Fall 1999

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Great Plains Research 9 (Fall 1999): 223-59

FEATURE ARTICLE

THE STRUCTURE AND FUNCTION OF ECOSYSTEMS IN THE CENTRAL NORTH AMERICAN GRASSLAND REGION

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ABSTRACT—The central grassland region occupies the center of North America in the United States, Canada and Mexico and is a unique resource for the continent. While there are no other areas with comparable features, the largest similar grassland areas occur in Europe and Asia. The uniqueness of the region derives from its size, its relative flatness, and the smoothness of its physical gradients. The smooth gradients in precipitation and temperature are the reasons why most gradients in ecosystem properties are also smooth. The west-east gradient in precipitation and the north-south gradient in temperature result in corresponding gradients in plant community types, net biomass production by plants, soil carbon storage, and nitrogen availability to plants. One of the most striking features of the present condition of the central grassland region is that a huge fraction of the original native grassland have been replaced by cropland.

Introduction

Grasslands have occupied portions of central North America since the retreat of the Wisconsin glaciers approximately 10,000 years ago (Stebbins 1981). Axelrod (1985) argued that the formation of the North American grassland biome began during the Miocene-Pliocene transition (7 - 5 million yrs BP), with intervening periods of dominance by forest or woodland vegetation. During the Wisconsin glacial maximum (~18,000 yrs BP), the northern portion of central North America was covered with ice and tundra. Boreal forest extended over much of the remaining area. Stebbins (1981) suggested that the plant communities observed and described by 19th century explorers were newly formed following the glacial retreat and had been substantially influenced by the immigration of bison and sheep from Eurasia. Based upon the paleobotanical data, Axelrod (1985) concluded that the current grassland biome in central North America arose during the Altithermal period, 3000-4000 yrs BP. There is little controversy about the fact that grasslands have occurred in central North America for the past 10,000 years. However, their extent, their composition and the degree to which fire has allowed grasses to dominate in areas that can support trees are less obvious, and research on these issues has occupied ecologists and geographers for the past 100 years (Pound and Clements 1898; Clements 1916; Sauer 1950; Wells 1970; Brown 1993).

Our overall objective is to describe the central grassland region of North America in terms of its climate, vegetation, biogeochemistry, and current landuse. Our specific objectives are to: 1) attempt to place the geographic distribution and size of the central North American grasslands in perspective with similar grasslands on other continents, and 2) to describe the spatial distribution of climate, soils, vegetation, net primary production (net biomass production by plants), carbon and nitrogen pools, and current landuse.

Global Perspective

Grasslands occur on every continent except Antarctica, from the tropics to the edge of the boreal forest (Coupland 1992). Estimates of the percentage of the terrestrial surface occupied by grasslands and savannas ranges from 16% (Whittaker and Likens 1975) to 30% (Ajtay et al. 1979). The variation in estimates occurs because of the difference between the potential grassland area in the absence of human alterations (climatically-determined grasslands) and the current distribution of grasslands. The central North American grassland ecoregions occupy 3.022 x 10^6 km^2, representing 12.5% of North America and 2% of the Earth's terrestrial surface (Bailey 1998). The central North American grasslands occupy two of Bailey's ecoregion domains (humid temperate and dry), three divisions (prairie, tropical/subtropical steppe and temperate steppe) and seven provinces (temperate prairies, coniferous wooded steppes, subtropical prairies, steppes and shrublands, dry steppes and shrublands, dry steppes and steppes).

Bailey (1998) defined ecoregions as "Any large portion of the Earth's surface over which the ecosystems have characteristics in common . . ." The key characteristics of ecoregions are determined by macroclimate, modified by the influences of latitude, continental position, and altitude. For our analysis, we identified all of the grassland ecoregions that occur in central North America (Fig. 1), specifically east of the Rocky Mountains in Canada and the United States and east of the Sierrra Madre Oriental in Mexico.

On which other continents do areas similar to the central North American grassland region occur? The answer is every continent, except Antarctica (Fig. 2). The African continent has the smallest area in similar grasslands, with 0.129 x 10^6 km^2 occurring in the extreme northern and southern parts (Table 1). Most of Africa is more tropical and subtropical than central North America. South America contains 0.369 x 10^6 km^2 of ecoregions that are similar to central North America, almost all occurring in the Río de la Plata grasslands of Uruguay and northeastern Argentina or in Patagonia. Similar grasslands occur in southeastern and southwestern Australia and occupy 0.505 x 10^6 km^2. The southeastern grasslands are in the subtropical zone, and the southwestern ones are in the temperate zone. The largest expanse of similar ecoregions are found in Europe and Asia. These grasslands stretch 9,000 km from Slovakia and Hungary on the west to China and Mongolia on the east. The total area of grassland ecoregions in Europe and Asia that are similar to those in central North America is 5.313 x 10^6 km^2, almost twice the area in North America. The Eurasian grassland ecoregions account for 57% of the Earth's total area similar to the grassland ecoregions in central North America.

While the central North American grassland ecoregions are not the largest of their types on Earth, they have some unique features. Compared to Eurasia, central North America is unique in its lack of political complexity. The Eurasian grassland ecoregions cross many international boundaries, which adds tremendous complexity to human activities in the region. Eurasian grassland research is seldom published in international journals,

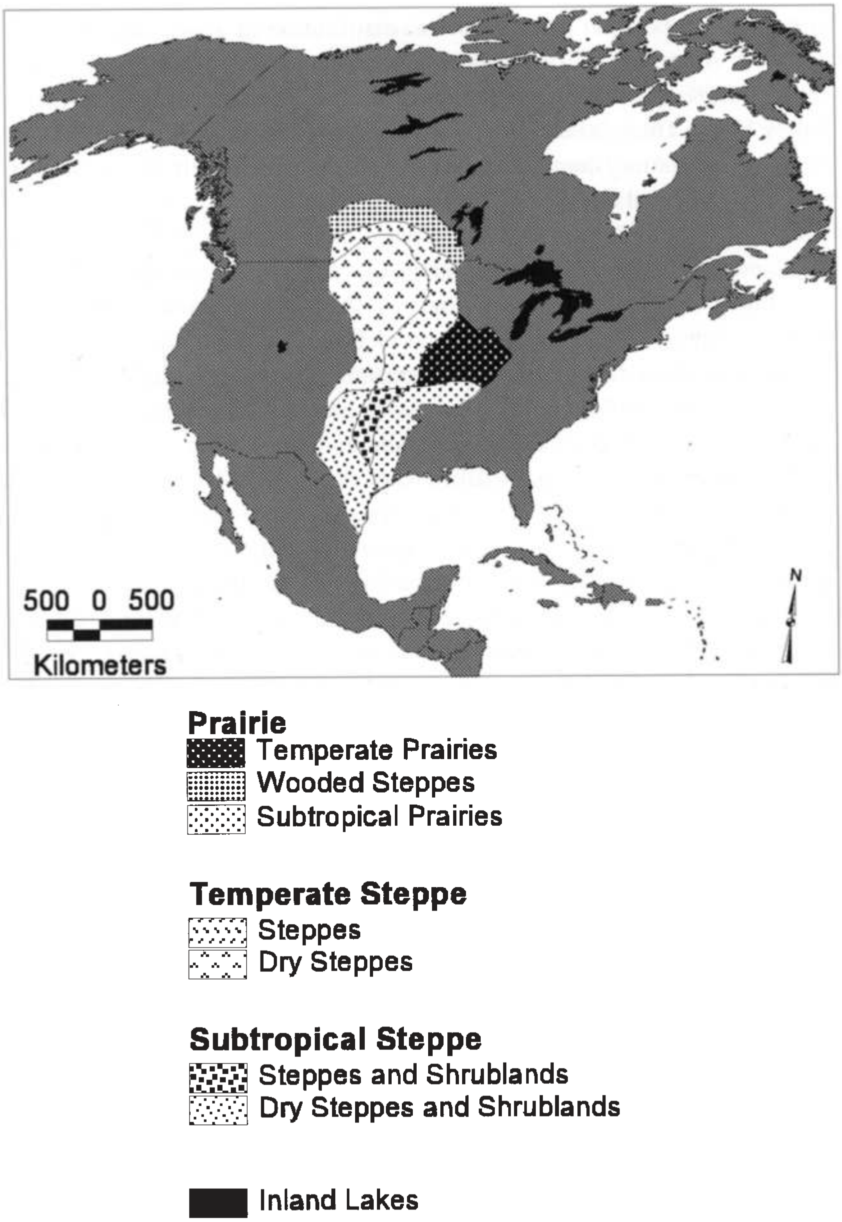

Figure 1. Grassland ecoregions in central North America (adapted from Bailey 1998).

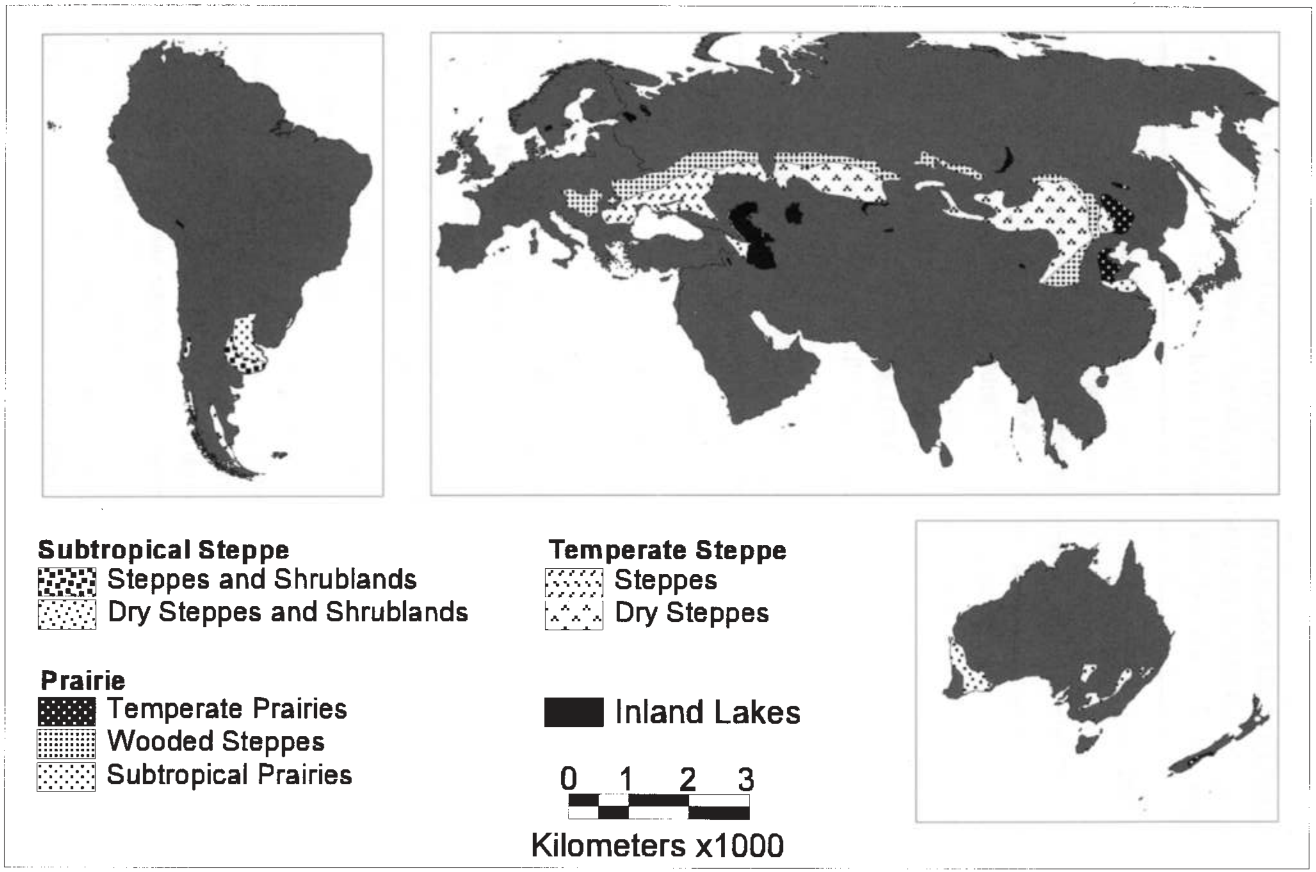

Figure 2. Ecoregions world wide (Africa omitted) that are similar to those in central North America (adapted from Bailey 1998).

TABLE 1
AREAS AND PERCENTAGES OF THE WORLD WIDE TOTAL AREA OF GRASSLAND ECOREGIONS THAT ARE SIMILAR TO THOSE IN CENTRAL NORTH AMERICA (ADAPTED FROM BAILEY 1998)

Continent	Area	
	km^2	%
Asia	3,570,523	38
Africa	128,684	1
Australia	505,007	5
Europe	1,742,351	19
North America	3,021,844	33
South America	368,922	4
Total	9,208,647	100

making access to results difficult. Information from the former Soviet Union is just now beginning to be made available to the international scientific community. By contrast, the central North American grassland region crosses only two international boundaries. Two of the countries (Canada and the United States) share the same language and many of the same research and application traditions. While differences in the kinds of data available occur, many of the most important types of data are widely available from both countries. Less than 2% of the grassland region occurs in Mexico.

The Eurasian grassland ecoregions are topographically and climatically more complex, crossing several major mountain ranges and two large areas of desert. In contrast, the central North American grassland region has little topographic variation. The relief occurs at the western edge of the region where it butts up against the foothills of the Rocky Mountains. The region itself slopes gently from 1500 m in the west to 300 m in the east. Compared to Eurasia, there are no major contrasting ecoregions embedded within the central grassland boundaries. The region interfaces with

Chihuahuan desert in the southwest, subtropical thorn woodlands in the south and forest vegetation on the remaining boundaries. The southeast boundary is formed by mixed deciduous-coniferous forest, the eastern boundary is formed by deciduous forest and in the north with boreal forest. Along the foothills of the Rocky Mountains the boundary is formed by coniferous forest.

The relative lack of complexity that makes the central grassland region of North America unique is the reason why it is the major source of information about temperate and subtropical grasslands in the world. The lack of topographic complexity means that gradients in climatic driving variables as well as those in organismal and ecosystem responses are relatively smooth across the region providing a template for analyses that could be conducted no where else on Earth. We will describe the spatial patterns of climate, soils, vegetation, and aboveground net primary production in the central grassland region of North America in the next section.

Characteristics of Central North American Grasslands

Environmental Conditions

An understanding of large-scale driving variables is crucial to understanding the behavior of ecosystems. In the central grassland region, precipitation and temperature are the most important variables. Two major gradients provide the key for defining the climate in the central grassland region: an uninterrupted north-south temperature gradient and a smooth west-east precipitation gradient. Mean annual precipitation ranges from greater than 1000 mm in the east-southeast to less than 300 mm in the west-northwest (Fig. 3). There is a clear southeast-northwest component to the precipitation as a result of the inflow of moisture from the southeast (Borchert 1950).

The seasonality of precipitation, and the amount received as snow, differ across the region. Winter is the dry season, although the degree of dryness changes from west to east. No location in the central grassland region receives more than 20% of its mean annual precipitation in the winter (Visher 1954). Areas west of the 700 mm/yr contour line receive less than 25 mm of precipitation in each of the winter months (December, January and February) (US Department of Commerce 1968). Areas to the east of this line receive more than 25 mm in each winter month. The amount of snowfall is less than 100 mm in the southern portion of the area, between 100 and 250

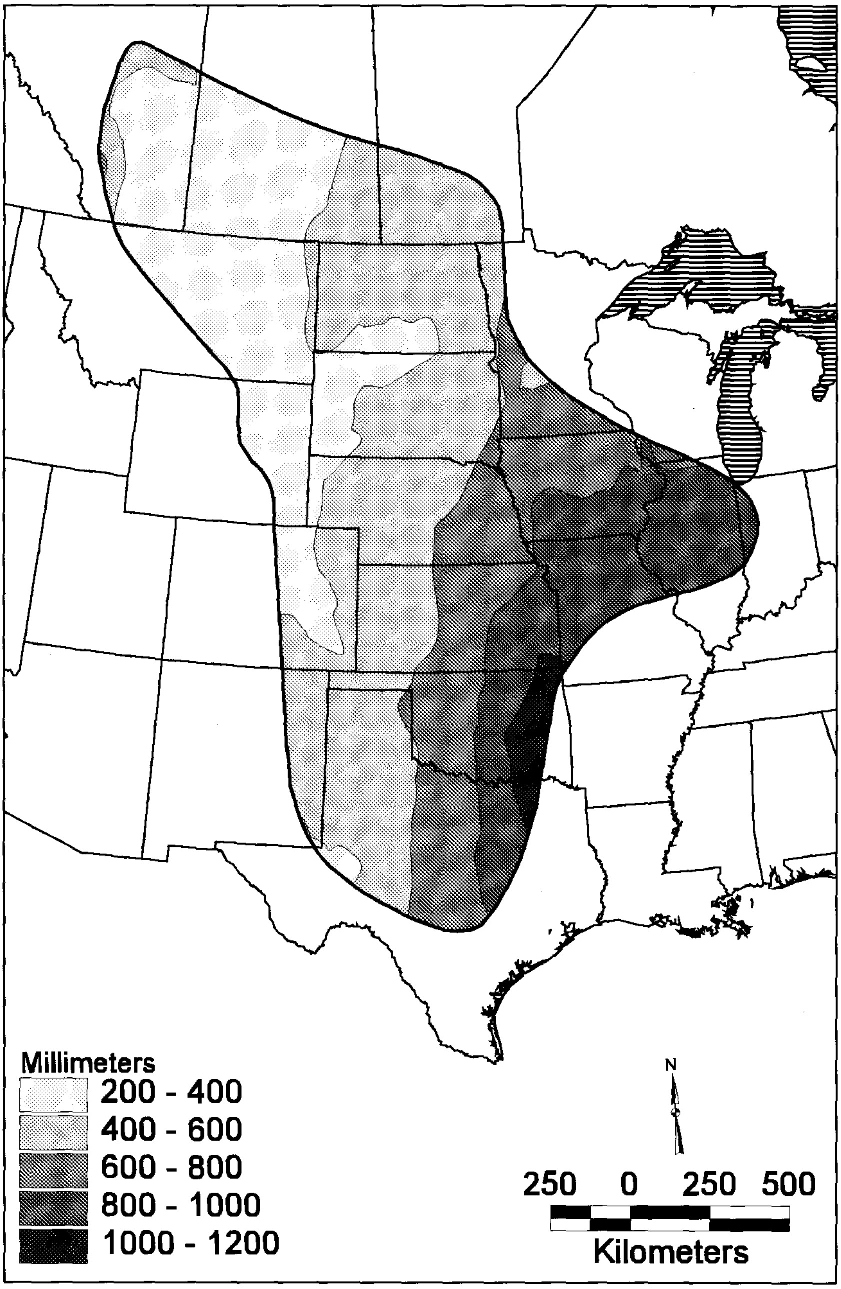

Figure 3. Spatial distribution of mean annual precipitation (mm) in the central grassland region of North America (data from Leemans and Cramer 1991).

mm in the central portion, and greater than 250 mm in the north (Visher 1954). The average number of days with at least 25 mm of snow cover range from 10 or less south of the Texas-Oklahoma border to greater than 80 for all of the area north of a line through central Iowa, northern Nebraska and along the Colorado-Wyoming border (Visher 1954). Winter snow cover is important to grasslands. It provides for recharge of soil water during spring melt, and protects plants from the cold, dry winter air.

Summer is the wet season in the central grassland region, and the proportion of mean annual precipitation received during the summer ranges from 30% to greater than 50% (Visher 1954). The highest percentages occur in the northeast and the lowest in the southeast. Because the highest proportion of precipitation occurs in summer, and much of that in convective thunderstorms, the drier portions of the region have the highest interannual variation in precipitation (Lauenroth and Burke 1995). The percentage of mean annual precipitation that falls in the summer ranges from 55% in the extreme northwestern portion to 15% in the extreme southeast. Two patterns influence these percentages. The first is a tendency towards bimodal precipitation peaks in the southeast. The second is an increase in spring, fall, and winter precipitation that diminishes the importance of the amount received in the summer. The percentage of mean annual precipitation received in the winter varies from 5% in the central portion to 15% in the southeast and northwest. The relatively high winter precipitation in the north is the result of the Alberta storm track (polar front) and in the south it is the effect of the Burmuda high (Borchert 1950).

Mean annual temperatures range from greater than 18°C in the south to less than 2°C in the north (Fig. 4). In the southern and central portion of the region, there is a small northwest-southeast component to the gradient as a result of the advection of warm air from the Gulf of Mexico and the increase in elevation toward the foothills of the Rocky Mountains. In the northern portion of the region, the tilt of the gradient reverses, so that there is a northeast-southwest component from the inflow of cold north Atlantic air (Borchert 1950). These deviations from the widely quoted orthogonal relationship of precipitation and temperature in the central grassland region result in a significant correlation between mean annual temperature and precipitation ($r = 0.68$; $p < 0.01$; $n = 5273$).

The entire region has its temperature maximum during the summer months (July or August), although the temperature range between the warmest and coldest month decreases from north to south. In the north, mean monthly temperatures for December and January are below 0°C, while in the

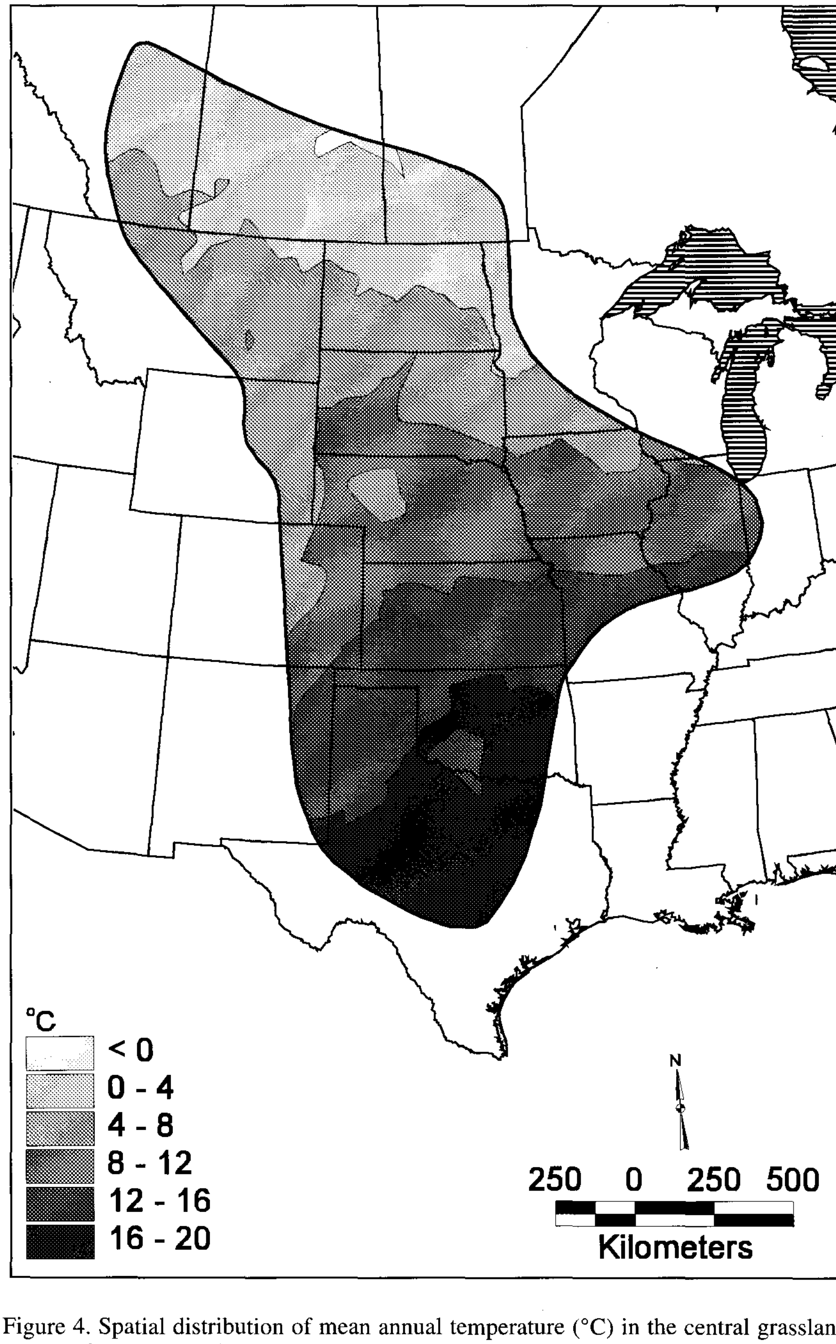

Figure 4. Spatial distribution of mean annual temperature (°C) in the central grassland region of North America (data from Leemans and Cramer 1991).

south they are equal to or above 0°C. The subtropical limit crosses the region from east to west through central Oklahoma and the panhandle of Texas. Sites south of this line have the lowest temperature amplitudes and sites to the north have the highest amplitudes. The timing of peak precipitation ranges from a unimodal peak in May or June in the northwestern portion of the region to bimodal peaks in the southern and eastern portions—one in April, May or June and the other in August, September or October.

The central grassland region, and especially the western portion of it, is commonly thought of as being arid. Analysis of the region using Bailey's (1958; 1979) widely used climatic classification method suggests that less than 1% of the region qualifies technically as arid (Fig. 5; Table 2). Sixty-six percent of the region is classified as dry subhumid and semiarid. The boundary between dry and moist subhumid classes represents the points at which water supply is equal to atmospheric demand. West of the boundary, demand exceeds supply. East of it, supply exceeds demand. Thirty-four percent of the central grassland region is classified as moist subhumid or humid.

Compared to the large-scale smooth gradients of climatic variables, spatial variability in soil characteristics are relatively small-scale, heterogeneous and without a directional gradient. Sand content is a good indicator variable to characterize the spatial variability in soil texture (Burke et al. 1994; 1997a; 1997b), because it is related to important factors for plant growth such as soil water holding capacity (Cosby et al. 1984) and soil fertility (Burke et al 1989). Because of these important relationships, the spatial distribution of soil texture influences vegetation type, net primary production, soil organic matter pools, nutrient availability, and landuse alternatives (Burke et al. 1989; 1994; 1997a; Küchler 1964; Epstein et al. 1998).

Ecosystem Structure and Function

In this section, we include two different approaches to describing the ecosystems of the central grassland region. First, we will treat the region as though it consists entirely of native grasslands. This approach provides background information about presettlement ecosystems, and it establishes the gradients one might expect to occur in remaining undisturbed ecosystems as well as in those undergoing restoration. Second, we will address the transformations that have occurred as a result of converting 60% of the region to row-crop agricultural ecosystems.

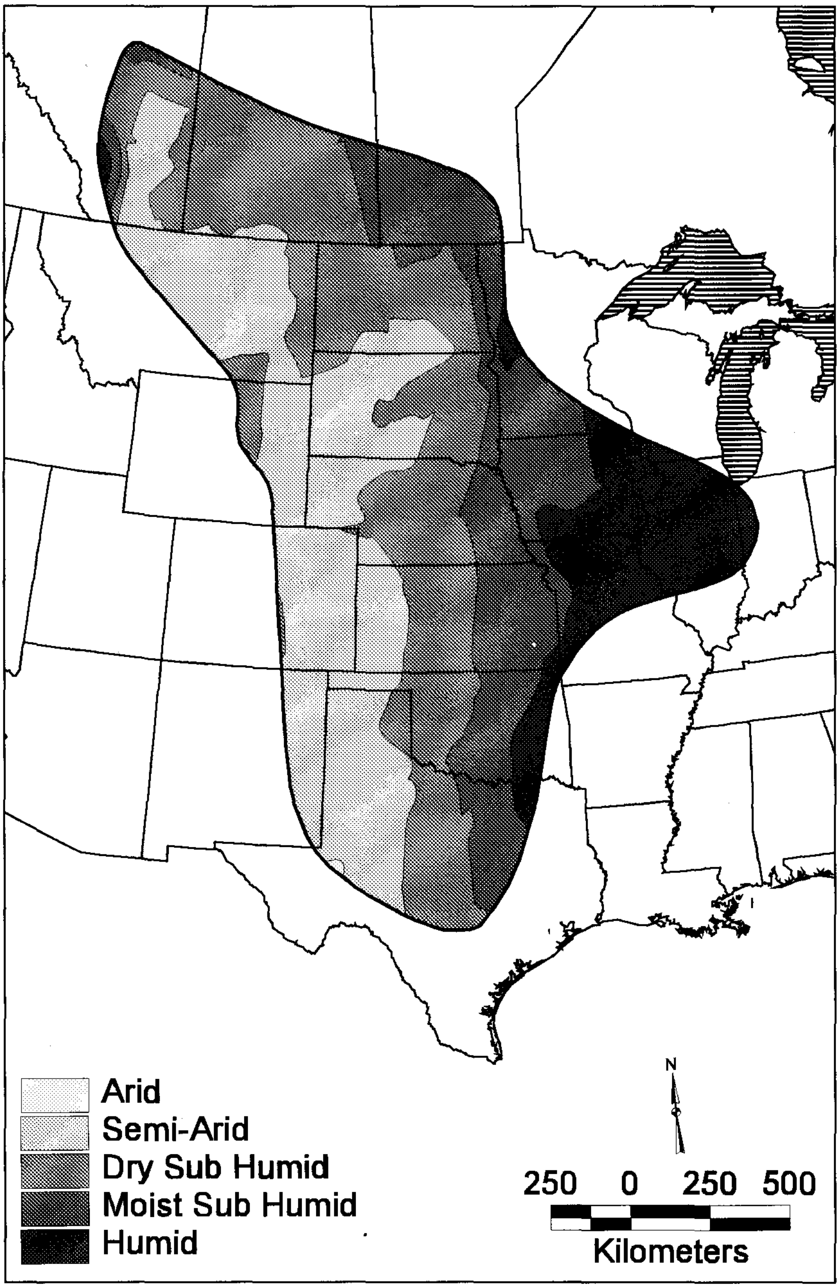

Figure 5. Spatial distribution of climate types in the central grassland region of North America (calculated from Bailey 1979).

TABLE 2
THE PERCENTAGE OF THE AREA IN THE CENTRAL GRASSLAND REGION OF NORTH AMERICA THAT FALLS WITHIN EACH OF THE CLIMATE TYPES IN FIGURE 5

Climate Type	Area	
	km^2	%
Arid	1,854	<1
Semi-arid	866,898	32
Dry Subhumid	906,742	34
Moist Subhumid	580,773	21
Humid	338,343	13
Total	2,694,610	100

Vegetation. The large-scale environmental gradients across the grassland region result in large-scale changes in vegetation. For instance, the west-east gradient in mean annual precipitation influences vegetation, with shortgrasses being most common in the west and tallgrasses in the east. Maximum canopy heights change along this gradient from less than 20 cm for shortgrasses to greater than 200 cm for tallgrasses (Lane et al. 2000; Hartnett and Fay 1998; Weaver 1954). The north-south temperature gradient is correlated with a change in the number of C_3 and C_4 grass species (Teeri and Stowe 1976). The C_3 species grow during the cool season and the C_4 species grow druing the warm season. The combination of the temperature and precipitation gradients create gradients in the relative contribution of C_3 and C_4 plant species to annual aboveground net primary production (plant biomass production) across the region (Epstein et al. 1997; Tieszen et al. 1997).

The C_3 species are most important in the coolest and driest portions of the region, while C_4 species are most important in the warmest and wettest areas (Fig. 6). Our analysis indicates that the wettest areas in which C_3 species contribute more to biomass production than C_4 species occur at a mean annual precipitation of approximately 550 mm and mean annual temperature of less than 2° C. Areas that are wetter and warmer than this are dominated by C_4 species. The warmest areas that are still dominated by C_3 species have a mean annual temperature of approximately 8° C and a mean

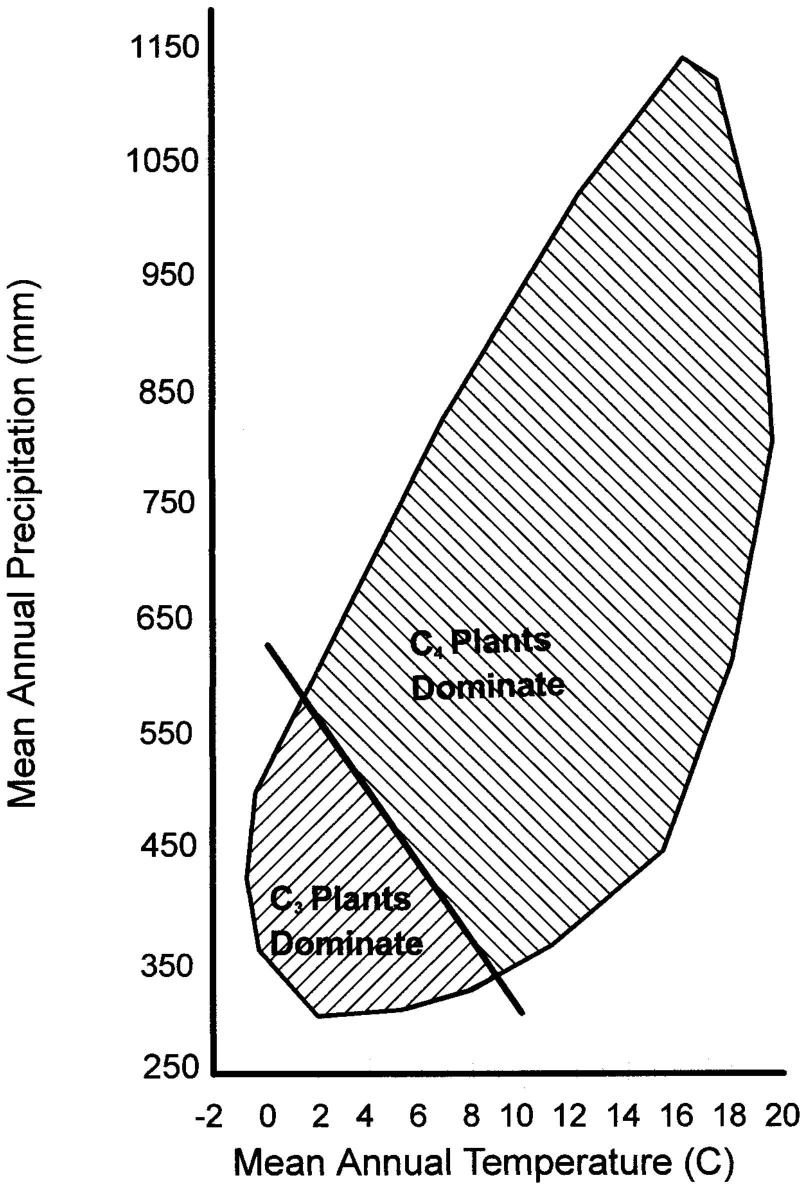

Figure 6. The environmental space of the central grassland region of North America defined by mean annual precipitation and mean annual temperature and the contributions of plant species with contrasting photosynthetic pathways (C_3 and C_4) to annual aboveground net primary production. The equation for the points of equal annual aboveground net primary production (C_3=C_4) is: Mean Annual Precipitation (mm) = 622 - 32*Mean Annual Temperature (°C) (adapted from Epstein et al. 1997a).

annual precipitation less than 350 mm (Fig. 6). Geographically, the major contributions of C_3 plants to annual aboveground net primary production are limited to the northwestern two-thirds of the region whereas C_4 species contribute to annual aboveground net primary production throughout the region (Fig. 7). These results appear to contradict the idea that C_3 species predominate in wet, cool areas, while C_4 species are most successful in hot, dry areas (Epstein et al. 1997). In the central grassland region, C_3 species reach their greatest relative importance in some of the driest parts of the region, while C_4 species are most important in the wettest portions. An important reason for this unexpected finding is that some tall, mid-height, and short-stature species in the central grassland region have the C_4 photosynthetic pathway. However, almost all of the C_3 species are mid-height and short in stature, so they are subject to being out competed for light by C_4 species in wet areas. Another important reason is that the positive correlation between temperature and precipitation results means that the wettest areas (southeast) are also some of the warmest (Figs. 3, 4). Therefore, C_4 species dominate annual, aboveground, net primary production (>50%) in all of the warmest areas, whether they are wet or dry; and, C_3 species dominate in the coolest areas, which are also relatively dry.

The multidimensional gradients in climate, soil and plant-type gradients across the central grassland region result in a complex spatial distribution of potential plant communities (Fig. 8) (Küchler 1964; Coupland 1950; Looman 1963). In the wettest, eastern and southeastern portions of the region, grasslands dominated by C_4 tallgrasses are intermixed with forests (Küchler 1964). Grassland vegetation extends eastward into the forest region, because North American airflow patterns force a wedge of dry, grassland air into the forest region just south of Lake Michigan, creating what E. N. Transeau referred to as the "prairie peninsula" (Transeau 1935; Borchert 1950). The prairie peninsula is the major area occupied by the grassland-forest mosaic. Forest vegetation also extends westward into the grassland region, as gallery forest along the major rivers.

In addition to the grassland-forest mosaic, there are two other community types dominated by C_4 tallgrasses: the bluestem type, which extends westward and northward from the tallgrass-forest mosaic; and, the Blackland prairie in Texas. West of the tallgrass-dominated communities is the mixed prairie, named by Weaver and Clements (1938) for its two-tiered canopy structure. In mixed praire, either tallgrasses are intermixed with mid-height grasses, or midgrasses form the upper canopy layer and shortgrasses the lower. These communities extend from southern and central Texas north

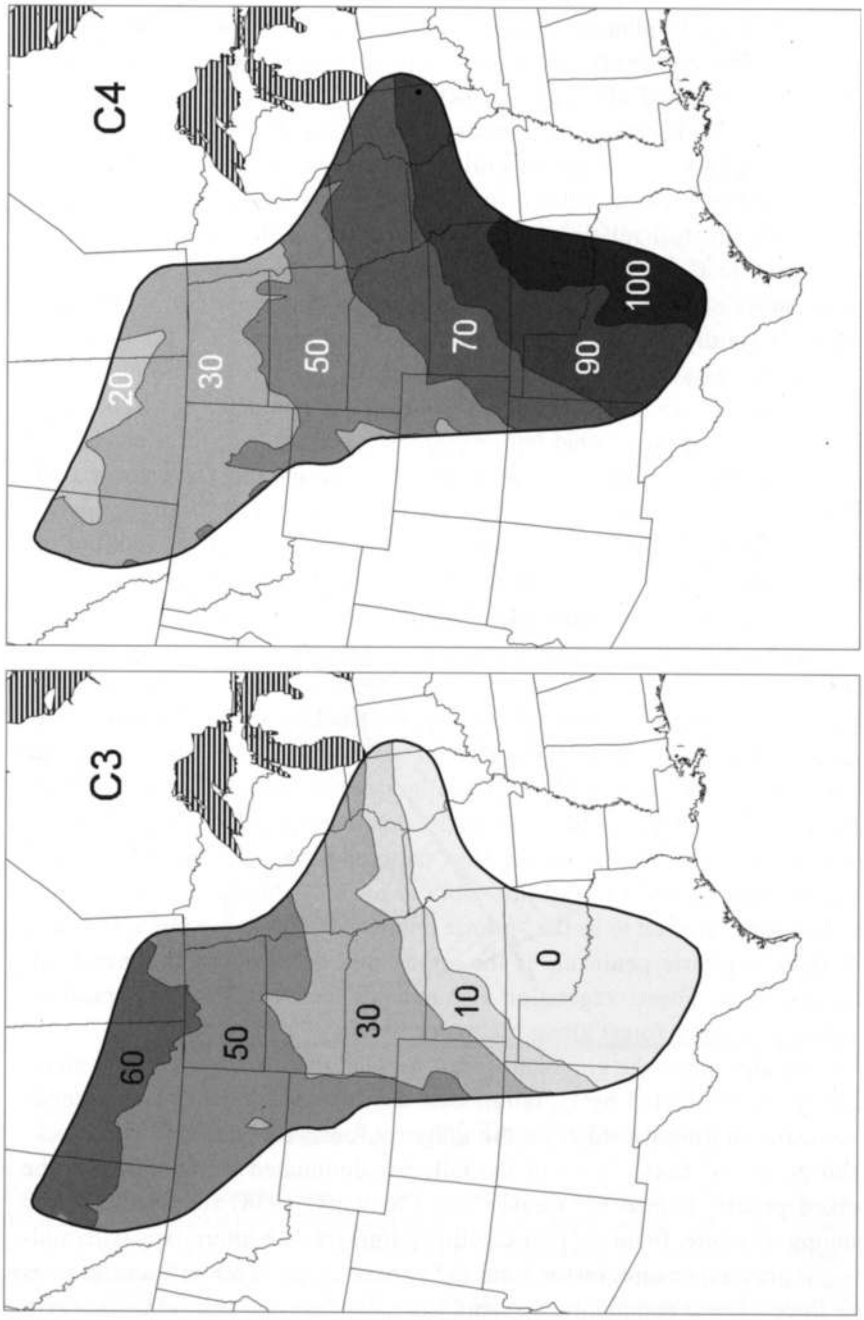

Figure 7. The spatial distribution of the percentage contribution by plants of contrasting photosynthetic pathway type (C_3, C_4) to total annual aboveground net primary production in the central grassland region of North America (adapted from Epstein et al. 1997a).

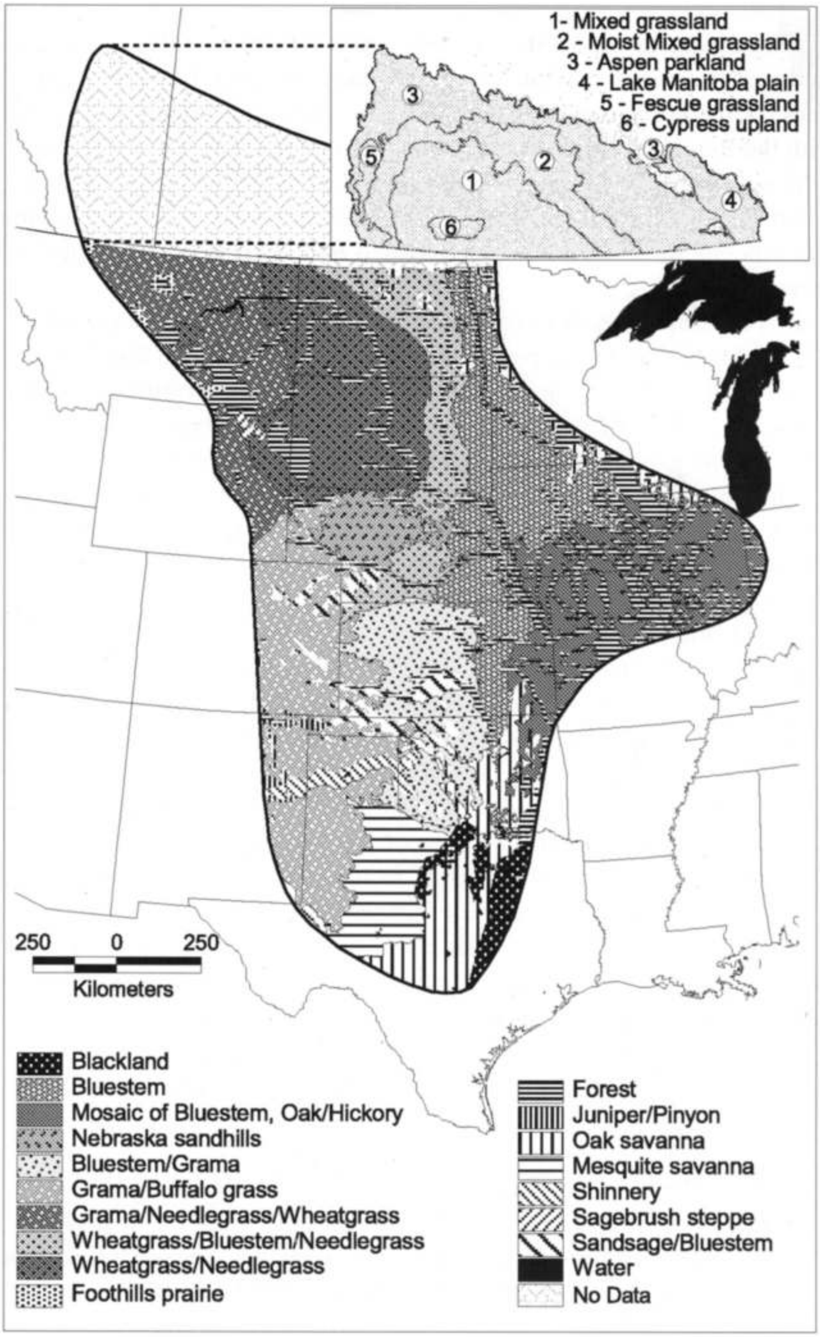

Figure 8. The spatial distribution of potential plant community types in the central grassland region of North America (adapted from Küchler 1964, Coupland 1950, and Looman 1963; inset for Canada downloaded and modified from the National Ecological Framework for Canada web site: [http://www1.ec.gc.ca/~soer/ANEF/default_e.htm]).

to central Alberta. All of the southern grassland communities occur in the subtropical zone and have an important woody component of shrubs and low trees. In the northernmost extension of the grasslands, along the interface with the Boreal forest, grassland communities are intermixed with aspen to form woodlands. In the southwestern portion of the region lies a community dominated by shortgrasses. This is the hottest and driest grassland community type; along its southwestern border it interfaces with the Chihuahuan desert.

An alternative way to conceptualize the vegetation of the region is to identify broad grassland types. Shantz (1923) and Shantz and Zon (1924), in early efforts to classify the grassland region vegetation, identified two types: a tallgrass type, "prairie grassland"; and, a shortgrass type, "plains grassland." Weaver and Clements (1938) recognized three grassland types: tallgrass prairie; true prairie; and mixed prairie. Within the mixed prairie, they used the term "short-grass disclimax" to identify areas dominated by blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloë dactyloides*). Our grassland map is a slight modification of Dodd's (1979) map which combines information from previous maps, especially the map of Küchler (1964), with information about the seasonality and the photosynthetic pathway types of the dominant species to define the tallgrass, mixed grass and shortgrass categories (Fig. 9). Our tallgrass prairie type combines the grassland-forest mosaic communities with the bluestem community types, including the sandhills prairie. The mixed prairie is split into a northern and southern type. The northern mixed prairie is "mixed" on the basis of a two tiered canopy (Weaver and Clements 1938), as well as the photosynthetic pathway type. The midgrasses are C_3 species and the shortgrasses are C_4 species. The southern mixed prairie is "mixed," only on the basis of the canopy heights of the dominant species, since both the midgrass and shortgrass co-dominants are C_4 species. We classify the shortgrass disclimax of Weaver and Clements (1938) and the Bouteloua-Buchloë community type of Küchler (1964) as the shortgrass steppe. This type occupies the driest portion of the grassland region.

Annual Net Primary Production. The gradients of precipitation, temperature and soil texture across the central grassland region also result in a complex spatial pattern of annual aboveground net primary production. Analysis of the relationships between the spatial variation in annual aboveground net primary production and environmental variables suggests that Walter's Law provides the greatest explanatory power for the pattern.

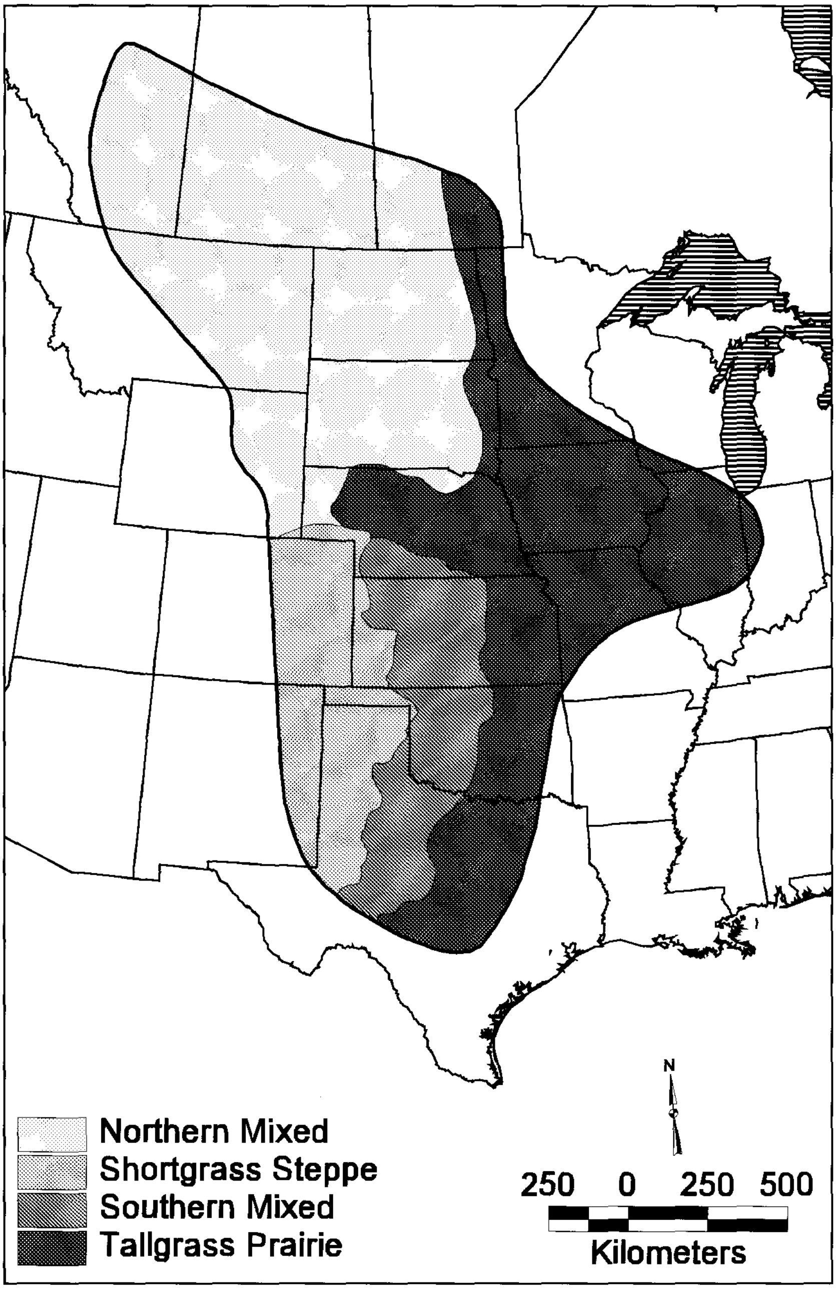

Figure 9. The spatial distribution of grassland types in the central grassland region of North America (adapted from Küchler 1964, Coupland 1950, Looman 1963 and Dodd 1979).

Walter's Law (Walter 1939, as cited in Rutherford 1980) states that the spatial distribution of annual aboveground net primary production in grasslands is directly proportional to the spatial distribution of mean annual precipitation. This is a widely verified relationship that has been reported at both regional (Sala et al. 1988; Epstein et al. 1997a) and global scales (Lauenroth 1979; Milchunas and Lauenroth 1993). Analysis of data collected for individual range sites by the USDA Natural Resource Conservation Service (USDA SCS 1976) results in the following equations for normal, favorable, and unfavorable years:

Normal:	ANPP = 0.53*MAP - 11	$r^2 = 0.56$	(1)
Favorable:	ANPP = 0.71*MAP - 41	$r^2 = 0.66$	(2)
Unfavorable:	ANPP = 0.38*MAP - 4	$r^2 = 0.43$	(3)

where ANPP is annual aboveground net primary production (g/m^2) and MAP is mean annual precipitation (mm) (Fig. 10) (Favorable years represent the wettest 10% of the years in the long term record, unfavorable the driest 10%, and normal the middle 80% (Soil Conservation Service 1973). These relationships are interesting because they substantiate the dominating importance of water availability in explaining the spatial pattern of annual aboveground net primary production in the grassland region. Further, these relationships provide us with a simple tool for predicting patterns in annual aboveground net primary production from mean annual precipitation.

There are, however, some important limitations of the equations. First, since mean annual precipitation and mean annual temperature are positively and significantly correlated for the central grassland region, the effects of precipitation cannot be separated from those of temperature. The relationship between annual aboveground net primary production and mean annual temperature in normal years is:

$$ANPP = 166 + 11.7*MAT \qquad r^2 = 0.14 \qquad (4)$$

where ANPP is annual aboveground net primary production (g/m^2) and MAT is mean annual temperature (°C). There are good reasons to expect the effects of water availability and temperature to interact. Lauenroth (1979) found at the global scale that precipitation explained 51% of the spatial variability in annual aboveground net primary production in grasslands, and that temperature explained only 4%. It was clear, however, that the least

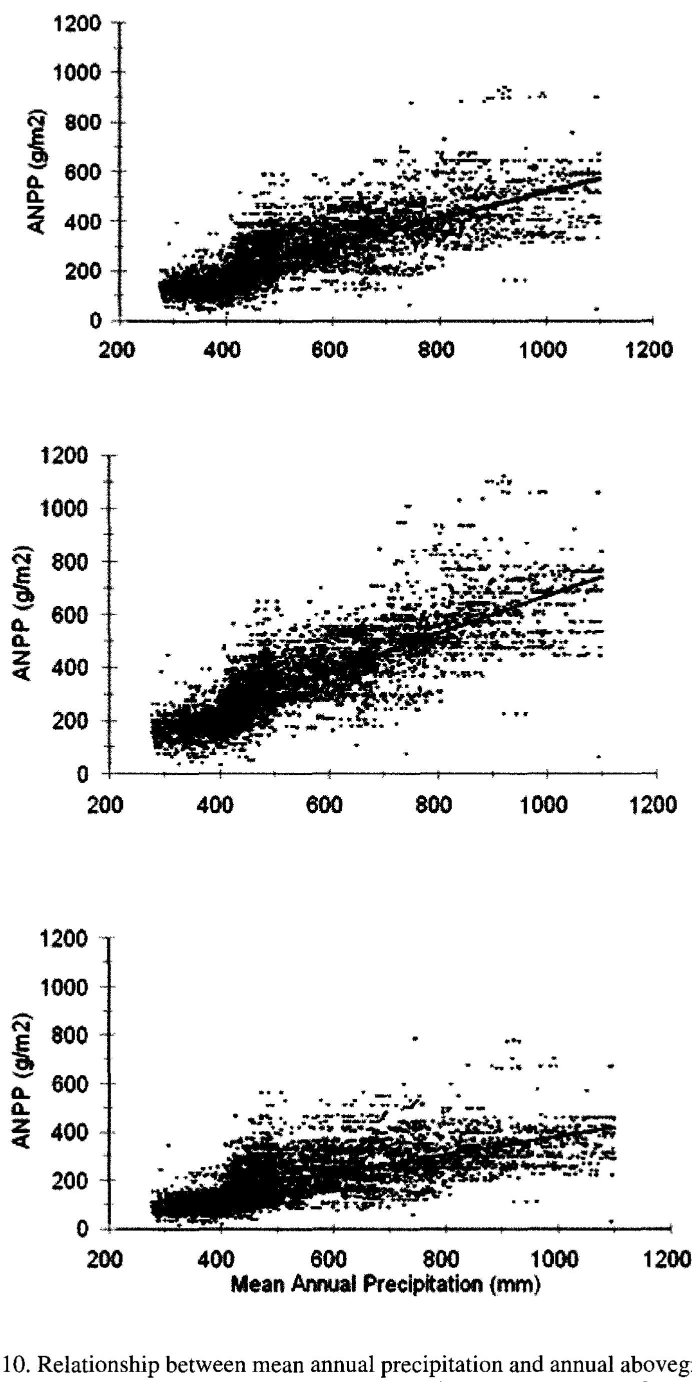

Figure 10. Relationship between mean annual precipitation and annual aboveground net primary production in (A) normal precipitation, (B) favorable (wet) and (C) unfavorable (dry) years in the US portion of the central grassland region of North America (ANPP=annual net primary production: see text).

productive sites were also the warmest and driest, while the most productive were the warmest and wettest. In the central grassland region, mean annual temperature explains 14% of the spatial pattern in annual aboveground net primary production.

Second, the spatial pattern of another of the important variables that affect annual aboveground net primary production, annual nitrogen availability, is also significantly related to mean annual precipitation (Burke et al. 1997b) (Fig. 11). Average annual nitrogen (N) mineralization (representing nitrogen availability to plants) ranges from less than 2.5 g N/m^2 in the driest and coldest portions of the region to greater than 10.5 g N/m^2 in the warmest and wettest parts. The high correspondence between mean annual precipitation and mean nitrogen availability makes it impossible to assess the independent influences of precipitation and nitrogen on annual aboveground net primary production.

Soil texture is another variable that influences annual aboveground net primary production through its effects on water and nitrogen availability. Noy-Meir (1973) suggested the "inverse texture effect" to explain the widely observed phenomenon of taller vegetation on coarse compared to fine textured soils in dry areas and the opposite in wet areas. Sala et al. (1988) tested whether the inverse texture effect held for annual aboveground net primary production as well as for plant height in the central grassland region; and, they found a small, but significant relationship. In the driest parts of the region, plant communities on coarse textured soils had greater annual aboveground net primary production than did those on fine textured soils. The opposite was true in the wettest portions. The relationship for normal years is:

$$ANPP = 32 + 0.45*MAP - 352*WHC + 0.95*MAP*WHC \qquad R^2 = 0.67 \quad (5)$$

where ANPP is annual aboveground net primary production in g/m^2, MAP is mean annual precipitation in mm, and WHC is water-holding capacity (an index of soil texture). This relationship predicts that below 370 mm/yr mean annual precipitation, sites with low water holding capacity (coarse texture) will be more productive than those with high water holding capacity (fine texture). Above 370 mm/yr, sites with high water holding capacity will be more productive than those with low water holding capacity. Epstein et al. (1997b), tested for an effect of texture on annual aboveground net primary production by stratifying the central grassland region into mean annual precipitation bands, using 50 mm increments. They also found an inverse texture effect on annual aboveground net primary production. Interestingly,

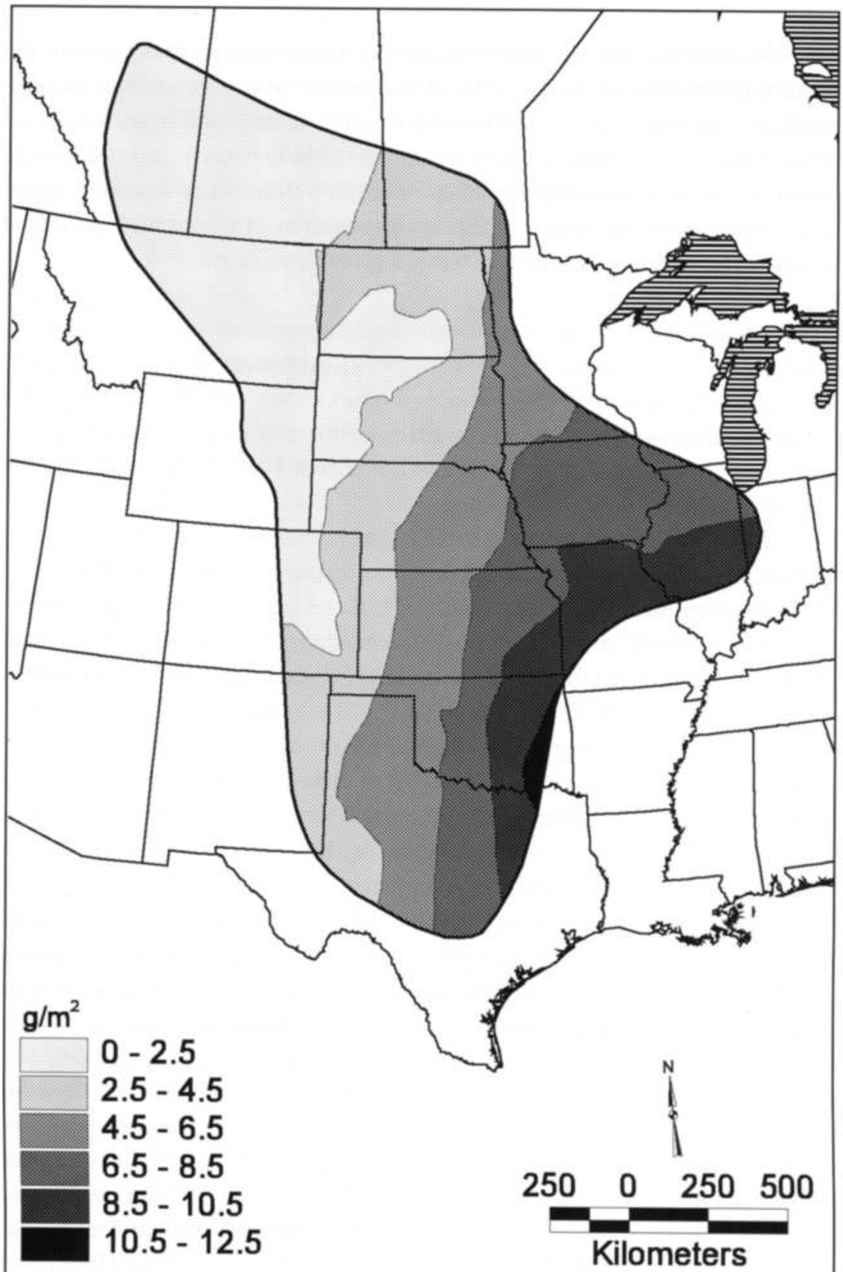

Figure 11. The spatial distribution of nitrogen availability to plants as annual net nitrogen mineralization (g N/m^2), in the central grassland region of North America (calculated from Burke et al. 1997b).

their results suggested the crossover point, where annual aboveground net primary production on coarse soils equals annual aboveground net primary production on fine soils, was 800 mm/yr, rather than 370 mm/yr (Sala et al. 1988). Even in the absence of additional data to help resolve this difference, we can reach two important conclusions at this time: 1) soil texture influences annual aboveground net primary production in the central grassland region, and 2) there is an inverse texture effect.

Biogeochemistry. Grassland soils are well-recognized for storing a large quantity of organic matter (Ajtay et al. 1979), with over 90% of total grassland ecosystem carbon located in the soil (Burke et al. 1997a). This large soil storage reflects both the large proportion of the primary production that is allocated belowground (Milchunas and Lauenroth 1992; Burke et al. 1997a), and the relatively low decomposition rates of that material (Dormaar 1992).

The strong environmental gradients across the central grassland region have created large gradients in soil organic carbon and nitrogen (Parton et al. 1987; Burke et al. 1989). Both soil carbon and nitrogen increase dramatically in an easterly direction along with mean annual precipitation, especially in the southern portion of the region. For example, along the gradient from eastern Colorado to eastern Kansas, soil organic carbon increases by a factor of two. And, along the gradient from western to eastern Texas, soil carbon increases by a factor of five. This strong gradient in soil organic carbon and nitrogen is the result of the annual aboveground net primary production gradient, which shows increasing inputs into soil organic matter from production with increasing precipitation.

Soil carbon and nitrogen decrease from north to south in the region (Burke et al. 1989). Previous interpretations have suggested that this gradient is due to the temperature dependence of decomposition. Decomposition increases as temperature increases, leading to lower soil organic matter levels in the southern portion of the region. Our recent analyses also suggest a role for the decrease in annual aboveground net primary production that occurs with increasing temperatures (Epstein et al. 2000). Soil texture also influences soil organic carbon and nitrogen in the central grassland region. Organic matter is highest in soils with high clay contents, and lowest in those with high sand content (Burke et al. 1989). The physical and chemical properties of clay protect organic matter from decomposition (Jenkinson 1977; Sorenson 1981). The ratio of carbon-to-nitrogen, which is an indicator of soil organic matter quality, follows the trends in total amounts. The highest ratios, and therefore lowest quality, occur at the: highest levels of precipitation, lowest temperatures, and highest clay contents.

Rates of biogeochemical cycling vary with the size and the quality of soil organic matter pools. Simulation analyses (Burke et al. 1997a) and field assessments indicate that nitrogen availability for plant growth (net nitrogen mineralization) increases with both mean annual temperature and precipitation. Although nitrogen availability increases with mean annual precipitation, the importance of nitrogen as a limiting factor for plant growth also increases with mean annual precipitation. The nitrogen content of litter (%) decreases across this gradient (Vinton and Burke 1997), suggesting that nitrogen availability becomes more limiting to plant growth as moisture increases. Litter decomposability, indexed by either carbon-to-nitrogen ratio or lignin-to-nitrogen ratio, also decreases as precipitation increases. The significance of these patterns for regional biogeochemistry is currently under study.

Current Land Use. A large fraction of the central grassland region has been converted to row-crop agriculture (Fig. 12). Since European settlers arrived in the region in the middle of the 19th century, the total area in native grasslands has decreased substantially, especially in the most productive areas. Most the areas with suitable soils and climatic conditions have been converted to cropland (Burke et al. 1994). The smallest proportion of native grassland remaining occurs in the tallgrass prairie region (Figs. 9, 12). Soil texture, mean annual precipitation, and mean annual temperature all play important roles in determining the probability of whether a location has been converted to cropland or not (Burke et al. 1994). The probability of conversion to cropland increases with increasing mean annual precipitation, and decreases with increasing mean annual temperature. Intermediate-textured soils (loams) have the highest probability of being cropped. Proximity to surface water or ground water for irrigation also increases the likelihood of cropping. Thus, the portion of the region with the largest amount of native vegetation is the shortgrass steppe, with nearly 50% remaining. The US portion of the northern mixed grass prairie has large areas in native vegetation, especially in western Nebraska and South Dakota, southeastern Montana, southwestern North Dakota, and eastern Wyoming. The Canadian portion of the northern mixed prairie has been extensively converted to cropland. Most of the remaining native grasslands are grazed by cattle (Lauenroth et al. 1994).

There are strong regional patterns in crop type and land management, as well. Much of the central, eastern half of the region has been converted into corn and soybeans (Figs. 13, 14). However, corn extends farther north than soybeans, into South and North Dakota in the US and Manitoba in

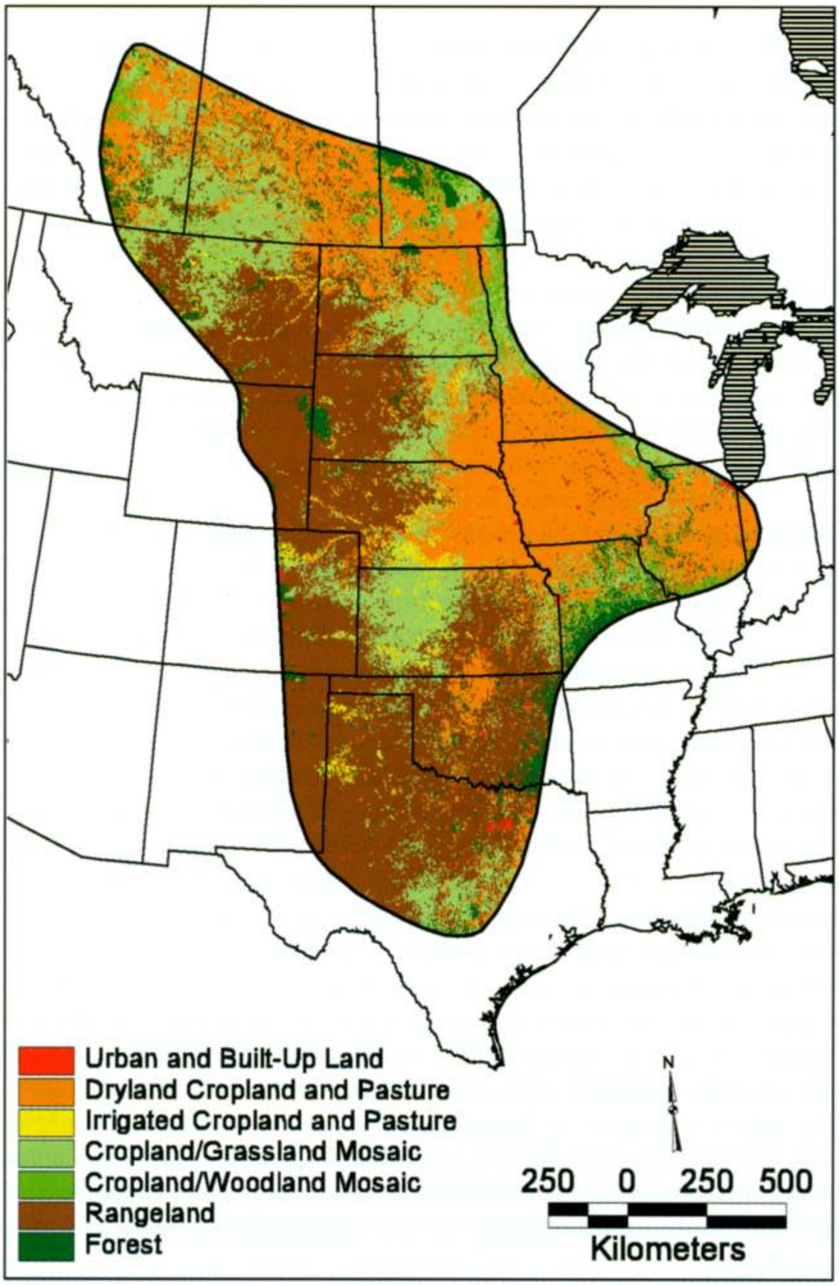

Figure 12. Spatial distribution of land use in the central grassland region of North America (data from the web site of the United States Geological Survey, North America Land Cover Characteristics Data Base: http://edcwww.cr.usgs.gov/landdaac/glcc/na_int.html).

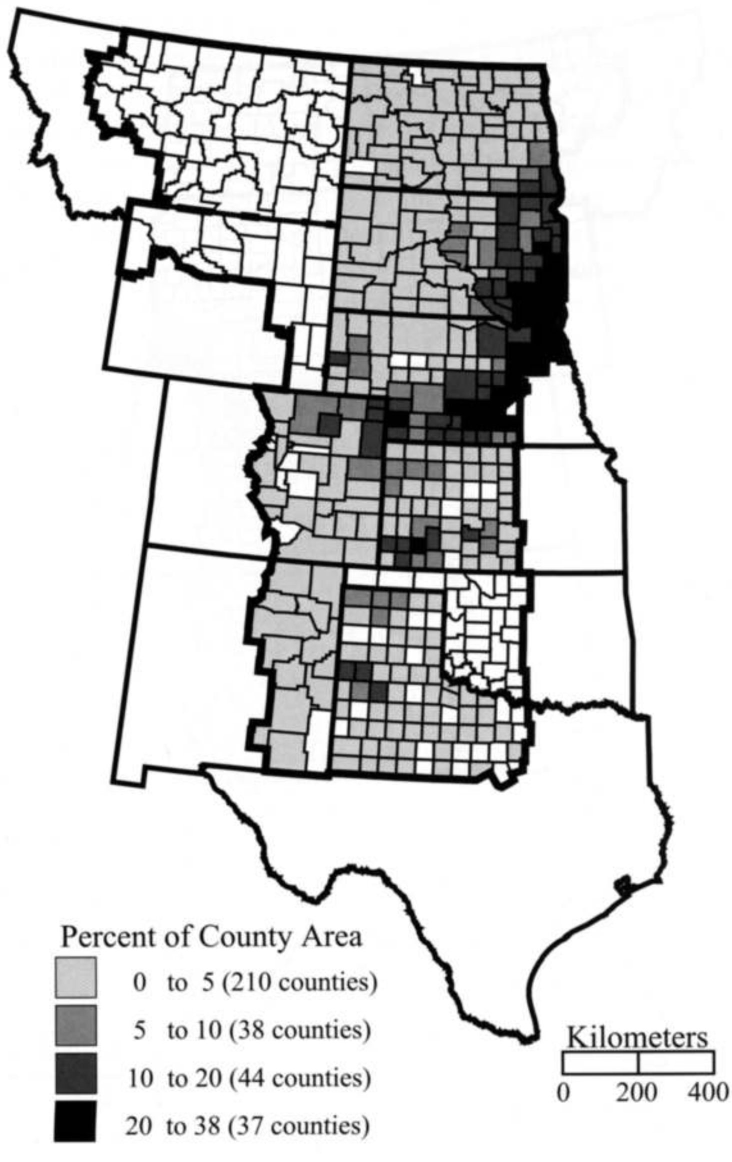

Figure 13. Corn in the US Great Plains: Acres harvested as a percent of county area, 1992 (original data from The United States Census of Agriculture (1992), collected in The University of Texas Population Research Center, Great Plains Population and Environment Database: Version 1.0, Austin: Texas Population Research Center, University of Texas at Austin, 1998).

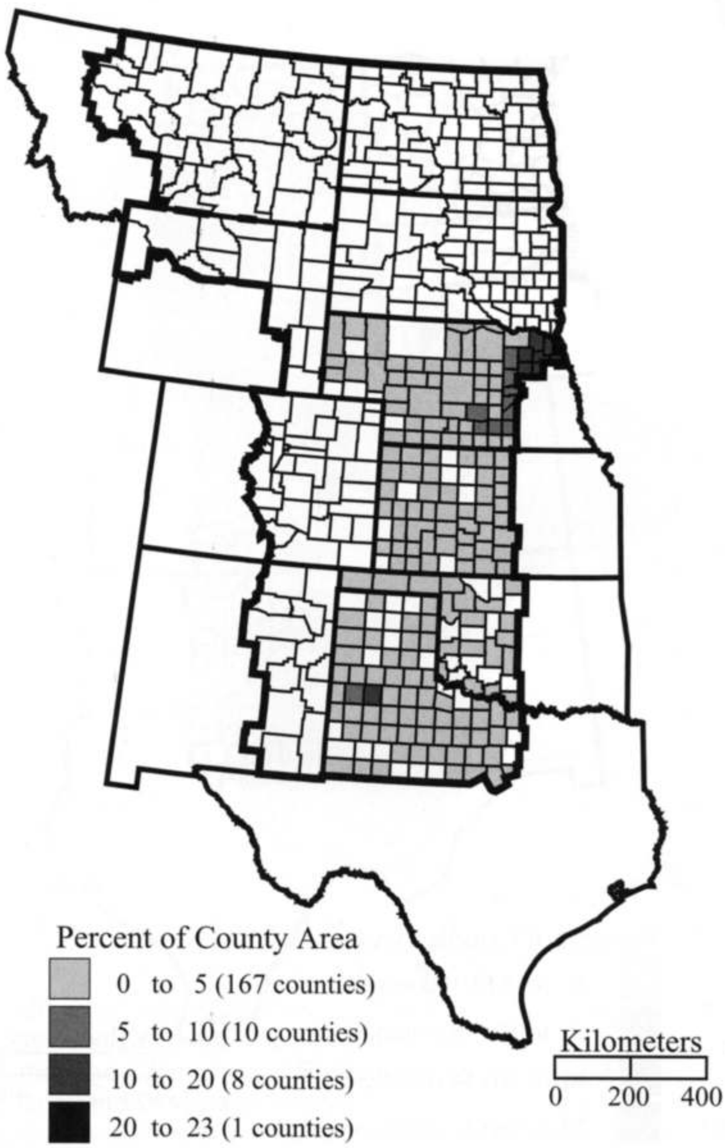

Figure 14. Soybeans in the US Great Plains: Acres harvested as a percent of county Area, 1992 (original data from The United States Census of Agriculture (1992), collected in The University of Texas Population Research Center, Great Plains Population and Environment Database: Version 1.0, Austin: Texas Population Research Center, University of Texas at Austin, 1998).

Canada (not shown). Wheat is grown throughout the entire central grassland region (Fig. 15). In the US, the amount of wheat grown increases from west to east, but its importance as a crop (percent of total cropped area) is highest in the west and north, especially in areas receiving less than 500 mm/yr precipitation. In the water-limited western portion, winter wheat is grown with a fallow rotation to allow soil water to accumulate during the fallow year. In the north, the crop is usually spring wheat. Cotton is an important crop in only the southern-most portion of the region (Fig. 16).

Conversion of native grasslands to croplands has had substantial effects on the vegetation, annual aboveground net primary production and nitrogen and carbon balance of the central grassland region. The loss of most of the tallgrass prairie exemplifies many of the negative influences of grassland conversion to cropland. Except for the Flint Hills in Kansas, the Osage Hills in Oklahoma and the Nebraska Sand Hills, the tallgrass prairie exists only as small fragments. These small parcels are difficult to manage, and they are extremely vulnerable to invasions by exotic plants. Although cultivation of corn and soybeans has increased annual aboveground net primary production, it also has resulted in a negative nitrogen and carbon balance and accelerated soil erosion (Paustian et al. 1997; Pimentel et al. 1995). In the drier portions of the central grassland region, conversion to cropland has likely increased annual aboveground net primary production in all but the very driest areas (Lauenroth et al. 2000), but soil carbon and nitrogen losses have been ubiquitous. Reports of soil carbon and nitrogen losses are common throughout the semiarid zone (Haas et al. 1957; Aguilar et al. 1988; Burke et al. 1989; Campbell and Zentner 1997; Jones et al. 1997). Such losses with cropping result from: a decrease in belowground net primary production, increased decomposition from tillage, removal of aboveground biomass for fodder or grain, and increased erosion associated with fallow treatments and tillage. Simulations for the central Great Plains have suggested that carbon losses after 50 years of cultivation (1900-1950) averaged 44% (Burke et al. 1994). Greatest losses were from summer-fallow winter wheat, where cropping intensity is lowest and fallow periods the longest; and, the smallest losses were from corn production.

Conclusions

The central grassland region, extending from the Gulf of Mexico to the southern edge of the boreal forest and from the foothills of the Rocky Mountains to the Mississippi River, is one of North America's most impor-

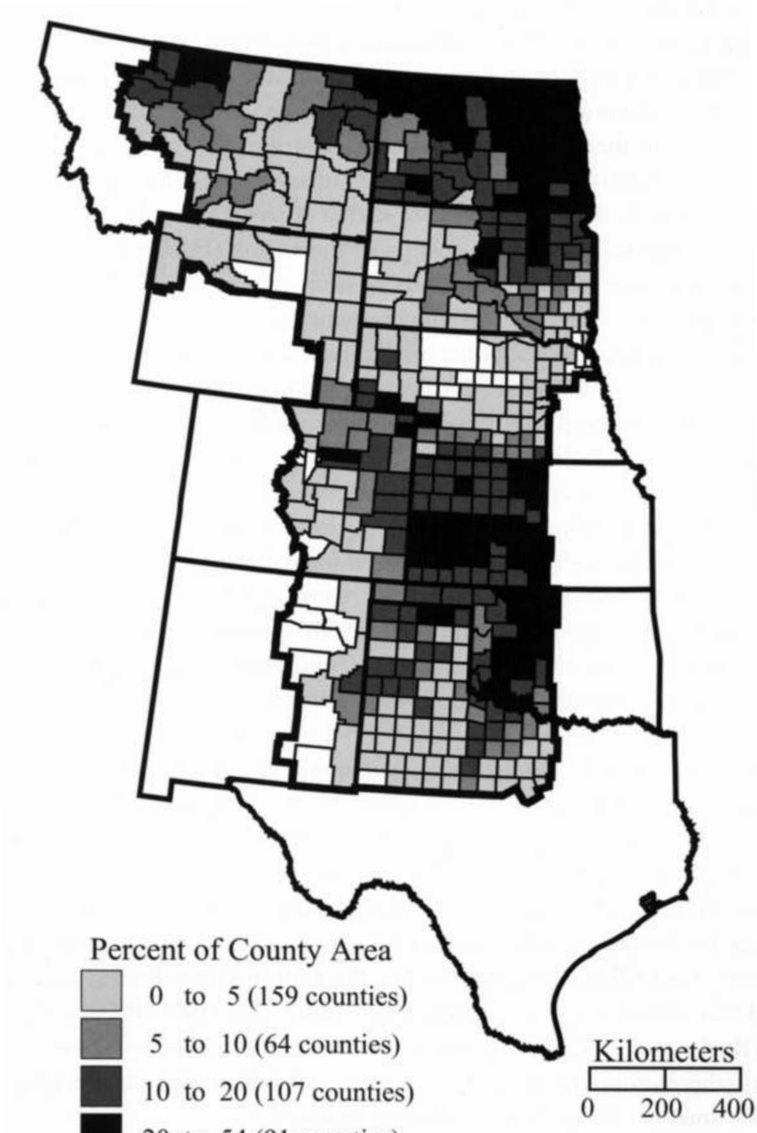

Figure 15. Wheat in the US Great Plains: Acres harvested as a percent of county area, 1992 (original data from The United States Census of Agriculture (1992), collected in The University of Texas Population Research Center, Great Plains Population and Environment Database: Version 1.0, Austin: Texas Population Research Center, University of Texas at Austin, 1998).

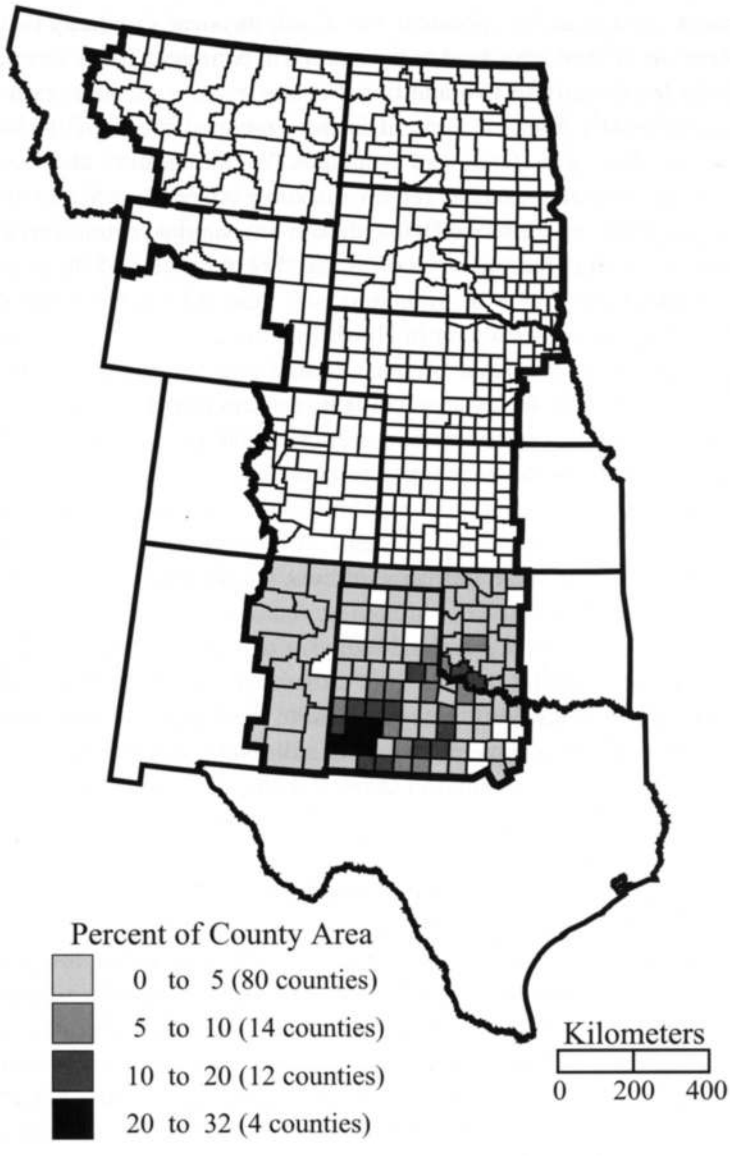

Figure 16. Cotton in the US Great Plains: Acres harvested as a percent of county Area, 1992 (original data from The United States Census of Agriculture (1992), collected in The University of Texas Population Research Center, Great Plains Population and Environment Database: Version 1.0, Austin: Texas Population Research Center, University of Texas at Austin, 1998).

tant and unique land resources. While similar grasslands occur on other continents, none have the political, social and physical simplicity that characterizes the central grassland region of North America. These characteristics have led directly to two additional characteristics of the region. First, from a scientist's point of view, it is the source of much of the world's knowledge about grasslands and croplands. We know more about ecosystems in the central grassland region of North America, whether they be native grasslands or agroecosystems, than in any similar region world-wide. Second, the central grassland region is the "bread basket" of the continent. It is an important source of grain and beef, and it contains more area of cropland than any other region in North America.

The physical gradients of precipitation and temperature provide an important framework for understanding ecosystem characteristics across the region. Plant biomass production, average plant height, annual nitrogen availability to plants and annual precipitation all increase from west to east. The relative importance of cool season (C_3) and warm season (C_4) plants change along the temperature gradient. As annual temperatures increase from north to south, the importance of cool season plants, both native and crop plants, decreases.

Because the central grassland region is of such continental and global importance, it is crucial that we have a thorough understanding of its ecological characteristics. Furthermore, because the forces that will shape the future states of ecosystems in the region will likely be different from those that have been most influential in shaping the current states, the knowledge that we gain now will be crucial to guide future management decisions.

Acknowledgments

We thank Chris Bennett and Sara Pullum for preparing the graphics. The participation of WKL and ICB in this work was partially supported by NSF grant (DEB 9350273) to the Shortgrass Steppe Long Term Ecological Research project at Colorado State University. WKL received additional support from the Colorado State Experiment Station (1-57661). MPG and ICB were supported by a grant from the National Institutes of Child Health and Human development (R01 HD33554).

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