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

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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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 1995

APPROVAL

of a thesis submitted by

Kerri Farnsworth Skinner

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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ACKNOWLEDGMENTS

My sincere thanks go to Dr. William P. Kemp for his guidance, encouragement, and support while supervising this thesis. Thanks also go to my committee members, Drs. John Wilson, Matt Lavin and Robert Moore, for their aid in developing, editing, and proofreading this work. I am indebted to Mark Carter, Jeffrey Holmes, and Ryan Nordsven for collecting, processing, and compiling the grasshopper and plant data. I am grateful to Tom Kalaris, Lisa Landenberger, Sue Osborne, Christine Ryan, and Robert Snyder for generously sharing their technical expertise, and to Chuck Griffin for helping me whenever things went wrong.

Special thanks go to Paul, for his unending support and patience, and to all those who encouraged me in the pursuit of this degree.

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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.

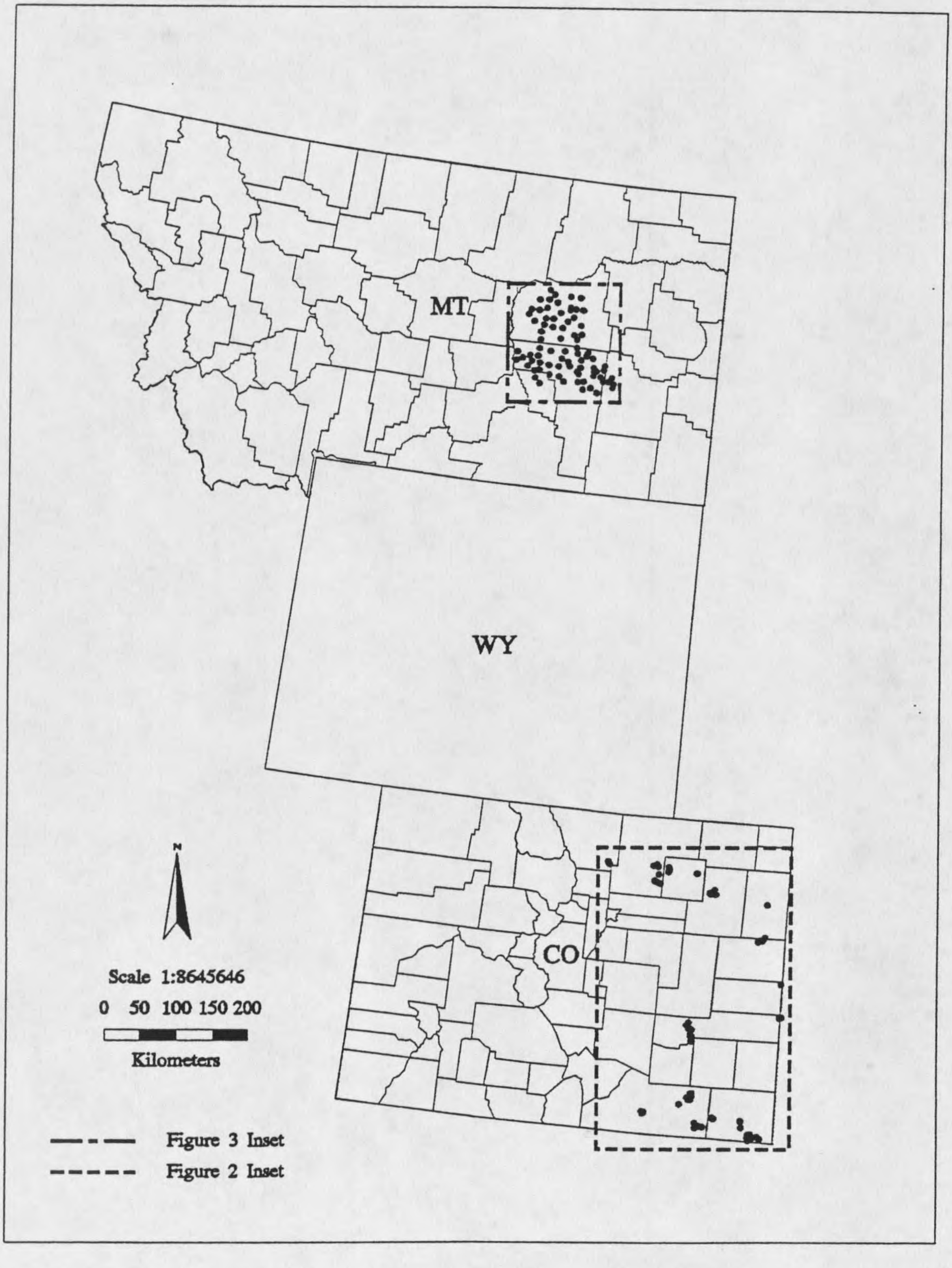

Figure 2. Sample sites in eastern Colorado with county boundaries.