-native species increased and shrub frequency surpassed the burn year frequencies (see MatBrn3 Appendix A: Fig. 6). Grasses increased in frequency (40 to 75%) in the year after the burn and three years later. Forb response to burning was mixed.

- In the **south**, vegetative cover increased from west to east (low to high elevation) and the overall proportions of grass, forbs, and shrubs varied considerably between the sites protected from grazing and those open to grazing by large mammals. Mean richness increased in both grazed and ungrazed areas, but the increases were not significant (Table 2-3). The exclosures and grazed sites were all sampled within the same years, so trends reflect real responses to restricted grazing and other environment stresses that are not affected by the boundary.

- **Trends outside of exclosures**
  - Richness was highest at most sights between the mid-1970s and early to late-1980s and again in 2002. Like the other ecoregions, spring temperatures were lower than normal during these intervals. Spring precipitation was considerably below average but winter precipitation was above the 30-year average. The low-elevation sites at Gardiner, Montana (see Fig. 2-1), had the highest richness only in the mid-1960s, which was one, but not the only, period of above-average precipitation in the 40 years of monitoring.
  - Overall, graminoid frequency decreased 11% between the initial sampling in 1958 or 1962 and 2002. However, in the mid-1970s to early 1980s, and again in 2002, graminoids expanded in dominance at most sites (Appendix A: Fig. 5). Diversity of grass species remained similar in all sample intervals.
  - Shrub frequency increased 8% in four decades. Shrub frequency remained lowest at low elevations (most years <8% of composition). At higher elevations (L-11 and I-12), shrub coverage was low until 1995 to-2002. Beginning in 1995, shrubs increased rapidly to account for15 to 20% of the total vegetation (Fig. 2-6).

  - Forb frequency increased an average of 3% in the grazed areas.
  - Mean differences in richness between the grazed and ungrazed sites were not significantly different (9.7 and 9.8, respectively; $p>0.1$).
  - Non-native species were not a significant disturbance factor in the historical records of either grazed or ungrazed sites.

- **Trends inside exclosures**:
  - Total vegetative cover increased shortly after the exclosure was erected.
  - Richness was generally highest between the mid-1970s and mid-1980s in most sites, but varied significantly at each location.
  - In early sample years, diversity of grasses was high, but the frequency of each was low. In later years, sites generally had less diversity in the grass species, but the remaining grasses occurred more frequently within the site.
  - Over 44 years, graminoids decreased 28 % in the exclosures. Total grass cover decreased at all locations except K-12 (see Fig. 2-1).
  - Shortly after construction of the exclosure, shrub cover expanded. In some plots, the increase in shrub frequency began in the mid-1970s to mid-1980s. In others, *Artemisia tridentata* increased exponentially around 1994 to exceed 20% of the plant

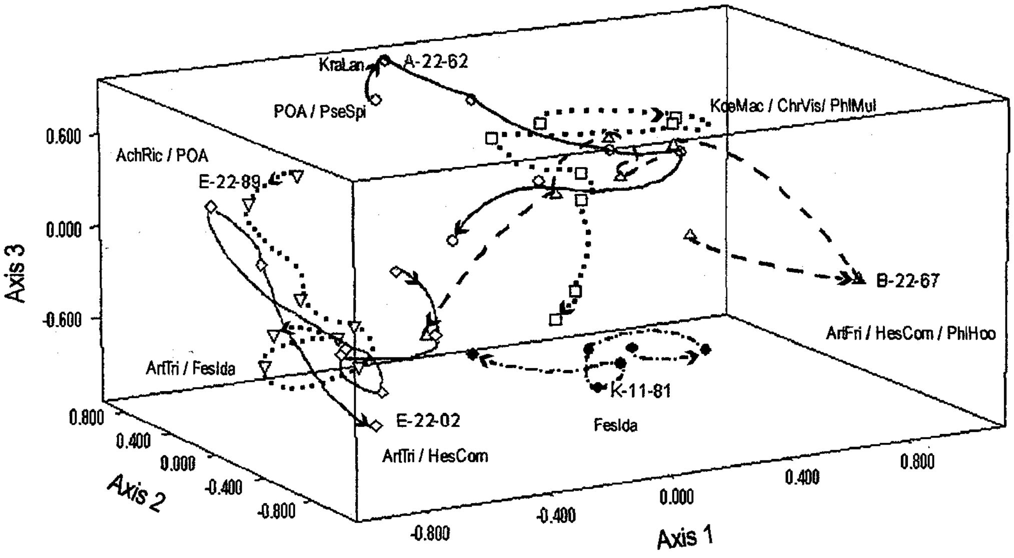
cover (Appendix A: Fig.5). The increase in shrub dominance was not always linear, however. Reversals in total cover occurred and frequency declined to zero between some intervals (K-11 in 1994, G-11 in 2002).

- Forbs expanded 8% in 44 years. *Phlox* expanded significantly in many sites during the mid-1970s to early 1980s. It also expanded in 2002 compared to the mid-1990s sampling.

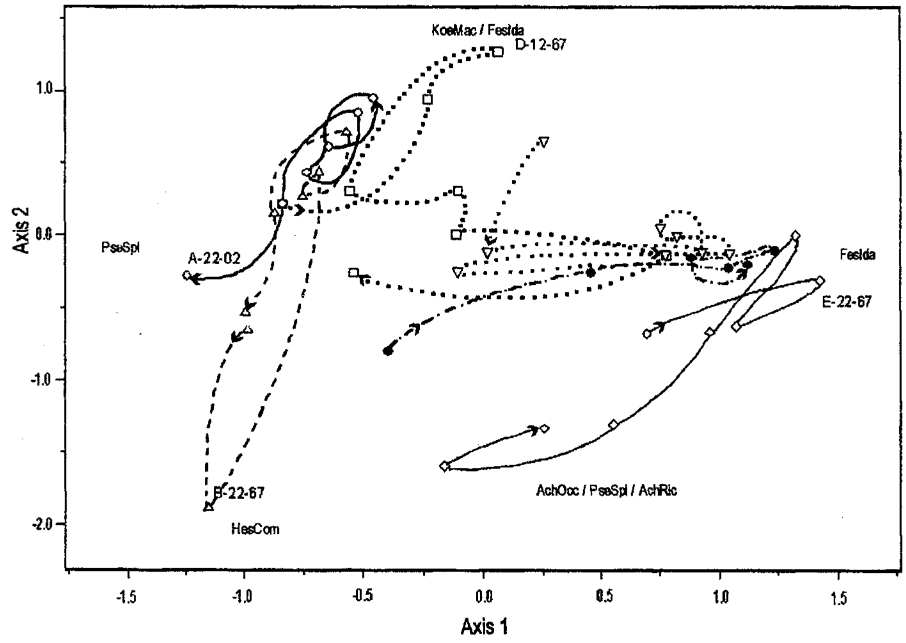
The effect of an earlier start date for monitoring on the perception of trends was compared for the south ecoregion (start year1958 or 1962) and for the northwest (start year of late 1960s or early 1970s). The trends in shrubs, grass, and forbs in both ecoregions were compared between the mid 1970s and 2002. The results show two opposite trends from the entire record, namely grass declined between the mid-1970s and 2002 in the northwest and forbs decreased in the south. All other trends for the lifeform groups remained the same between these two intervals.

As the descriptions in the preceding paragraphs show, lifeform groups seem to show different trends in each ecoregion. Using the south (ungrazed) ecoregion as a case study, the trends for grass, forbs, and shrubs were examined individually to define their change patterns and to determine if one group affected perceptions of change within the community more than any other group (Fig. 2-7). In the exclosures, where grazing was eliminated as a factor affecting change patterns, NMS vector directions all fluctuated widely in species space over time. All lifeforms showed significantly long vectors between most, but not all, sample intervals, which indicates significant variation in proportions over time. The full community (Fig. 2-7a) showed trends in vector direction toward more *A. tridentata* and *F. idahoensis* (lower left corner, Fig. 2-7a). Likewise, the shrub NMS showed a general trend toward *A. tridentata* over time. Of the three lifeforms, the graminoid NMS was most similar to the full community in general direction and magnitude of movement for each plot (Fig. 2-7b). The similarities are not surprising because grass has been the dominant lifeform in most plots for the longest time. However, the shorter vectors and tighter patterns of the community analysis compared to the graminoid analysis suggest that the variation in the grasses has been damped by either shrub or forb variations in different directions (see D-12 and K-11 in Figs. 4b-4d).

The change patterns represented by the NMS vectors in species space were quite varied for each ecoregion (Table 2-4) so change in the bunchgrass communities could not be depicted by one type of pattern. The most common vector trend was a non-equilibrium pattern characterized by irregular directions, unequal magnitudes, and reversals in direction at some point in the sample history (Table 2-4). This pattern was present in 30% of the lifeform change patterns at the 50 sites. Over 18% of the vector patterns oscillated around a centralized area before or after a major change in composition (Fig. 2-7b, K-11, A-22). A related zig-zag pattern was also common (15%). Non-equilibrium patterns were not universal in the grasslands, however. Linear pathways were found in approximately 7% of the cases. They occurred in all lifeforms, and were especially common in ungrazed plots and plots with less than four resamples in their history (Fig. 2-7d, A-22, AMAZN, and IC1).

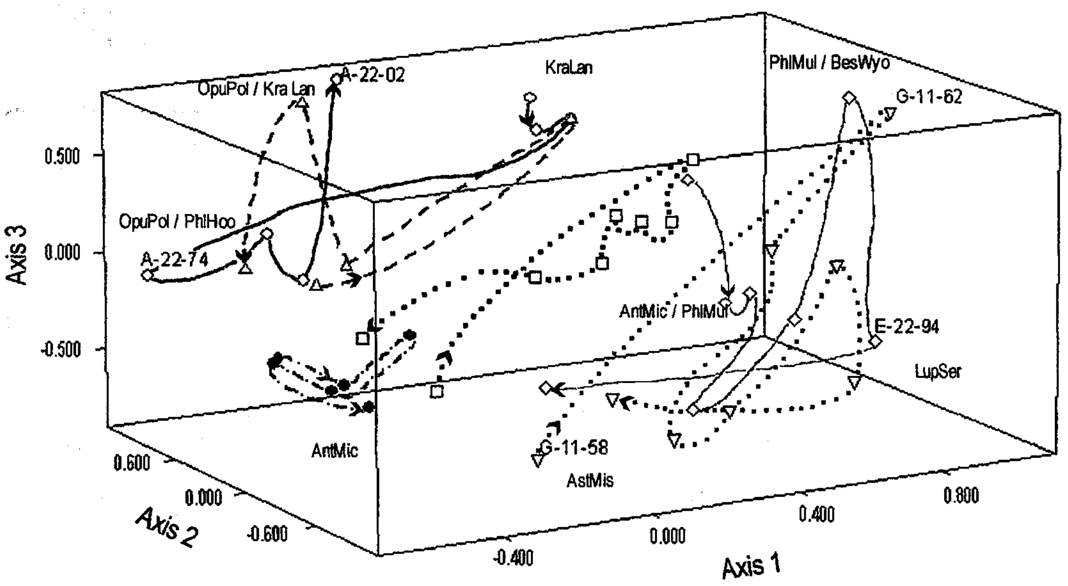


A. All species

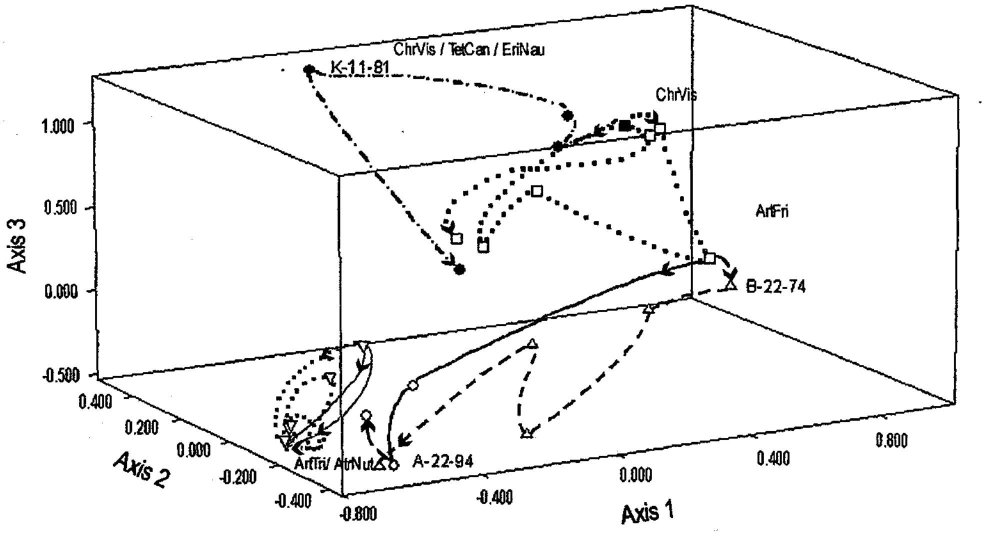


B. Grasses

Figure 2-7: Plot movements in NMS ordination space for ungrazed plots of the south ecoregion. **(A)** All species in community; **(B)** perennial grasses and sedges only; **(C)** perennial forbs only; and **(D)** shrubs and sub-shrubs only. The vectors connect consecutive sampling units and show directions (first and last arrows only), magnitudes, and compositional trends at each site over the monitoring period of each plot. (Note: Grazed and ungrazed plots are processed together in NMS by lifeform but plotted in separate diagrams to highlight differences.)



C. Forbs



D. Shrubs

Figure 2-7 (continued): Plot movements in NMS ordination space for ungrazed plots of the south ecoregion. **(A)** All species in community; **(B)** perennial grasses and sedges only; **(C)** perennial forbs only; and **(D)** shrubs and sub-shrubs only. The vectors connect consecutive sampling units and show directions (first and last arrows only), magnitudes, and compositional trends at each site over the monitoring period of each plot. (Note: Grazed and ungrazed plots are processed together in NMS by lifeform but plotted in separate diagrams to highlight differences.)

Table 2-4: Classification of vector-patterns from the NMS analyses of compositional change by lifeforms and by community, all ecoregions[1]

	Northwest ecoregion grazed				Southwest ecoregion grazed				South ecoregion grazed				South ecoregion ungrazed				
Change pattern[2]	***Full***[4]	Graminoid	Forb	Shrub	***Full***	Graminoid	Forb	Shrub	***Full***	Graminoid	Forb	Shrub	***Full***	Graminoid	Forb	Shrub	Total in category
Linear or near linear[3]	--	--	--	--	***2***	3	4	--	--	--	--	1	--	--	--	1	11
Zig-zag	***2***	1	3	--	***7***	9	3	2	***2***	--	1	--	--	1	--	1	30
Oscillating around point(s) or spaces	--	1	1	--	***8***	4	5	6	***1***	--	3	--	***3***	3	1	1	37
Irregular directions	***5***	5	4	--	***6***	8	7	5	***1***	3	--	2	***2***	2	3	2	50
Other	***1***	1	0	--	***8***	7	12	17	--	1	--	1	***1***	--	2	1	51

[1] Lifeform division in west region did not produce meaningful NMS

[2] See conceptual diagram (Fig. 2) for relationship of patterns to theoretical models

[3] Columns contain number of times pattern occurred in each lifeform analysis using relativized raw data

[4] NMS analysis of entire plant community (all vegetative species)

Correlations of change patterns with environmental factors

Climatic and substrate factors correlated most with community change in the western Montana bunchgrass communities. Variations in temperature and precipitation determined what annuals sprouted in a given year, what forbs flourished to produce seeds, which exotic species had the conditions needed to increase in communities, and which grasses had high yields and produced seed to expand to new sites. For the case study area (south ecoregion), the movement of each community in species space was correlated most significantly with variations in the substrate variables and temperature (Fig. 2-8). Richness was high in years with spring temperatures that were lower than the 30-year average and winter precipitation was higher than average. Correlations of community change with mean spring and winter temperatures were significant along NMS axes one (t=3.26 and 2.01) and three (t=-2.20, and 3.23, respectively). Spring precipitation correlated significantly only along axis two (t=1.99).

Not all ecoregions yielded NMS values that could be tested with path analysis. For the ecoregions that were tested, each had different combinations of substrate, temperature, and precipitation factors that correlated most strongly with change (Table 2-5). Surprisingly, non-native species were not a significant driver for change in any ecoregion but the southwest (t=-3.43), at least over the time periods and regions that were tested. In the west and northwest regions, the influence of non-native species may have been more significant (see chapter 1 results), but a meaningful NMS was not produced for these areas to test the correlations or non-native species in combination with climatic fluctuations.

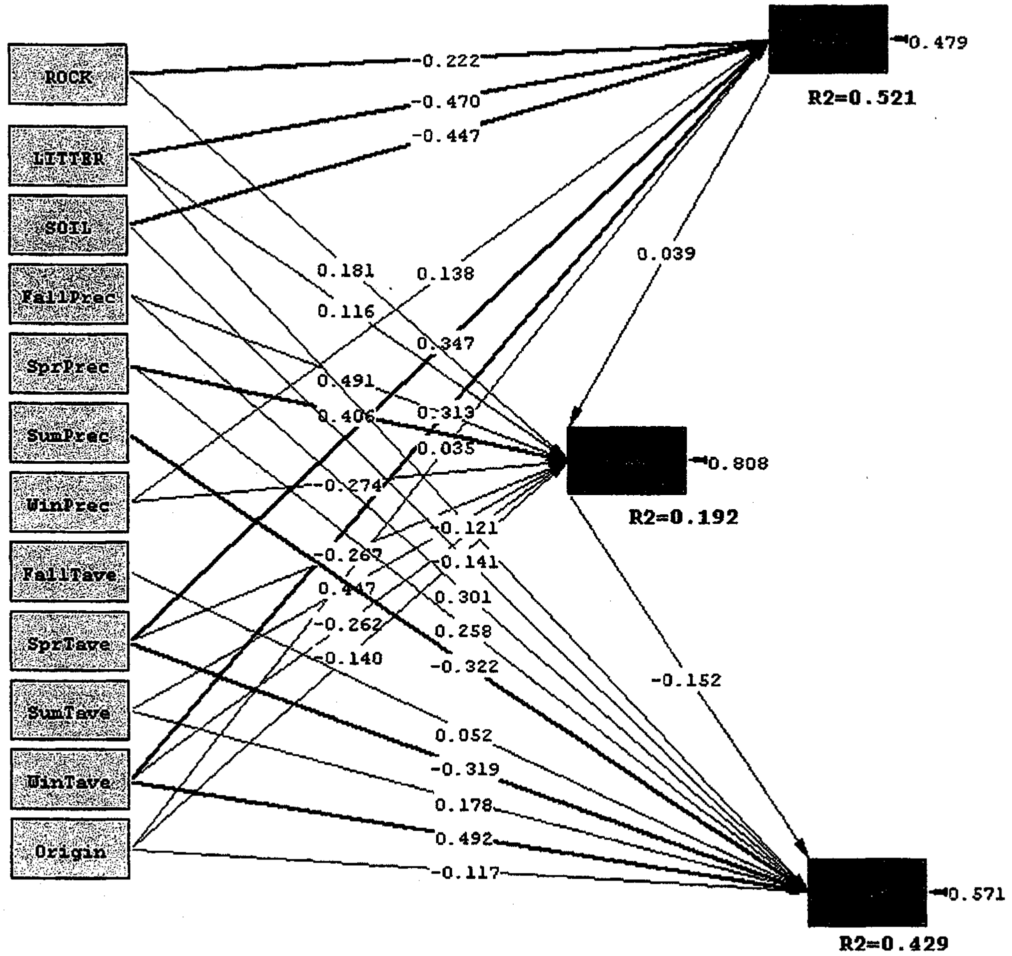


Figure 2-8: Path coefficients for south ecoregion. Paths with significant t-values are shown with bold lines. Chi-square=5.60, df=11, p value=0.89894, RMSEA=0.000, n=63.

Table 2-5: Path analysis coefficients for the relationships between the variations in community composition, abiotic factors, climatic fluctuation, and non-native species

	Western Montana Landscape [4]			**South Ecoregion** [5]			**Southwest Ecoregion** [6]		
NMS Axis	**NMS 1**	**NMS 2**	**NMS 3**	**NMS 1**	**NMS 2**	**NMS 3**	**NMS 1**	**NMS 2**	**NMS 3**
R^2 of NMS axis[1]	0.48	0.27	0.134	0.389	0.344	0.164	0.38	0.261	0.172
R^2 of Y variable in structual model[2]	0.075	0.133	0.091	0.521	0.192	0.429	0.297	0.265	0.227
Substrate[3]									
M/L	- -[7]	**0.258**	0.102						
ROCK	-0.105	**-0.144**	**0.163**	**-0.222**	0.173	-0.026	0.024	-0.054	**0.343**
LITTER	- -	**0.183**	0.123	**-0.47**	0.098	-0.136	-0.047	0.025	**0.294**
SOIL	0.06	- -	-0.104	**-0.447**	-0.017	-0.138	-0.077	0.035	-0.213
Precipitation variables[3]									
FallPrec	0.13	**0.158**	**-0.185**	- -	0.491	0.227	- -	**0.282**	- -
SprPrec	- -	0.082	- -	- -	**0.406**	0.196	-0.172	-0.057	-0.146
SumPrec	**0.168**	-0.097	-0.027	- -	- -	-0.322	0.179	0.113	-0.026
WinPrec	- -	**-0.156**	- -	0.138	-0.269	0.041	**0.518**	**-0.227**	0.116
Temperature variables[3]									
FallTave	**0.18**	- -	-0.123	- -	- -	0.052	0.097	**0.342**	0.032
SprTave	0.109	- -	- -	**0.347**	-0.253	**-0.281**	**0.268**	0.077	-0.111
SumTave	0.103	-0.11	- -	- -	0.447	0.11	**0.318**	0.101	0.161
WinTave	-0.083	- -	-0.085	**0.313**	-0.25	**0.53**	**0.23**	-0.072	0.068
Non-native coverage[3]									
Origin	-0.112	- -	0.047	0.035	-0.139	-0.096	**-0.328**	-0.147	0.026

[1] R^2 value from NMS in PCOrd. Represents the amount of variance in the raw data explained by each NMS axis, respectively

[2] R^2 value from path analysis. Represents the fit of the measurement models with each respective axis

[3] Bold numbers have significant T-values for the regression of matrix y (NMS axes values) on x (measured variables) in each path model

[4] Path analysis results: Chi-square = 4.32, df=18, p-value=0.99959, Root Mean Square Error of Approximation (RMSEA)=0.000, n=246

[5] Path analysis results: Chi-square=5.60, df=11, p-value=0.89894, RMSEA=0.000, n=63

[6] Path analysis results: Chi-square=0.75, df=8, p-value=0.99938, RMSEA=0.000, n=118

[7] --Path removed from model because the coefficients were near zero. Removal of path had no significant effect on R^2 of each axis.

The explanatory power of both the NMS results and the path models also varied with spatial area. At the landscape scale, the NMS axes, which represent community change over time, explained variation in the species difference-matrix data quite well (R^2 ranging from 0.13 to 0.48). The fit of the path model to the variations in NMS and measurement data was also good (see chi-square and p-values in Table 2-5 footnotes); but the path model explained very little of the variation within each y (i.e. NMS axis) value (R^2=0.07 to 0.13). In the south ecoregion, the explanatory power and fit of the model were best. The NMS explained from 16 to 39% of the variation in the species difference matrix and the path model explained from 19 to 52% of the variation in measurement data (Table 2-5). Similar variation was explained in the NMS of the southwest ecoregion, but the path model did not fit the data quite as well as in the south (R^2=0.23 to 0.30). The correlations within each of these path models should be used with caution, however. All were created using fewer samples than the number of parameters in the model, so the results should be considered tentative (Joreskog & Sorbom 1996).

Discussion

The nature of change in the bunchgrass communities of western Montana is recorded in vegetation monitoring records that, when originally written, probably seemed less significant to their authors than to those with historic perspective. Taken collectively, however, these snapshots in time now provide unique insights into how Montana's bunchgrass communities have changed within the relatively natural settings of the intermountain area during the past 20-50 years. That these grasslands have changed is not surprising – change is inevitable in any community after long time periods. What may be surprising, however, is the constant variation in composition within an ecosystem that, in general, appears so stable over time at relatively small spatial scales.

Natural experiments, like this study, are not unaffected by disturbance or environmental variation. Each of the sites has experienced, either directly or indirectly, many changes over the past five decades, including changes in the abundance of both domestic grazers and wildlife, introductions of non-native vegetation, and increases in human population on the adjacent landscape (Fig. 2-3). They are also pressured by climate variability (Fig. 2-4). All of these changes have undoubtedly affected each site, although not under experimental conditions that are easy to manage and correlate.

The dynamic nature of the Montana bunchgrass communities in response to disturbance and environmental factors is quite evident from this study, and the results challenge traditional concepts of stability and equilibrium within grasslands. At the plot scale, change is characterized by wide fluctuations in species frequency and community membership. Neither the facies diagrams at any single location, nor the vector movements of individual plots within the ordination species space, portray the same change patterns through time at all locations. Little evidence exists at each plot for the directionality that is characteristic of succession in the classical sense (Heady & Child 1994: Fig 10-1). The change patterns do not show any discrete stages or phases in either the ordinations or facies diagrams to indicate that the species move through time as one unit or follow a distinct development path. All species, whether they are categorized as common, rare, non-native or indicators, vary in space and time. The transient nature of the majority of species at the ecoregion scales results in very high turnover rates and gives the impression that the communities are in a constant state of flux, which argues against their past classifications as stable "climax" vegetation (Mueggler & Stewart 1980). The high turnover rates in these communities are comparable, however, to turnover rates found in other grasslands where long-term perspectives are available (e.g., Ward and Jennings (1990)).

Grouping the plots together into ecoregions, however, does show obvious trends in richness and lifeforms during the 20-50 years. The trends are not the same for each ecoregion nor do they last for the entire data record, but each has directionality over relatively long time frames. One of the most obvious trend patterns is an increase in richness between the mid-1970s and mid-1980s in each ecoregion. Lifeform groups also exhibit distinct trends over time.

Plant functional types (PTFs), or lifeforms, recently have become important analysis units in other vegetation studies because each group plays a unique role in community interactions, and each responds to external environmental factors in different ways (Cousins & Lindborg 2004, Epstein *et al.* 2002, Rodriguez *et al.* 2003). Cousins and Lindborg (2004) found that PFTs had no association with successional gradients in abandoned grasslands in Sweden, but other studies have found that PFTs were helpful in generalizing change patterns within grasslands and assessing their correlations with external factors (Epstein *et al.* 1997, Jobbagy & Sala 2000, Kahmen *et al.* 2002). In this study, I also found PFTs helpful in minimizing the significant variation in individual species at each location so more general trends could be detected. The analyses suggested that lifeform groups may be responding differently to environmental stresses in the four ecoregions because they varied independently from each other in frequency and composition over time (Fig. 2-6 and Appendix A). For example, the increase in shrubs and decrease in grasses in the grazed and ungrazed plots of the south ecoregion contrasted sharply with a significant increase in grass and no change in shrub cover in grazed plots of the northwest. The trend toward increased grass frequency and decreased forb frequency occurred in three of the four ecoregions (Appendix A). Knapp *et al.* (2004) suggested that forbs increased under more mesic conditions, but forb frequency was also affected by grazing to varying degrees (Stohlgren *et al.* 1999). Either climate fluctuation or increased grazing pressure from increasing wildlife populations could explain these trends in Montana. While some of the trend differences in each ecoregion were likely due to differences in the start dates of the monitoring, the analysis of equal-intervals (mid-1970s to 2002 in both) in two ecoregions with contrasting trends using the full historic record also showed contrasting trends for the restricted interval. Therefore, the trends appear consistent within a spatial area.

The ordination results reiterate that lifeforms may be responding in different directions to stress. The full community ordination for the ungrazed area of the south region (Fig. 2-7a) shows that change vectors trend in many directions over the 44 years, but the final vectors for 2002 all trend to communities with more *A. tridentata*, *F. idahoensis*, and *H. comata* than the original sample descriptions. In the ordinations of separate lifeform groups, the change vectors tell the same general story but some are longer than those of the full community and some are shorter. In most cases, the patterns depicting the full compliment of species are more confined in species space because the effects of one lifeform (e.g., forbs) are dampened by offsetting patterns from another.

The directions and magnitudes of the vectors depicting community change in this study vary considerably in species space and show that there are no set trajectories for change within an ecoregion. Some years the vectors are short and indicate that a community experienced very little change in either species or the relative dominance of each species between sample periods. In many years, the vectors are long and indicate significantly different combinations or proportions of species at a plot location. Short intervals between sample periods also do not guarantee that the time-series samples will plot close to each other in species space (e.g., there are long vectors between samples taken in 1997 and 1998 at CO13 in the northwest ecoregion, but very short vectors between the samples taken between 1994 and 1997). It is obvious from the ordination diagrams that impressions of community trends would be very different if one happened to sample between periods when (a) fluctuations were great; (b) fluctuations were very small; or (c) the community was following a very long vector in the transition between two different compositional states.

For this study, the correlation of community change with change drivers focused on four environmental stresses: fire, non-native species, grazing, and climatic fluctuation. Burning was a factor at only two sites but its effects agreed with many other grassland fire studies (Antos *et al.* 1983, Redmann *et al.* 1993). In the year directly following the burn, shrubs declined and grasses increased significantly but by three years after the burn, shrubs, grass, and non-native species all exceeded pre-burn levels. Burning effects on forbs were mixed.

Non-native species increased in all of the ecoregions in the past 30 years (Fig. 2-3b) but their statistical correlations with community change were significant only in the southwest ecoregion. In the southwest, they affected overall richness values in over 60% of the sites, especially between 1970 and 1980 when both richness and domestic livestock numbers were higher. However, neither the grazed nor ungrazed areas of the south ecoregion had significant correlations with increases in non-native species, at least at the plot locations measured for this study. The northwest ecoregion needs more analysis because the facies diagrams indicated that increases in non-natives were important during some time frames, but sites that were included in the statistical analyses failed to produce a meaningful NMS to correlate the outbreaks with.

Attributing grazing effects specifically to lifeform or community trends in the case study area was not clear cut. Lifeforms followed the same trends in the exclosures as in the grazed areas (i.e. shrubs and forbs increased in both; grasses declined significantly). The declines or increases for each lifeform type were just greater in exclosures. The decline in grass frequency over the 45-year record did not correspond with results from other grassland studies where grass coverage increased over time in areas protected from grazing (Anderson & Holte 1981, Floyd *et al.* 2003). The greater increases in shrub frequency inside the exclosures supported previous research that showed shrub dominance increased significantly over time in semi-arid temperate grasslands when protected from grazing (Anderson & Holte 1981, Floyd *et al.* 2003, Van Auken 2000). Recently, Rodriguez *et al.* (2003) used NMS to show that forbs and graminoids from a temperate grassland, which was released from grazing nine years prior to their study, had near-linear trends and a decreasing change rate over time (see Rodriquez et al. 2003, Fig. 2-1a and 1b). Neither the grazed (Fig. 2-7a-d) nor ungrazed plots in this study show linear trends. However, some of the pathways in the south ecoregion would appear near-linear during portions of their sample history if their time series were shorter (e.g., Fig. 2-7b K-11). The south ecoregion sites have been under the same management regimes for the past 40 years but the lifeform components do not exhibit a consistent decrease in change rate during that time (Figs. 4b-4d). Therefore, the change patterns in this ungrazed grassland differ from those of Rodriquez *et al.* (2003). Two to five decades of monitoring give a relatively restricted look at the disturbance histories in each of these ecoregions. Whether the trends in each ecoregion represent (a) the grasslands rebounding from disturbances that happened prior to 1950, such as the cattle-boom era of the late 1800s; or (b) adjustments to a combination of changes in agricultural land use and species invasions since 1950, or (c) other disturbance factors are as yet unclear. Longer, more detailed records on grazing history than were used within this study will be required to determine the specific importance of each alternative.

The fluctuation of community positions in NMS ordination space that represent compositional change correlate most closely with fluctuations in substrate, temperature, and precipitation (Table 2-5). The fluctuations in substrate variables are directly related to fluctuations in biomass coverage of individual species during sampling – high species cover translates to low proportions of bare soil and exposed rock. Table 2-5 reiterates that these correlations are significant at each spatial scale; but the substrate variation really represents indirect effects of more basic causal mechanisms that control the quantity of plant growth in the community, such as climate conditions and/or grazing intensity or duration. Ultimately, seasonal temperature and precipitation variables correlate most significantly with community change.

The significance of each climate variable to community change varies with ecoregion (Table 2-5). Temperature is not the most important causal mechanism for change in all of the ecoregions, although it has been widely accepted that temperature is the principle control on the distribution of C_3 and C_4 grasses in temperate grassland ecosystems. Similarly, precipitation does not universally explain multi-decadal change in these semi-arid communities, even though seasonal distribution of precipitation is becoming more widely recognized as an important factor in the distribution and change patterns in all types of grassland vegetation (Fay *et al.* 2003, Kaiser 2001, Knapp & Smith 2001, Paruelo & Lauenroth 1996). In this study, precipitation variables are most important in ecoregions that have the most variation in latitude and topography among the plots (e.g. landscape and southwest ecoregion, Table 2-5). In these spatial areas, change correlates most with fall and winter precipitation, probably because they contribute significantly to deeper soil moisture (Schwinning *et al.*, Svejcar & Brown 1991). Each ecoregion experienced drought conditions (i.e. below mean total yearly precipitation by area) during at least 20 of the years between 1958 and 2002, so soil moisture would be critical to whether individual species thrive or struggle in the community during each sample period

In the south and southwest ecoregions, community change correlates with the variations in spring and winter mean temperatures. The temperature correlations are important on several dimensions (see Table 2-5, NMS1, NMS2 and NMS3) in each ordination, which indicates that they are strongly affecting many different types of species. However, the general lifeform categories can not be equally affected by temperature in the two areas because the south and southwest have opposite trends in lifeforms over time. The trends in shrub frequency in the south (+8% to +20%) contrast with the southwest (-3%). The trends in grass frequency in the south (-11% to -28%) differ from the southwest (4%). Paruelo and Lauenroth (1996) suggest that the abundance of shrubs should be controlled more by winter precipitation than by temperature, but this study shows that winter precipitation is not statistically significant in the area where shrub increase is the greatest. The discrepancy may be explained by the differences in spatial scale between the two study areas.

Although the path models suggest that climatic factors explain long-term change in these ecoregions, the R^2 values for each NMS axis suggest that the models are still missing some key elements to explain the amount of variation in the species matrices (see Table 2-5, R^2 values of the y variables). At best, the variables tested within the path models predict only 52% of the variation in community change (Table 2-5). The low predictive ability of some of the path models may have two possible explanations. First, the plot movement in species space had to be represented by three different axes values instead of one comprehensive number, which dispersed variation. Second, an unmeasured change factor (such as grazing, disturbance history, soil moisture, or soil nutrients) was fundamentally missing from the model. Further study will be required to determine if fit can be improved between the path model and the bunchgrass data with more factors added. In addition, the results need to be tested on a data set that is independent of the set that was used to create the path model to further verify these relationships (Knapp *et al.* 2004).

How well do these grassland communities fit the current theoretical models to describe succession in plant communities? The strength of correlations in the path models reiterates that external forces are important drivers of change in these grasslands, which would generally place them within the non-equilibrium class of successional models (Briske *et al.* 2003). The compositional changes in the historic data that are portrayed by time-series vectors in NMS species space, however, suggest that the change patterns – whether they are examined from the perspective of the entire community or separate lifeforms within each community - cannot be pigeon-holed into a single successional model. Theoretically, one hopes to find compositional changes in bunchgrass communities that fit one successional model better than any of the others. In reality, however, the data from these grasslands tell a much more complex story. Some of the sites are excellent examples of the equilibrium model proposed by Clements (1916) with clear linear and unidirectional trends over time (Fig. 2-2). Many, but not all, of these linear sites have a sparse sampling history or are from locations undergoing progressive shrub invasion. The most common change pattern in the bunchgrass communities is an irregular pattern consistent with the persistent non-equilibrium model (Fig. 2-2; Table 2-4). The irregular directions and constantly changing magnitudes are consistent with a model that is very sensitive to fluctuations in precipitation and/or temperature (Knapp & Smith 2001). The significant correlations with climatic variation support a model driven by external influences (i.e. a non-equilibrium model). The irregular patterns, along with the variations in species that are apparent from the facies diagrams, would most closely fit Gleason's (1926) individualistic concept of community succession.

Several sites also exhibit change patterns consistent with patterns predicted by the state-and-transition model. Oscillations of plots around a single point or area of species space suggest relative stability during some intervals but sudden changes in vector directions away from these oscillation points suggest the influence of external forces at other intervals. These are the second most identified pattern in the ordination analyses (Table 2-4).

Two theoretical succession models that have little support from the long-term data are the threshold model (Friedel 1991) and the deterministic chaos model (Stone & Ezrati 1996). For the threshold model, there are no concentrations of oscillating patterns that are strictly unidirectional in species space. All reverse their direction toward a previous compositional state one or more times during their history. Even the shrub-invaded sites, which would be expected to fit the threshold model best, had periods when shrub cover decreased significantly and compositional trends reversed. Similarly, the analyses show no clear evidence of dominance-driven cycles predicted by the deterministic chaos model. Although both grass and shrub species appear to be more abundant at certain times in the historic record, neither the facies diagrams nor the ordinations suggest that they reach some upper frequency limit that leads to a rapid decline in the population.

The nature of change in western Montana's bunchgrass communities can only be described as extremely dynamic at both the site and ecoregion scales. Recently, Kahmen and Poschlod (2004) suggested that the course of succession in grasslands may be unique for each site and year. At the local scale, the Montana bunchgrass communities appear to support such a view. They are truly communities in constant motion that have experienced unique external forces at each spatial scale to shape their historic change patterns. They have been affected to varying degrees by climatic fluctuations, grazing intensity, and invasive species. These particular environmental stresses will increasingly shape the change pathways of their future.

Acknowledgements

Several government agencies provided data and technical assistance to make this project possible, including the Bureau of Land Management regional offices in Missoula, Butte and Dillon; Montana Department of Fish, Wildlife and Parks offices in Missoula and Bozeman; the National Fish and Wildlife Service; and Yellowstone National Park (under permit YELL-2001-SCI-0229). I thank numerous personnel from these agencies who helped locate historic records that were stored in long-forgotten places and who assisted in locating and sampling some of the sites used in this paper. I also acknowledge the work and skill of many unnamed field workers who sampled the agencies' monitoring sites during the past several decades. Access to ArcGIS for analysis and computer time for SOGS computations were provided by the University of Montana, Missoula. Kristin Sikkink assisted with data entry. Art Sikkink provided field assistance at 50 locations in 2002 to describe site conditions.

Appendix A: Representative facies diagrams for ecoregions

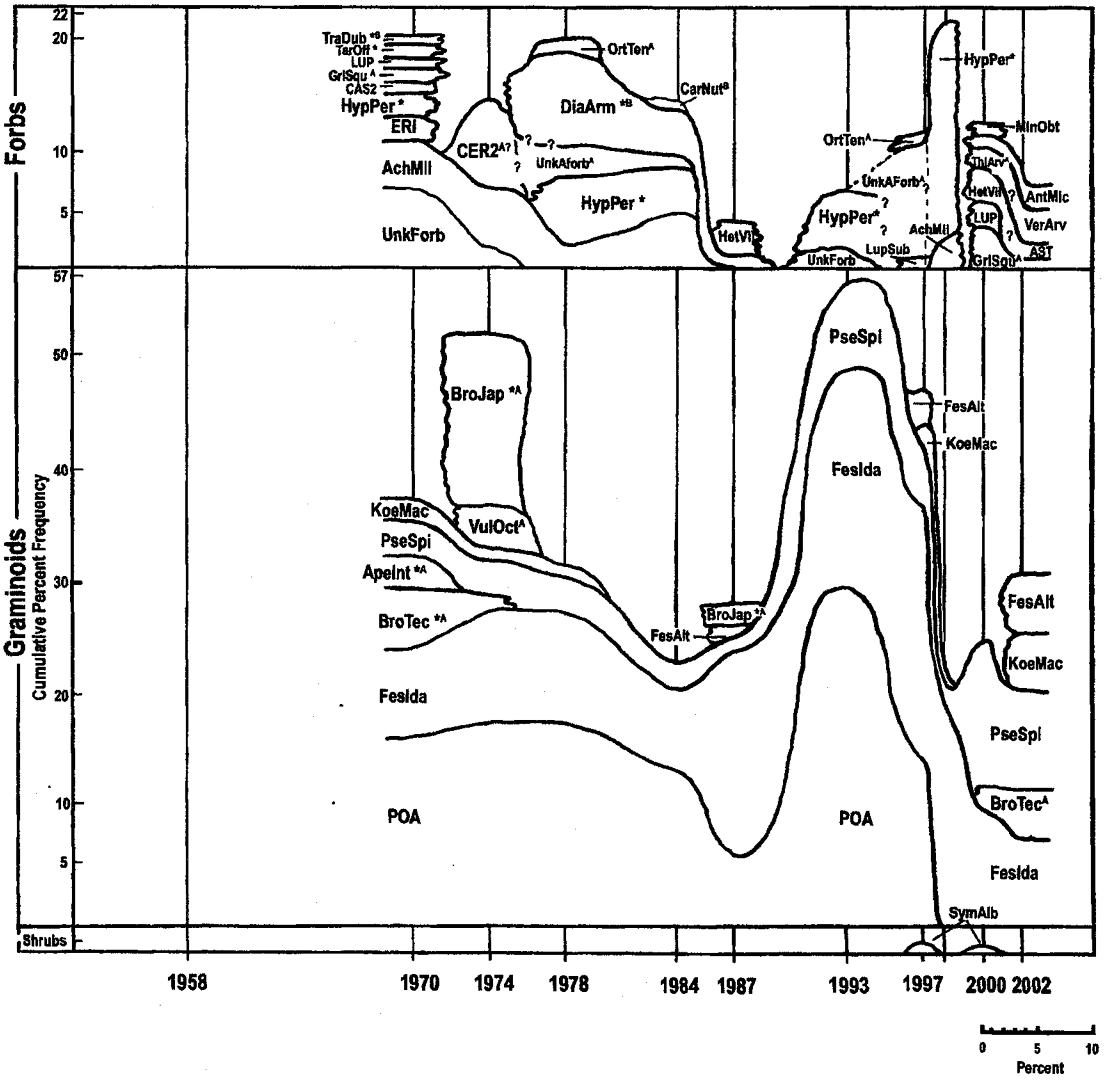


Fig.1: Facies diagram for CO23 in northwest ecoregion, National Bison Range, Montana. Sample years are at vertical lines. Intervals between samples conceptualized. Cumulative frequency percents are diagrammed to scale by lifeform. * = non-native species; A= annual; B= biennial (Species abbreviations listed in Appendix B).

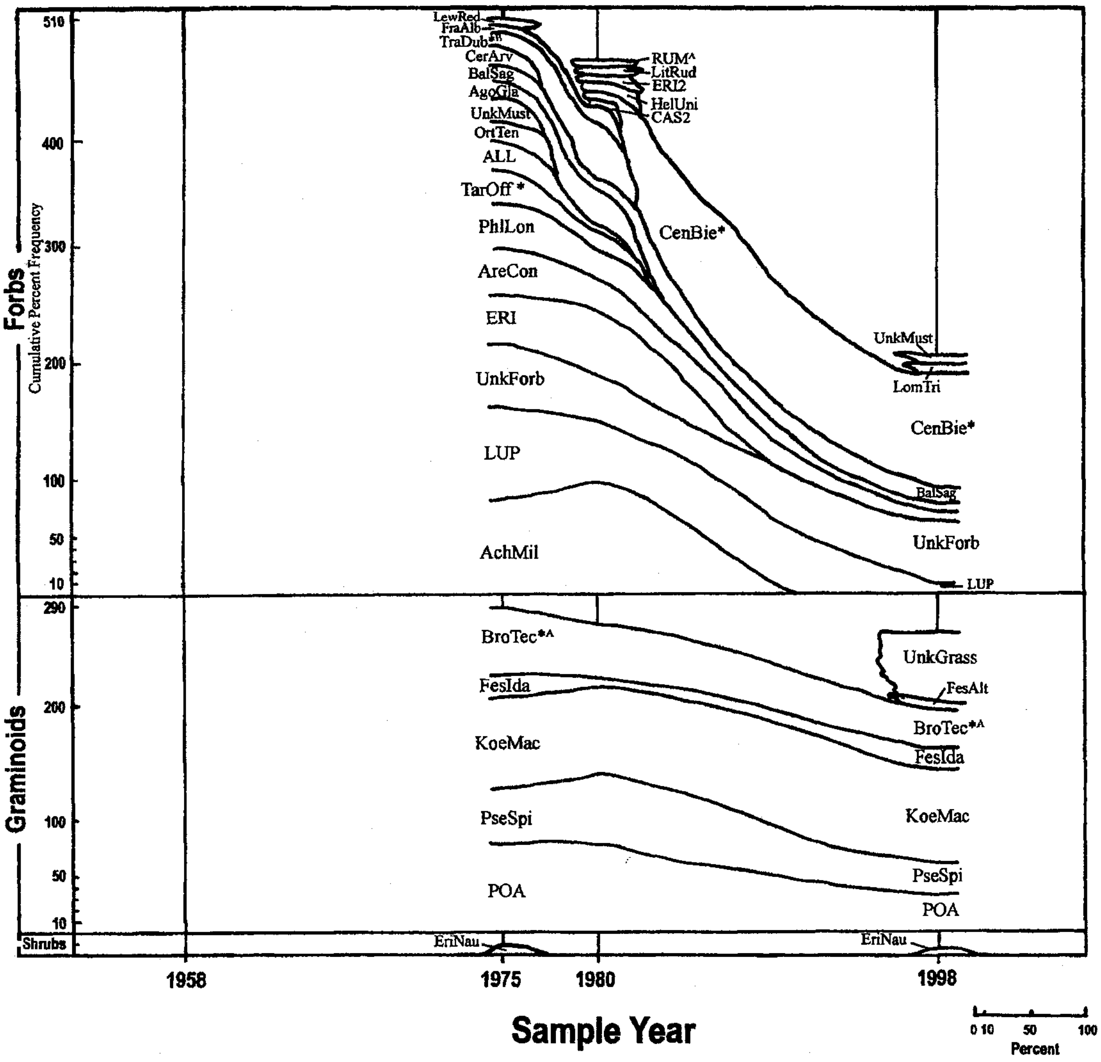


Fig.2: Facies diagram for BA1 in west ecoregion, southern edge Sapphire Mountains, Montana. Sample years are at vertical lines. Intervals between samples conceptualized. Cumulative frequency percents are diagrammed to scale by lifeform. * = non-native species; A= annual; B= biennial (Species abbreviations listed in Appendix B).

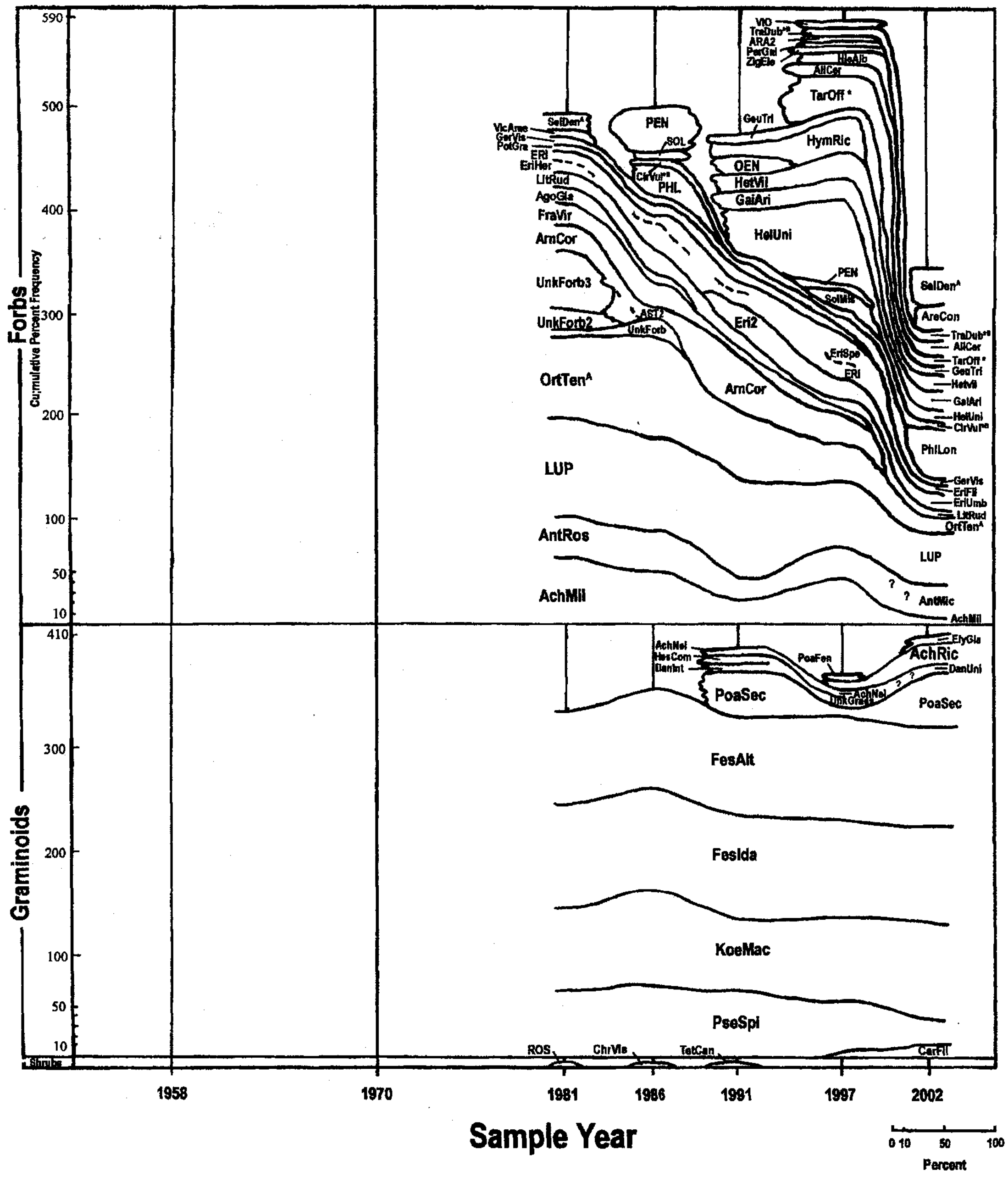


Fig.3: Facies diagram for SL1 in southwest ecoregion, Sapphire Mountains, Montana. Sample years are at vertical lines. Intervals between samples conceptualized. Cumulative frequency percents are diagrammed to scale by lifeform. * = non-native species; A= annual; B= biennial (Species abbreviations listed in Appendix B).

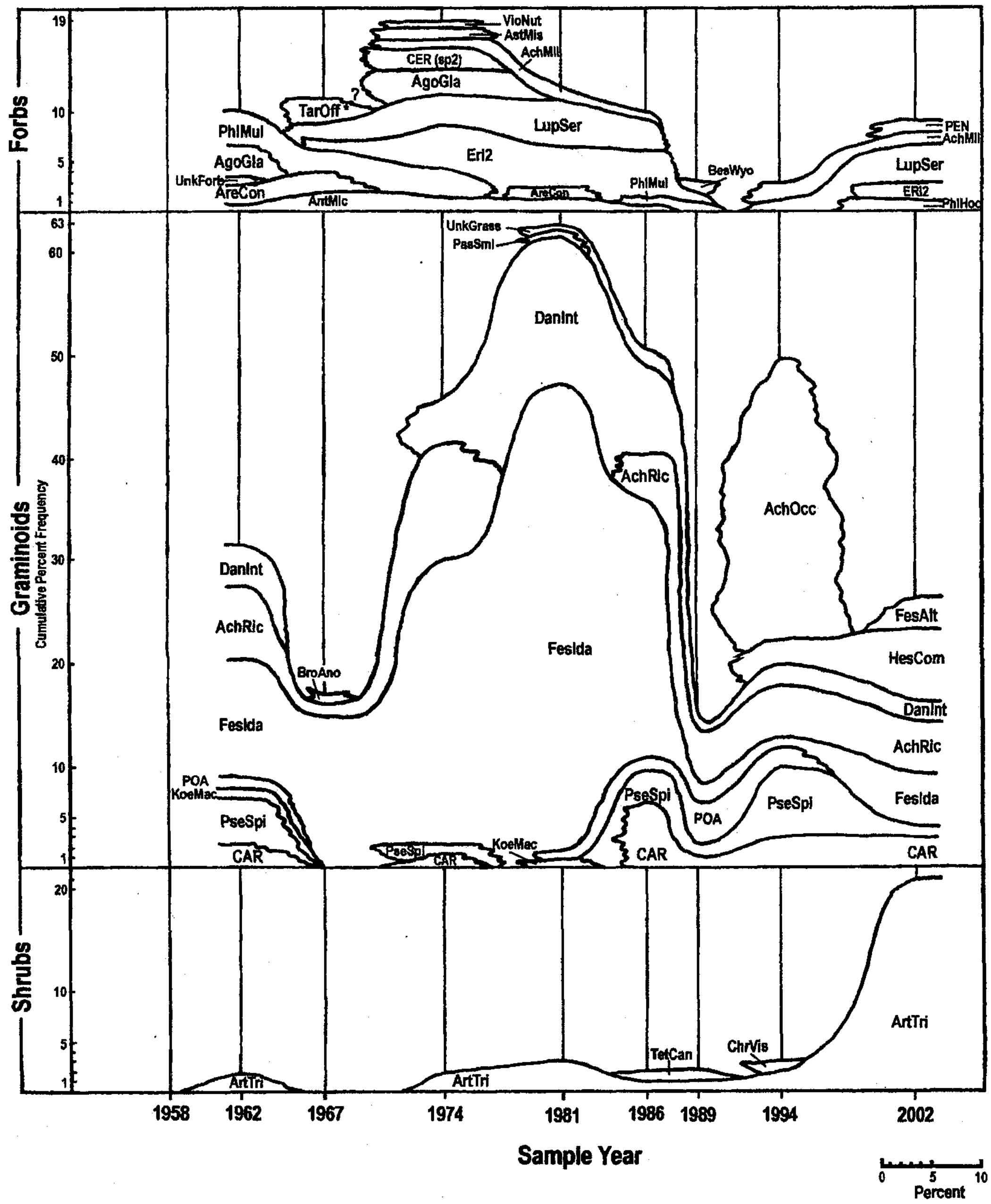


Fig.4: Facies diagram for E-22 in south ecoregion, inside Blacktail exclosure (ungrazed area), Yellowstone National Park. Sample years are at vertical lines. Intervals between samples conceptualized. Cumulative frequency percents are diagrammed to scale by lifeform. * = non-native species; A= annual; B= biennial (Species abbreviations listed in Appendix B).

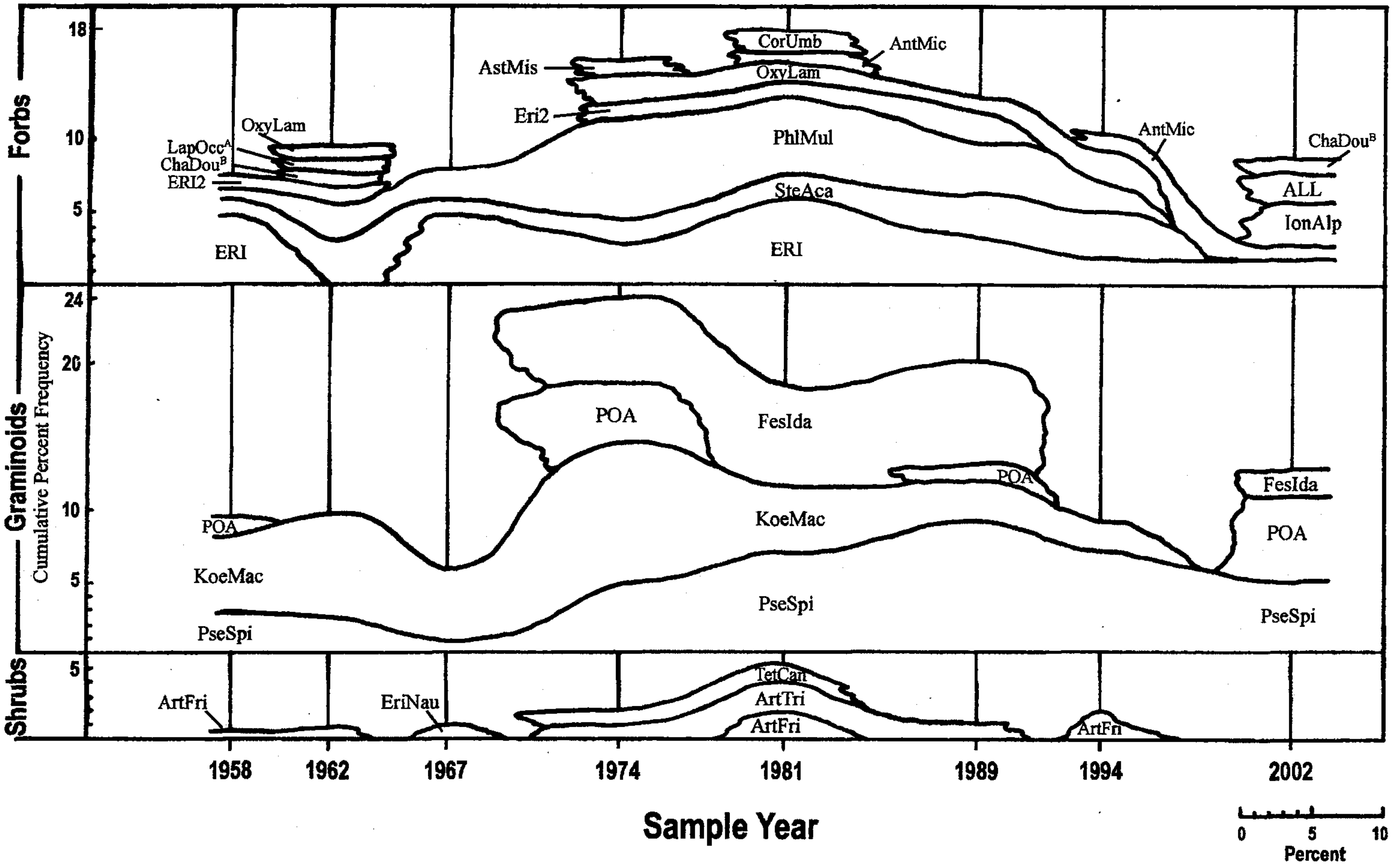


Fig.5: Facies diagram for F-11 in south ecoregion, located outside of Blacktail exclosure (grazed area). Sample years are at vertical lines. Intervals between samples conceptualized. Cumulative frequency percents are diagrammed to scale by lifeform. * = non-native species; A= annual; B= biennial (Species abbreviations listed in Appendix B).

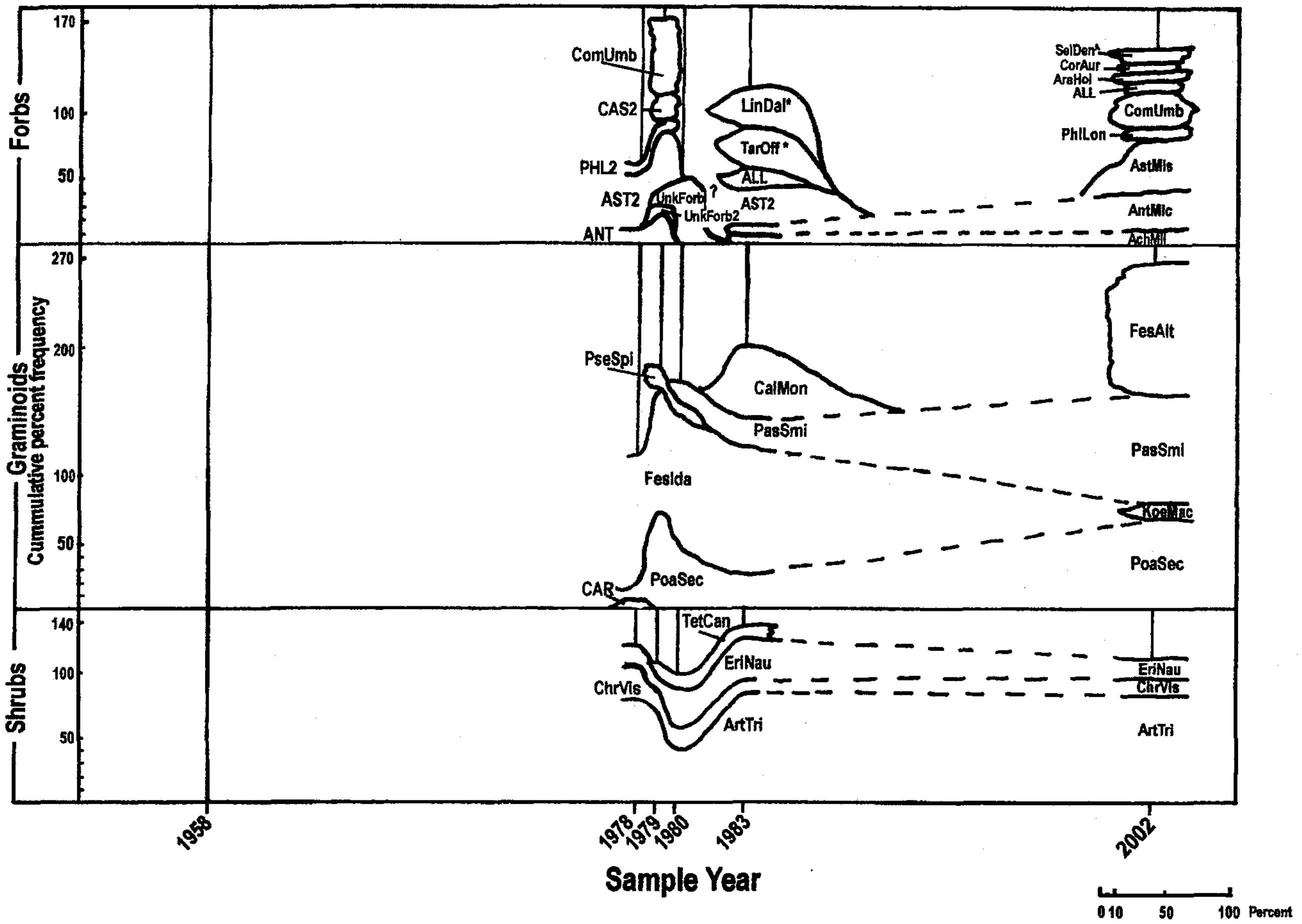


Fig.6: Facies diagram for MatBrn3 in southwest ecoregion. Area burned in 1978. Transect adjacent to MatBrn2. Sample years are at vertical lines. Intervals between samples conceptualized. Dashed lines indicate possible, but not verified, continuation of species. Cumulative frequency percents are diagrammed to scale by lifeform. * = non-native species; A= annual; B= biennial (Species abbreviations listed in Appendix B).

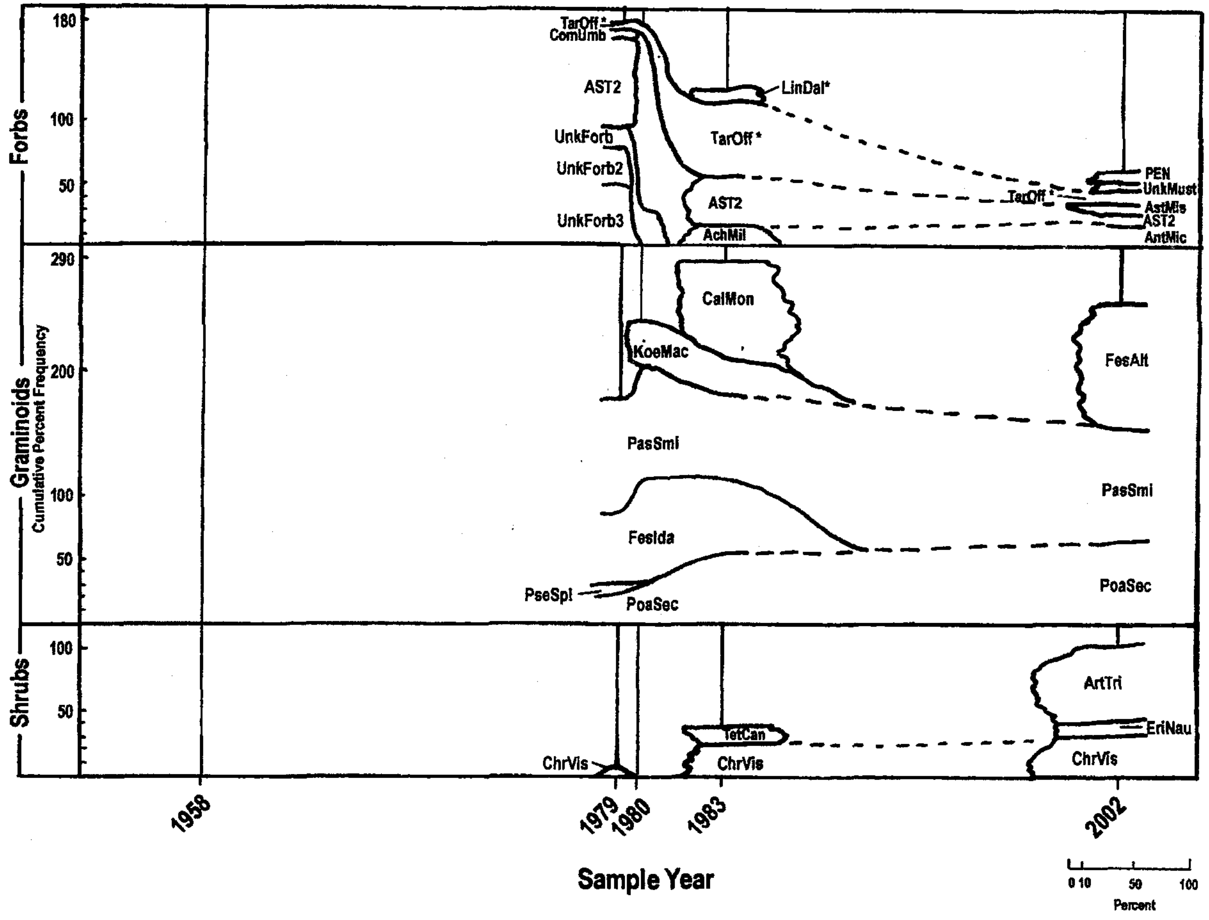


Fig.7: Facies diagram for MatBrn2 in southwest ecoregion. Area burned in 1978. Transect adjacent to MatBrn3. Sample years are at vertical lines. Intervals between samples conceptualized. Dashed lines indicate possible, but not verified, continuation of species. Cumulative frequency percents are diagrammed to scale by lifeform. * = non-native species; A= annual; B= biennial (Species abbreviations listed in Appendix B).

Appendix B: Species codes and characteristics

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Code	Genus/species	Common name	Lifecycle	Origin	Family
AchMil	Achillea millefoilum	Yarrow or Milfoil	Perennial	Native	Asteraceae
AchNel	Achnatherum nelsonii (Stipa nelsonii Scribn.)	Nelson's needlegrass	Perennial	Native	Poaceae
AchOcc	Achnatherum occidentale (Stipa occidentalis Thurb.ex S. Wats)	western needlegrass	Perennial	Native	Poaceae
AchRic	Achnatherum richardsonii (Stipa richardsonii Link)	spreading needlegrass	Perennial	Native	Poaceae
AgoGla	Agoseris glauca	False dandelion	Perennial	Native	Asteraceae
ALL	Allium sp.	wild onion	Perennial	Native	Liliaceae
AllCer	Allium cernuum	Nodding Onion	Perennial	Native	Liliaceae
ANT	Antennaria sp.	pussytoes	Perennial	Native	Asteraceae
AntMic	Antennaria microphylla	Rosy Pussytoes	Perennial	Native	Asteraceae
AntRos	Antennaria rosea	Rosy Pussytoes	Perennial	Native	Asteraceae
ApeInt	Apera interrupta (Agrostis interrupta L.)	Interupted bentgrass	Annual	Introduced	Poaceae
ARA2	Arabis sp.	rockcress	Biennial/Peren	Undetermin	Brassicaceae
AraHol	Arabis holboellii	Holboell's Rockcress	Biennial	Native	Brassicaceae
AreCon	Arenaria congesta	Ballhead Sandwort	Perennial	Native	Caryophyllaceae
ArnCor	Arnica cordifolia	Heartleaf Arnica	Perennial	Native	Asteraceae
ArtFri	Artemisia frigida	Fringed sagewort	Perennial	Native	Asteraceae
ArtTri	Artemisia tridentata	Big Sagebrush	Perennial	Native	Asteraceae
AST	Aster sp.	aster	Unknown	Undetermined	Asteraceae
AST2	Astragalus sp.	milk-vetch	Annual/Perennial	Native	Fabaceae
AstMis	Astragalus miser Dougl.	Weedy Milkvetch	Perennial	Native	Fabaceae
BalSag	Balsamorhiza sagittata	Arrowleaf balsamroot	Perennial	Native	Asteraceae
BesWyo	Besseya wyomingensis	Prairie kittentails	Perennial	Native	Scrophulariaceae
BroAno	Bromus anomalus	Nodding brome	Perennial	Native	Poaceae
BroJap	Bromus japonicus	Japanese Brome	Annual	Introduced	Poaceae
BroTec	Bromus tectorum	Cheatgrass or Downy Brome	Annual	Introduced	Poaceae
CalMon	Calamagrostis montanensis	Prairie Reedgrass	Perennial	Native	Poaceae
CAR	Carex sp.	sedge	Perennial	Native	Cyperaceae

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Code	Genus/species	Common name	Lifecycle	Origin	Family
CarFil	Carex filifolia	Threadleaf Sedge	Perennial	Native	Cyperaceae
CarNut	Carduus nutans	Musk Thistle Nodding Thistle	Biennial	Introduced	Asteraceae
CAS2	Castilleja sp.	paintbrush	Perennial	Native	Scrophulariac
CenBie	Centaurea biebersteinii (C. maculosa auct.non Lam)	spotted knapweed	Biennial/Perenial	Introduced	Asteraceae
CER2	Cerastium sp.	chickweed	Annual/Perenial	Undetermined	Caryophyllac
CerArv	Cerastium arvense L.	Field Chickweed	Perennial	Native	Caryophyllac
ChaDou	Chaenactis douglasii	Dusty maiden	Biennial/Perenial	Native	Asteraceae
ChrVis	Chrysothamnus viscidiflorus	Rabbitbrush	Perennial	Native	Asteraceae
CirVul	Cirsium vulgare	Common Thistle	Biennial	Introduced	Asteraceae
ComUmb	Comandra umbellata	Pale bastard toadflax	Perennial	Native	Santalaceae
CorAur	Corydalis aurea	Golden Corydalis	Biennial	Native	Funariaceae
DanInt	Danthonia intermedia	Timber Oatgrass	Perennial	Native	Poaceae
DanUni	Danthonia unispicata	One-spike oatgrass	Perennial	Native	Poaceae
DiaArm	Dianthus armeria L.	Deptford Pink	Biennial	Introduced	Caryophyllaceae
DraNem	Draba nemorosa L.	Woods Draba	Annual	Native	Brassicaceae
ElyGla	Elymus glaucus	Blue Wild Rye	Perennial	Native	Poaceae
ERI	Erigeron sp.	fleabane	Unknown	Undetermin	Asteraceae
ERI2	Eriogonum sp.	wild buckwheat	Annual/Perennial	Undetermined	Polygonaceae
EriCou	Erigeron coulteri	Coulter's daisy	Perennial	Native	Asteraceae
EriFil	Erigeron filifolius	Thread-leafed fleabane	Perennial	Native	Asteraceae
EriHer	Eriogonum heracleoides	Parsnip-flower wild	Perennial	Native	Polygonacea
EriNau	Ericameria nauseosus (Chrysothamnus nauseosus(Pallas) Britton)	Gray rabbitbrush	Perennial	Native	Asteraceae
EriSpe	Erigeron speciosus	Showy Fleabane	Perennial	Native	Asteraceae
FesAlt	Festuca altaica (F. scabrella Torr.ex Hook.)	Rough fescue	Perennial	Native	Poaceae
FesIda	Festuca idahoensis	Idaho fescue	Perennial	Native	Poaceae
FraAlb	Frasera albicaulis	White std Frasera	Perennial	Native	Gentianaceae

Appendix B: Species codes and characteristics

Code	Genus/species	Common name	Lifecycle	Origin	Family
FraVir	Fragaria virginiana	Blueleaf or Virginia	Perennial	Native	Rosaceae
GaiAri	Gaillardia aristata	Blanket Flower	Perennial	Native	Asteraceae
GerVis	Geranium viscosissium	Sticky Wild Geranium	Perennial	Native	Geraniaceae
GeuTri	Geum triflorum	Prairie Smoke-Old Man's	Perennial	Native	Rosaceae
GriSqu	Grindelia squarrosa	Curly-cup gumweed	Biennial	Native	Asteraceae
HelUni	Helianthella uniflora	Rocky Mountain dwarf	Perennial	Native	Asteraceae
HesCom	Hesperostipa comata (Stipa comata Trin.&Rupr.)	needle and thread	Perennial	Native	Poaceae
HetVil	Heterotheca villosa (Chrysopsis villosa	Hairy false golden aster	Perennial	Native	Asteraceae
HieAlb	Hieracium albiflorum	White-flower hawkweed	Perennial	Native	Asteraceae
HymRic	Hymenoxys richardsonii	Colorado rubberweed	Perennial	Native	Asteraceae
HypPer	Hypericum perforatum	St. John's wort or Goatweed	Perennial	Introduced	Hypericaceae
IonAlp	Ionactis alpina (Aster scopulorum Gray)	crag aster/ lava aster	Perennial	Native	Asteraceae
KoeMac	Koeleria macrantha (K. cristata auct. P.p. non Pers.)	Prairie Koeler's grass/junegrass	Perennial	Native	Poaceae
LapOcc	Lappula occidentalis (Lappula redowskii (Hornem.) E.	Flat-spine sheepburr	Annual	Native	Boraginaceae
LewRed	Lewisia rediviva	Bitterroot	Perennial	Native	Portulacaceae
LinDal	Linaria dalmatica	Dalmatian Toadflax	Perennial	Introduced	Scrophulariac
LinSep	Linanthus septentrionales	Northern Linanthus	Annual	Native	Polemoniaceae
LitRud	Lithospermum ruderale	Wayside Gromwell Puccoon	Perennial	Native	Boraginaceae
LomTri	Lomatium triternatum	Nine-leaf lomatium	Perennial	Native	Umbelliferae
LUP	Lupinus sp.	lupine	Annual/Peren	Native	Fabaceae
LupSer	Lupinus sericeus	Blue-bonnet Lupine Silky Lupine	Perennial	Native	Fabaceae
LupSub	Lupinus subcarnosus	Texas bluebonnet	Perennial	Native	Fabaceae
MinObt	Minuartia obtusiloba (Arenaria obtusiloba)	alpine stitchwort	Perennial	Native	Caryophyllaceae
OEN	Oenothera sp.	Primrose	Annual/Peren	Native	Onagraceae
OrtTen	Orthocarpus tenuifolius	Twin-leaved Owl Clover	Annual	Native	Scrophulariaceae
OxyLa	Oxytropis lambertii	Colorado Loco Purple	Perennial	Native	Fabaceae
PasSmi	Pascopyrum smithii (Agropyron smithii Rydb.)	Western wheatgrass	Perennial	Native	Poaceae
PEN	Penstemon sp.	penstemon	Perennial	Native	Scrophulariac

Appendix B: Species codes and characteristics

Code	Genus/species	Common name	Lifecycle	Origin	Family
PerGai	Perideridia gairdneri	Yampah	Perennial	Native	Umbelliferae
PHL2	Phlox sp.	phlox	Perennial	Undetermin	Polemoniace
PhlHoo	Phlox hoodii	Hood's phlox	Perennial	Native	Polemoniaceae
PhlLon	Phlox longifolia	Long-leaf phlox	Perennial	Native	Polemoniaceae
PhlMul	Phlox multiflora	Rocky mountain phlox	Perennial	Native	Polemoniace
POA	Poa sp.	bluegrass	Annual/Perennial	Undetermined	Poaceae
PoaFen	Poa fendleriana	Fendler's Muttongrass	Perennial	Native	Poaceae
PoaSec	Poa secunda (P. sandbergii and juncifolia Scribn.)	Curly bluegrass	Perennial	Native	Poaceae
PotGra	Potentilla gracilis	Soft Cinquefoil	Perennial	Native	Rosaceae
PseSpi	Pseudoroegneria spicata (Agropyron spicatum Pursh)	Bluebunch wheatgrass	Perennial	Native	Poaceae
ROS	Rosa sp.	rose	Perennial	Native	Rosaceae
RUM	Rumex sp.	sorrel	Annual/Perenial	Undetermined	Polygonaceae
SelDen	Selaginella densa	Compact clubmoss	Annual	Native	Sellaginellac
SOL	Solidago sp.	goldenrod	Perennial	Native	Asteraceae
SolMis	Solidago missouriensis	Missouri Goldenrod	Perennial	Native	Asteraceae
SteAca	Stenotus acaulis (Haplopappus acaulis (Nutt.) Gray)	stemless mock goldenweed	Perennial	Native	Asteraceae
SymAlb	Symphoricarpos albus	Common Snowberry	Perennial	Native	Caryophyllac
TarOff	Taraxacum officinale	Common Dandelion	Perennial	Introduced	Asteraceae
TetCan	Tetradymia canescens	Gray horse-brush	Perennial	Native	Asteraceae
ThlArv	Thlapsi arvense	Fanweed Penny-Cress	Annual	Introduced	Brassicaceae
TraDub	Tragopogon dubius	Goat's-beard	Biennial	Introduced	Asteraceae
UnkMust	unknown mustard (Crucifera)	unknown mustard	Annual/Perenial	Undetermined	Brassicaceae
VerArv	Veronica arvensis	Common speedwell	Perennial	Native	Scrophulariac
VicAme	Vicia americana	American Vetch	Perennial	Native	Fabaceae
VIO	Viola sp.	violet	Unknown	Undetermin	Violaceae
VioNut	Viola nuttallii	Nuttall's violet	Perennial	Native	Violaceae
VulOct	Vulpia octoflora	Common Sixweeksgrass	Annual	Native	Poaceae
ZigEle	Zigadenus elegans	mountain death-camas	Perennial	Native	Liliaceae

CHAPTER 3

The dynamic nature of "climax" habitat and potential vegetation types: 30 years of grassland monitoring in Montana

Summary

1. Potential vegetation or habitat types are used extensively in many parts of the U.S. to inventory and classify grasslands for resource management. This classification assumes that plant community indicator species are faithful to specific abiotic site conditions and persist unchanged on a landscape until the area undergoes a climatic shift.

2. I test key assumptions of species-based classification methods - namely community equilibrium and indicator species stability - using monitoring data from 35 grassland sites located across western Montana. Each site was periodically resampled over 30 years.

3. I found little support in the historical data for grassland stability as predicted by the habitat type concept. Using the habitat type key, 55% of the sites changed their classification over 30 years. At several sites, changes occurred within 5-10 years. Similar patterns of change were detected in moist and dry sites.

4. Indicator species were actually found to be more dynamic over time than plant communities in general, as indicated by Bray-Curtis ordination and similarity indices. Changes in dominance of several indicator species correlated with fluctuations in temperature and precipitation over 30 years, but the specific factors vary by species.

5. The dynamics of Montana's bunchgrass communities over the past 30 years are better supported by non-equilibrium, multiple-pathway models of succession than linear, climatic-climax models on which some classification systems are based. Accurate assessment and monitoring of these grasslands require more realistic models of plant communities that are developed from regular sampling protocols spanning at least 15 years and that incorporate their dynamic nature.

Key-words: bunchgrass, habitat type, monitoring, multiple pathways, potential vegetation, succession, vegetation dynamics.

Introduction

Classification of biotic communities is essential in ecology to organize information efficiently, communicate community characteristics easily, and treat like groups similarly. In the classification process, names are assigned to a community based on a classification key, the key indicates some expected potential for the community under specific assumptions, and the community is managed according to guidelines designed to meet those potentials. Once a classification name is assigned to a plant community, the label usually has a profound effect on how each plant community is treated by managers on a day-to-day basis and how its long-term fate is perceived. Management practices usually consist of techniques or policies that have worked successfully for the particular named community in the past. Recently, however, the debate over how to classify ecosystems has resurfaced because some conservationists feel that species-based data is the best tool to portray changes in biodiversity over time while others argue that habitat or spatial classifications based on changes in environmental characteristics capture trends better (Pickup *et al.* 1998, Pressey 2004). The controversy over the merits of species-based versus land type-based classifications to conservation indicates that ecologists and managers alike are concerned with what a community is named because it affects assessment, management and planning (Brooks *et al.* 2004). What are the consequences, however, when a community is assigned a label that does not accurately portray its true character? A specific classification at a local site may often be questioned by managers. Rarely, however, is the classification system itself examined for its appropriateness to the community or for its underlying premises once it is in common use.

The dynamic nature of ecosystems and their abiotic controls are increasingly well-recognized at both the community and ecosystem scales. Rapidly-changing communities present several challenges to both ecologists and managers – challenges to reevaluate old tools and concepts and challenges to develop new methods of assessing plant communities that incorporate their dynamic qualities. Grassland communities are particularly problematic because they have been shown to be very sensitive to fluctuations in temperature and precipitation (Alward *et al.* 1999, Brown *et al.* 2001, Knapp & Smith 2001, Shaw *et al.* 2002), to grazing intensity (Frank & McNaughton 1993, Mack & Thompson 1982, Schlesinger 1990), and to fire (Singer & Harter 1996). Their functioning and processes are also affected by non-native species (Mack 1989).

In the past three decades, successional theory in plant communities has undergone a shift from stable equilibrium models (Clements 1916, Tansley 1935) to non-equilibrium models, including the state-and-transition model (Westoby 1989), threshold model

(Friedel 1991, Laycock 1991, May 1977), multiple steady states and pathways model (Blatt *et al.* 2001, Cattelino *et al.* 1979, McCune & Allen 1985, Tausch *et al.* 1993), and chaos model (Stone & Ezrati 1996). The shifts reflect the challenge of reevaluating old successional models in terms of increasing amounts of long-term data. During the same time period, however, many tools that rangeland managers use to classify and monitor grasslands and to assess range quality have remained unchanged. In the United States, habitat-type classifications, range site, and range condition are all firmly rooted in equilibrium and climax theory (Daubenmire 1942, Dyksterhuis 1949, Hall 1985, Sampson 1919). In Europe and parts of North America, Braun-Blanquet classifications are rooted in the stability of indicator species to particular site conditions.

This paper investigates the fallibility of classifying communities within a dynamic landscape using a static classification system (i.e. one created at a specific point in time) and what it means to managers who must plan appropriate land use practices and preserve long-term biodiversity within them. The study focuses on western Montana grasslands as a case study. The communities within these grasslands are classified according to the habitat-type system. However, the results are equally applicable to any dynamic environment that is classified using a species-based system. The classification of the Montana bunchgrass communities as "habitat types" infers that they exist in stable "climax" conditions and that they represent potential vegetation - if external disturbance is minimized and there is no severe change in climate. For the Montana grasslands, I utilize the original data that were used to create the grassland classification system in Montana (Mueggler & Stewart 1980). I also utilize monitoring data from several different agencies, which span over 30 years. The data sets are used to: (1) test assumptions of stability in communities considered “climax” or potential vegetation; (2) characterize the patterns of change within the individual classifications; and (3) determine what environmental factors correlate with classification changes that occur in these grasslands.

Methods

DATA SETS

Monitoring data from 35 sites managed by the Bureau of Land Management and Montana Fish, Wildlife and Parks in southwestern Montana were obtained for this study (Fig. 3-1). The sites were chosen to represent the range of microclimates, elevations, and years of sampling record that exist within the study area. All sites were permanently marked locations with at least 15 years of data records. Site selection was limited to those that were: (a) sampled at least three times in their historic record; (b) sampled using estimates of canopy cover within 2 x 5 dm microplots; and (c) last described between 1999 and 2002. Canopy cover measures were used because the habitat-type classification was created using these methods (Daubenmire 1959). Cover classes were the same as those used in the western Montana grassland classification study (Mueggler & Stewart 1980) and by Daubenmire (1959). The most recent sampling intervals were limited to sites sampled after 1999 to minimize climatic variation. Between 1999 and 2002, temperatures were comparable throughout southwestern Montana and the state was in drought conditions (Western Regional Climatic Center 2002).

When the plots were last sampled, most were relatively undisturbed by grazing, weed control, or other recent anthropogenic disturbances but they did contain introduced species. Sites were not eliminated from analysis if they contained non-native species because non-natives were also part of the grassland community in the 1970s when the habitat-type classification was created (Mueggler & Stewart 1980) and they have been considered part of the community in many other habitat-type classifications (Hansen *et al.* 1984, Hirsch 1985, Tisdale 1986).

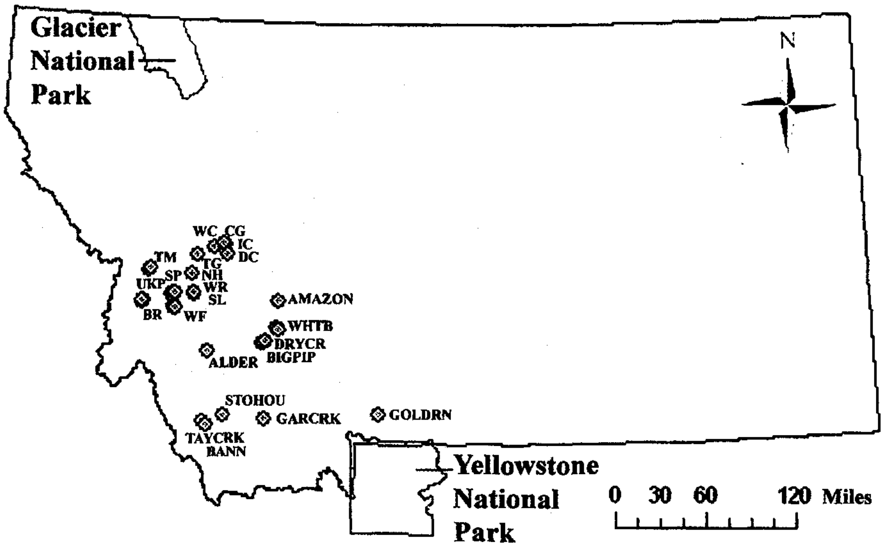

Figure 3-1: Location of permanently-marked monitoring sites. All sites are between 45.1° and 46.9° N latitude and 110.8° and 114.0° W longitude.

Because none of the 35 monitoring sites were sampled in the 1970s for the original habitat-type classification, it was necessary to recreate some of the habitat-type classification process to test whether classifications that were made in 2002 might have different outcomes if they had been done 30 years ago. Originally, the habitat-type classification for Montana grasslands was created by: a) collecting detailed coverage data on the current vascular plant species, non-vascular lifeforms, and surface characteristics between 1971-1973; b) classifying the current vegetation data into groups with similar characteristics using Sorenson's similarity coefficient (Sorensen 1948), Bray-Curtis ordination (Bray & Curtis 1957) and cluster analysis (Sneath & Sokal 1973); and c) determining the soil characteristics and moisture regimes of each habitat type to characterize the future yield potential. Using the results of similarity analyses and the physiological requirements for the groups, a classification key to the different habitat types was ultimately created for western Montana grasslands. For this investigation, I obtained the original microplot data from all 365 plots that were used to create Mueggler and Stewart's (1980) classification so I could recreate the similarity analysis and the ordination. I also obtained a list of plot numbers that were originally assigned to each habitat type in the 1970s and the habitat-type key for these grasslands.

NOMENCLATURE

During the 30 years covered by this study, nomenclature has changed dramatically. Over 40% of the indicator species used in the habitat-type key for western Montana grasslands have been renamed. While name changes are an ongoing and often controversial process, nomenclature in this study was standardized to the currently accepted genus and species listed on the Biology of North America Program web site (Kartesz 1998). In all analyses, origin designations for introduced species in Montana followed Rice (2004). Life form and life history designations followed Hitchcock and Cronquist (1973). Response to grazing by species was designated according to the American Society of Range Management (Willard 2003a) and Wroe et al. (2000).

DATA ANALYSIS

To test whether habitat-type classifications changed over time, data sets were analyzed in three ways. First, the community data for each sampling period was habitat-typed using the classification key – just as a manager would use the key to monitor the rangeland in each sample year. Second, a Sorenson's similarity coefficient was calculated between each historic and each monitoring plot to determine which were most similar to each other. Third, the position of current plots in relation to locations of similar habitat-types in ordination space was tested using Bray-Curtis ordination.

To measure the stability of the classifications using the habitat type key, the historic data were divided into three moisture categories and seven five-year sampling intervals. The moisture categories assigned were based on the relative moisture needs of individual species within each sample and on the distribution of sites within a non-metric multidimensional scaling diagram that had a distinct moisture gradient along its dominant axis (see chapter 1 results). Within each five-year interval, sites with sampling dates that fell within the interval were classified to habitat type according to cover class data and indicator species in the key developed by Mueggler and Stewart (1980). Past field investigators had classified some of the sites to habitat type on their field forms during sampling, which helped validate many decisions during the keying process. The field classification was especially important at sites where the key required a decision as to whether the landscape was considered shrub- or grass- dominated at the time of the sampling. The canopy coverage of key grasses and shrubs was graphed to show the amount of variation in coverage of individual species during all the years of record and the long-term trends in the species over time. Short-term (5-6 year) trends in key grass species were analyzed by tallying the amount of change in canopy cover within only the last sampling interval (1995 to 2002). The trends were compared with classification changes to determine whether the changes in coverage of the key species were great enough over the six years to ultimately affect classification.

Many of the test sites had data gaps at some point in their sampling history. The effect of data gaps on change patterns was tested by grouping plots with similar sampling histories and then comparing the percentage of plots that changed with the percentage of plots that had different gap lengths in the data. The minimal sampling time for change patterns to emerge was examined by grouping plots into five-year intervals and computing a percentage of change for each interval.

To test whether the habitat-type classification for each monitoring plot would have been different if the classifications had been done in the 1970s with the original data set rather than 2002, the sites were compared using the same similarity indices that were used in the original grassland work. Sorenson's similarity index was calculated on entire plot compositions between each monitoring plot and each original Mueggler and Stewart (1980) sample plot. It was calculated within VTAB Ecosystem Reporter (Emanuel 1999) as follows: SI= (2*sum(x or y, whichever is lower)/ (N1+N2)), where x and y are the percent cover of each species in samples 1 and 2 multiplied by 1000; N1 and N2 are the total percent cover for all species in samples 1 and 2 multiplied by 10 (Mueller-Dombois & Ellenburg 1974). Calculations were made on raw percent canopy cover data from each plot (i.e. no data standardizations or transformations). No species were omitted from the calculations if they occurred in the composition data. The compositions were based on mean percent cover values for each plant species found in the microplots. From the similarity analysis, the one Mueggler and Stewart (1980) plot with the highest similarity to each monitoring plot was determined. The monitoring plots were then given the same habitat-type classification as their most similar Mueggler and Stewart plot and examined for changes in classification between the oldest and most recent time intervals.

Bray-Curtis ordination analysis was used to examine how the overall compositions of monitoring plots related to the compositions of original habitat-type samples in ordination space and to examine whether the composition of monitoring plots changed in that ordination space over time. If compositions were stable over the sampling intervals, the historic and current monitoring plots for the same locations were expected to lay in close proximity to each other within the ordination diagram. The Bray-Curtis analysis used the same data format as described above for the similarity analysis, and the ordination was conducted within PCOrd (McCune & Mefford 1999). All historic and monitoring data were analyzed together and both the historic and current sites were well-integrated within the ordination space, indicating that the monitoring sites did not have significantly different compositions than bunchgrass sites used to create the grassland classification in the 1970s. Sorensen (Bray-Curtis) distances and variance-regression endpoints were used for the ordination. Variance-regression endpoints were used instead of the original Bray-Curtis endpoints because, according to McCune (2002)), the variance-regression endpoints were in use in this ordination by 1973 – well before ordination analysis on the western Montana grasslands would have been started.

The influence of variations in non-native species and grazing on changes in classification over the short-term was measured using Kruskal-Wallis non-parametric tests. For each site that had data in both the 1995-1999 and 2000-2002 intervals, the total percentage of species that were classified as non-native or as a grazing indicator (i.e. increaser, decreaser, or invader) were tallied by plot and by time interval using VTAB Ecosystem Reporter (Emanuel 1999). For each variable, the differences in cover between the two intervals were computed and compared for significant statistical differences between three site groups: (1) those that had completely changed classification; (2) those that had changed only in phase; and (3) those that had not changed. Differences were analyzed using Kruskal-Wallis rank sum tests for multiple comparisons within S-Plus (Insightful Corporation 2001).

Correlations between variations in temperature and moisture, the percent cover of select indicator species, and the changes in site classification were tested within S-Plus using linear regression and Kruskal-Wallis tests. Precipitation and temperature data from the nearest climate station to each site was obtained from the Western Regional Climatic Center (2002). Nine climate stations were paired with the 35 sites. All climate data were matched to site by the year sampling was done and were averaged into seasonal values for each sample year. Seasons included fall (September - October), winter (November - March), spring (April – May), and summer (June – August).

The effects of climate variables on actual canopy cover of individual grass species were tested using linear regression in S-Plus. Total canopy cover of nine key indicator grasses and shrubs were correlated with mean precipitation and temperature by season. The correlations used all stations that contained the select indicator plant and all monitoring years in which it was present during sampling. Canopy cover was compared with each of the eight seasonal climatic variables separately to determine whether temperature or precipitation during certain seasons influenced canopy cover changes in the select grasses over the 30 years. In addition, total canopy coverage was also related to total yearly precipitation and average annual temperature on a site-by-site basis to determine if less restricted climate measures would also show significant correlations.

To test whether seasonal climatic variations correlated with how much classification changed at each site using the habitat-type key, data were divided into short-term variations (i.e. differences in temperature and precipitation between the 1995-1999 and 2000-2002 time intervals) and long-term variations (differences in temperature and precipitation between the time the site was first sampled and the time it was last sampled). Kruskal-Wallis rank sum tests were used to show whether one of three classification groups (i.e. changed habitat type, phase change or no change) was significantly different from the other two based on the influence of eight seasonal temperature and precipitation variables. Differences between each of the eight climate variables were tested for group effects separately. In the Kruskal-Wallis analyses, if all of the sites that changed classification correlated with a general increase in spring precipitation during the sample year, for example, then significant statistical differences should be apparent among the three groups.

Results

Over the past 30 years, grasslands in western Montana have varied enough in both composition and structure to significantly affect the way sites were classified through time. In the three methods of analysis used to explore compositional changes, classifications have changed in 43-55% of the sites. The temporal scale of change depended on the resolution of the sample data.

COMMUNITY CHANGES PORTRAYED BY USING CLASSIFICATION KEY

The habitat-type key developed by Mueggler and Stewart (1980) gave the highest percentage of sites that changed classification (55%). Keying each sample interval showed that sufficient changes in indicator species coverage could occur in as little as five years to change classification and that a similar magnitude of change occurred in dry to moist grassland environments (Table 3-1). Both shrub-dominated and grass-dominated sites experienced change to varying degrees. Some sites completely changed classification (GARCRK, BR1, FG1, and TG1). One shrub-dominated site (GARCRK) exhibited a complete change in community structure due to shrub invasion. GARCRK had a five-fold increase in woody shrubs on the site in the 23 years, resulting in succession from a grass-dominated to shrub-dominated community that dramatically changed its habitat-type classification over time. Similarly, the BIGPIP7 site showed evidence of succession in that one type of shrub replaced another (Table 3-1). *Purshia tridentata* was gradually eliminated from BIGPIP7 over 20 years, while desirable bunchgrasses remained fairly stable and *Artemisia tridentata* doubled in canopy coverage. Other grass- and shrub-dominated sites did not change their main type at all; but they did change phase within the type quite frequently as minor species fluctuated in dominance over time (ALDER, SL1). Some grass-dominated sites even showed complete reversals in phase within five years (DRYCR3).

Table 3-1: Plant association changes at select locations in southwestern Montana from 1970 to 2002 using grassland habitat-type (indicator species) key

Site Code[1]	Yrs of record	Elevation (m)	Sampling Period 1970-1975	1976-1980	1981-1984	1985-1989	1990-1994	1995-1999	2000-2002	Degree of change
Dry sites										
BIGPIP7	20	1748	-[2]	-	k[3]	j	-	j	j	h.t.
BIGPIP9	21	1667	-	j	j	j	-	-	j	none
DRYCR3	22	1636	-	d1	d	d1	-	d1	d1	phase
DRYCR6	22	1667	-	d	d	d1	-	-	d1	phase
GOLDRN	22	2182	-	a	-	a	a	a	a	none
STOHOU1	20	1736	-	d	-	d	-	d	-	none
WHTB28	21	1519	-	e	h	-	h	h	h	h.t.
WHTB34	21	1515	-	d1	h	h1	d	h1	h	h.t.
Intermediate sites										
AMAZON	20	1833	-	-	a	b	b	b	b	h.t.
BANN1	20	1824	-	j	-	j	-	j	-	none
BR2	28	1542	d1	b	-	-	-	d	d	h.t.
BR3	28	1417	d	d	-	-	-	d	d	none
CG1	21	1628	-	-	d1	d1	d1	d1	d1	none
DC2	18	1436	-	-	i	i	-	-	i	none
GARCRK1	23	2246	-	a	-	-	j	i	i	h.t.
MP1	15	1824	-	-	-	b	b	b	c	h.t.
SL1	21	1828	-	c2	-	c2	c2	c1	c1	phase
TAYCR1	20	1955	-	i	i	-	-	i	-	none
TM1	27	1302	d1	d1	-	-	-	-	d1	none
TM2	27	1314	d1	d	-	-	-	-	d1	phase
TM3	27	1517	a	a	-	-	a	-	a	none
UKP	15	1947	-	-	-	a	a	a	a	none
WC3	21	1620	-	-	d1	d1	d1	d	d	phase
WF2	21	1824	-	c	-	c	c	c	c	none
WF3	21	1771	-	a	-	b	b	b	b	h.t.
WF4	21	1848	-	a	c	b	b	b	a	h.t.
WR1	20	1798	-	-	a	a	a	a	a	none
Moist sites										
ALDER	20	1848	-	i1	i1	i	i	i1	-	phase
BR1	28	1599	a	a	-	-	-	a	b	h.t.
FG1	18	1850	-	-	e1	e1	f	f	c1	h.t.
IC1	15	1798	-	-	-	c	c	c	c	none
NH1	15	1733	-	-	a	a	a	a	-	none
SP2	13	1818	-	-	-	f	f	c1	-	h.t.
TG1	18	1738	-	-	d1	a	a	a	a1	h.t.
WF1	22	1776	-	c	-	c	c	c	c	none

[1] Abbreviations for sites follow agency codes. See Figure 1 for location of sites.

[2] - = gap in data over time interval

[3] Letter changes denote change in habitat type
Number changes denote change in phase within a particular habitat type

Table 3-1 (continued): Plant association changes at select locations in southwestern Montana from 1970 to 2002 using grassland habitat-type (indicator species) key

Key to abbreviations

***Festuca idahoensis* Series**

a = Festuca idahoensis/Pseudoroegneria spicata
    a1 = Festuca idahoensis/Pseudoroegneria spicata (Achnatherum occidentale phase)
f = Festuca idahoensis/Carex filifolia

***Festuca altaica* Series**

b = Festuca altaica/Pseudoroegneria spicata
c = Festuca altaica/Festuca idahoensis
    c1 = Festuca altaica/Festuca idahoensis (Achnatherum richardsonii phase)
    c2 = Festuca altaica/Festuca idahoensis (Geranium viscosissimum phase)

***Pseudoroegneria spicata* Series**

d = Pseudoroegneria spicata/Poa secunda
    d1 = Pseudoroegneria spicata/Poa secunda (Hesperostipa comata phase)
h = Pseudoroegneria spicata/Bouteloua gracilis
    h1 = Pseudoroegneria spicata/Bouteloua gracilis (Liatris punctata phase)

***Hesperostipa comata* Series**

e = Hesperostipa comata/Bouteloua gracilis
    e1 = Hesperostipa comata/Bouteloua gracilis (Pascopyrum smithii phase)

***Artemisia tridentata* Series**

i = Artemisia tridentata/Festuca idahoensis
    i1 = Artemisia tridentata/Festuca idahoensis (Geranium viscosissimum phase)
j = Artemisia tridentata/Pseudoroegneria spicata

***Purshia tridentata* Series**

k = Purshia tridentata/Pseudoroegneria spicata

Both shrub and grass-dominated communities also had sites that appeared relatively stable with time. For some (e.g. IC1, UKP), the data covered only 15 years, which may have been too short to exhibit change at these particular sites. Although many sites changed classification within five years in Table 3-1, most sites retained the new classification for at least 10 years after the change occurred. Only the change from grassland to shrubland (e.g. FesIda/PseSpi to ArtTri/PseSpi at GARCRK) could not be shown to have occurred within five years because the site lacks 10 years of monitoring data before the transformation occurred. Therefore, sites with short sampling records or gaps of >15 years may appear stable in the sampling record. Species turnover averaged about 15 years before there was enough difference in composition or dominance to alter the assigned classification. WHTB34 was the only site that appeared to change more often. *Bouteloua gracilis* and *Poa secunda* coverage in WHTB34 varied with time, and the resulting phase changes gave the appearance of change every five years (Table 3-1). Many of the classification changes, except for shrub increases, were also shown to be reversible within the same short time frames. Whether the communities changed to shrubs because they reached some critical transition state (Westoby 1989), exceeded some ecological buffer (Jeltsch *et al.* 2000), reached a new polyclimax (Ellenburg 1959, Whittaker 1951), or experienced critical competitive interactions can not be determined with this limited data set.

The influence of data gaps on perceptions of change is shown in Table 3-2. No clear pattern was evident from the gap analysis. Similar percentages of plots changed classification (43-57%) whether they had long periods of sampling records or whether they had short or long gaps in those sampling records (Table 3-2). For example, plots with gaps ranging from 0 to10 years in 19 year records had similar percentages of classification change (i.e. 43%) as those with 10-15 year gaps in 30 year records (i.e. 50%). Regular sampling is crucial, however, to decipher trends in individual species and determine what causes the communities to change their composition at distinct points in time.

Over both the long and short term, fluctuations in the coverage of individual indicator species have significantly influenced the classification at current sites. In the past 30 years, the trends in the coverage of individual indicator species have varied by location, by year, across moisture gradients, and across a range of latitudes (Fig. 3-2). No clear change pattern that spanned all elevations or all moisture levels could be determined for any of the key species. Indicator species commonly increased quite significantly at one site (e.g. *P. spicata* 1992 at TG1 in Fig. 3- 2) while decreasing in the same year at another site (e.g. *P. spicata* 1992 at WHTB34). From 1995 to 2002 when western Montana experienced severe drought conditions, major grass species that define these bunchgrass communities decreased significantly at many locations (Table 3-3). Total grass coverage declined in 70% of the plots and many important bunchgrass species contributed to the total decline. Coverage of *Pseudoroegneria spicata* declined between 1995 and 2002 in almost 70% of the sites. *Festuca idahoensis* declined in 65% of them (Table 3-3). Corresponding decreases in total forb coverage were found in 75% of the sites. Ten plots had slight increases in moss and lichen coverage. Although some plots increased in the same indicator species over the six years, the increases were relatively small (most <10%) and they occurred only in a small number of plots (Table 3-3).

Table 3-2. Influence of gaps in sampling records on changes in habitat-type classifications

# Years of record	Total # plots	% of plots that changed h.t.	% Plots with No Gap	% Plots with 5 yr gap	% Plots with 10 yr gap	% Plots with >15 yr gap
<15 yrs	1	100%	0.00	100.00	0.00	0.00
15-19 yrs	7	43%	14.29	71.43	14.29	0.00
20-24	21	57%	9.52	71.43	19.05	0.00
25-30	6	50%	0.00	0.00	16.67	83.33

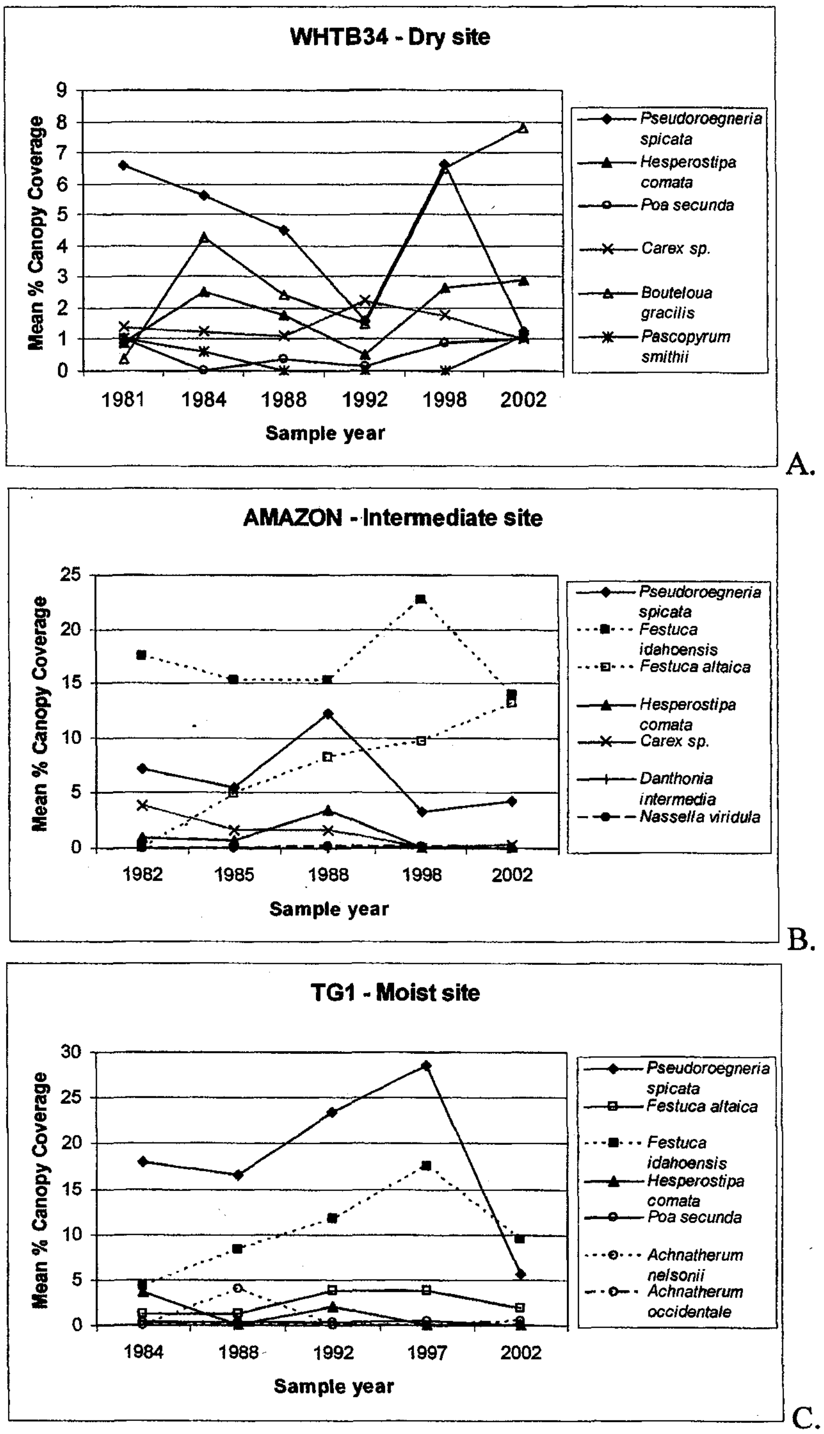

Figure 3-2: Fluctuations in key species used in habitat typing on three representative sites. a) Dry environment, lowest latitude, *Pseudoroegneria spicata/Bouteloua gracilis* h.t. in 2002; b) intermediate moisture, mid-latitude, *Festuca altaica/Pseudoroegneria spicata* h.t. in 2002; c) moist environment, highest latitude, *Festuca idahoensis/Pseudoroegneria spicata Achnatherum occidentale* phase in 2002.

Table 3-3: Percent of total plots[1] undergoing canopy cover change of key indicator species between 1995 and 2002

	Stable	**Decrease in canopy coverage**					**Increase in canopy coverage**				
Percent Change[1]	<1%	1-10%	11-20%	21-30%	>30%	total %	1-10%	11-20%	21-30%	>30%	total %
Festuca idahoensis	25.0	55.0	10.0	0.0	0.0	65.0	5.0	0.0	5.0	0.0	10.0
Festuca altaica	13.3	40.0	6.7	6.7	0.0	53.3	26.7	6.7	0.0	0.0	33.3
Pseudoroegneria spicata	9.1	50.0	4.5	9.1	4.5	68.2	22.7	0.0	0.0	0.0	22.7
Poa secunda	23.1	38.5	0.0	0.0	7.7	46.2	30.8	0.0	0.0	0.0	30.8
Artemisia tridentata	28.6	14.3	0.0	0.0	0.0	14.3	28.6	28.6	0.0	0.0	57.1

[1] Based on 23 of the study plots that have complete data between 1995 and 2002

Because the habitat-type key is based on minimum quantities and/or presence/absence of key indicator species, variations in these species – in both the long term and short term - significantly affect how the communities are classified.

The variations in the canopy coverage of indicator species and the fluctuation of supporting species within each community over time clearly suggest that these relatively undisturbed grassland sites are not static or stable in composition. A summary of the change pathways and how they affect classification of the Montana grasslands for the past 30 years are summarized in Fig. 3-3.

COMMUNITY CHANGES PORTRAYED BY SIMILARITY INDICES

Using similarity analysis, 43% of the sites changed classification over time (Table 3-4). However, over one third of the sites that changed were not in the same locations that changed names using the keying process in the previous section. Sites that showed phase changes using the key (BR2, DRYCR6, TM2, and WC3) converted fully to a different classification using similarity analysis. Of the ten sites that changed classification in both analyses, only two agreed in both analyses in 2002.

One of the major problems with comparing classifications using similarity analyses was that the compositions of some of the plots did not contain key indicators that were used in creation of the original classification groupings. Even though compositions would be relatively similar between an historic and current plot, the species that defined the actual classification was not present at the site or it was present in such low percentages that it would not be considered an indicator species to name the type. More often than not, the key indicators from the original compositions were missing from

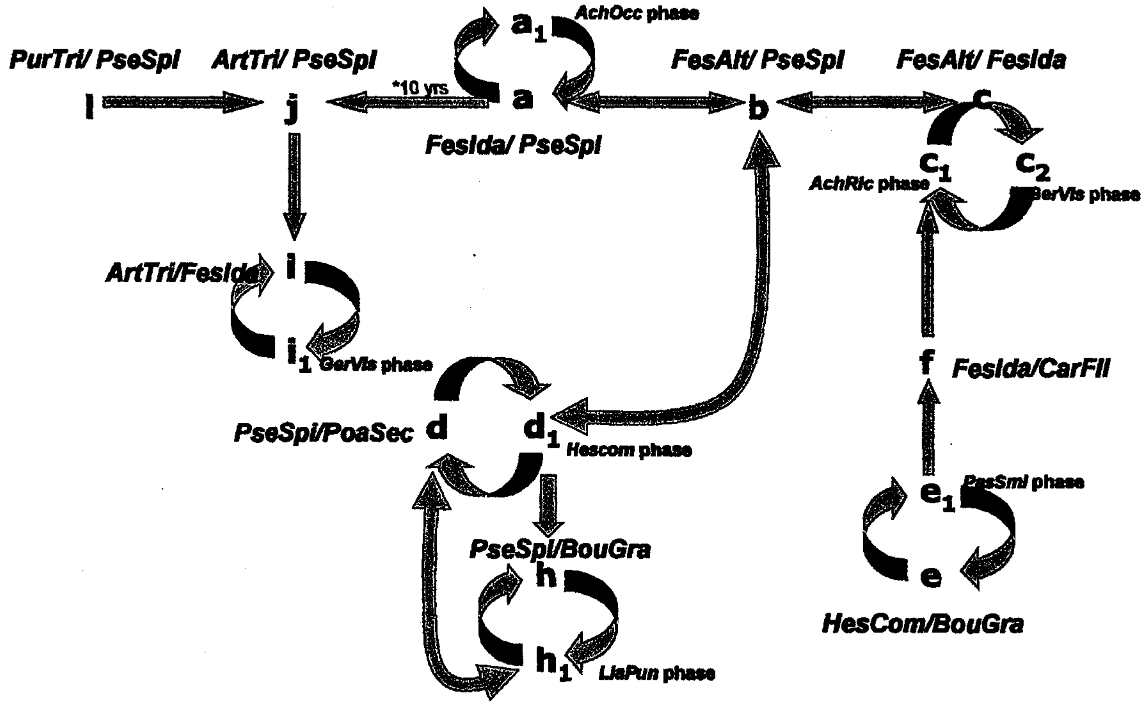

Figure 3-3: Observed change pathways in western Montana grassland classifications from 1970-2002. All pathways can change classification in as little as five years except a-j = 10 years. Classification codes are listed in Table 3-1.

Table 3-4: Classification changes over time obtained by comparing total community compositions of current sites with original Mueggler and Stewart (1980) grassland sample sites using Sorensen's similarity index.

Site Code	Elevation (m)	Year First Sampled	Habitat Type	Year Last Sampled	Habitat Type	Degree of Change	Notes
Dry Sites							
BIGPIP7	1748	1982	ArtTri/PseSpi [1]	2002	ArtTri/PseSpi	- [2]	
BIGPIP9	1667	1980	PseSpi/PasSmi-ElyLan	2001	PseSpi/PasSmi-ElyLan	-	No PasSmi or ElyLan in 1980 or 2001
DRYCR3	1636	1980	PseSpi/BouGra	2002	PseSpi/BouGra	-	
DRYCR6	1667	1980	PseSpi/PasSmi-ElyLan	2002	PseSpi/BouGra	h.t. [3]	No PasSmi, ElyLan or BouGra in either 1980 or 2002
GOLDRN	2182	1979	FesIda/PseSpi	2001	FesIda/PseSpi	-	
STOHOU1	1736	1979	Hescom/BouGra	1999	PseSpi/BouGra	h.t.	AchNel (not Hescom) in 1979 and 1999; no BouGra in 1979
WHTB28	1519	1981	PseSpi/BouGra	2002	PseSpi/BouGra	-	
WHTB34	1515	1981	PseSpi/BouGra	2002	PseSpi/BouGra	-	
Intermediate Sites							
AMAZON	1833	1982	FesIda/PseSpi	2002	FesAlt/FesIda	h.t.	
BANN1	1824	1979	ArtTri/PseSpi	1999	ArtTri/PseSpi	-	
BR2	1542	1974	PseSpi/BouGra	2002	FesIda/PseSpi	h.t.	No BouGra in1974
BR3	1417	1974	PseSpi/PasSmi-ElyLan	2002	PseSpi/PasSmi-ElyLan	-	No PasSmi or ElyLan in 1974 or 2002
CG1	1628	1981	PseSpi/BouGra	2002	PseSpi/BouGra	-	No BouGra in 1981 or 2002
DC2	1436	1984	ArtTri/FesIda	2002	FesIda/PseSpi	h.t.	
GARCRK1	2246	1979	FesIda/PseSpi	2002	ArtTri/FesIda	h.t.	
MP1	1824	1986	FesAlt/PseSpi	2001	FesAlt/PseSpi	-	FesIda dominates in both 1986 and 2001
SL1	1828	1981	FesAlt/PseSpi	2002	FesAlt/PseSpi	-	
TAYCR1	1955	1979	ArtTri/FesIda	1999	ArtTri/FesAlt	h.t.	No FesAlt in 1979 or 1999
TM1	1302	1975	PseSpi/PoaSec	2002	PurTri/FesIda	h.t.	No FesIda or PurTri in 1975 or 2002; PoaSan 0.12 in 2002
TM2	1314	1975	PseSpi/PoaSec	2002	PseSpi/BouGra	h.t.	No BouGra in 1975 or 2002
TM3	1517	1975	FesIda/PseSpi	2002	FesIda/PseSpi	-	
UKP	1947	1986	FesIda/PseSpi	2001	FesIda/PseSpi	-	
WC3	1620	1981	FesAlt/PseSpi	2002	FesIda/PseSpi	h.t.	
WC4	1824	1980	FesAlt/PseSpi	2001	FesAlt/PseSpi	-	No PseSpi in 1980 or 2001
WC5	1771	1980	FesAlt/PseSpi	2001	FesAlt/PseSpi	-	
WC6	1848	1980	FesIda/PseSpi	2001	FesAlt/PseSpi	h.t.	
WC7	1798	1981	FesIda/PseSpi	2001	FesIda/PseSpi	-	
Moist Sites							
ALDER	1848	1979	FesIda/PseSpi	1999	FesIda/PseSpi	-	
BR1	1599	1974	FesIda/PseSpi	2002	FesAlt/PseSpi	h.t.	
FG1	1850	1984	FesIda/ElyCan	2002	FesIda/AchRic	h.t.	No ElyCan or FesIda in 1984; Hescom dominant in 1984
IC1	1798	1987	FesAlt/FesIda	2002	FesAlt/PseSpi	h.t.	No PseSpi in 1987 or 2002
NH1	1733	1984	FesIda/PseSpi	1999	FesIda/PseSpi	-	
SP2	1818	1986	FesIda/PseSpi	1999	FesIda/ElyCan	h.t.	No PseSpi or ElyCan in 1986 or 1999
TG1	1738	1984	FesIda/PseSpi	2002	FesIda/PseSpi	-	
WF1	1776	1979	FesAlt/PseSpi	2001	FesAlt/PseSpi	-	

[1] Species Abbreviations:

AchNel = Achnatherum nelsonii (Scribn.) Barkworth
AchRic = Achnatherum richardsonii (Link) Barkworth
ArtTri = Artemisia tridentata Nutt.
BouGra = Bouteloua gracilis (Willd. Ex Kunth) Lag. Ex Griffiths
ElyCan = Elymus caninus (L.) L.
ElyLan = Elymus lanceolatus (Scribn. & J.g. Sm.) Gould
FesAlt = Festuca altaica Trin.
FesIda = Festuca idahoensis Elmer
HesCom = Hesperostipa comata Trin. & Rupr.) Barkwork
PseSpi = Pseudoroegneria spicata (Pursh) A. Love
PasSmi = Pascopyrum smithii (Rydb.) A. Love
PurTri = Purshia tridentata (Pursh) DC.

[2] - = no change in habitat-type classification

[3] h.t. = change in habitat-type classification

the current sites during sampling. In many cases, the species was never in the plot during several decades of sampling history. For example, DRYCR6 was most similar to a *Pseudoroegneria spicata/Pascopyrum smithii – Elymus lanceolatus* phase in 1980 and to *Pseudoroegneria spicata / Bouteloua gracilis* in 2002. However, the site had neither *Pascopyrum smithii* nor *Elymus lanceolatus* in its coverage data during 1980 or 2002 and never contained *Bouteloua gracilis* (Table 3-4). Even though habitat-type literature warns users that key species may be missing from plots when they are sampled because of chance, past history, or present competitive interactions (Barnes *et al.* 1998), this problem was encountered quite frequently using the similarity analysis. Users are left wondering whether their classification truly represents the physiographic requirements, potential vegetation, and potential yield of the proper grassland community even if they compare their data with the original data used to make the classification key.

COMMUNITY CHANGES PORTRAYED BY ORDINATION ANALYSIS

Composition of our monitoring sites was not significantly different than sites that were used to create the grassland classification in western Montana. Most monitoring sites grouped well with the historic sites at the **series** level of the classification (i.e. *Pseudoroegneria spicata* series). However, grouping at the more specific **habitat-type** level was not consistent, mostly because the original habitat types varied so much in composition that they were quite spread out in three-dimensional ordination space. Species dominating the ends of each axis were easy to distinguish using the composition data. The movements of plots along the ordination axis corresponded to gains or losses in these individual species over time. However, there was no correlation between the shifts in ordination space and whether a site changed in classification using the habitat-type key or not (Fig. 3-4). For example, WHTB 28 lost *Hesperostipa comata,* but added *Bouteloua gracilis* and *Pseudoroegneria spicata* over time. Its movement downward along axis 3 reflected these changes and underwent a corresponding change in classification using the habitat-type key (Fig. 3-4). GOLDRN, however, moved a similar distance in the reverse direction along axis 3 because it lost coverage of *Festuca idahoensis* and gained in *Hesperostipa comata,* but it did not change classification. Some sites had only phase shifts that caused the site to move long distances in ordination space; others experienced similar changes in phase but moved only short distances (SL1). Contrary to notions of stability through time, however, all sites change positions in dimensional space after 15-30 years (except CG1, Fig. 3-4). The directions and magnitude of change varied for each site; and there was no evidence of widespread change trends in any species that would move plots toward any particular region of the graph because of climate changes.

CORRELATIONS OF COMMUNITY CHANGE WITH CONTROL FACTORS

No one factor stands out as clearly responsible for driving the classification changes in this case study over the 30 years. Changes occurred at the full range of elevations and latitudes using all methods of analysis. There was no clear pattern that dry areas changed more frequently than moist areas (Fig. 3-2, Tables 3-1 and 3-4). In the short term, the degree of change in classification did not correlate with an increase or decrease in coverage of introduced species ($p>0.35$), annual species ($p>0.18$), or grazing indicators ($p>0.10$) using Kruskal-Wallis tests.

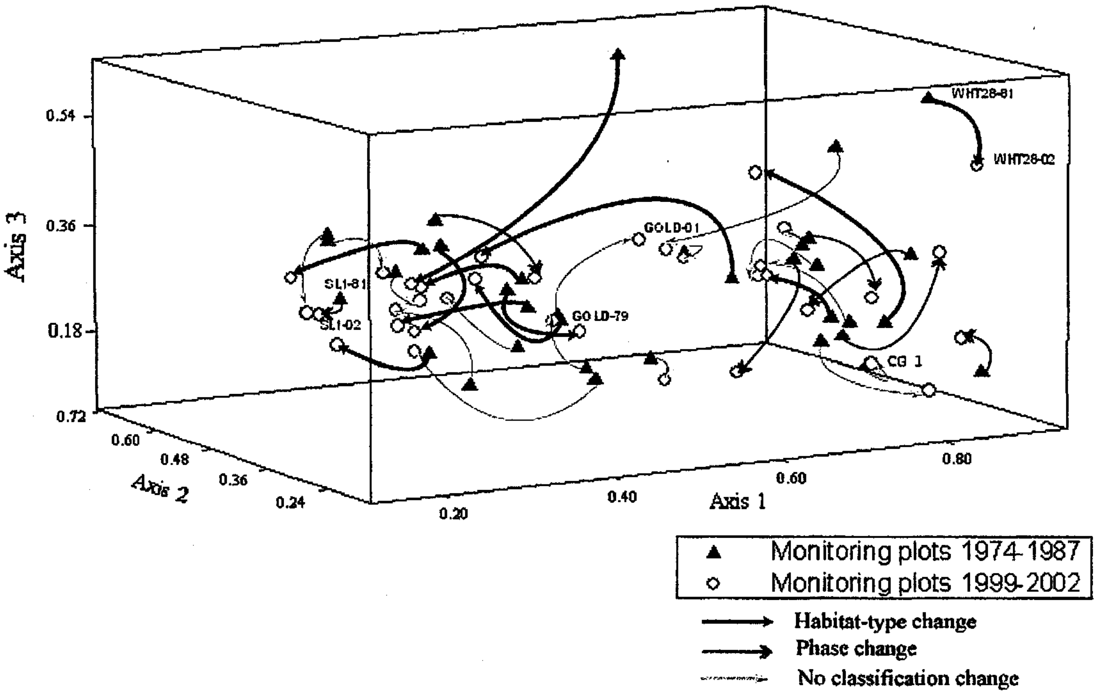

Figure 3-4: Shifts in individual plot composition over time within ordination space (Bray-Curtis ordination). Classification changes were determined using the habitat-type key of Mueggler and Stewart (1980). Note: Ordination was run with monitoring plots and historic Mueggler and Stewart plots together. The historic plots have been removed from this diagram to more clearly show the movements of only monitoring plots through time.

Variations in climatic factors had no direct correlation with how a site was classified in the past using the habitat-type key. When compared with variation in eight climatic variables, no significant statistical differences were found between sites that had changed classification in the past 30 years and sites that had either changed phase or stayed within the same classification (χ^2 0.43 to 4.3, df = 2, all $p>0.11$). Similarly, changes in classification were not correlated with climatic variation during the last six years.

Climatic variation had mixed effects on canopy cover of key indicator species. Analyses using total yearly precipitation and mean annual temperatures on a site-by-site basis had no significant correlations with changes in canopy cover of the indicators in dry, intermediate, or moist sites ($P>0.10$). The overall decrease in total grass and forb coverage and increase in bare ground in plots over the time period did correspond with a general decrease in precipitation in southwestern Montana between 1981 and 2002 for many of the sites (Western Regional Climatic Center 2002). The most important climatic correlations were with individual indicator species. Over the three decades, the canopy cover of individual indicator grasses correlated significantly with variations in precipitation and temperature among seasons of each year and each indicator species responded to a different set of factors. *Pseudoroegneria spicata* correlated significantly with winter precipitation over the 30 years ($R^2=0.13$, $p<0.001$). *Carex filifolia* correlated with mean fall temperatures ($R^2=0.21$, $p<0.05$). Although the correlations between the remaining six indicator species that were tested in this study were not as strong as those for *Pseudoroegneria spicata* or *Carex filifolia* ($R^2< 0.10$), linear regression did show that all correlated significantly with one to four climatic variables, but no two species had all of the same climatic correlations in common. Changes in the abundance of indicators shown in Fig. 3-2 related to these seasonal variations in precipitation and temperature over time.

Discussion

Only the perspective of time can clearly illuminate how susceptible plant communities are to change or how rapidly change can occur. When one looks at a short time span, most plant communities appear relatively stable and structural change may be indistinguishable. When viewed in geologic terms, all plant communities are in a constant state of flux and stability does not exist (Brubaker 1988, Johnson & Mayeux 1992, Tausch *et al.* 1995). In between these two extremes, however, lie time perspectives critical to ecosystem classification, assessment, and management - multiple decades that Magnuson (1990) calls the "invisible present". Using 30 years of monitoring data from the Montana bunchgrass communities, the previously "invisible present" clearly reveals that these grasslands consist of very dynamic communities that have their own managerial challenges for classifying types, assessing change, and modeling succession.

One major challenge facing managers is choosing a classification system that is efficient, yet best captures trends in focal grass species and changes in biodiversity over time. In the case study, the communities are classified with a species-based system meant to portray stable climax and potential vegetation. If the communities are properly classified and the classification is appropriate to the ecosystem, classifications should not change during the monitoring period unless they experience catastrophic disturbance events or a severe change in climate. The bunchgrass communities have experienced neither; but, as the analyses show, their classifications change often and some change relatively rapidly. More importantly, the change patterns are also multidirectional - not linear or unidirectional (Fig. 3-3). Reversals in classification occur as a matter of course.

Most sites changed classification because the dominance of one or more key species varied during favorable climatic or grazing conditions. Physiographic conditions did not specifically relate to classification change. Classifications changes were not limited to plots within a specific range of elevations, latitudes, or moisture regimes. Changes in classification occurred because individual indicator species varied in dominance over time and because overall community structure changed.

Indicator species fluctuated enough to affect classifications in as little as five years and some sites changed classification several times over three decades (Fig. 3-3). Some species were present in a plot during the entire time span but, during good years for growth, reproduction, and competitive interactions, they increased in canopy coverage relative to other community members to affect classification. The patterns of dominance for grass and forb species did not indicate what specific interactions drove the changes in vegetation or whether interactions were positive or negative toward other community members (Callaway 1997), but dominance of all community members did vary in both time and in space. From the time perspective, compositional stability was very short-lived in these grassland communities.

Structurally, the communities also varied in time and space. Overall grass coverage declined over the past 30 years. Forbs increased significantly and the proportions of key grasses fluctuated enough to be considered phase changes within the classification. Whether a remote-sensed, land-type classification system would have detected the decreases in total grass cover or these phase changes is debatable. A land-type system would certainly have detected the significant increases in shrub cover at several of the sites, but the changes in community composition associated with the increase in shrub coverage would certainly have been missing if species-based data had not been collected.

Many factors were examined to explain why classifications changed over 30 years. The factors included variations in the coverage of several types of grazing indicators, variations in the cover of non-native species, and the effect of seasonal climatic variables. Differences in the coverage of grazing indicators and of non-native species had no correlation with whether a site changed classification over time in either the short-or long-term. The changes in grazing indicators and non-native species affected overall composition of many plots and their positions in dimensional space in ordination analysis, but the increase or decrease in coverage of these variables did not specifically correlate with changes in classification names. Because the classification theoretically described stable climax communities with minimized external disturbances (Daubenmire 1952, Mueggler & Stewart 1980), the lack of correlation between classification changes and external disturbances like grazing or introduced species was expected.

The sensitivity of these grasslands to climatic variability, however, was not factored into this species-based system. Seasonal variation in temperature and precipitation correlated significantly with the canopy coverage of several key indicator species used in the habitat-type key. The importance of variations in temperature and precipitation to individual indicator species on an annual basis is crucial to understanding grassland change patterns and community dynamics. In this study, there is no synchronicity to either the magnitude or direction of change for all the sites in the ordination analyses (Fig. 3-4). The effects of these climatic variables vary by species and lend support to current research that shows these ecosystems are particularly sensitive to short-term climatic variability (Alward *et al.* 1999, De Valpine & Harte 2001, Knapp & Smith 2001, NSF 2002, Weltzin *et al.* 2003).

The sensitivity of indicator species to climatic variables also suggests that assignment of classification names may depend on when a site is sampled. The original habitat-type or "potential vegetation" classification was created using vegetation on the ground at one point in time. According to Brubaker (1988, p.1), when change is considered in such dynamic systems, "it is probably unrealistic to think that future vegetation changes can be precisely anticipated from observation of present vegetation." In the decades covered by this study alone, there is so much variation in both the frequency and canopy coverage of the dominant grasses and community compositions over time that predicting future trends even 10 years ahead is uncertain (see Figs. 3-2 and 3-3). The classification would probably look quite different if it had been created in 1850, 1930, 1970, or 2000 because of the different climatic conditions in these years. Since 1970, southwest Montana has undergone gradual warming and drying (Sikkink & Alaback, Western Regional Climatic Center 2002), but this study shows that classification changes also occurred at monitoring sites in the 1970s when this trend would not have been a factor.

These grasslands follow many different change pathways (Fig. 3-3). These pathways are more similar to current non-equilibrium models than they are to linear, unidirectional succession models. The inherent instability of indicator species with environmental variation and the multiple pathways of change patterns suggest that alternative methods are needed to assess stability and succession within them. Current non-equilibrium models, such as the multiple steady-state models (Cattelino *et al.* 1979, Tausch *et al.* 1993, Westoby 1989) or the threshold models (Friedel 1991, Laycock 1991, May 1977), appear to fit the changes exhibited by western Montana grasslands over the past 30 years better than equilibrium models, which form the basis of the habitat type, range type and range condition classifications. The data from this study neither supports nor disputes older theories that promote multiple climax communities (i.e. a polyclimatic climax) for a vegetation type instead of multiple pathways of non-equilibrium succession (Meeker & Merkel 1984). The differences between these theories will only be answered through very long-term vegetation monitoring. However, at this point in time, evidence supports current successional theories of multiple pathways because of the frequent changes in species dominance and short time spans for change within many different vegetation types. Currently, grassland research worldwide faces similar challenges in determining how stable grasslands are over time and what factors drive compositional change within them (Brown *et al.* 2001, Hirst *et al.* 2003, Kahmen & Poschloda 2004, Schutz *et al.* 2000, Shaw *et al.* 2002).

The principles behind the habitat-type classification and, by extension, other species-based systems that rely on "climax", potential vegetation, or indicator species clearly do not withstand scrutiny of the change patterns indicated by long-term data. How then can such systems be made more appropriate for use in grasslands? Records detailing plant changes and fluctuations within a particular area are usually not available or taken into consideration during the process of creating a classification. As a result, a static classification provides a very narrow perception of community interactions, climatic influences, and stability of a vegetation type in a particular area on the landscape over time. If a classification system is to be used to assess change and track compositional trends in communities, the system must consider the natural range of variation inherent in the communities being classified and the drivers that control it. Capturing the range of variability in each community requires frequent resampling at each location so that the variations in important species can be identified before the classification is constructed. It may also involve new methods of sampling individual target species, including measuring fecundity and demographic structure (Buhler & Schmid 2001, Oostermeijer & Van't Veer 1994). Ideally, monitoring should include yearly samples for at least 15 years to cover an adequate range of temperature and precipitation variations and cover the transitions between community types. With repeat sampling over longer time frames, more robust statistical methods, such as time-series techniques, can be applied to the data to determine if focal species are affected by climatic fluctuation, grazing intensity, or introduced species within short time periods or whether lag effects exist that must be considered when assessing community change. Auxiliary data on grazing history and soil samples for each sample interval would enable more robust statistical correlations to be conducted. New monitoring sites should be selected away from ecotones or other locations that would inflate variation or affect composition in the short-term. In the intermountain grasslands, this means sites should be located away from forest edges and reflect a variety of physiographic conditions. For the temporal scales important to management, species-based classification systems should be much more sensitive than remote-sensed systems at capturing compositional change due to grazing or introduced species especially if they are constructed correctly from the start and use spatial scales appropriate to management. Creating a classification system for these dynamic systems with highly detailed, or super-fine, categories, however, seems doomed to failure.

Assessing change in any community requires that historical links remains intact. Sampling procedures and techniques must remain the same at each permanently-marked monitoring site through time or this link is broken. All records must also be saved, which is sometimes a challenge after several decades. Incorporating new techniques to improve community descriptions is often desirable, but requires trade-offs between maintaining this historical link and allotting time for extra work. Above all, the historical links must be maintained. Sample frequency, however, may be increased without any loss of historical integrity to adequately capture the nature of change in these communities and new techniques can be added to the historical base.

When Mueggler and Stewart published their grassland classification for western Montana in 1980, they predicted that it would certainly experience changes through the years because they thought their examples of pristine "climax" communities were so limited and they expected that new discoveries on how grassland communities responded to grazing would significantly affect the original classification (Mueggler & Stewart 1980). Ultimately, the problems of habitat typing in grassland ecosystems were even more fundamental than their lack of foresight about grazing effects or a scarcity of sample sites; but, hopefully, their prediction for change will be fulfilled. The challenge now is to develop assessment tools that more realistically reflect the dynamic nature of these communities without breaking the ties that bind each one to the past.

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References

Alward R.D., Detling J.K. and Milchunas D.G. 1999. Grassland vegetation changes and nocturnal global warming. Science 283: 229-231.

Anderson J.E. and Holte K.E. 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. Journal of range management 34: 25-29.

Andrews R., Biggs M., Seidel M. and others (eds). 1996. The Columbia world of quotations, Quotation #5566 (from 1900 version of Roadmender, V. 3 no.3), Cd Rom edition. Columbia University Press, New York.

Antos J.A., McCune B. and Bara C. 1983. The effect of fire on an ungrazed western Montana grassland. The American Midland Naturalist 110: 354-364.

Bailey A.W. and Anderson M.L. 1978. Prescribed burning of a Festuca-Stipa grassland. Journal of range management 31: 446-449.

Bais H.P., Vepachedu R., Gilroy S., Callaway R.M. and Vivanco J.M. 2003. Allelopathy and exotic plant invasion: From molecules and genes to species interactions. Science 301: 1377-1380.

Bamforth D.B. 1987. Historical documents and bison ecology on the Great Plains (USA). Plains Anthropologist 32: 1-16.

Barnes B.V., Zak D.R., Denton S.R. and Spurr S.H. 1998. Site quality and ecosystem evaluation. In: Forest Ecology. John Wiley & Sons, Inc., New York, NY, p 298-329.

Bartlein P.J., Whitlock C. and Shafer S.L. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology 11: 782-792.

Bedunah D.J. 1992. The complex ecology of weeds, grazing and wildlife. Western Wildlands: 6-11.

Blatt S.E., Janmaat J.A. and Harmsen R. 2001. Modelling succession to include a herbivore effect. Ecological Modelling 139: 123-136.

Bray J.R. and Curtis J.T. 1957. An ordination of upland forest communities of southern Wisconsin. Ecological Monographs 27: 325-349.

Briggs J.M. and Knapp A.K. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. Journal of American Botany 82: 1024-1030.

Briske D.D., Fuhlendorf S.D. and Smeins F.E. 2003. Vegetation dynamics on rangelands: a critique of the current paradigms. Journal of Applied Ecology 40: 601-614.

Brooks T.M., da Fonseca G.A.B. and Rodrigues A.S.L. 2004. Species, Data, and Conservation Planning. Conservation Biology 18: 1682-1688.

Brown J.H., Whitham T.G., Ernst S.K.M. and Gehring C.A. 2001. Complex species interactions and the dynamics of ecological systems: Long-term experiments. Science 293: 643-650.

Brubaker L.B. 1988. Vegetation history and anticipating future vegetation change. In: Agee J.K. and Johnson D.R. (eds), Ecosystem management for parks and wilderness. University of Washington Press, Seattle, p 41-61.

Buhler C. and Schmid B. 2001. The influence of management regime and altitude on the population structure of *Succisa pratensis*: implications for vegetation monitoring. J Appl Ecology 38: 689-698.

Burke M.J.W., and Grime, J.P. 1996. An experimental study of plant community invasibility. Ecology 77: 776-790.

Cale W.G., Henebry, Geoffrey M., and Yeakley, J. Alan. 1989. Inferring Process from Pattern in Natural Communities - Can we understand what we see? BioScience 39: 600-605.

Callaway R.M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112: 143-149.

Callaway R.M., Mahall B.E., Wicks C., Pankey J. and Zabinsky C.A. 2003. Soil fungi and the effects of an invasive forb on grasses: neighbor identity matters. Ecology 84: 129-135.

Cattelino P.J., Noble I.R., Slatyer R.O. and Kessell S.R. 1979. Predicting the multiple pathways of plant succession. Environmental Management 3: 41-50.

Clarke K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Botany 18: 117-143.

Clements F.E. 1916. I. Concept and causes of succession. Carnegie Institution of Washington, Washington, D.C.

Coffin D.P. and Lauenroth W.K. 1996. Transient responses of North-American grasslands to changes in climate. Climatic Change 34: 269-278.

Collins S.L., Knapp A.K., Briggs J.M., Blair J.M. and Steinauer E.M. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280: 745-747.

Copeland R.T. (ed) 1992. Natural grasslands: Introduction and western hemisphere, Vol 8A. Elsevier, New York.

Coughenour M.B., Singer F.J. and Reardon J. 1991. The Parker transects revisited: Long-term herbaceous vegetation trends on Yellowstone's northern winter range. In: Plants and their environments: Proceedings of the first biennial scientific conference on the greater Yellowstone ecosystem (conference procedings), Yellowstone National Park, Wyoming. USDA National Park Service Rocky Mountain Region Yellowstone National Park, 73-95.

Cousins S.A.O. and Lindborg R. 2004. Assessing changes in plant distribution patterns--indicator species versus plant functional types. Ecological Indicators 4: 17-27.

Daubenmire R. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33: 43-64.

Daubenmire R.F. 1942. An ecological study of the vegetation of southeastern Washington and adjacent Idaho. Ecological Monographs 12: 53-79.

Daubenmire R.F. 1952. Forest vegetation of northern Idaho and adjacent Washington and its bearing on concepts of vegetation classification. Ecological Monographs 22: 301-330.

Daubenmire R.F. 1970. Steppe vegetation of Washington. Washington Agric. Exp. Sta. Tech Bull. 62, Pullman, WA, 131 pp.

Daubenmire R.F. 1975. Floristic plant geography of eastern Washington and northern Idaho. Journal Biogeography 2: 1-18.

De Valpine P. and Harte J. 2001. Plant responses to experimental warming in a montane meadow. Ecology 82: 637-648.

Dyksterhuis E.J. 1949. Condition and management of range land based on quantitative ecology. Journal of range management 2: 104-115.

Ellenburg H. 1959. Typen tropischer Urwalder in Peru. Schweiz Z. Forstw 110:

Ellis J.E. and Swift D.M. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. Journal of range management 41: 450-459.

Elzinga C.L., Salzer D.W. and Willoughby J.W. 1998. Measuring and monitoring plant populations. Bureau of Land Management Technical Reference 1730-1, Denver, CO, 477 pp.

Emanuel J. 1999. VTAB Ecosystem Reporter Professional Edition Version 1999-07a. University of British Columbia, Vancouver.

Epstein H.E., Gill R.A., Paruelo J.M., Lauenroth W.K., Jia G.J. and Burke I.C. 2002. The relative abundance of three plant functional types in temperate grasslands and shrublands of North and South America: effects of projected climate change. J Biogeography 29: 875-888.

Epstein H.E., Lauenroth W.K., Burke I.C. and Coffin D.P. 1997. Productivity patterns of C3 and C4 functional types in the U.S. Great Plains. Ecology 78: 722-732.

Fay P.A., Carlisle J.D., Danner B.T., Lett M.S., McCarron J.K., Stewart C., Knapp A.K., Blair J.M. and Collins S.L. 2002. Altered rainfall patterns, gas exchange, and growth in grasses and forbs. International Journal of Plant Sciences 163: 549-557.

Fay P.A., Carlisle J.D., Knapp A.K., Blair J.M. and Collins S.L. 2003. Productivity responses to altered rainfall patterns in a C_4 -dominated grassland. Oecologia 137: 245-251.

Fleischner T.L. 1994. Ecological Costs of Livestock Grazing in Western North America. Conservation Biology 8: 629-644.

Floyd M.L., Fleischner T.L., Hanna D. and Whitefield P. 2003. Effects of Historic Livestock Grazing on Vegetation at Chaco Culture National Historic Park, New Mexico. Conservation Biology 17: 1703-1711.

Frank D.A. and McNaughton S.J. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96: 157-161.

Friedel M.H. 1991. Range condition assessment and the concept of thresholds: A viewpoint. Journal of range management 44: 422-426.

Fuhlendorf S.D., Briske D.D. and Smeins F.E. 2001. Herbaceous vegetation change in variable rangeland environments: The relative contribution of grazing and climatic variability. Applied Vegetation Science 4: 177-188.

Fuhlendorf S.D. and Smeins F.E. 1996. Spatial scale influence on longterm temporal patterns of a semi-arid grassland. Landscape ecology 11: 107-113.

Gleason H.A. 1917. The structure and development of the plant association. Bulletin of the Torrey Botanical Club 44: 463-481.

Gleason H.A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53: 1-20.

Grace J.B. 2003. Examining the relationship between environmental variables and ordination axes using latent variables and structural equation modeling. In: Pugesek B.H., Tomer A. and von Eye A. (eds), Structural Equation Modeling. Cambridge University Press, Cambridge, p 171-193.

Greig-Smith P. 1983. Quantitative plant ecology. University of California Press, Berkeley, CA.

Hall F.C. 1985. Viewpoint: The habitat type controversy; two common concepts. Rangelands 7: 170-171.

Hansen P.L., Hoffman G.R. and Bjugstad A.J. 1984. The vegetation of Theodore Roosevelt National Park, North Dakota: A habitat type classification. USDA Forest Service Rocky Mountain Forest and Range Experiment Station General Technical Report RM-113, Fort Collins, CO, 35 pp.

Harding J.S., Benfield E.F., Bolstad P.V., Helfman G.S. and Jones E.B.D. 1998. Stream biodiversity: the ghost of land use past. In: Proceedings of the National Academy of Sciences of the United States of America (conference procedings), 14843-14847.

Hayes G.F. and Holl K.D. 2003. Cattle Grazing Impacts on Annual Forbs and Vegetation Composition of Mesic Grasslands in California. Conservation Biology 17: 1694-1702.

Heady H.F. and Child R.D. 1994. Rangeland ecology and management. Westview Press, Boulder.

Herben T., Krahulec F., Hadincova V. and Pechackova S. 1995. Climatic variability and grassland community composition over 10 years: separating effects on module biomass and number of modules. Functional ecology 9: 767-773.

Hirsch K.J. 1985. Habitat type classification of grasslands and shrublands of southwestern North Dakota. *Dissertation*, North Dakota State University, Fargo, North Dakota.

Hirst R.A., Pywell R.F., Marrs R.H. and Putwain P.D. 2003. The resistance of a chalk grassland to disturbance. Journal of Applied Ecology 40: 368-379.

Hitchcock C.L. and Cronquist A. 1973. Flora of the Pacific Northwest: an illustrated manual. University of Washington Press, Seattle, WA.

Horn B.E. and Redente E.F. 1998. Soil nitrogen and plant cover of an old-field on the shortgrass steppe in southeastern Colorado. Arid soil research and rehabilitation 12: 193-206.

Insightful Corporation. 2001. S-Plus 6.1 for Windows Professional Version 3. Seattle, WA.

Jackson R.B., Sala O.E., Paruelo J.M. and Mooney H.A. 1998. Ecosystem water fluxes for two grasslands in elevated CO_2: a modeling analysis. Oecologia 113: 537-546.

Jacobs M.J. and Schloeder C.A. 2002. Fire frequency and species associations in perennial grasslands of south-west Ethiopia. African J Ecol 40: 1-9.

Jeltsch F., Weber G.E. and Grimm V. 2000. Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. Plant Ecology 161: 161-171.

Jobbagy E.G. and Sala O.E. 2000. Controls of grass and shrub aboveground production in the Patagonian steppe. Ecological Applications 10: 541-549.

Johnson H.B. and Mayeux H.S. 1992. Viewpoint: A view on species addiitions and deletions and the balance of nature. Journal of range management 45: 322-333.

Jolly W.M., Graham J.M., Michaelis A., Nemani R. and Running S.W. 2004. A flexible, integrated system for generating meterological surfaces derived from point sources across multiple geographic scales. Environmental Modeling and Software 20: 873-882.

Joreskog K. and Sorbom D. 1996. Submodel 2: Causal models for directly observed variables. In: Lisrel 8: User's Reference Guide. Scientific Software International, Lincolnwood, IL, p 143-170.

Jöreskog K.G. and Sörbom D. 2003. Interactive LISREL 8.54. Scientific Software International, Inc.,

Kahmen S., Poschlod P. and Schreiber K.-F. 2002. Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. Biological Conservation 104: 319-328.

Kahmen S. and Poschloda P. 2004. Plant functional trait responses to grassland succession over 25 years. Journal of Vegetation Science 15: 21-32.

Kaiser J. 2001. How rain pulses drive biome growth. Science 291: 413-414.

Kaiser V.G. 1961. Historical land use and erosion in the Palouse - a reappraisal. Northwest Science 35: 139-153.

Kartesz J. 1998. A synonymized checklist of the vascular flora of the United States, Puerto Rico, and the Virgin Islands, Full text index. Biota of North America Program (BONAP): North Carolina Botanical Garden, University of North Carolina, Chapel Hill. www.csdl.tamu.edu/FLORA/b98/check98.htm, 2/9/04.

Knapp A.K. and Smith M.D. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291: 481-484.

Knapp A.K., Smith M.D., Collins S.L., Zambatis N., Peel M., Emery S., Wojdak J., Horner-Devine M.C., Biggs H., Kruger J. and Andelmanb S.J. 2004. Generality in ecology: testing North American grassland rules in South African savannas. Frontiers in Ecology and the Environment 2: 483-491.

Koterba W.D. and Habeck J.R. 1971. Grasslands of the North Fork Valley, Glacier National Park, Montana. Canadian Journal Botany 49: 1627-1636.

Krebs C.J. 1999. Ecological methodology. Addison-Welsey Educational Publishers, Inc., Menlo Park, CA.

Kruskal J.B. and Wish M. 1978. Multidimensional Scaling. Sage Publications, Inc., Beverly Hills and London.

Lauenroth W.K. and Sala O.E. 1992. Long-term forage production of north American shortgrass steppe. Ecological Applications 2: 397-403.

Laycock W.A. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. Journal of range management 44: 427-433.

Leach M.K. and Givnish T.J. 1996. Ecological determinants of species loss in remnant prairies. Science 273: 1555-1558.

LeJeune K.D. and Seastedt T.R. 2001. Centaurea Species: The forb that won the West. Conservation Biology 15: 1568-1574.

Lesica P. and Hanna D. 2002. Monitoring composition of foothills grassland using frequency of indicator species. Natural areas journal 22: 148-153.

Li C.C. 1975. Path analysis. A primer. The Boxwood Press, Pacific Grove, CA.

Lonsdale W.M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522-1536.

Mack R.N. 1989. Temperate grasslands vulnerable to plant invasions: Characteristics and consequences. In: Drake J.A. and Mooney H.A. (eds), Biological Invasions: a global perspective. John Wiley & Sons, New York, p 155-179.

Mack R.N. and Lonsdale W.M. 2001. Humans as global plant dispersers: Getting more than we bargained for. BioScience 51: 95-102.

Mack R.N. and Thompson J.N. 1982. Evolution in steppe with few large, hooved mammals. The American Naturalist 119: 757-773.

Manning R. 1995. Grassland: The history biology, politics, and promise of the American prairie. Penguin Books, New York.

Marler M.J., Zabinsky C.A. and Callaway R.M. 1999. Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. Ecology 80: 1180-1186.

May R.M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269: 471-477.

McCune B. 1994. Improving community analysis with the Beals smoothing function. Ecoscience 1: 82-86.

McCune B. and Allen T.F.H. 1985. Will similar forests develop on similar sites? Can. Journal of Botany 63: 367-376.

McCune B. and Grace J.B. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McCune B. and Mefford M.J. 1999. PC-Ord Version 4.33. MjM Software Design, Gleneden Beach, Oregon.

Meeker D.O. and Merkel D.L. 1984. Climax theories and a recommendation for vegetation classification - a viewpoint. Journal of range management 37: 427-430.

Merrill E.H., Stanton N.L. and Hak J.C. 1994. Responses of bluebunch wheatgrass, Idaho fescue, and nematodes to ungulate grazing in Yellowstone National Park. Oikos 69: 231-240.

Microsoft Corporation. 2001. Microsoft Access 97 for Windows

Montana Department of Fish Wildlife and Parks. 2003. Region two deer and elk survey and inventory progress report - July 1, 2002 to June 30, 2003. Montana Department of Fish Wildlife and Parks Missoula, Montana, 95 pp.

Morris M.S. and Brunner J.D. 1971. Primary productivity of the fescue grassland in western Montana. The University of Montana School of Forestry U.S. International Biological Program Grassland Biome Technical Report No. 113, Missoula, 71 pp.

Mueggler W.F. 1992. Cliff Lake Bench Research Natural Area: Problems encountered in monitoring vegetation change on mountain grasslands. U.S. Department of Agriculture Forest Service Intermountain Research Station INT-454, Ogden, Utah, 13 pp.

Mueggler W.F. and Stewart W.L. 1980. Grassland and shrubland habitat types of western Montana. USDA Forest Service General Technical Report INT-66, Ogden, Utah, 154 pp.

Mueller-Dombois D. and Ellenburg H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

NSF. 2002. Increase in rainfall variability related to global climate change; impacts on ecosystems are greater than previously anticipated. NSF web site release. http://www.nsf.gov/cgi-bin/getpub?pr0298, Dec. 12, 2002.

Oostermeijer J.G.B. and Van't Veer R. 1994. Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. Journal of Applied Ecology 31: 428-439.

Paruelo J.M. and Lauenroth W.K. 1996. Relative Abundance of Plant Functional Types in Grasslands and Shrublands of North America. Ecological Applications 6: 1212-1224.

Pickup G., Bastin G.N. and Chewings V.H. 1998. Identifying trends in land degradation in non-equilibrium rangelands. J Appl Ecology 35: 365-377.

Potyondi B. 1995. In Palliser's Triangle. Purich Publishing, Saskatoon, Saskatchewan.

Pressey R.L. 2004. Conservation Planning and Biodiversity: Assembling the Best Data for the Job. Conservation Biology 18: 1677-1681.

Preston F.W. 1948. The commonness and rarity of species. Ecology 29: 185-215, 410-432.

Redmann R.E., Romo J.T. and Pylypec B. 1993. Impacts of burning on primary productivity of Festuca and Stipa-Agropyron grasslands in central Saskatchewan. American Midland Naturalist 130: 262-273.

Rice P.M. 2004. INVADERS DATABASE SYSTEM. Division of Biological Sciences, University of Montana, Missoula, MT. http://invader.dbs.umt.edu, Ridenour W.M. and Callaway R.M. 2001. The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126: 444-450.

Rodriguez C., Leoni E., Lezama F. and Altesor A. 2003. Temporal trends in species composition and plant traits in natural grasslands of Uruguay. Journal of Vegetation Science 14: 433-440.

Sampson A.W. 1919. Plant succession in relation to range management. USDA Dept Bulletin 791, pp.

Savory A. 1988. Holistic resource management. Island Press, Washington, D.C.

Scheiner, Mitchell and Callahan. 2000. Using path analysis to measure natural selection. J Evolution Biol 13: 423-433.

Schenk H.J., Callaway R.M. and Mahall B.E. 1999. Spatial root segregation: are plants territorial? Advances Ecological Research 28: 146-180.

Schirokauer D.W. 1996. The effects of 55 years of vegetative change on bighorn sheep habitat in the Sun River Area of Montana. *Master Science*, The University of Montana, Missoula, MT.

Schlesinger W.H., Reynolds, James F., Cunningham, Gary L., Huenneke, Laura F., Jarrell, Wesley M., Virginia, Ross A., Witford, Walter G. 1990. Biological feedbacks in global desertification. Science 240: 1043-1048.

Schutz M., Krusi B.O. and Edwards P.J. 2000. Succession research in the Swiss National Park: From Braun-Blanquet's permanent plots to models of long-term ecological change. Swiss Federal Research Institute WSL, Bermensdorf, Switzerland.

Schwinning S., Starr B.I. and Ehleringer J.R. 2005. Summer and winter drought in a cold desert ecosystem (Colorado Plateau) II: effects on plant carbon assimilation and growth. Journal of Arid Environments In Press, Corrected Proof:

Shaw M.R., Zavaleta E.S., Chiariello N.R., Cleland E.E., Mooney H.A. and Field C.B. 2002. Grassland Responses to Global Environmental Changes Suppressed by Elevated CO_2. Science 298: 1987-1990.

Shea D., Olin S. and Asebrook. J. 2003. Glacier National Park East-side Grasslands Ecology Project Final Report (Draft). Glacier National Park West Glacier, MT., 22 pp.

Sims P.L., Singh J.S. and Lauenroth W.K. 1978. The structure and function of ten western North American grasslands: I. Abiotic and vegetational characteristics. Journal of Ecology 66: 251-285.

Singer F.J. and Harter M.K. 1996. Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. Ecological Applications 6: 185-199.

Singer F.J., Swift D.M., Coughenour M.B. and Varley J.D. 1998. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation 1968-1993. Wildlife Society Bulletin 26: 375-390.

Smith S.D., Bunting S.C. and Hironaka M. 1986. Sensitivity of frequency plots for detecting vegetation change. Northwest Science 60: 279-286.

Sneath P.H.A. and Sokal R.R. 1973. Numerical taxonomy. W.H. Freeman, San Francisco.

Solow A.R. 1994. Detecting change in the composition of a multispecies community. Biometrics 50: 556-565.

Sorensen T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. F. danke vidensk. Selsk. 5: 1-34 (translation).

Stohlgren T.J., Barnett D.T. and Kartesz J.T. 2003. The rich get richer: patterns of plant invasions in the United States. Frontiers in Ecology and the Environment 1: 11-14.

Stohlgren T.J., Schell L.D. and Heuvel B.V. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9: 45-64.

Stone L. and Ezrati S. 1996. Chaos, cycles and spatiotemporal dynamics in plant ecology. Journal of Ecology 84: 279-291.

Stringer P.W. 1973. An ecological study of grasslands in Banff, Jasper, and Waterton Lakes National Parks. Canadian Journal Botany 51: 383-411.

Svejcar T. and Brown J.R. 1991. Failures in the assumptions of the condition and trend concept for management of natural ecosystems. Rangelands 13: 165-167.

Tansley A.G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16: 284-307.

Tausch R., J., Nowak C., L. and Nowak R., S. 1995. Climate change and plant species responses over the Quaternary; implications for ecosystem management. In: Interior West Global Change Workshop (conference procedings), Fort Collins, CO. USDAForest Service, Rocky Mountain Forest and Range Experiment Station, 14-19.

Tausch R.J., Wigand P.E. and Burkhardt J.W. 1993. Viewpoint: Plant community thresholds, multiple steady states, and multiple successional pathways: legacy of the Quaternary? Journal of range management 46: 439-447.

Tilman D. and Wedin D. 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72: 1038-1049.

Tisdale E.W. 1986. Canyon grasslands and associated shrublands of west-central Idaho and adjacent areas. Forest, Wildlife and Range Experiment Station University of Idaho Bulletin No. 40 Contribution No. 284, Moscow, Idaho, 42 pp.

U.S. Bureau of the Census. 2000. County Population Estimates for July 1, 1999. Population Estimates Program, Population Division. http://www.cunsus.gov/population/estimates/county/co-99-1/99C1_30.txt, 11/13/00.

U.S. Dept. of Agriculture. 2002. 2002 Census ofAgriculture - Counties and State Tables, Montana and Wyoming. USDA National Agricultural Statistics Service. www.nass.usda.gov/census/, Feb. 1, 2005.

U.S. Dept. of Commerce Bureau of the Census. 1952. 1950 Agricultural Census - Counties and State Economic Areas. U.S. Government Printing Office

USDA Natural Resources Conservation Service National Soil Survey Center. 2004. Montana SSURGO Soil Data. Montana Natural Resources Conservation Service and the Montana Natural Resource Information System of the Montana State Library. http://www.nris.state.mt.us/nrcs/soils/soilstatus.html,

Van Auken O.W. 2000. Shrub invasions of North American semiarid grasslands. Annual review of ecology and systematics 31: 197-215.

van der Waerden B.L. 1969. Mathematical Statistics. Springer-Verlag, New York.

Veseth R. and Montagne C. 1980. Geologic parent materials of Montana soils. USDA Soil Conservation Service Bulletin 721, Bozeman, MT, pp.

Wallace L.L. and Macko S.A. 1993. Nutrient acquisition by clipped plants as a measure of competitive success: the effects of compensation. Functional ecology 7: 326-331.

Wallen R. 2004. Personal communication, Wildlife biologist, Bison Ecology and Management Program. 2/3/04.

Ward L.K. and Jennings R.D. 1990. Succession of disturbed and undisturbed chalk grassland at Aston Rowant National Nature Reserve: Dynamics of species changes. Journal of Applied Ecology 27: 897-912.

Weltzin J.F., Loik M.E., Schwinning S., Williams D.G. and al e. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53: 941-952.

Western Regional Climatic Center. 2002. Western region climate summaries. Western Regional Climatic Center. http://www.wrcc.dri.edu/climsum.html, Feb. 2, 2004.

Westoby M., Walker, Brian, and Noy-Meir, Imanuel. 1989. Opportunistic management for rangelands not at equilibrium. Journal of range management 42: 266-274.

White P. 2004. Personal communication, Wildlife biologist, Yellowstone Center for Resources. 2/03/04.

Whittaker R.H. 1951. A criticism of the plant association and climatic climax concepts. Northwest Science 15: 17-31.

Willard E. 2003a. American Society of Range Management International Mountain Section Field guide to range plant classification unpublished, Missoula, MT, 9 pp.

Willard E. 2003b. Personal communication, Professor of range management, College of Forestry and Conservation, The University of Montana. 12/05/2003.

Willms W.D. and Quinton D.A. 1995. Grazing effects on germinable seeds on the fescue prairie. Journal of range management 48: 423-430.

Wilsey B.J., Coleman J.S. and McNaughton S.J. 1997. Effects of elevated CO-2 and defoliation on grasses; A comparative ecosystem approach. Ecological Applications 7: 844-853.

Woods A.J., Omernik J., M., Nesser J.A., Shelden J. and Azevedo S.H. 1999. Ecoregions of Montana (color poster with map, descriptive text, summary tables, and photographs). U.S. Geological Survey, Reston, Virginia.

Wroe R.A., Smoliak S. and Wheeler G.W. 2000. Alberta Range Plants and their Classification. Alberta Agriculture, food and rural development.

http://ww1.agric.gov.ab.ca/$department/deptdocs.nsf/all/agdex146?opendocument, April 20, 2004.

Young F.W. 1987. Multidimensional scaling: History, theory and applications. Lawrence Erlbaum Associates, Hillsdale, New Jersey.

Zabinski C.A., Quinn L. and Callaway R.M. 2002. Phosphorus uptake, not carbon transfer, explains arbuscular mycorrhizal enhancement of *Centaurea maculosa* in the presence of native grassland species. Functional ecology 16: 758-765.

Zuur A. 2000. Brodgar: Software package for multivariate analysis and multivariate time series analysis. HIGHLAND STATISTICS LTD, Aberdeenshire, Scotland.