MONTANA STATE UNIVERSITY

Plant and grasshopper community composition : indicators and interaction across three spatial scales
by Kerri Farnsworth Skinner

A thesis submitted in partial fulfillment . of the requirements for the degree of Master of Science in Biological Sciences
Montana State University
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Abstract:
Grasshopper communities in the Great Plains display broad species heterogeneity, varying with vegetation and local habitat. Knowledge of the specific composition of grasshopper communities and their pattern across space is necessary for the development of efficient grasshopper management strategies. This information can be integrated with habitat classification data to identify areas which are prone to grasshopper outbreaks. Plant and grasshopper communities at 170 sites in Montana and Colorado in 1992 were compared to identify differences in species composition and factors which influence grasshopper communities in the two states. Species proportions and percentages were analyzed using detrended correspondence analysis (DCA). Percent bare ground, litter, total cover, proportions of grasses and forbs, and plant height were not useful in distinguishing between plant communities in either state. Individual plant species DCA did detect differences among plant communities. Plant and grasshopper community compositions differ significantly between the two states, with Buchloe dactyloides and Bouteloua curtipendula distinguishing Colorado sites. Because both grasshopper communities and the vegetation resource vary between Montana and Colorado, the same pest management activities may have varied results when implemented in shortgrass versus mixed-grass prairie. Spearman rank correlations found grasshopper DCA results for Montana were correlated with percent bare ground, mode plant height, and plant species which increase with grazing. Such factors are thus important in determining grasshopper community composition, though they are not useful in distinguishing among plant communities. To identify spatial attributes which distinguish plant and grasshopper communities on a state-wide scale, plant and grasshopper species composition data were collected at 128 sites in three areas of Montana in 1993. A geographic information system (GIS) was used to associate each sampling site with Omernik’s ecoregions and the Montana State Soil Geographic Database (STATSGO). DCA and statistical analyses were used to test differences and correlations among sampling areas, ecoregions, available water, and soil permeability. Three plant and four grasshopper species were correlated with soil permeability. Available water was correlated with six grasshopper species, but with none of the plant species. Soil permeability values differed significantly over all sampling areas and ecoregions. STATSGO plant percentages did not correlate with field percentages, indicating inadequate resolution for the scale of this study. Ecoregions were useful in categorizing habitat and grasshopper community gradients across Montana, from mountains to plains. GIS data are thus useful for grasshopper community analysis and can be used as input for grasshopper forecasting or decisionmaking models.

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APPROVAL

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Date May 5, 1995

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ABSTRACT

Grasshopper communities in the Great Plains display broad species heterogeneity, varying with vegetation and local habitat. Knowledge of the specific composition of grasshopper communities and their pattern across space is necessary for the development of efficient grasshopper management strategies. This information can be integrated with habitat classification data to identify areas which are prone to grasshopper outbreaks. Plant and grasshopper communities at 170 sites in Montana and Colorado in 1992 were compared to identify differences in species composition and factors which influence grasshopper communities in the two states. Species proportions and percentages were analyzed using detrended correspondence analysis (DCA). Percent bare ground, litter, total cover, proportions of grasses and forbs, and plant height were not useful in distinguishing between plant communities in either state. Individual plant species DCA did detect differences among plant communities. Plant and grasshopper community compositions differ significantly between the two states, with *Buchloe dactyloides* and *Bouteloua curtipendula* distinguishing Colorado sites. Because both grasshopper communities and the vegetation resource vary between Montana and Colorado, the same pest management activities may have varied results when implemented in shortgrass versus mixed-grass prairie. Spearman rank correlations found grasshopper DCA results for Montana were correlated with percent bare ground, mode plant height, and plant species which increase with grazing. Such factors are thus important in determining grasshopper community composition, though they are not useful in distinguishing among plant communities. To identify spatial attributes which distinguish plant and grasshopper communities on a state-wide scale, plant and grasshopper species composition data were collected at 128 sites in three areas of Montana in 1993. A geographic information system (GIS) was used to associate each sampling site with Omernik's ecoregions and the Montana State Soil Geographic Database (STATSGO). DCA and statistical analyses were used to test differences and correlations among sampling areas, ecoregions, available water, and soil permeability. Three plant and four grasshopper species were correlated with soil permeability. Available water was correlated with six grasshopper species, but with none of the plant species. Soil permeability values differed significantly over all sampling areas and ecoregions. STATSGO plant percentages did not correlate with field percentages, indicating inadequate resolution for the scale of this study. Ecoregions were useful in categorizing habitat and grasshopper community gradients across Montana, from mountains to plains. GIS data are thus useful for grasshopper community analysis and can be used as input for grasshopper forecasting or decision-making models.

CHAPTER ONE

PLANT AND GRASSHOPPER COMMUNITY COMPOSITION: INDICATORS AND INTERACTIONS ACROSS THREE SPATIAL SCALES

General Introduction

Grasshoppers, as agricultural pests, have long been in conflict with humans. When pioneers settled in the western prairie of the United States, they endured years in which great clouds of grasshoppers destroyed crops, forage, trees, gardens, and household items such as canvas and clothing. Over 200 species of grasshoppers occur on the Great Plains, and up to 40 species might be observed in a single field. Despite the large number of species that inhabit rangeland and their extensive distributions, only a few species reach the outbreak numbers that result in widespread economic losses.

Prior to the 1940's, many attempts at grasshopper control in the western United States were unsuccessful because of the immense area of land infested and the cost of poison bait. Research into the species and factors responsible for outbreaks began in the 1940's at the request of stock growers. In the years following, insecticide sprays and powders replaced poison bait for grasshopper control and, more recently, baits containing grasshopper pathogens have been developed and incorporated into pest management

systems. Current research on viral pathogens holds much promise for grasshopper management with minimum impact on nontarget organisms.

Grasshoppers and locusts belong to the insect order Orthoptera, and related orthopteroids include crickets, mantids, cockroaches, termites and katydids. The term "grasshopper" is generally used for non-swarming species of the family Acrididae, while gregarious species are commonly referred to as "locusts". Most North American acridids do not form migrating swarms. A notable exception is the Rocky Mountain grasshopper (*Melanoplus spretus* [Walsh]), a species responsible for frequent and severe crop damage in the late 1800's, but which is now considered extinct.

North American grasshoppers feed mainly on vegetation, and a surprising number of species supplement that diet by cannibalizing dead or dying grasshoppers. Some species prefer dry plant material on the ground to green leaves, and immature nymphs may prefer different food plants from adults. Grasshoppers use posturing to regulate body temperature and may bask in the sun in bare patches when conditions are cool or climb plant stems when the soil becomes too warm.

Most grasshopper species found on the North American Great Plains overwinter as eggs buried in the ground, though a few species hatch in the fall and spend the winter as flightless nymphs. Diapause of eggs commences in the fall when the embryo is 60 to 80% developed and hatching occurs in the spring when temperatures exceed 24°C for several days. Hatchlings pass through 4 or 5 instars before becoming mature adults. Nymphs are not particularly damaging to vegetation before the 4th instar of their development.

Contrary to the popular perception that grasshoppers will eat anything, most species show preferences for particular food plants and some are oligophagous, feeding on only a few plant species. Feeding habits may change as nymphs develop or with environmental conditions. Vegetation structure and soil characteristics influence microhabitat selection and, consequently, species distribution. Thus, the heterogeneity of plants and soils across the landscape result in a mosaic of grasshopper communities with differing species compositions.

Though there has been much research on the population dynamics of grasshopper communities, little is known about the heterogeneity of those communities across the rangeland landscape. Knowledge of the specific composition of plant and grasshopper communities and their pattern in space and time is needed for the development of effective grasshopper management strategies. Because grasshopper control can be implemented over a range of scales, from a single ranch to multiple states, there is a need to demonstrate these community differences on different scales. This is the focus of Chapter 2, in which plant and grasshopper communities are compared on two different scales: between Montana and Colorado rangeland and within eastern Montana rangeland.

A large body of research has identified the environmental factors that influence grasshopper species distribution. The integration of this knowledge with habitat classification schemes can assist control efforts through the identification of areas where outbreaks are likely to develop. The focus of Chapter 3 is to evaluate two sources of habitat classification data for their usefulness as indicators of plant and grasshopper community change within Montana.

The community analyses in Chapters 2 and 3 also identify factors which determine grasshopper distribution in space at different scales. This information, with baseline data about the composition and spatial patterns of grasshopper communities, can be incorporated into decision-making processes to facilitate an approach to grasshopper management that considers the entire ecosystem.

CHAPTER TWO

COMPOSITION OF PLANT AND GRASSHOPPER COMMUNITIES: INTERACTIONS AT THE WATERSHED AND REGIONAL SCALES

Introduction

The Great Plains region of the United States is composed of many different ecosystems in a patchy, heterogeneous landscape and the amount of variability observed in the landscape is scale-dependent. To fully understand any ecological system, research must consider three levels of investigation: the phenomenon of interest, the mechanisms that give rise to it, and the larger context that gives it significance (Allen & Hoekstra 1992). While the large body of grasshopper research encompasses a range of scales, from microhabitat selection to global diversity, little has been done to integrate the information across these spatial scales, so that mechanisms and context become clear. There is a need to describe grasshopper community variability at the regional (multi-state) scale and compare it with the variability that exists at the watershed scale. With this information, regional trends in grasshopper communities will emerge and management efforts can then be tailored to local differences in community composition.

The main objectives in this study are to 1) determine the plant and grasshopper communities of rangeland sites in Montana and Colorado and establish how they may differ; 2) determine whether the plant and grasshopper species compositions differ

between sites within Montana; and 3) identify factors which influence grasshopper community composition at sites distributed in major grassland areas of the two states. Montana and Colorado were chosen for study because their plant and grasshopper communities are fundamentally different and thus allow meaningful comparisons. This information will establish the level of heterogeneity that can be found in rangeland at the landscape scale by comparison of sites which are widely separated in space and will provide information that will form the basis for grasshopper management within the larger sphere of ecosystem management.

As of 1987, 239 million hectares in the United States were used as grassland pasture (USDA 1992) and grasshopper management issues on these lands are extremely complex. The APHIS Rangeland Grasshopper Cooperative Management Program covers the 17 states west of the Mississippi River and parts of Alaska (USDA APHIS-PPQ 1987) that incorporate great differences in biodiversity. Grasshoppers are a part of that biodiversity, which may be important to maintain for moral, aesthetic and economic reasons, and because ecosystems provide benefits like nutrient cycling (West 1993). The design of pest management options which disrupt grassland ecosystems as little as possible requires an understanding of interactions among the communities which are potentially affected by grasshopper pest management practices. Is it reasonable to use the same management options in different states, or is there a need to tailor control measures to more localized characteristics of grasshopper communities?

Efforts to categorize habitat diversity has produced varied results, with the number of categories depending on the spatial scale, resolution, and factors used in

classification. For example, at the statewide level, Ross and Hunter (1976) identified 62 categories of climax vegetation in Montana, based on prevailing climate and soil conditions. Among these, 42 were non-forested grassland and shrubland range sites. Payne (1973) described 16 vegetative types, based on topography, soils, and plant species, within Montana rangeland alone. At a smaller spatial scale, Mueggler and Stewart (1980) divided the nonforested portions of the western third of Montana into 29 rangeland habitat types, based on plant dominance, cover, and frequency. Rangeland is defined here to be non-forested, open areas where the dominant plants are shrubs, grasses, and forbs.

Like the grasslands with which they are associated, grasshopper communities also display broad heterogeneity. For example, Kemp et al. (1990b) collected 40 species of grasshoppers from seven habitat types in the Gallatin Valley of Montana, and Quinn and Walgenbach (1990) found 31 species on 29 sites in South Dakota. Grasshopper species differ in the amount of damage caused to range and cropland. While over 600 species of grasshoppers occur in the United States, only a few can be considered serious pests and some are considered beneficial (Hewitt 1977). In Kansas, 219 species occur, but only 14 become occasionally abundant enough to be economically important (Smith 1954). Similarly, only four economic species were recognized by Smith and Holmes (1977) in Alberta. In Montana, Kemp (1992b) collected 57 species and found the only species which contributed proportionately less of the community in non-outbreak versus outbreak years was *Melanoplus sanguinipes*. Because most research is focused on economically important species rather than whole communities, little is known about the

effects of grasshopper management activities on the dynamics of species which do not reach damaging numbers.

Grasshoppers are an economically and ecologically important part of the fauna found in the Great Plains of the United States, at times causing extensive losses of forage and crops (see Hewitt 1977). Densities commonly range from less than one to over 40 grasshoppers per m^2 (Hewitt and Onsager 1983) and may exceed 100 grasshoppers per m^2 during outbreaks (W.P. Kemp, personal communication). Densities reached 54/m^2 in east-central Arizona in 1954, destroying over 99% of the vegetation (Nerney and Hamilton 1969). There is a positive relationship between grasshopper densities and the extent of an infestation (Smith and Holmes 1977). Outbreaks of high grasshopper densities occur cyclically (Capinera and Sechrist 1982b, Smith 1954, Onsager 1986), but may not be synchronized over large multi-state areas (Onsager 1986, Capinera and Horton 1989).

Pest management activities may extend across state boundaries when grasshopper infestations are widespread (USDA APHIS-PPQ 1987). However, the rangeland covered by cooperative management programs will likely vary in vegetation, and grasshopper community composition can be expected to change along vegetational gradients. Fielding and Brusven (1993a), for example, found a high proportion of grass-feeding grasshoppers at sites which had been seeded with perennial grasses, while sites with annual grasses had high proportions of polyphagous species. Quinn et al. (1991) also found that grasshopper communities changed along a gradient of percent coverage of grasses, particularly *Buchloe dactyloides*. Studies by Miller and Onsager (1991) and Quinn and Walgenbach

(1990) on the effects of cattle grazing show that grazing resulted in changes in canopy structure and increased areas of bare ground, which may be important for oviposition in some species. Kemp et al. (1990b) found grasshopper species composition was correlated to precipitation, elevation, proportion of grasses and total number of plant species. Scoggan and Brusven (1973) found that plant community, soil characteristics and climate determined grasshopper community composition. Patch size and plant succession impact the species richness and composition of grasshopper communities through changes in vegetation structure and litter (Bergmann and Chaplin 1992).

Climate has been shown to influence grasshopper abundance, with warmer temperatures usually associated with higher grasshopper numbers. Edwards (1960), using data from 19 weather stations in Saskatchewan, found a relationship between grasshopper populations and mean July-September temperature of the previous three years. Capinera and Horton (1989) examined grasshopper infestation maps and weather data for four western states from 1930 through 1986. They found spring and summer precipitation to be important for grasshopper infestations in Colorado and New Mexico, while summer and fall temperatures were more important in Montana and Wyoming. Grasshopper species richness was significantly reduced in eastern and south-central Montana following the 1988 drought, although species differed in their sensitivity to the resulting temporal variation in vegetation (Kemp and Cigliano, 1994).

The studies noted above illustrate the spatial differences that exist among grasshopper communities. The grasshopper species present at a given site and their relative abundance is related to local habitat, resulting from moisture gradients (Kemp

1992a), vegetation and soil characteristics (Quinn et al. 1991), or disturbance (Fielding and Brusven 1993a, Scoggan and Brusven 1973). Differences in composition influence the need for and success of grasshopper management efforts, because these depend upon the presence and abundance of economically damaging species.

There is a need for fundamental knowledge of the structure of grassland heterogeneity and its implications for grasshopper communities. There is abundant evidence that plants influence grasshoppers (Anderson 1964, 1973; Capinera and Sechrist 1982a; Evans 1988; Fielding and Brusven 1993a,b; Kemp et al. 1990; Miller and Onsager 1991; Pfadt 1984; Quinn et al. 1991) and even polyphagous species show preferences for a limited number of host plants (Isely 1938). Knowledge of specific relationships between grasshopper species composition and plant species composition may permit the use of indicator plants to identify sites on which grasshopper species might reach economically damaging densities. For example, Hewitt (1980) found that the flowering of many forbs, such as Prairie sunflower (*Helianthus petiolaris*), pricklypear (*Opuntia polyacantha*) and Scarlet globemallow (*Sphaeralcea coccinea*), coincides with stages of grasshopper development during which control is recommended. Kemp et al. (1991) found that hatching occurred about 10 days after the onset of purple lilac (*Syringa vulgaris*) blooms and the ideal time for application of control agents occurred about 10 days after the end bloom phase of Zabeli honeysuckle (*Lonicera krolkowii*).

In some areas, pest management activities are aimed at protecting cropland from grasshoppers which invade from adjacent rangeland (see Fielding and Brusven 1990). Where the forage produced on the range is not valuable enough to justify control for

forage alone, knowing how grasshoppers respond to changes in plant heterogeneity can help to identify areas and conditions in which grasshoppers are likely to migrate to valuable cropland.

An understanding of the spatial variability of grasshopper populations is also important for proper sampling and hazard assessment. Early work by Gage and Mukerji (1977), which calculated a damage index based on a ratio of heat to precipitation, demonstrated the value of quantifying existing survey data in order to evaluate change in grasshopper populations over time. Recent developments in mapping technology have allowed the spatial variability in grasshopper densities to be quantified and used as an indicator for hazard maps. Johnson and Worobec (1988) and Kemp et al. (1989), using the geographic information system SPANS, found a spatial auto-correlation between grasshopper counts and spatial separation between sites, and both produced maps which could be used in predicting grasshopper densities during the subsequent year. Johnson (1989) found, by comparing maps of predicted and observed field counts, that roadside counts are reliable predictors of field populations and are sufficient for making population density maps to be used in hazard prediction.

Despite the need for information on an ecologically large scale to make informed management decisions, research into the relationships between plant community composition and grasshopper community composition has been focused on small-scale investigations, most commonly at the field scale and only occasionally at the valley (watershed) scale or larger. Pfadt (1984) found in Colorado that the abundance of grass affected the number of grasshopper species and the density of graminivorous

grasshoppers at a 2.2 ha site. Capinera and Sechrist (1982a) linked grasshopper community composition with grazing intensity in a study of six 130 ha pastures in northeastern Colorado. Quinn and Walgenbach's (1990) study of 29 sites in south-central South Dakota covered just two counties. Evans (1988) studied the influences of fire frequency, topography, and vegetation on grasshoppers in Kansas tallgrass prairie, using 38 sites that ranged from 14 to 134 ha in size. However, Bergelson (1990) found that the spatial scale at which herbivory was measured affected the interactions discovered. Thus, there is a need to identify the scale on which grasshopper and plant sampling should be performed in order to adequately capture heterogeneity and plant-grasshopper interactions. Studies done on multiple scales are needed to address the problems identified by Bergelson and others.

Studies of local grasshopper populations often describe plant and grasshopper community composition, giving specifics on grasshopper species distribution and food preferences, but provide no generalities concerning interrelationships between grasshopper distributions and the presence of preferred food plants (Anderson 1964, 1973; Banfill and Brusven 1973). Little research has been carried out at scales above the local level. Studies done on the state or province level often use historical counts taken from annual surveys (e.g., Gage and Mukerji 1977, Johnson 1989). Studies comparing density data from multiple states, such as Capinera and Horton's (1989) study on the effects of weather on grasshopper infestation, are uncommon. On the global scale, Otte (1976) compared the species richness of grasshoppers on 2500 m^2 plots in North and South American deserts and found that higher numbers of grasshopper species

were associated with more heterogeneous vegetation. Large-scale investigations such as this are needed to test whether general relationships discovered between grasshopper and plant communities at small ecological scales apply to large spatial areas.

Basic information is needed to assist land managers with decisions concerning management of problem grasshopper densities. For example, a computer program has been developed (HOPPER) that assists in decision-making by evaluating control options (Kemp et al. 1988, Berry et al. 1991, USDA APHIS-PPQ 1991). Such decision support systems can help to decide which pest management actions are cost-efficient given the conditions under which the control is to be carried out. The traditional minimum threshold for grasshopper control requires densities to be higher than 9.6 grasshoppers per m^2 before some management activity is considered (USDA APHIS-PPQ 1987). One threshold, however, is not valid for every situation (Davis et al. 1992). In 1979, only about 68% of the western range produced forage worth more than the average cost of historical cooperative chemical control (Hewitt and Onsager 1983).

It follows, then, that the costs and benefits need to be analyzed for each case where management is considered to demonstrate that it is economically and biologically justifiable. While treatments such as carbaryl bait expose fewer nontarget arthropods and wildlife to less environmental hazards than chemical sprays, the potential for indirect effects still exists (George et al. 1992), and mortality rates for baits differ with grasshopper species (Onsager et al. 1980). Thus, fundamental knowledge of the relationships between grasshopper and plant community composition must be incorporated into decision support programs to make better management decisions.

Methods

Vegetation Sampling

Plant cover was measured at 80 sites near Jordan, Montana, and at 90 sites in eastern Colorado during two sampling periods in 1992 (Figures 1-3). The first set of samples was collected during the first two weeks of June, while the second set of samples were collected between the end of July and the third week of August. The Montana sites were located in a roughly triangular area near Jordan, Hysham, and Miles City, Montana, between longitudes -107° 10′ and -105° 55′ and between latitudes 46° 15′ and 47° 35′. Colorado sites were located between longitudes -105° 12′ and -102° 25′ and between latitudes 37° 00′ and 40° 41′.

The Colorado sites were numbered 1 through 90 (Figure 2). These sites were characterized by shortgrass prairie (Sims 1988). In contrast, the Montana sites (Figure 3) are located in mixed-grass prairie (Weaver and Albertson 1956, Sims 1988). Montana sites were chosen in three different climax vegetation types, arbitrarily designated A, B, and C. The definition of a climax plant community, as used by Ross and Hunter (1976), is the plant community which develops under the prevailing climatic and edaphic conditions in the absence of disturbance. This view is equivalent to the "climatic climax" used by Daubenmire (1978). While this native plant community may not be evident because of disturbance, each vegetation type is distinguished by the potential for the development of a specific kind and amount of vegetation.

Figure 1. Montana and Colorado study areas, with 80 sample sites in eastern Montana and 90 sites in eastern Colorado in 1992.

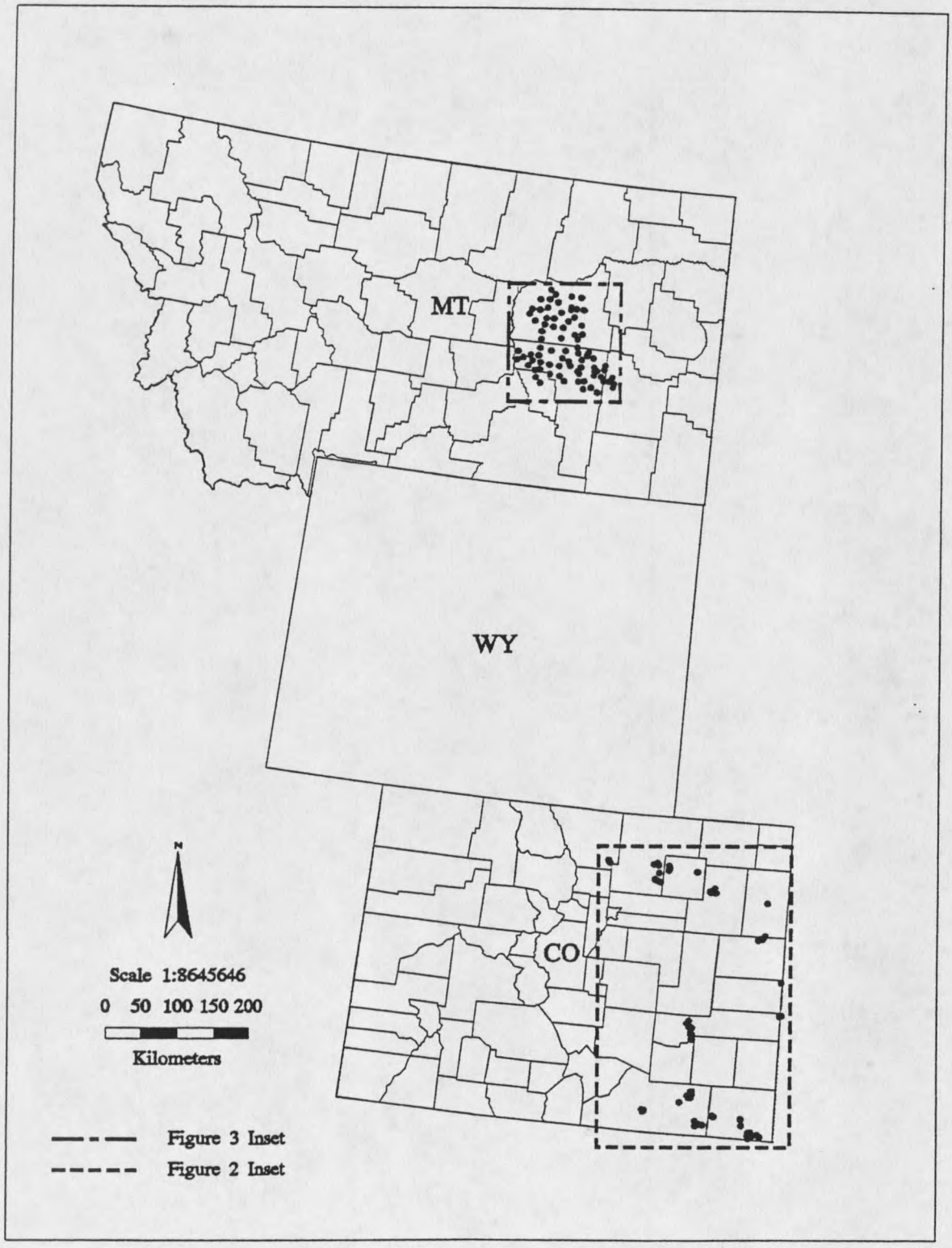


Figure 2. Sample sites in eastern Colorado with county boundaries.

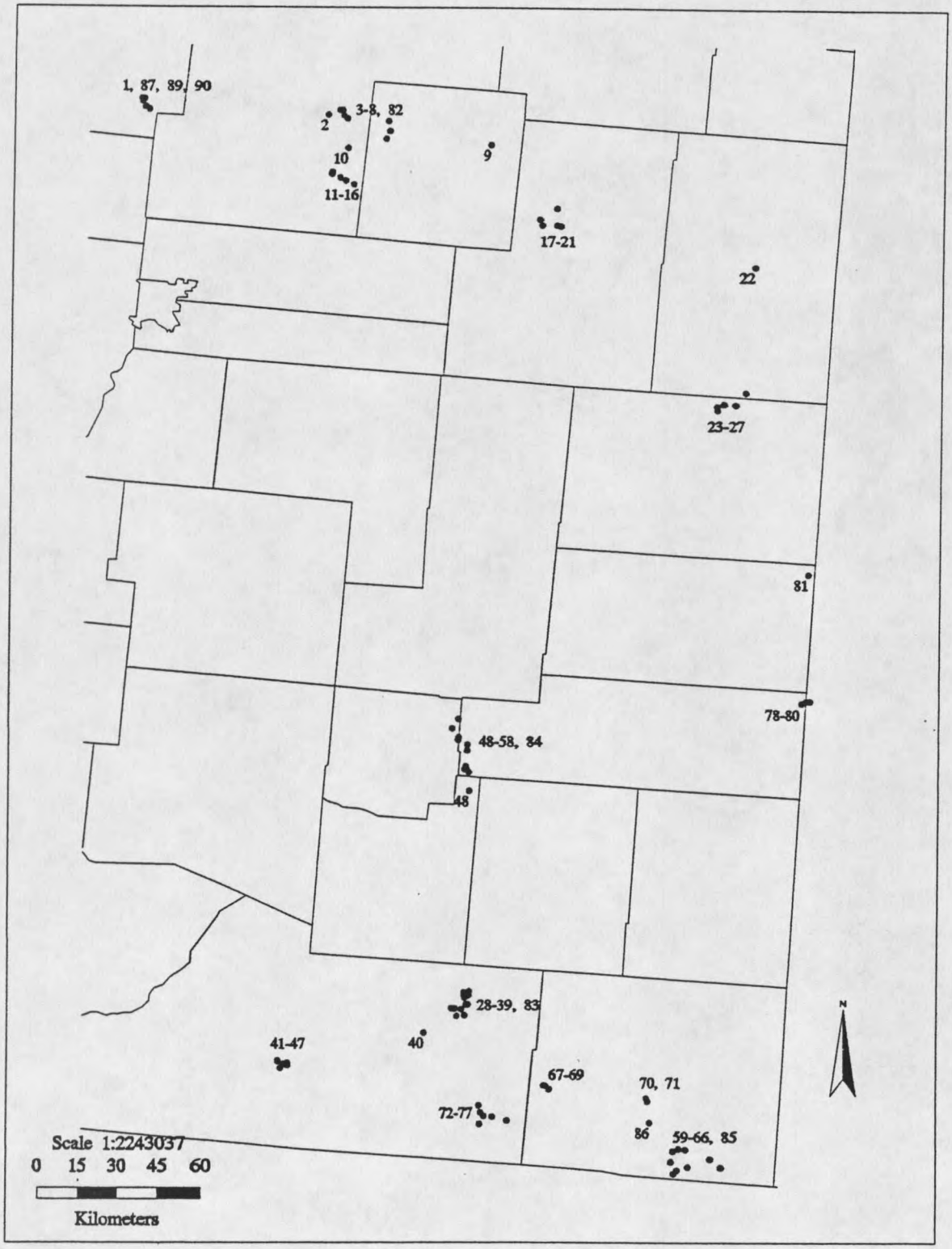
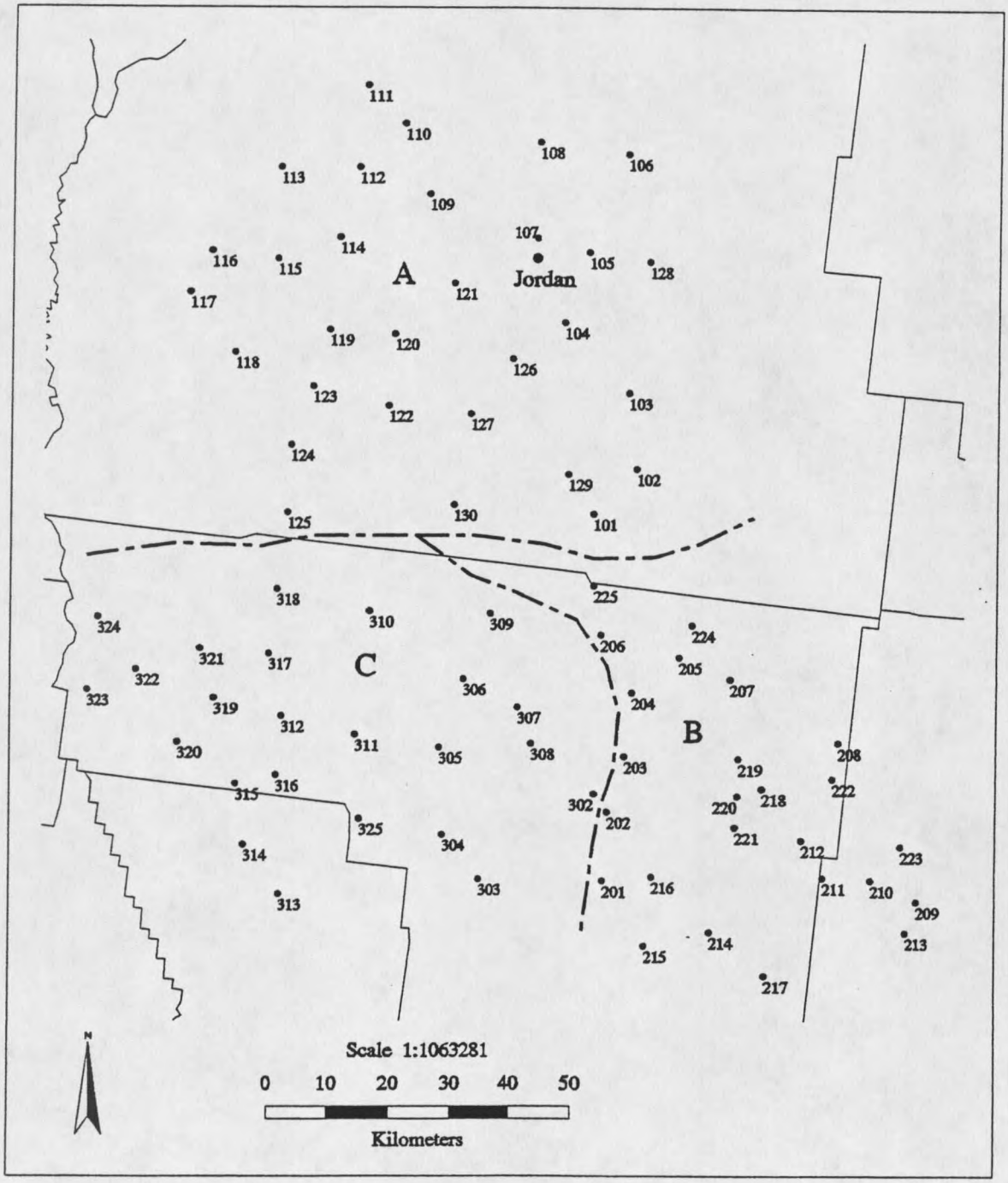


Figure 3. Sample sites near Jordan, Montana, for 1992 with county boundaries and associated vegetation types. Solid lines represent county boundaries, while dashed lines represent the boundaries of climax vegetation types A, B, and C. Sites located in vegetation type A have silty soils and are dominated by wheatgrass and needleandthread; vegetation type B has silty or clayey soil with wheatgrass and green needlegrass; type C has dense clayey or saline soil with wheatgrass, green needlegrass and wildrye (Ross and Hunter 1976).



For the Montana sites, climax vegetation in type A (Figure 3) occurs on silty range sites in the 10-14" precipitation zone and is dominated by western and thickspike wheatgrass, needleandthread, green needlegrass, little and big bluestem, bluebunch wheatgrass, and silver sagebrush (Ross and Hunter 1976). Type B represents silty or clayey range sites in the 10-14" precipitation zone with wheatgrass, green needlegrass, little bluestem, and big sagebrush (Ross and Hunter 1976). Type C is found on upland range sites with dense clay, clayey or saline soils in the 10-14" precipitation zone with wheatgrass, green needlegrass, wildrye, big sagebrush, and greasewood (Ross and Hunter 1976). Sites in Montana were chosen in more than one vegetation type to determine whether the plant community at a site (approximately 0.05 km^2) in this area (approximately 16,000 km^2) influences the grasshopper community at that site. Sites that were located in vegetation type A were numbered 101 to 130, sites within type B numbered 201 to 225, and in type C, were numbered 301 to 325.

At the Colorado and Montana sites, the vegetation contained in five Daubenmire (1959) frames of 0.10 m^2 each were examined at each site. The percent cover by bare ground, leaf litter, and individual species were recorded. Total cover, tallest plant height, and mode plant height were also measured. The data were averaged over the five frames by summing the percent cover or heights for each site and dividing by five. Therefore, if a plant species was not present in one of the frames, the percent cover for that frame was zero, and this value was averaged with the other four frames to obtain the site average for that species.

The percent cover and plant height data were used to establish three different data sets for each state to determine which attributes of the plant community most strongly affect the grasshopper community. One data set, "general site characteristics", consisted of the proportions of bare ground, leaf litter, and total cover. Because of overlap, these measurements do not sum to 100%, so the proportion of each measure was calculated by summing the percent cover of bare ground, litter, and total cover at each site, then dividing each measurement by this total. Tallest plant height and mode plant height were averaged from the direct measurements by summing the heights over the five frames and dividing by five.

A second data set, "plant groups", consisted of the proportions of perennial grass, annual grass, perennial forbs, and annual forbs calculated for each site. Classification of plants was done using Dorn (1984), GPFA (1986), Hitchcock and Cronquist (1973) and Stubbendieck et al. (1992). Any plant species which could not be reliably classified in these groups was grouped into a category called "other". It should be noted that only one species, found at one of the 80 Montana sites, was classified as "other" in the Montana plant data set. A third data set, "individual species", consisted of the proportion of plant cover contributed by each plant species found at each site. The codes used to abbreviate plant species names are listed in the Appendix. Montana and Colorado data sets were processed in separate files.

Grasshopper Sampling

Grasshoppers were collected via sweep nets at the same sites where plant sampling was done, although Colorado site 87 was missing from the grasshopper data.

The number of first through fifth instars, adult males and adult females were recorded for each grasshopper species collected in 200 sweeps at each site. Sweeps were taken between 0930 and 1600 h when cloud cover was less than 15% and winds were less than 25 kmh^{-1}, with each sweep covering a low 180° arc through vegetation with a net. Crickets were counted at the Montana sites, but were not included in the data. Montana and Colorado data were processed in separate files.

The raw data were pooled over phenological stage and over the two sampling periods in the statistical software package SAS (SAS 1985) to sum counts for each species at each site. The proportion that each species contributed to the local community was calculated by dividing the number of grasshoppers of a given species by the total number of grasshoppers collected at that site. These proportions comprised a data file of "all species" collected. Species were then classified by the phenological stage in which they spend the winter months, using Otte (1981, 1984), Capinera and Sechrist (1982b), and Vickery and Kevan (1985). Those species which overwinter as nymphs were classified as overwintering species, while those which spend the winter as eggs were classified as "spring-emergers" (see Appendix). The proportion of spring-emerging species at each site was calculated by excluding over-wintering species from the total number of grasshoppers at each site, then dividing the number of grasshoppers of a given species by the new total. A second data file consisted of the proportions for only spring-emergers at Montana sites.

Data Analysis

Species proportions and percentages, whether plant or grasshopper, were analyzed using detrended correspondence analysis (DCA) via the computer program CANOCO. DCA is a nonlinear, weighted averaging method of measuring the variance among species and site data in a single analysis, in which sites and species are ordered along four axes (the most available in CANOCO) according to their similarities to each other. The result is a list of eigenvalues for each species and site, representing the variance accounted for by each ordination axis (Ter Braak 1988). Eigenvalues for each axis are directly proportional to the importance of that axis in separating species and sites. DCA scales axes in uniform and natural units, so scores from different data sets may be compared (Gauch 1982). Using the computer ordination program CANOCO (Ter Braak 1988), the first DCA run was conducted on all sites and variables (site characteristics, plant groups, or species) in each data set. Axis 1 and 2 scores resulting from each final DCA were imported into SAS programs (SAS 1985) to produce graphs of the distributions of sites and species. Codes from the Appendix were used for plotting plant and grasshopper species.

The first null hypothesis considered was that the grassland sites sampled within Montana did not have different plant stand structure (hypothesis 1, Table 1). This hypothesis was tested using two DCAs, one based on the Montana general site characteristics data set and another from the Montana plant groups data set. In these two analyses, what are input as "species" by CANOCO are actually plant groups or general measures which characterize sites. Low eigenvalues resulting from DCA would support

Table 1. Hypotheses used to test interactions between plant and grasshopper community compositions in Montana and Colorado rangeland in 1992.

Hypothesis	Test
1) Montana sites do not differ in plant stand structure	DCA on general site characteristics, DCA on plant groups
2) Montana sites do not differ in plant species composition	DCA on individual plant species
3) Colorado sites do not differ in plant stand structure	DCA on general site characteristics, DCA on plant groups
4) Colorado sites do not differ in plant species composition	DCA on individual plant species
5) Montana and Colorado sites do not differ in plant species composition	DCA on the 20 most frequently collected plant species
6) Montana sites do not differ in grasshopper species composition	DCA on all grasshopper species, DCA on spring-emerging grasshopper species
7) Colorado sites do not differ in grasshopper species composition	DCA on all grasshopper species
8) Montana and Colorado sites do not differ in grasshopper species composition	DCA on all grasshopper species
9) No correlations exist between grasshopper species composition and vegetation characteristics at Montana sites	Spearman correlation

the null hypothesis, since low values indicate little separation between sites. Therefore, if the sum of the eigenvalues for the first two axes was less than 0.60, the null hypothesis would not be rejected. This same subjectively-chosen criterion was used to test each

subsequent null hypothesis, so that null hypotheses were not rejected unless over half of the variation in the samples was accounted for in the first two axes.

A second null hypothesis developed was that the Montana sites do not differ in their plant species composition (hypothesis 2). To test this hypothesis, a DCA was conducted using the percent cover contributed by each plant species collected at each site (Montana individual species data set).

Hypothesis 3 stated that Colorado sites were not different in terms of plant stand structure. This hypothesis was tested in the same way as hypothesis 1, using Colorado general site characteristics and plant groups data sets. Hypothesis 4 was that the Colorado sites do not have different plant community compositions. This hypothesis was tested using percent cover of the Colorado individual species (similar to hypothesis 2).

Where comparisons of Montana and Colorado sites were to be made, the data sets for the two states were merged and the DCA was conducted on the combined data set. To test the hypothesis that Montana sites and Colorado sites do not differ in plant community composition (hypothesis 5), the frequency of occurrence for individual species was calculated for sites within each state. The percent cover for each of the 20 most frequently collected species in each state was merged into a file for this analysis. A second DCA was conducted using all plant species collected in both states to be sure that inferences made using only these 20 plant species were valid.

To test the null hypothesis that Montana sites do not differ in grasshopper community composition (hypothesis 6), a DCA was conducted using the Montana all species data set. In the Montana grasshopper data, only one species had been collected

at sites 318 and 325. This skewed the axis scores, resulting in the other sites being so similar to one another that they were indistinguishable. Thus, sites 318 and 325 were removed from subsequent analyses to allow better separation among the remaining sites and species. Because proportions were equally distributed among 3 and 4 species at sites 307 and 322, respectively, these sites were omitted from DCA of the Montana all species data set to obtain better distinction between the remaining sites.

Because grasshopper species which spend the winter as nymphs may attain higher abundance at an earlier date than those that overwinter as eggs, hypothesis 6 was tested again, using data for the Montana spring-emerger data set (see Appendix). In this DCA, sites 307, 315, 318, 322 and 325 were omitted because of species proportions, as explained above, for better dispersion between the remaining sites.

A similar null hypothesis for Colorado sites stated that the sites were not different in terms of grasshopper species composition (hypothesis 7). This was tested using a DCA analysis of the Colorado all species data set. To test the null hypothesis that Montana and Colorado sites do not differ in grasshopper community composition (hypothesis 8), the Montana all species data set was merged with the Colorado all species data set and DCA was conducted on the combined data. Montana sites 307, 318, and 325 were omitted from the analysis for better distinction between sites.

To evaluate the relationships between the plant measurements and grasshopper community composition, grasshopper DCA axis scores for sites were correlated with the plant proportion values. The statistical package SAS (SAS 1985) was used to calculate (1) Spearman rank correlations between axes 1 and 2 scores and the plant variables, as

well as among the plant variables, and (2) the test statistic t. To obtain the fast and precise results, the P-value for each value of t was determined in the statistical program MSUSTAT (Lund 1991) and P-values of less than 0.05 were considered statistically significant, resulting in rejection of the null hypothesis.

To test for relationships between grasshopper species compositions and vegetation characteristics at Montana sites (hypothesis 9), three statistical tests were performed. The first was a Spearman rank correlation between axis 1 and 2 grasshopper site scores and general site characteristics (bare ground, leaf litter, and so on). A second correlation was conducted using grasshopper site scores and plant group proportions, although correlations could not be tested with species coded as "other" because this category occurred at only one site. A third correlation test used the percent cover of individual plant species and grasshopper DCA scores. This step was not taken for the Colorado sites because those sites were chosen without regard to climax vegetation types. Thus, while gradients might have been identified by performing correlation tests, whether these gradients resulted from changes in climax vegetation type or some other environmental factor could not be determined.

Results

Montana Vegetation

General Site Characteristics. For the Montana general site characteristics data, (percent bare ground, leaf litter, total cover, and plant heights), eigenvalues for axis 1 and 2 were 0.011 and 0.003, explaining little of the variation among sites and species.

These small eigenvalues supported the null hypothesis that these sites do not have different plant community characteristics. Thus, although the sites were chosen in different climax vegetation types (Ross and Hunter 1976), the differences among sites were not large enough for the null hypothesis to be rejected (Figure 4).

The scatter-plot of Montana sites based on general site characteristics (Figure 4) showed overlap between sites located in different vegetation types. Although some sites in vegetation type C ordinated separately from the other sites, suggesting different plant community composition from types A and B, these differences are not statistically significant, given the very low eigenvalues for this analysis.

Plant Groups. The analysis on plant groups classified each plant species as annual or perennial and either grass or forb as a further test of hypothesis 1. Eigenvalues for axis 1 and 2 of this analysis were 0.182 and 0.068, explaining little variation among sites and species in these first two axes (Figure 5). These small values supported the null hypothesis that these sites do not have different plant community compositions and confirmed the general site characteristics analysis results.

Individual Species. The eigenvalues for individual Montana plant species on axis 1 and 2 were .593 and .385, respectively, explaining a high degree of the variation among sites and species. These values supported the alternative hypothesis that these sites have different plant community compositions. Thus, analysis using plant species resulted in detection of differences large enough for null hypothesis 2 to be rejected.

Figure 4. Results of detrended correspondence analysis based on general site characteristics for 80 sites near Jordan, Montana in 1992. Sites located in vegetation type A have silty soils and are dominated by wheatgrass and needleandthread; vegetation type B has silty or slayey soil with wheatgrass and green needlegrass; type C has dense clayey or saline soil with wheatgrass, green needlegrass and wildrye (Ross and Hunter 1976). Unlabeled sites include 103, 104, 116, 123, 202, 204, 205, 212, 215, 217, 223, 225, 310, 311, and 313.

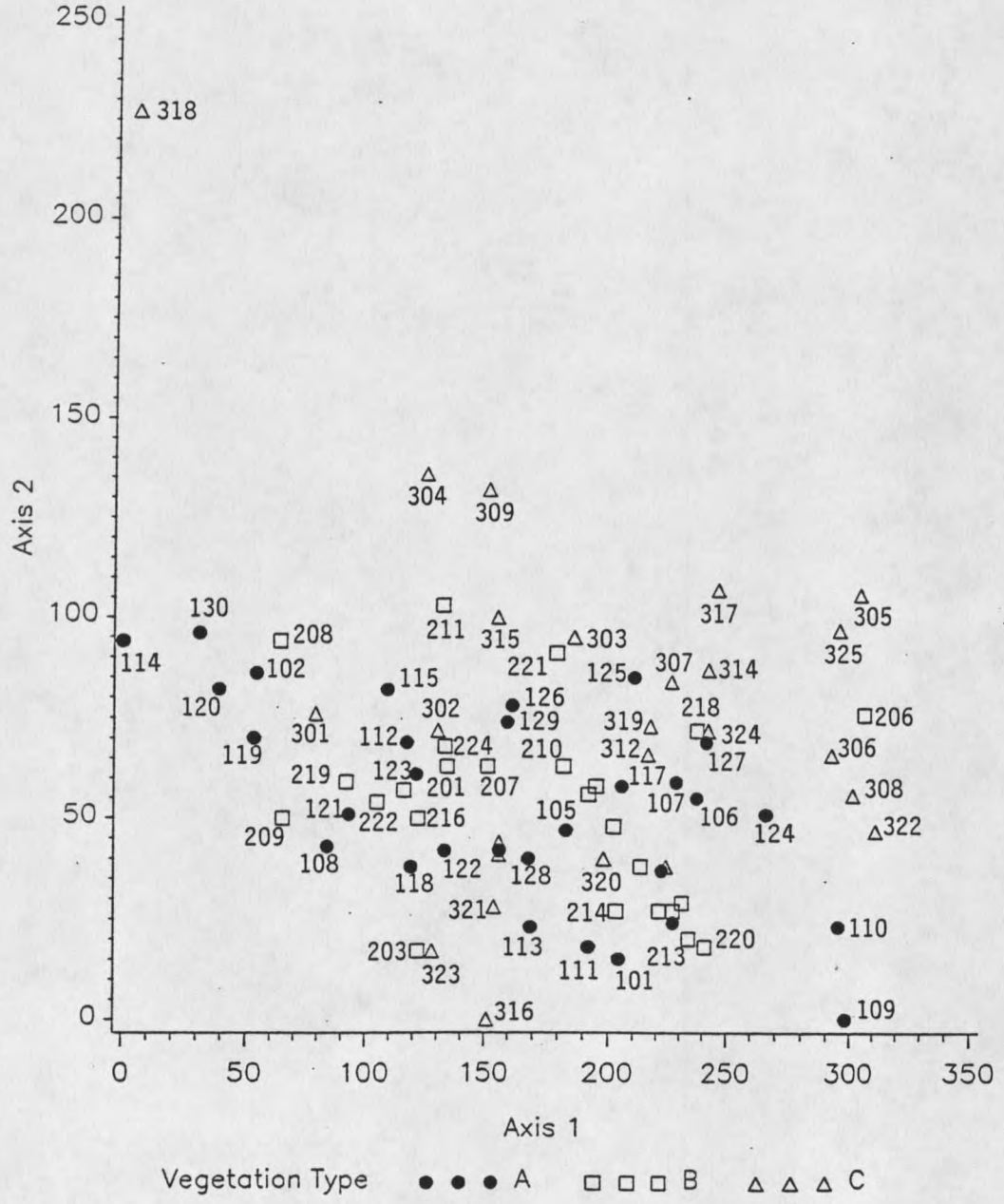
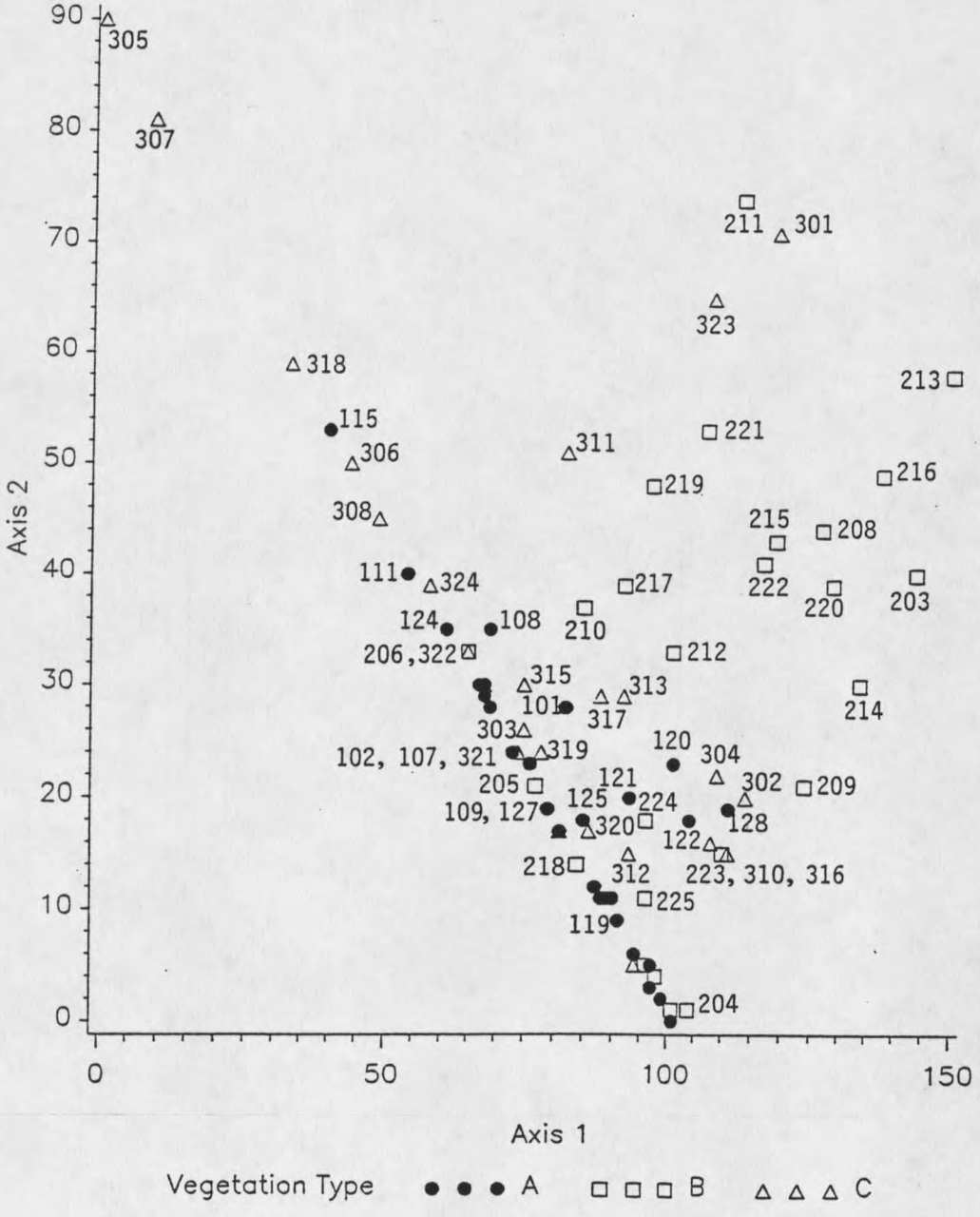


Figure 5. Results of detrended correspondence analysis based on plant groups for 80 sites near Jordan, Montana in 1992. Sites located in vegetation type A have silty soils and are dominated by wheatgrass and needleand thread; vegetation type B has silty or clayey soil with wheatgrass and green needlegrass; type C has dense clayey or saline soil with wheatgrass, green needlegrass and wildrye (Ross and Hunter 1976). Unlabeled sites include 103-106, 110, 112-114, 116-118, 123, 126, 129, 130, 201, 202, 207, 309, 314, and 325.



The site plot based on individual species of Montana plants (Figure 6) showed sites in vegetation type C well-separated from sites in types A and B. Sites within vegetation types A and B did not separate well in Figure 6, suggesting that these sites are similiar in plant community composition.

The species plot (Figure 7) was coded to show the growth form of each plant species. Plant species with low axis 1 scores were *Artemisia ludovisciana*, *Calamovilfa longifolia*, *Linum perenne*, and *Lupinus sericeus*. *Eriogonum ovalifolium* and *Penstemon* spp. had high axis 1 scores. For axis 2, *Astragalus gilviflorus*, *Sitanion hystrix*, *Sporobolus airoides*, and *Vicia americana* had low scores while *Artemisia arbuscula*, *Bromus japonicus*, and *Poa scabrella* had high scores. No pattern regarding differences in growth form was evident.

Colorado Vegetation

General Site Characteristics. DCA analysis of Colorado general site characteristics resulted in eigenvalues of 0.033 and 0.015 for axes 1 and 2 (Figure 8). These low values indicate that very little of the variability between sites was accounted for by measuring bare ground, leaf litter, cover, and plant heights. Therefore, the null hypothesis that the sites have similar stand structures (hypothesis 3) was not rejected using this test.

Plant Groups. An analysis of Colorado plant data based on plant growth form was also used to test hypothesis 3. The eigenvalues for axis 1 and 2 from this DCA were 0.322 and 0.112, respectively. While these values are much higher than those for

Figure 6. Results of detrended correspondence analysis based on individual plant species for 80 sites near Jordan, Montana in 1992. Sites located in vegetation type A have silty soils and are dominated by wheatgrass and needleand thread; vegetation type B has silty or slayey soil with wheatgrass and green needlegrass; type C has dense clayey or saline soil with wheatgrass, green needlegrass and wildrye (Ross and Hunter 1976). Unlabeled sites include 101, 102, 104, 106, 108-110, 112, 114, 116-122, 126, 129, 130, 201, 203, 209-213, 215-217, 219, and 223.

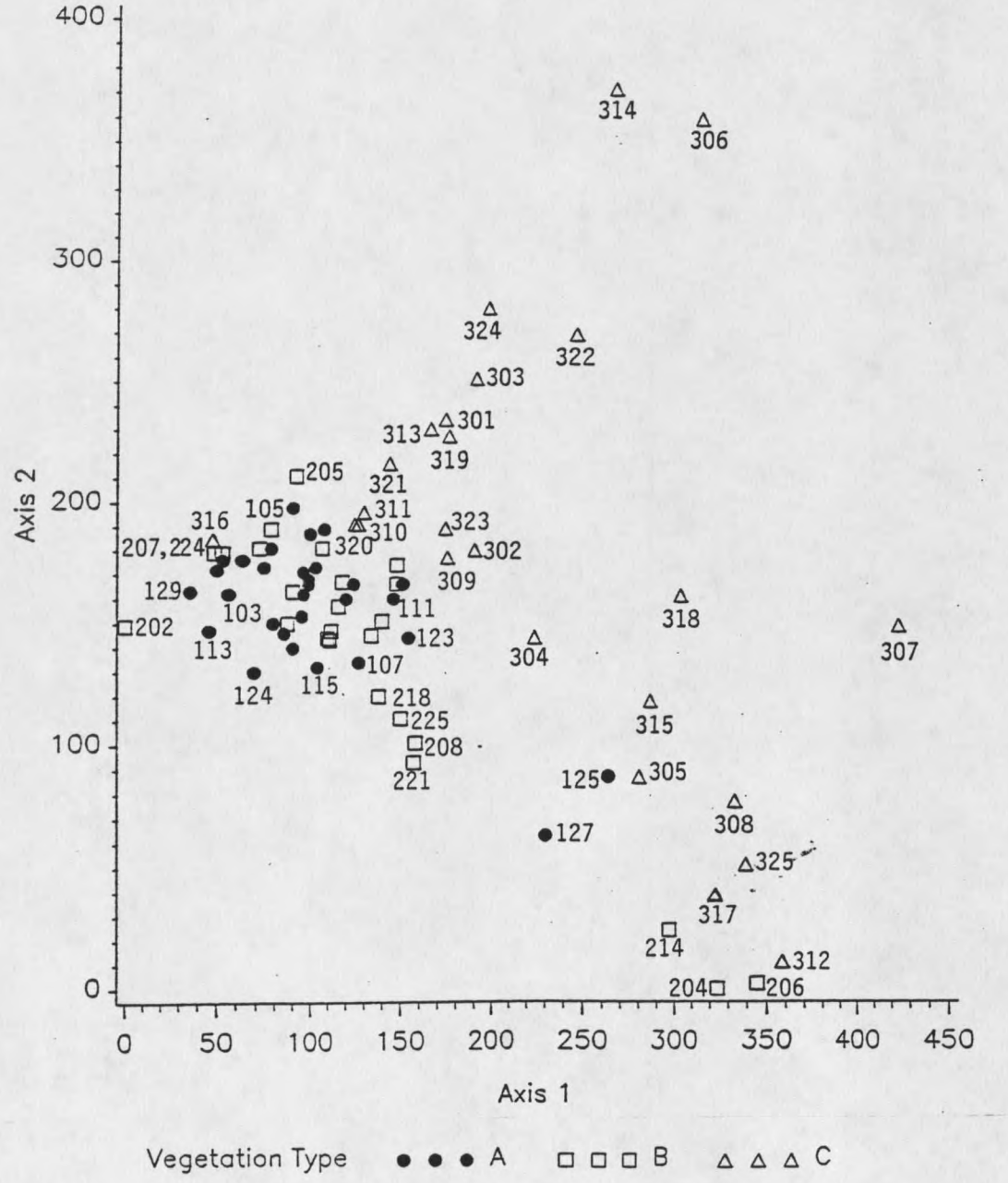


Figure 7. Results of detrended correspondence analysis based on individual plant species for 80 sites near Jordan, Montana in 1992. "AF" refers to species which are annual forbs, "AG" refers to annual grasses, "PF" refers to perennial forbs, "PG" refers to perennial grasses, and "OT" are other plants not identified by species. Species abbreviation codes are given in the Appendix. Unlabeled species at 1 are CHVI, OPPO, and OXY?, and at 2 are ARCA, COUM, and ERPA.

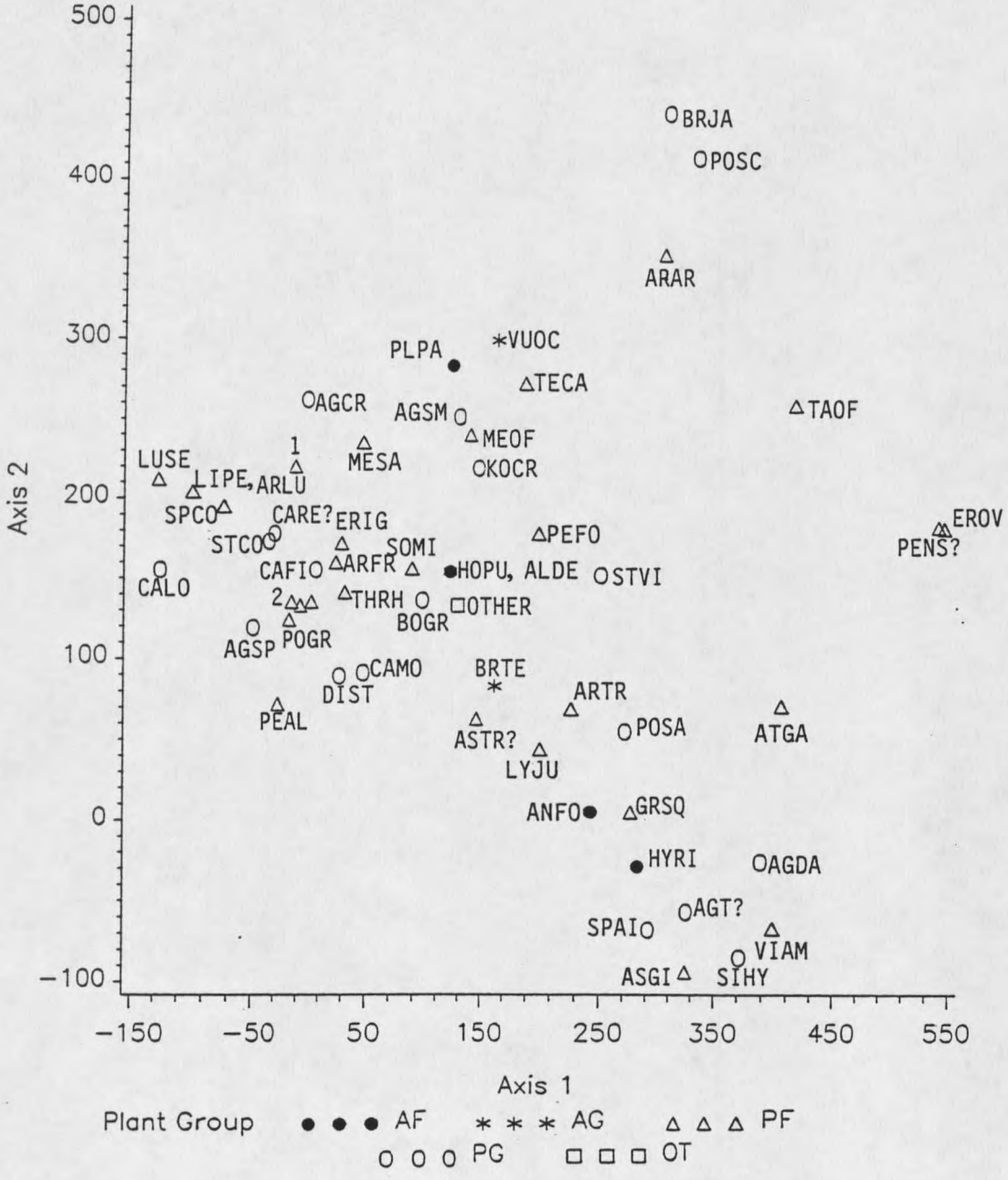
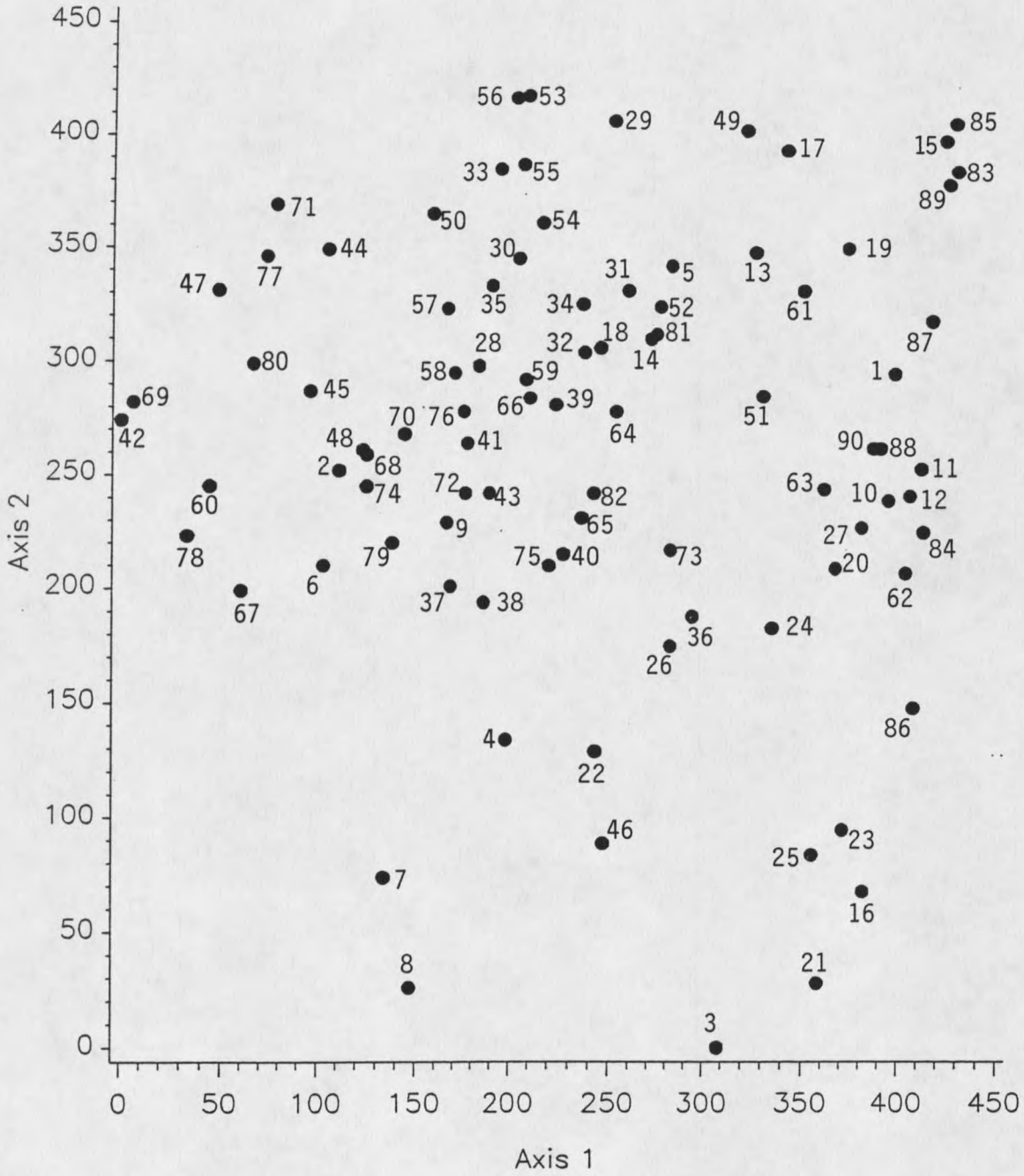


Figure 8. Results of detrended correspondence analysis based on general site characteristics for 90 sites in eastern Colorado in 1992: scatter-plot of sites.



the general measures, they are too low to provide sufficient evidence for rejecting the null hypothesis. Thus, hypothesis 3 is not rejected on the basis of either test.

The plot of Colorado sites based on plant group DCA scores (Figure 9) showed sites 1, 85, and 87 to have low axis 1 scores but high axis 2 scores. Site 84 had low scores for both axes. Sites 13 and 83 also had low axis 2 scores. A number of sites had high axis 1 scores, making it difficult to distinguish between sites. The clustering of these sites indicates their similarity with respect to plant groups.

Individual Species. Eigenvalues for analysis of Colorado sites based on individual plant species were 0.678 and 0.511 for axes 1 and 2, respectively. These values were very high, indicating that the sites differ in plant species composition. Thus, the null hypothesis that the sites do not have different plant communities (hypothesis 4) was rejected.

A site plot based on Colorado individual plant species (Figure 10) shows some sites clumped around 195 on axis 2. Sites 1, 11, and 13 had low axis 1 scores; 61, 71, and 86 had high axis 1 scores; 1, 5, 12, and 88 had low axis 2 scores; and sites 18, 63, 85, and 89 had high axis 2 scores.

The plot showing distribution of the individual plant species (Figure 11) was more dispersed than the site plot. Species with low axis 1 scores were *Carex* spp., *Erigeron bellidiastrum*, and *Picradeniopsis oppositifolia*. *Andropogon gerardi*, *Dyssodia aurea*, and *Schizachyrium scoparium* had high axis 1 scores. On axis 2, *Artemisia frigida*, *Artemisia campestris*, and *Stipa viridula* had low scores while *Chenopodium leptophyllum*, *Equisetum arvense*, and *Gaura coccinea* had high scores. This plot used

Figure 9. Results of detrended correspondence analysis based on plant groups for 90 sites in eastern Colorado in 1992: scatter-plot of sites. Unlabeled sites include 2-8, 10, 16, 20-22, 24, 25, 28, 29, 31, 32, 35-37, 39, 40, 42, 44-62, 64-80, 82, 86, 89, and 90.

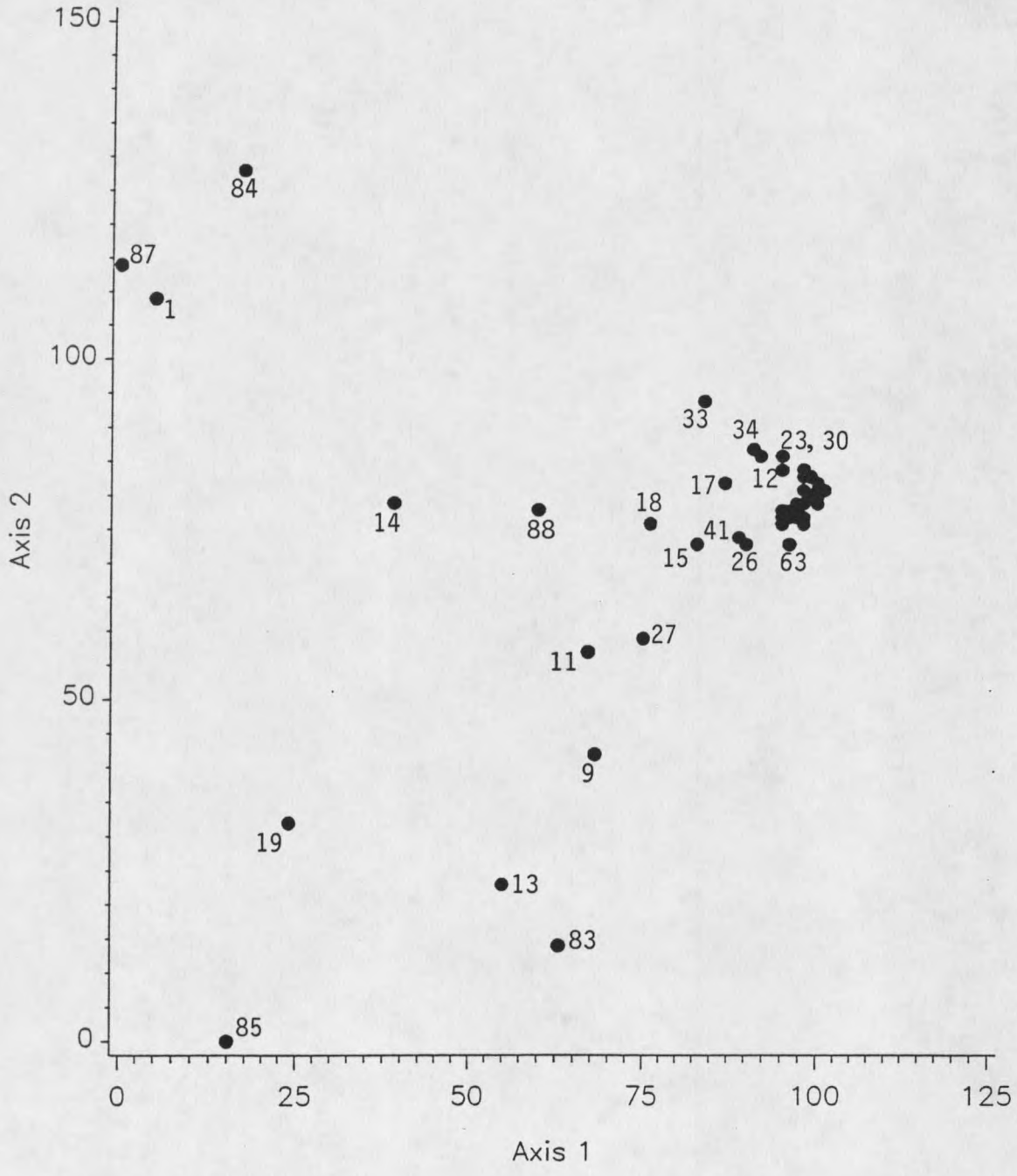


Figure 10. Results of detrended correspondence analysis based on individual plant species for 89 sites in eastern Colorado in 1992: scatter-plot of sites. Unlabeled sites include 2, 3, 6-8, 21, 22, 28-47, 51, 53, 55-58, 60, 67, 70, 72-76, 78, and 81.

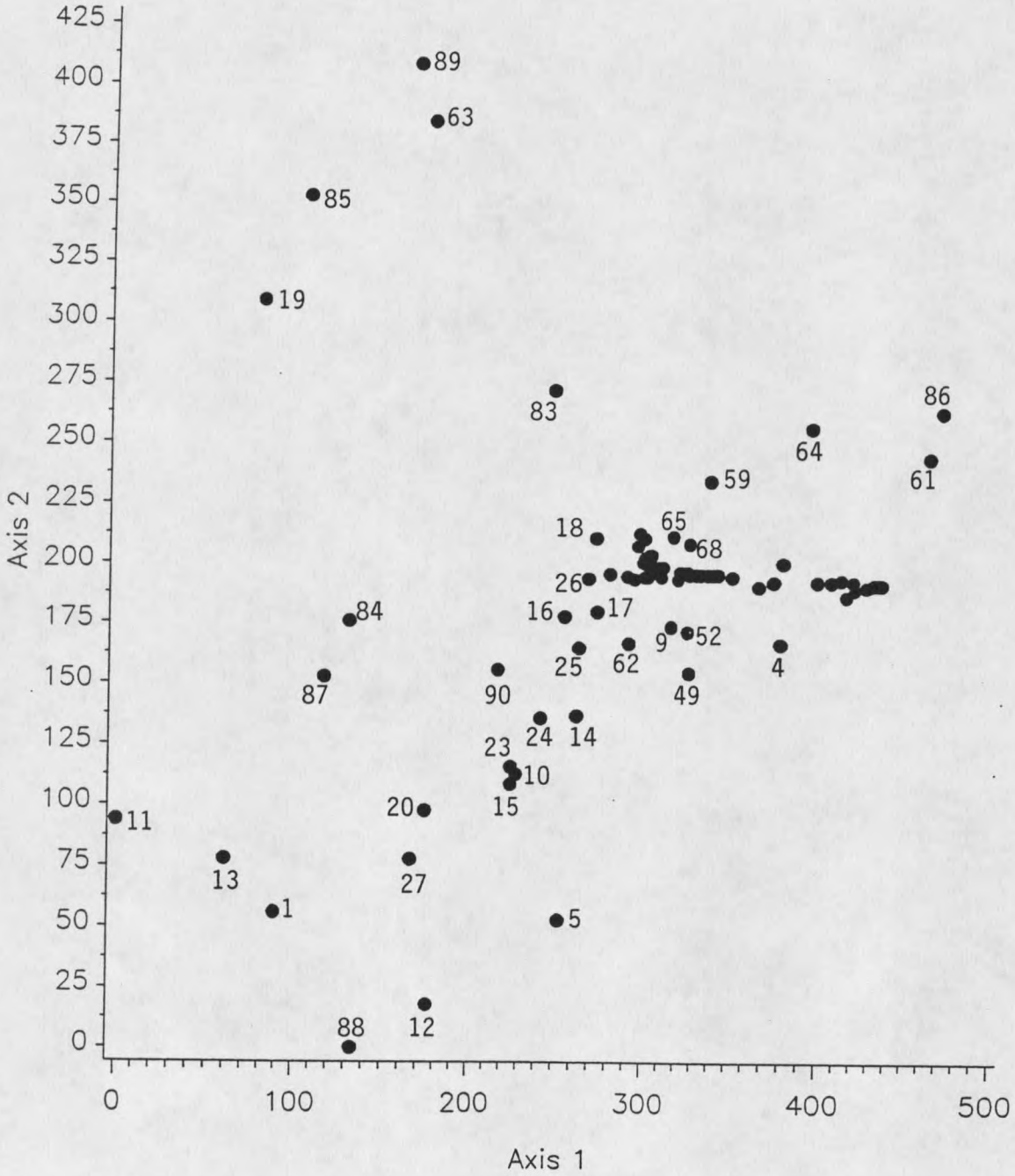
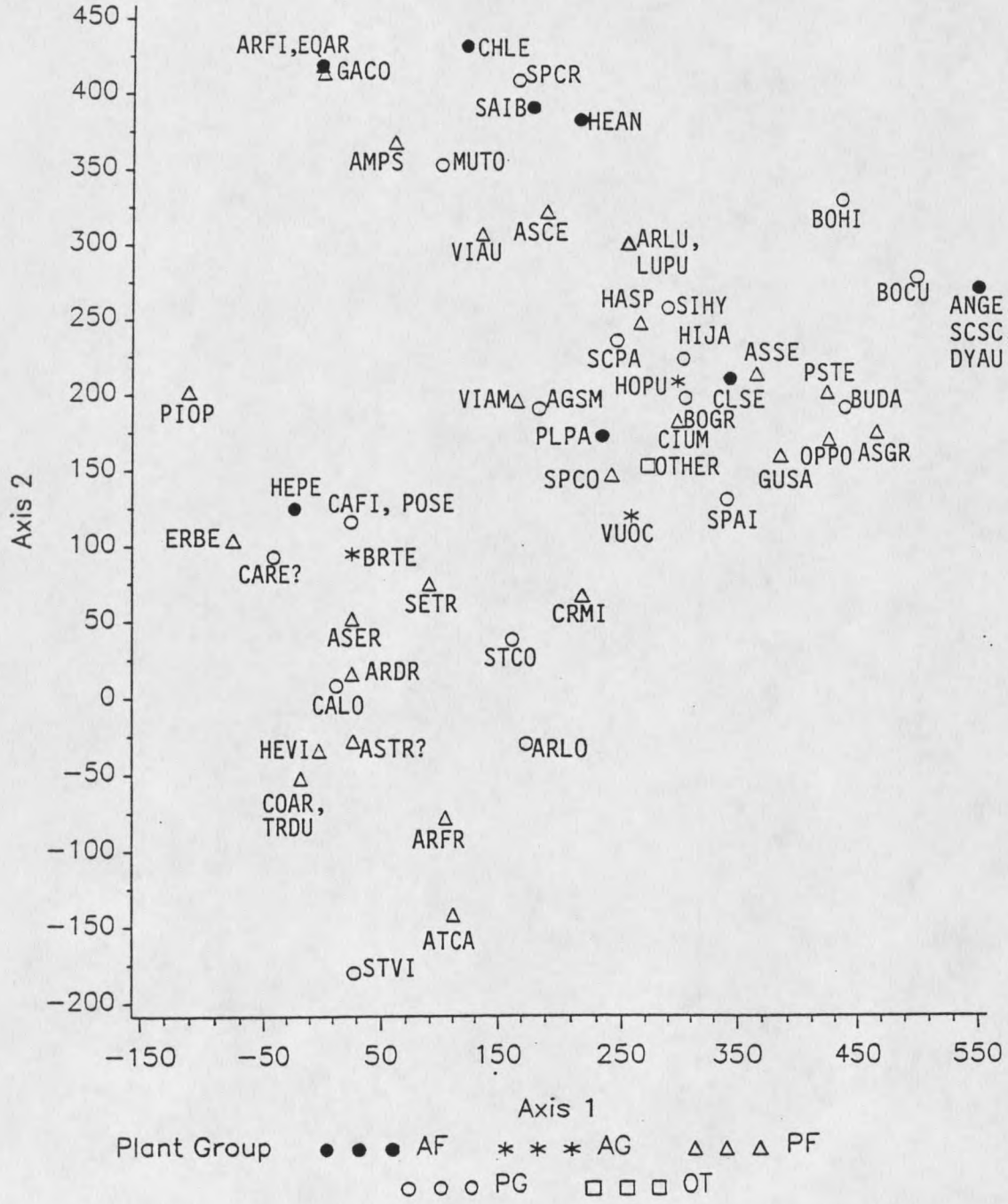


Figure 11. Results of detrended correspondence analysis based on individual plant species for 89 sites in eastern Colorado in 1992. "AF" refers to species which are annual forbs, "AG" refers to annual grasses, "PF" refers to perennial forbs, "PG" refers to perennial grasses, and "OT" are other plants not identified by species. Species abbreviation codes are given in the Appendix.

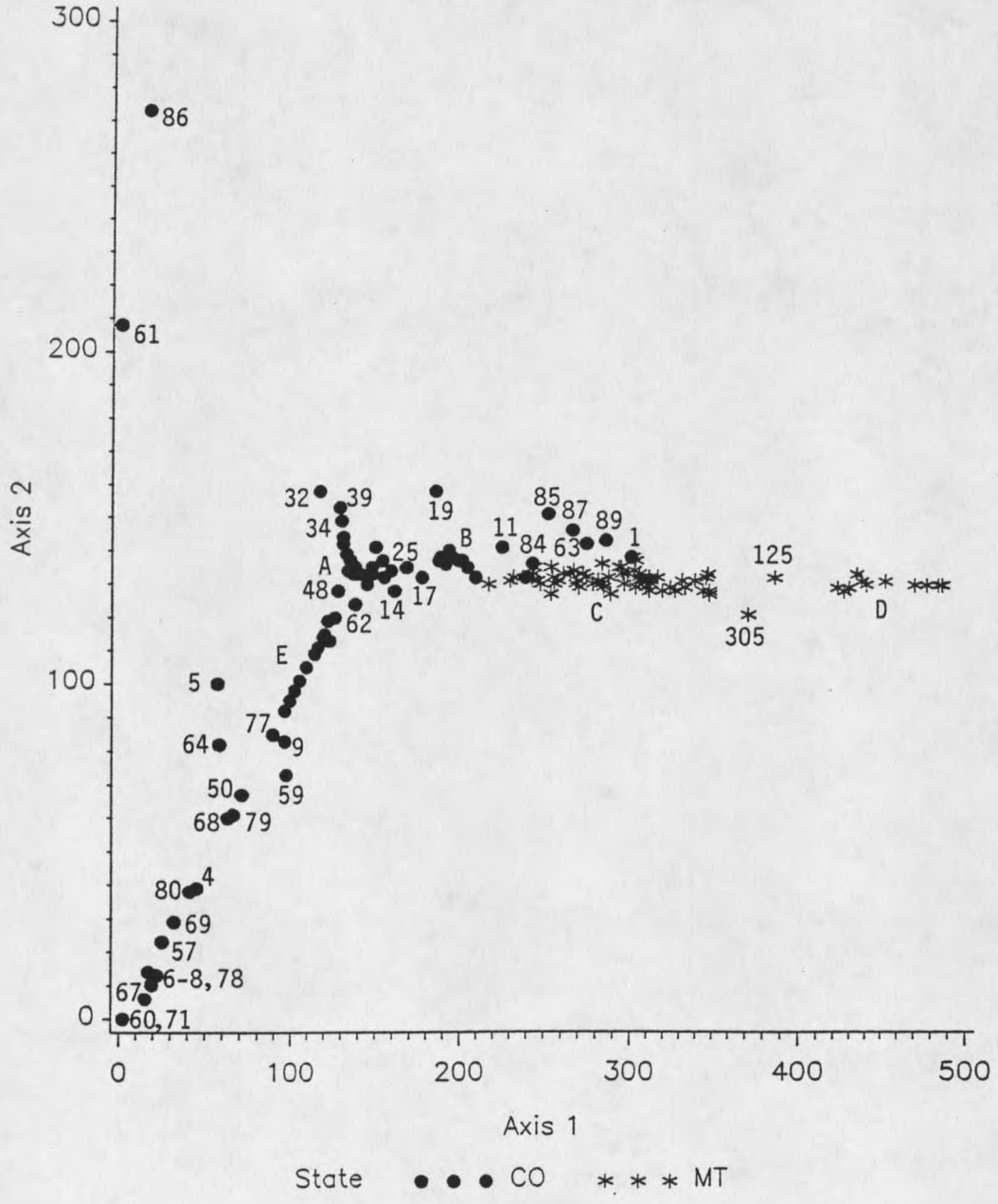


different symbols to display the growth form for each species. Although several perennial forbs had low scores for both axes, no pattern was apparent for the groups as a whole, as in Figure 7. These results show that plants in Montana and Colorado are not distributed by growth form, and that plant communities are composed of species which have a variety of growth forms.

Montana and Colorado Vegetation Comparisons

Top 20 Plants. DCA analysis of the 20 most frequently collected plant species in each state was done to test null hypothesis 5. This resulted in eigenvalues of 0.728 and 0.540 for axes 1 and 2, respectively. These two axes were thus very important in explaining the variability between sites in the two states sampled. The large eigenvalues indicate that species were well-separated along the ordination axes and supported the alternative hypothesis that Colorado sites differ significantly from Montana sites with regard to plant community composition (Figure 12). The null hypothesis was thus rejected. The orientation of the Montana sites suggested that axis 2 is much less important in their ordination than axis 1. The alignment of many Colorado sites along an approximate 60 degree line can be explained by examination of species composition for those sites. Sites with low axis 2 scores had high proportions of *Buchloe dactyloides*. The diagonal line represents a gradient of decreasing percentages of this species. Sites with axis 2 scores above 120 had no *Buchloe dactyloides*, a fact which explains the placement of Montana sites, where it was not found at all. Colorado sites 61 and 86 had much higher axis 2 scores than any other sites. This may be explained by their relatively large proportions of *Bouteloua curtipendula*, a species found at Colorado sites, but not

Figure 12. Results of detrended correspondence analysis based on the 20 most common plant species for 89 sites in eastern Colorado and 80 sites near Jordan, Montana, in 1992. "CO" refers to sites which are located in Colorado and "MT" refers to sites located in Montana. Unlabeled sites near "A" are 12, 18, 21, 22, 26, 28-31, 33, 35-38, 40-47, 49, 51-54, 62, 72, 73, 82, and 83; near "B" are 10, 13, 15, 16, 20, 23, 24, 27, 88; near "C" are 90, 101-106, 108-124, 126-130, 201-203, 205, 207-213, 215-225, 301-304, 309-311, 313, 314, 316, 319-324; near "D" are 204, 206, 214, 306-308, 312, 315, 317, 318, 325; near E are 2, 3, 55, 56, 58, 65, 66, 70, 74-76, and 81.



at the Montana sites. These data support Capinera's (1987) assertion that, in Colorado, *Buchloe dactyloides* replaces some of the species found in Wyoming and Montana.

The species plot (Figure 13) displayed axis 1 and 2 for the 20 most frequently collected plants, coded by growth form. While species with axis 1 scores below 100 were all perennial grasses, there is no obvious pattern among growth forms. Comparison of this plot with the species plot coded by state (Figure 14) showed that all growth forms are found in both states, although perennial forbs are more common in Montana and perennial grasses are more common in Colorado. Figure 14 shows a locational gradient along axis 1, with species collected in Colorado having low axis 1 scores while Montana species have high scores. Plant species common to both states had intermediate axis 1 scores. This pattern confirms the inference of a species gradient in Figure 12.

All Species. Comparison of these results with the analysis using all species collected in both states confirmed the validity of using only the 20 most frequently collected species. The plot of sites for all plant species was almost indistinguishable from the plot using 20 species, and the species plots shared overall similarity in the distributions of both species and growth form. These results affirmed the validity of using the 20 most frequently collected plants in the plant community analysis.

A plot of the percent of bare ground against the mode plant height for both states (Figure 15) showed differences in general vegetation characteristics between sites in Colorado and sites in Montana. There is some overlap in the mode plant height between the states, with Colorado sites 15, 83, 85, and 89 having heights above 25 cm. Sites 83, 85 and 89 have higher proportions of tall plant species such as *Sporobolus cryptandrus*,

Figure 13. Results of detrended correspondence analysis based on the 20 most common plant species for 89 sites in eastern Colorado and 80 sites near Jordan, Montana, in 1992. "AF" refers to species which are annual forbs, "AG" refers to annual grasses, "PF" refers to perennial forbs, and "PG" refers to perennial grasses. Species abbreviation codes are given in the Appendix. Unlabeled species include AGSM, ARFR, ARTR, ASTR?, CAFI, KOCR, AGSP, and PHHO.

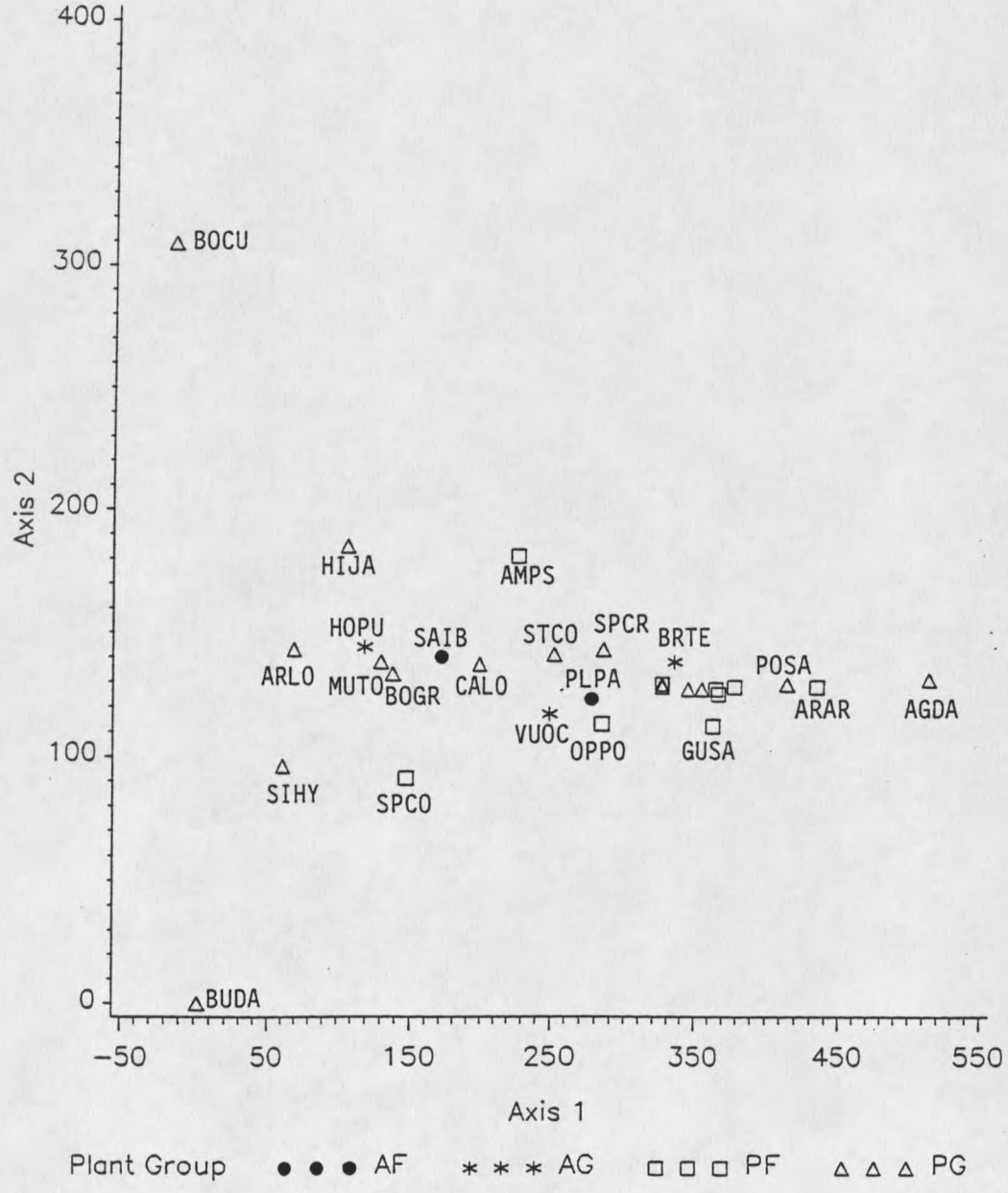


Figure 14. Results of detrended correspondence analysis based on the 20 most common plant species for 89 sites in eastern Colorado and 80 sites near Jordan, Montana, in 1992. "CM" refers to species which are common in both Montana and Colorado, "CO" refers to species which are common at Colorado sites and "MT" refers to species common at Montana sites. Unlabeled species include AGSM, ARFR, ARTR, ASTR?, CAFI, KOCR, AGSP, and PHHO.

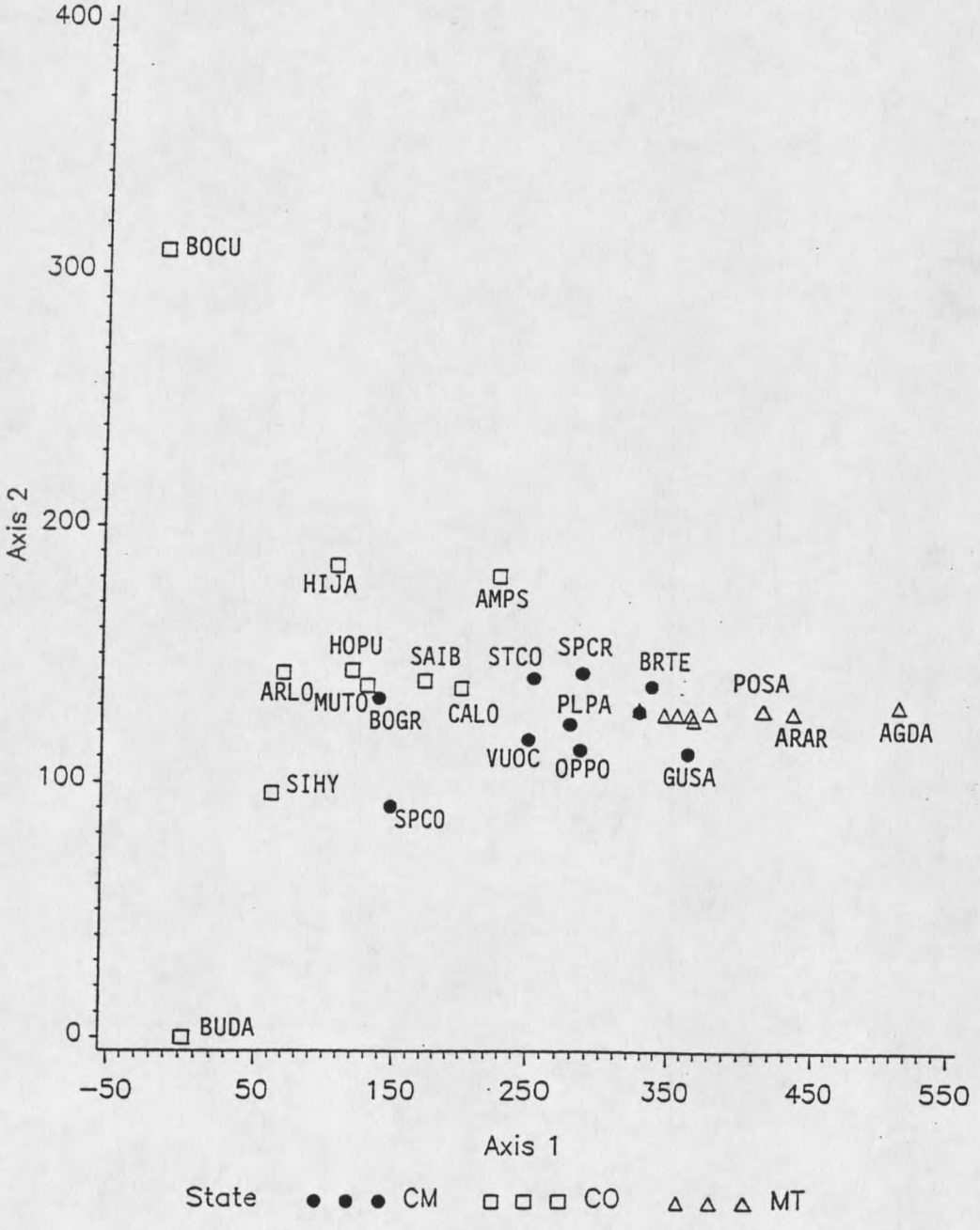
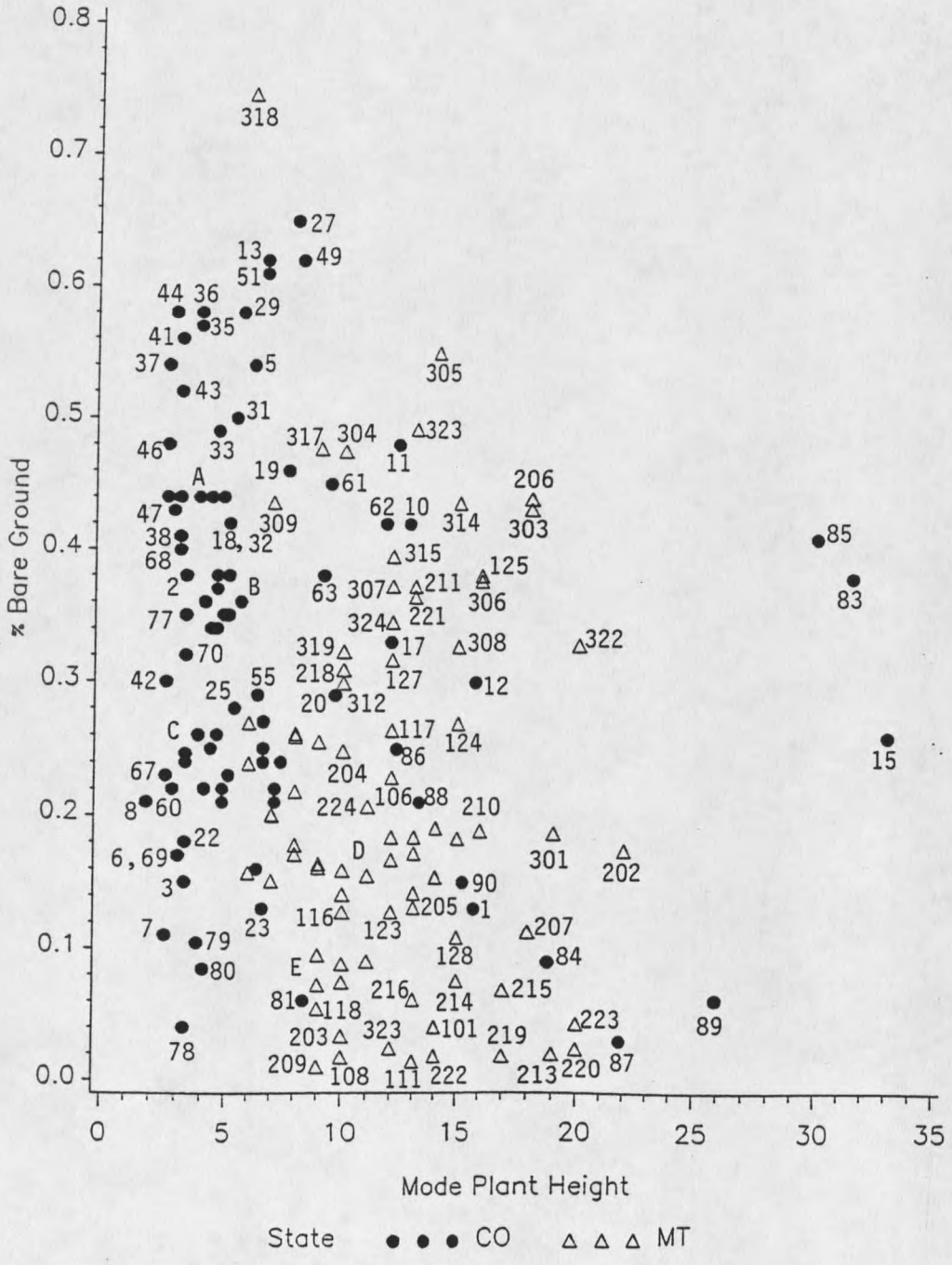


Figure 15. Percent cover by bare ground plotted against mode plant height (cm) for 89 sites in eastern Colorado and 80 sites near Jordan, Montana, in 1992. Unlabeled sites near "A" include 9, 28, 34, 45, 48, 82; near "B" are 26, 30, 39, 40, 50, 54, 57, 59, 73; near "C" are 4, 14, 16, 21, 24, 52, 53, 58, 65, 66, 71, 72, 74, 75, 76, 102, 107, 112, 115, 126, 129, 130, 208; near "D" are 103, 104, 110, 114, 120, 201, 212, 225, 301, 310, 311, 313, 320; near "E" are 113, 121, 217, 316, and 321.



Ambrosia psilostachya, and *Salsola iberica* than other sites, and there may also be some site characteristic that allows taller plant growth.

The sites within Montana had more plant species per site than those in Colorado (Table 2). This is due, in part, to the fact that only 3 grasses and 3 forbs were measured at each of the Colorado sites. This is also a reflection of differences in community structure between the two states, with Montana sites having a higher diversity of plant species than sites in Colorado, even when only the 20 most common species are examined.

Montana Grasshoppers

All Species. In the analysis of all Montana grasshopper species, the eigenvalues for axis 1 and 2 were 0.613 and 0.261, respectively. Thus, a large part of the variation among sites, with respect to grasshopper species, was explained in these first two axes. The large eigenvalues supported the alternative hypothesis that there are different grasshopper community compositions between the Montana sites. Accordingly, null hypothesis 6, that the sites did not differ with respect to grasshopper community, was rejected.

The site plot (Figure 16) showed most of the sites numbered over 300 to be separate from the other sites. This suggests that the grasshopper community composition of sites within vegetation type C were somewhat unique. The fact that all sites which were removed initially for better resolution were in vegetation type C corroborates this. These results are consistent with those from analysis on Montana plant species, which

Table 2. Number of plant and grasshopper species collected per site for Colorado and Montana, 1992.

	Minimum	Maximum	Mean	Variance	N
Montana plants	3	18	9.66	9.64	80
Colorado plants	1	13	4.39	5.27	90
Montana grasshoppers	1	15	8.76	11.93	80
Colorado grasshoppers	3	21	11.46	16.16	89

showed type C sites to be unique in terms of species composition. Sites within vegetation types A and B did not clearly separate from each other.

Sites that were similar to sites in other vegetation types may be spatially located near the transition zone between vegetation types. Such is the case with sites 101, 129, 201, 202, 205, 225, 302, 309, and 310.

The species plot (Figure 17) was less dispersed. Species which fell at the extremes of axis 1 were *Melanoplus angustipennis*, *Eritettix simplex*, *Dissosteira carolina*, and *Pseudopomala brachyptera* with low scores; *Encoptolophus costalis*, *Melanoplus packardii* and *Mermiria maculipennis* had high scores. For axis 2, scores for *Aeropedellus clavatus*, *Arphia conspersa*, and *Spharagemon equale* were low, while scores for *Melanoplus bowditchi* and *Aeoloplides turnbulli* were high. No obvious pattern could be discerned for subfamily groups.

Spring-Emergers. For the DCA conducted on the data set with only Montana spring-emerging grasshoppers, the eigenvalues for axis 1 and 2 were 0.621 and 0.275, respectively. A great deal of the variation among sites and species was thus explained

Figure 16. Results of detrended correspondence analysis based on grasshopper species composition for 80 sites near Jordan, Montana in 1992. Sites located in vegetation type A have silty soils and are dominated by wheatgrass and needleandthread; vegetation type B has silty or slayey soil with wheatgrass and green needlegrass; type C has dense clayey or saline soil with wheatgrass, green needlegrass and wildrye (Ross and Hunter 1976). Unlabeled sites near "A" include 108, 111, 217, 222, 320; near "B" are 101-105, 107, 109, 110, 112, 114-124, 130, 201, 202, 205, 208-212, 219, 301, and 309-311.

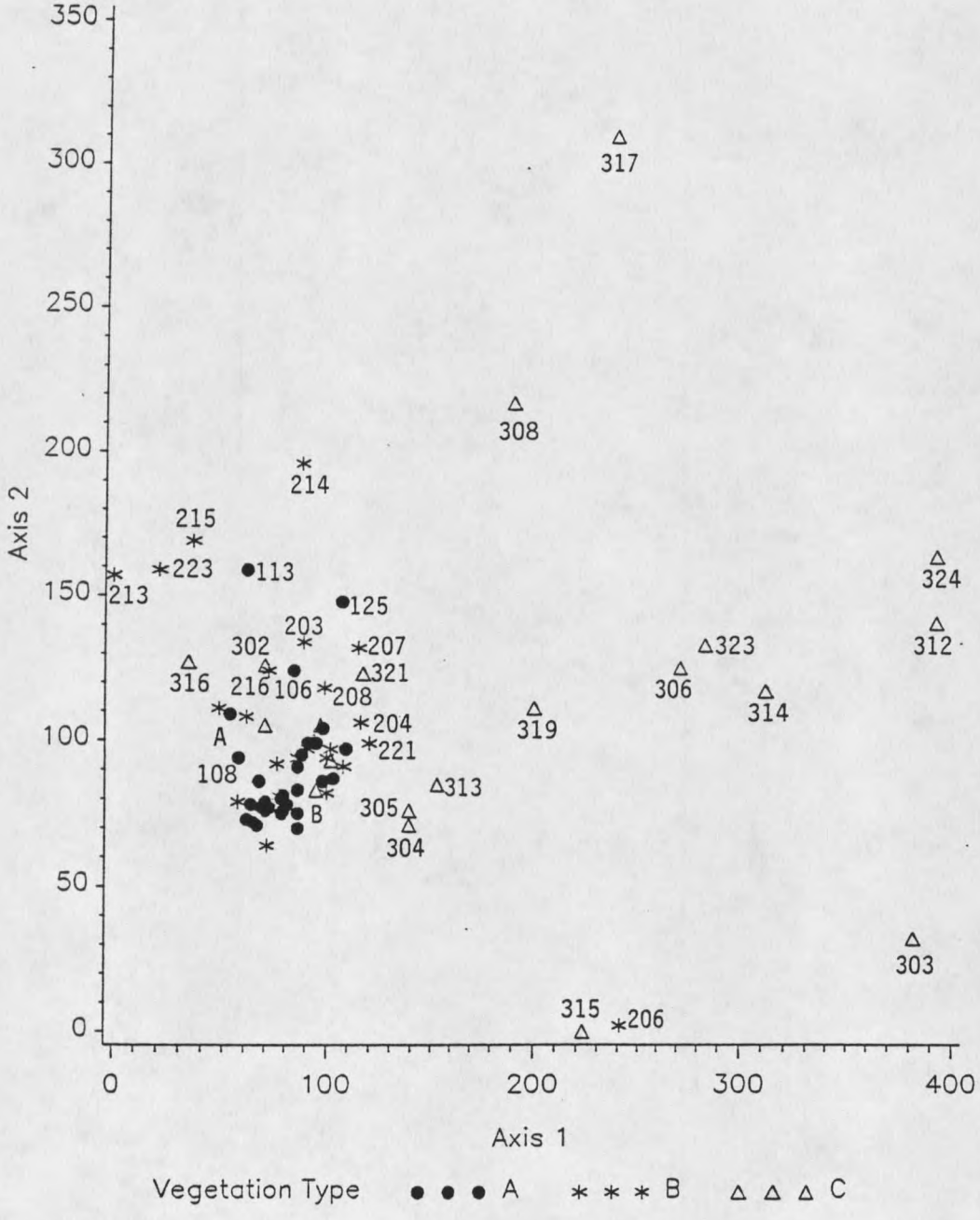
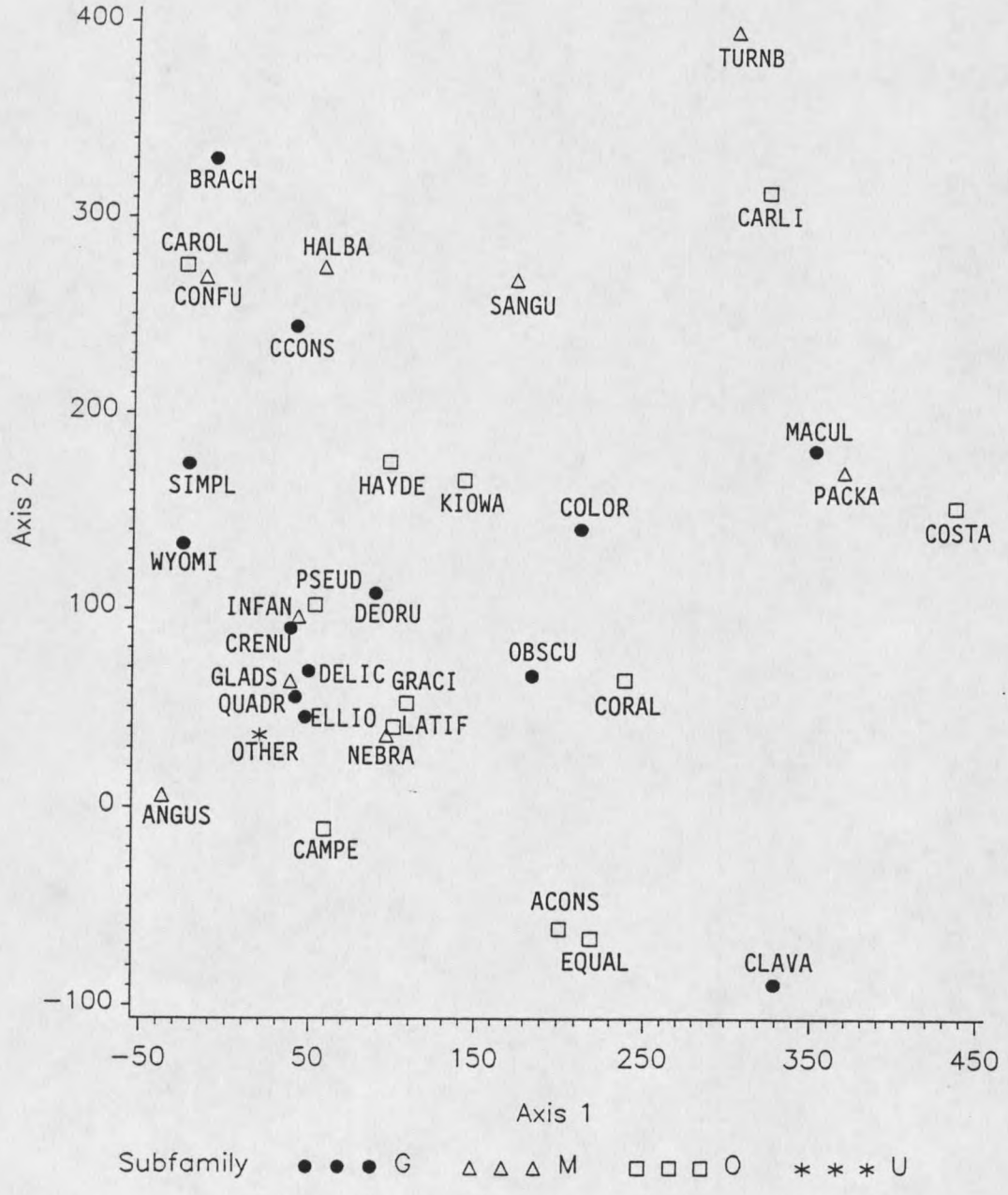


Figure 17. Results of detrended correspondence analysis based on grasshopper species composition for 80 sites near Jordan, Montana in 1992. Species abbreviation codes are given in the Appendix. "Other" and "U" refer to grasshoppers not identified by species. "G" refers to the subfamily Gomphocerinae, "M" refers to the subfamily Melanoplinae, and "O" refers to the subfamily Oedipodinae.



in these first two axes. These values led to the rejection of the null hypothesis that the sites do not have different grasshopper community compositions (hypothesis 6).

The site plot (Figure 18) again showed most of the sites numbered over 300 to be separate from the other sites. While sites within vegetation types A and B did not clearly separate from each other, sites which were numbered between 100 and 130 had lower axis 1 scores, in general, than did sites which were numbered between 200 and 225. Sites that may be located in a transition zone between vegetation types include 101, 127, 202, 205, 224, 225, 302, 308, and 309.

Species which fell at the extremes of axis 1 in the species plot (Figure 19) were *Melanoplus angustipennis*, *Dissosteira carolina*, and *Melanoplus gladstoni* with low scores; *Encoptolophus costalis*, *Melanoplus packardii* and *Mermiria maculipennis* had high scores. For axis 2, scores for *Phoetaliotes nebrascensis*, *Trimerotropis gracilis*, and *Spharagemon campestris* were low, while scores for *Melanoplus bowditchi* and *Hypochlora alba* were high. No obvious pattern could be discerned in the distribution of subfamilies.

Colorado Grasshoppers

All Species. Using the Colorado grasshopper all species data set, the DCA produced eigenvalues of 0.501 and 0.296 for axis 1 and 2, respectively, and a large portion of the variation among sites and species was explained by these two axes. These large values support the alternative hypothesis that these sites do have different grasshopper community compositions and null hypothesis 7 was rejected.

Figure 18. Results of detrended correspondence analysis based on spring-emerging grasshopper species for 80 sites near Jordan, Montana in 1992. Sites located in vegetation type A have silty soils and are dominated by wheatgrass and needleandthread; vegetation type B has silty or slayey soil with wheatgrass and green needlegrass; type C has dense clayey or saline soil with wheatgrass, green needlegrass and wildrye (Ross and Hunter 1976). Unlabeled sites include 107, 112, 116, 117, 120, and 224.

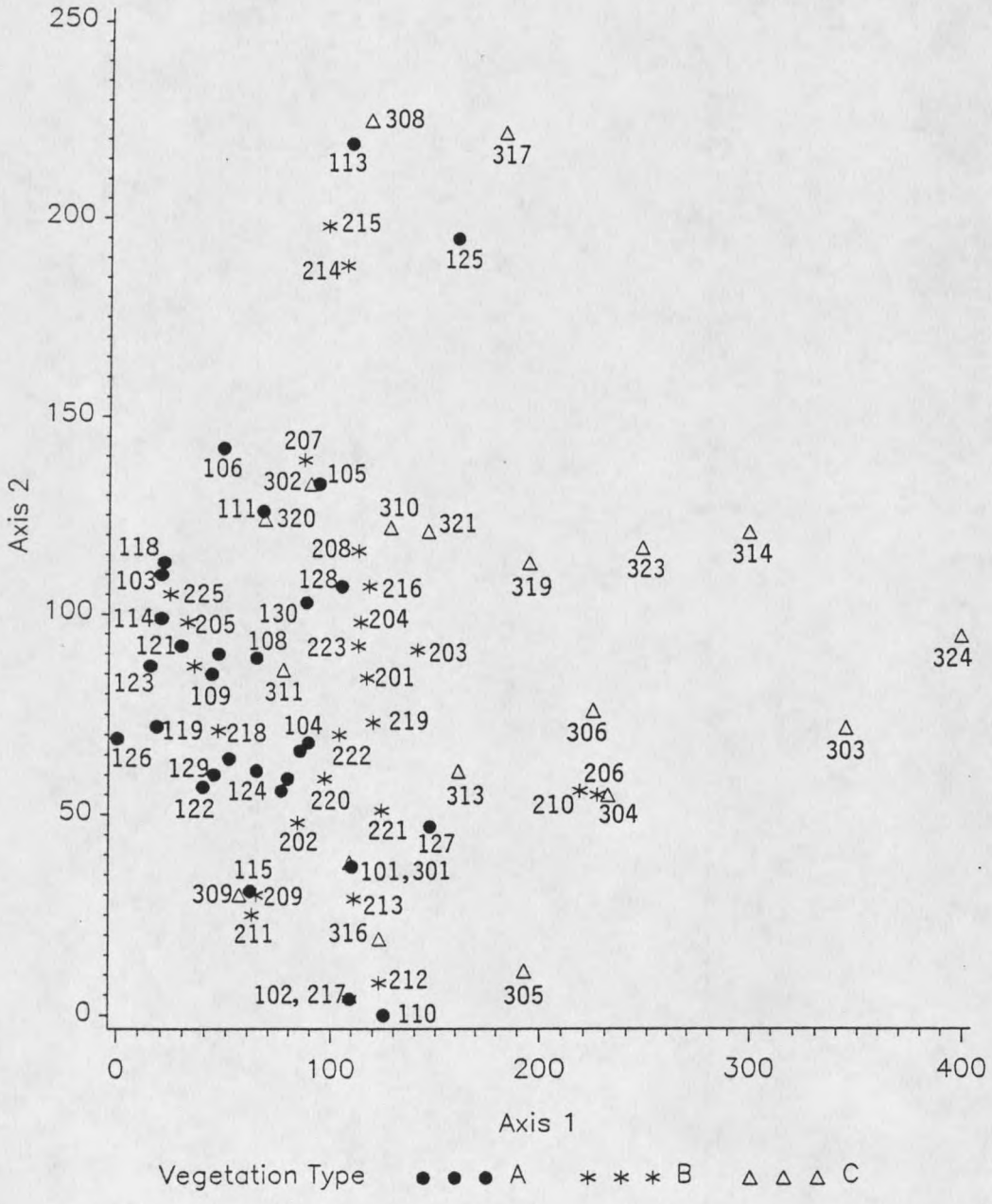
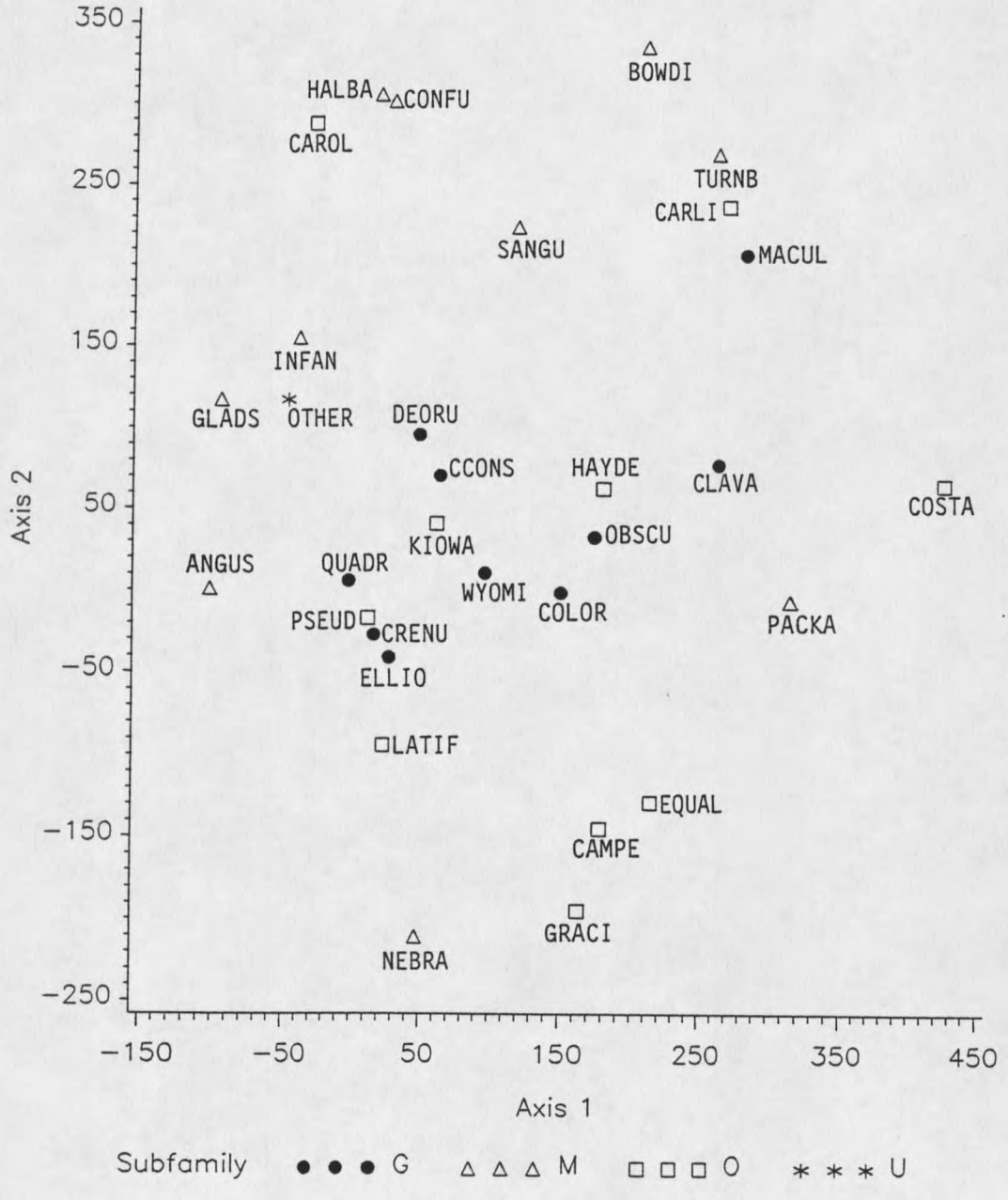


Figure 19. Results of detrended correspondence analysis based on spring-emerging grasshopper species for 80 sites near Jordan, Montana in 1992. Species abbreviation codes are given in the Appendix. "Other" and "U" refer to grasshoppers not identified by species. "G" refers to the subfamily Gomphocerinae, "M" refers to the subfamily Melanoplinae, and "O" refers to the subfamily Oedipodinae.



The site plot (Figure 20) showed few sites which were very dissimilar from the others. These included sites 13, 22, 48, 54, 55, 81, 84, 86, 88, 89, and 90. Sites with similar numbers which were grouped together may be spatially located near one another. Such may be the case with sites 30 through 37, 40 through 47, and 73 through 77.

The species plot (Figure 21) was not as tightly clustered. Species which fell at the extremes of axis 1 were *Pardalophora haldemanii* and *Derotmema haydeni* with low scores; *Melanoplus bivittatus*, *Melanoplus keeleri*, and *Pseudopomala brachyptera* had high scores. For axis 2, scores for *Melanoplus flavidus*, *Dactylotum bicolor*, and *Schistocerca alutacea* were low, while scores for *Melanoplus femurrubrum*, *Orphulella speciosa* and *Melanoplus lakinus* were high.

When species were classified by subfamily, with two exceptions, all species which had axis 1 scores above 300 were members of the subfamily Melanoplinae (Figure 22). The exceptions were *Pseudopomala brachyptera*, a Gomphocerinae species which spends winter months as a nymph, and *Schistocerca alutacea*, the only Cyrtacanthacridinae species collected. No pattern was apparent for axis 2 scores.

Montana and Colorado Grasshopper Comparisons

All Species. In the analysis combining Montana and Colorado grasshopper species, the eigenvalues for axis 1 and 2 were 0.606 and 0.308, respectively. Thus, much of the variation among sites and species was explained in these first two axes. These large values support the alternative hypothesis that there are different grasshopper community compositions between the two states. Therefore, the null hypothesis (hypothesis 8) was rejected.

Figure 20. Results of detrended correspondence analysis based on grasshopper species composition for 89 sites in eastern Colorado in 1992. Unlabeled sites near "A" include 9, 56, 67, 75, 77; other unlabeled sites are 3, 33, 40, and 47.

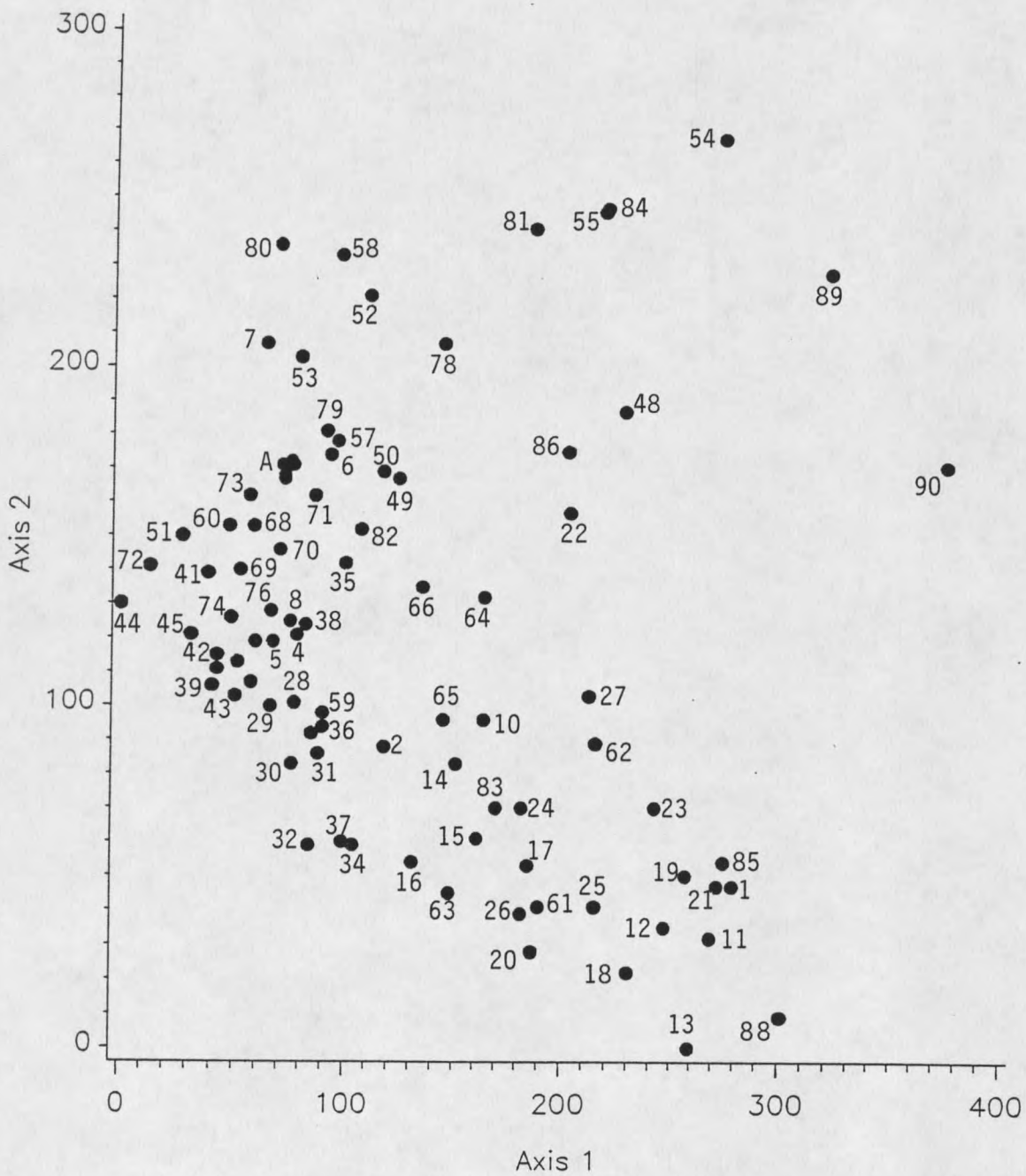


Figure 21. Results of detrended correspondence analysis based on grasshopper species composition for 89 sites in eastern Colorado in 1992. "CM" refers to species which were collected in both Colorado and Montana, and "CO" refers to species which were collected only in Colorado. Species abbreviation codes are given in the Appendix.

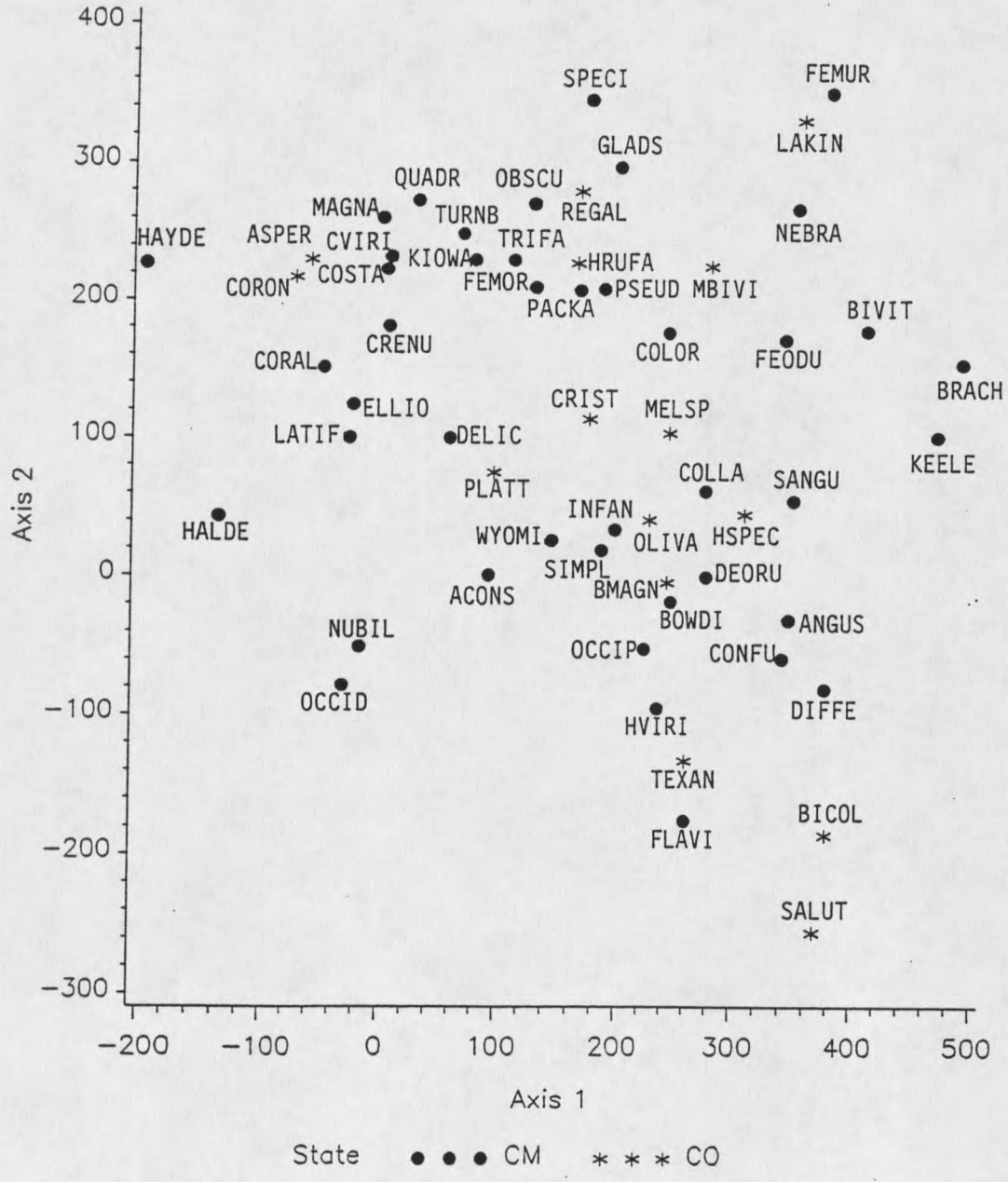
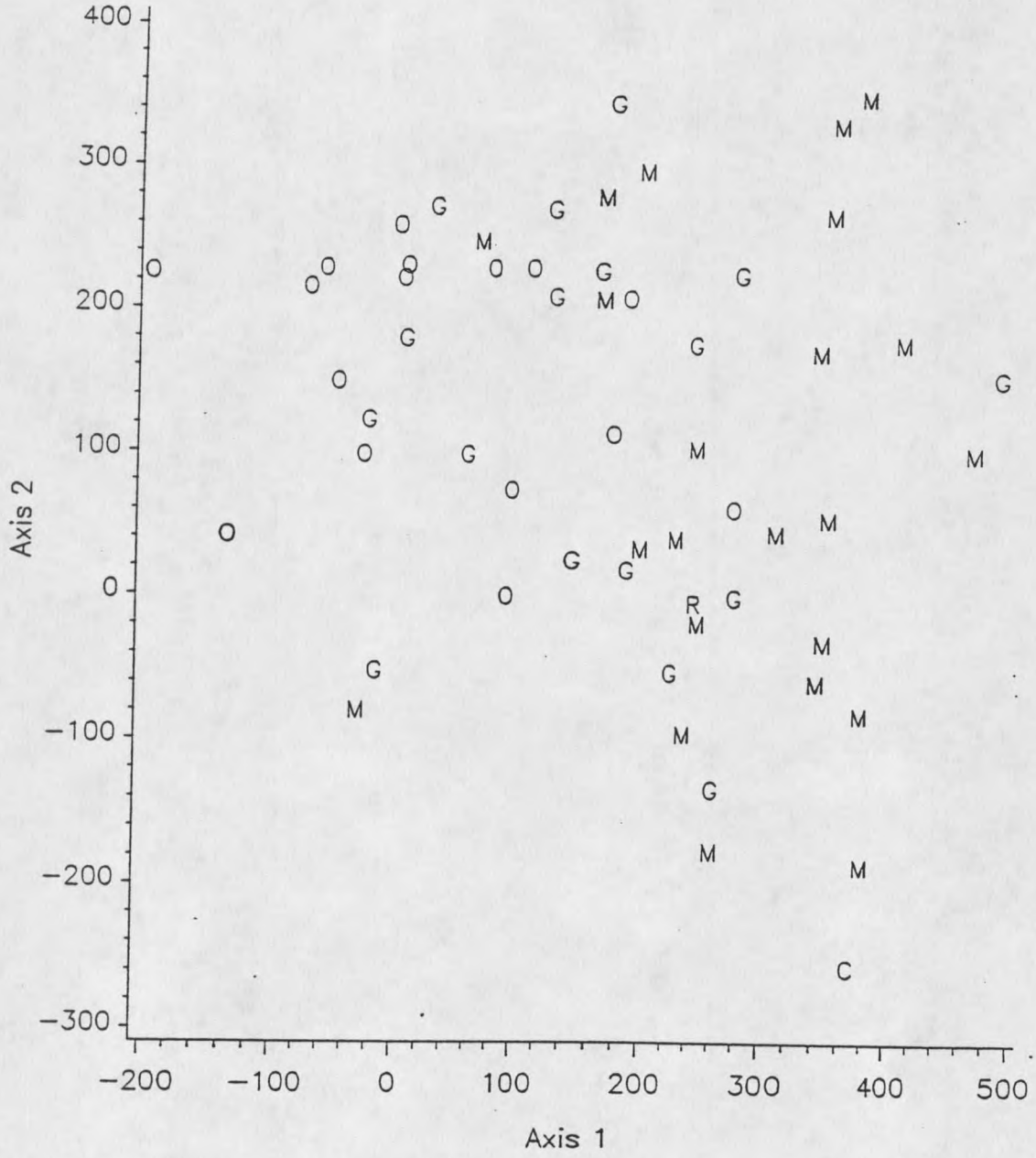


Figure 22. Results of detrended correspondence analysis based on grasshopper species composition for 89 sites in eastern Colorado in 1992. "G" refers to the subfamily Gomphocerinae, "M" refers to the subfamily Melanoplinae, "O" refers to the subfamily Oedipodinae, and "U" refers to grasshoppers not identified by species.



The site plot (Figure 23) showed the Montana sites (numbered over 100) to be grouped together, separate from the Colorado sites, with little overlap. This result suggests that the grasshopper community composition of sites within the states differ significantly. Overlap between Montana and Colorado sites may represent similarities in plant communities as seen in Figure 14.

The species plot (Figure 24) showed that grasshopper species which are found in Colorado, but not in Montana, tended to have low axis 1 scores. These species may be associated with some plant species not found in Montana. Species having low axis 1 scores were *Melanoplus bivittatus*, *Melanoplus femurrubrum*, *Melanoplus keeleri*, and *Melanoplus lakinus*, while *Encoptolophus costalis*, *Melanoplus packardii*, and *Mermiria maculipennis* had high axis 1 scores. For axis 2, *Aulocara femoratum* and *Trachyrachys coronata* had low scores and *Chloealtis conspersa*, *Melanoplus confusus*, and *Pseudopomala brachyptera* had high scores. As in Figures 17 and 19, no pattern was apparent in the distribution of grasshopper subfamilies (Figure 25).

Grasshopper/Plant Correlations

Results of the Spearman rank correlation between Montana grasshoppers and general site characteristics (Table 3) showed axis 1 site scores were positively correlated with bare ground (P-value < 0.05). Axis 1 and bare ground were both negatively correlated with leaf litter and total cover. Thus, grasshopper axis 1 scores are related to some measure of the openness of the plant cover at the site. Low scores represent more plant cover and a more closed canopy and high axis 1 scores represent relatively open areas with more bare ground and less litter. Axis 2 was positively correlated with

Figure 23. Results of detrended correspondence analysis based on grasshopper species composition for 89 sites in eastern Colorado and 80 sites near Jordan, Montana, in 1992. "CO" refers to sites which are located in Colorado and "MT" refers to sites located in Montana. Unlabeled sites near "A" include 111, 128, 207, 216, 302; near "B" are 3-5, 8, 20, 25, 28, 30, 31, 33, 34, 38-40, 42, 43, 46, 47, 51, 59, 82, 87, 101-105, 107-110, 112, 114-124, 126, 127, 129, 130, 201, 202, 208-212, 218-221, 224, 301, 309-312; near "C" are 49, 50, 56, 57, 60, 76, 78, and 81.

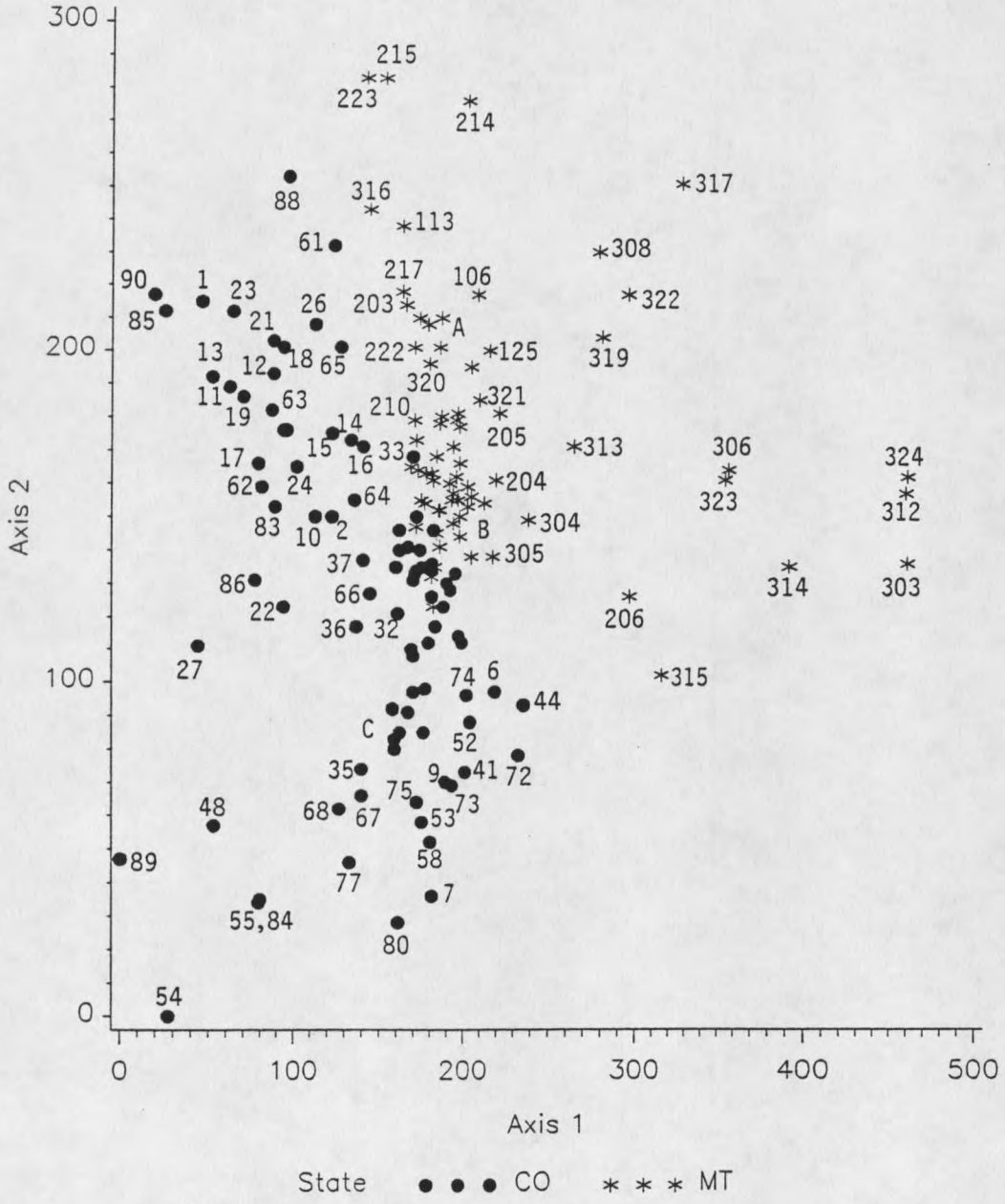


Figure 24. Results of detrended correspondence analysis based on grasshopper species composition for 89 sites in eastern Colorado and 80 sites near Jordan, Montana, in 1992. "CM" refers to species which were collected in both Colorado and Montana, and "CO" refers to species which were collected only in Colorado. Species abbreviation codes are given in the Appendix.

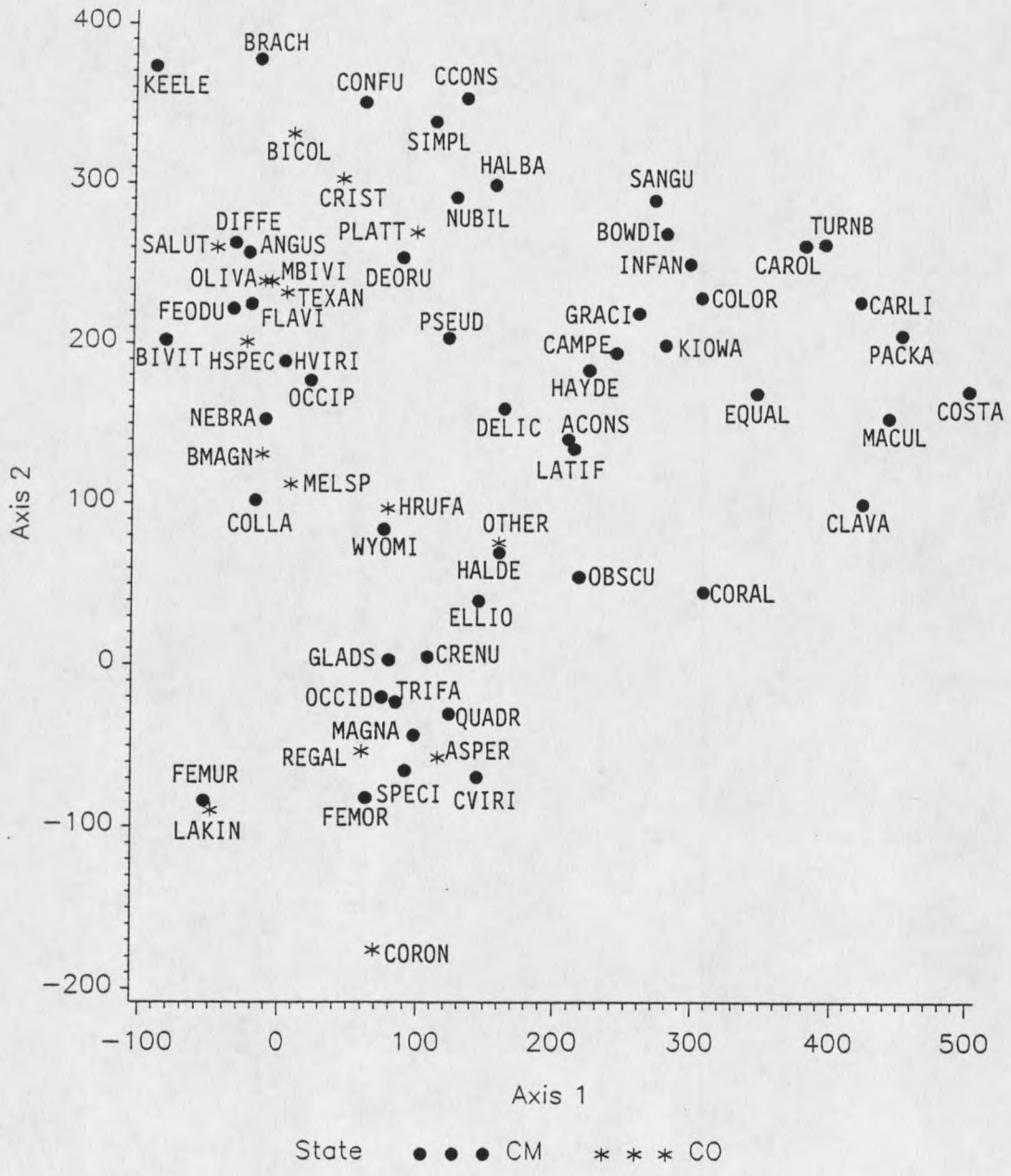
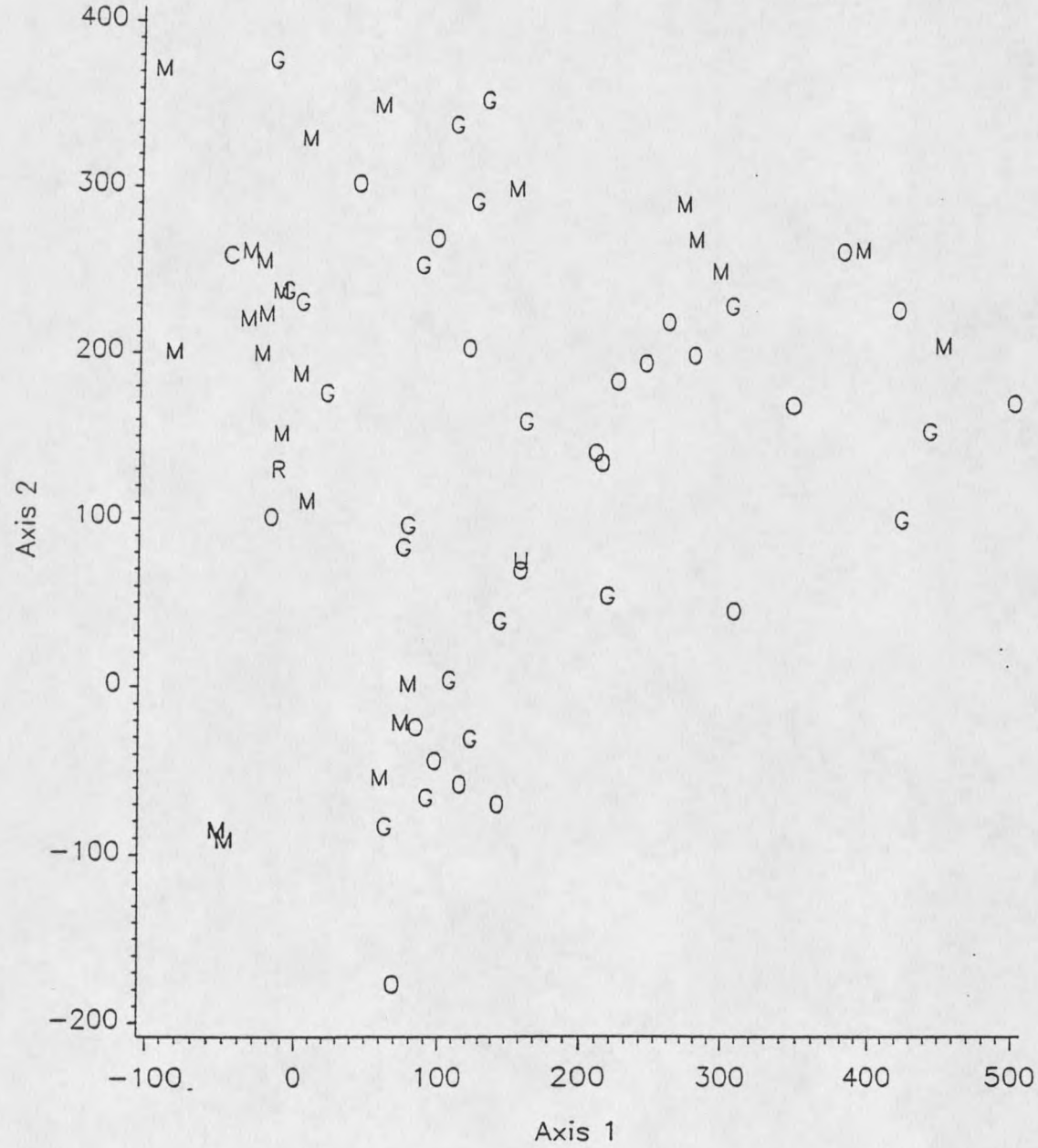


Figure 25. Results of detrended correspondence analysis based on grasshopper species composition for 89 sites in eastern Colorado and 80 sites near Jordan, Montana, in 1992. "C" refers to species of the subfamily Cyrtacanthacridinae, "G" refers to the subfamily Gomphocerinae, "M" refers to the subfamily Melanoplinae, "O" refers to the subfamily Oedipodinae, and "R" refers to the family Romaleinae.



mode plant height, which may be related to the vegetation type or to the amount of grazing at the site. Tallest and mode plant height were positively correlated with one another, while total cover was not correlated with mode plant height.

Results of the Spearman rank correlation between grasshopper community and plant groups (Table 4) showed axis 1 of the sites was positively correlated with perennial grasses. Axis 1 was also negatively correlated with both annual grasses and perennial forbs.

The Spearman rank correlation of individual plant species with grasshopper DCA scores (Table 5) showed that axis 1 was positively correlated with *Poa* spp., *Artemisia* spp., and *Opuntia polycantha*. Axis 1 was negatively correlated with *Bromus* spp. Grasshopper axis 2 scores were positively correlated with *Bromus* spp. and negatively correlated with *Bouteloua gracilis*.

Statistically significant correlations found in each of these three tests resulted in rejection of the null hypothesis that grasshopper species are not influenced by vegetation characteristics (hypothesis 9). No correlations were tested for Colorado, as previously discussed.

Discussion

Vegetation Community Differences

Within States. The level of heterogeneity observed depends on the scale at which site is examined: general measurement can be regarded as at a larger scale of resolution than percent coverage of individual species. For Montana, general site characteristics

Table 3. Results of Spearman rank correlation between grasshopper axis scores and general site characteristics. "Axis 1" and "Axis 2" refer to eigenvalues for axes 1 and 2, respectively, resulting from detrended correspondence analysis of grasshopper species composition data. "Bare Ground" refers to the percent cover by bare ground, "Leaf Litter" is the percent cover by leaf litter, "Total Cover" is the total plant cover expressed as percent, "Tallest Plant" is the tallest plant height (cm) and "Mode Plant" is the mode plant height (cm).

Correlation on	r_s	t	P-value*
Axis 1 by Axis 2	0.112	0.9696	0.3354
Axis 1 by Bare Ground	0.638	7.1273	0.0000[1]
Axis 2 by Bare Ground	-0.202	-1.7742	0.0802
Axis 1 by Leaf Litter	-0.530	-5.3765	0.0000[1]
Axis 2 by Leaf Litter	0.202	1.7742	0.0802
Axis 1 by Total Cover	-0.596	-6.3849	0.0000[1]
Axis 2 by Total Cover	0.019	0.1635	0.8706
Axis 1 by Tallest Plant	-0.070	-0.6036	0.5480
Axis 2 by Tallest Plant	0.187	1.6375	0.1058
Axis 1 by Mode Plant	0.094	0.8122	0.4192
Axis 2 by Mode Plant	0.237	2.0985	0.0392[2]
Bare Ground by Leaf Litter	-0.877	-15.7011	0.0000[1]
Bare Ground by Total Cover	-0.714	-8.7725	0.0000[1]
Leaf Litter by Total Cover	0.374	3.4690	0.0000[1]
Tallest Plant by Mode Plant	0.665	7.6596	0.0000[1]
Total Cover by Mode Plant	0.093	0.8035	0.4242

* P-value was calculated for a two-tailed t distribution.
[1] Significant at $\alpha=0.01$ level.
[2] Significant at $\alpha=0.05$ level.

Table 4. Results of Spearman rank correlation of grasshopper axis scores and plant groups. "Axis 1" and "Axis 2" refer to eigenvalues for axes 1 and 2, respectively, resulting from detrended correspondence analysis of grasshopper species composition data. "Perennial Grass" refers to the percent cover by perennial grasses, "Annual Grass" is the percent cover by annual grasses, "Perennial Forb" is the percent cover by perennial forbs, and "Annual Forb" is the percent cover by annual forbs.

Correlation on	r_s	t	P-value*
Axis 1 by Axis 2	0.112	0.9696	0.3354
Axis 1 by Perennial Grass	0.638	7.1273	0.0000[1]
Axis 2 by Perennial Grass	-0.202	-1.7742	0.0802
Axis 1 by Annual Grass	-0.530	-5.3765	0.0000[1]
Axis 2 by Annual Grass	0.202	1.7742	0.0802
Axis 1 by Perennial Forb	-0.596	-6.3849	0.0000[1]
Axis 2 by Perennial Forb	0.019	0.1635	0.8706
Axis 1 by Annual Forb	-0.070	-0.6036	0.5480
Axis 2 by Annual Forb	0.187	1.6375	0.1058
Perennial Grass by Annual Grass	-0.877	-15.7011	0.0000[1]
Perennial Grass by Perennial Forb	-0.714	-8.7725	0.0000[1]
Perennial Grass by Annual Forb	-0.316	-2.8651	0.0054[1]
Annual Grass by Perennial Forb	0.374	3.4690	0.0000[1]
Annual Grass by Annual Forb	0.187	1.6375	0.1058
Perennial Forb by Annual Forb	0.355	3.2666	0.0016[1]

* P-value was calculated for a two-tailed t distribution.
[1] Significant at $\alpha=0.01$ level.

Table 5. Results of Spearman rank correlation of grasshopper axis scores and individual plant species. "Axis 1" and "Axis 2" refer to eigenvalues for axes 1 and 2, respectively, resulting from detrended correspondence analysis of grasshopper species composition data. Correlations use only those sites at which the individual species are found.

Correlation on	r_s	*t*	*P*-value*
Axis 1 by Axis 2	0.045	0.9696	0.1677
Axis 1 by *Agropyron smithii*	0.041	0.3530	0.7252
Axis 2 by *Agropyron smithii*	0.070	0.6036	0.5482
Axis 1 by *Bouteloua gracilis*	-0.053	-0.4566	0.6496
Axis 2 by *Bouteloua gracilis*	-0.284	-2.5480	0.0132[2]
Axis 1 by *Bromus* spp.	-0.240	-2.1267	0.0384[2]
Axis 2 by *Bromus* spp.	0.326	2.9664	0.0046[1]
Axis 1 by *Carex* spp.	0.167	1.4571	0.1532
Axis 2 by *Carex* spp.	0.110	0.9520	0.3470
Axis 1 by *Poa* spp.	0.245	2.1738	0.0334[2]
Axis 2 by *Poa* spp.	0.085	0.7339	0.4656
Axis 1 by *Sporobolus cryptandrus*	-0.037	-0.3185	0.7514
Axis 2 by *Sporobolus cryptandrus*	0.206	1.8109	0.0764
Axis 1 by *Artemesia* spp.	0.348	3.1932	0.0020[1]
Axis 2 by *Artemesia* spp.	0.002	0.0172	0.9864
Axis 1 by *Phlox hoodii*	0.192	1.6830	0.1022
Axis 2 by *Phlox hoodii*	0.025	0.2151	0.8310
Axis 1 by *Opuntia polyacantha*	0.275	2.4605	0.0196[2]
Axis 2 by *Opuntia polyacantha*	0.033	0.2840	0.7782

* *P*-value was calculated for a two-tailed *t* distribution.
[1] Significant at $\alpha=0.01$ level.
[2] Significant at $\alpha=0.05$ level.

(Figure 4) and plant group (Figure 5) analyses showed little variation among sites, suggesting that potential differences in climax vegetation were not detected at the coarse level of resolution of these two data sets. However, ordination based on individual plant species composition did find significant variation among Montana sites (Figure 6). This result suggests that at this scale, percent cover by individual species is the best method for distinguishing among areas in which the potential climax community differs, although the grasshopper community is also influenced by other site characteristics (Tables 3 and 4).

DCA results for individual plant species (Figure 6) supported Ross and Hunter's (1976) classification which separates the Montana study area into different vegetation types. The more dense clay and saline soils of vegetation type C may be the basis for the plant community differences shown in the ordination (Ross and Hunter 1976). Vegetation type B has soil and plant characteristics similar to both type A and type C, which made distinguishing between types difficult when ordination was done on plant group data or general site characteristics (Figures 4 and 5). For the purpose of identifying unique plant communities at this scale, vegetation types A and B might be combined and treated as one vegetation type.

For Colorado, general site characteristics (Figure 8) and plant group (Figure 9) analyses did not differentiate between sites, although analysis of individual species indicated differences in plant communities did exist (Figure 10). These results confirm the conclusion reached for Montana DCA analyses: individual plant species data is better than coarse variables for measuring variability among sites. Because vegetation type was

not used in choosing the Colorado sites, no information about the validity of using vegetation type is available for those sites.

Between States. Montana and Colorado grassland vegetation, as expected, had very different species compositions, although there is some overlap (Figures 12 and 14). The species which ordinated at the extremes of the two axes were entirely different between the two states (Figures 7, 11, and 14), indicating differences in the importance of these species to the plant communities in each state. In general, vegetation in Colorado is shorter than in Montana (Figure 15), consistent with Sims' (1988) classification of Montana as mixed-grass and Colorado as shortgrass prairie. Thus, the vegetation resource available to grasshoppers in each state is fundamentally different.

The mean number of plant species per site for Montana is over twice that for Colorado (Table 2). This difference in plant species diversity may result in different plant community characteristics as individual species respond to disturbances such as grazing. For example, Olson et al. (1985) found that the reaction of Montana rangeland vegetation to precipitation and grazing regimes is species-specific. These responses, in turn, have implications for the associated grasshopper species. Grazing has been associated with increased coverage by shortgrasses and bare ground (Quinn and Walgenbach 1990), higher overall grasshopper densities (Capinera & Sechrist 1982a, Joern 1982), and increases in Oedipodine grasshopper species (Capinera & Sechrist 1982a).

Grasshopper Community Differences

Within States. Although vegetation types in Montana could not be distinguished by stand structure (Figures 4 and 5), the correlations between grasshopper DCA scores and general plant variables indicate that grasshopper species respond to changes in these site characteristics, particularly the openness of the vegetation (Tables 3 and 4). Thus, vegetation types capture differences in these variables in grasshopper community ordination but not in plant community ordination, so that the level of resolution at which vegetation types are meaningful differs between grasshopper and plant communities within the Jordan study area.

Most sites from Montana in climax vegetation type C ordinated differently from the other two types (Figure 16 and 18) and *Encoptolophus costalis* comprised a large proportion of the grasshopper community at some of these sites. A comparison of species characteristics and habitat preferences with the position of species in the DCA output indicated that axis 1 might represent a gradient of body size and axis 2 may indicate a gradient of soil aridity (Vickery and Kevan 1985). Soil characteristics are important to the distributions and densities of some grasshopper species (Isely 1938, Quinn et al. 1991, Scoggan & Brusven 1973). The lack of pattern in the subfamily plots (Figures 17 and 19) shows that grasshopper subfamily groupings are not a factor in their response to the gradients represented by axes 1 and 2.

The spring-emerger data set supported findings from the whole data set, with the same species again having high axis 1 scores (Figure 18). This suggests that

overwintering species do not have much influence on ordination, and the entire data set can be used for ordination without concern that numbers of overwintering species are given too much weight. Based on comparison of species habitat and food-plant preferences with the position of species in the DCA output, axis 1 may represent a soil moisture and texture gradient and axis 2 may be related to the amount of sagebrush and other forbs in the diet (Vickery and Kevan 1985). However, such generalities must be made with caution because consistent and detailed diet and habitat information is not available for all the grasshopper species in the analysis.

The correlation between grasshopper ordination scores and individual plant species (Table 5) supports by the approaches of Banfill and Brusven (1973), Fielding and Brusven (1992), Isely (1938), Pfadt (1984), and Quinn et al. (1991), which identify individual plant species and their importance to each grasshopper species. Because the presence and abundance of individual plant species at a given site are indicators of other habitat variables, correlation of grasshopper species with coarser-scale variables (eg, Fielding and Brusven 1993a, Kemp 1992a, Quinn and Walgenbach 1990, Scoggan and Brusven 1973) is a less direct approach to studying the association between vegetation and grasshopper community composition. However, sampling general site characteristics is less expensive and less time-consuming than sampling individual plant species cover.

In Colorado, sites differed significantly from one another in grasshopper species composition, but examination of the raw data showed that sites having similar grasshopper communities may be spatially located close to one another. All species having the highest axis 1 scores were Melanopline species (Figure 22), indicating that

axis 1 represents a gradient to which Melanoplines are sensitive. Such factors could include disturbance by grazing (Joern 1982), amount of cover by forbs (Capinera & Sechrist 1982a) or other habitat characteristics, although this family is so large and diverse that such generalizations should be made with caution.

Between States. As with vegetation, Montana and Colorado grasshopper communities are significantly different from one another, but with some overlap (Figures 23 and 24). Differences may be due to differing plant communities, because changes in vegetation correspond with different densities and distributions of grasshopper species (Anderson 1964, Anderson and Wright 1952, Bergmann and Chaplin 1992, Capinera and Sechrist 1982a, Pfadt 1984). Changes in plant diversity and vegetation structure influence the species richness and composition of grasshopper communities (Bergmann and Chaplin 1992, Evans 1988, Kemp et al. 1990), and may account for the different numbers of grasshopper species per site for the two states (Table 2).

The difference in latitude and weather patterns between the states may also be a factor in determining grasshopper community composition, although there are not sufficient data to test this hypothesis here. During summer, grasshopper development depends upon precipitation in Colorado, while in Montana precipitation is less limiting and degree-days become more important (Capinera and Horton 1989). Grasshopper species which overwinter as eggs and develop during late spring and summer may be sensitive to these climate differences, resulting in the observed spatial distributions. The lack of a pattern for the subfamily plot (Figure 25) indicates that grasshopper communities are not organized by taxonomic units such as subfamily, but are

assemblages of species from different taxa that fulfill various roles within the community. In addition, Kemp (1992a) found that grasshopper communities are comprised of species which are facultatively associated and apparently not interdependent.

Correlations Between Grasshoppers and Vegetation

In Montana, general site characteristics and plant groupings were not useful in ordinating sites but were significantly correlated with grasshopper ordination scores (Tables 3 and 4). Factors such as bare ground, plant height, and percent of annual grasses are important in determining grasshopper community composition (Anderson 1964, Bock and Bock 1991, Quinn and Walgenbach 1990, Quinn et al. 1991), though they may not be helpful in distinguishing between plant communities. Grasshoppers are likely responding to factors such as bare ground or total plant cover at a resolution finer than that which is important for ordination of vegetation.

Positive correlations were found between grasshopper DCA scores and species which tend to increase under grazing regimes (*Artemisia* spp. and *Opuntia polycantha*) (Smith 1940, Ellison 1960). These results support the findings of Capinera and Sechrist (1982a), Evans (1988), Miller and Onsager (1991), and Quinn and Walgenbach (1990), which link grasshopper community composition to the changes in canopy structure which result from grazing. Daddy et al. (1988) found that heavily grazed sites had high losses of soil water, a factor which is be relevant to oviposition for some grasshoppers (see Hewitt 1985), especially species of the subfamily Oedipodinae (Isely 1938, Scoggan and Brusven 1973).

Landscape-scale Relationships and Management

The fact that grasshopper communities differ between vegetation types and states is important and should be recognized in efforts to manage grasshopper communites. While the three vegetation types sampled within Montana could not be distinguished on the basis of general site characteristics or plant groups, the classification of sites into climax types may still be useful (although some vegetation types could be combined), because grasshopper communities are not the same across all types. However, sampling at scales coarser than that which measures individual plant species results in a "smoothing" effect, so that differences between vegetation types are not detected. This has been demonstrated in this study for two kinds of grassland: the mixed-grass prairie of Montana and the shortgrass prairie of Colorado. The implication for management at the valley level is that vegetation sampling must be done at a finer scale if the purpose is to detect the heterogeneity that exists in the plant community, but may be done at a coarser scale if the purpose is to identify grasshopper community heterogeneity.

Although there is some overlap in grasshopper community composition (Figure 23), the differences between the states suggest that pest management activities may have very different results in Montana versus Colorado. Because grasshopper communities change in response to vegetation, grazing and climate, management decisions need to take each of these factors into account. The use of cultural methods, such as reseeding, to manage range should recognize the effects of changing vegetation on grasshopper community composition (Fielding and Brusven 1993a). The changes in canopy structure that result from grazing and fire regimes likewise need to considered. These

disturbances work within the context of climate at a site to determine grasshopper community composition (*sensu* Allen and Hoekstra 1992, Clements 1936).

More work is necessary to evaluate the effects of landscape pattern on grasshopper communities and their distributions. Interactions between vegetation and grasshoppers at the rangeland-cropland interface, for example, may differ significantly from those within rangeland alone. The migration of roadside grasshoppers into cropland depends on the density of both grasshoppers and vegetation (Gage and Mukerji 1977), but it is not known if this relationship holds true for rangeland. Studies at multiple spatial scales are also needed to see if ecosystem relationships hold true across different scales (Allen and Hoekstra 1992). The findings between plant and grasshopper communities uncovered here address a regional scale which begins to meet this need. Knowledge of the conditions which lead to grasshopper outbreaks will be enhanced by further studies which characterize the relationships between the vegetation resource and grasshopper community dynamics over large spatial areas.

Summary and Conclusions

The main findings of this study were (1) grasshopper communities ordinate on different factors than do plant communities, (2) plant and grasshopper communities vary on both local and regional scales, and (3) grasshopper community composition is determined by general site characteristics as well as by the presence of individual plants. The implications of ordination results for studies which seek to find interactions between plants and grasshoppers is that sampling must be planned carefully so the factors measured for ordination reflect the heterogeneity of the system studied. Factors which

determine the distribution of a given grasshopper species may differ from the emergent properties which determine the composition of the grasshopper community. These communities vary in both time and space, so pest management activities can have varied results when implemented across different spatial scales. Research on control measures which is performed at local or watershed scales may not be readily applied to larger spatial areas. Finally, because general site and vegetation characteristics have been shown to influence grasshopper communities, sampling these factors or using them to categorize habitat can aid grasshopper research by reducing costs and sampling time.

CHAPTER THREE

COMPOSITION OF PLANT AND GRASSHOPPER COMMUNITIES: INDICATORS AT THE STATE SCALE

Introduction

The species composition of rangeland grasshopper communities (Orthoptera: Acrididae) varies with vegetation and local habitat (Anderson 1964, Bergmann & Chaplin 1992, Capinera & Sechrist 1982a, Joern 1979, Kemp 1992a, Kemp et al. 1990b, Quinn et al. 1991). While grasshoppers can cause significant losses of rangeland forage (Hewitt & Onsager 1983), the amount of damage caused by a grasshopper community depends on not only abundance but also the species present and their proportions (Anderson & Wright 1952). To focus management efforts on those species which are likely to cause forage and crop losses, it is necessary to know the species composition of the grasshopper community found in a given type of habitat.

Although certain conditions correlate with the distribution and abundance of individual grasshopper species, the parameters which dictate the structure and composition of specific grasshopper communities have not been delineated. Detailed knowledge of the relationship between grasshoppers and habitat is necessary to pinpoint areas where economically damaging species occur and thus are likely to require grasshopper control.

Historically, control efforts have not incorporated the fact that grasshopper species composition varies in space. Instead, large areas of land are treated as if the grasshopper communities on them are homogeneous (USDA APHIS-PPQ 1987). However, the plants and soils on the landscape are not homogeneous, and grasshopper species with different habitat requirements should be expected to find the food plants and soils needed for growth and reproduction in different places (Uvarov 1957). Considerable money could be saved and ecosystem disturbance avoided if management was directed only at economically damaging species.

An understanding of how grasshoppers respond to changes in habitat requires detailed habitat information and analysis of grasshopper communities within each type of habitat. Vegetation and soil maps are inexpensive alternatives to field surveys as sources of habitat information, and are available in digital form and at various degrees of resolution. For example, the State Soil Geographic Data Base (STATSGO) for Montana contains generalized plant and soil data at a map scale of 1:250,000 (USDA-SCS 1991). These digital map data can provide the environmental variables necessary for grasshopper community analysis and modelling and may help to predict grasshopper community characteristics, but only if the data accurately describe field conditions which are important to grasshopper community composition.

To evaluate two digital data sources that might be helpful in characterizing grasshopper habitat, this study compared map information with plant and grasshopper species data collected in the field. The objectives of the study were to (1) identify differences in plant and grasshopper community composition between three

geographically separate sampling areas within Montana; (2) determine whether the ecoregion level of classification is a useful indicator of grasshopper community change on a state-wide scale; and (3) determine whether the Montana State Soil Geographic Data Base (STATSGO) is useful for characterizing grasshopper communities on a state-wide scale.

While a number of grasshopper species exist in Montana rangeland, only a few species become economically important pests. Kemp (1992b) found that of 57 species collected at sites across Montana, less than a third of all species were important to the change in densities from non-outbreak to outbreak conditions. Montana counties differ in the probability for outbreak to occur or persist (Kemp 1987), so whether a given density of grasshoppers warrants control depends on the county and the probability that population levels will decrease in subsequent years. It is likely that areas within a county also differ in outbreak probabilities, but the target habitat has yet to be identified. This is where habitat classification schemes can be useful.

The classification of land based on vegetation and climate has been of interest to biologists for many years. Clements (1936) developed a scheme for classifying biotic regions by comparison with the "climax" vegetation that would develop in the absence of disturbance. Both Bailey (1980) and Omernik (1987) outlined ecoregions for the conterminous United States based on physical and biological characteristics. Omernik's (1987) ecoregion map was used in this study because of its finer level of detail. The map was compiled from a composite of potential vegetation, land use, topography, and soil maps to delineate ecoregions for the conterminous United States. The map scale is

1:7,500,000 and while maps at the more detailed scale of 1:250,000 are in progress for several states, none are available for Montana at this time.

Kemp (1992a; Kemp et al. 1990b) has demonstrated the usefulness of habitat types for grasshopper community comparisons, and ecoregions are a similarly useful habitat classification scheme that can identify habitat where economically damaging grasshoppers may occur. Because both acridid abundance and weather conditions are closely linked to habitat type (Capinera & Sechrist 1982a, Clements 1936, Dempster 1963, Kemp 1992a, Kemp et al. 1990b, Quinn et al. 1991), the classification of grasshopper habitat is an important step that will aid in clarifying the mechanisms that regulate acridid populations.

It has been established that most grasshopper species need a habitat mosaic where they can find bare soils for oviposition sites and green vegetation for food and shelter, to complete their life cycles (see Uvarov 1957). Densities of grasshoppers increase with human activities that disturb rangeland (Fielding & Brusven 1993a, 1993b; Joern 1982; Scoggan & Brusven 1973), as grasshoppers respond to increases in the amount of bare ground and altered vegetation structure that result from overgrazing, tilling, and burning (Anderson 1964, Bergmann & Chaplin 1992, Capinera & Sechrist 1982a, Miller & Onsager 1991, Quinn & Walgenbach 1990).

Weather has a great effect on grasshopper populations, with warm temperatures and low precipitation favorable to the development of outbreaks (Capinera & Horton 1989, Edwards 1960, Fielding & Brusven 1990, Gage & Mukerji 1977, Johnson & Worobec 1988, Jones 1939, Smith 1954, Wakeland 1961). The previous year's

population level is also important in determining grasshopper abundance (Gage & Mukerji 1977, Johnson & Worobec 1988, Kemp 1987) and affects whether favorable conditions will result in outbreaks.

Soil type and soil moisture also affect grasshopper populations through the choice of oviposition sites. Edwards & Epp (1965) observed the choice of oviposition sites by *Melanoplus sanguinipes* in laboratory experiments. They found that this pest species prefers moist sand to loam or clay, avoids completely dry soil, and, when only dry soil is available, prefers coarse soil over fine soil. The subsurface moisture content was more important than surface moisture in selection of oviposition sites. Time lost looking for oviposition sites in unsuitable habitat reduces oviposition rates, and thus impacts the population level of a species in a given habitat. Because the permeability and available water content of soil influence grasshopper hatching and oviposition (Hewitt 1985), these soil attributes were chosen from the Montana STATSGO database as possible indicators of grasshopper community composition.

The combined impacts of weather, soil conditions, vegetation, and abundance determine whether grasshopper populations will reach economically damaging levels. It is not known which habitats have a favorable combination of these factors most frequently and are thus more prone to outbreaks, nor is it known where those habitats exist in the landscape of a state the size of Montana. If such habitat can be identified, it can serve as an indicator for grasshopper community classification, to identify grasshopper communities which may become economically damaging.

The value of descriptive studies such as this one is in their application to new spatial areas and temporal periods. Once the usefulness of ecoregions and STATSGO soil attributes have been tested for Montana rangelands, the results are useful for extrapolating to the future (as with population models) and to other geographic areas. The results of this study provide the groundwork for grasshopper community analysis in Montana by demonstrating how digital data sources can be applied to rangelands.

Methods

The scale of grasshopper habitat research can range from the microenvironment around an individual plant to a multi-state region. The question of scale is important in the study of spatial issues, as the proper scale of study must be identified for each question that is addressed to ensure that the correct context and constraints are examined. Unfortunately, the term "scale" means different things to different scientists. Ecologists use scale to pertain to spatial and sometimes temporal size (Allen & Hoekstra 1992), while geographers use scale to refer to the ratio between an object's size on a map and the objects actual size on the ground.

In this study, the term "scale" will be used in the ecological sense to refer to the spatial extent of the study, and "resolution" will refer to the amount of detail captured by the data. Thus, small-scale concepts apply to small areas of land, such as a single site, and large-scale concepts apply to larger areas such as multiple watersheds, a state, or a multi-state region.

Site Selection

Plant and grasshopper communities were sampled at 80 sites near Jordan, Montana, at 22 sites in the Madison river area of Montana, and at 26 sites near Big Timber, Montana, during 1993 (Figure 26). Grasshoppers were sampled twice at the Jordan sites; the first set of samples were collected during the first two weeks of June, while the second sample dates were during the second and third weeks of August. Because the Madison and Big Timber sites were sampled only once during mid-August, to maintain consistency, the data from the first sampling dates at Jordan were not used.

The Jordan sampling area was located in a roughly triangular area near Jordan, Hysham, and Miles City, Montana, between longitudes -107° 10′ and -105° 55′ and between latitudes 46° 15′ and 47° 35′. The Madison sampling area was located between longitudes -111° 30′ and -111° 54′ and between latitudes 44° 50′ and 45° 48′. The Big Timber sampling area was located between longitudes -109° 25′ and -110° 04′ and between latitudes 45° 52′ and 46° 18′.

The Jordan sites were numbered between 101 and 325 (Figure 27) and were chosen in three different climax vegetation types, arbitrarily designated A, B, and C. The climax plant community, as used by Ross and Hunter (1976) is defined as that plant community which develops under the prevailing climatic and edaphic conditions in the absence of disturbance. For the Jordan sites, climax vegetation in type A (Figure 27) is characterized as a silty range site in the 10-14" precipitation zone dominated by western and thickspike wheatgrass, needleandthread, green needlegrass, little and big bluestem, bluebunch wheatgrass, and silver sagebrush. Type B represents silty or clayey

Figure 26. Sampling sites for 1993 with Montana county boundaries.

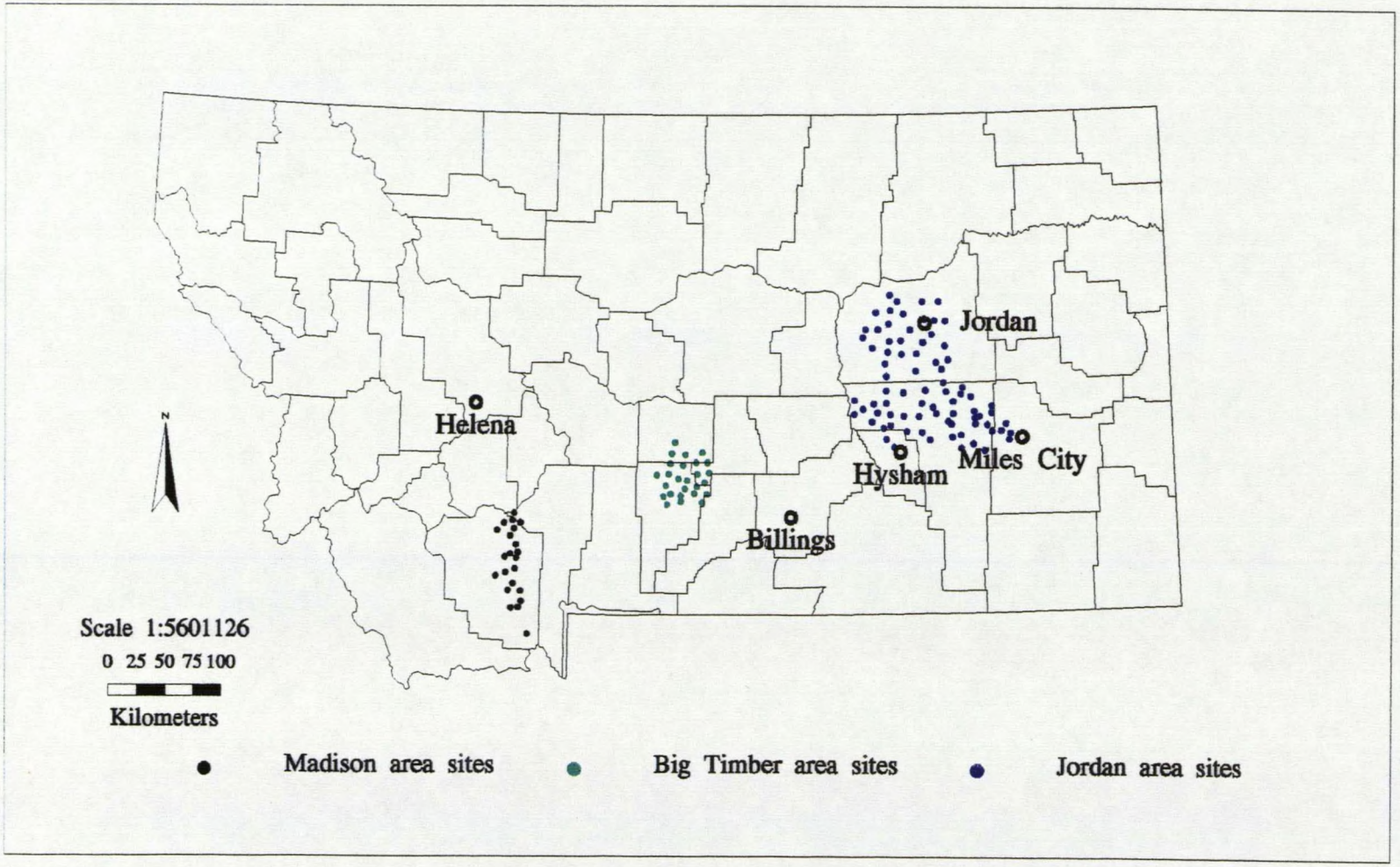
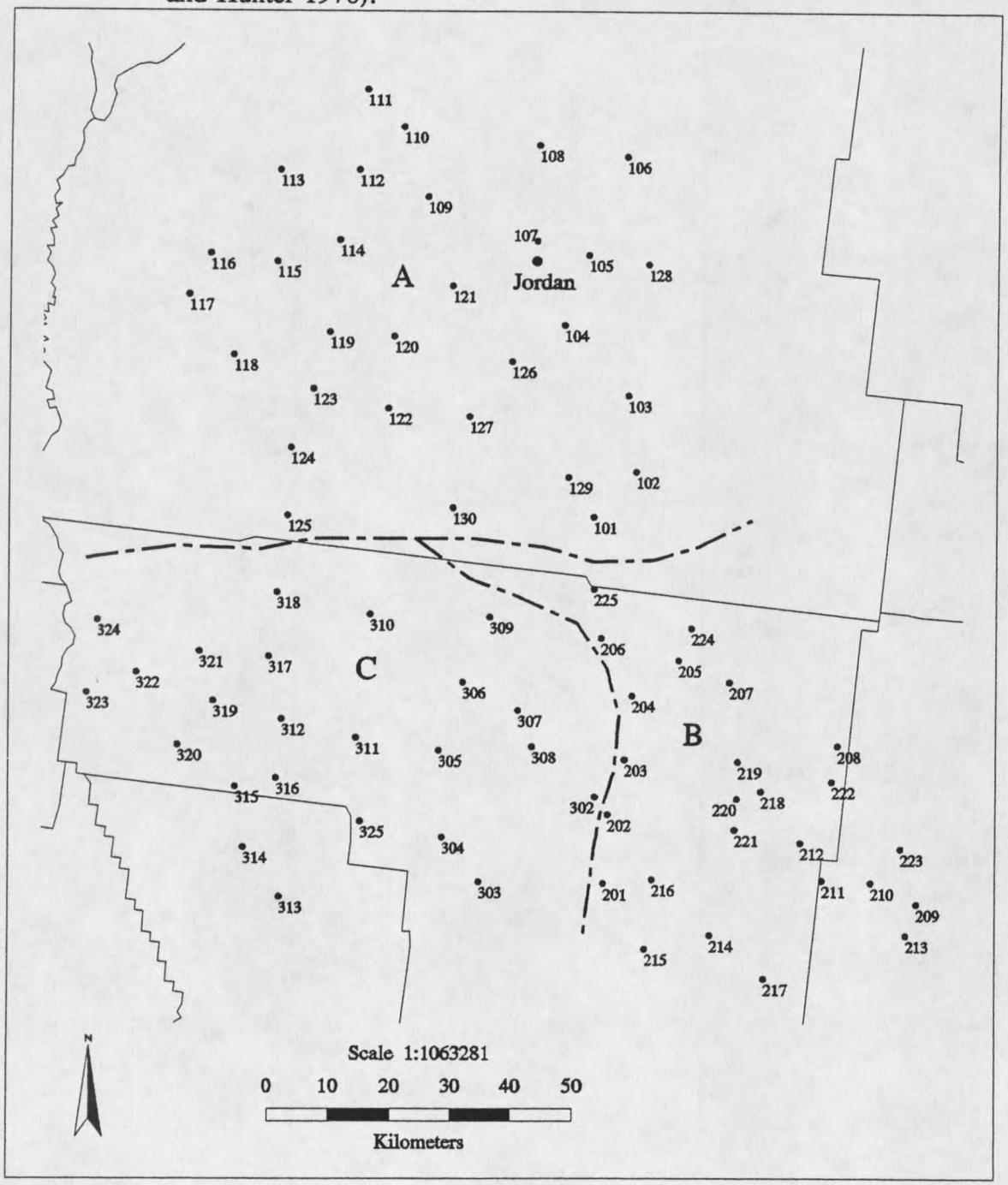


Figure 27. Sample sites near Jordan, Montana, where vegetation and grasshopper communities were sampled during 1993. Solid lines represent county boundaries, while dashed lines represent the boundaries of climax vegetation types A, B, and C. Sites located in vegetation type A have silty soils and are dominated by wheatgrass and needleandthread; vegetation type B has silty or clayey soil with wheatgrass and green needlegrass; type C has dense clayey or saline soil with wheatgrass, green needlegrass and wildrye (Ross and Hunter 1976).



range sites in the 10-14" precipitation zone with wheatgrass, green needlegrass, little bluestem, and big sagebrush. Upland range sites in the 10-14" precipitation zone comprise type C, with dense clay, clayey or saline soils and wheatgrass, green needlegrass, wildrye, big sagebrush, and greasewood.

The climax vegetation types represented by the Madison and Big Timber areas were determined using a map from Ross and Hunter (1976). The Madison area sites were located on silty or clayey range sites in the 10-14" or 15-19" precipitation zone dominated by fescues, bluebunch wheatgrass, needleandthread, and basin wildrye. Sites in the Big Timber area were located on silty, clayey, or shallow clay range sites in the 10-14", 12-14", or 15-19" precipitation zone, which are dominated by wheatgrasses, needlegrass, big sagebrush, fescues, and prairie junegrass.

Sites near Jordan (Figures 26 and 27) were chosen in more than one vegetation type to determine whether the plant community influences the grasshopper community at a small scale. More detailed analyses of differences between site in the vegetation types near Jordan are included in Chapter 2. Sites that were located in vegetation type A were numbered 101 to 130, sites within type B numbered 201 to 225, and in type C, were numbered 301 to 325. Sites in the Madison area were numbered 401 to 422 and sites in the Big Timber area were numbered 501 to 526. The latitude and longitude of each sampling site was obtained with a global positioning system (GPS) receiver accurate to $\pm$ 12 m horizontal distance (Magellan 1992). Topographic maps were used to find the altitude of each site for input into the receiver and the location of each sampling site was the average of 100 points.

Vegetation Sampling

The vegetation contained in five Daubenmire (1959) frames of 0.10 m^2 each were examined at each site. The percent cover by bare ground, leaf litter, and individual species were recorded. Total cover, tallest plant height, and mode plant height were also measured. At the Jordan sites, a list of common species, based on the previous year's collections, was compiled (Table 6) and only plant species on this list were recorded. Species encountered but not on the list were recorded as either "other grasses" or "other forbs". To ensure uniformity among the datasets, the plant data collected from the Madison and Big Timber sites were generalized to match the Jordan species list.

The plant cover data were averaged over the five frames by summing the percent cover or heights for each site and dividing by five. Therefore, if a plant species was not present in one of the frames, the percent cover for that frame was zero, and this value was averaged with the other four frames to obtain the site average for that species. For correlation purposes, the proportion of grasses, forbs, and "other" plants at each site were calculated using programs in the statistical package SAS (SAS 1985) to sum the percent cover in each category, then divided by the total. Nine plant species and genera were selected for correlation testing based on mean percent cover and frequency at each of the sampling areas (see Table 6). The percent cover for a given genus is equal to the sum of the percent cover values of all species collected for that genus.

Grasshopper Sampling

Grasshoppers were collected via sweep nets at the same sites where plant sampling was conducted, except site 105, which was missing from the grasshopper data.

Table 6. Plant species names and codes used in analyses for collections made at Jordan, Madison, and Big Timber sampling areas of Montana, in 1993. Codes in bold type were used in Spearman rank correlations.

Code	Species
AGROS	All *Agropyron* spp.
ARFR	*Artemisia frigida* Willd.
ARTEM	All *Artemisia* spp.
ATGA	*Atriplex gardneri* (Moq.) D.Dietr.
BOGR	*Bouteloua gracilis* (H.B.K.) Lag.
BRTE	*Bromus tectorum* L.
CAFI	*Carex filifolia* Nutt.
CAREX	All *Carex* spp.
FEID	*Festuca idahoensis* Elmer
GUSA	*Gutierrezia sarothrae* (Pursh) Britt. & Rusby
KOCR	*Koeleria cristata* Pers.
OPPO	*Opuntia polyacantha* Haw.
OTHER	Other plants
OTHFB	Other forbs
OTHGR	Other grasses
PHHO	*Phlox hoodii* Rich.
PLPA	*Plantago patagonica* Jacq.
POAS	All *Poa* spp.
STIPA	All *Stipa* spp.
STCO	*Stipa comata* Trin. & Rupr.
VUOC	*Vulpia octoflora* (Walt.) Rydb.

The number of first through fifth instars, adult males and adult females were recorded for each grasshopper species collected in 200 sweeps at each site. Sweeps were taken between 0930 and 1600 h when cloud cover was less than 15% and winds were less than 25 kmh^{-1}, with each sweep covering a low 180 degree arc through vegetation with a net. Crickets were counted and included in the data set.

The raw data were pooled over phenological stage via programming in SAS (SAS 1985) to sum counts for each species at each site. By dividing the number of

grasshoppers of a given species by the total number of grasshoppers collected at that site, the proportion each species contributed to the local community was calculated. Grasshopper species abbreviations are given in Table 7. Thirteen species were selected for correlations based on average proportion of community and frequency and each of the sampling areas (see Table 7).

GIS Processing

The location of each sampling site was converted to decimal degrees in SAS (SAS 1985) and used to create digital maps, called coverages, in the workstation version 6.0 of the geographic information system ARC/INFO (ESRI 1992) via the GENERATE command. Locational data for the three sampling areas were treated separately. Each of the three ARC/INFO coverages were converted to an Albers Conic Equal Area map projection using the PROJECT command.

Ecoregions. A digital map of Omernik's ecoregions (Omernik, 1993) for the United States, at a scale of 1:7,500,000, was obtained. A coverage of state boundaries with a scale of 1:2,000,000 (USGS-ESIC 1991) was used to extract ecoregions within the boundary of Montana from the United States ecoregion coverage using the CLIP command. Spatial overlay using the IDENTITY command was performed between the Montana ecoregion coverage and each of the sample site coverages. In the resulting coverages, the number of the ecoregion in which each site lies is a spatial attribute of that site (Figure 28).

STATSGO. Additional spatial attributes were associated with each site and extracted in the following manner: The Montana State Soil Geographic Data Base

Table 7. Grasshopper species names, codes used for analyses, and subfamily classifications* for collections made at sites in Montana, 1993. Codes in bold type were used in Spearman rank correlations.

Code	Species	Subfamily*
ACONS	*Arphia conspersa* (Scudder)	O
ANGUS	*Melanoplus angustipennis* (Dodge)	O
BIVIT	*Melanoplus bivittatus* (Say)	M
BOWDI	*Melanoplus bowditchi* Scudder	M
BRUNE	*Melanoplus bruneri* Scudder	M
BRUNN	*Stenobothrus brunneus* Thomas	G
CAMPE	*Trimerotropis campestris* McNeill	O
CARLI	*Circotettix carlinianus* (Thomas)	O
CAROL	*Dissosteira carolina* (Linneaus)	O
CLAVA	*Aeropedellus clavatus* (Thomas)	G
COLLA	*Spharagemon collare* (Scudder)	O
COLOR	*Amphitornus coloradus* (Thomas)	G
CONFU	*Melanoplus confusus* Scudder	M
CORAL	*Xanthippus corallipes* Haldeman	O
COSTA	*Encoptolophus costalis* (Scudder)	O
CRENU	*Cordillacris crenulata* (Bruner)	G
CRICK	Cricket	
CURTI	*Chorthippus curtipennis* (Harris)	G
DAWSO	*Melanoplus dawsoni* (Scudder)	M
DELIC	*Psoloessa delicatula* (Scudder)	G
DEORU	*Ageneotettix deorum* (Scudder)	G
ELLIO	*Aulocara elliotti* (Thomas)	G
EQUAL	*Spharagemon equale* (Say)	O
FEMOR	*Aulocara femoratum* (Scudder)	G
FEMUR	*Melanoplus femurrubrum* (DeGeer)	M
GLADS	*Melanoplus gladstoni* Scudder	M
GRACI	*Trimerotropis gracilis* (Thomas)	O
HALBA	*Hypochlora alba* (Dodge)	M
HALDE	*Pardalophora haldemanii* (Scudder)	O
HAYDE	*Derotmema haydeni* (Thomas)	O
HIRTI	*Acrolophitus hirtipes hirtipes* (Say)	G
HVIRI	*Hesperotettix viridis* (Scudder)	M
INFAN	*Melanoplus infantilis* (Scudder)	M
KIOWA	*Trachyrhachys kiowa* (Thomas)	O

Table 7. Continued on following page.

Table 7. Continued.

LATIF	*Trimerotropis latifasciata* Scudder	O
MACUL	*Mermiria maculipennis* Bruner	G
NEBRA	*Phoetaliotes nebrascensis* (Thomas)	M
NEGLE	*Cratypedes neglectus* (Thomas)	O
OBSCU	*Opeia obscura* (Thomas)	G
OCCID	*Melanoplus occidentalis* (Thomas)	M
OCCIP	*Cordillacris occipitalis* (Thomas)	G
OTHER	Other, not identified to species	
PACKA	*Melanoplus packardii* Scudder	M
PARDA	*Metator pardalinus* (Saussure)	O
PELLU	*Camnula pellucida* (Scudder)	O
PISTR	*Trimerotropis pistrinaria* Saussure	O
PSEUD	*Arphia pseudonietana* (Thomas)	O
QUADR	*Phlibostroma quadrimaculatum* (Thomas)	G
RABUL	*Circotettix rabula* Rhen and Hebard	O
SANGU	*Melanoplus sanguinipes* (Fabricius)	M
SIMPL	*Eritettix simplex* (Thomas)	G
TRIFA	*Hadrotettix trifasciatus* (Say)	O
TURNB	*Aeoloplides turnbulli turnbulli* (Thomas)	M
WYOMI	*Paropomala wyomingensis* (Thomas)	G

* "G" refers to the subfamily Gomphocerinae, "M" refers to the subfamily Melanoplinae, and "O" refers to the subfamily Oedipodinae.

** Denotes stage in which species spends the winter months.

(MTSTATSGO) (USDA-SCS 1991), compiled at a map scale of 1:250,000, was projected into an Albers Conic Equal Area map projection (Figure 29), then spatially joined with each of the sampling area coverages in ARC/INFO using the INTERSECT command. The resulting coverages consisted of the sampling points and the number of the MTSTATSGO map unit in which each lies (Figures 30-32). This map unit identification number (MUID) was later used to determine the physical attributes of each

Figure 28. Omernik's Ecoregions for Montana and 1993 sampling areas

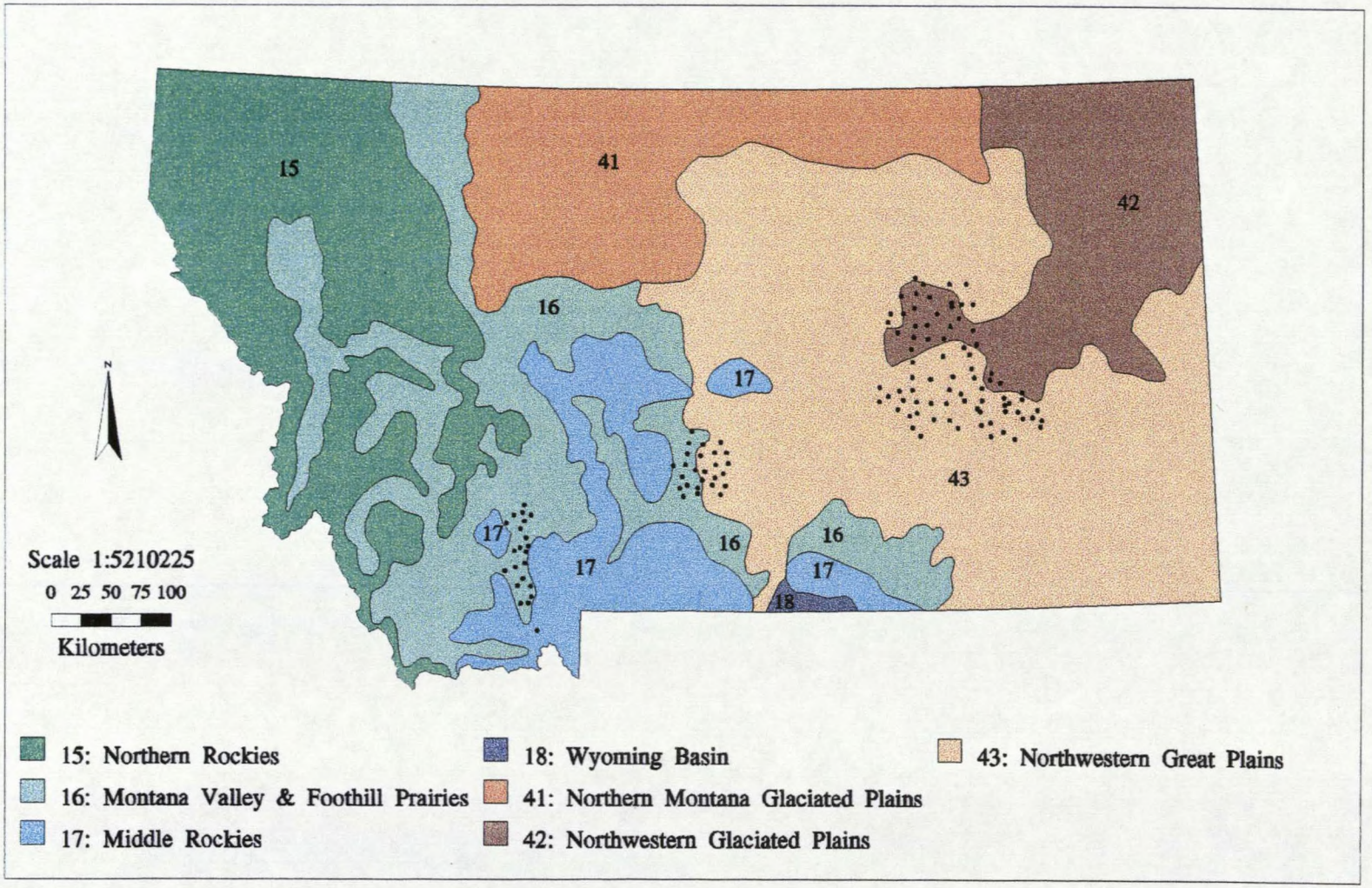


Figure 29. Sampling sites for 1993 with Montana STATSGO mapping units

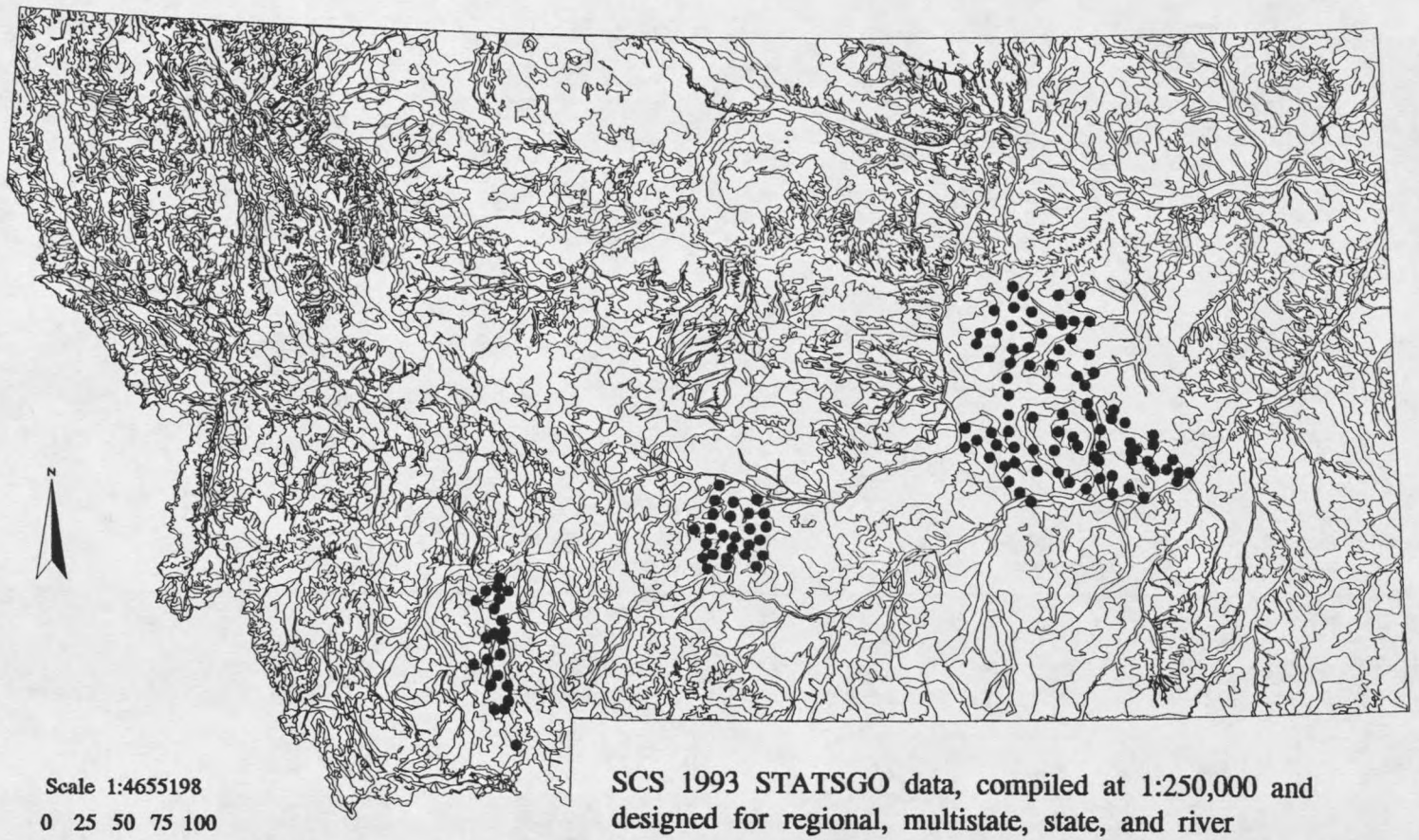


Figure 30. Sampling sites near Jordan, Montana, with STATSGO mapping units

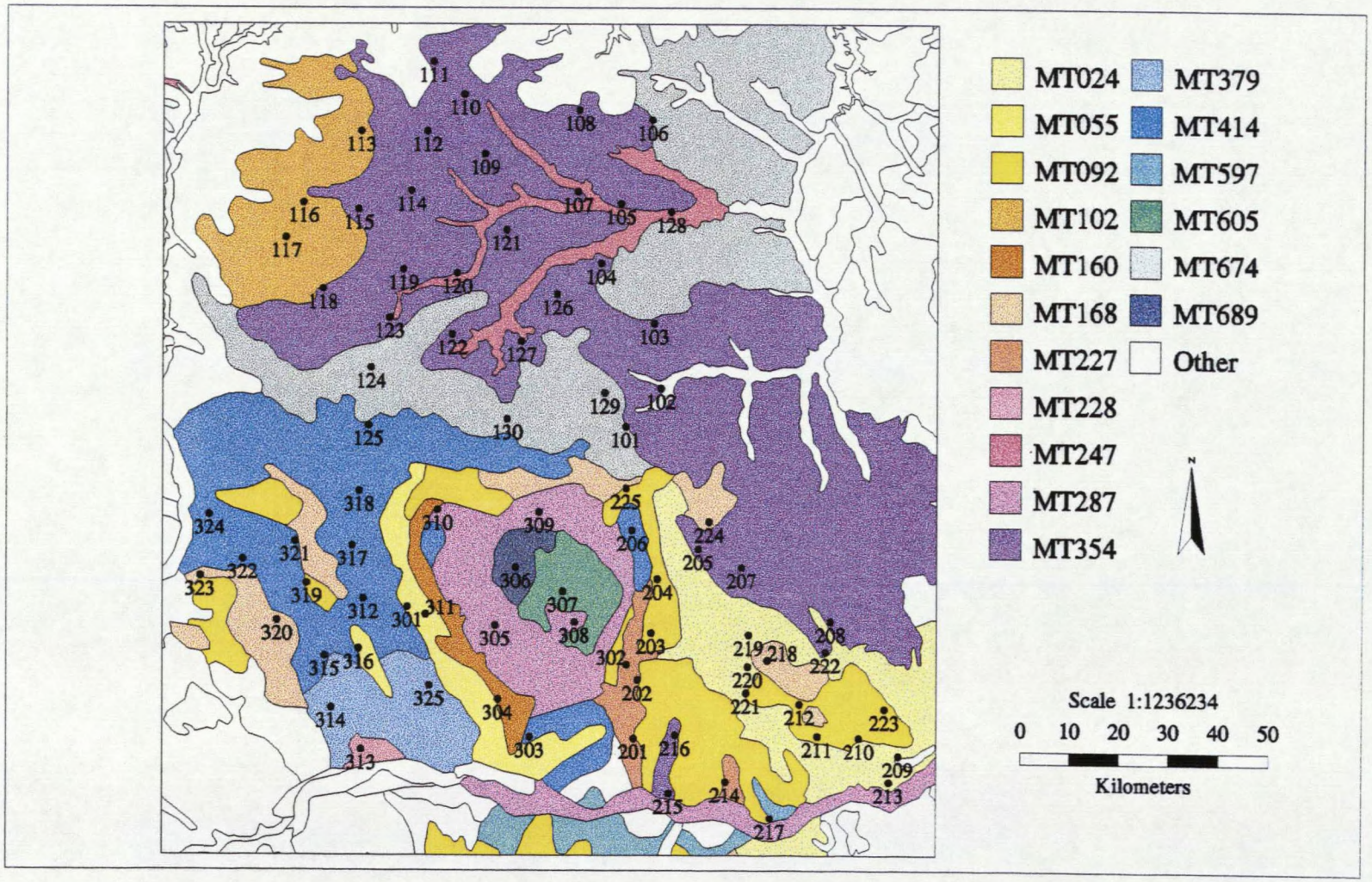


Figure 31. Sampling sites in the Madison river area of Montana with STATSGO mapping units

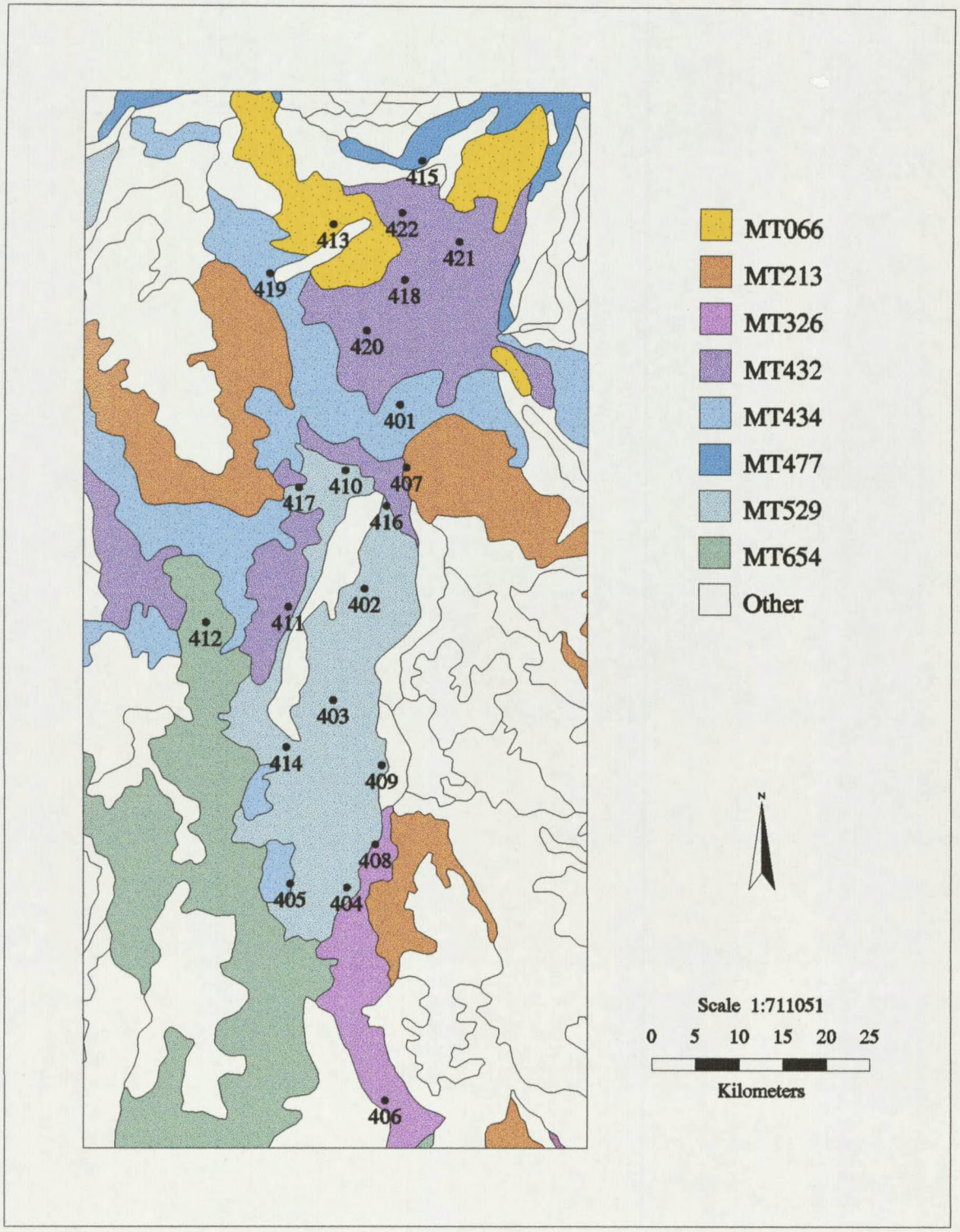
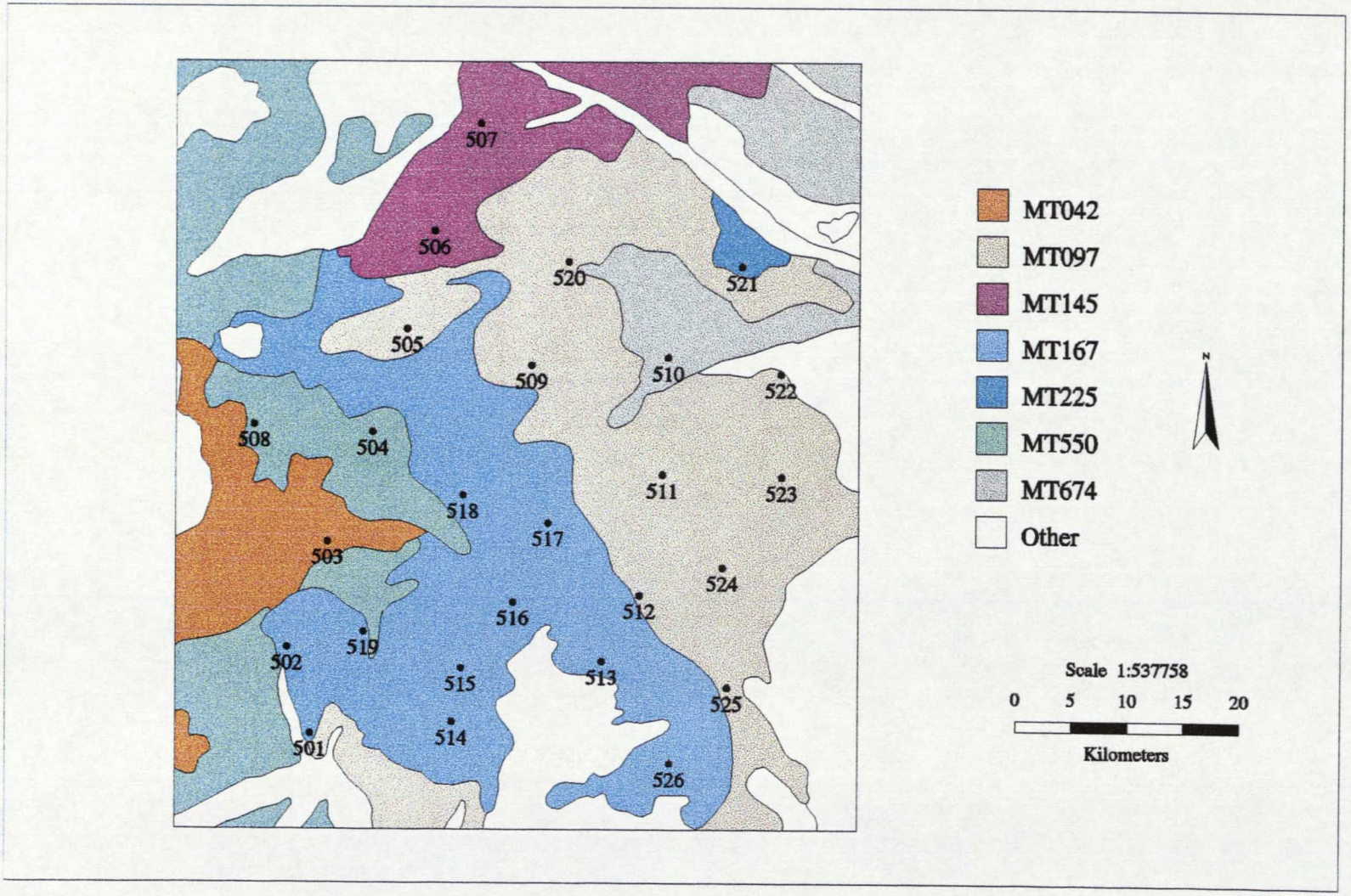


Figure 32. Sampling sites near Big Timber, Montana, with STATSGO mapping units



sampling site by extracting specific MTSTATSGO attributes for the MUIDs which overlap the Jordan, Madison, and Big Timber sampling areas.

Data Analysis

Ecoregions. Species proportions and percentages, whether plant or grasshopper, were first analyzed using detrended correspondence analysis (DCA). DCA is a nonlinear, weighted averaging method of measuring the variance among species and site data in a single analysis, in which sites and species are ordered along four axes according to their similarities to each other (Ter Braak 1988). The result is a list of eigenvalues for each species and site, representing roughly the proportion of the variance accounted for by each ordination axis. Eigenvalues for each axis are directly proportional to the importance of that axis in separating species and samples. DCA scales axes in uniform and natural units, so scores from different data sets may be compared (Gauch 1982). Using the program CANOCO (Ter Braak 1988), the first DCA run was conducted on all sites and variables in each data set. For the grasshopper data, site 307 was omitted from a second DCA to allow greater separation among the remaining sites.

Each DCA results in two sets of axis scores, one for species and one for sites, although eigenvalues are the same for both sets of scores. Axis 1 and 2 scores resulting from each final DCA were imported into SAS programs to produce graphs of the distributions of sites and species. Codes from Tables 6 and 7 were used for plotting plant and grasshopper species, respectively.

The first null hypothesis (hypothesis 1, see Table 8) tested was that the Jordan, Madison, and Big Timber sampling areas do not differ from one another in plant

Table 8. Hypotheses to be tested in a study on indicators of plant and grasshopper community composition in Montana, 1993.

Hypothesis	Test
1) Sampling areas do not differ in plant species composition	DCA
2) Ecoregions do not differ in plant species composition	DCA
3) Sampling areas do not differ in grasshopper species composition	DCA
4) Ecoregions do not differ in grasshopper species composition	DCA
5) Sampling areas do not differ in mean grasshopper densities	pairwise *t* test
6) Ecoregions do not differ in mean grasshopper densities	pairwise *t* test
7) No correlations exist between proportions of grasses, forbs and other plants and DCA scores based on percent cover of individual plant species	Spearman correlation
8) No correlations exist between proportions of grasses, forbs and other plants and DCA scores based on proportions of grasshopper species	Spearman correlation
9) No correlations exist between DCA scores based on grasshopper species and DCA scores based on percent cover of individual plant species	Spearman correlation
10) No correlations exist between Montana STATSGO attributes and plant species composition	Spearman correlation
11) No correlations exist between Montana STATSGO attributes and grasshopper species composition	Spearman correlation

Table 8. Continued next page.

Table 8. Continued.

12) No correlations exist between Montana STATSGO attributes and ecoregion	Kruskal-Wallis test, Wilcoxon test
13) No correlations exist between Montana STATSGO attributes and sampling area	Kruskal-Wallis test, Wilcoxon test
14) No correlations exist between Montana STATSGO plant production values and plant cover as measured at sampling sites	Spearman correlation
15) No correlations exist between proportions of grasshopper species and plant cover	Spearman correlation

community composition. This hypothesis was tested using DCA. Low eigenvalues resulting from DCA would support the null hypothesis, because low values indicate little separation between sites. Therefore, for this study, if the sum of the eigenvalues for the first two axes was less than 0.60, the null hypothesis was not rejected. This general criterion was used in testing each subsequent null hypothesis that was tested using DCA.

Hypothesis 2 stated that the ecoregions do not differ in plant community composition. This hypothesis was tested using the same DCA used in hypothesis 1, but using different symbols to plot the results. This hypothesis tested the validity of using the ecoregion concept for Montana rangeland: can two ecoregions be combined and treated as one? For example, are ecoregions 16 and 43 or 42 and 43 (Figure 28) distinct from one another in terms of plant species composition? If the ecoregions do not cluster separately (i.e., overlap in the DCA plot), there is support for dissolving ecoregion

boundaries. Differences between ecoregion 17 and the other ecoregions could not be tested because only 1 sampling site is located in ecoregion 17.

The third null hypothesis (hypothesis 3) was that the three sampling areas do not differ in grasshopper species composition. This hypothesis was tested in the same manner as hypothesis 1, using DCA. Hypothesis 4 stated that the ecoregions do not differ in grasshopper community composition, and was tested similarly, using the same DCA results as hypothesis 3 but using different symbols to plot the sites.

Hypothesis 5 stated that mean grasshopper densities of the three sampling areas do not differ from one another. To test for differences between each of the study areas and ecoregions, the mean number of grasshoppers per area or ecoregion was calculated in SAS (SAS 1985). Pairwise differences between resulting means were tested using the TTEST procedure, and results were interpreted at the $\alpha=0.05$ level of significance. *P*-values of less than 0.05 for the test statistic t resulted in rejection of the null hypothesis.

Hypothesis 6 stated that there are no correlations between proportions of grasses and forbs and the percent cover by individual plant species. Hypothesis 7 stated that there are no correlations between proportions of grasses and forbs and the composition of the grasshopper community. Both these hypotheses were tested using Spearman rank correlations performed between plant and grasshopper DCA axis scores for sites and the proportions of grasses and forbs at each site. SAS was used to perform the correlations and to calculate the test statistic t. The *P*-value for each value of t was determined in MSUSTAT (Lund 1991) and *P*-values of less than 0.05 resulted in rejection of the null hypotheses.

Hypothesis 8 stated that no correlations exist between grasshopper species DCA scores and DCA scores for percent cover of individual plant species. This was tested using Spearman rank correlations in a manner similar to that used for hypothesis 7.

STATSGO. The MTSTATSGO data base includes a number of tabular data files which contain information about the soil and vegetation within each map unit (Figures 29-32). Because each map unit may encompass up to 21 components (soil series), each component is comprised of several soil layers, and components are not spatially referenced, there is no one map unit value for a given attribute. To reduce this one-to-many relationship and correlate STATSGO attributes with plant and grasshopper community data, the weighted average of each soil attribute was calculated to find one value for the entire mapping unit, as described below.

The STATSGO attribute data were exported from ARC/INFO to ASCII files and formatted using SAS. Only those MUIDs which contained sampling points from the spatial overlay on the MTSTATSGO coverage were used in subsequent steps.

Two soil attributes, available water capacity (AWC) and permeability rate (PERM), were selected for study. For each of these attributes, STATSGO lists a maximum and minumum value for each soil layer. The AWC values for each layer within a meter of the soil surface were averaged by adding the minimum and maximum values together and dividing by two. The result was multiplied by the thickness of the soil layer, and the layer values were summed over the soil profile, giving the weighted AWC in inches per inch for each soil component. The mean of these component values was calculated in SAS (SAS 1985) using PROC MEANS using the percent of the map unit covered by each

component to weight the values. The soil permeability rate (PERM) was weighted similarly, except layer values were averaged rather than summed to get a mean PERM value for each component, because the water available to a plant is cumulative over soil layers, but permeability rates are not cumulative. The result was a weighted average value for soil permeability rate in inches per hour over all soil layers and map components.

Hypothesis 9 stated that there are no correlations between MTSTATSGO soil attributes and plant community composition. This hypothesis was tested using Spearman rank correlations between AWC and PERM values and the percent cover of selected plant species and genera (see Table 6). The results were interpreted at the $\alpha=0.05$ level of significance using a table of critical values (Zar 1974). Hypothesis 10 was that there are no correlations between MTSTATSGO soil attributes and grasshopper community composition, and was tested using Spearman rank correlations between AWC and PERM values and selected grasshopper species (see Table 7). Results were interpreted in the same manner as for hypothesis 9.

Null hypothesis 11 stated that there are no correlations between MTSTATSGO soil attributes and ecoregion. To test this hypothesis, AWC and PERM values for each site were merged with ecoregion numbers, and nonparametric statistical tests for differences in soil attributes among the ecoregions were performed using the NPAR1WAY procedure in SAS (SAS 1985). If the *P*-value of the Kruskal-Wallis test, as output by SAS, was significant at the $\alpha=0.05$ level, then Wilcoxon tests on AWC and PERM values were done between pairs of ecoregions. Correlations between MTSTATSGO attributes and

sampling area (hypothesis 12) were tested in a similar manner. Again, differences between ecoregion 17 and other ecoregions could not be tested because only 1 sampling site is located in ecoregion 17.

The MTSTATSGO attribute data include plant cover information, including the percent of total site production attributed to a given plant species for each map unit component. Percentages for selected plant species and genera (see Table 8) were weighted by the percent of the map unit covered by each component. The mean of the component values was used as the map unit average production. Hypothesis 13 stated that no correlations exist between MTSTATSGO plant production data and plant cover data collected at field sites. This was tested using Spearman rank correlations between the MTSTATSGO value for a given plant species and the site value for that species. Results were interpreted using the same criterion as for hypothesis 9.

The final null hypothesis tested (hypothesis 14) was that there are no correlations between selected plant species and genera (see Table 8) and selected grasshopper species (see Table 9). This was tested by conducting Spearman rank correlations using the criterion for hypothesis 9.

Results

Sampling Areas

Differences in plant communities between the Jordan, Madison and Big Timber sampling areas were tested by DCA. Eigenvalues for DCA of plant species were 0.339 and 0.293 for axes 1 and 2, respectively. The sum of the first two axes was thus 0.632,

a value high enough to reject the null hypothesis that sampling areas do not differ in plant species composition (hypothesis 1).

Figure 33 shows the plant species plot that resulted from the DCA. There was not obvious pattern in the growth form of the plant species (forb/grass/annual/perennial). "Other" plants had high axis 2 scores. There are only two species categorized as annual grasses, and only one annual forb, so any gradient in percent cover is not revealed by the DCA plot. Figure 34 shows the DCA plot of sites by sampling area. The Jordan area sites (A-C) had low axis 2 scores, while Madison and Big Timber area sites had high axis 2 scores. Because "other" plants had high axis 2 scores, this result could be an artifact of the sampling method, since more plant species were pooled as "other" at the Madison and Big Timber sites. There is no apparent pattern along axis 1 for site number.

Differences in grasshopper species composition between the sampling areas (hypothesis 3) were also tested using DCA. Eigenvalues were 0.735 and 0.416 for axes 1 and 2, respectively. Because the sum of the first two axes was very high (1.151), the null hypothesis was rejected. Thus, DCA showed that both plant and grasshopper communities varied over the three major areas sampled.

Figure 35 shows the DCA plot of grasshopper species, and Figure 36 shows the separation of sampling sites coded by number (A-E). As in Figure 34, the Jordan area sites clustered separately from the Madison and Big Timber area sites, with generally lower axis 2 scores. Because grasshoppers were collected in the same manner in each of the minor areas, overlap between the Jordan sites and other areas represents

Figure 33. Results of detrended correspondence analysis based on plant species composition for 128 sites across Montana in 1993. "AF" refers to species which are annual forbs, "AG" refers to annual grasses, "PF" refers to perennial forbs, "PG" refers to perennial grasses, and "OT" are other plants not identified by species. Species abbreviation codes are given in Table 6.

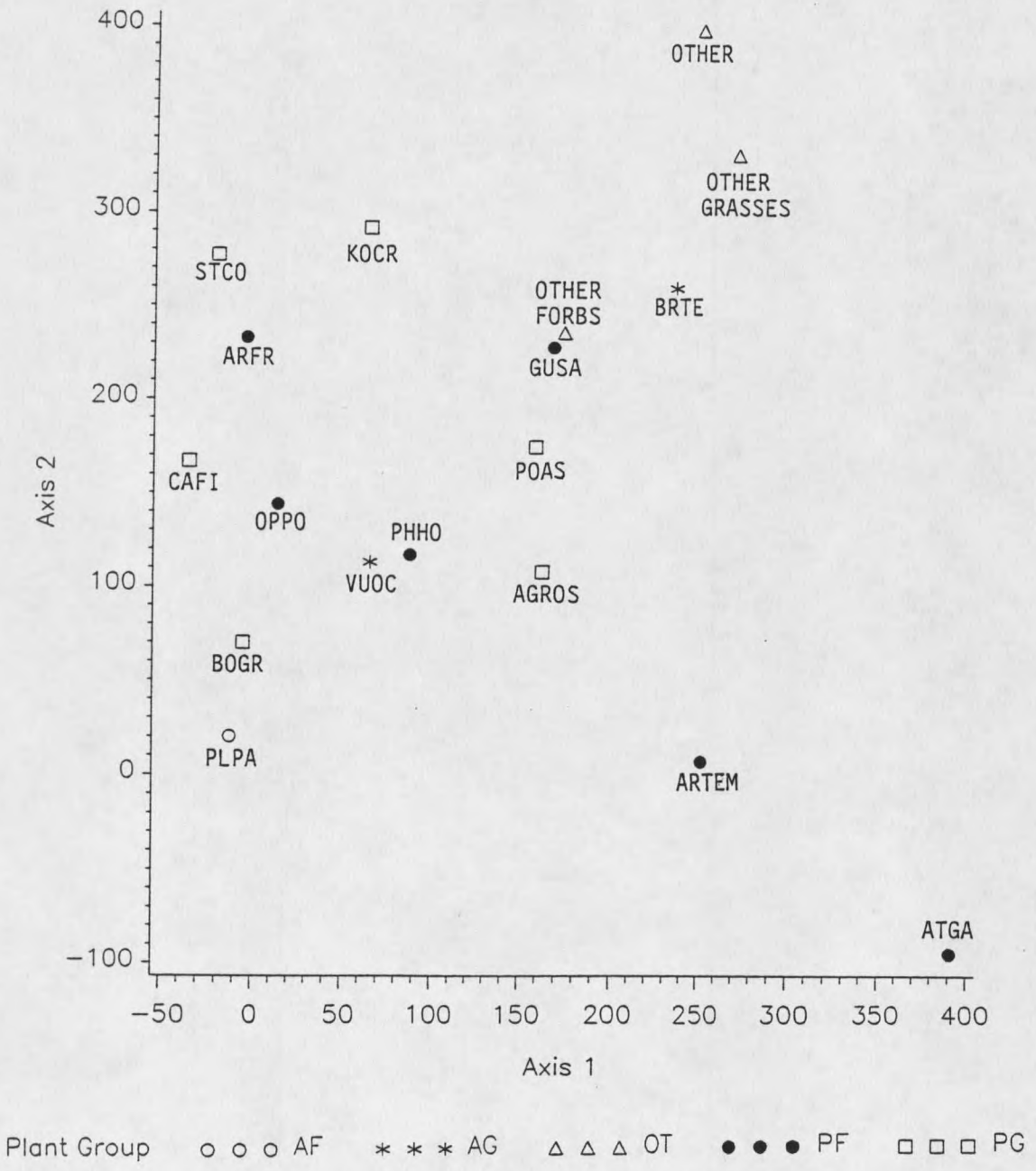


Figure 34. Results of detrended correspondence analysis based on plant species composition for 128 sites across Montana in 1993. "A", "B", and "C" refer to vegetation types at the Jordan sampling area; "D" refers to Madison area sites; and "E" refers to Big Timber area sites. Unlabeled sites include 106, 108, 110, 112, 118, 122, 128, 201, 203-205, 220, 222, 225, 302, 308, 311, 312, 323, 418, 511, 513, and 515.

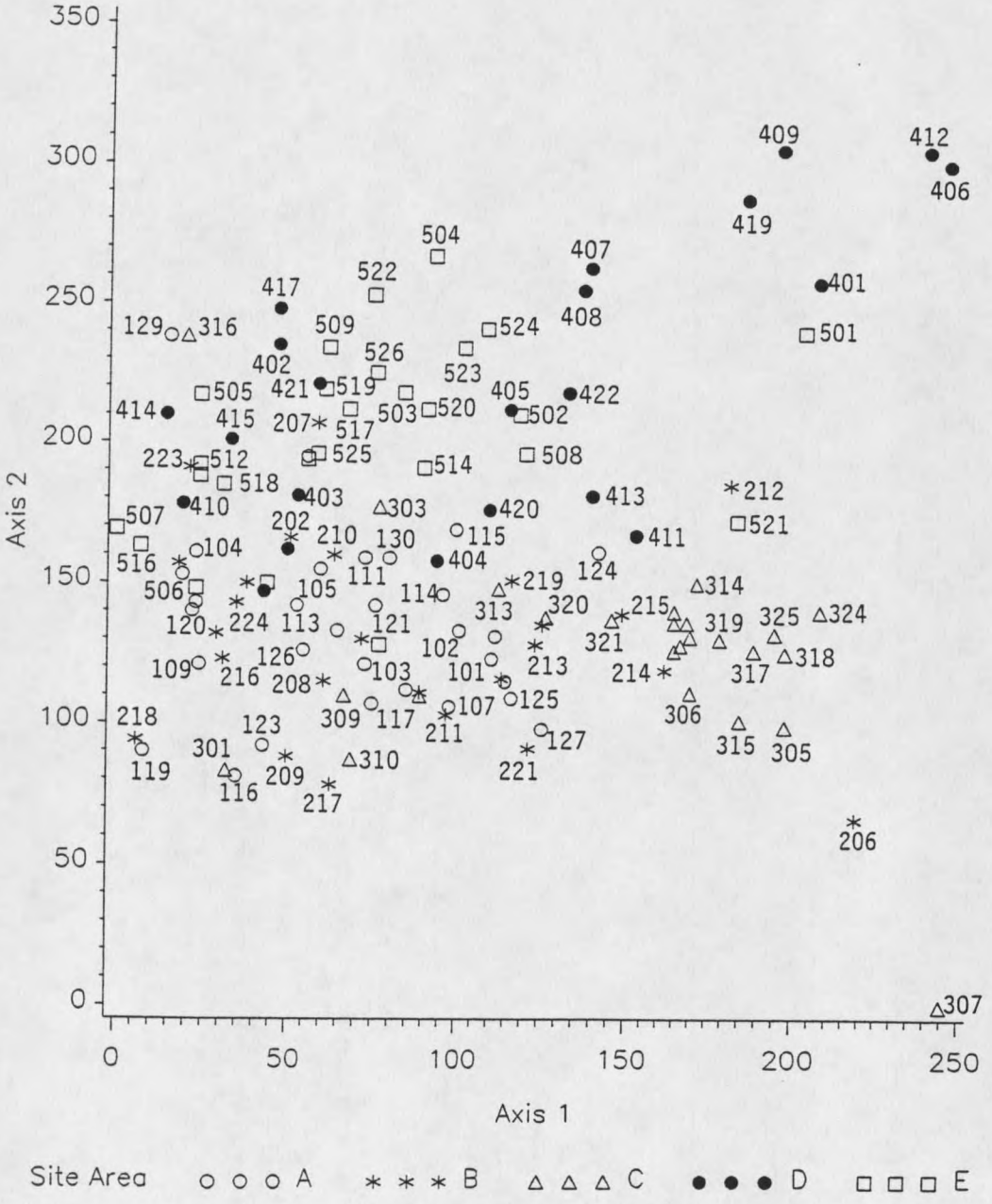


Figure 35. Results of detrended correspondence analysis based on grasshopper species composition for 128 sites across Montana in 1993. Species abbreviation codes are given in Table 7.

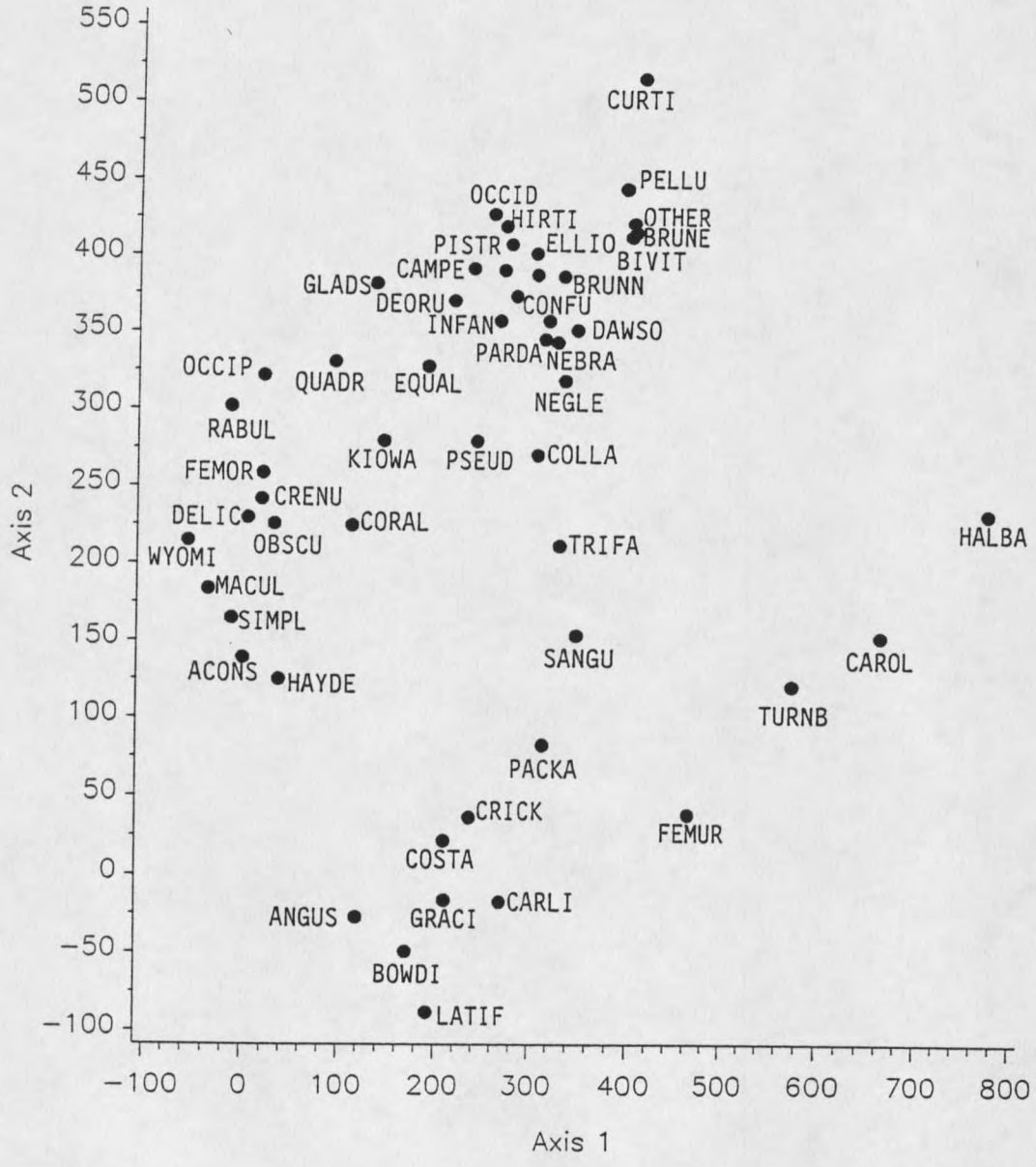
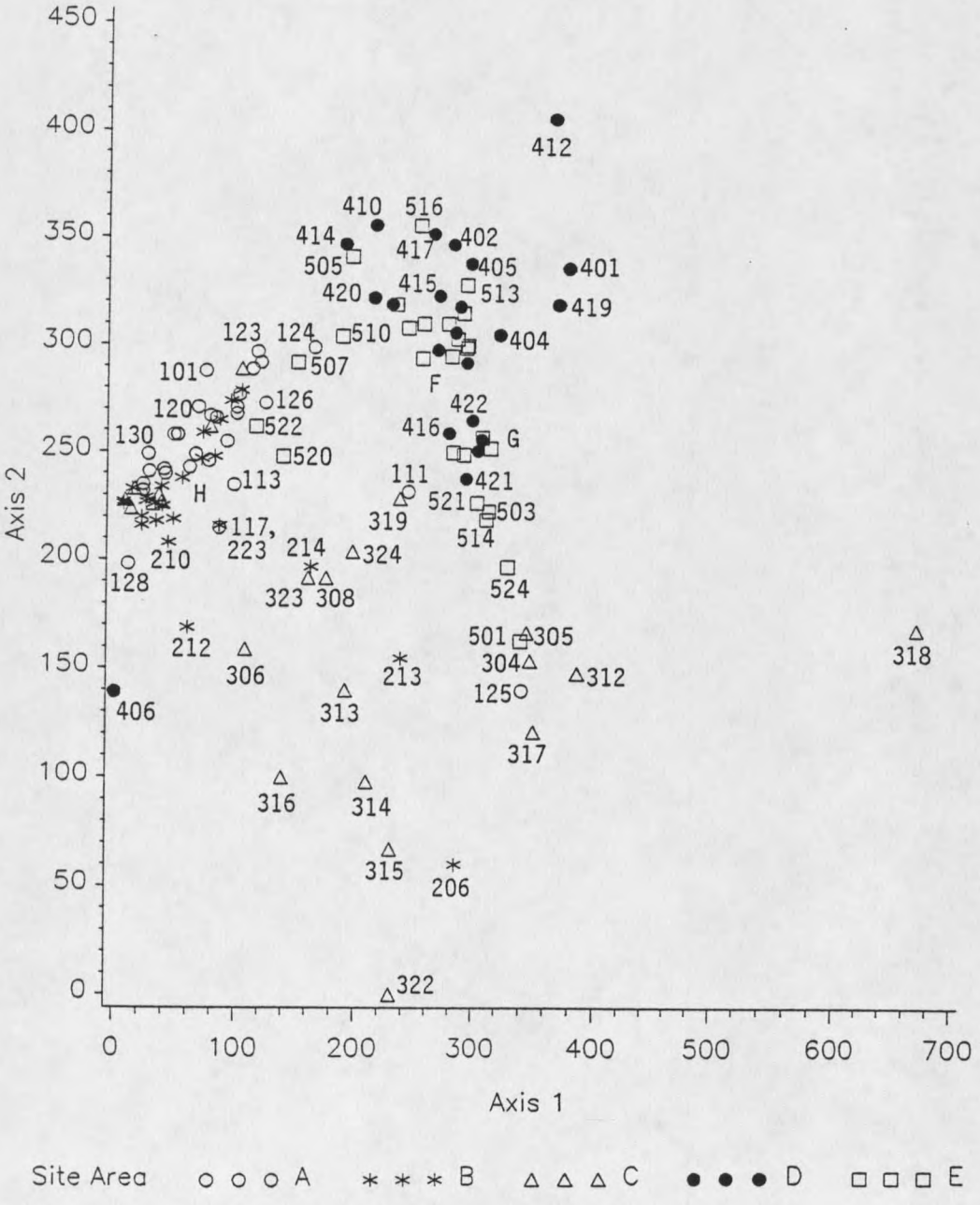


Figure 36. Results of detrended correspondence analysis based on grasshopper species composition for 128 sites across Montana in 1993. "A", "B", and "C" refer to vegetation types at the Jordan sampling area; "D" refers to Madison area sites; and "E" refers to Big Timber area sites. Unlabeled sites near "F" include 403, 407, 408, 411, 504, 508, 509, 511, 512, 517, 519, 523, 525; near "G" are 409, 413, 502, 515, 518, 526; near "H" are 103, 104, 106-109, 112, 114-116, 118, 122, 129, 130, 201-205, 207-209, 211, 215-222, 224, 225, 301-303, 307, 309-311, 320, 321, 325.



differences in grasshopper communities between the plains area of Jordan and the mountain/transition areas of Madison and Big Timber.

Differences in mean grasshopper densities between the sampling areas (hypothesis 5) were tested by pairwise *t*-tests. The results are shown in Table 9. No significant differences in grasshopper numbers (at $\alpha=0.01$ level) were found between any of the sampling areas.

Ecoregions

The null hypothesis that ecoregions do not differ in plant species composition (hypothesis 2) was tested with the same DCA used to test hypothesis 1. Because the eigenvalues are high for this DCA (0.632 for the first two axes), the null hypothesis was rejected. Figure 37 shows the DCA plot of sites by ecoregion. Because there is only one site in ecoregion 17 (Middle Rockies), generalizations about this ecoregion could not be made from the plot, although this site was closer to other mountain-area sites than to plains sites. The fact that ecoregion 42 (Northwestern Glaciated Plains) and 43 (Northwestern Great Plains) sites had generally low axis 2 scores indicates a gradient on axis 2 from plains sites to mountain sites. Ecoregion 43 overlaps ecoregions 16 (Montana Valley and Foothill Prairies) and 42 on both axes. Ecoregion 43 may be a transitional ecoregion, having some plains attributes and some mountain attributes, given the fact that it is adjacent to both mountain and plains ecoregions.

The null hypothesis that ecoregions do not differ in grasshopper species composition (hypothesis 4) was tested using the same DCA as for hypothesis 2. The very high eigenvalues resulted in rejecting the null. Figure 38 shows the DCA plot for

Table 9. Results of pairwise *t*-tests for differences in mean grasshopper abundance between the Jordan, Madison, and Big Timber sampling areas of Montana, 1993.

Area	N	Mean	S.D.*	Variances	*t*	D.F.	Prob > |*t*|
Jordan	80	66.66	69.58	Unequal	-1.6539	25.8	0.1103
Madison	22	107.55	110.05	Equal	-2.1282	100.0	0.0358
For H_o: Variances are equal, F'=2.50, DF=(21,79), Prob>F'=0.0037							
Jordan	80	66.66	69.58	Unequal	-1.9702	29.3	0.0583
Big Timber	26	121.73	136.89	Equal	-2.64968	104.0	0.0082
For H_o: Variances are equal, F'=3.87, DF=(25,79), Prob>F'=0.0000							
Madison	22	107.55	110.05	Unequal	-0.3978	45.9	0.6926
Big Timber	26	121.73	136.89	Equal	-0.3906	46.0	0.6979
For H_o: Variances are equal, F'=1.55, DF=(25,21), Prob>F'=0.3131							

sites, coded by ecoregion. Here the site in ecoregion 17 is closer to sites in ecoregion 43 than those in 16, in contrast with Figure 37. Again, ecoregion 43 appears to be transitional, as sites in 43 overlap those in ecoregions 42 and 16, although all sites with low axis 2 scores are in ecoregion 43. Sites in ecoregion 43 that overlap 16 and 42 in Figure 37 are not consistently closer to the ecoregion boundaries than are other sites.

The sixth hypothesis tested was that ecogregions do not differ in mean grasshopper abundance. The results of the pairwise *t*-tests are given in Table 10. At the α=0.05 level of significance, mean grasshopper numbers were significantly different between Jordan and Big Timber sites within ecoregion 43, between ecoregions 42 and 43 (at Jordan and over all sampling areas), and between ecoregions 16 and 43 (over all

Figure 37. Results of detrended correspondence analysis based on plant species composition for 128 sites across Montana in 1993. Ecoregion 16 is Montana Valley and Foothill Prairies, 17 is Middle Rockies, 42 is Northwestern Glaciated Plains, and 43 is Northwestern Great Plains. Site numbers are as in Figure 34.

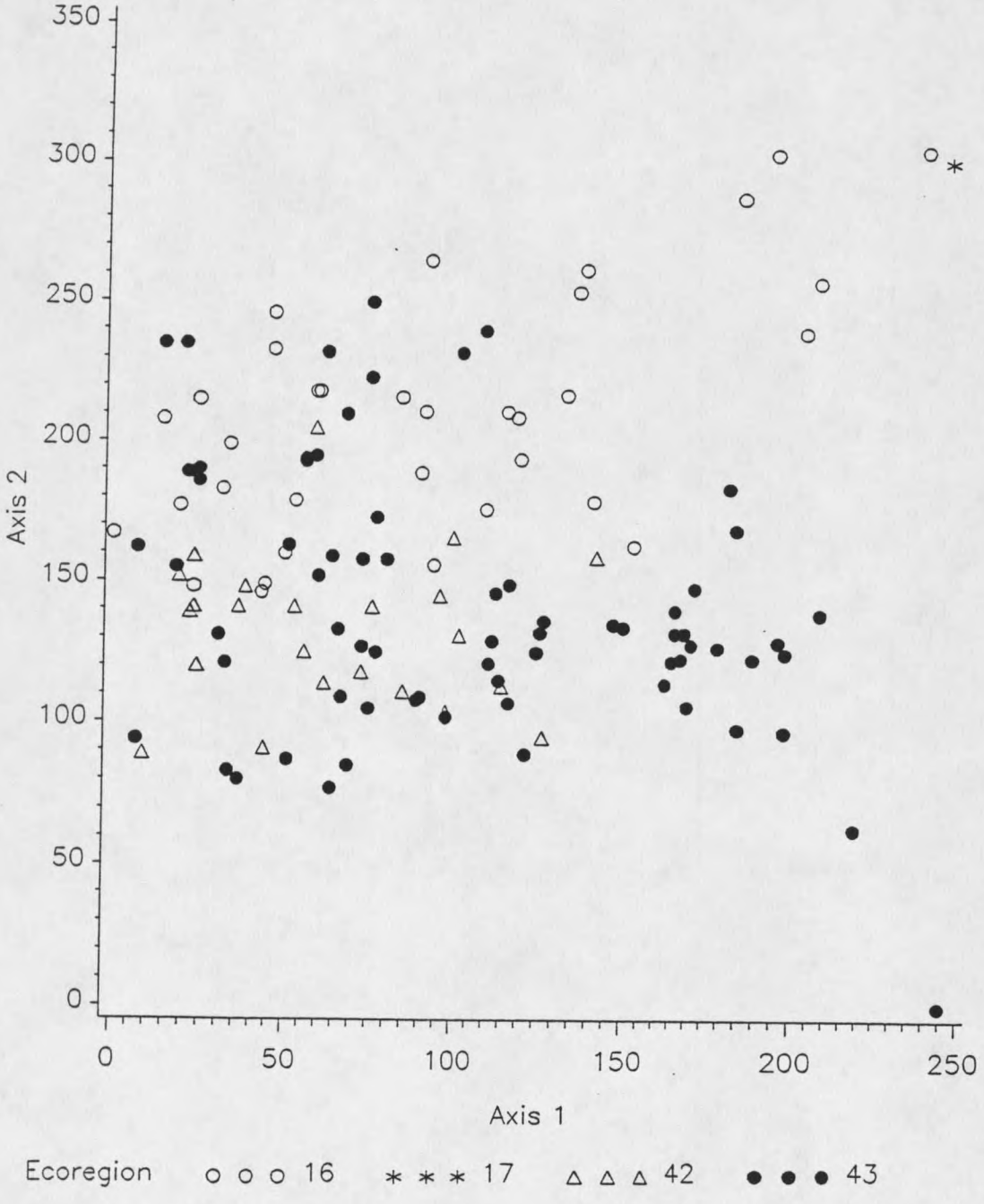


Figure 38. Results of detrended correspondence analysis based on grasshopper species composition for 128 sites across Montana in 1993. Ecoregion 16 is Montana Valley and Foothill Prairies, 17 is Middle Rockies, 42 is Northwestern Glaciated Plains, and 43 is Northwestern Great Plains. Site numbers are as in Figure 36.

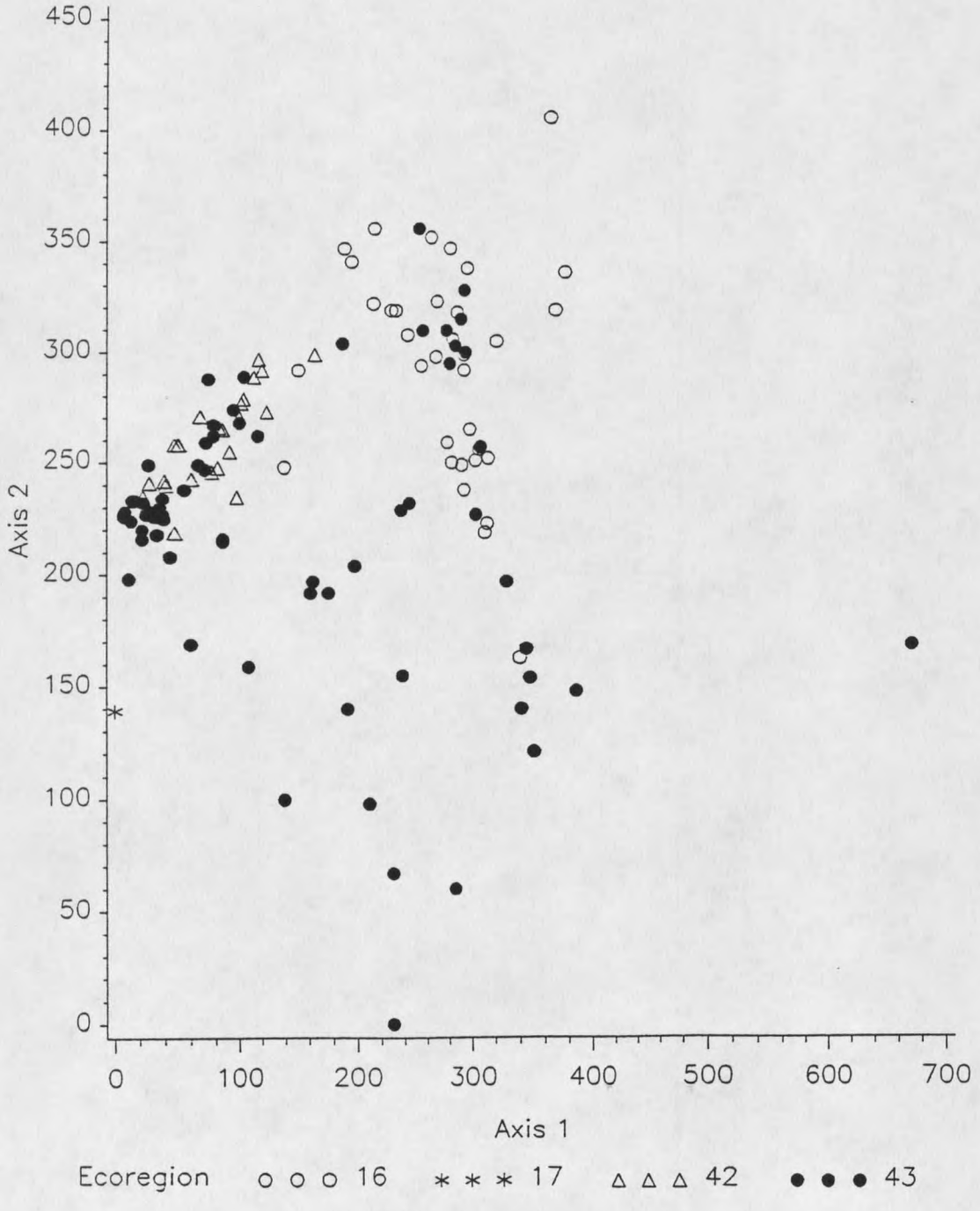


Table 10. Results of pairwise *t*-tests for differences in mean grasshopper abundance between ecoregions at the Jordan, Madison, and Big Timber sampling areas of Montana, 1993.

Area	Ecoregion	N	Mean	S.D.*	Variances	*t*	D.F.	Prob > |*t*|
Madison	16	21	112.62	110.10	Unequal	-0.3552	18.0	0.7266
Big Timber	16	13	131.85	174.90	Equal	-0.3948	32.0	0.6956
For H_o: Variances are equal, F' = 2.52, DF = (12,20), Prob > F' = 0.0650								
Jordan	43	57	52.65	57.95	Unequal	-2.2415	14.3	0.0414[2]
Big Timber	43	13	111.62	90.72	Equal	-2.9540	68.0	0.0043
For H_o: Variances are equal, F' = 2.45, DF = (12,56), Prob > F' = 0.0242								
Big Timber	16	13	131.85	174.90	Unequal	0.3702	18.0	0.7155
Big Timber	43	13	111.62	90.72	Equal	0.3702	24.0	0.7145
For H_o: Variances are equal, F' = 3.72, DF = (12,12), Prob > F' = 0.0311								
Jordan	42	23	101.39	84.05	Unequal	2.5475	30.8	0.0161[1]
Jordan	43	57	52.65	57.95	Equal	2.9734	78.0	0.0039
For H_o: Variances are equal, F' = 2.10, DF = (22,56), Prob > F' = 0.0263								
All	16	34	119.97	136.24	Unequal	0.6361	54.6	0.5274
All	42	23	101.39	84.05	Equal	0.5824	55.0	0.5627
For H_o: Variances are equal, F' = 2.63, DF = (33,22), Prob > F' = 0.0205								
All	42	23	101.39	84.05	Unequal	1.9537	32.2	0.0595
All	43	70	63.60	68.49	Equal	2.1672	91.0	0.0328[2]
For H_o: Variances are equal, F' = 1.51, DF = (22,69), Prob > F' = 0.2023								
All	16	34	119.97	136.24	Unequal	2.2270	41.3	0.0280[2]
All	43	70	63.60	68.49	Equal	2.8149	102.0	0.0059
For H_o: Variances are equal, F' = 3.96, DF = (33,69), Prob > F' = 0.0000								

*Standard Deviation.
[1]Significant at $\alpha = 0.01$ level.
[2]Significant at $\alpha = 0.05$ level.

sampling areas). Significant differences in abundance were not found between the Madison and Big Timber sampling areas. In the Big Timber area, sites in ecoregion 16 were not significantly different from sites in ecoregion 43 with respect to grasshopper abundance, so distinguishing between ecoregions has no meaning for grasshoppers there. When the Madison area sites in ecoregion 16 were included in the test, there were still no differences between ecoregions 16 and 42. If there is a gradient in grasshopper species across the three sampling areas, as supported by DCA eigenvalues and Figure 38, it affects overall abundance most in ecoregion 43 at Jordan. This conclusion is confirmed by the fact that all ecoregion 43 sites which do not overlap other ecoregions in Figure 38 are located at Jordan.

Correlations

Hypothesis 7 stated that no correlations exist between proportions of grasses, forbs, and other plants and DCA scores based on percent cover of individual plant species. The results of the Spearman correlations (Table 11) show significant positive correlations between axis 1 and both forbs and "other" plants, while grasses were negatively correlated with that axis. Axis 2 was negatively correlated with grasses and positively correlated with "other" plants (see also Figure 33).

Grasshopper axes 1 and 2 are correlated, and thus are not independent. This could result if axis 1 and 2 are both correlated with or are gradients of the same environmental or plant variables. The results of correlations between DCA of plant species and proportions of grasses, forbs, and other plants suggests that this is the case, since both axes 1 and 2 are correlated with grasses and "other" plants. As a result, the

Table 11. Spearman rank correlations on axis scores from plant and grasshopper community DCAs. "Grasses" refers to the proportion of cover by grass species, "forbs" refers to the proportion of cover by forb species, and "other" refers to the proportion of cover by plants which were not identified to species. "GH" refers to grasshopper site DCA axis scores and "PL" refers to plant site DCA axis scores.

Correlation on	N	r_s	P-value*
DCA axis scores for plant sites			
Axis 1 by axis 2	128	-0.069	$0.20<P<0.50$
Axis 1 by grasses	128	-0.590	$P<0.001$[1]
Axis 2 by grasses	128	-0.186	$0.02<P<0.05$[2]
Axis 1 by forbs	128	0.522	$P<0.001$[1]
Axis 2 by forbs	128	0.015	$P>0.50$
Axis 1 by other	44	0.669	$P<0.001$[1]
Axis 2 by other	44	0.439	$0.002<P<0.005$[1]
DCA axis scores for grasshopper sites			
Axis 1 by axis 2	125	0.237	$0.005<P<0.01$[1]
Axis 1 by grasses	125	-0.387	$P<0.001$[1]
Axis 2 by grasses	125	-0.001	$P>0.50$
Axis 1 by forbs	125	0.282	$0.001<P<0.002$[1]
Axis 2 by forbs	125	-0.090	$0.20<P<0.50$
Axis 1 by other	44	0.162	$0.20<P<0.50$
Axis 2 by other	44	-0.206	$0.10<P<0.20$
DCA axis scores for plant and grasshopper sites			
GH axis 1 by PL axis 1	125	0.310	$P<0.001$[1]
GH axis 1 by PL axis 2	125	0.421	$P<0.001$[1]
GH axis 2 by PL axis 1	125	-0.372	$P<0.001$[1]
GH axis 2 by PL axis 2	125	0.416	$P<0.001$[1]

*Two-tailed P-values for $a=0.05$, $N\leq 100$ were taken from Table D.24 and P-values for $a=0.05$, $N>100$ from Table D.21 of J.H. Zar, 1974.

[1]Significant at $\alpha=0.01$ level.

[2]Significant at $\alpha=0.05$ level.

correlations between grasshopper axes and plant form or plant DCA scores are not reliable (Gauch 1982). Hypotheses 8 and 9 could not be tested, but correlation results are given in Table 11.

Spearman rank correlations were conducted on grasshopper species proportions and percent cover by selected plant species. Significant positive correlations were found between *Agropyron* spp. and *Melanoplus packardii*; between *Koeleria cristata* and both *Melanoplus infantilis* and *Melanoplus sanguinipes*; and between *Poa* spp. and *Ageneotettix deorum*, *Melanoplus infantilis*, and *Opeia obscura*. Negative correlations exist between *Bouteloua gracilis* and *Melanoplus sanguinipes* and between *Stipa* spp. and both *Melanoplus gladstoni* and *Xanthippus corallipes* (Table 12). Hypothesis 15, that no correlations exist between grasshopper and plant species, was thus rejected.

STATSGO

Hypothesis 10, that no correlations exist between Montana STATSGO attributes and plant species composition, was tested using Spearman correlations. Significant positive correlations were found between PERM and both *Koeleria cristata* and *Stipa* spp., while PERM was negatively correlated with *Agropyron* spp. There were no significant correlations between AWC and any plant species or genus (Table 13). Thus, null hypothesis 10 was rejected for PERM but could not be rejected for AWC.

Spearman rank correlations were also used to test for correlations between Montana STATSGO attributes and grasshopper species composition (hypothesis 11). There were significant negative correlations between AWC and *Ageneotettix deorum*, *Amphitornus coloradus*, *Melanoplus infantilis*, *Melanoplus packardii*, and *Melanoplus*

Table 12. Spearman rank correlation between selected plant species and selected grasshopper species. Plant species codes are given in Table 6 and grasshopper species codes are given in Table 7.

Correlation on	r_s	N	*t*	*P*-value*
AGROS by CLAVA	0.078	37	0.46137	0.6474
AGROS by COLOR	-0.042	39	-0.25546	0.7998
AGROS by CORAL	0.025	69	0.20463	0.8384
AGROS by DELIC	0.207	71	1.71836	0.0902
AGROS by DEORU	-0.187	51	-1.30803	0.1970
AGROS by ELLIO	-0.144	22	-0.64331	0.5274
AGROS by GLADS	-0.047	61	-0.36100	0.7194
AGROS by INFAN	-0.191	75	-1.63106	0.1072
AGROS by KIOWA	0.007	71	0.05815	0.9538
AGROS by OBSCU	0.019	56	0.13962	0.8894
AGROS by PACKA	0.384	35	2.19432	0.0354[2]
AGROS by PELLU	0.156	18	0.62303	0.5420
AGROS by SANGU	0.093	79	0.81598	0.4170
BOGR by COLOR	-0.294	27	-1.46443	0.1556
BOGR by CLAVA	-0.120	33	-0.66782	0.5088
BOGR by CORAL	0.114	62	0.88285	0.3808
BOGR by DELIC	0.104	65	0.82533	0.4122
BOGR by DEORU	-0.148	45	-0.97000	0.3374
BOGR by ELLIO	-0.235	16	-0.87561	0.3960
BOGR by GLADS	0.212	55	1.54201	0.1290
BOGR by INFAN	-0.259	61	-1.98699	0.0516
BOGR by KIOWA	-0.012	66	-0.09600	0.9238
BOGR by OBSCU	-0.116	54	-0.83627	0.4068
BOGR by PACKA	-0.332	25	-1.58362	0.1270
BOGR by PELLU	-0.100	9	-0.26419	0.7992
BOGR by SANGU	-0.327	64	-2.56982	0.0126[2]
CAREX by CLAVA	-0.272	16	-1.01191	0.3288
CAREX by COLOR	-0.028	19	-0.11544	0.9094
CAREX by CORAL	0.232	34	1.31006	0.1996
CAREX by DELIC	0.043	35	0.24700	0.8064
CAREX by DEORU	-0.190	28	-0.96742	0.3422
CAREX by ELLIO	0.407	8	0.96339	0.3726
CAREX by GLADS	-0.027	37	-0.15973	0.8740
CAREX by INFAN	-0.002	35	-0.01149	0.9910

Table 12. Continued next page.

Table 12. Continued.

Correlation on	r_s	N	*t*	*P*-value*
CAREX by KIOWA	-0.113	32	-0.61866	0.5408
CAREX by OBSCU	-0.119	30	-0.62937	0.5342
CAREX by PACKA	0.196	16	0.73127	0.4766
CAREX by PELLU	-0.718	5	-0.67041	0.5506
CAREX by SANGU	-0.131	35	-0.75214	0.4572
FEID by CLAVA	1.000	3	-.-----	-.----
FEID by COLOR	--.---	2	-.-----	-.----
FEID by CORAL	--.---	0	-.-----	-.----
FEID by DELIC	--.---	1	-.-----	-.----
FEID by DEORU	--.---	0	-.-----	-.----
FEID by ELLIO	--.---	1	-.-----	-.----
FEID by GLADS	--.---	2	-.-----	-.----
FEID by INFAN	0.800	4	-.-----	-.----
FEID by KIOWA	--.---	1	-.-----	-.----
FEID by OBSCU	--.---	0	-.-----	-.----
FEID by PACKA	1.000	3	-.-----	-.----
FEID by PELLU	0.800	4	-.-----	-.----
FEID by SANGU	0.300	5	0.50219	0.6500
KOCR by CLAVA	-0.091	34	-0.51464	0.6104
KOCR by COLOR	0.128	30	0.67691	0.5040
KOCR by CORAL	-0.380	27	-1.88713	0.0708
KOCR by DELIC	-0.254	26	-1.24076	0.2266
KOCR by DEORU	-0.067	38	-0.40195	0.6900
KOCR by ELLIO	-0.062	19	-0.25557	0.8014
KOCR by GLADS	-0.224	37	-1.32320	0.1944
KOCR by INFAN	0.365	55	2.64952	0.0106[2]
KOCR by KIOWA	-0.027	35	-0.15510	0.8776
KOCR by OBSCU	-0.189	18	-0.75425	0.4616
KOCR by PACKA	-0.021	28	-0.10708	0.9156
KOCR by PELLU	-0.143	16	-0.53426	0.6016
KOCR by SANGU	0.357	46	2.36020	0.0228[2]
POAS by CLAVA	0.242	28	1.23101	0.2294
POAS by COLOR	-0.131	30	-0.69275	0.4942
POAS by CORAL	0.081	51	0.56692	0.5734
POAS by DELIC	-0.002	47	-0.01342	0.9894
POAS by DEORU	0.394	34	2.21596	0.0340[2]

Table 12. Continued next page.

Table 12. Continued.

Correlation on	r_s	N	*t*	*P*-value*
POAS by ELLIO	-0.082	17	-0.31744	0.7552
POAS by GLADS	-0.131	45	-0.85868	0.3952
POAS by INFAN	0.274	58	2.04745	0.0454[2]
POAS by KIOWA	0.206	52	1.45535	0.1518
POAS by OBSCU	0.458	37	2.68894	0.0110[2]
POAS by PACKA	-0.371	27	-1.84312	0.0772
POAS by PELLU	0.374	16	1.38303	0.1884
POAS by SANGU	0.049	58	0.36667	0.7152
STIPA by CLAVA	-0.139	38	-0.83354	0.4098
STIPA by COLOR	0.101	39	0.61419	0.5428
STIPA by CORAL	-0.310	51	-2.16529	0.0352[2]
STIPA by DELIC	0.167	56	1.22654	0.2254
STIPA by DEORU	0.221	47	1.48082	0.1456
STIPA by ELLIO	0.246	22	1.09660	0.2858
STIPA by GLADS	-0.343	57	-2.53758	0.0410[2]
STIPA by INFAN	0.184	70	1.51652	0.1340
STIPA by KIOWA	0.147	58	1.09961	0.2762
STIPA by OBSCU	0.005	45	0.03279	0.9740
STIPA by PACKA	-0.176	32	-0.96296	0.3432
STIPA by PELLU	-0.240	19	-0.98598	0.3380
STIPA by SANGU	0.138	71	1.14599	0.2558
PHHO by CLAVA	-0.378	24	-1.75949	0.0924
PHHO by COLOR	-0.010	22	-0.04472	0.9648
PHHO by CORAL	-0.008	39	-0.04866	0.9614
PHHO by DELIC	-0.065	35	-0.37335	0.7112
PHHO by DEORU	0.004	32	0.02191	0.9826
PHHO by ELLIO	-0.303	11	-0.89873	0.3922
PHHO by GLADS	-0.137	39	-0.83291	0.4102
PHHO by INFAN	0.197	46	1.30555	0.1984
PHHO by KIOWA	-0.076	37	-0.44955	0.6558
PHHO by OBSCU	-0.257	26	-1.25532	0.2214
PHHO by PACKA	0.069	20	0.29266	0.7732
PHHO by PELLU	-0.643	7	-1.21835	0.2774
PHHO by SANGU	0.134	42	0.84710	0.4020
ARTEM by CLAVA	0.025	35	0.14361	0.8866
ARTEM by COLOR	-0.013	36	-0.07580	0.9400

Table 12. Continued next page.

Table 12. Continued.

Correlation on	r_s	N	*t*	*P*-value*
ARTEM by CORAL	0.233	50	-1.61234	0.1134
ARTEM by DELIC	-0.008	52	-0.05657	0.9552
ARTEM by DEORU	-0.064	48	-0.43403	0.6662
ARTEM by ELLIO	-0.225	20	-0.95176	0.3538
ARTEM by GLADS	0.114	54	0.82186	0.4150
ARTEM by INFAN	0.190	67	1.53095	0.1306
ARTEM by KIOWA	-0.127	59	-0.95855	0.3418
ARTEM by OBSCU	0.053	40	0.32669	0.7456
ARTEM by PACKA	-0.021	33	-0.11692	0.9076
ARTEM by PELLU	0.081	18	0.32387	0.7502
ARTEM by SANGU	0.072	65	0.57144	0.5698

*P-values were calculated using SAS programs.
[1]Significant at $\alpha=0.01$ level.
[2]Significant at $\alpha=0.05$ level.

sanguinipes; and between PERM and *Xanthippus corallipes*. AWC was positively correlated with *Melanoplus gladstoni* and PERM was positively correlated with *Ageneotettix deorum*, *Aulocara elliotti*, and *Melanoplus infantilis* (Table 14). Null hypothesis 11 was rejected.

No significant correlations were found between MTSTATSGO plant production values and plant cover as measured at sampling sites (Table 15). Thus, null hypothesis 14 could not be rejected. The lack of any significant correlations indicates that MTSTASGO plant data do not correlate with plant cover on the ground, and should not be used for indications of the vegetation of an area, even at a statewide scale.

Kruskal-Wallis tests were used to look for correlations between MTSTATSGO soil attributes and ecoregion (hypothesis 12). Significant differences were found for both

Table 13. Spearman rank correlations on STATSGO soil attribute values and proportions of plant species. "AWC" is the average available water capacity and "PERM" is the average soil permeability rate for the mapping unit in which a given site is located. Plant species and genera codes are given in Table 6.

Correlation on	N	r_s	*P*-value*
AWC by PERM	31	0.021	$P>0.50$
AWC by AGROS	125	-0.028	$P>0.50$
AWC by ARTEM	102	0.012	$P>0.50$
AWC by BOGR	97	0.186	$0.05<P<0.10$
AWC by CAREX	50	0.034	$P>0.50$
AWC by FEID	7	0.109	$P>0.50$
AWC by KOCR	68	-0.081	$P>0.50$
AWC by PHHO	60	0.062	$P>0.50$
AWC by POAS	96	0.012	$P>0.50$
AWC by STIPA	97	-0.093	$0.20<P<0.50$
PERM by AGROS	125	-0.507	$P<0.001$[1]
PERM by ARTEM	102	-0.150	$0.10<P<0.20$
PERM by BOGR	97	0.192	$0.05<P<0.10$
PERM by CAREX	50	-0.165	$0.20<P<0.50$
PERM by FEID	7	-0.509	$0.20<P<0.50$
PERM by KOCR	68	0.384	$0.001<P<0.002$[1]
PERM by PHHO	60	0.113	$0.20<P<0.50$
PERM by POAS	96	0.115	$0.20<P<0.50$
PERM by STIPA	97	0.341	$P<0.001$[1]

*Two-tailed *P*-values for $a=0.05$, $N\leq 100$ were taken from Table D.24 and *P*-values for $a=0.05$, $N>100$ from Table D.21 of J.H. Zar, 1974.
[1]Significant at $\alpha=0.01$ level.

AWC and PERM over the four ecoregions (Table 16). Subsequent pairwise tests found significant differences between values of both AWC and PERM for all pairs of ecoregions (Table 17), although ecoregion 17 was omitted from testing because of sample size n=1.

Table 14. Spearman rank correlations on STATSGO soil attribute values and proportions of grasshopper species. "AWC" is the average available water capacity and "PERM" is the average soil permeability rate for the mapping unit in which a given site is located. Grasshopper species codes are listed in Table 7.

Correlation on	N	r_s	P-value*
AWC by PERM	31	0.021	$P>0.50$
AWC by CLAVA	38	-0.148	$0.20<P<0.50$
AWC by COLOR	40	-0.429	$0.005<P<0.01$[1]
AWC by CORAL	69	0.191	$0.10<P<0.20$
AWC by DELIC	71	-0.006	$P>0.50$
AWC by DEORU	52	-0.331	$0.01<P<0.02$[2]
AWC by ELLIO	22	-0.049	$P>0.50$
AWC by GLADS	62	0.269	$0.02<P<0.05$[2]
AWC by INFAN	76	-0.315	$0.005<P<0.001$[1]
AWC by KIOWA	71	-0.056	$P>0.50$
AWC by OBSCU	61	-0.061	$P>0.50$
AWC by PACKA	35	-0.390	$0.02<P<0.05$[2]
AWC by PELLU	19	-0.240	$0.20<P<0.50$
AWC by SANGU	97	-0.453	$P<0.001$[1]
PERM by CLAVA	38	0.037	$P>0.50$
PERM by COLOR	40	0.183	$0.20<P<0.50$
PERM by CORAL	69	-0.339	$0.005<P<0.01$[2]
PERM by DELIC	71	-0.161	$P>0.50$
PERM by DEORU	52	0.302	$0.02<P<0.05$[2]
PERM by ELLIO	22	0.464	$0.02<P<0.15$[2]
PERM by GLADS	62	0.002	$P>0.50$
PERM by INFAN	76	0.362	$0.001<P<0.002$[1]
PERM by KIOWA	71	0.017	$P>0.50$
PERM by OBSCU	61	-0.242	$0.05<P<0.10$
PERM by PACKA	35	-0.256	$0.10<P<0.20$
PERM by PELLU	19	-0.251	$0.20<P<0.50$
PERM by SANGU	97	0.150	$0.10<P<0.20$

*Two-tailed P-values for $a=0.05$, $N\leq 100$ were taken from Table D.24 and P-values for $a=0.05$, $N>100$ from Table D.21 of J.H. Zar, 1974.

[1]Significant at $\alpha=0.01$ level.

[2]Significant at $\alpha=0.05$ level.

Table 15. Spearman rank correlations between selected MTSTATSGO plant species proportions and percent cover of selected plant species collected at sampling sites. MTSTATSGO values are listed as "AGROS1", etc. while site values are listed as "AGROS2", etc. Plant species and genera codes are listed in Table 6.

Correlation on	r_s	N	*P*-value*
AGROS1 by AGROS2	-0.135	126	$0.10<P<0.20$
BOGR1 by BOGR2	0.012	29	$P>0.50$
CAREX1 by CAREX2	-0.097	40	$P>0.50$
FEID1 by FEID2	0.327	7	$0.20<P<0.50$
POAS1 by POAS2	0.118	57	$0.20<P<0.50$
STIPA1 by STIPA2	0.149	97	$0.10<P<0.20$
PHHO1 by PHHO2	-.--	0	---
ARTEM1 by ARTEM2	-0.096	92	$0.20<P<0.50$

*Two-tailed *P*-values for $a=0.05$, $N\leq 100$ were taken from Table D.24 and *P*-values for $a=0.05$, $N>100$ from Table D.21 of J.H. Zar, 1974.

Table 16. Kruskal-Wallis test results for MTSTATSGO soil attributes and ecoregion. Wilcoxon scores are rank sums and average scores were used for ties.

Wilcoxon Scores for Available Water Capacity (AWC)

Ecoregion	N	Sum of Scores	Expected Under H0	Std Dev Under H0	Mean Score
43	70	4163.00	4515.00	207.815906	59.471429
42	23	2458.00	1483.50	160.278155	106.869565
16	34	1542.50	2193.00	184.382268	45.367647
17	1	92.50	64.50	36.755102	92.500000

Kruskal-Wallis Test (Chi-Square Approximation)
CHISQ = 41.341 DF = 3 Prob > CHISQ = 0.0001*

Wilcoxon Scores for Permeability Rate (PERM)

Ecoregion	N	Sum of Scores	Expected Under H0	Std Dev Under H0	Mean Score
43	70	3039.00	4515.00	207.815906	43.414286
42	23	1468.00	1483.50	160.278155	63.826087
16	34	3635.50	2193.00	184.382268	106.926471
17	1	113.50	64.50	36.755102	113.500000

Kruskal-Wallis Test (Chi-Square Approximation)
CHISQ = 69.577 DF = 3 Prob > CHISQ = 0.0001*

*Significant at α=0.01 level.

Table 17. Wilcoxon 2-sample test results for MTSTATSGO soil attributes and ecoregion. Sample sizes for ecoregions are as follows: for ecoregion 16, n=34; for 42, n=23; and for 43, n=70. Values given within the table are probabilities from the Normal approximation with continuity correction of 0.5.

Values for pairwise tests of AWC classified by ecoregion

Ecoregion	16	42	43
16	---		
42	0.0001*	---	
43	0.0437**	0.0001*	---

Values for pairwise tests of PERM classified by ecoregion

Ecoregion	16	42	43
16	---		
42	0.0001*	---	
43	0.0001*	0.0019*	---

*Significant at α=0.01 level.
**Significant at α=0.05 level.

A second set of Kruskal-Wallis tests for hypothesis 13, correlating MTSTATSGO attributes with sampling area, resulted in significant differences among the sampling areas for both AWC and PERM (Table 18). Pairwise tests found differences between values of AWC for sampling area A with areas C, D, and E; and for area B with areas C, D, and E. Values of PERM were different for all pairs of sampling areas (Table 19).

Table 18. Kruskal-Wallis test results on MTSTATSGO soil attributes and sampling area. Wilcoxon scores are rank sums and average scores were used for ties.

Wilcoxon Scores for Available Water Capacity (AWC)

Area	N	Sum of Scores	Expected Under H0	Std Dev Under H0	Mean Score
A	30	2671.00	1935.00	176.843635	89.0333333
B	25	2037.50	1612.50	165.502434	81.5000000
C	25	1228.00	1612.50	165.502434	49.1200000
D	22	1066.00	1419.00	157.499813	48.4545455
E	26	1253.50	1677.00	167.958709	48.2115385

Kruskal-Wallis Test (Chi-Square Approximation)
CHISQ = 32.137 DF = 4 Prob > CHISQ = 0.0001*

Wilcoxon Scores for Permeability Rate (PERM)

Area	N	Sum of Scores	Expected Under H0	Std Dev Under H0	Mean Score
A	30	1663.00	1935.00	176.843635	55.433333
B	25	1171.50	1612.50	165.502434	46.860000
C	25	616.00	1612.50	165.502434	24.640000
D	22	2532.00	1419.00	157.499813	115.090909
E	26	2273.50	1677.00	167.958709	87.442308

Kruskal-Wallis Test (Chi-Square Approximation)
CHISQ = 88.103 DF = 4 Prob > CHISQ = 0.0001*

*Significant at α=0.01 level.

Table 19. Wilcoxon 2-sample test results on MTSTATSGO soil attributes and sampling area. Sampling areas A, B, and C are vegetation types at the Jordan area, while D is the Madison sampling area and E is the Big Timber sampling area. Sample sizes are as follows: for area A, n=30; for B, n=25; for C, n=25; for D, n=22; and for E, n=26. Values given within the table are probabilities from the Normal approximation with continuity correction of 0.5.

Values for pairwise tests of AWC classified by sampling area

Area	A	B	C	D	E
A	-----				
B	0.0994	-----			
C	0.0001*	0.0017*	-----		
D	0.0010*	0.0010*	0.9914	-----	
E	0.0001*	0.0001*	0.9621	0.5651	-----

Values for pairwise tests of PERM classified by sampling area

Area	A	B	C	D	E
A	-----				
B	0.0338**	-----			
C	0.0001*	0.0002*	-----		
D	0.0001*	0.0001*	0.0001*	-----	
E	0.0001*	0.0001*	0.0001*	0.0001*	-----

*Significant at α=0.01 level.
**Significant at α=0.05 level.

Discussion

Sampling Areas

DCA results showed that the three geographic areas of Montana differ in plant species composition (Figure 34). This supports the distinctions in climax vegetation made by Ross and Hunter (1976) and ecoregions outlined by Omernik (1987). The sampling areas also differ in grasshopper species composition, supporting the previous small-scale assertions that grasshopper communities are not homogeneous across Montana (Anderson 1964, Kemp et al. 1989, Kemp 1992a) and should not be treated as such for management purposes.

Results show that Jordan sites were different from the Madison and Big Timber sites (Figures 34 and 36). The sites near Jordan are thus distinct from the other sampling areas in both plant and grasshopper communities, indicating important environmental differences between plains and mountain valley sites. I expected the Big Timber sites to be transitional, having characteristics of both plains and mountain areas, but either there is a qualitative difference between plains and mountain sites, rather than a gradient in species composition, or the sites near Big Timber do not represent the gradient well.

The ordination of grasshopper species (Figure 35) was similar to the results of Kemp et al. (1990b). *Aeropedellus clavatus*, *Arphia conspersa*, and *Psoloessa delicatula* were at the edges of the DCA plot, while *Melanoplus packardii* was in the middle. While the study of Kemp et al. (1990b) covered a smaller spatial area than this research, the similar positions of these species in the two community analyses indicates their

comparable role and importance in the two studies. However, *Ageneotettix deorum* and *Arphia pseudonietana* are well-separated and *Hadrotettix trifasciatus* is at the edge of the DCA plot produced by Kemp et al., in contrast with Figure 35. These differences reflect the differences in species composition that distinguish individual communities.

Grasshopper densities were the same over all the sampling areas (Table 9) during 1993, contrary to what might be expected, given the drier conditions of the plains are generally beneficial to grasshopper abundance (Uvarov 1957). However, yearly densities are greatly affected by temperature and precipitation patterns (Edwards 1960, Fielding and Brusven 1990, Gage and Mukerji 1977, Johnson and Worobec 1988), and it is possible that there are not significant differences in the scale studied here to detect grasshopper response to weather patterns. Weather extremes may have suppressed grasshopper populations to a common level, as 1993 was a very wet and cool summer.

Ecoregions

DCA results also showed that the ecoregions differ in both plant and grasshopper species composition (Figures 37 and 38). Thus, Omernik's ecoregions capture the variability of the plant and grasshopper communities across the areas sampled. There is a gradient in the plant community composition between ecoregions 16, 42 and 43 (Figure 37), and there must be some overlap in species composition, since the ecoregions do not cluster separately. Ecoregion 43, Northwestern Great Plains, has plant species in common with both of the other two ecoregions, and can be considered a transitional region between foothill prairies and glaciated plains (Figure 37, Omernik 1987). There was not sufficient data in this study to test whether ecoregion 16 is a transitional

ecoregion between the high mountains of ecoregion 17 (Middle Rockies) and the plains ecoregions.

Grasshopper abundances differed in all tests that included sites in ecoregion 43 (Northwestern Great Plains) at Jordan. Thus, the combination of grassland and grazing land with open hills and tablelands in ecoregion 43 (Omernik 1987) supports lower grasshopper densities than the other ecoregions. Omernik was unable to discern a clear pattern in soils for ecoregion 43 nor land-surface form for ecoregion 16, and the basis for the difference in grasshopper abundance with ecoregion 42 (Northwestern Glaciated Plains) is unclear. It could be due to soils (Gage and Mukerji 1977, Isely 1938, Quinn et al. 1991, Scoggan and Brusven 1973), plant species composition (Anderson 1964, 1973; Anderson and Wright 1952, Evans 1988, Kemp et al. 1990b, Pfadt 1984, Quinn et al. 1991), precipitation and temperature regimes (Capinera and Horton 1989, Edwards 1960, Fielding and Brusven 1990, Gage and Mukerji 1977, Johnson and Worobec 1988, Kemp and Cigliano 1994), the previous year's densities (Kemp 1987, Kemp 1992b), or disturbance (Fielding and Brusven 1993a, 1993b; Joern 1982).

Between ecoregions 16 and 42, grasshopper species composition changes while overall abundance does not (Figure 38, Table 10). This indicates replacement of species across ecoregions 16 and 42, such that the geographic range of a species is determined by habitat characteristics (expressed by ecoregion), while yearly densities are constrained by weather patterns and resource conditions.

Grasshopper communities within each ecoregion are similar, because they ordinated closely in DCA, though ecoregion 43 shows overlap in species composition

with ecoregions 16 and 42 (Figure 38). Omernik's ecoregions are thus good indicators of similarities among grasshopper communities, but this may not hold true for other herbivore insect communities because the sensitivity to spatial patchiness is species-specific (Kemp 1992a, Allen and Hoekstra 1992).

The usefulness of Omernik's ecoregions in Montana may depend on the distance between sampling points and the ecoregion boundary. The resolution of Omernik's ecoregion map may be too coarse to test ecoregion differences within a state. Even very small mistakes in the placement of a boundary on a map of scale 1:7,500,000 means a difference of many kilometers on the ground. Because all the sampling points lie close (0 to 100 km) to at least one ecoregion boundary (Figure 28), differences between ecoregions should not be expected, or at least should be interpreted cautiously. All of the sampling sites may be located in ecotones between ecoregions, though the relative proportions of each type of habitat may differ depending on location. Omernik (1987) stated the appropriate use of his map is to identify attainable resource quality through knowledge of natural spatial patterns. The map identifies changes in the resource over space by combining several indicators of resource quality: soils, topography, and land use. Ecoregion boundaries might be drawn in very different places, depending on the criterion used, but it is interesting that Omernik's map is useful in distinguishing between real communities (Figures 37 and 38) despite its coarse scale.

Correlations

In the DCA of plant communities, axis 1 is correlated with proportions of grasses and forbs (Table 11). There is thus a gradient in plant growth form across the sites

sampled, which may be responsible for differences detected between the ecoregions by DCA (Figure 37). It is not possible to distinguish which ecoregions have more grasses and which have more forbs from DCA, but this could be easily done with statistical tests and could then be incorporated into grasshopper community classification schemes.

Axes 1 and 2 of the DCA on grasshopper communities are correlated. This presents a problem for interpreting which factors underlie the grasshopper community ordination. One disadvantage of DCA is that isolating the causes of such problems is difficult. It may be that both axes are ordinating on a similar environmental variable, but it was not possible to confirm this by examining the raw data.

The results of the Spearman rank correlations between plant and grasshopper species (Table 12) contrast somewhat with host plant reports in the literature. For example, *Melanoplus infantilis* was positively correlated with *Koeleria cristata*, although the main food plants were *Bouteloua gracilis*, *Stipa comata*, and other grasses in North Dakota (Mulkern et al. 1969) and *Carex filifolia*, dry material, and *Agropyron smithii* in southcentral Montana (Anderson and Wright 1952). The correlation may be an indicator of factors other than diet which affect the distribution and abundance of *M. infantilis*, although Isely's (1938) findings would suggest that, as a member of the subfamily Melanoplinae, this species would be distributed according to the availability of food plants.

Ageneotettix deorum was positively correlated with *Poa* spp., contrasting with the preference for *Agropyron smithii* observed by Anderson and Wright (1952). In Idaho, *A. deorum* is common in dry, alkaline or saline sites (Scoggan and Brusven 1973) and

Vickery and Kevan (1985) state that this species prefers sandy soils with little vegetation. This grasshopper frequently reaches high densities in the North Central Great Plains (Mulkern et al. 1969) and Montana (Shotwell 1941). Like *M. infantilis*, *A. deorum* may be distributed according to factors other than food plants, such as available shelter (Isely 1938), with range or abundance limited by the proportion of bare ground to vegetation.

Similarly, *Melanoplus infantilis* was positively correlated with *Poa* spp., although this species was observed by Anderson and Wright (1952) feeding on only *Agropyron smithii* and *Carex filifolia*. In Nebraska, most of the diet for this species consisted of *Bouteloua gracilis* and *Stipa comata* (Mulkern et al. 1969). Again, correlations between grasshopper and plant species may be due to factors other than diet, or the contrasting results may be due to variation in the resolutions and areas covered by different studies.

Agropyron spp. were negatively correlated with *Melanoplus packardii*, which agrees with the characterization of *M. packardii* as a forb feeder by Vickery and Kevan (1985) and Anderson and Wright (1952). This is also consistent with Isely's (1938) finding that food plant distribution is the greatest factor affecting the distribution of Melanopline species. This species reaches high densites in Alberta (Johnson 1989, Smith and Holmes 1977), Missouri (Jones 1939), and Montana (Shotwell 1941), so the proportions of *Agropyron* spp. and forbs could be used as indicators of areas where management efforts should be focused.

Bouteloua gracilis was also negatively correlated with *Melanoplus sanguinipes*, a species positively correlated with *Koeleria cristata*. These results contrast with the finding of Mulkern et al. (1969) that *B. gracilis* represented 22 to 25% of this species'

diet in Kansas and Nebraska. However, this common and numerous grasshopper is highly polyphagous and can tolerate a range of conditions (Anderson and Wright 1952, Banfill and Brusven 1973, Scoggan and Brusven 1973). A negative correlation between *M. sanguinipes* and *B. gracilis* has implications for range management, because grazing regimes impact the proportion of forbs to grasses (Smoliak et al. 1972). Miller and Onsager (1991) found densities of this grasshopper were lowest on a site with low-intensity, short-duration grazing. *M. sanguinipes* is an important economic pest in Alberta (Johnson 1989, Smith and Holmes 1977), Missouri (Jones 1939), and Montana (Kemp 1992b, Shotwell 1941).

Stipa spp. were negatively correlated with *Melanoplus gladstoni*, a mixed (grass and forb) feeder (Mulkern et al 1969) that prefers *Agropyron smithii* in Montana (Anderson and Wright 1952). Because *M. gladstoni* is an economic pest in Montana (Shotwell 1941), this relationship has implications for range management, as discussed for *M. sanguinipes*.

The correlations between economically important grasshopper species in Montana and plant species which are not food plants shows that vegetation may be used as an indicator of habitat that is favorable in some other way for those pests, providing another clue as to where economic species are and are not likely to occur. This information can be used with further data on the relation between grasshopper species and environmental variables in community or population models to predict which species are expected to be abundant given a known set of environmental factors. Additional research is necessary before it will be clear exactly which factors should be included in such models.

STATSGO

Several grasshopper species were correlated with STATSGO soil attribute values. The correlations between economically important species such as *Ageneotettix deorum*, *Melanoplus packardii*, and *Melanoplus sanguinipes* with measures of soil moisture and permeability are important, since soil characteristics are important to oviposition and fecundity (Hewitt 1985). Efforts to categorize and map habitat that is likely to support economically damaging grasshopper communties will be aided by the use of digital soil information such as that available in the STATSGO data base.

The lack of any correlation between STATSGO plant percentages and field measurements (Table 15) shows that the STATSGO values are too coarsely estimated for prediction of the plant community composition, even at the state scale. The STATSGO data are compiled by generalizing soil survey maps and making interpretations for rangeland, crop, and forest uses (Reybold and TeSelle 1989). Thus, the plant cover data from STATSGO was inferred rather than sampled, and caution should be used in the application of STATSGO range production values to plant community classification or analysis. It should be noted that these data usually are not distributed with STATSGO soil data, because of the generality of the range information (M. Hanson, USDA Soil Conservation Service Field Office, Bozeman, Montana; personal communication). Users of STATSGO data who are not familiar with the methods used in compiling the range production data may be unaware of this generality and mistakenly use the data to infer vegetation patterns or trends which are unreliable.

The data user's guide to the STATSGO database states the data can be used for broad land use planning and understanding soil resources at the state or regional scale, although the notation that must be included on hard copy maps suggests that the data could also be used at the watershed scale (USDA-SCS 1991). My conclusion concerning the STATSGO data for Montana is that the soil data are useful and at a level of resolution that captures community variability, but plant values should not be used for even gross approximations of general trends in plant cover.

Summary and Conclusions

The main findings of this study were (1) grasshopper communities vary across geographic areas and ecoregions in Montana and (2) both Omernik's ecoregions and STATSGO soil attributes are useful in distinguishing among grasshopper and plant communities in Montana. The spatial variability of grasshopper communities within a state has implications for grasshopper management efforts, which may have differing results in plains versus mountain valley rangeland. This study also demonstrates that ecoregions and soil characteristics can be used as indicators for community composition, and because these data are more easily and inexpensively acquired than field data, they can be used as input for grasshopper forecasting or decision-making models to tailor management efforts to the local environment. However, caution should be exercised in applying these conclusions across different sampling years, since plant and grasshopper communities vary temporally as well as spatially. More research on grasshopper community dynamics and the influence of fluctuations in the plant resource is needed to clarify these relationships.

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APPENDIX

PLANT AND GRASSHOPPER SPECIES NAMES AND CODES

Plant species names and codes used in analyses for sites in Montana and Colorado, 1992.

Code	Species
AGCR	*Agropyron cristatum* (L.) Gaertn.
AGDA	*Agropyron dasystachyum* (Hook.) Scribn.
AGSM	*Agropyron smithii* Rydb.
AGSP	*Agropyron spicatum* (Pursh) Scribn. & Smith
AGT?	*Agropyron trachycaulum* (Link) Malte
ALDE	*Alyssum desertorum* Stapf
AMPS	*Ambrosia psilostachya* DC.
ANFO	Annual forb
ANGE	*Andropogon gerardii* Vitman
ARAR	*Artemisia arbuscula* Nutt.
ARCA	*Arenaria capillaris* Poir.
ARDR	*Artemisia dracunculus* L.
ARFI	*Artemisia filifolia* Torr.
ARFR	*Artemisia frigida* Willd.
ARLO	*Aristida longiseta* Steud.
ARLU	*Artemisia ludovisciana* Nutt.
ARTR	*Artemisia tridentata* Nutt.
ASCE	*Astragalus ceramicus* Sheld.
ASER	*Aster ericoides* L.
ASGI	*Astragalus gilviflorus* Sheld.
ASGR	*Astragalus gracilus* Nutt.
ASSE	*Astragalus sericoleucus* Gray
ASTR?	*Astragalus* spp.
ATCA	*Artemisia campestris* L.
ATGA	*Atriplex gardneri* (Moq.) D.Dietr.
BOCU	*Bouteloua curtipendula* (Michx.) Torr.
BOGR	*Bouteloua gracilis* (H.B.K.) Lag.
BOHI	*Bouteloua hirsuta* Lag.
BRTE	*Bromus tectorum* L.
BUDA	*Buchloe dactyloides* (Nutt.) Engelm.
CAFI	*Carex filifolia* Nutt.
CALO	*Calamovilfa longifolia* (Hook.)
CAMO	*Calamogrostis montanensis* (Scribn.) Scribn.
CARE?	*Carex* spp.
CHLE	*Chenopodeum leptophyllum* (Moq.) Wats.
CHVI	*Chrysopsis villosa* (Pursh) Nutt.

Plant Species Names and Codes. Continued on following page.

Plant Species Names and Codes. Continued.

CIUN	*Cirsium undulatum* (Nutt.) Spreng.
CLSE	*Cleome serrulata* Pursh
COAR	*Convolvulus arvensis* L.
COUM	*Comandra umbellata* (L.) Nutt.
CRMI	*Cryptantha minima* Rydb.
DIST	*Distichlis spicata* (L.) Greene
DYAU	*Dyssodia aurea* (A.Gray) A. Nels.
EQAR	*Equisetum arvense* L.
ERBE	*Erigeron bellidiastrum* Nutt.
ERIG	*Erigeron* spp.
EROV	*Eriogonum ovalifolium* Nutt.
ERPA	*Eriogonum pauciflorum* Pursh
GACO	*Gaura coccinea* (Nutt.) Pursh
GRSQ	*Grindelia squarrosa* (Pursh) Dun.
GUSA	*Gutierrezia sarothrae* (Pursh) Britt. & Rusby
HASP	*Haplopappus spinulosus* (Pursh) DC.
HEAN	*Helianthus annuus* L.
HEPE	*Helianthus petiolaris* Nutt.
HEVI	*Heterotheca villosa* (Pursh) Britt. & Rusby
HIJA	*Hilaria jamesii* (Torr.) Benth.
HOPU	*Hordeum pusillum* Nutt.
HYRI	*Hymenoxys richardsonii* (Hook.) Cockerell
KOCR	*Koeleria cristata* Pers.
LIPE	*Linum perenne* L.
LUPU	*Lupinus pusillus* Pursh
LUSE	*Lupinus sericeus* Pursh
LYJU	*Lygodesmia juncea* (Pursh) D.Don
MEOF	*Melilotus officinadis* (L.) Lam.
MESA	*Medicago sativa* L.
MUTO	*Muhlenbergia torryei* (Kunth) Hitchc. *ex* Bush
OPPO	*Opuntia polyacantha* Haw.
OXY?	*Oxytropis* spp.
PEAL	*Penstemon albidus* Nutt.
PENS?	*Penstemon* spp.
PEFO	Perennial forb
PHHO	*Phlox hoodii* Rich.
PIOP	*Picradeniopsis oppositifolia* (Nutt.) DC.
PLPA	*Plantago patagonica* Jacq.

Plant Species Names and Codes. Continued on following page.

Plant Species Names and Codes. Continued.

POGR	*Potentilla gracilis* Dougl.
POSA	*Poa sandbergii* Vasey
POSC	*Poa scabrella* (Thurb.) Benth.
POSE	*Poa secunda* Presl
PSTE	*Psoralea tenuiflora* Pursh
SETR	*Senecio tridenticulatus* Rydb.
SIHY	*Sitanion hystrix* (Nutt.) J.G.Smith
SAIB	*Salsola iberica* Sennen & Pau
SCPA	*Schedonnardus paniculatus* (Nutt.) Trel.
SCSC	*Schizachyrium scoparium* (Michx.) Nash
SOMI	*Solidago missouriensis* Nutt.
SPAI	*Sporobolus airoides* (Torr.) Torr.
SPCO	*Sphaeralcea coccinea* (Nutt.) Rydb.
SPCR	*Sporobolus cryptandrus* (Torr.) Gray
STCO	*Stipa comata* Trin. & Rupr.
STVI	*Stipa viridula* Trin.
TAOF	*Taraxacum officinale* Weber
TECA	*Tetradymia canescens* DC.
THRH	*Thermopsis rhombifolia* Nutt.
TRDU	*Tragopogon dubius* Scop.
VIAU	*Iva axillaris* Pursh
VIAM	*Vicia americana* Muhl. *ex* Willd.
VUOC	*Vulpia octoflora* (Walt.) Rydb.

Grasshopper species names, codes used for analyses, subfamily classifi-cations*, and overwintering habit** for collections made at sites in Montana and Colorado, 1992.

Code	Species	Subfamily*	Habit**
ACONS	*Arphia conspersa* (Scudder)	O	overwintering
ANGUS	*Melanoplus angustipennis* (Dodge)	O	spring-emerging
ASPER	*Trachyrhachys aspera* (Scudder)	O	spring-emerging
BICOL	*Dactylotum bicolor* (Thomas)	M	spring-emerging
BIVIT	*Melanoplus bivittatus* (Say)	M	spring-emerging
BMAGN	*Brachystola magna* (Girard)	R	spring-emerging
BOWDI	*Melanoplus bowditchi* Scudder	M	spring-emerging
BRACH	*Pseudopomala brachyptera* (Scudder)	G	overwintering
CAMPE	*Trimerotropis campestris* McNeill	O	spring-emerging
CARLI	*Circotettix carlinianus* (Thomas)	O	spring-emerging
CAROL	*Dissosteira carolina* (Linneaus)	O	spring-emerging
CCONS	*Chloealtis conspersa* (Harris)	G	spring-emerging
CLAVA	*Aeropedellus clavatus* (Thomas)	G	spring-emerging
COLLA	*Spharagemon collare* (Scudder)	O	spring-emerging
COLOR	*Amphitornus coloradus* (Thomas)	G	spring-emerging
CONFU	*Melanoplus confusus* Scudder	M	spring-emerging
CORAL	*Xanthippus corallipes* Haldeman	O	overwintering
CORON	*Trachyrhachys coronata* (Scudder)	O	overwintering
COSTA	*Encoptolophus costalis* (Scudder)	O	spring-emerging
CRENU	*Cordillacris crenulata* (Bruner)	G	spring-emerging
CRIST	*Spharagemon cristatum* (Scudder)	O	spring-emerging
CVIRI	*Chortophaga viridifasciata* (DeGeer)	O	overwintering
DELIC	*Psoloessa delicatula* (Scudder)	G	overwintering
DEORU	*Ageneotettix deorum* (Scudder)	G	spring-emerging
DIFFE	*Melanoplus differentials* (Thomas)	M	spring-emerging
ELLIO	*Aulocara elliotti* (Thomas)	G	spring-emerging
EQUAL	*Spharagemon equale* (Say)	O	spring-emerging
FEMOR	*Aulocara femoratum* (Scudder)	G	spring-emerging
FEMUR	*Melanoplus femurrubrum* (DeGeer)	M	spring-emerging
FLAVI	*Melanoplus flavidus* Scudder	M	spring-emerging
FOEDU	*Melanoplus foedus* (Scudder)	M	spring-emerging
GLADS	*Melanoplus gladstoni* Scudder	M	spring-emerging
GRACI	*Trimerotropis gracilis* (Thomas)	O	spring-emerging
HALBA	*Hypochlora alba* (Dodge)	M	spring-emerging
HALDE	*Pardalophora haldemanii* (Scudder)	O	overwintering

Grasshopper Species Names and Codes. Continued on following page.

Grasshopper Species Names and Codes. Continued.

HAYDE	*Derotmema haydeni* (Thomas)	O	spring-emerging
HRUFA	*Heliaula rufa* (Scudder)	G	spring-emerging
HSPEC	*Hesperotettix speciosus* (Scudder)	M	spring-emerging
HVIRI	*Hesperotettix viridis* (Scudder)	M	spring-emerging
INFAN	*Melanoplus infantilis* (Scudder)	M	spring-emerging
KEELE	*Melanoplus keeleri* (Dodge)	M	spring-emerging
KIOWA	*Trachyrhachys kiowa* (Thomas)	O	spring-emerging
LAKIN	*Melanoplus lakinus* (Scudder)	M	spring-emerging
LATIF	*Trimerotropis latifasciata* Scudder	O	spring-emerging
MACUL	*Mermiria maculipennis* Bruner	G	spring-emerging
MAGNA	*Hadrotettix magnificus* (Rehn)	O	spring-emerging
MBIVI	*Mermiria bivittata* (Serville)	G	spring-emerging
NEBRA	*Phoetaliotes nebrascensis* (Thomas)	M	spring-emerging
NUBIL	*Boopedon nubilum* (Say)	G	spring-emerging
OBSCU	*Opeia obscura* (Thomas)	G	spring-emerging
OCCID	*Melanoplus occidentalis* (Thomas)	M	spring-emerging
OCCIP	*Cordillacris occipitalis* (Thomas)	G	spring-emerging
OLIVA	*Campylacantha olivacea* (Scudder)	M	spring-emerging
PACKA	*Melanoplus packardii* Scudder	M	spring-emerging
PLATT	*Mestobregma plattei* (Thomas)	O	spring-emerging
PSEUD	*Arphia pseudonietana* (Thomas)	O	spring-emerging
QUADR	*Phlibostroma quadrimaculatum* (Thomas)	G	spring-emerging
REGAL	*Melanoplus regalis* (Dodge)	M	spring-emerging
SALUT	*Schistocerca alutacea* Scudder	C	spring-emerging
SANGU	*Melanoplus sanguinipes* (Fabricius)	M	spring-emerging
SIMPL	*Eritettix simplex* (Thomas)	G	overwintering
SPECI	*Orphulella speciosa* (Scudder)	G	spring-emerging
TEXAN	*Psoloessa texana* Scudder	G	overwintering
TRIFA	*Hadrotettix trifasciatus* (Say)	O	spring-emerging
TURNB	*Aeoloplides turnbulli turnbulli* (Thomas)	M	spring-emerging
WYOMI	*Paropomala wyomingensis* (Thomas)	G	spring-emerging
XMONT	*Xanthippus montanus* (Thomas)	O	overwintering

* "C" refers to the subfamily Cyrtacanthacridinae, "G" refers to the subfamily Gomphocerinae, "M" refers to the subfamily Melanoplinae, "O" refers to the subfamily Oedipodinae, and "R" refers to the family Romaleinae.

** "Overwintering" species spend the winter months as nymphal instars and "spring-emerging" species spend the winter months in the egg stage.

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