12

Net Primary Production in the Shortgrass Steppe

William K. Lauenroth
Daniel G. Milchunas
Osvaldo E. Sala
Ingrid C. Burke
Jack A. Morgan

Net primary production (NPP), the amount of carbon or energy fixed by green plants in excess of their respiratory needs, is the fundamental quantity upon which all heterotrophs and the ecosystem processes they are associated with depend. Understanding NPP is therefore a prerequisite to understanding ecosystem dynamics. Our objectives for this chapter are to describe the current state of our knowledge about the temporal and spatial patterns of NPP in the shortgrass steppe, to evaluate the important variables that control NPP, and to discuss the future of NPP in the shortgrass steppe given current hypotheses about global change. Most of the data available for NPP in the shortgrass steppe are for aboveground net primary production (ANPP), so most of our presentation will focus on ANPP and we will deal with belowground net primary production (BNPP) as a separate topic. Furthermore, our treatment of NPP in this chapter will ignore the effects of herbivory, which will be covered in chapter 16.

Our approach will be to start with a regional-scale view of ANPP in shortgrass ecosystems and work toward a site-scale view. We will begin by briefly placing ANPP in the shortgrass steppe in its larger context of the central North American grassland region. We will then describe the regional-scale patterns and controls on ANPP, and then move to the site-scale patterns and controls on ANPP. At the site scale, we will describe both temporal and spatial dynamics, and controls on ANPP as well as BNPP. We will then discuss relationships between spatial and temporal patterns in ANPP and end the chapter with a short, speculative section on how future global change may influence NPP in the shortgrass steppe.

Aboveground Net Primary Production of the Shortgrass Steppe in the Context of the Central North American Grassland Region

Temperate grasslands in central North America are found over a range of mean annual precipitation from 200 to 1200 mm·y^{-1} and mean annual temperatures from 0 to 20 °C (Lauenroth et al., 1999). The widely cited relationship between mean annual precipitation and average annual ANPP allows us to convert the precipitation gradient into a production gradient (Lauenroth, 1979; Lauenroth et al., 1999; Noy-Meir, 1973; Rutherford, 1980; Sala et al., 1988b). Therefore, the position of the central North American grasslands on the production gradient is from less than 100 g·m^{-2}·y^{-1} to more than 600 g·m^{-2}·y^{-1} (Lauenroth et al., 1999).

The shortgrass steppe contains a large proportion of the least productive sites in the region. Paruelo and Lauenroth (1995) used normalized difference vegetation index (NDVI) data, which are correlated with ANPP (Paruelo et al., 1997), to compare sites within the grassland region. They found large differences among grassland types, supporting the idea that the shortgrass steppe is the least productive of the grassland types (Fig. 12.1).

Lane et al. (1998, 2000) sampled a transect across the precipitation gradient from the northern shortgrass steppe through the northern mixed prairie and into the tallgrass prairie. Their results also support the idea of low NPP in the shortgrass steppe compared with the remainder of the grassland region. They estimated annual ANPP and made measurements of leaf area index (LAI), and found that both increased significantly with increasing mean annual precipitation (Fig. 12.2A). Aboveground NPP ranged from 40 to 75 g·m^{-2} at the three shortgrass steppe sites, from 165 to 300 g·m^{-2} at three northern mixed prairie sites,
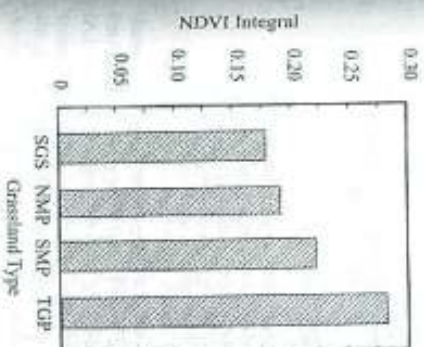

Figure 12.1 Normalized difference vegetation index (NDVI) integrated over the growing season for the shortgrass steppe (SGS), northern mixed prairie (NMP), southern mixed prairie (SMP), and tallgrass prairie (TGP). Each bar represents the average over several sites. (Adapted from Paruelo and Lauenroth [1995])

ANPP (g m⁻²)

LAI (m² m⁻²)
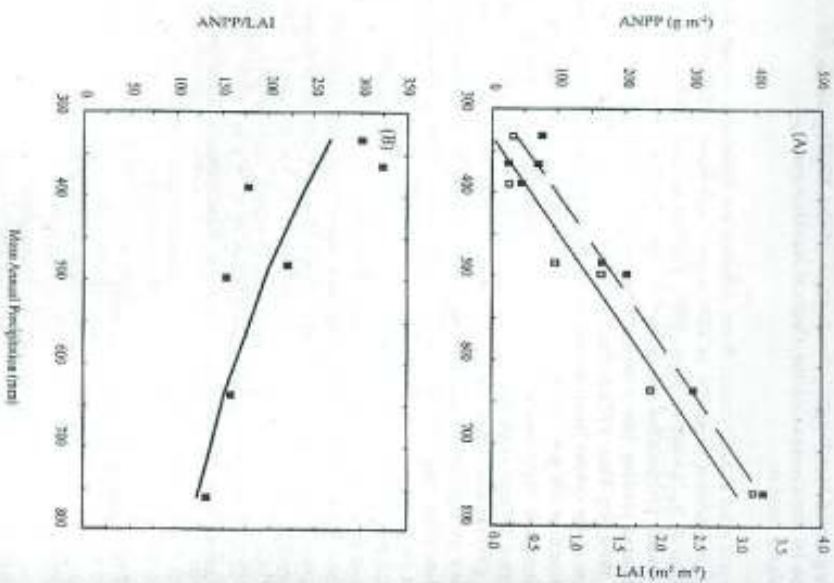
ANPP/LAI

Mean Annual Precipitation (mm)

Figure 12.2 The relationship among annual aboveground net primary production (ANPP), leaf area index (LAI), mean annual precipitation (A); and ANPP per unit of LAI as a function of mean annual precipitation across the central grassland region (B). (Data from Lane et al. [1998, 2000].)

and was 410 g·m⁻² for a tallgrass prairie site. Leaf area index averaged approximately 0.25 at the shortgrass sites, ranged from 0.75 to 1.9 at the northern mixed prairie sites, and was 3.15 at the tallgrass site. The relationship between LAI and ANPP suggests that the amount of NPP produced per unit LAI decreases along the precipitation gradient from the shortgrass steppe to the tallgrass prairie (Fig. 12.2B). Lane et al. (2000) estimated the amount of light reaching the soil

Mean Annual Temperature (C)

Mean Annual Precipitation (cm)

C_3 Dominant

C_4 Dominant

Shortgrass Steppe

Great Plains

C_3 Grasses (%)
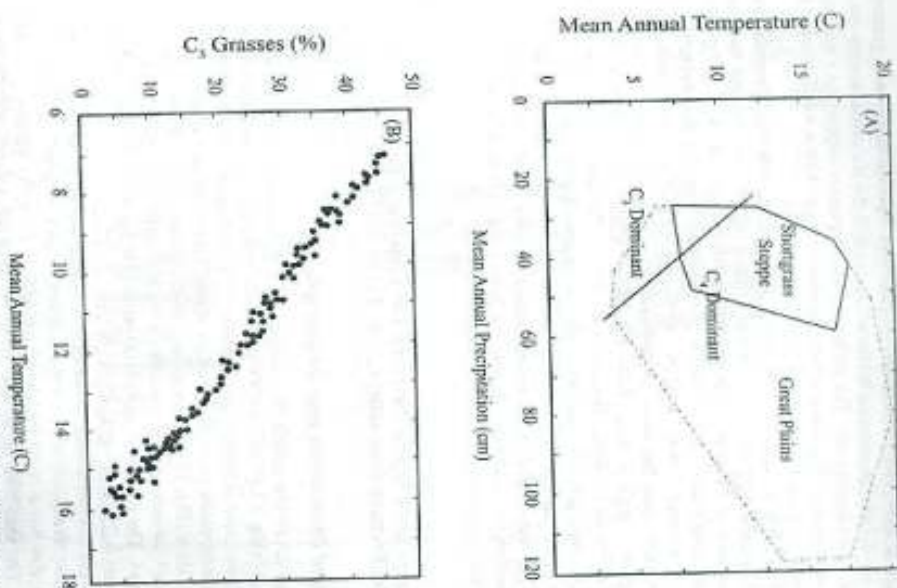
Mean Annual Temperature (C)

Figure 12.3 (A) The location of the shortgrass steppe in the parameter space defined by mean annual precipitation and mean annual temperature relative to the entire Great Plains. The solid diagonal line divides the space into portions dominated by C_3 or C_4 plants. (Adapted from Epstein et al. [1997b].) (B) The relationship between the percentage contribution of C_3 grasses to aboveground net primary production and mean annual temperature in the shortgrass steppe. (Data from Fan [1993].)

surface at maximum canopy development and reported that it was greater than 90% for the shortgrass sites, between 0% and 10% for the mixed prairie sites, and 0% for the tallgrass site. The picture of the shortgrass steppe that emerges from this work is one of a low-productivity environment with a small amount of the soil surface shaded by the leaves of plants.

The shortgrass steppe combines low precipitation with high temperatures. It is found in areas with mean annual temperatures more than 7 °C and mean annual precipitation less than 625 mm (Fig. 12.3A). Based upon the work of Epstein et al. (1997b) a very small portion of the environmental space of the shortgrass steppe (Fig. 12.3A) favors the dominance of C_3 species. Regression relationships from this work suggest that the percentage that C_3 grasses contribute to ANPP in the shortgrass steppe on sandy loam soils should range from more than 40% in the north to 0% in the south (Epstein et al., 1997b). The decrease in C_3 grasses from north to south is linear with increasing mean annual temperature (Fig. 12.3B).

Thus, the shortgrass steppe is a dry grassland that is dominated by short-statured C_4 grasses that develop a sparse canopy with a low LAI. These characteristics combine to result in its having the lowest annual ANPP in the central North American grassland region.

Regional-Scale Spatial Patterns and Controls on Net Primary Production

Effects of Precipitation and Temperature

Average ANPP throughout the shortgrass steppe ranges from 50 g·m⁻² to more than 300 g·m⁻² (Fig. 12.4 [USDA, 1967]). The mean of estimates for average years is 178 g·m⁻², with a spatial coefficient of variation (CV) of 38%. Predictably, the distribution during unfavorable years shifts toward smaller values; and in favorable years, toward larger values (Fig. 12.4). During unfavorable years, 10% of the sites have ANPP ≤50 g·m⁻², whereas during favorable years 10% of the sites have ANPP more than 400 g·m⁻². The mean for unfavorable years is 103 g·m⁻² (CV, 50%), and for favorable years is 250 g·m⁻² (CV, 35%).

The key environmental variables that explain the differences among locations within the shortgrass steppe are precipitation and temperature (Fig. 12.5). Soil texture also has a small but significant influence on the regional distribution of ANPP. The sites with the lowest ANPP occur in the warmest and driest parts of the region (western Texas and southeastern New Mexico, Fig. 12.5B). Sites with the greatest ANPP occur at a mean annual precipitation of more than 400 mm·y⁻¹ in three areas: (1) northeastern Colorado, southeastern Nebraska, and northeastern Kansas; (2) the northeastern portion of the panhandle of Texas and northeastern New Mexico; and (3) southern Colorado adjacent to the mountains. These are the sites with the greatest amounts of effective precipitation. As mean annual temperature (MAT) increases, mean annual potential evapotranspiration also increases (MAPET [measured in centimeters] = 94 + 5 × MAT, r^2 = 0.71 [Lauenroth and Burke, 1995]), resulting in a requirement for greater precipitation to maintain
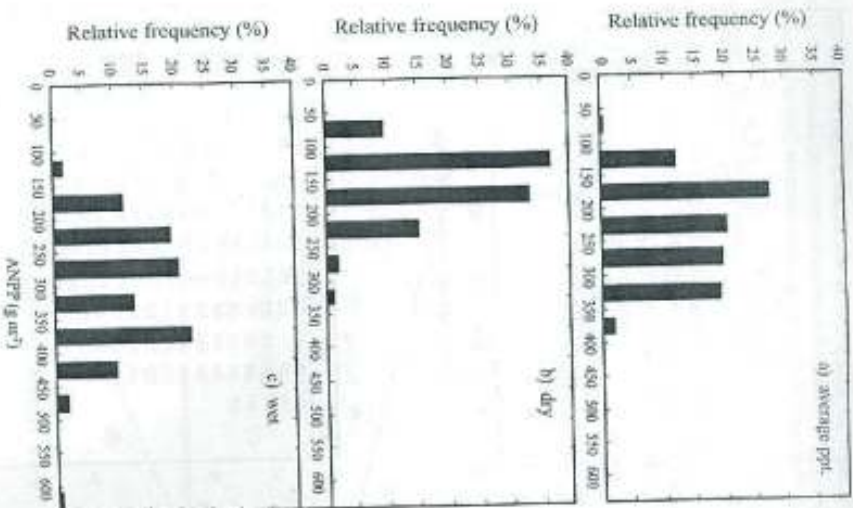

Figure 12.4 Frequency distributions of annual aboveground net primary production (ANPP) in the shortgrass steppe for normal (average) (A), unfavorable (dry) (B), and favorable (wet) (C) years. These data were collected by the Natural Resources Conservation Service as part of their Range Site database (USDA, 1967). The data represent ANPP for different sites throughout the shortgrass region.

a similar amount of ANPP. Vertical slices through Figure 12.5A provide examples of this effect. For instance, at a mean annual precipitation of 450 mm, ANPP ranges from 240 g·m⁻²·yr⁻¹ at 9 °C mean annual temperature to 175 g·m⁻²·yr⁻¹ at 16 °C.

Effects of Soil Texture

The role that soil texture plays in influencing ANPP can be illustrated by an analysis of data collected by the NRCS in north-central Colorado (Fig. 12.6A). Aboveground NPP decreases as water-holding capacity increases. Water-holding
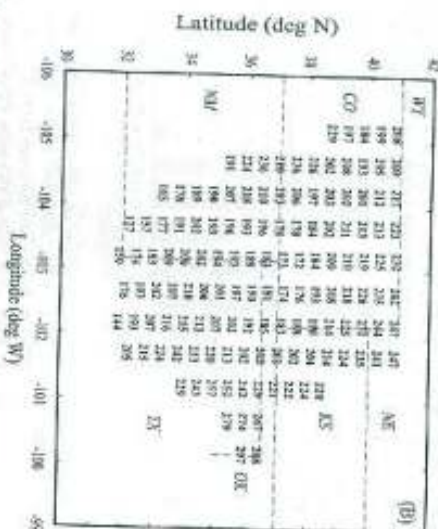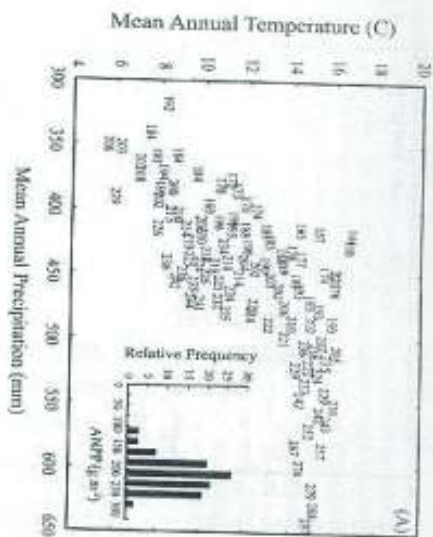
Figure 12.5 Distribution of annual aboveground net primary production (ANPP) in the shortgrass steppe. (A) Distribution of ANPP (measured in grams per square meter) as a function of mean annual precipitation and mean annual temperature. (B) Distribution of ANPP (measured in grams per square meter) as a function of longitude and latitude. See Figure 12.4 for description of the database.
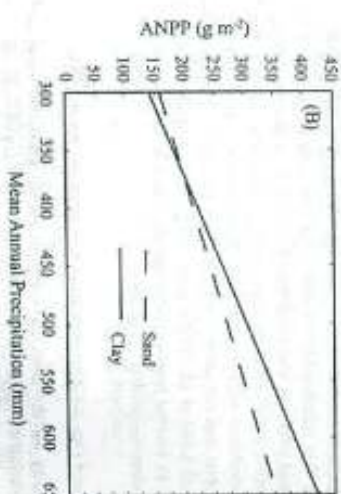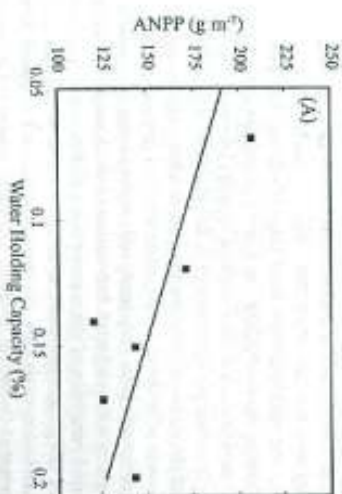
Figure 12.6 Relationship between (A) waterholding capacity of soils and average annual aboveground net primary production (ANPP) and (B) mean annual precipitation and ANPP for two soil texture classes from sites in Weld County, Colorado. See Figure 12.4 for a description of the database.

capacity is largely determined by soil texture and has a large influence on soil water availability and water balance (Cosby et al., 1984; Lauenroth and Bradford, 2006). A decrease in ANPP in dry areas as water-holding capacity increases is consistent with the inverse texture effect (Noy-Meir, 1973), which states that in dry areas, coarse-textured soils should be more productive than fine-textured soils and the reverse should be true for wet areas (Fig. 12.6B). The explanation lies in the relative roles of bare soil evaporation and percolation below the root zone. Coarse-textured soils have low water-holding capacity and low losses to bare soil evaporation. This results in more water available for plant growth in dry areas and less in wet areas. This effect can be best illustrated by evaluating the two extreme cases of clay and sand (Fig. 12.6B). At the wettest sites (≈650 mm·y⁻¹), ANPP on clay soils averages 70 g·m⁻² more than that on sandy soils, at the dry end of the gradient (300 mm·y⁻¹), sandy soils have an ANPP that is approximately 20 g·m⁻² more than that found on clay. The inverse texture effect (Fig. 12.6B) provides an explanation for why the relationship between ANPP and water-holding capacity for sites in north-central Colorado decreases as water-holding capacity increases (Fig. 12.6A). These sites have mean annual precipitation that is less than 375 mm, which puts them on the dry side of the crossover point for the inverse texture effect (Fig. 12.6B).

Another source of evidence for the existence of an inverse texture effect can be found in the observation that deep sandy soils in the shortgrass region tend to support taller vegetation than adjacent fine-textured soils. Küchler (1964) mapped the potential natural vegetation of the conterminous United States and indicated that on deposits of deep sand associated with major rivers in the shortgrass region, tallgrasses (*Andropogon* sp.) are dominant, whereas the adjacent fine-textured soils are dominated by the shortgrasses *Bouteloua gracilis* and *Buchloe dactyloides*. Fan (1993) evaluated the distribution of species and functional groups in eastern Colorado and found that production of C₄ grasses was significantly and positively related to sand content of the soil (r²=0.56; P = .0001). Investigation of the details of this relationship revealed that the largest proportion of ANPP at the highest sand contents was contributed by tallgrass species. Average ANPP at low sand contents (<60%) was 65 g·m⁻², and at high sand contents was 120 g·m⁻². Most of the evidence supports the idea of an inverse texture effect at both the shortgrass steppe and the central grassland region scales. The single contrasting study is that of Lane et al. (1998); and it is possible that the lack of support in these data for an inverse texture effect was the result of insufficient sample size to deal with quadrat-to-quadrat variability.

Effects of Land Use on Aboveground Net Primary Production

A current reality for the shortgrass steppe and all grassland areas worldwide is that only a portion of the original area of grassland remains in native vegetation (Lauenroth et al., 1999). More than half the area within the shortgrass steppe remains in native vegetation (Lauenroth and Milchunas, 1992; Lauenroth et al., 1999; Hart, chapter 4, this volume). The remainder is split between dryland and irrigated crops. The major dryland crop is winter wheat and the key irrigated crop is corn. Although other crops are grown under dryland and irrigated conditions, these two account for the largest part of the area harvested each year.

It is difficult to estimate NPP for crops, but by making some assumptions we can get approximate numbers for corn and wheat. If we assume that all corn produces the same amount of aboveground biomass as the corn grown for silage, then on average, production is 4250 to 4790 g·m⁻². This is under irrigated and fertilized conditions, and is approximately 20 times the average ANPP of the native shortgrass steppe. This level of production is restricted to those areas with either surface irrigation water, such as along the major rivers, or where water can be pumped to the surface.

Dryland wheat production can be statistically related to environmental variables, so that we can make comparisons with native grasslands. In the central Great Plains, including the shortgrass steppe, winter wheat is grown using the summer-fallow rotation system (USDA, 1974). This rotation system produces one crop in 2 years. Lauenroth et al. (2000) analyzed summer-fallow wheat production for the central Great Plains and found the following relationship between ANPP of winter wheat and mean annual precipitation (MAP):

$$\text{ANPP} \ (g \cdot m^{-2}) = 197 + 0.2 \times \text{MAP}$$
$$(mm) \ (r^2 = 0.67)$$

This equation incorporates the fact that at a particular location, only one wheat crop is produced in 2 years.

Over the range of mean annual precipitation found in the shortgrass steppe, grassland ANPP increases more rapidly with increasing precipitation than does wheat (Fig. 12.7). Between 325 and 575 mm mean annual precipitation, ANPP of winter wheat is greater than that of the native shortgrass steppe. At a mean annual precipitation more than 575 mm, native steppe production is greater than wheat. The likely explanation for greater production of wheat in the driest locations is that the
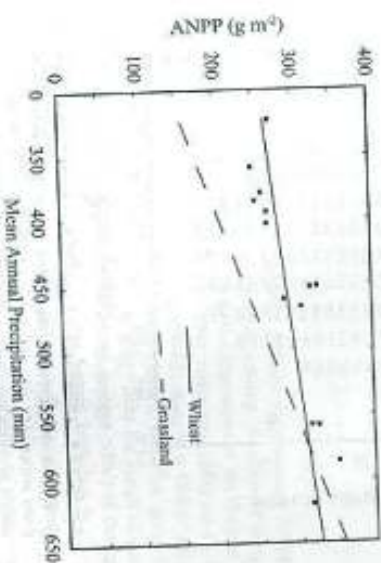

Figure 12.7 Relationship between mean annual precipitation and annual aboveground net primary production (ANPP) for native grasslands and summer-fallow winter wheat in the shortgrass steppe. (Adapted from Lauenroth et al. [2000].)

summer-fallow rotations system on average produces more favorable soil water conditions for plant growth and less variability among years than in the adjacent grasslands. The crossover point at 575 mm is the point at which there is no advantage to the summer/fallow system, and continuous cropping would be more desirable.

The decreased variability of winter wheat ANPP relative to the native shortgrass steppe is very apparent from a spatial analysis (Fig. 12.9). Although the

Figure 12.8. Distribution of annual aboveground net primary production (ANPP) for summer-fallow winter wheat in the shortgrass steppe. (A) Distribution of ANPP as a function of mean annual precipitation (MAP) and mean annual temperature. (B) Distribution of ANPP as a function of longitude and latitude. Aboveground NPP was calculated from the regression equation $ANPP (g \cdot m^{-2}) = 197 + 0.2 \times MAP (mm)$ ($r^2 = .67$) (Lauenroth et al., 2000).

spatial distribution of average grassland ANPP ranges from 125 g·m⁻² in the extreme southwestern portion of the steppe to almost 300 g·m⁻² in the southeast (Fig. 12.5). winter wheat ANPP only varies from 261 to 328 g·m⁻². One caution about these results is that the relationship between winter wheat ANPP and mean annual precipitation was developed with data from the northern portion of the steppe and may not do as good a job representing the southern portion. The intercepts for the two equations relating ANPP to mean annual precipitation lead to additional speculation about the differences. Noy-Meir (1973) interpreted the x-in-tercept of such relationships as the amount of precipitation required to maintain zero production. In the case of grasslands, 57 mm is required to maintain zero production. The winter wheat equation had a positive y-intercept, suggesting that if precipitation is zero, ANPP would still be greater than zero. This is consistent with the idea of water storage during the fallow period. Average winter wheat ANPP over the shortgrass steppe precipitation gradient is 294 g·m⁻². The y-in-tercept (197 g·m⁻²) suggests that, on average, 67% of ANPP is attributable to the fallow period.

Site-Scale Spatial Patterns and Controls on Net Primary Production

Controls, or at least correlates, of the spatial pattern of ANPP are much clearer at the regional scale than at the site scale. Climatic influences seem to be the key controls at the regional scale. At the site scale, climatic conditions are either constant or vary only a small amount. All the work on site-scale spatial variability of ANPP in the shortgrass steppe has been conducted at the Central Plains Experimental Range (CPER).

Effects of Soil Texture

One of the techniques that holds the greatest promise for assessing ANPP at the square kilometer scale is satellite-based remote sensing. Analysis of imagery for the CPER indicates the spatial variability in the vegetation at the scale of tens of square kilometers (Anderson, 1991; Todd, 1994). Anderson (1991) used a Landsat Thematic Mapper scene to create a spectral classification of a 42-km² area in the northeast portion of the CPER into greenness classes. Data for green biomass from harvested plots ranged from 43 to 190 g·m⁻² over the range of greenness classes and green biomass. His equation for the August 1989 data is

$$\text{Green Biomass } (g \cdot m^{-2}) = 30.8 + 434.5 \times NDVI \ (r^2 = 0.95)$$

Regressions for two other periods produced coefficients of determination of 0.71 and 0.95 (Anderson, 1991). Although Anderson (1991) did not attempt to relate green biomass to environmental variables, a qualitative analysis of the relationship between his spatial distribution of green biomass and a soil texture map

for the CPER (not shown) suggests that landscape position and surface horizon soil texture both may influence green biomass.

The soils at the CPER, similar to most other sites in the shortgrass steppe that have remained in native vegetation, are predominantly coarse in texture. The most common texture is fine sandy loam. Todd (1994) used Landsat Thematic Mapper data for the entire CPER (65 km²) to investigate relationships between spectral indices and standing crop biomass. She found a number of significant relationships between indices derived from satellite data and standing crop of grazed sites, but fewer for ungrazed sites. Reanalysis of the data presented by Todd (1994) revealed a significant relationship between soil texture (clay content) and standing crop (Fig. 12.9), but it is possible that the key controlling variable is landscape position rather than clay (see the next section on landscape effects). One of the things that argues against the importance of clay in this relationship is that the majority of our field data indicate that ANPP is greatest on sandy soils.

The data from the two Thematic Mapper images used by Todd (1994) produced relationships with different y-intercepts but otherwise similar forms. The June 22, 1984, image produced standing crop values that were, on average, 32 g m⁻² more than the July 12, 1991, image. Precipitation in 1991 was very near the long-term average, and in 1984 was 30% greater than the average. This likely accounts for the difference in standing crop between the 2 years.

Seven years of data from the CPER collected on a loamy sand and a clay loam site approximately 5 km apart support the idea that ANPP on coarse-textured soils is greater than on fine-textured soils (Fig. 12.10). Six of the seven ratios
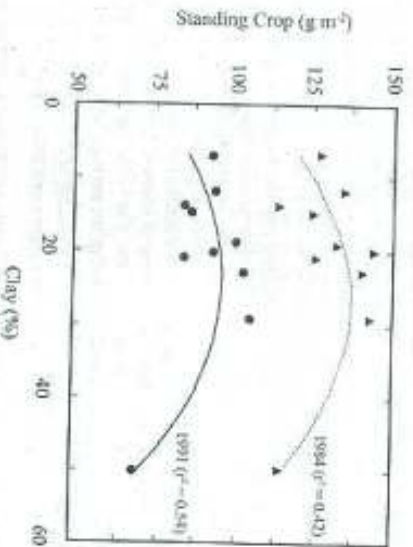
Figure 12.9 Relationship between standing crop biomass for the CPER predicted from Thematic Mapper data and clay content. (Data from Todd [1994].)
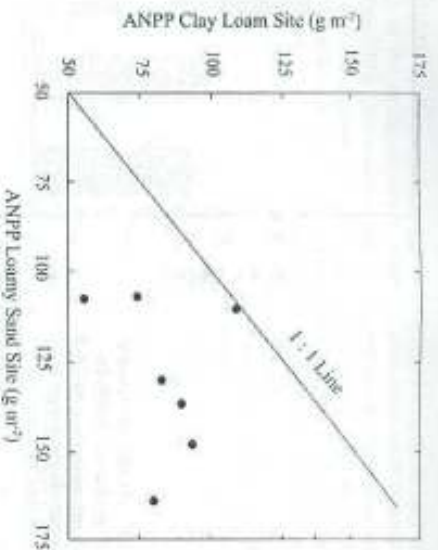

Figure 12.10 Relationship between annual aboveground net primary production (ANPP) on a loamy sand and a clay loam site at the CPER.

of ANPP fine to ANPP coarse were between 0.45 and 0.80 and were not significantly related to annual precipitation. In 1 year, the ratio was approximately one. Dodd and Lauenroth (1997) used a soil water simulation model to compare these two sites and found that, on average, over 50 years, a greater fraction of soil water was lost via transpiration from the loamy sand than from the clay loam site. Conversely, a greater fraction of the water was lost to bare soil evaporation on the clay loam than the loamy sand site. These results are consistent with greater ANPP for the coarse- versus the fine-textured site.

Landscape Effects

In addition to the effects of soil texture, landscape position has a complex effect on ANPP that is not easy to partition into individual controlling factors. Sixteen years of data collected from three landscape positions at the CPER indicate that there are small differences in ANPP between upland and midslope positions, but large differences between swales and either of the other two landscape positions (Fig. 12.11). A simple soil texture explanation does not account for these differences because in this example both the midslope and swale positions have the same soil textures. The upland position has a clay loam soil and the midslope and swale positions both are on sandy clay loam soils. The most likely explanation for these differences lies in a combination of effects of soil texture, soil water, and nitrogen. Swale positions can receive additional water via runon or interflow and in some cases have higher soil carbon and nitrogen contents (Burke et al., 1999, Yonker et al., 1988).

Figure 12.11 Annual aboveground net primary production (ANPP) for three landscape positions at the CPER. Each bar represents the average of 17 years. The vertical lines are 1 SE.

ANPP (g m⁻²)
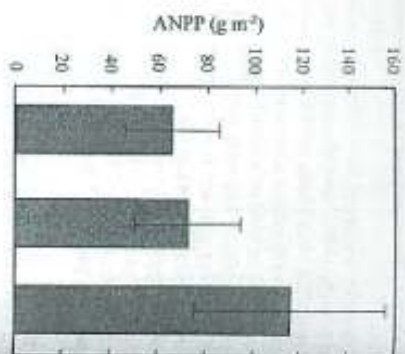
Temporal Patterns and Controls

Ecophysiology of Shortgrass Plants

The physiological responses of shortgrass steppe plants have often been studied within the context of functional types (e.g., morphological groups, such as shrubs, grasses, forbs, succulents; or photosynthetic groups, such as C_3, C_4, and crassulacean acid metabolism [CAM]; and generally in response to variation in water and temperature, the two most important environmental constraints to plant production in this region (Detling et al., 1978; Dickinson and Dodd, 1976; Kemp and Williams, 1980; Sala et al., 1992). These functional types have frequently been discussed in regard to plant distribution, but they have significance for temporal variation in primary production as well. For instance, shrubs can be important on soils (Dodd and Lauenroth, 1997; Lane et al., 1998; Lauenroth and Milchunas, 1992; Sala et al., 1997) or in climates (Knight, 1994; Sala et al., 1997) that encourage deep percolation of water. Deep-rooted shrubs and forbs can take advantage of water stored below surface layers where roots of grasses and succulents dominate (Coffin and Lauenroth, 1990). Similarly, variation in seasonal ANPP of a site and of individual species depends to a large extent on the interactions among seasonality and amount of precipitation, soils, and plant types (Epstein et al., 1997a). On sites with a significant shrub component, large precipitation events will likely lead to substantial production responses of both grasses and shrubs, whereas small precipitation events will enhance primary grass production (Dodd and Lauenroth, 1997). Because deep soil water is less variable and ephemeral than shallow soil water, the seasonal dynamics of shrub production should be less variable than for shallow-rooted grasses (Sala and Lauenroth, 1982).

Similar kinds of morphological differences in rooting apply as well to the majority of the shortgrass steppe, which is grass-dominated (Lauenroth and Milchunas, 1992). Cool-season grasses such as Agropyron smithii tend to be more deep-rooted than the warm-season, dominant B. gracilis (Coupland and Johnson, 1965; Weaver and Albertson, 1956), and these differences in rooting characteristics can result in different soil-plant water dynamics (Dodd and Lauenroth, 1997; Sala et al., 1992). Furthermore, leaf water potential and leaf conductance of B. gracilis sometimes appear to be more sensitive to changes in soil water compared with A. smithii (Morgan et al., 1998; Sala and Lauenroth, 1982; Sala et al., 1982), responses that could be related to differences in rooting characteristics.

The other important functional typing that has often framed physiological studies on the shortgrass steppe involves the photosynthetic pathway—specifically, the categorization of plants into C_3, C_4, and CAM (Black, 1971, 1973). Of the three types, CAM plants are the smallest group represented in the shortgrass steppe and are especially noted for their adaptations to xeric environments. Opuntia is the most prominent CAM genus of the region (Lauenroth and Milchunas, 1992). An abundance of both C_3 and C_4 perennial grasses dominates the shortgrass steppe, although the majority of physiological studies have focused on contrasting two important, representative species: the C_4 A. smithii and the C_4 B. gracilis. Bouteloua gracilis has a higher temperature optimum for photosynthesis (Brown, 1977; Kemp and Williams, 1980; Monson et al., 1983; Read et al., 1997), requires more light to saturate photosynthesis (Brown and Trlica, 1977; Williams and Kemp, 1978), and has greater water use efficiency (Monson et al., 1986; Morgan et al., 1998) compared with the C_3 native A. smithii. These traits partly explain the dominance of B. gracilis in this semiarid steppe; they have also been used to explain the temporal variation in production between these two grasses as a mechanism for niche separation (Monson et al., 1983).

At the site level, seasonal and yearly variation in the dynamics of precipitation and temperature account for most of the temporal and precipitation variation in physiological activity. The period when both temperature and precipitation create favorable conditions is, to a large extent, limited to May, June, and July (Lauenroth and Milchunas, 1992; Sala et al., 1992). The early part of this period is most favorable for photosynthesis and growth of cool-season C_3 grasses and sedges (Kemp and Williams, 1980; Monson et al., 1983; Reed and Morgan, 1996; Read et al., 1997). Furthermore, the distribution of soil water tends to be deeper in the profile early during the growing season than at other times (Sala et al., 1992), a factor that may be important for deeply rooted C_3 grasses.

As the growing season progresses and temperatures warm, growth of the dominant C_4 species B. gracilis and B. dactyloides commence, about a month to a month and a half after C_3 grasses and sedges first begin growth (Dickinson and Dodd, 1976; Monson and Williams, 1982). Precipitation amounts peak, and photosynthetic and growth rates reach seasonal maxima in May and June, resulting in rapid increases in biomass (Brown and Trlica, 1977; LeCain et al., 2002).

After the first of July, increased evaporative demand means that recharge of the soil water stores is unlikely, and water from precipitation is held only briefly in the surface soil layers before being transpired or evaporated (Sala et al., 1992;

These drier and warmer conditions in mid to late summer strongly favor growth of C_4 grasses. Rates of community photosynthesis tend to be less this time of year because of water stress (Brown and Trlica, 1977; LeCain et al., 2002). Continued photosynthesis and growth of C_4 grasses in late summer is due in large part to their warm-season C_4 metabolism, which can maintain photosynthetic activity up to relatively high temperatures (Brown and Trlica, 1977; Detling et al., 1978; Kemp and Williams, 1980; Monson et al., 1983; Read and Morgan, 1996; Reed et al., 1997), plus their shallow root system that is able to utilize soil water efficiently that is available mostly near the soil surface. The characteristic high water use efficiency (Monson et al., 1986; Morgan et al., 1998) and stomatal sensitivity (Morgan et al., 1998; Sala and Lauenroth, 1982; Sala et al., 1982) of the C_4 grass *B. gracilis* may be important adaptations that allow continued growth of this species at this time of year. High light saturation of photosynthesis in *B. gracilis* (Brown and Trlica, 1977; Williams and Kemp, 1978) may also be important in the dominance and functioning of this species during summer months in a region characterized by low leaf area and few cloudy days.

LeCain et al. (2002) illustrated how the seasonality of CO_2 fluxes on the shortgrass steppe is tied to soil water. They used chambers to measure CO_2 exchange every 2 to 3 weeks during the 1995 to 1997 growing seasons, and measurements were adjusted to subtract soil respiration, giving an estimate of community net photosynthesis. Precipitation in 1996 was close to long-term norms for the site (Fig. 12.12). In contrast, spring in 1995 was unusually wet, followed by a dry summer, whereas 1997 had below-average precipitation late during the second half of the growing season. The effects of these different precipitation patterns on soil water content, and consequently on net photosynthesis of the plant community in this semiarid steppe, are evident (Fig. 12.12), and illustrate how seasonal and year-to-year variability in precipitation are, in large part, the basis for differences in NPP.

In summary, the temporal variation in productivity of the shortgrass steppe occurs primarily in response to variations in water and temperature, and involves the coexistence of different plant types in this grassland that are capable of growing and utilizing resources at different times of the year. The cool-season C_3 grasses take advantage of early-season cool temperatures and water stores that are deepest at that time of year. Both C_3 and C_4 grasses typically exhibit their highest growth rates in mid to late spring and on into early summer, but the typically warm, dry conditions of midsummer clearly favor the warm-season and shallow-rooted C_4 grasses that tend to have higher water use efficiency. The actual rates of NPP and the contribution made by different species can vary dramatically and depend on seasonal and year-to-year variability in soil water and temperature (LeCain et al. 2002).

Aboveground Net Primary Production

The combined patterns in the seasonality of precipitation and temperature in the central grassland region result in all the grasslands having similar temporal patterns of NPP. Average NDVI data from 1991 for a number of sites in each of the
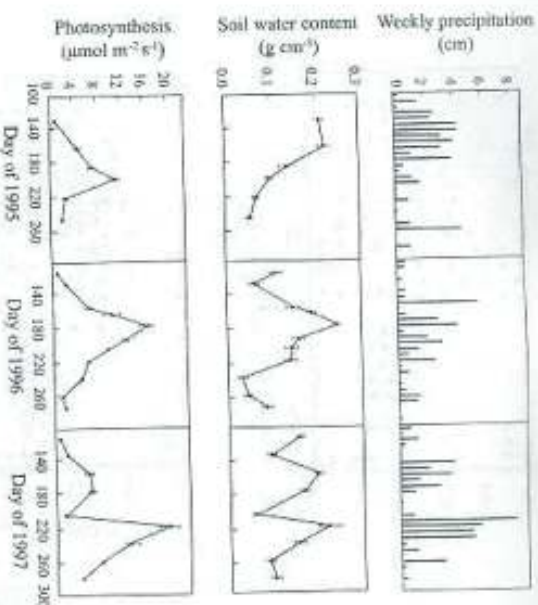
four grassland types suggests that the peak in green biomass for all types occurs between June 1 (day 152) and August 1 (day 213; Fig. 12.13A). Although average shortgrass steppe greenness is clearly lower than other types and shows strong seasonality, it is highly variable across sites (Fig. 12.13B). The peak in green biomass for these sites occurs between May 1 (day 121) and September 1 (day 244). Because of the important influence of the amount and timing of water availability in promoting ANPP, we should not be surprised to see such site-to-site variability in both the magnitude and timing of maximum green biomass. In addition to site-to-site variability in the same year, year-to-year variability in water availability results in differences in the timing and amount of green biomass. Lauenroth et al. (1980) found three distinct patterns of green biomass dynamics for 3 years at the CPER. Three peaks in green biomass occurred in 1973: one in early June, another in early August, and another in early September. In 1974, a single broad peak lasted from early July until early August, and 1975 was characterized by a single sharp peak in late June.
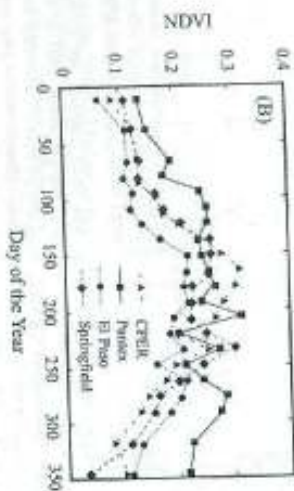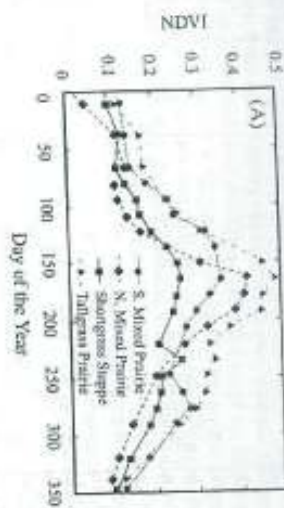

Photosynthesis (μmol m^{-2} s^{-1}) Soil water content (g cm^{-3}) Weekly precipitation (cm)

Day of 1995 Day of 1996 Day of 1997

Figure 12.12 Weekly precipitation, soil water content, and chambered-determined photosynthesis rates of the shortgrass steppe 1995 to 1997 at the CPER. Photosynthesis measurements are gross rates, corrected for static chamber measurements of soil respiration. Photosynthesis data represent 5 means ± SEs. Soil water contents are 3 means ± SEs. For more details, see LeCain et al. (2002).

Figure 12.13 (A) Season dynamics of NDVI for the four grassland types in the central grassland region. (Adapted from Paruelo and Lauenroth [1995]) (B) Season dynamics of NDVI for four short-grass steppe sites. (Adapted from Paruelo and Lauenroth [1995])

Effects of Precipitation

Interannual variability in precipitation results in variability in water availability, and subsequent variability in annual NPP. Lauenroth and Sala (1992) analyzed 52 years of forage production data for the CPER and found a significant positive relationship between forage production and ANPP, making it possible to express the data in terms of ANPP. The 52-year average ANPP was 97 g·m⁻² and deviated positively (maximum, 45 g·m⁻²) and negatively (minimum, −36 g·m⁻²) from the average (Fig. 12.14). During this time period, annual precipitation deviated positively (maximum, 267 mm) and negatively (minimum, −214 mm) from the 52-year mean of 321 mm·y⁻¹. Although there was a relatively good correspondence between the wet years and high ANPP, and dry years and low ANPP (r = 0.63, n = 52, P < .01), there was substantial residual variability not explained by annual precipitation. Using growing season precipitation improved the correlation a small
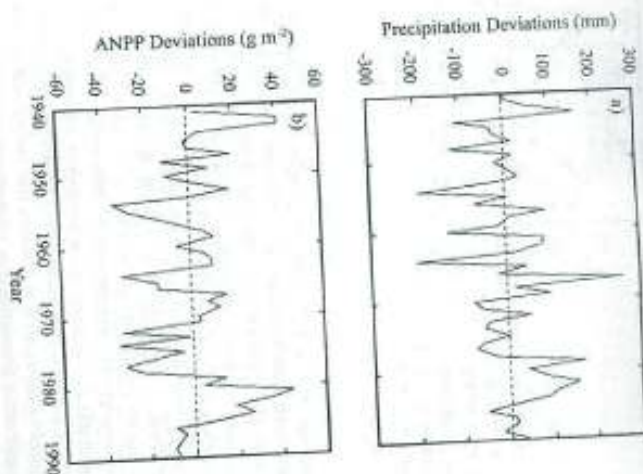
amount (r = 0.66), but using different-size precipitation events did not result in any additional improvement (r = 0.67).

Figure 12.14 Deviations of annual precipitation (A) and deviations of annual aboveground net primary production (ANPP) (B) from their long-term means for the period 1939 to 1990 at the CPER. (Adapted from Lauenroth and Sala [1992])

Landscape Effects

The results found by Lauenroth and Sala (1992) were from a number of sites, representing a variety of landscape positions. In at least some cases, individual landscape positions can have substantially different temporal dynamics of ANPP. Three landscape positions from a single catena were sampled at the CPER from 1983 to 1997 (Fig. 12.15). Interannual fluctuations of ANPP were similar for 1983 to 1997 (Fig. 12.15). Interannual fluctuations of ANPP were similar for the midslope and upland positions, but quite different for the swale. All three

ANPP (g m^{-2})

Year (19xx)
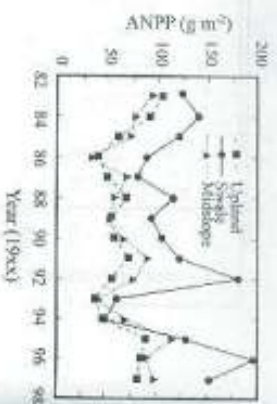
landscape positions followed the same large-scale trends, but ANPP on the swale fluctuated more widely between low-production and high-production years. Minimum ANPP was similar for all three landscape positions, but maximum ANPP for the swale position was almost 200 g·m^{-2}, whereas for the upland and midslope positions it was between 100 and 125 g·m^{-2}. Aboveground NPP for all landscape positions was related to annual precipitation (Fig. 12.16).

The greater slope for the swale compared with the other two landscape positions suggests that the controlling factors may be different among the landscape positions. The classic catena model (Gerrard, 1981) is based upon the downslope movement of material as a result of the movement of water. Although many hill slopes at the CPER do not fit the classic catena model because of the importance of wind movement of material, it is possible that during certain years there is movement of water either aboveground or belowground from the upland and mid-slope positions to the swale position (Singh et al., 1998). Another characteristic of swales is that many of them have higher soil organic carbon and nitrogen, as well as higher nitrogen availability (Burke et al., 1999; Hook and Burke, 2000; Yonker et al., 1988). Higher nitrogen availability in the swale position would explain the greater slope.

Nitrogen Effects

Nitrogen additions increase ANPP in most nonforested terrestrial ecosystems, and the shortgrass steppe is not an exception (Dodd and Lauenroth, 1979; Hart et al., 1995; Lauenroth et al., 1978). Burke et al. (1997) reported that the shortgrass steppe has a low nitrogen use efficiency (ANPP/annual net nitrogen mineralization) compared with other locations in the central North American grassland region. One of many possible interpretations of this is that ANPP is more limited by water than by nitrogen. Several experiments have been conducted at the CPER that provide additional information about this issue, although only two provide direct information about the response of ANPP to nitrogen addition.

Hart et al. (1995) reported the results of an experiment that was carried out between 1979 and 1985, and consisted of the addition of 2.2 g N·m^{-2} annually

ANPP (g m^{-2})

(A) upland

ANPP = 5.8 + 0.17*AP
r^2 = 0.40

ANPP (g m^{-2})

(B) midslope

ANPP = 6.3 + 0.18*AP
r^2 = 0.62

ANPP (g m^{-2})

(C) swale

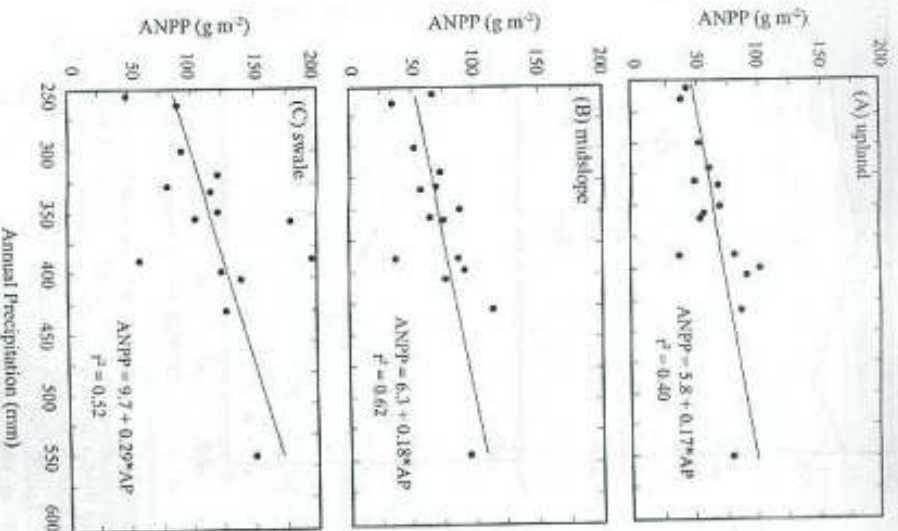ANPP = 9.7 + 0.29*AP
r^2 = 0.52

Annual Precipitation (mm)

Figure 12.16 Relationship between annual precipitation (AP) and annual aboveground net primary production (ANPP) for upland (A), midslope (B), and swale (C) landscape positions at the CPER.
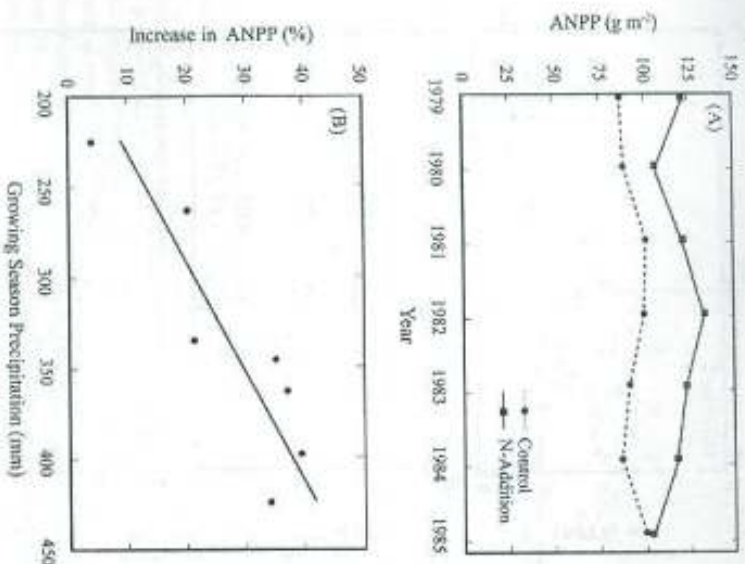
ANPP (g m⁻²)

(A)

150
125
100
75
50
25
0

1979 1980 1981 1982 1983 1984 1985
Year

Control
N-Addition

Increase in ANPP (%)

(B)

50
40
30
20
10
0

200 250 300 350 400 450
Growing Season Precipitation (mm)

Figure 12.17 (A) The effect of nitrogen addition on annual aboveground net primary production (ANPP) at the CPER. (Data from Hart et al. [1995]) (B) Relationship between growing season precipitation and the amount by which ANPP was increased by nitrogen fertilization at the CPER. (Data from Hart et al. [1995])

in the fall to two 32.4-ha pastures. Two similar-size pastures were used as control. Nitrogen addition increased ANPP in each of the years of the experiment (Fig. 12.17A). The average increase in ANPP compared with the control was 27%. The variability in the response of ANPP to nitrogen addition was related to growing season precipitation (Fig. 12.17B). The largest increases occurred in years with high growing season precipitation, and the smallest increases occurred in years with low growing season precipitation. *Bouteloua gracilis* was the dominant species in terms of contributions to total ANPP in both

Table 12.1 Average Annual ANPP for Species and Species Groups with and without Nitrogen Fertilization

Species or Group	Control, kg·ha⁻¹	Nitrogen Addition, kg·ha⁻¹
Bouteloua gracilis	450 a	680 b
Cool-season grasses	40 c	80 d
Other grasses	80 e	60 e
Forbs	40 f	130 g

ANPP within a species or group not followed by the same letter are significantly different at P <0.05. (Data from Hart et al. [1995])

the control and nitrogen addition pastures, increasing by 50% as a result of nitrogen addition (Table 12.1). The forb group had the greatest percentage increase to nitrogen addition of 225%. Forbs contributed only 7% of total ANPP under control conditions, but increased to 14% with nitrogen addition. These results suggest an interaction between water and nitrogen availability in controlling ANPP at the CPER.

One of the most important experiments for understanding the long-term effects of resource availability on ANPP, as well as community structure of the shortgrass steppe, was started during the International Biological Program (IBP). (Results of this long-term experiment are reported in many other chapters in this book.) The interactive effects of water and nitrogen on ANPP were clearly illustrated in this experiment, which consisted of a factorial combination of nitrogen and water additions (Dodd and Lauenroth, 1979; Lauenroth et al. 1978). The unwatered nitrogen treatment consisted of an addition of inorganic nitrogen as ammonium nitrate at the rate of 5 g N·m⁻² over the 5 years of the experiment to the nitrogen addition plots. The watered nitrogen treatment consisted of annual additions of 10 g N·m⁻² for a total of 50 g N·m⁻² to the water-plus-nitrogen plots in 5 years. The objective of the water addition treatment was to maintain soil water potential in the top 10 cm of the soil greater than −0.08 Mpa. This resulted in an average addition to the water-only plots of 550 mm per growing season and to the water-plus-nitrogen plots of 600 mm per growing season.

The addition of water and nitrogen increased ANPP in all but the first year of the experiment, when the treatments were not begun early enough to influence the experiment (Fig. 12.18). Nitrogen on average increased ANPP by 100%, water addition increased ANPP by 250%, and water-plus-nitrogen increased ANPP by 700% (Fig. 12.18). The decreases in ANPP for the water and water-plus-nitrogen treatments during the last year of the experiment were the result of limited water additions. In both the Hart et al. (1995) nitrogen addition and Lauenroth et al. (1978) water and nitrogen experiments, the group of plants that had the greatest relative response to the addition of nitrogen was the forbs. In the results of Hart et al. (1995), grasses increased 44% and forbs increased 225%. The dominant grass, *B. gracilis*, increased by 50%. Hyder et al. (1975) suggested that on average during the 7 years of their experiment, the addition of 2.2 g N·m⁻² had negative
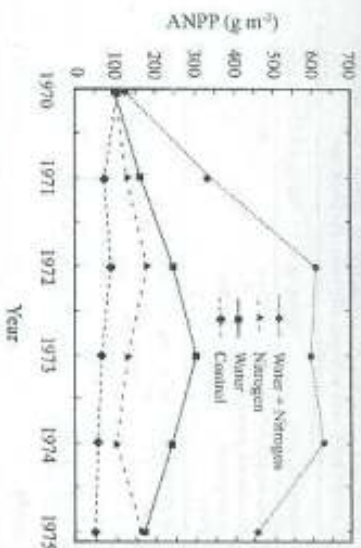
Figure 12.18 Effects of water, nitrogen, and water-nitrogen additions on annual aboveground net primary production (ANPP) at the CPER. (Adapted from Dodd and Lauenroth [1979].)

effects on the frequency of occurrence of perennial species and positive effects on annual species. In the water and nitrogen experiment by Lauenroth et al. (1978), nitrogen addition increased grasses by 70%, forbs by 425%, and the dominant grass by 50%. Water increased grasses by 175%, forbs by 725%, and the dominant grass by 175%. Water-plus-nitrogen increased grasses by 575%, forbs by 1600%, and the dominant grass by 650%. These results suggest two important conclusions. First, that it is not possible to speak of water or nitrogen as the single factor that controls ANPP at the CPER. Water addition had the greatest absolute and relative effect on ANPP, but the effects of nitrogen addition were also substantial. Second, there is a clear, positive interaction between water and nitrogen availability. With a similar amount of nitrogen available in the soil, increasing water availability had a similar positive influence. Average ANPP of the water-plus-nitrogen treatment was 3.7 times greater than ANPP of the nitrogen addition treatment. It is also true that with similar amounts of water availability, the addition of nitrogen had a huge effect on ANPP. Average ANPP of the water-plus-nitrogen treatment was 2.3 times that of the water treatment. Interestingly, many of the effects of nitrogen have persisted decades after the nitrogen additions were halted (Burke et al., chapter 13, this volume; Lauenroth, chapter 5, this volume; Milchunas and Lauenroth, 1995).

Effects of Carbon Dioxide

The CO_2 concentration of the atmosphere has increased 30% during the past 150 years and is expected to continue to increase into the foreseeable future (IPCC, 2007; Korner, 2000). Because the atmosphere is the source of carbon to plants,

there are good theoretical reasons to expect that increasing CO_2 concentrations will result in increases in NPP in many ecosystems, and especially those dominated by C_3 species (Bowes, 1993). There are also good theoretical reasons for ecosystems such as the shortgrass steppe that are dominated by C_4 species to experience minimal increases in NPP (Bowes, 1993). In contrast to theoretical predictions, many C_4-dominated ecosystems, including the shortgrass steppe, have shown positive responses of NPP to elevated CO_2 (Ghannoum et al. 2000; Hunt et al. 1996; Morgan et al., 2001; Wand et al., 1999). We have conducted two CO_2 enhancement experiments for the shortgrass steppe, one in the greenhouse (Hunt et al., 1996; LeCain and Morgan, 1998; Morgan et al., 1998) and another in large open-top field chambers experiencing ambient weather conditions (LeCain et al., 2003; Morgan et al., 2001, 2004).

Under a greenhouse treatment of 700 μL·L^{-1} CO_2, biomass responses of both B. gracilis (C_4) and A. smithii (C_3) were greater than the control, but not different from each other (Hunt et al., 1996). For both species, their response to elevated CO_2 was enhanced with water addition. The response of A. smithii was increased by elevated CO_2 at ambient temperatures, but the response of B. gracilis was greatest at ambient temperatures (Hunt et al., 1996).

In open-top field chambers and 720 μL·L^{-1} CO_2, ANPP was increased an average of 42% over 2 years, both of which were wetter than average (Morgan et al., 2001, 2004). The increase in ANPP was spread proportionately over C_4 and C_3 species, suggesting an equal response of plants of the two photosynthetic pathway types. The chamber effect resulted in an average increase of 57% in ANPP, suggesting a positive effect of elevated temperature. The available information suggests that the shortgrass steppe will have a positive response of ANPP to increasing CO_2 concentrations and perhaps to warming.

Belowground Net Primary Production

Belowground NPP has been a major hurdle in our understanding of shortgrass steppe ecosystem structure and function. The challenge has been finding a method that will produce reliable results. This is a problem that is common to the study of all ecosystems, not just the shortgrass steppe (Lauenroth, 2000), but the magnitude of belowground allocation and its importance for consumers in this ecosystem (see Moore et al., chapter 11, this volume) makes it especially important that we understand BNPP. We have used two methods in the shortgrass steppe. The first, sequential harvesting of soil cores, has been used at two sites: the CPER (Colorado) and Pantex (located in the panhandle of Texas near Amarillo). The second method, ^{14}C turnover, has been used at the CPER.

One of the key difficulties in estimating BNPP is separating the annual increment from the standing crop of belowground plant biomass. A defining characteristic of semiarid grasslands is that a large fraction of the total plant biomass occurs belowground. In the shortgrass steppe, 70% to more than 80% of the total plant biomass (live+dead) occurs belowground (Table 12.2) (Sims et al., 1978). There are two components to belowground biomass: crowns and roots (including rhizomes). Crowns represent the transition zone between above- and belowground

Table 12.2 Above- and Belowground Biomass Components for Two Sites in the Shortgrass Steppe

|		CPER		Pantex	
	Year	Ungrazed	Grazed	Ungrazed	Grazed
Aboveground					
Live	1970	63	48	25	62
	1971	58	82	76	103
	1972	89	57	107	93
	Mean	70	62	70	86
Recent dead	1970	—	—	20	19
	1971	—	—	70	71
	1972	35	28	10	10
	Mean	35	28	33	33
Old dead	1970	—	—	52	45
	1971	—	—	101	84
	1972	39	37	136	109
	Mean	39	37	96	79
Litter	1970	180	164	182	185
	1971	140	91	273	214
	1972	210	128	242	247
	Mean	177	128	232	215
Total	1970	243	212	279	311
	1971	198	173	522	472
	1972	373	250	495	459
	Mean	271	212	432	414
Belowground					
Crown	1970	—	—	123	186
	1971	340	322	289	302
	1972	258	308	349	410
	Mean	299	315	254	299
Roots	1970	1631	1701	1212	1638
	1971	1014	996	344	402
	1972	803	1290	580	562
	Mean	1149	1329	620	725
Total	1970	1631	1701	1335	1817
	1971	1354	1338	633	704
	1972	1061	1598	929	972
	Mean	1349	1539	966	1164
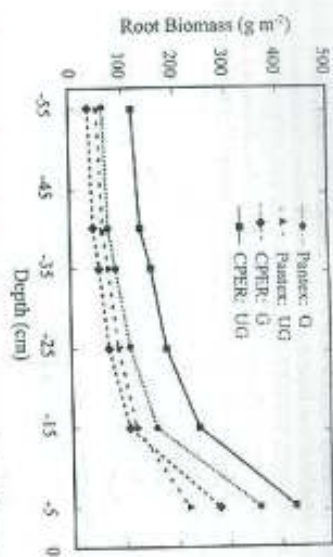
Figure 12.19 Relationship between root biomass and depth for two shortgrass steppe sites. Pantex is the Texas Tech University Research Farm in Amarillo, Texas, and CPER is the Central Plains Experimental Range. G, grazed; UG, ungrazed treatments. (Data from Sims and Singh [1978])

organs in grasses, and in the shortgrass steppe, this includes all the perennial aboveground material. At the CPER and Pantex sites, crowns represent 20% to 26% of belowground biomass. Roots and rhizomes represent the remaining 74% to 80%.

Root biomass is distributed as a negative exponential function with depth (Fig. 12.19). Both sites have more than 30% of their roots in the top 10 cm of the soil regardless of whether they are grazed. The top 30 cm of the soil contains 70% to 80% of the root biomass and, because all the crowns are at or just below the soil surface, the 0 to 30-cm-depth increment includes more than 70% to 80% of the total belowground biomass.

Sims and Singh (1978) reported estimates of BNPP using sequential harvesting and summation of significant increments in biomass (Table 12.3) (Singh et al., 1975). Estimates of BNPP ranged from approximately 400 to almost 1000 g·m^{-2}. These values are associated with ANPP-to-BNPP ratios of 0.39 to 0.22, suggesting that BNPP is 2.5 to 4.5 times greater than ANPP. However, analysis of methods of estimating BNPP from harvest data has suggested that there is a high likelihood that all estimates based upon harvest data have a positive bias (Singh et al., 1984; Sala et al., 1988a).

Carbon isotope labeling resulted in values of BNPP substantially smaller than those reported by Sims and Singh in 1978 (Milchunas and Lauenroth, 1992). This method requires a pulse label with a carbon tracer (either ^{14}C or ^{13}C) and relies on an estimate of the time required for all of the tracer to be lost from the belowground organs (turnover time). Milchunas and Lauenroth (1992) estimated values of BNPP ranging from 202 to 262 g·m^{-2} and ANPP-to-BNPP ratios ranging from

Table 12.3 Estimates of Aboveground and Belowground ANPP for Two Sites in the Shortgrass Steppe

	CPER		Pawnee	
	Ungrazed	Grazed	Ungrazed	Grazed
Aboveground				
1970	160	123	155	155
1971	218	108	289	218
1972	138	77	322	302
Mean	172	103	257	225
Belowground				
1970	411	471	417	410
1971	686	722	606	987
1972	607	429	870	968
Mean	568	541	633	788

Data from Sims and Singh (1978, Table 2 and 4).

0.42 to 0.72. These results suggested that BNPP is 1.4 to 2.4 times greater than ANPP in the shortgrass steppe. With further sampling of these plots, we found some complications with the measurement of roots by soil (Milchunas and Lauenroth, 2001). Correction for contamination resulted in a 22% increase in the 10-year average annual root production from 183 to 223 g·m⁻². Because the 10-year uncorrected average production for roots is essentially identical to the original 4-year average (183 g·m⁻² vs. 175 g·m⁻²), it seems reasonable to assume that the average for crowns will be similar. If that is true, the average ANPP-to-BNPP ratio is approximately 0.36, suggesting that BNPP is 2.8 times greater than ANPP. This falls within the lower portion of the range reported by Sims and Singh (1978) of 2.5 to 4.5.

Comparison of Spatial and Temporal Patterns

Shortgrass scientists have conducted a great deal of research on the spatial patterns in ANPP across grassland regions (e.g., Epstein et al., 1997a, b; Sala et al., 1988b), as well as conducted long-term monitoring and experimental analyses (Lauenroth and Sala, 1992; Lauenroth et al., 1978). These experiments have all demonstrated that precipitation is a key control over NPP. However, are the relationships gained from analysis of large spatial gradients the same as those from long-term, site-level analyses? Conceptually, the relationships differ. In the temporal case, the relationship is between ANPP in a specific year and the amount of precipitation received during that year, in the spatial case, the relationship is between mean annual ANPP and mean annual precipitation. The temporal model reflects the ability of the vegetation to capitalize on the amount of precipitation and nitrogen made available as a result of the amount and timing of water inputs in a specific year.

Because water availability is a key control on NPP in the shortgrass region, one of the ways to compare spatial and temporal patterns is to ask whether the slopes of regressions between ANPP and precipitation are similar for spatial and temporal data sets. Lauenroth and Sala (1992) summarized 52 years of ANPP data for the CPER and developed a regression model between ANPP and annual precipitation:

$$ANPP_t = -56 + 0.131 \times APPT_t$$

where $ANPP_t$ is ANPP in year t (measured in grams per square meter) and $APPT_t$ is annual precipitation in year t (measured in millimeters). They then compared this temporal model with a spatial model developed for the entire grassland region by Sala et al. (1988b):

$$ANPP_s = -34 + 0.60 \ MAP$$

where $ANPP_s$ is mean ANPP (measured in grams per square meter) and MAP is mean annual precipitation (measured in millimeters). It is clear from this comparison that the temporal relationship is different from the spatial relationship (Fig. 12.20). That is, the response of ANPP to precipitation for a given year and at a single site is not what we would predict, based upon relationships generated from regional average precipitation and production data. In dry years (APPT, < MAP), the vegetation (the number, identity, and size of plants) and the biogeochemistry (the size and quality of organic matter pools) reflect the average wetter conditions of the site, and ANPP exceeds the value one would expect for a site
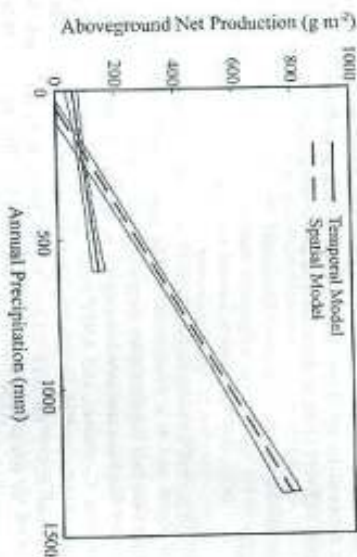

Figure 12.20 Relationships between annual aboveground net primary production (ANPP) from a spatial model for the central grassland region (Sala et al., 1988b) and a temporal model for the CPER (Lauenroth and Sala, 1992). The shaded areas are the 95% confidence interval. The spatial model is ANPP=0.60×AP − 34 and the temporal model is ANPP=0.13×AP+56. AP, annual precipitation. (Adapted from Lauenroth and Sala [1992].)

that had $APPT_i=MAP$. In a wet year, ($APPT_i > MAP$), the vegetation and biogeochemical processes at a single site reflect drier conditions, and cannot capitalize on the extra water available, so that ANPP is lower than the spatial model would predict for a site with $APPT_i=MAP$.

Our results from the shortgrass steppe have substantial implications for understanding the response of ecosystems to changes in climate—short term or long-term. For instance, simulation models that utilize such long-term spatial relationships to reflect the relationship between climate and production cannot adequately predict how a single site will change.

Furthermore, our results (Lauenroth and Sala, 1992) have been validated at other locations. For instance, Paruelo et al. (1999) evaluated relationships between spatial and temporal models for the entire grassland region precipitation gradient (200 mm < MAP < 1200 mm). They found that temporal precipitation use efficiency ($PUE_t = \Delta ANPP/\Delta APPT$) was low at both the dry (shortgrass steppe) and wet (tallgrass prairie) ends of the gradient. Their interpretation was that at the dry end of the precipitation gradient, vegetation constraints were the dominant influence (that is, that the ability of vegetation to respond to changes in precipitation limited ANPP response). At the wet end of the gradient, they inferred that biogeochemical constraints dominated (that is, that the ability of ANPP to respond was limited by nitrogen or other nutrient availability). These results suggest that the low slope of the shortgrass steppe temporal model reported by Lauenroth and Sala (1992) is the result of the low productive potential of the dominant shortgrass species (*B. gracilis* and *B. dactyloides*).

Our results have been further validated in the tallgrass prairie (Briggs and Knapp, 1995). The slope of the relationship between ANPP and annual precipitation was substantially lower than that reported by Sala et al. (1988b) for the grassland region and very close to the similar slope for the shortgrass steppe.

Summary

The shortgrass steppe occupies the warmest and driest portion of the central grassland region and as a consequence is the least productive of the grassland types. More than half the shortgrass steppe remains in native grasslands, whereas the remainder has been converted to croplands. Native grasslands are dominated by short-stature C_4 grasses, and ANPP ranges from 50 to more than 300 g·m⁻². Major crops include corn on irrigated fields and wheat under dryland conditions. Average annual ANPP for corn ranges from 4250 to 4700 g·m⁻² and average annual ANPP for wheat ranges from 260 to 330 g·m⁻². The key variables influencing the spatial pattern of ANPP for both crops and native grasslands are water and soil texture. The major effects of soil texture are through its effects on the storage and availability of both water and nutrients.

The seasonality of temperature and precipitation account for an early- to mid-summer peak in ANPP of native grasslands. Interannual variability in precipitation is the key determinant of interannual availability of soil water, which is the most frequent control on annual ANPP. Other factors that can affect temporal variability of ANPP include landscape effects, soil nitrogen, and atmospheric CO_2. Landscape position influences water and nutrient availability through topography (runoff and runon) and soil texture. Although connections between annual variability in nitrogen supply and ANPP are difficult to find, additions of nitrogen as fertilizer have consistently resulted in increases in ANPP. The increases are largest in the wettest years, or when nitrogen addition is combined with water addition. Effects of CO_2 have been demonstrated with open-top chambers and resulted in an average 42% increase over 2 years.

Annual belowground NPP is one of the most difficult quantities to estimate for any ecosystem, including the shortgrass steppe, and is particularly important for this system. We have estimated BNPP for shortgrass ecosystems using biomass harvest and carbon isotope turnover techniques. Biomass harvest estimates range from 400 to almost 1000 g·m⁻², and carbon isotope turnover estimates seem to have the fewest problems and therefore represent the best estimates of annual BNPP for shortgrass ecosystems.

References

Anderson, G. L. 1991. *Using simulation models and spatial information systems for evaluating rangeland ecosystems*. PhD diss., Colorado State University, Fort Collins, Colo.

Black, C. C. 1971. Ecological implications of dividing plants into groups with distinct photosynthetic production capacities. *Advances in Ecological Research* 7:87–114.

Black, C. C., Jr. 1973. Photosynthetic carbon fixation in relation to net CO2 uptake. *Annual Review of Plant Physiology* 24:253–286.

Bowes, G. 1993. Facing the inevitable: Plants and increasing atmospheric CO_2. *Annual Review of Plant Physiology and Plant Molecular Biology* 44:309–332.

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

Brown, L. F., and M. J. Trlica. 1977. Interacting effects of two dominant grasses of the shortgrass prairie. Irradiance on CO_2 exchange rates of soil water, temperature and *Journal of Applied Ecology* 14:197–204.

Burke, I. C., W. K. Lauenroth, and W. J. Parton. 1997. Regional and temporal variation in net primary production and net nitrogen mineralization in grasslands. *Ecology* 78:1330–1340.

Burke, I. C., W. K. Lauenroth, R. Riggle, P. Brannen, B. Madigan, and S. Beard. 1999. Spatial variability of soil properties in the shortgrass steppe: The relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. *Ecosystems* 2:422–438.

Coffin, D. P., and W. K. Lauenroth. 1990. A gap dynamics simulation model of succession in a semiarid grassland. *Ecological Modelling* 49:229–266.

Cosby, B. J., G. M. Hornberger, R. B. Clapp, and T. R. Ginn. 1984. A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils. *Water Resources Research* 20:682–690.

Coupland, R. T., and R. E. Johnson. 1965. Rooting characteristics of native grassland species in Saskatchewan. *Ecology* 53:475–507.

Detling, J. K., W. J. Parton, and H. W. Hunt. 1978. An empirical model for estimating CO₂ exchange of *Bouteloua gracilis* (H.B.K.) Lag. in the shortgrass prairie. *Oecologia* 33:137–147.

Dickinson, C. E., and J. L. Dodd. 1976. Phenological pattern in the shortgrass prairie. *American Midland Naturalist* 96:367–378.

Dodd, J. L., and W. K. Lauenroth. 1979. Analysis of the response of a grassland ecosystem to stress, pp. 43–58. In: N. R. French (ed.). *Perspectives in grassland ecology*. Springer-Verlag, New York.

Dodd, M. B., and W. K. Lauenroth. 1997. The influence of soil texture on the soil water dynamics and vegetation characteristics of a shortgrass steppe ecosystem. *Plant Ecology* 133:13–28.

Epstein, H. E., W. K. Lauenroth, and I. C. Burke. 1997a. Effects of temperature and soil texture on aboveground net primary production in the U.S. Great Plains. *Ecology* 78:2628–2631.

Epstein, H. E., W. K. Lauenroth, I. C. Burke, and D. P. Coffin. 1997b. Productivity patterns of C₃ and C₄ functional types in the U.S. Great Plains. *Ecology* 78:722–731.

Fan, W. 1993. *Regional analysis of plant species and environmental variables in eastern Colorado*. PhD diss., Colorado State University, Fort Collins, Colo.

Ghannoum, O., S. von Caemmerer, L. H. Ziska, and J. P. Conroy. 2000. The growth response of C₄ plants to rising atmospheric CO₂ partial pressure: A reassessment. *Plant, Cell, and Environment* 23:931–942.

Gerrard, A. 1981. *Soils and landforms*. George Allen and Unwin, Boston, Mass.

Hart R. H., M. C. Shoop, and M. M. Ashby. 1995. Nitrogen and atrazine on shortgrass: Vegetation, cattle and economic responses. *Journal of Range Management* 48:165–171.

Hook, P. B., and I. C. Burke. 2000. Biogeochemistry in a shortgrass landscape: Control by topography, soil texture, and microclimate. *Ecology* 81:2686–2703.

Hunt, H. W., E. T. Elliot, J. K. Detling, J. A. Morgan, and D.-X. Chen. 1996. Responses of a C₃ and a C₄ perennial grass to elevated CO₂ and temperature under different water regimes. *Global Change Biology* 2:35–47.

Hyder, D. N., R. E. Bement, E. E. Remmenga, and D. F. Hervey. 1975. *Ecological responses of native plants and guidelines for management of shortgrass range*. USDA technical bulletin no. 1503 U. S. Government Printing Office, Washington, D.C.

IPCC. 2007. Climate change 2007: Mitigation. Contribution of working group III to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Kemp, P. R., and G. J. Williams, III. 1980. A physiological basis for niche separation between *Agropyron smithii* (C₃) and *Bouteloua gracilis* (C₄). *Ecology* 61:846–858.

Knight, D. H. 1994. *Mountains and plains*. Thomson-Shore, Dexter, Mich.

Korner, C. 2000. Biospheric responses to CO2 enrichment. *Ecological Applications* 10:1590–1619.

Küchler, A. W. 1964. *Potential natural vegetation of the conterminous United States*. American Geographical Society, New York.

Lane, D. R., D. P. Coffin, and W. K. Lauenroth. 1998. Effects of soil texture and precipitation on above-ground net primary productivity and vegetation structure across the central grassland region of the United States. *Journal of Vegetation Science* 9:239–250.

Lane, D. R., D. P. Coffin, and W. K. Lauenroth. 2000. Changes in grassland canopy structure across a precipitation gradient. *Journal of Vegetation Science* 11:359–368.

Lauenroth, W. K. 1979. Grassland primary production: North American grasslands in perspective, pp. 3–24. In: N. R. French (ed.). *Perspectives in grassland ecology*. Springer-Verlag, New York.

Lauenroth, W. K. 2000. Methods of estimating belowground net primary production, pp. 58–71. In: Sala, O. E., R. B. Jackson, H. Mooney and R. W. Howarth (eds.). *Methods in ecosystem science*. Springer-Verlag, New York.

Lauenroth, W. K., and J. B. Bradford. 2006. Ecohydrology and the partitioning AET between transpiration and evaporation in a semiarid steppe. *Ecosystems* 9:756–767.

Lauenroth, W. K., and I. C. Burke. 1995. Great Plains, climate variability. *Encyclopedia of Environmental Biology* 2:237–249.

Lauenroth, W. K., and I. C. Burke, and M. P. Gutmann. 1999. The structure and function of ecosystems in the central North American grassland region. *Great Plains Research* 9:223–259.

Lauenroth, W. K., I. C. Burke, and J. M. Paruelo. 2000. Patterns of production and precipitation use efficiency in winter wheat and native grasslands in the central Great Plains of the United States. *Ecosystems* 3:344–351.

Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water and nitrogen induced stresses on plant community structure in a semiarid grassland. *Oecologia* 36:211–222.

Lauenroth, W. K., J. L. Dodd, and C. E. Dickinson. 1980. Biomass dynamics of blue grama in a shortgrass prairie and evaluation of a method for separating live and dead material. *Journal of Range Management* 33:210–212.

Lauenroth, W. K., and D. G. Milchunas. 1992. Shortgrass steppe, pp. 183–226. In: R. T. Coupland (ed.). *Natural grasslands: Introduction and western hemisphere*. Elsevier, Amsterdam.

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

LeCain, D. R., J. A. Morgan. 1998. Growth, gas exchange, leaf nitrogen and carbohydrate concentrations in NAD-ME and NADP-ME C-4 grasses grown in elevated CO₂. *Physiologia Plantarum* 102:297–306.

LeCain, D. R., J. A. Morgan, A. R. Mosier, and J. A. Nelson. 2003. Soil and plant water relations determine photosynthetic responses of C-3 and C-4 grasses in a semi-arid ecosystem under elevated CO₂. *Annals of Botany* 92(1):41–52.

LeCain, D. R., J. A. Morgan, G. E. Schuman, J. D. Reeder, and R. H. Hart. 2002. Carbon exchange and species composition of grazed pastures and exclosures in the shortgrass steppe of Colorado. *Agriculture, Ecosystems and the Environment* 93:421–435.

Milchunas, D. G., and W. K. Lauenroth. 1992. Carbon dynamics and estimates of primary production by harvest, C-14 dilution and C-14 turnover. *Ecology* 73:1593–1607.

Milchunas, D. G., and W. K. Lauenroth. 1995. Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress. *Ecological Applications* 5:452–458.

Monson, R. K., R. O. Littlejohn, Jr., and G. J. Williams, III. 1983. Photosynthetic adaptation to temperature in four species from the Colorado shortgrass steppe: A physiological model for coexistence. *Oecologia* 58:43–51.

Monson, R. K., M. R. Sackschewsky, and G. J. Williams, III. 1986. Field measurements of photosynthesis, water-use efficiency, and growth in *Agropyron smithii* (C₃) and *Bouteloua gracilis* (C₄) in the Colorado shortgrass steppe. *Oecologia* 68:400–409.

Monson, R. K., and G. J. Williams, III. 1982. A correlation between photosynthetic temperature adaptation and seasonal phenology patterns in the shortgrass prairie. *Oecologia* 54:58–62.

Morgan, J. A., D. R. LeCain, A. R. Mosier, and D. G. Milchunas. 2001. Elevated CO_2 enhances water relations and productivity and affects gas exchange in C_3 and C_4 grasses of the Colorado Shortgrass Steppe. *Global Change Biology* 7:1–16.

Morgan, J. A., D. R. LeCain, J. J. Read, H. W. Hunt, and W. G. Knight. 1998. Photosynthetic pathway and ontogeny affect water relations and the impact of CO_2 on *Bouteloua gracilis* (C_4) and *Pascopyrum smithii* (C_3). *Oecologia* 114:483–493.

Morgan, J. A., A. R. Mosier, D. G. Milchunas, D. R. LeCain, J. A. Nelson, and W. J. Parton. 2004. CO_2 enhances productivity, alters species composition, and reduces digestibility of shortgrass steppe vegetation. *Ecological Applications* 14:208–219.

Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4:25–51.

Paruelo, J. M., H. E. Epstein, W. K. Lauenroth, and I. C. Burke. 1997. ANPP estimates from NDVI for the central grassland region of the United States. *Ecology* 78:953–958.

Paruelo, J. M., and W. K. Lauenroth. 1995. Regional patterns of normalized difference vegetation index in North American shrublands and grasslands. *Ecology* 76:1888–1898.

Paruelo, J. M., W. K. Lauenroth, I. C. Burke, and O. E. Sala. 1999. Grassland precipitation-use efficiency varies across a resource gradient. *Ecosystems* 2:64–67.

Read, J. J., and J. A. Morgan. 1996. Growth and partitioning in *Pascopyrum smithii* (C_3) and *Bouteloua gracilis* (C_4) as influenced by carbon dioxide and temperature. *Annals of Botany* 77:487–496.

Read, J. J., J. A. Morgan, N. J. Chatterton, and P. A. Harrison. 1997. Gas exchange and carbohydrate and nitrogen concentrations in leaves of *Pascopyrum smithii* (C_3) and *Bouteloua gracilis* (C_4) at different carbon dioxide concentrations and temperatures. *Annals of Botany* 79:197–206.

Rutherford, M. C. 1980. Annual plant production precipitation relations in arid and semi-arid regions. *South African Journal of Science* 76:53–56.

Sala, O. E., M. E. Biondini, and W. K. Lauenroth. 1988a. Bias in estimates of primary production: An analytical solution. *Ecological Modelling* 44:43–55.

Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events, an ecological role in semi-arid regions. *Oecologia* 53:301–304.

Sala, O. E., W. K. Lauenroth, and R. A. Golluscio. 1997. Plant functional types in temperate semiarid regions, pp. 217–233. In: T. M. Smith, H. H. Shugart, and F. I. Woodward (eds.), *Plant functional types*. Cambridge University Press, Cambridge, UK.

Sala, O. E., W. K. Lauenroth, and W. J. Parton. 1992. Long term soil water dynamics in the shortgrass steppe. *Ecology* 73:1175–1181.

Sala, O. E., W. K. Lauenroth, and C. P. P. Reid. 1982. Water relations: A new dimension for niche separation between *Bouteloua gracilis* and *Agropyron smithii* in North American semi-arid grasslands. *Journal of Applied Ecology* 19:647–657.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988b. Primary production of the central grassland region of the United States. *Ecology* 69:40–45.

Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands: III. Net primary production, turnover and efficiencies of energy capture and water use. *Journal of Ecology* 66:573–597.

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

Singh, J. S., W. K. Lauenroth, and R. K. Steinhorst. 1975. Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. *Botanical Review* 41:181–232.

Singh, J. S., W. K. Lauenroth, H. W. Hunt, and D. M. Swift. 1984. Bias and random errors in estimators of net root production: A simulation approach. *Ecology* 65:1760–1764.

Singh, J. S., D. G. Milchunas, and W. K. Lauenroth. 1998. Soil water dynamics and vegetation patterns in a semiarid grassland. *Plant Ecology* 134:77–89.

Todd, S. W. 1994. Spatiotemporal estimation of biomass on the shortgrass steppe using Landsat TM vegetation and soil indices, field data, and simulation models. PhD diss., Colorado State University, Fort Collins, Colo.

USDA. 1967. *National handbook for range and related grazing lands*. Soil Conservation Service, U.S. Department of Agriculture, Washington, D.C.

USDA. 1974. *Summer fallow in the western United States*. Conservation research report no. 17. U.S. Department of Agriculture, Agricultural Research Service, Washington, D.C.

Ward, J. K., J. E. G. F. Midgley, M. H. Jones, and P. S. Curtis. 1999. Responses of wild C_3 and C_4 grass (Poaceae) species to elevated atmospheric CO_2 concentration: A meta-analytic test of current theories and perceptions. *Global Change Biology* 5:723–741.

Weaver, J. E., and F. W. Albertson. 1956. *Grasslands of the Great Plains: Their nature and use*. Johnsen, Lincoln, Neb.

Williams, G. J., III, and P. R. Kemp. 1978. Simultaneous measurements of leaf and root gas exchange of shortgrass prairie species. *Botanical Gazette* 139:150–157.

Yonker, C. M., D. S. Schimel, E. Paroussis, and R. D. Heil. 1988. Patterns of organic carbon accumulation in a semiarid shortgrass steppe. *Soil Science Society of America Journal* 52:478–483.