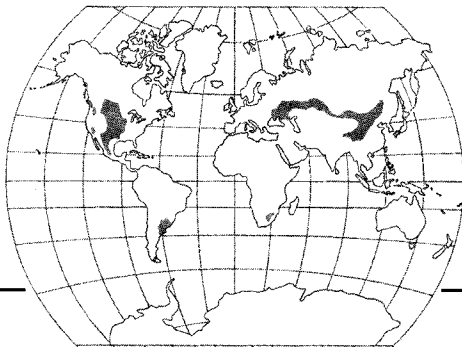# 12

Productivity of Temperate Grasslands

Osvaldo E. Sala

I. Introduction

Grasslands are located in areas with precipitation ranging between 150 and 1200 mm yr^{-1} and temperature between 0 and 25°C (Lieth and Whittaker, 1975). Along a precipitation gradient, in temperate regions, grasslands are located between forests and deserts. Sites with annual precipitation higher than 1200 mm yr^{-1} usually support forests whereas sites receiving less than 150 mm yr^{-1} usually are occupied by deserts. Temperature interacts with precipitation, moving the grassland–forest and grassland–desert boundaries to wetter or drier areas. For example, as temperature and potential evapotranspiration decrease, the grassland–forest boundary occurs at lower precipitation. In the Great Plains of North America where isohyets run in a north–south direction, the boundary between the tallgrass prairie and the temperate forest has a clear SE–NW direction (Barbour and Billings, 1988).

The grassland biome is large, potentially covering an area of 49×10^6 km^2, which is equivalent to 36% of the Earth's surface (Shantz, 1954). This estimate of the grassland area excludes savannas but includes both grass and shrub deserts. The area covered exclusively by grasslands is 15×10^6 km^2, which accounts for 11% of the Earth's surface. There are large expanses of grasslands in North America, South America, and Asia, whereas smaller pieces are found in Europe, Southern Africa, and Australia (Singh *et al.*,

1983). In North America, most of the Great Plains potential natural vegetation is grassland, and encompasses large areas from subtropical Texas in the United States to the boundary with temperate deciduous forest in Canada. In South America, the vast pampas and the Patagonian steppe are considered grasslands. Finally, in Asia, grasslands cover a large region from Ukraine to China.

This chapter is constrained to a discussion of climatically determined grasslands, in contrast with grasslands resulting from human action. Climatically determined grasslands occur in areas where, during at least part of the year, water availability is not enough to support forests, although they receive sufficient precipitation to sustain grasses as the dominant component of vegetation (Lauenroth, 1979). Anthropogenically determined grasslands are usually located in areas where the potential vegetation is forest. These forest areas have been logged, burnt, and sown with grasses and legumes, and consequently transformed into cultivated pastures that do not resemble natural grasslands in their functioning and relationships with the environment. Seldom, cultivated pastures occur in areas where potential vegetation was grassland because, when the transformation is feasible, crops are usually a more economically beneficial option.

Although the vast grassland biome is largely determined by environmental conditions, most of the biome is currently managed in one way or the other. Grasslands have provided food and fiber for our ancestors for millennia and have been at the epicenter of civilization (Stebbins, 1981). Grassland management ranges from pastoralism, which is still common in parts of Africa, to the improvement of cattle and sheep production via the organization of herds in categories, subdivision of ranches into paddocks, development of new water holes, intense veterinary care, and control of predators and parasites (Oesterheld *et al.,* 1992). Management practices rarely include fertilization or irrigation of native grasslands because these practices are reserved for cultivated pastures.

Four major functional types of plants—grasses, shrubs, herbs, and succulents—form the grassland biome. The relative contribution of these four functional types in grasslands depends on the seasonality of precipitation and the soil texture (Sala and Lauenroth, 1993). The two major functional types, grasses and shrubs, have contrasting root patterns. In general, grasses have shallow roots and shrubs have deep root systems. Sites where water availability tends to concentrate in the upper layers of the soil are dominated by grasses, whereas sites where water is predominantly located in deeper layers are dominated by shrubs (Sala *et al.,* 1993). The location of water in the soil depends on soil texture and seasonality of precipitation. The same amount of precipitation penetrates deeper into a soil with a coarse texture and lower water-holding capacity compared to a fine-texture soil with higher water-holding capacity. For example, in Mediterranean ecosystems where

the wet and warm seasons do not coincide, soils tend to have water at deeper layers than do regions with a continental climate, where most of the precipitation occurs during the warm season. In Mediterranean ecosystems, during the rainy season, potential evapotranspiration is low and the upper layers stay wet, so when it rains, the upper layers are saturated and water penetrates into deeper soil layers. In contrast, in regions with a continental climate, most of the rain occurs during the warm season when evaporation is high, maintaining the upper layers dry, so when it rains water wets repeatedly the upper layers but rarely reaches deeper layers. Two contrasting examples are the shortgrass steppe in North America and the Patagonian steppe in South America. The shortgrass steppe receives most of the precipitation during the warm season; the wettest layer is located at 5–15 cm of depth, and is dominated by grasses (Sala *et al.*, 1992). In contrast, the Patagonian steppe receives most of the precipitation during fall and winter; the soil layer with the highest probability of being wet during the entire year is located at 80 cm of depth, and primary production is evenly distributed between shrubs and grasses (Paruelo and Sala, 1995).

C_3 and C_4 grasses, differentiated by their photosynthetic pathway, are two major groups within the grass functional type. Physiological differences of the two groups are associated with different ecological characteristics that separate them in space and time. C_4 species, in general, dominate in areas that are warmer and with less available water than C_3 species. Analysis of the distribution of these two types of grasses showed that the proportion of C_3 decreases southward in North America and northward in South America (Paruelo *et al.*, 1998). Many grasslands have both types of grasses but in those cases their phenology and production patterns are separated during the year. For example, the C_3 *Agropyron smithii* dominates the shortgrass steppe during the cool spring but the C_4 grass *Bouteloua gracilis* dominates during late spring and summer (Lauenroth and Milchunas, 1992). Similarly, very little overlap occurs between C_3 and C_4 species in the vast Pampas of South America; productivity of C_3 grasses peaks in early spring to almost disappear in the summer when C_4 grasses reach their maximum (Sala *et al.*, 1981).

Grasslands are utilized for grazing of cattle, sheep, goats, and native animals, all of which produce meat, milk, blood, wool, and hair—important goods for society. In arid and semiarid grasslands, these products represent one of the only ways of harvesting the production of these ecosystems. Grasslands also provide an array of goods and services besides those just mentioned above. These other goods and services, which currently have no market value, include the maintenance of the composition of the atmosphere by sequestering carbon, ameliorating weather, maintaining the genetic library, and conserving the soil. Economic analysis indicates that those services with no market value may in the future exceed the traditional goods and services provided by grasslands. For example, for some grasslands, car-

bon sequestration may be valued at $200 ha^{-1}, which can exceed the current price of the land in the region (Sala and Paruelo, 1997).

The objectives of this chapter are twofold: to review the patterns and controls of aboveground productivity in temperate grasslands and to evaluate the impact of expected global change on those patterns. The literature on primary productivity of grasslands is abundant; productivity in grasslands has been measured extensively since the days of the International Biological Programme (Sims and Singh, 1978). The focus here is on those papers that contribute new understanding about the general patterns and controls of productivity in grasslands.

II. Productivity Patterns and Controls

A. Productivity and Precipitation

Grasslands cover a broad range of environmental conditions and consequently show a large range of aboveground net primary productivity (ANPP), from 50 to 800 g m^{-2} yr^{-1}. Precipitation is the major control of aboveground primary production in grasslands at a regional scale (Sala *et al.*, 1988). The United States Department of Agriculture (USDA) Soil Conservation Service developed an exhaustive data set that included estimates of annual average primary production for 9498 sites across the Central Grassland Region of the United States (Joyce *et al.*, 1986). Analysis of the data set indicated that annual precipitation (APPT) was the best predictor of annual primary production and that a straight line was the best model relating precipitation and production (Fig. 12-1) (Sala *et al.*, 1988). Not only was precipitation the best predictor but addition of other variables such as temperature, potential evapotranspiration, or the precipitation/potential evapotranspiration ratio did not improve the estimates of production. The model can be written using the form proposed by Noy-Meir (1973):

$$\text{ANPP (g m}^{-2}) = 0.6[\text{APPT (mm yr}^{-1}) - 56],$$

where each term in the equation now has an ecological meaning. The slope 0.6 is the average water use efficiency for grasslands in the region and 56 is the zero-yield intercept or ineffective precipitation (the threshold below which no production can occur).

The model presented in Fig. 12-1 was developed using a large number (9498) of sites, but all from only one continent, North America. How general is this model? McNaughton *et al.* (1993) and Paruelo *et al.* (1998) tested this model against data from other continents. They fitted similar models to data collected for 14 sites located in temperate South America, which is a region with a climate similar to that of the Central Grassland Region, but which belongs to a different biotic realm (Udvardy, 1975) and has a differ-
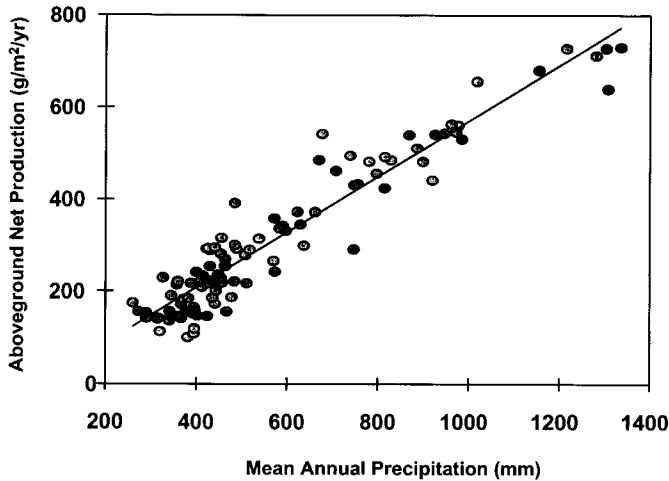
Figure 12-1 Relationship between average aboveground net primary production (ANPP) and mean annual precipitation (APPT) for 100 ecological regions encompassing 9498 sites along the Central Grassland Region of the United States. ANPP (g m^{-2}) = $-34 + 0.6$ APPT (mm yr^{-1}); $r^2 = 0.90$ and $p < 0.01$. Redrawn from Sala *et al.* (1988).

ent evolutionary grazing history (Sala *et al.*, 1986; Milchunas and Lauenroth, 1993). McNaughton *et al.* (1993) also developed similar models of production for distinct regions using data from 20 sites in the Serengeti ecosystem (McNaughton, 1985), 33 sites in Eastern and Southern Africa (Deshmukh, 1984), and 45 North African locations (Le Houérou and Hoste, 1977). Rodin (1979) reported aboveground primary productivity data for 13 sites in Central Asia ranging in annual precipitation from 99 to 217 mm yr^{-1}. I performed the regression analysis of ANPP versus annual precipitation on the Asian data and obtained a model [ANPP (g m^{-2}) = $-30 + 0.59$APPT (mm yr^{-1}); $p < 0.01$, $r^2 = 0.63$] that is quite similar to the one reported for the Central Grassland Region of the United States (Fig. 12-1). In all cases there is a remarkable similarity among the models, the efficiencies ranged between 0.48 and 0.85 g m^{-2} mm^{-1} yr^{-1}, encompassing the efficiency of the Central Grassland region and that of other global studies (Lauenroth, 1979; Rutherford, 1980).

B. Productivity and Temperature

Precipitation exerts an overwhelming control over production at the regional scale, although our ecological understanding suggests that other variables should also be important controls of production. Epstein *et al.* (1996), using the database for the Central Grassland Region of the United States, isolated sites along a north–south transect encompassing a broad tempera-
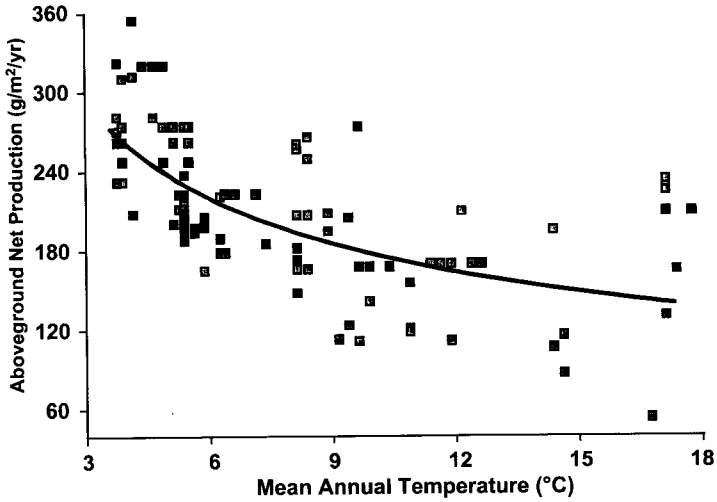
Figure 12-2   Relationship between average aboveground net primary production (ANPP) and mean annual temperature (MAT) for sites along a north–south transect in the Central Grassland Region of North America. ANPP = $456\text{MAT}^{(-0.4)}$; $r^2 = 0.4$ and $p < 0.001$. Redrawn from Epstein *et al.* (1996).

ture range (5–18°C) with little variation in precipitation. Once the precipitation variability was eliminated, a temperature effect was visible (Fig. 12-2). Surprisingly, the temperature effect was negative, with production decreasing with increasing temperature. Because biological processes, and certainly those related to plant growth, increase with temperature, the explanation for this pattern is that of an indirect effect on productivity through changes in water availability. As temperature increases, it simultaneously increases the evaporative demand, therefore temperature increases result in a reduction in water availability if precipitation input is maintained constant (Epstein *et al.,* 1996).

C. Productivity and Soil Texture

Soil characteristics also influence primary production in grasslands. Soil texture modifies water-holding capacity, which affects production, but there is an interesting interaction with precipitation (Sala *et al.,* 1988). Analysis of ANPP and soil patterns for 9498 sites in the Central Grassland Region of the United States indicated that production decreases with increasing water-holding capacity for sites with an annual precipitation below 370 mm yr^{-1} and production increases with increasing water-holding capacity at sites with annual precipitation higher than 370 mm (Fig. 12-3). The interaction be-

tween water-holding capacity and precipitation, i.e., the inverse texture hypothesis, is based on the ecosystem water balance (Sala *et al.*, 1988). Water losses in grasslands occur via transpiration, deep percolation, and bare soil evaporation and the relative magnitude of the last two pathways varies with precipitation. Bare soil evaporation occurs only from the uppermost layer of the soil. In wetter grasslands, those receiving more than 370 mm yr^{-1}, the major path for water loss is deep percolation and the magnitude of the loss decreases with increasing water-holding capacity. In drier grasslands, receiving less than 370 mm of annual precipitation, precipitation rarely penetrates beyond shallow deep layers and the major path for water loss is bare soil evaporation, which increases with increasing water-holding capacity. A given amount of water penetrates deeper into a coarse-textured soil with low water-holding capacity than into a fine-textured soil and consequently a smaller fraction of water will be located in the uppermost layer where evaporation occurs. In summary, in drier locations the major loss is soil evaporation, which increases with increasing water-holding capacity, whereas in
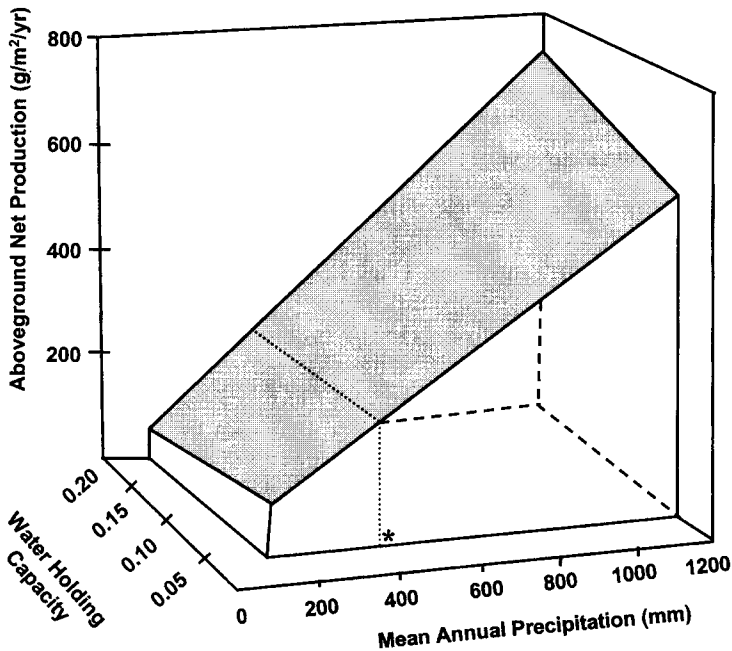

Figure 12-3 Relationship between aboveground net primary production (ANPP), soil water-holding capacity (WHC; proportion of soil dry mass), and mean annual precipitation (APPT) for 9498 sites located in the Central Grassland Region of North America. ANPP = 32 + 0.45APPT − 352WHC + 0.95WHC·APPT; r^2 = 0.67 and $p < 0.01$. Redrawn from Sala *et al.* (1988).

wetter sites the major loss is deep percolation, which decreases with in-
creasing water-holding capacity. Consequently, in drier areas, available wa-
ter for transpiration and plant growth decreases with increasing water-hold-
ing capacity and vice versa in wetter sites.

D. Spatial versus Temporal Controls

Up to this point, analyses of patterns and controls of primary production
have been based on comparisons among sites. The correlative models were
constructed using data on mean production and average precipitation or
temperature for different sites. Implicit in the models was the assumption
that spatial variability was a good analog of temporal variability and that
models developed using spatial data were appropriate tools to predict
changes through time. Lauenroth and Sala (1992) analyzed a 52-yr time se-
ries of production data for a site, the Central Plains Experimental Range, in
the shortgrass steppe of North America. They found that annual precipita-
tion was the variable that accounted for most of the variability in production
among years, as precipitation accounted for most of the variability in pro-
duction among sites. The model for the shortgrass steppe site developed us-
ing data for the 52-year period is

$$\text{ANPP (g m}^{-2}\text{ yr}^{-1}) = 56 + 0.13[\text{APPT (mm yr}^{-1})],$$

or, written in the form proposed by Noy-Meir (1973)

$$\text{ANPP (g m}^{-2}\text{ yr}^{-1}) = 0.13[\text{APPT (mm yr}^{-1}) + 430].$$

The striking finding was that the temporal model developed using the time
series had a much lower slope compared to the spatial model developed us-
ing average data from many sites (Fig. 12-4). In the temporal model, each
data point represents the precipitation and production for a different year,
but all from the same site, whereas in the spatial model, each data point rep-
resents the average production and average annual precipitation for a dif-
ferent site. The large difference between the two models shows that the as-
sumption that it was possible to exchange space for time was incorrect.

  The explanation for the difference between the spatial and temporal
models is associated with the existence of time lags in the response of ecosys-
tems to changes in water availability. In the 52-yr data set, the lowest pro-
duction year (1954) corresponds to one of the three driest years during the
period. The following year, 1955, had a precipitation slightly above the long-
term average; however, production (72 g m^{-2}) was substantially below the
long-term production average of 97 g m^{-2}. Production did not reach and
pass the long-term average until 1957, which was an extraordinarily wet year.
The explanation for the lags in the ability of ecosystems to respond to
changes in water availability is related to the inertia of vegetation structure.
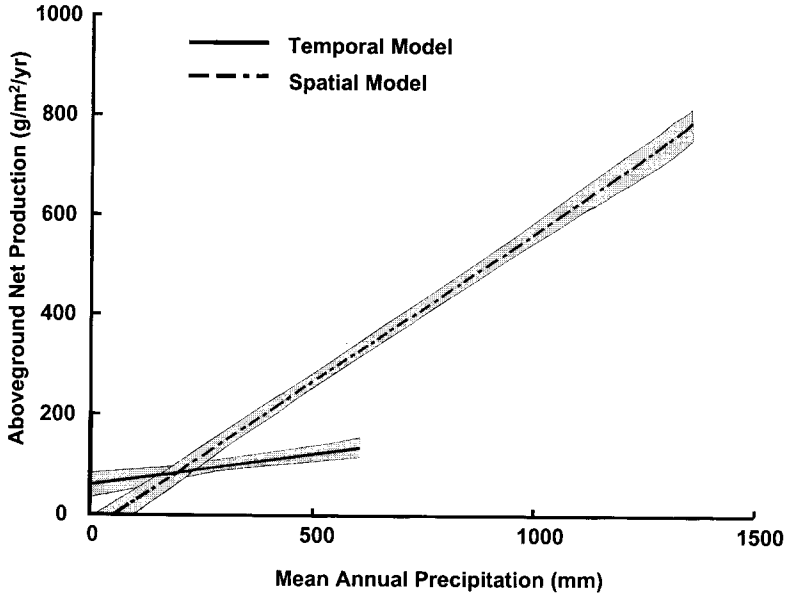 Lags occur because what represents the optimal ecosystem structure

Figure 12-4   Relationship between aboveground net primary production and annual precipitation for a site in the shortgrass steppe during a 52-yr period (solid line), and the model described in Fig. 12-1 (dashed line). Shaded areas represent confidence intervals. Redrawn from Lauenroth and Sala (1992).

changes from year to year. The optimal ecosystem structure is characterized by a leaf area, a density of individuals, and a species composition that result in maximum resource acquisition. The structure of a grassland ecosystem has inertia and does not change immediately with changes in water availability. The different components of the ecosystem structure show different time lags in their ability to respond to increases in water availability. Leaf expansion may respond in a matter of hours after a rainfall event whereas changes in density of individuals or in species composition may take several years. Tilman and Downing (1994) showed how several years were required for species composition in a tallgrass prairie ecosystem to recover after a severe drought. Lags in altering the structure of the ecosystem may be responsible for the differences between the temporal and spatial models. For example, the wettest year during the 52-yr period analyzed for the shortgrass steppe had a precipitation of 588 mm and a production of only 115 g m^{-2}, whereas a site with 588 mm of average annual precipitation has an average production of 318 g m^{-2}. The structure of the ecosystem constrained the production during the wet year.

Burke *et al.* (1997) suggested another explanation for the differences between the spatial and temporal models and the occurrence of lags in the response to changes in water availability. Their modeling exercise using the ecosystem model CENTURY (Parton *et al.,* 1987) suggested that nutrient availability may constrain productivity in wet years. During dry years the model shows higher N mineralization than does the spatial model, because current-year mineralization depends on previous-year production and the resulting active organic matter. Similarly, during wet years N mineralization is lower than expected from the spatial model. Their modeling exercise reproduced the inertial behavior reported in the field data (Lauenroth and Sala, 1992). The nutrient constraint and the structural constraint hypotheses can easily complement each other. Further experimental work is necessary to evaluate the relative importance of these two hypotheses.

The difference between the temporal and spatial models is not restricted to the shortgrass steppe. Knapp *et al.* (1998) found a similar pattern using a 20-yr data set for the tallgrass prairie. Paruelo *et al.* (1999) reviewed data from 11 temperate grasslands (7 in the United States and 4 in Eurasia) with long-term data sets of productivity. They found that the ratio of the slopes of the temporal and spatial models changed along a precipitation gradient from 200 to 1200 mm yr^{-1}; both slopes become similar at intermediate precipitation (475 mm yr^{-1}) but the differences increase toward the dry and wet ends of the gradient. They hypothesized that structural constraints are maximum at the dry end of the gradient and decrease with increasing precipitation. On the contrary, biogeochemical constraints would be maximal at the wettest end of the gradient and decrease with decreasing precipitation. According to this hypothesis, the slope of the temporal model is maximum and equals that of the spatial model at intermediate precipitation values because at that point both the structural and the biogeochemical constraints are minimal.

The temporal model not only had a smaller slope than the spatial model but also accounted for a smaller fraction of the variability in production. A possible explanation for that fact is that different functional groups respond differently to environmental factors that vary from year to year, such as precipitation amount or seasonality. In the tallgrass prairie, grass production increases while forb production decreases with increasing water availability (Knapp *et al.,* 1998). In the Patagonian steppe, which has predominantly winter precipitation, grass production depends on spring and summer precipitation and shrub production depends on the precipitation accumulated during the previous 18 months (Jobbágy and Sala, 2000).

E. Biome Level Productivity

Grasslands occur in all continents and occupy a broad range of temperature, precipitation, and soil conditions. Consequently, estimating production for the entire biome requires taking into account spatial variability of the con-

trols. Accuracy of the estimate depends on the quality of both the information on patterns of the controls as well as the functions relating NPP to the different drivers. Melillo *et al.* (1993) used the terrestrial ecosystem model (TEM) to estimate total NPP (sum of above- and belowground production) for all terrestrial biomes. Although the carbon cycle was the primary interest of their exercise, TEM also simulated the nitrogen cycle and the carbon–nitrogen interactions. The authors divided the grassland biome in two categories, short and tall grasslands, and reported mean NPP values of 428 for short grasslands and 670 g dry matter (DM) $m^{-2} yr^{-1}$ for tall grasslands. The mean NPP for the grassland biome when the two categories were weighted by their areas was 533 g DM $m^{-2} yr^{-1}$. This exercise has since been repeated using 17 different ecosystem models and of course a different set of parameters (Kicklighter *et al.*, 1999). Results of this second exercise were comparable, although higher than those of the first exercise, with values of NPP ranging between 600 and 900 g DM $m^{-2} yr^{-1}$.

Aboveground biomass and primary production are two different concepts; the former is a state variable and the latter is a flow or an ecosystem process. Although conceptually they are different and they even are represented by different units, aboveground biomass and aboveground net primary production in grasslands usually have the same values. Grasslands have an annual turnover of biomass of approximately 1. Consequently, the most common way of estimating aboveground net primary productivity is equating peak biomass with annual productivity (Sala and Austin, 2000). Therefore, mean estimates of biomass for grasslands have an absolute value that is quite similar to those of NPP, although units are different; biomass is represented in mass per unit area whereas productivity also has a unit time.

III. Secondary Productivity Patterns and Controls

A thorough analysis of the literature including 104 sites and encompassing nine different ecosystem types yielded an important conclusion that, at the global scale, there is a highly significant relationship between primary production and herbivore biomass, herbivore consumption, and secondary production (McNaughton *et al.*, 1989). The authors concluded that secondary production, herbivore biomass, and consumption are strong correlates of primary production. Secondary productivity varies linearly with primary productivity, indicating that changes in primary production are directly reflected in changes in secondary productivity. On the contrary, herbivore biomass and consumption vary exponentially with primary production, indicating that as primary production increases, consumption increases more than proportionally and that the fraction of total production consumed increases with increasing primary productivity.

The striking relationship between primary and secondary productivity

across all kind of environmental and evolutionary conditions is not unique to terrestrial ecosystems or natural ecosystems. Similar patterns were described for aquatic ecosystems (Cyr and Pace, 1993) and managed ecosystems (Oesterheld *et al.*, 1992). In managed grasslands, analyses of livestock biomass censuses from Argentina and Uruguay showed that there is a tight, exponential relationship between herbivore biomass and primary productivity (Oesterheld *et al.*, 1992). The managed systems showed a relationship with primary production that had the same slope as the relationship found for natural systems but a higher *y* intercept. In managed systems, regardless of socioeconomic differences among regions, herbivore biomass or stocking rate increased exponentially with primary production. The difference in the *y* intercept between the models derived for natural and human-managed systems is an estimate of the effect of animal husbandry on herbivore-carrying capacity at a regional scale.

IV. Grassland Primary Production, Carbon Balance, and Global Change

The carbon balance of an ecosystem depends on inputs and outputs, and for most terrestrial ecosystems, primary production is the major input and soil erosion and decomposition are the major outputs. Four global change drivers will affect the primary production and carbon balance of grasslands: land use change, climate change, changes in the composition of the atmosphere, and biotic exchange or biodiversity change.

Land use change has the largest impact on the carbon balance of grasslands, not only because of the extent of land use change in grassland areas, but because of the effects per unit area. IMAGE 2 (Alcamo, 1994) is a global model of land use dynamics and it predicts large changes in the land use of grasslands for the next century. In the developing world, large areas of native grasslands will be converted into agricultural land, whereas the opposite will occur in North America, where large expanses of cropland will be abandoned. The processes of cultivation and abandonment have opposite effects, but of significantly different magnitude. Consequently, losses due to cultivation would not be compensated equally by an increase in abandoned area. Transformations of grasslands into croplands result in a net carbon flux to the atmosphere, because tillage increases decomposition by breaking soil aggregates and placing organic matter particles that were previously protected in contact with decomposers. Losses during the first 10 to 20 yr of cultivation can be enormous. For example, in the Great Plains of North America, Burke *et al.* (1991) found that agriculture has resulted in carbon losses of 1400 g m^{-2} during this century.

Most of the current climate change scenarios agree on the global warming trend, although there are differences among regions and models re-

garding the patterns of precipitation change (Kattenberg *et al.*, 1996). A review of the effects of climate change on the carbon balance of grasslands indicated that the expected increase in temperature will result in a decrease of the soil organic matter pool as a result of the increase in decomposition (Sala *et al.*, 1996). The effects of temperature on primary production are likely to be small and indirect, through changes in water availability (see Section II,B). The global circulation models predict decreases in precipitation for most of the temperate grassland region, although for some grasslands they predict small increases. Decreases in precipitation coupled with the increases in temperature will result in a large negative carbon balance. In the small area where precipitation may increase, the increase in production may compensate for the increase in decomposition resulting from the temperature increase.

The direct effects of elevated CO_2 on grassland primary production vary among ecosystems and from year to year. For example, in the annual grasslands of California, elevated CO_2 resulted in a stimulation of productivity in the shallow-soil serpentine ecosystem and a reduction in the deep-soil sandstone (Field *et al.*, 1995). In tallgrass prairie, similar experiments suggested an increase in production of the C_4 grasses during dry years and possibly an accumulation of carbon in surface soils as a result of elevated CO_2 (Owensby *et al.*, 1995).

Finally, our current understanding does not provide a quantitative answer to the question of the effects of changes in biodiversity on primary production. Experimental evidence suggested that production decreases as a result of losses of biodiversity (Mooney *et al.*, 1995a,b; Tilman *et al.*, 1996). However, we do not know yet how general those results are and what is the level of biodiversity change at which production will start to decrease.

The relative importance of the four drivers of global change on the production of grasslands is difficult to assess quantitatively because of the uncertainties in the predictions and in the response of the different grasslands. Burke *et al.* (1991) compared the effects of expected climate change versus the observed changes in land use in the Great Plains of the United States, regarding carbon emissions. They concluded that land use change had a larger effect than did climate change, 1400 versus 200 g m^{-2} of carbon losses. Our difficulty in assessing the relative importance of the four drivers is compounded by the expected change of the relative importance of the drivers. Land use seems the major driver now, but it may be surpassed by biodiversity or climate change in the future.

Acknowledgments

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