Chapter 11

GRAZING, FIRE, AND CLIMATE EFFECTS ON PRIMARY PRODUCTIVITY OF GRASSLANDS AND SAVANNAS

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INTRODUCTION

Grasslands and savannas share a number of biotic and abiotic features that differentiate them from other vegetation types. Their major characteristic is the dominance of a herbaceous layer largely composed of grasses and sedges (Walter, 1977). In grasslands, the herbaceous component forms a unique vegetation layer, whereas in savannas there is an additional woody layer which can range from sporadic, isolated shrubs or trees to relatively dense woodlands. Climatically, grasslands and savannas extend over a broad range of mean annual precipitation (200–1300 mm) and temperature (0–30°C) (Lauenroth, 1979). However, all of them have a negative water balance and undergo marked dry seasons (Lauenroth, 1979; McNaughton et al., 1982).

Grasslands and savannas are fuzzy segments of a climatic gradient from deserts through closed forests. In many regions of the world, deserts turn gradually into grasslands, as grasses become more important in response to an increase in mean precipitation (Paruelo and Lauenroth, 1996; Paruelo et al., 1998). A southeast–northwest gradient in eastern Europe from *Artemisia* desert to *Stipa* steppe (Walter, 1977), an east–west gradient in southern South America, from *Nassauvia glomerulosa* semi-desert to the western steppe with *Festuca pallescens* (León and Facelli, 1981), and a west–east gradient in North America from the Chihuahuan Desert with *Larrea tridentata* to shortgrass steppe with *Bouteloua gracilis* (Gosz, 1993) are all examples of this transition. At the other end of the gradient, dense grasslands and savannas are replaced by forests. In some regions, this transition is sharp enough for no intermediate regions with savannas to be distinguishable at the scale of world or continental maps. For example, in Patagonia, *Festuca pallescens* grassland turns into a *Nothofagus* forest (Soriano, 1983; Schulze et al., 1996). In other regions, particularly in the tropics, there is a gradual increase in the tree/grass ratio as precipitation increases: grasslands are progressively replaced by savannas whose woody component becomes more important as precipitation increases (Sinclair, 1979; Walker and Noy-Meir, 1982; McNaughton, 1983a; Belsky, 1990).

The broad range of mean annual precipitation of the grassland/savanna biome is one of the most important causes of its structural and functional diversity. Plant cover, plant biomass, leaf area, and canopy height of the herbaceous layer predictably increase along gradients of increasing precipitation. For example, the heterogeneity of the grassland region of North America has been repeatedly described on the basis of a gradient from the relatively dry, shortgrass steppe in the West through the more humid, tallgrass prairie in the East (Coupland, 1992). Similar gradients are observed in southern South America (Oesterheld et al., 1992) and East Africa (McNaughton, 1983a). Parallel to these changes in structural features, ecosystem function also changes dramatically and predictably along the precipitation gradient. In particular, more than 75% of the variation in above-ground net primary production of the herbaceous layer of grasslands and savannas can be accounted for by their mean annual precipitation (McNaughton, 1985; Sala et al., 1988a; McNaughton et al., 1993). Precipitation also explains a substantial proportion of the seasonal variability of carbon gains (Paruelo and Lauenroth, 1996, 1998). Taken together, these observations suggest that mean annual precipitation causes a great deal of variation among grasslands and savannas, but, for this same reason, it becomes a highly integrative variable to be used when generalizations about the whole biome are needed. This conceptual gradient of precipitation will be an important framework for this chapter.

In addition to this variation associated with mean annual precipitation and primary productivity, there is a finer scale of variation associated with soil types. The gently rolling landscape of many grasslands and savannas determines wide differences in hydrologic regime, nutrient cycling, vegetation structure, and ecosystem function without difference in mean annual precipitation (McNaughton, 1983a; Schimel et al., 1985; Soriano, 1992; Corona et al., 1995). At a broader scale, grasslands and tropical savannas differ significantly as a result of soil texture and mineralogy, with important consequences not only for vegetation structure and composition, but also for herbivore populations (Huntley, 1982; East, 1984; Epstein et al., 1997).

In addition to the important role of mean annual precipitation and soil type as determinants of grassland and savanna structure and function, there is the role of disturbance regimes. The world-wide expansion of grasslands and savannas since the Miocene has been paralleled by the evolution of large mammalian grazers and browsers (McNaughton et al., 1993), the occurrence of fire (Vogl, 1974; Collins, 1990), and the marked climatic fluctuations that characterize these subhumid and semiarid environments (Anderson, 1982).

Thus, three types of disturbance are particularly important in shaping the structure and function of grasslands and savannas. First, the type and magnitude of herbivore load determines a pattern of biomass removal, trampling, defecation, and urination, with profound consequences for the entire system (McNaughton, 1983a; Detling, 1988; McNaughton et al., 1988). For example, grazing can turn a tall grassland into a short one (McNaughton, 1984; Facelli, 1988), and its exclusion may have opposite effects (McNaughton, 1984; Sala et al., 1986). Second, the frequency and intensity of fires determine a pattern of biomass removal, nutrient volatilization, and ash deposition which affect the whole ecosystem (Daubenmire, 1968; Vogl, 1974; Hulbert, 1988; Hobbs et al., 1991). For example, in Australian savannas, fire can remove up to 94% of nitrogen, 53% of phosphorus, and 82% of potassium present in plant biomass (Cook, 1994); and, in the tallgrass prairie of North America, a single fire event can remove approximately twice the annual input of nitrogen (Seastedt, 1995). Finally, year-to-year changes, and even larger-scale trends in climatic variables, can affect water availability, a major driving force of the structure and function of these systems (Risser, 1985; Le Houérou et al., 1988; Briggs et al., 1989; Lauenroth and Sala, 1992). These disturbance factors become particularly important at the boundaries of the biome because they may be responsible for changing the biome status of the system: at the drier boundary, grazing and climatic variations have been repeatedly identified as likely causes of desertification, the transformation of a grassland into a system with desert features (Dodd, 1994), whereas at the humid end of the gradient interactions among grazing, fire, and climate have been identified as the cause for woody-plant encroachment, and the transformation of a grassland or savanna into a closed woodland or forest (Archer et al., 1988; Archer, 1989, 1995).

The objective of this chapter is to show the major effects of these three disturbances on grasslands and savannas of the world. This subject has been reviewed many times in the past (e.g., Daubenmire, 1968; Vogl, 1974; Anderson, 1982; Risser, 1985; Detling, 1987, 1988; Collins, 1990). Our contribution will focus on those aspects that we believe have received less attention and that we are in the position of analyzing now because of the existence of new data and the development of new ideas. Most reviews have concentrated on structural aspects of vegetation at the community level while neglecting the more functional, ecosystem-level attributes. Thus, we have chosen a single functional response variable as the center of our chapter: aboveground net primary productivity (ANPP). In addition, most researchers, while agreeing on the importance of grazing, fire, and climate fluctuations as agents of disturbance, have tended to treat them separately, so that a measure of their relative importance is lacking. Thus, we have attempted to study their effects on productivity in comparable ways, so that they can be ranked. Finally, we believe that there have been good reviews focusing on particular grassland/savanna regions, but less effort has been devoted to integrating patterns for all kinds of systems. Thus, we have framed all our analysis in the context of a gradient of annual precipitation that encompasses a wide range of grassland and savanna ecosystems. Naturally, this approach has tradeoffs. We will lose spatial detail and diversity of response variables. The rest of the chapter is organized in the following way: first, we will describe the disturbance regime of grasslands and savannas;

second, we will show how disturbances affect above-ground net primary productivity.

DISTURBANCE REGIMES

The frequency and intensity of grazing, fire, and climatic fluctuations change with mean annual precipitation. Because precipitation is linearly related to above-ground net primary productivity, mean annual precipitation is associated with both the availability of forage, which partially determines grazing regime, and the production of flammable fuel, which partially determines fire regime. Grazing and fire are alternative consumers of productivity: grazing may preclude the accumulation of fuel and completely suppress fire, and fire, in turn, may either consume productivity that could be used by herbivores or change its quality as forage (Kucera, 1981). Finally, mean annual precipitation is associated with year-to-year variations in precipitation. Thus, there is a gradient of mean annual precipitation along which the likelihood of a system being grazed, burned, or struck by drought or exceptionally wet conditions, vary.

Grazing regime

It may not be surprising that populations of herbivores and the amount of energy they consume increase with productivity across a wide range of ecosystem types, from deserts through tropical forests (McNaughton et al., 1989, 1991). However, it is more intriguing that different ecosystem types form a single cohesive function, and that the shape of that function is exponential: as ecosystems become more productive, they have a growing herbivore load per unit of primary production and, as a result, a growing proportion of their productivity is consumed by herbivores (McNaughton et al., 1989, 1991). Considering only foliage production (i.e., excluding wood), consumption by herbivores across all these ecosystem types dominated by native herbivores was related to production by:

$$\log C = -4.8 + 2.04 \log \mathrm{NFP} \qquad (r^2 = 0.59, \quad P < 0.0001, \quad \mathrm{d.f.} = 73) \tag{11.1}$$

where C is consumption, NFP is net foliage production, and units are $\mathrm{kJ\,m^{-2}\,yr^{-1}}$ (McNaughton et al., 1989). Being significantly greater than 1, the slope of this log–log relationship indicates an exponential shape. Discussing this result, McNaughton et al. (1991) argued that it could stem from the fact that the most productive end of the data set was heavily influenced by data points from tropical grasslands and savannas of East Africa, with their high density of megafauna, whereas the low end of the productivity gradient was influenced by temperate grasslands that currently lack an important population of large herbivores because of hunting and other habitat alterations by humans. The key question concerns the extent to which the exponential increase of consumption is an intrinsic property of the productivity gradient or simply a result of human-induced extinctions.

We extracted from the data set of McNaughton et al. (1989, 1991) only the data points classified as grasslands and savannas (Fig. 11.1). The relationship between consumption and productivity, which should be regarded here as the pattern of consumption along the gradient of mean annual precipitation, was of the form:

$$\log C = -5.16 + 2.2 \log \mathrm{ANPP} \qquad (r^2 = 0.75, \quad P < 0.0001, \quad \mathrm{d.f.} = 42) \tag{11.2}$$

This relationship is not significantly different from the

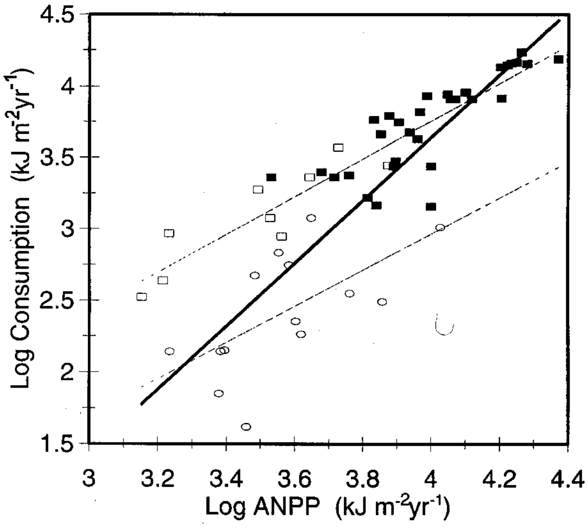

Fig. 11.1. Relationship between herbivore consumption and above-ground net primary production (ANPP) of grasslands and savannas dominated by native herbivores. Solid squares are tropical sites ($n = 31$) dominated by vertebrates and open circles are temperate sites ($n = 14$) dominated by invertebrates (from McNaughton et al., 1989, 1991). The solid line is the best-fit line for both types of system taken together. Open squares are sites ($n = 9$) from Yellowstone National Park, a temperate, vertebrate-dominated system (from Frank and McNaughton, 1992). The two parallel dashed lines are best-fit lines for vertebrate-dominated systems (top) and invertebrate-dominated systems (bottom).

general relationship obtained for all ecosystem types, but it is stronger, as shown by its higher coefficient of determination ($r^2 = 0.75$, as against 0.59 for all ecosystem types). However, Fig. 11.1 shows that this function actually connects two parallel point clouds: a high-consumption cloud formed by the tropical, vertebrate-dominated grasslands, and a low-consumption cloud formed by the temperate, invertebrate-dominated grasslands. Frank and McNaughton (1992) have provided a crucial handful of data points by measuring consumption along a productivity gradient in a temperate ecosystem dominated by large herbivores: Yellowstone National Park with its dominant population of elk (*Cervus canadensis*). They showed that consumption data for that system perfectly fit the line of the tropical, vertebrate-dominated systems, suggesting that the highly exponential nature of the general relationship was indeed influenced by the lack of large herbivores in the temperate grasslands included in the original data set. When considered separately, the functions relating consumption and productivity of vertebrate-dominated and invertebrate-dominated systems are much less exponential than the general relationship:

$$\log C = -1.54 + 1.32 \log \text{ANPP} \quad \left(r^2 = 0.83, \quad P < 0.0001, \quad \text{d.f.} = 38\right) \tag{11.3a}$$

for vertebrate systems, and

$$\log C = -2.08 + 1.26 \log \text{ANPP} \quad \left(r^2 = 0.39, \quad P < 0.02, \quad \text{d.f.} = 12\right) \tag{11.3b}$$

for invertebrate systems. These relationships indicate that consumption, as a percentage of productivity, grows from 30 to 75% across the productivity gradient of vertebrate-dominated systems, but only from 5 to 10% across the productivity gradient of invertebrate-dominated systems (Fig. 11.2).

The relationships shown in Figs. 11.1 and 11.2, however, seem to be influenced by spatial scale. Independent data sets on herbivore densities and biomass suggest that the consumption data discussed above represent areas within regions with particularly high levels of herbivory. Consumption rates derived from large-scale surveys of herbivore density are much lower.

The consumption data discussed above were extracted from studies aimed at exploring the effects of herbivory on various aspects of community (and ecosystem) structure and function, and it is reasonable to expect that they were conducted in areas where herbivory was particularly important. For example, McNaughton (1985) explicitly stated that his regional study sites were located in areas of the Serengeti with high animal utilization. When animal biomass is measured for large regions, such as an entire national park or reserve, however, the data suggest that consumption rates are lower. Coe et al. (1976) and East (1984) reported such data sets, included also in McNaughton et al. (1989, 1991), and showed that herbivore biomass of East African grasslands and savannas varies roughly between 10 and 50 kg ha^{-1} and only rarely reaches values near 100 kg ha^{-1}. Considering that a 300 kg ruminant consumes approximately 11 kg kg^{-1} yr^{-1} of dry matter, consumption in grasslands with herbivore biomass between 10 and 50 kg ha^{-1} should be around 110 to 550 kg ha^{-1} yr^{-1}. The range of productivity for those grasslands is 2400–12 000 kg ha^{-1}, which indicates a 5 to 10% consumption rate. A similar pattern arises from Yellowstone. Herbivore biomass in the grassland/shrubland areas of the park is estimated as 36.9 kg ha^{-1} and is largely dominated by elk (D. Frank, pers. commun.). Thus, consumption should be around 400 kg ha^{-1} yr^{-1}, nearly an order of magnitude lower than the maximum reported by Frank and McNaughton (1992) for particular study sites. Densities of predators change with scale in the same way as those of mammalian herbivores; density of mammalian carnivores has a close negative relationship to the size of the study area (Smallwood and Schonewald, 1996).

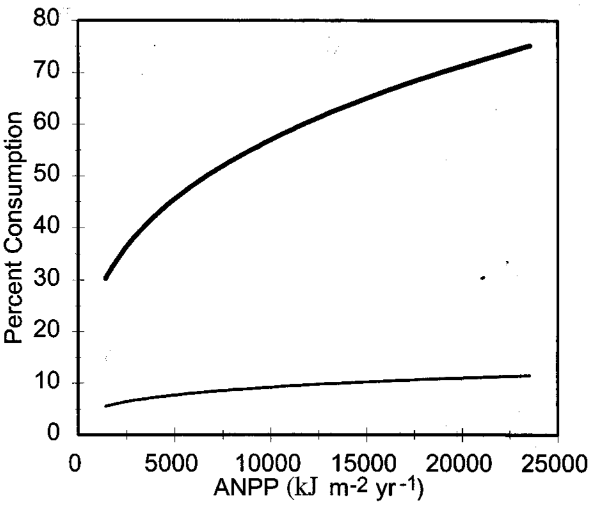

Fig. 11.2. Percentage of ANPP (above-ground net primary production) consumed by herbivores along a gradient of ANPP as predicted by the two parallel models of Fig. 11.1. Top, thick line: systems dominated by vertebrates. Bottom, thin line: systems dominated by invertebrates.

Most of the area covered by grasslands and savannas of the world, however, is populated by livestock rather than by native herbivores, and the patterns of consumption in that situation differ in some respects from those just described. Livestock biomass per unit area at a county level across a wide range of mean annual precipitation in rangelands of southern South America (Argentina and Uruguay) increased exponentially with precipitation, and was an order of magnitude greater than herbivore biomass of native systems around the world (Oesterheld et al., 1992). Rough calculations of consumption based on these data for livestock biomass indicate that percent consumption along the productivity gradient ranged from 20% to 75%. Thus, animal husbandry on rangelands has made an entire region look very much like the relatively small portions of a landscape such as the Serengeti National Park or Yellowstone that are heavily grazed by native herbivores.

These results suggest that (1) herbivore biomass and consumption increase along the precipitation gradient in an exponential fashion; (2) the relationship is very different among vertebrate-dominated and invertebrate-dominated systems; (3) consumption rates measured directly in particular communities or study sites likely represent the upper boundary of a range with great spatial variability; (4) consumption rates inferred from large-scale herbivore densities are much lower and likely reflect the actual average values that result from that spatial variability; and (5) livestock biomass and plant consumption also increase exponentially with precipitation but animal husbandry makes them both drastically larger and spatially more uniform within extended regions of grasslands and savannas.

Fire regime

There is a high degree of consensus about the way in which fire frequency varies along the gradient of annual precipitation that characterizes grasslands and savannas. In order to occur, fire requires a minimum amount of flammable fuel and the proper conditions for ignition and spread (Vogl, 1974). Since the rate of production of biomass (productivity) increases linearly with precipitation, fire frequency is thought to increase monotonically along the mean annual precipitation gradient that we have been analyzing (Kucera, 1981; Frost and Robertson, 1987; Risser, 1990). For example, researchers have experienced serious difficulties studying fires in areas with precipitation below 450 mm yr^{-1} because of repeated failures with experimental burning (Trollope, 1984). Our own set of data on fire effects, which will be presented later, lacks data for grasslands below 400 mm yr^{-1}. At the other extreme of the gradient, annual burning is a common practice both in research and management.

It is less clear, however, what mechanisms underlie the pattern of increased fire with increased precipitation. One mechanism, which has been repeatedly invoked, is that as precipitation increases so does the difference between production and losses of biomass, resulting in an increasing net accumulation of flammable fuel (standing dead material plus litter). This would be so if biomass losses by grazing and decomposition increased less with precipitation than primary productivity.

Regarding grazing, we have shown in the previous section (Figs. 11.1 and 11.2) that consumption by herbivores accounts for an increasing proportion of productivity as precipitation increases. We calculated the amount of above-ground primary productivity which would remain unconsumed on an annual basis according to those patterns (Fig. 11.3). Unconsumed productivity indeed increases along a gradient of mean annual productivity, as this mechanism for fire-

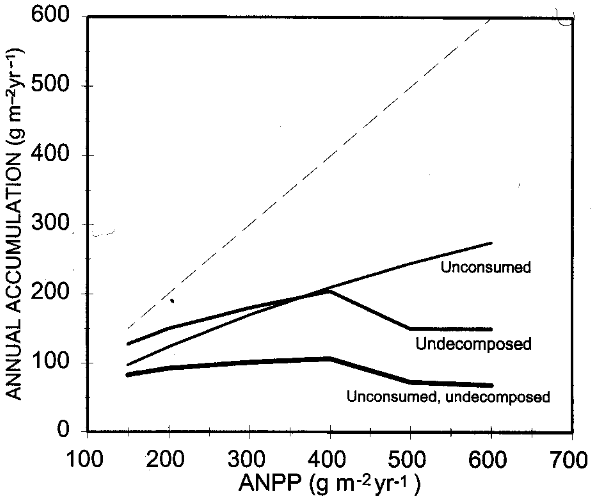

Fig. 11.3. Annual accumulation of above-ground biomass along a gradient of mean annual ANPP (above-ground net primary production), which is linearly related to precipitation. The dashed line represents the hypothetical accumulation if biomass were neither grazed nor decomposed (equality line). The other three lines with increasing thickness respectively represent the accumulation of biomass left unconsumed by herbivores (derived from the equation for vertebrate systems in Fig. 11.1), the accumulation of biomass left undecomposed without grazers (derived from decomposition rates by Schimel et al., 1990), and the accumulation of unconsumed biomass left undecomposed (derived from a combination of the two previous curves).

frequency gradients predicts, but the increase is much less steep than would be expected if grazers either were absent or consumed a constant proportion of productivity.

Regarding litter decomposition, there is a great deal of evidence for forest ecosystems that the proportion of litter annually lost by microbial decomposition is a positive function of actual evapotranspiration (AET), and a negative function of lignin content (Meentemeyer, 1978; Couteaux et al., 1995). Actual evapotranspiration is a close linear positive function of precipitation in grasslands (Ripley, 1992), and the few available data indicate that lignin content, particularly above-ground, decreases with precipitation (Schimel et al., 1990). Thus a higher, not lower, proportion of litter should be lost annually to decomposers as precipitation increases. Actually, Risser et al. (1981) have shown that, in the North American tallgrass prairie, litter losses by decomposition nearly equal the inputs on an annual basis.

The CENTURY model, which includes a number of biogeochemical processes in grasslands (Parton et al., 1987), predicts that annual decomposition rates of the Great Plains in North America should range from 20% at the low end of the precipitation gradient to 85% at the high end (Schimel et al., 1990). We used these data to estimate the amount of above-ground net primary productivity that would remain undecomposed annually in the absence of herbivores across a gradient from the north-west of the region through the south-east (Fig. 11.3). The increase in this accumulation rate was very low: a 270% increase in above-ground net primary productivity, from 150 to 400 $\mathrm{g\,m^{-2}\,yr^{-1}}$, resulted in an increase of fuel of 60% (deviations from this curve are obtained if the gradient of productivity is considered at low or high latitudes, instead of the NW–SE diagonal we utilized, because of the effect of temperature on decomposition rates). If above-ground net primary productivity exceeds 400 $\mathrm{g\,m^{-2}\,yr^{-1}}$, decomposition rates increase more than productivity, resulting in a decrease in accumulation of undecomposed above-ground material. If these decomposition rates are applied to the unconsumed productivity, simulating a more real system with herbivores and decomposers, fuel accumulation is obviously lower (Fig. 11.3). Figure 11.3 also reveals that the CENTURY model predicts a decrease in the above-ground inputs to the soil pool of carbon from subhumid to humid systems. However, belowground inputs continuously increase along the gradient (Schimel et al., 1990), and seem to be responsible for the associated increase in soil organic matter with increasing precipitation (Burke et al., 1989). Thus, high fire frequency in humid grasslands and savannas does not seem to be a consequence of litter accumulation through years due to larger differences between productivity and losses by grazing and decomposition. Standing-dead accumulation during the current year, instead, seems to account for regional patterns of fire frequency.

Another set of mechanisms consistent with predictions of an increase in fire frequency with mean annual precipitation or productivity has been provided by Wedin (1995). He proposed the existence of strong feedbacks involving nitrogen, soils, plants, herbivores, and fire, and related them to disturbance regimes. His conceptual model is integrative and thought-provoking, and is highly relevant here because it covers the same gradient from low precipitation and low productivity to high precipitation and high productivity that we have been considering.

The model assumes that, along this gradient of increasing precipitation and productivity, animal biomass and forage quality decline. This unexplained assumption leads to predictions about the major consumers of productivity (herbivores, decomposers, and fire) and, as a consequence, about disturbance regimes. The model stresses the importance of carbon and nitrogen stoichiometry of plants in regulating the consumer pathway that primary production will follow in a particular ecosystem. Unlike fire, herbivores and decomposers have a minimum nitrogen requirement to consume biomass. Thus, grazing and fire regimes operating along the gradient should depend on the carbon/nitrogen ratio of the dominant grasses. Consequently, one would expect herbivory and decomposition to be the major consumers in low-production systems with high quality of forage and litter, and fire to be the major "consumer" in high-production ecosystems with lower quality of forage and litter.

We have shown in the previous section that the pattern of consumption along the gradient is opposite to that assumed by this model. We will concentrate now on the second assumption: that forage quality decreases along the gradient. [This assumption was based on a set of data published by Breman and de Wit (1983) who showed, using an adjusted curve, that protein concentration and biomass production were inversely correlated in the Sahel region of Africa.]

We compiled information from the literature about nitrogen content in biomass of grasslands and savannas located along a broad range of mean annual precipitation to test this assumption (Table 11.1). Approximately 200 potentially relevant articles were surveyed, and 28, representing 61 data sets, were used in the analysis. The general criteria for data selection and analysis were as follows:

(1) we selected data from climatically-determined native grasslands or savannas (alpine communities, anthropogenic pastures, and wetlands were excluded);
(2) these data had to be taken from the field;
(3) data from the same site but obtained on different dates within a year were pooled and averaged;
(4) data from studies of individual species were included only when they were a dominant component of the community;
(5) the variable used for analysis was nitrogen concentration in above-ground green biomass. In the cases reported by Turner et al. (1993) and Jackson et al. (1990), this variable was estimated from nitrogen concentration of the above-ground dead biomass according to a linear regression obtained from cases where both variables were reported:

$$y = 0.535 + 1.06x; \quad (r^2 = 0.7; \quad P = 0.0003; \quad \text{d.f.} = 12) \tag{11.4}$$

where y is nitrogen concentration in green biomass and x is nitrogen concentration in dead biomass;
(6) data used by Breman and de Wit (1983) were not included in the analysis because they were not available (their paper only presented an adjusted curve).

Figure 11.4 shows that the two variables were not significantly correlated:

$$[\mathrm{N}] = 1.59 - 0.00024 \times \mathrm{ppt}, \quad (r^2 = 0.026; \quad P = 0.20; \quad \text{d.f.} = 60) \tag{11.5}$$

where [N] is nitrogen concentration in above-ground biomass and ppt is mean annual precipitation. This result does not support Wedin's assumption. Multiple regression models including grazing regime (ungrazed or grazed) or the proportion of C_3 vs. C_4 plants did not add to the proportion of the variance being explained. Figure 11.4 suggests that greater productivity of more humid systems does not necessarily involve a trade-off with nitrogen concentration, which is related to forage quality and presumably to litter quality (Wedin, 1995). High fire frequency in more productive grasslands is neither a consequence of lower nitrogen content of the forage, which would reduce herbivore consumption, nor of low litter quality, which would reduce decomposition. Wedin's model has been extremely helpful in leading the way to an integrated explanation for disturbance regimes of grasslands and savannas, but a fully satisfactory picture is still lacking.

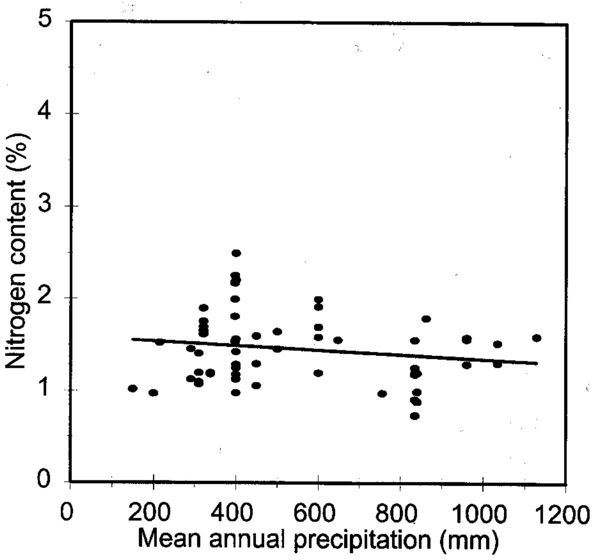

Fig. 11.4. Nitrogen content (%) in above-ground green biomass along a gradient of mean annual precipitation of grasslands and savannas.

Perhaps too much importance is being given to the annual balance between production and decomposition to explain fire frequency, and, in any case, this exaggerated importance is being applied to the wrong side of the gradient. In order to burn, very productive grasslands do not need to accumulate litter for many years. On the contrary, a highly productive season followed by a dormant season is enough. For example, in a North American tallgrass prairie, grasslands burnt in March were able to carry a second fire in October of the same year (Bragg, 1982). Grasslands with such a high productivity simply need a dormant season that kills most green tissue, an ignition event, and atmospheric conditions that favor the spread of fire (Vogl, 1974). Differences between production and litter decomposition may indeed be very important for fire occurrence on the drier (<600 mm), but not the wetter, side of the gradient. Low productivity will not generate enough flammable biomass in a single season, and only by year-to-year accumulation will these grasslands be able to carry fires.

Climatic fluctuations

The gradient of grasslands and savannas we have been considering is one of mean annual precipitation,

Table 11.1
Nitrogen concentration values based on green above-ground biomass[1](characteristics of information shown in Fig. 11.4)

Site	MAP[2]	Ungrazed[3]	Grazed[4]	Reference
Mixed grass prairie (North Dakota, USA)	400	0.98	1.19	Biondini and Manske (1996)
	400	–	1.98	
	400	1.43	1.13	
	400	–	1.25	
	400	1.18	1.57	
	400	–	1.21	
Oak savanna (California, USA)	600	1.92	2.00	Center et al. (1989)
Subhumid grassland (Buenos Aires, Argentina)	960	1.30	1.57	Chaneton et al. (1996)
Shrub steppe (Wyoming, USA)	290	1.13	1.46	Coughenour (1991)
Shortgrass steppe (South Dakota, USA)	450	–	1.06	Day and Detling (1990)
Shrub steppe (Wyoming, USA)	398	–	2.00	Frank and McNaughton (1992)
Shrub steppe (Wyoming, USA)	398	–	2.18	Frank et al. (1994)
	398	–	2.17	
	398	–	1.81	
	398	–	1.54	
	398	–	1.53	
Oak savanna (California, USA)	600	–	1.20	Hart et al. (1993)
Tallgrass prairie (Kansas, USA)	835	0.91	1.20	Hobbs et al. (1991)
Shortgrass steppe (Colorado, USA)	310	–	1.20	Hunt et al. (1988)
Oak savanna (California, USA)	600	1.59	–	Jackson et al. (1990)
	600	1.70	–	
Mixed grass prairie (South Dakota, USA)	338	–	1.20	Jaramillo and Detling (1992)
Mediterranean grassland (Andalucía, Spain)	648	1.56	–	Joffre (1990)
Semiarid grassland (Thessaloniki, Greece)	215	–	1.53	Mamolos et al. (1995)
	215	–	1.19	
Shortgrass steppe (Colorado, USA)	321	1.76	–	Milchunas et al. (1995)
	321	–	1.62	
	321	–	1.65	
	321	1.70	–	
Tallgrass prairie (Kansas, USA)	840	1.20	1.20	Owensby et al. (1993)
Dehesa savanna (Salamanca, Spain)	500	–	1.46	Pérez Corona et al. (1995)
	300	–	1.65	
Tallgrass prairie (Oklahoma, USA)	840	0.89	0.89	Risser and Parton (1982)
Semiarid steppe (Chubut, Argentina)	150	1.02	1.02	Sala et al. (1991)
Shortgrass steppe (Colorado, USA)	310	–	1.10	Schimel et al. (1985)
	310	–	1.08	
	310	–	1.41	
Tallgrass prairie (Kansas, USA)	835	1.19	–	Schimel et al. (1991)
Subhumid grassland (Serengeti, Tanzania)	862	–	1.80	Seagle and McNaughton (1992)
Tallgrass prairie (Oklahoma, USA)	756	–	0.98	Seastedt et al. (1988)

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Table 11.1, *continued*

Site	MAP[2]	Ungrazed[3]	Grazed[4]	Reference
Subhumid grassland (Buenos Aires, Argentina)	960	1.59	1.59	Semmartin and Oesterheld (1996)
Savanna (Sonbhadra, India)	1035	1.31	–	Singh (1993)
		1.53	–	
Tallgrass prairie (Kansas, USA)	835	1.74	1.20	Turner et al. (1993)
	835	1.26	1.56	
Mixed grass prairie (South Dakota, USA)	450	–	1.30	Whicker and Detling (1988)
		–	1.60	
Semiarid steppe (Beer Sheva, Israel)	200	–	0.97	Zaady et al. (1996)

[1] Different values within a study represent different years or different topographic positions.

[2] Mean Annual Precipitation (mm).

[3] [N] of ungrazed plots (%).

[4] [N] of grazed plots (%).

which integrates in a single figure a variable that fluctuates from year to year. In this section we examine whether that variability changes along the gradient of mean annual precipitation of grasslands and savannas. Evidence from such dispersed sources as the North American Great Plains, the Serengeti National Park (Tanzania), and Patagonia (Argentina) clearly shows that absolute interannual variability in precipitation is positively correlated with its mean (Sinclair, 1979; Jobbágy et al., 1995; Lauenroth and Burke, 1995). The standard deviation of annual precipitation, which provides a measure of absolute variability, increases with mean precipitation. However, the coefficient of variation (CV), which provides a measure of variation relative to the mean, decreases with precipitation. For example, in the North American Great Plains, a grassland with annual precipitation around 200 mm has a standard deviation of 50 mm and a coefficient of variation of 25%, whereas a grassland with annual precipitation around 800 mm has a standard deviation of 150 mm and a coefficient of variation of 19% (Lauenroth and Burke, 1995). In Patagonia, a mean annual precipitation gradient from 150 to 500 mm is associated with a decrease in the coefficient of variation from 40% to 20% (Jobbágy et al., 1995). Thus, drier grasslands have a greater chance of experiencing more important relative changes in precipitation from year to year than more humid grasslands.

The variability of water demand by the atmosphere is much lower than the variability of precipitation. The standard deviation of the mean annual potential evapotranspiration in the Great Plains ranges from 15 to 30 mm, whereas the standard deviation of precipitation ranges from 50 to 250 mm (Lauenroth and Burke, 1995). The coefficient of variation of the mean annual potential evapotranspiration ranges between 1 and 2.5%, whereas that of the annual precipitation ranges between 15 and 35%. Thus, drier systems have a greater chance of experiencing drought or unusually high water status because of variation in the input rather than in the output of water.

EFFECTS OF GRAZING, FIRE, AND CLIMATE FLUCTUATIONS ON PRODUCTIVITY

Researchers have repeatedly emphasized the importance of grazing, fire, and climatic fluctuations, largely drought, in shaping the structure and function of grasslands and savannas (Anderson, 1982; McNaughton, 1983a; Medina and Silva, 1990; Risser, 1990). In this section, we address the effects of these disturbances on above-ground net primary productivity, a single but important functional variable that not only indicates the amount of energy that enters an ecosystem but also integrates many other attributes (Odum, 1969; McNaughton et al., 1989). We focus our attention on two major sets of questions. First, what is the relative magnitude of these three disturbance effects? We accept they are all important, but are they equally important, or do they differ in this respect? Secondly, are these effects and responses different along a

Table 11.2
Data on ANPP (above-ground net primary production) of grazed and ungrazed plots of grassland and savanna sites from publications that appeared after Milchunas and Lauenroth's (1993) analysis[1]

Site	MAP[2]	Ungrazed[3]	Grazed[4]	Reference
Yellowstone National Park (Wyoming, USA)	379	55	85	Frank and McNaughton (1993)
	379	400	590	
	379	190	340	
	379	175	295	
	379	205	235	
	379	110	130	
Shortgrass steppe (Colorado, USA)	275	26	26	Hobbs et al. (1996)
	275	26	27	
	275	26	23	
Tropical savanna (India)	926	548	794	Pandey and Singh (1992)
	926	432	626	
	1145	693	819	
	1145	703	732	
	1145	741	876	
	1145	590	614	

[1] Different values within a study represent different years or different topographic positions.
[2] Mean Annual Precipitation (mm).
[3] ANPP of ungrazed plots ($g\,m^{-2}\,yr^{-1}$).
[4] ANPP of grazed plots ($g\,m^{-2}\,yr^{-1}$).

precipitation gradient that encompasses a wide range of grasslands and savannas? For example, are drier systems more or less sensitive to each of these disturbances than more humid systems? And does the ranking of importance of these disturbances change along the gradient?

In order to address these questions, we used two different approaches, one for the effects of grazing and fire, and the other for the effects of climatic fluctuations. To study the effects of grazing and fire, we searched the literature and compiled two data sets from studies in which above-ground net primary productivity had been simultaneously measured in either grazed and ungrazed or burned and unburned conditions. The data set encompassed a wide variety of grasslands (see criteria below), and methodologies, both for treatments and data collection. To study the effects of climate, we used a surrogate for above-ground net primary productivity, the integral of the normalized difference vegetation index (NDVI-I). This index corresponds to the relative difference between red and infra-red reflectance of the Earth's surface as detected by satellite imagery. It has been shown for many areas that the normalized difference vegetation index is strongly correlated with the above-ground net primary productivity (Paruelo et al., 1997). We looked at how the normalized difference vegetation index fluctuated from year to year in a wide variety of grassland types, and translated that to above-ground net primary productivity based on the relationship mentioned.

Grazing and fire

We based our analysis on published data (Tables 11.2 and 11.3) complying with the following criteria. We only considered sites that received a mean annual precipitation within the range 200–1200 mm, and were occupied by climatically-determined grasslands or savannas grazed by ungulates (i.e., we excluded cultivated pastures, shrublands, and azonal communities such as wetlands and salt marshes). We only included data for above-ground net primary production measured on an annual basis. Peak biomass data

Table 11.3
Annual above-ground primary production (ANPP) of burned and unburned plots of different grassland sites along a wide precipitation gradient[1]

Site	MAP[2]	Unburned[3]	Burned[4]	Reference
Tallgrass prairie (Stillwater, Oklahoma, USA)	810	475	500	Bidwell et al. (1990)
	810	475	470	
Mixed grass prairie (South Dakota, USA)	440	118	162	Bragg (1995)
	440	249	218	
	440	249	246	
Bunchgrass steppe (Alberta, Canada)	439	118	137	
	439	118	115	
Tallgrass prairie (Illinios, USA)	843	389	648	
Tallgrass prairie (Iowa, USA)	782	420	544	
Tallgrass prairie (Kansas, USA)	846	170	340	
Tallgrass prairie (Nebraska, USA)	681	129	315	
	681	129	174	
	681	129	258	
Sandhills (Nebraska, USA)	472	269	208	
	472	242	240	
	472	111	80	
Mixed grass prairie (Nebraska, USA)	472	525	500	
Mixed grass prairie (Kansas, USA)	582	238	120	
	582	238	157	
Mixed grass prairie (Oklahoma, USA)	804	132	216	
Shortgrass steppe (Kansas, USA)	582	303	71	
	582	303	215	
	582	442	167	
Annual grassland (California, USA)	529	551	354	
Tallgrass prairie (Konza, Kansas, USA)	880	358	367	Briggs and Knapp (1995)
	880	404	506	
	810	500	530	
	810	500	580	
Tallgrass prairie (Konza, Kansas, USA)	880	510	903	Hulbert (1988)
Tallgrass prairie (Illinois, USA)	843	302	1321	Kucera (1981)
	843	361	591	
Tallgrass prairie (Missouri, USA)	897	509	933	
	897	482	522	
Tallgrass prairie (Iowa, USA)	782	349	750	
Tallgrass prairie (Eastern Kansas, USA)	880	186	340	
Mixed grass prairie (Western Kansas, USA)	582	380	171	
Serengeti National Park (Tanzania)	1129	374	491	McNaughton (1985)
	1129	374	337	
Tallgrass prairie (Manhattan, Kansas, USA)	880	205	516	Owensby et al. (1970)

continued on next page

Table 11.3, *continued*

Site	MAP[2]	Unburned[3]	Burned[4]	Reference
Mediterranean grassland (Thessaloniki, Greece)	500	203	176	Papanastasis (1980)
	500	203	119	
	500	203	58	
Tallgrass prairie (Kansas, USA)	880	473	380	Risser et al. (1981)
	880	180	340	
Tallgrass prairie (Illinois, USA)	843	395	1397	
	843	634	756	
Tallgrass prairie (Iowa, USA)	782	364	455	
Mixed grass prairie (South Dakota, USA)	440	243	200	Steuter (1987)
	440	243	234	
	440	243	237	
	440	106	116	
	440	106	88	
	440	106	95	
Texas high plains (Amarillo, Texas, USA)	542	123	84	Trlica Jr and Schuster (1969)
	542	123	96	
	542	123	91	
	542	123	84	
	542	123	82	
	542	87	57	
	542	87	51	
	542	87	51	
	542	87	48	
	542	87	68	
Juniper community (Callahan County, Texas, USA)	600	131	185	Wink and Wright (1973)
	600	103	90	
	782	369	447	

[1] Different values within a study represent different years or different topographic positions.

[2] Mean Annual Precipitation (mm).

[3] ANPP of unburned plots ($g\,m^{-2}\,yr^{-1}$).

[4] ANPP of burned plots ($g\,m^{-2}\,yr^{-1}$).

were considered equivalent to above-ground net primary productivity only for sites with a well-defined growing season (Sala et al., 1988b). Most data on grazing effects were obtained from Milchunas and Lauenroth's (1993) meta-analysis, whereas the data on fire effects were obtained from reviews by Kucera (1981), Risser et al. (1981) and Bragg (1995), and a literature search. Data for above-ground net primary productivity were transformed into logarithms for normality.

It is widely recognized that grazing alters primary production of grasslands and the herbaceous layer of savannas. However, the direction of the change it provokes at the community level is currently a matter of debate. While there is evidence that grazing may promote productivity (e.g., McNaughton, 1979, 1993),

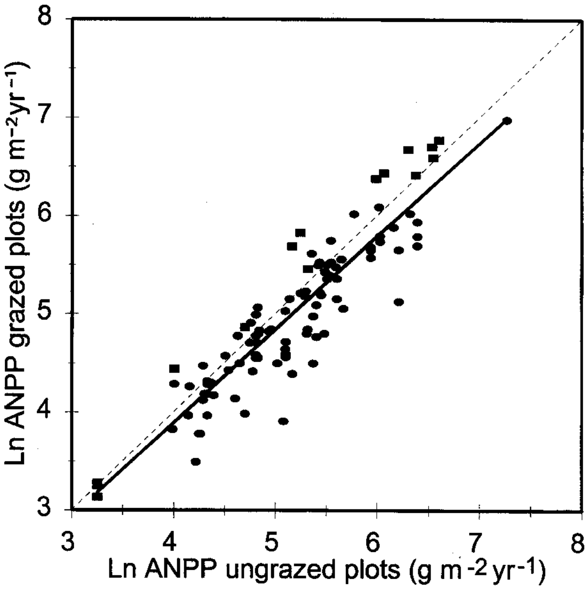

Fig. 11.5. Relationship between ANPP (above-ground net primary production) of grazed and ungrazed plots of grassland and savanna sites comprising a wide range of primary productivity. The solid line corresponds to the best-fit line, and the dashed line represents the equality line, where ANPP of grazed plots is equal to the ANPP of ungrazed plots. The solid circles belong to the data set of Milchunas and Lauenroth (1993), and the solid squares to papers published after 1990, which were not included in their review.

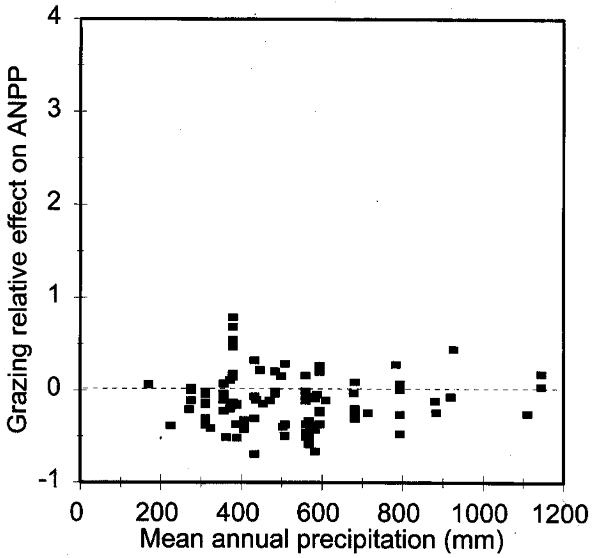

Fig. 11.6. Effects of grazing on ANPP (above-ground net primary production) (calculated as $(\mathrm{ANPP_{grazed}} - \mathrm{ANPP_{ungrazed}})/\mathrm{ANPP_{ungrazed}}$) of grassland and savanna sites along a gradient of mean annual precipitation. The dashed line indicates the null effects of grazing on ANPP.

in other circumstances grazing has been shown to have detrimental effects on productivity (e.g., Painter and Belsky, 1993; see also Bradbury, Chapter 24, this volume). Figure 11.5 shows that, for a wide range of environments, productivity of grazed plots is linearly related with the productivity of their ungrazed counterparts by:

$$\ln \mathrm{ANPP_{grazed}} = 0.1017 + 0.9475 \times \ln \mathrm{ANPP_{ungrazed}}$$
$$\left(r^2 = 0.84, \quad P < 0.00001, \quad \text{d.f.} = 103\right), \tag{11.6}$$

where $\ln \mathrm{ANPP_{grazed}}$ and $\ln \mathrm{ANPP_{ungrazed}}$ are the natural logarithms of the above-ground net primary production ($\mathrm{g\,m^{-2}\,yr^{-1}}$) of grazed and ungrazed plots, respectively. The intercept, not different from 0, the slope, marginally lower than 1 ($P < 0.10$), and the high r^2 value, all indicate that the effects of grazing on productivity are small, can be either positive or negative, but are more frequently negative.

The effects of grazing on productivity were in general no larger than a 50% increase or decrease and showed no relationship with mean annual precipitation (Fig. 11.6). Grazing increased productivity in 28% of the cases and decreased it in 72% of the cases.

Productivity of burned plots was linearly related with the productivity of their unburned counterparts by:

$$\ln \mathrm{ANPP_{burned}} = -0.63 + 1.118 \times \ln \mathrm{ANPP_{unburned}}$$
$$\left(r^2 = 0.62, \quad P < 0.00001, \quad \text{d.f.} = 64\right), \tag{11.7}$$

where $\ln \mathrm{ANPP_{burned}}$ and $\ln \mathrm{ANPP_{unburned}}$ are the natural logarithms of the ANPP ($\mathrm{g\,m^{-2}\,yr^{-1}}$) of burned and unburned plots respectively (Fig. 11.7). A slope not significantly different from one ($P > 0.14$) and an intercept not significantly different from zero ($P > 0.28$) indicate that fire may have both positive and negative effects on productivity.

The effects of fire on productivity were relatively larger than the effects of grazing, and showed a significant pattern along the precipitation gradient. The dispersion of the points around the equality line of Fig. 11.7 is larger than the dispersion of the points around the grazed vs. ungrazed line of Fig. 11.5. Thus, both positive and negative effects of fire on productivity appear to be more intense than the effects of grazing. This is clearly shown by Fig. 11.8: fire might increase productivity by 300%, or reduce it to less than 20% of control treatments. The proportional effect of fire on productivity was positively associated with mean annual precipitation ($r^2 = 0.30$, $P < 0.00001$, d.f. $= 62$): the positive cases were on the more humid side of the

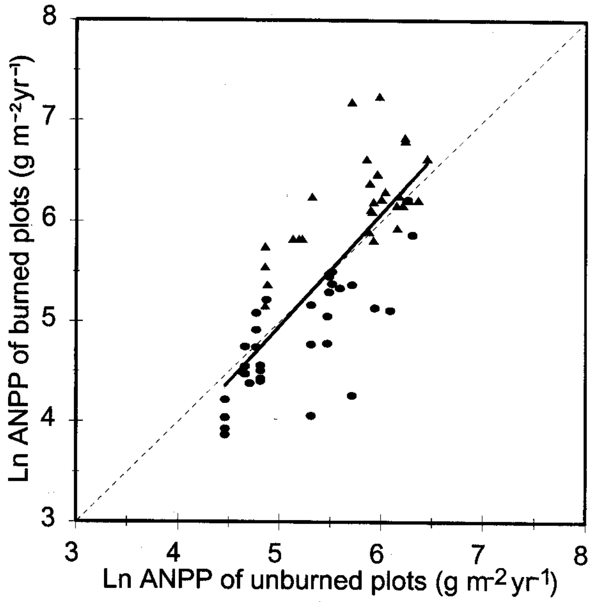

Fig. 11.7. Relationship between ANPP (above-ground net primary production) of burned and unburned plots of grassland and savanna sites comprising a wide range of primary productivity. The full line corresponds to the best-fit line, and the dashed line represents the equality line, where ANPP of burned plots is equal to the ANPP of unburned plots. Solid circles and triangles correspond to sites receiving less and more than 600 mm of mean annual precipitation respectively.

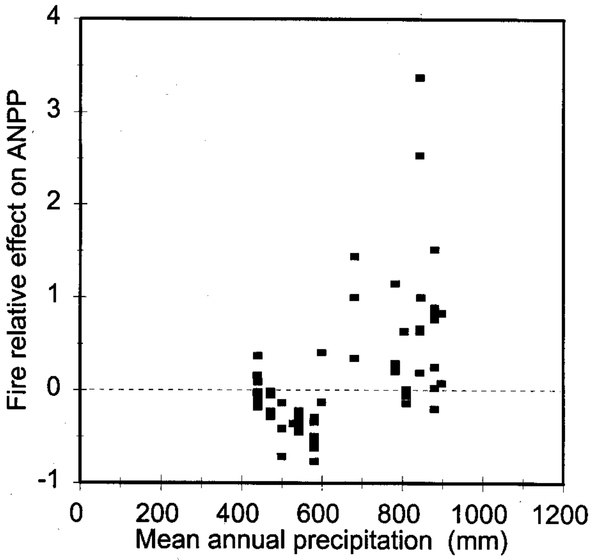

Fig. 11.8. Effects of burning on ANPP (above-ground net primary production) (calculated as $(\text{ANPP}_{\text{burned}} - \text{ANPP}_{\text{unburned}})/\text{ANPP}_{\text{unburned}}$) of grassland and savanna sites along a gradient of mean annual precipitation. The dashed line indicates the null effects of burning on ANPP.

gradient and the negative cases on the drier side of the gradient, with a transition between 600–700 mm.

Climatic fluctuations

We compiled a data set of the normalized difference vegetation index (a surrogate for above-ground net primary productivity) for 13 grassland sites in North and South America. Site selection was based on the following criteria: a broad gradient of precipitation had to be encompassed, annual precipitation data had to be available, and natural grassland had to be the dominant vegetation type within the scanning unit or pixel. We used the Pathfinder Land Program data set (National Oceanic and Atmospheric Administration/National Aeronautic and Space Administration; James and Kalluri, 1994), which covers the 1981–1992 period and is based on maximum composites for ten-day periods. Spatial resolution is 8 km. Data for normalized difference vegetation index were transformed into productivity by means of the equation provided by Paruelo et al. (1997).

To make this analysis comparable to our previous analyses, we plotted maximum and minimum productivity for the 12-year period as a function of average productivity (Fig. 11.9). The figure shows that variations in productivity were, in relative terms, much greater on the drier side of the gradient. Both regression lines significantly differed from the equality line. The relationship between maximum and average productivity was

$$\ln \text{ANPP}_{\text{MAX}} = 0.84 + 0.90 \times \ln \text{ANPP}_{\text{AVG}} \quad (r^2 = 0.98, \quad P < 0.00001, \quad \text{d.f.} = 12). \tag{11.8}$$

The intercept was significantly larger than 0 and the slope significantly lower than 1.

The relationship between minimum and average productivity was

$$\ln \text{ANPP}_{\text{MIN}} = -2.11 + 1.31 \times \ln \text{ANPP}_{\text{AVG}} \quad (r^2 = 0.96, \quad P < 0.00001, \quad \text{d.f.} = 12). \tag{11.9}$$

It had the opposite pattern: the intercept was significantly lower than 0 and the slope significantly greater than 1. Thus, relative fluctuations in productivity from year to year tend to be smaller as mean annual rainfall increases (Fig. 11.10). Extreme productivity values were 80–90% greater or smaller than the mean in dry sites, and only 20% in humid sites.

We investigated to what extent this interannual variability in productivity was related to precipitation fluctuations. We analyzed the relationship between the relative variations in productivity shown in Fig. 11.10 and the relative variation of the precipitation of the year in which the maximum or the minimum productivity was recorded [(annual precipitation for maximum or minimum ANPP – mean precipitation)/mean precipitation]. This analysis showed that 50% of the interannual fluctuations in productivity were accounted for by the year's relative deviation in precipitation with respect to the mean ($r^2 = 0.50$, $P < 0.0001$).

Discussion of disturbance effects

The relatively mild effects of grazing and their uniformity throughout the gradient of rainfall reflect the importance of compensatory mechanisms in all sorts of systems and conditions. Compensatory growth, the increase in production per unit of remaining biomass after grazing (McNaughton, 1983b), is responsible not only for the positive effects of grazing on productivity but also for the relatively low magnitude of the negative effects. Since percent consumption increases along the gradient, our results indicate that compensatory growth also increases as precipitation increases. Without this increasing compensatory growth, the effects of grazing should have been all negative and directly related to consumption: more negative from the dry to the wet end of the gradient. Thus, the lack of strong effects on productivity and the common pattern along the gradient are in fact the result of strong feedback processes, which, through drastic changes in species composition, canopy structure, canopy photosynthesis, within-plant resource allocation, nutrient cycling, and water economy, among others, buffer potential changes in the functional, ecosystem-level variable, productivity (McNaughton, 1979, 1983b; Detling, 1987). It is particularly interesting that grazing effects on species composition are strongly influenced by the position of a system along the precipitation gradient (Milchunas and Lauenroth, 1993); grazing has minor effects on species composition of dry grasslands and large effects in more humid grasslands and savannas. Thus, the more or less similar relative effects of grazing on productivity along the gradient are maintained despite strong structural changes.

A challenging, and promising, aspect of our analysis is the difference between fire and grazing effects along the gradient. It has been stated many times that fire effects on productivity vary from predominantly negative in arid sites to positive in humid sites (Daubenmire, 1968; Vogl, 1974; Anderson, 1982; Bragg, 1995). However, we do not know of a quantitative test of

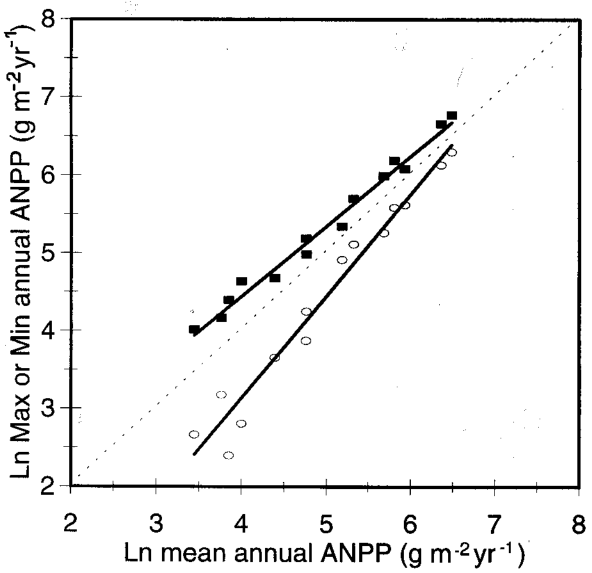

Fig. 11.9. Fluctuation of ANPP in grasslands along a gradient of productivity. Solid squares correspond to maximum ANPP (above-ground net primary production) and open circles correspond to minimum ANPP in a series of 12 years between 1981 and 1992.

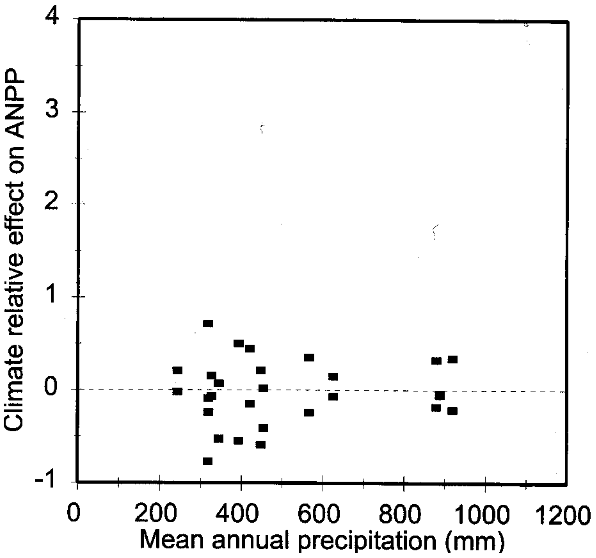

Fig. 11.10. Relative variation of ANPP (above-ground net primary production) of grasslands along a gradient of mean annual precipitation. The relative variation was calculated as $(ANPP_{MAX} - ANPPAVG)/ANPPAVG$ for the maximum data and as $(ANPP_{MIN} - ANPPAVG)/ANPPAVG$ for the minimum data. The dashed line is the equality line that indicates the null effects of climate fluctuations on ANPP.

that statement such as the one we have presented. The observation that fire generally does not have negative effects on productivity in humid sites, as grazing does, and does not have positive effects in drier sites, as grazing does, poses interesting questions regarding the different mechanisms through which these two agents of disturbance affect productivity.

Interannual variability in productivity has been an important aspect of ecosystem studies because it affects one's ability to predict productivity. Lauenroth and Sala (1992) have shown that 40% of the variation in productivity of a shortgrass site was explained by annual precipitation. Thus, productivity would fluctuate following the wide relative fluctuations in precipitation that characterize those semiarid environments (Le Houérou et al., 1988; Lauenroth and Burke, 1995). Our analysis based on patterns of the normalized difference vegetation index suggests that this pattern of variation closely matches the pattern of the coefficient of variation of rainfall along the gradient. For North American grasslands, the relative variability of the integral of normalized difference vegetation index (our estimator of above-ground net primary productivity) decreased exponentially with an increase in mean annual precipitation (Paruelo and Lauenroth, 1998).

Our analysis fails to consider the interaction among disturbances, a potentially important aspect of disturbance phenomena, which has received particular attention recently (Collins, 1987; Hobbs et al., 1991; Briggs and Knapp, 1995; Noy-Meir, 1995). We do not have enough data to study these interactive effects at the large scale we have selected for our chapter. In any case, the patterns we have shown are strong enough, despite any potential interactive effect that we have not accounted for.

A CONCEPTUAL MODEL

Our analyses allowed us to build a conceptual model of the relative effects of three types of disturbance in grasslands and savannas (Fig. 11.11). The central element of this model is that both the regimes and the ranking of importance of the effects of these three types of disturbance depend on the position of a particular system on the gradient of mean annual precipitation. The effect of a disturbance on the productivity of a system located at any point along the gradient will be a function of the disturbance regime at that point, and the way that system responds to disturbances with changes in productivity.

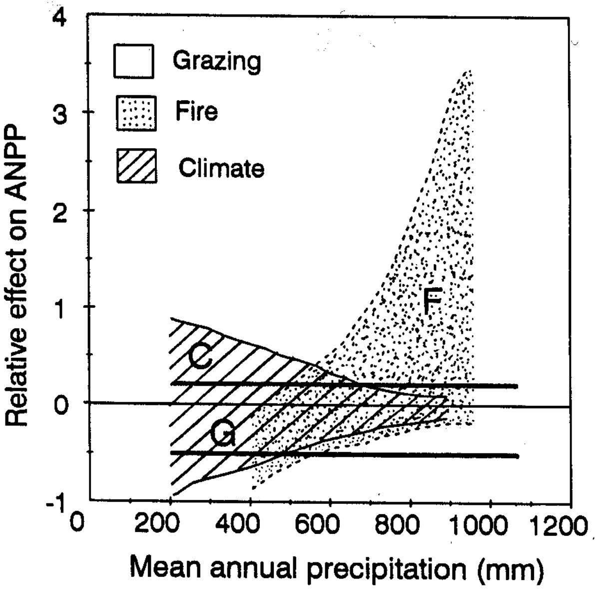

Fig. 11.11. A conceptual model of the relative effects of grazing, fire, and climate on ANPP (above-ground net primary production) along a gradient of precipitation. The lines enclosing the response areas for each disturbance represent approximate boundaries of variation of ANPP according to Figs. 11.6, 11.8 and 11.10. Grazing effects are bounded by thick lines, fire effects are bounded by dashed lines and enclose a dotted area, climate effects are bounded by thin lines and enclose an area with stripes.

Between 200 and 450 mm, herbivory rates as a proportion of consumption and fire frequency are very low. In contrast, the systems are exposed to wide relative climatic fluctuations from year to year that can drastically change water economy, largely on the input side. Grazing in these systems may either increase or decrease productivity, but its effects are relatively mild compared to the interannual variation in productivity. One does not know what the effect of an eventual fire will be, but an extrapolation of our curve suggests that it may be severe. Productivity of these systems will fluctuate greatly around the mean, mainly as a consequence of interannual climatic fluctuations, reaching values ranging from less than one third of the mean to twice the mean.

Between 450–700 mm of precipitation, grazing intensity increases, but still is a low proportion of productivity. This, together with slow decomposition rates limited by low soil water and high lignin content of the litter, sets the stage for the occurrence of fire with increasing frequency. Fire depends on fuel accumulation over more than one year. Grazing, as in any segment of the gradient, may have both positive and negative effects on productivity, negative effects being more frequent than positive. Fire in these systems, however, usually decreases productivity. The relative effects of fire and grazing in this segment of the gradient are of the same magnitude. Year-to-year variations in precipitation are much lower than in the driest end of the gradient, and so is the variation in productivity. It is therefore in this intermediate portion of the gradient that the three agents of disturbance have effects of similar relative magnitude. The presence or absence of grazing, the occurrence of fire, or the occurrence of an unusual year may be equally important in changing productivity.

Above 700 mm of rainfall, grazing intensity in systems dominated by large ungulates may be very high, with a more patchy distribution in native systems than in livestock production systems. Fire frequency is much higher, favored by high annual production and the occurrence of a dormant season. Interannual fluctuations in weather are minimal in relative terms. Grazing has minor relative effects on productivity due to compensatory growth, but fire increases productivity up to five times the mean. Climatic fluctuations, in contrast, can only change productivity by less than 25%. Thus, productivity of these systems will fundamentally depend on fire occurrence in the first place, and grazing in the second. Grazing may have a larger effect in these systems through the regulation of the fire regime than by herbage removal *per se*.

Ecologists have known for decades that mean annual productivity of grasslands and savannas is linearly related to mean annual precipitation (Walter, 1939 cited by Rutherford, 1980; McNaughton, 1985; Sala et al., 1988a; McNaughton et al., 1993). Our results provide a quantitative measure of the variation that may be observed around that mean as a consequence of disturbance agents. These results have several implications. First, livestock and wildlife managers can use them when making decisions about setting long-term levels of herbivore populations: the food base will fluctuate in different ways for different systems, and that variation may cascade to affect animal populations and the human societies based upon their production of economic goods. Second, these results can be used to rank the potential importance of each of these agents in driving productivity fluctuations for particular ecosystems along the precipitation gradient. Instead of the qualitative suggestions from fire ecologists, grazing ecologists, climatologists, and grassland ecologists in general stressing the importance of one factor or considering them all equally important, a more balanced, broader view of their relative effects is now available, together with a more precise reference to the heterogeneity of responses across the biome. Finally, the results suggest that grasslands and savannas of intermediate mean precipitation are the most stable in terms of fluctuations in productivity, whereas the two extreme ends of the gradient are more prone to change. However, by controlling fire regime, grazing may reduce fluctuations in productivity at the humid end of the gradient, providing more stability to those systems. This may actually be a byproduct of human utilization of grasslands and savannas with livestock at much higher densities than wildlife (Oesterheld et al., 1992).

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