Chapter 18

Comparative Ecology of African and South American Arid to Subhumid Ecosystems

Samuel J. McNaughton, Osvaldo E. Sala, and Martin Oesterheld

I. Introduction

The arid to subhumid ecosystems of Africa and South America have identical origins in vast tracts of West Gondwana before the two continents were separated by continental drift and seafloor spreading (Raven and Axelrod 1974). Monocotyledons, including the Poaceae, appear to have originated during this period, although the grasses may have spread into South America later, in the Paleocene or Upper Cretaceous (Stebbins 1981). The earliest grass fossils, customarily taken as diagnostic of arid to subhumid ecosystems, appear in Patagonian deposits of Eocene age (Frenguelli 1930; Teruggi 1955), but they did not become common until the Miocene, by which time the Poaceae was almost fully differentiated, suggesting previous radiation in rare habitats or locations not lending themselves to fossil formation (Stebbins 1981). On both continents, the expansion and contraction of wet tropical forest associated with polar shifts and glaciation at higher elevations resulted in periodic fragmentation and subsequent reemergence of contiguous dryland ecosystems (Aubréville 1962). There were also substantial radiations of large, mammalian browser and grazer faunas in both South America and Africa contemporaneous with these climatic and vegetation oscillations. Thus, the arid to subhumid ecosystems of the two continents apparently had identi-

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cal origins and very similar developments through geological time.

II. Ecosystems Considered

We concentrate here on ecosystems where mean annual precipitation ranges from an approximate lower limit of 20 cm to an upper limit near 150 cm, although, like all such boundaries, these are subject to modification by local edaphic conditions, evaporative demand, altitude, and topography. In general, we consider ecosystems where members of the Poaceae are important in the herbaceous layer and woody vegetation can range from scattered dwarf shrubs to an almost continuous canopy of small-statured trees.

South American ecosystems considered include the Patagonian steppe, the pampas, open grassland called "campo," grass and savanna woodland known as "llano" or "cerrado," the open dry thorny woodlands called "chaco," and the dry thorn scrub named "caatinga." African ecosystems of these types (Huntley 1982; Werger 1983) would simply be known as grassland, bushland, or by the indefinite Spanish term derived from Amerindian languages (Sarmiento 1984), "savanna," and are commonly distinguished from woodland vegetation called "miombo."

Approximately 40 percent of earth's total area covered by arid to subhumid ecosystems occurs on the two continents considered here (FAO 1987). Therefore, these two continents are major sites of arid to subhumid ecosystems, although the proportion of continental area covered by them is less than in Australia. In Africa, they fringe the Mediterranean shore before being interrupted by the Sahara Desert, then sweep across the continent south of there to be bifurcated by rainforest except along the east, and continue southward more or less uninterrupted. In South America, they occur as disjunct areas north of the Amazon basin, scattered areas throughout that basin, and then sweep southward to near the continent's southern tip (figure 18.1).

The contemporary African and South American ecosystems are remarkably similar. Although the species of major herbaceous and woody plants are largely different, many grass and dicotyledonous genera and families appear on both continents, and the physiognomy of the vegetation on both continents is strikingly similar and varies in a similar fashion with precipitation and thermal climate. There is, however, one notable exception to the general similarity between African and South American ecosystems: South America's diverse and abundant browser and grazer fauna was comparable to that of Africa through the Tertiary, but it almost totally failed to survive the Pleistocene extinctions of large herbivorous mammals, whereas Africa preserves earth's greatest remnant of that fauna (Keast et al. 1972). The reasons for this notable difference are by no means clear (see Chapter 13), but it has significant implications for ecosystem structure and function on the two continents.

The ecosystems considered here are associated with climates characterized by pronounced dry seasons, high fire frequencies, and highly variable, but often anomalous, soil properties (Werger 1979; Walter 1979; Huntley and Walker 1982; Sarmiento 1984; Cole 1986). It is far beyond the scope of this chapter to consider such patterns in detail; instead we concentrate on variation

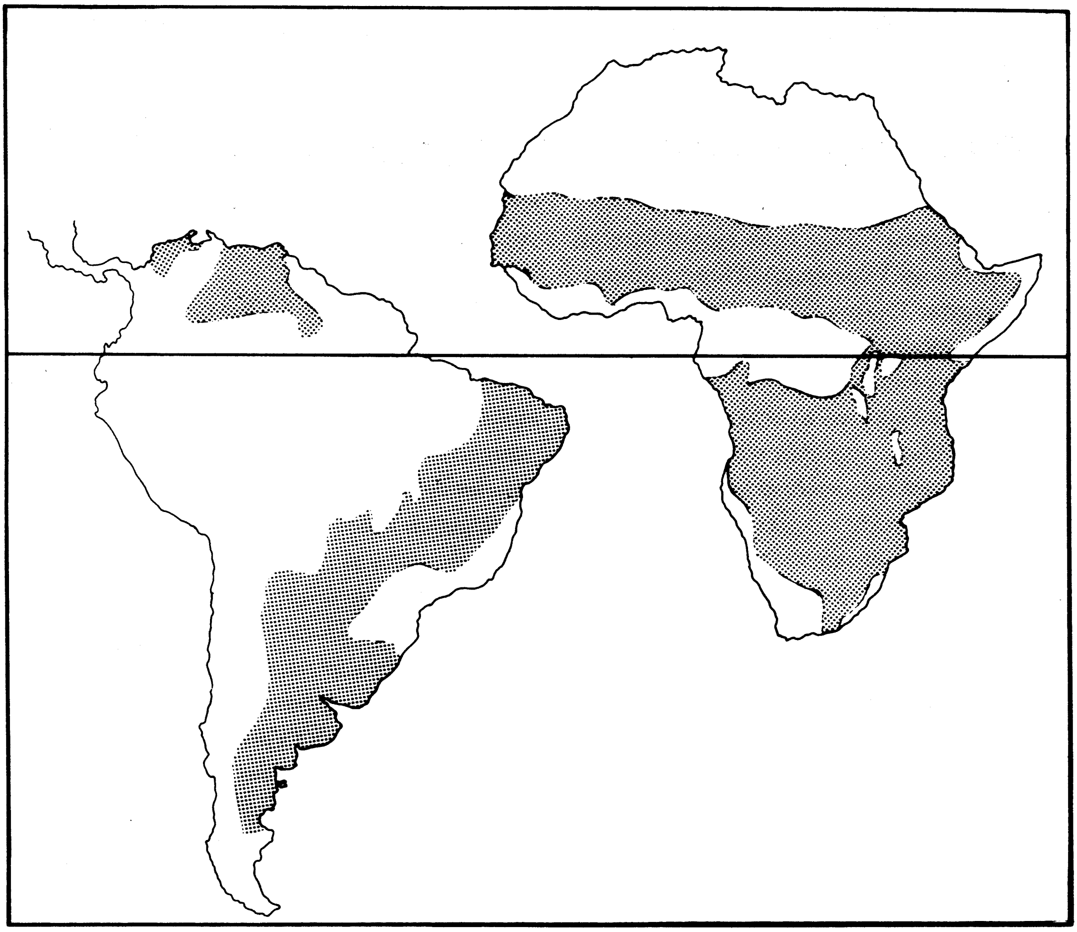

Figure 18.1. Map of South America and Africa with regions occupied by extensive arid to subhumid ecosystems indicated with dark shading.

in major structural and functional properties of semi-arid to subhumid ecosystems, comparing and contrasting the two continents ecologically.

III. Vegetation Structure

On both continents, the herbaceous layer is commonly dominated by grasses, species with the C_4 photosynthetic pathway most common in equatorial locations and species with the C_3 pathway becoming more important away from the tropics. In subtropical to temperate localities, such as the Argentinean pampas, there often is seasonal alternation of dominance by C_3 and C_4 grasses (Sala et al. 1982, Oesterheld and Léon 1987). Peak productivity of C_3 species occurs in early spring, whereas C_4 species have maximum productivity in late spring or early summer, a pattern also observed in mixed grass prairies of the northern Great Plains in North America (Ode et al. 1980).

Walter (1971) hypothesized that there is a vertical partitioning of soil resources, comparable to the two-phase aboveground structure, which reduces niche overlap between the herbaceous layer and the shrubs and trees. This could be a major attribute of these ecosystems tending to augment and stabilize productivity compared to a uniphasic ecosystem containing only herbs or only woody plants (Walker and Noy-Meier 1982). This hypothesis states that grasses absorb water from the upper soil layers, whereas trees absorb water from both upper and lower layers. It is based upon the morphological differences in the roots of grasses and woody plants. Grasses have finely branched roots that densely permeate the surface soil, whereas woody species have an extensive root system with coarse roots extending much farther into the soil profile.

Experimental data from southern African savannas provide support for the hypothesis (Knopp and Walker 1985). Removal of the herbaceous layer had a negligible effect on tree growth in a broad-leaved savanna with a low ratio of herbaceous to woody cover. In an *Acacia* savanna with sparser tree cover and a denser herbaceous layer, however, removal of the herbaceous layer resulted in significant increases in tree growth. Soil water and nutrient data suggested that this effect was due to the grasses intercepting percolating water in shallow soil layers, thus preventing water from light showers from reaching tree roots lower in the profile.

The two-layer hypothesis has also been extended to the shrub-grass balance in temperate steppes and tested with a removal experiment in Patagonia (Sala et al. 1989). Results support the overall hypothesis since shrubs and grasses used mainly different water resources. The data suggest a different distribution of resources between the two life forms. Patagonian shrubs absorb water almost exclusively from lower soil layers, whereas grasses take up water mostly from the upper layers. The major effect of grasses, then, is indirect: they intercept water that, in their absence, would percolate to lower layers where shrub roots have access to them. Consequently, grasses are not able to use the resources freed by shrub removal but shrubs can use the water freed by grass removal, but with a very low efficiency, about 25 percent.

These patterns of soil water partitioning pose similar questions regarding the mineral nutrition of grasses and woody plants in arid to subhumid ecosystem: do both life forms absorb nutrients from the same location in the soil at which water absorption is concentrated? If so, the woody plants would be at a clear disadvantage in competition for mineral nutrients since mineral cycles in these ecosystems are concentrated very near the soil surface (Clark 1977; Cole et al. 1977; Woodmansee et al. 1981). Data from tracer experiments in Patagonia (Sala et al. 1991) confirm the idea that shrubs absorb nutrients from the lower soil layers whereas grasses absorb principally from upper, nutrient-rich layers. These results suggest that shrubs must have effective strategies for coping with the differential mineral nutrient supply: (a) conservation and retranslocation of acquired nutrients at higher efficiency than grasses, (b) exploitation of nutrients from sporadic leaching events associated with exceptionally high rainfall, or (c) by percolation during periods when grasses are not actively growing.

The replacement of grasslands by shrublands is a serious worldwide problem in arid to subhumid ecosystems, a phenomenon commonly referred to as bush encroachment. The biphasic models just discussed suggest that intense and selective removal of grasses by livestock can lead to a redistribution of resources making conditions more favorable to the woody plants. This would probably lead to an associated decline of net primary productivity due to the low efficiency with which woody plants use the resources freed by grass decline. The existence of underexploited resources under the shrub-dominated condition suggests that this phase could be reversed by reducing herbivore pressure. However, the shrubs' advantage in aboveground competition would place them at a decided advantage once encroachment had become pronounced, perhaps leading to irreversibility in the absence of fire to kill back aboveground portions of woody plants.

At moderate to low precipitation levels, tree spacing in savannas appears to result from competition between trees for soil resources (Smith and Goodman 1986). In studies at a location with mean annual precipitation of 610 mm, a variety of lines of evidence implicated competition in tree spacing. First, there was a positive correlation between nearest neighbor distance of canopy trees and the combined canopy volume of those neighbors. Second, the slope of the regression between combined canopy cover of nearest neighbors and distance between them was positively related to both water available from the soil and total exchangeable bases. And, third, removal of surrounding trees resulted in significantly enhanced growth of the remaining experimental trees, in spite of the fact that canopies were widely spaced and nonoverlapping. These results indicate that the spacing of trees in some savannas is due to competition for soil-borne resources.

It is also important to recognize the potential importance of fire in maintaining the balance between the herb layer and the arborescent canopy (Vesey-Fitzgerald 1971), particularly in higher rainfall locations. Experimental fire plots established in Zambia in 1933 at a location with a mean rainfall near 1200 mm included annual treatments of (a) a late dry season, hot burn, (b) an early dry season, cool burn, and (c) no burning. The vegetation on these plots came to be decidedly different, documenting the role of fire in the balance of arborescent and herbaceous vegetation in subhumid ecosystems (Trapnell 1959; Werger 1983). Hot fires almost completely destroyed the woody overstory, resulting in a very open savanna with an extremely sparse overstory of large trees. Cool fires produced the typical open miombo woodland that is characteristic of that region of Africa. The unburned vegetation developed into a closed woodland of dry evergreen forest. These long-term studies provide convincing evidence that fire plays a central role in maintaining the open character of savannas toward the higher end of the rainfall gradient. Early burning, at the wet-dry season transition when grass biomass still has a good deal of moisture and fires are, therefore, "cool" is now a common management practice throughout Africa to maintain the tree canopy (Stronach and McNaughton 1989).

Regular flooding also can influence the balance between grasses and woody vegetation in arid to subhumid ecosystems by leading to open grassland, whereas better-drained areas support savanna or woodland. These hydrologic grasslands are common in the Brazilian Mato Grosso and Venezuelan-Colombian llanos (Sarmiento 1984). Conspicuous African examples are the floodplain of the Kafue flats in Zambia (Werger and Ellenbrook 1980), the Okavango Delta in Botswana (Cole 1986), and the Ndabaka Plains in the western Serengeti ecosystem (McNaughton 1983). Both the South American and the African ecosystems of this type are characterized by inundation during the wet season and severe drought during the dry season. Anoxia for significant periods appears to deter the colonization of and suppress the growth of trees much more severely than it affects grasses. Although it has been argued that the pampas were anthropogenic grasslands maintained through burning by the aboriginal Amerindian population (Schmieder 1927), they are more plausibly recognized as edapho-climatic grasslands (Walter 1979).

Even gentle topographic relief in hydrologic grasslands leads to alternating patches flooded for extended periods and unflooded areas (Leon et al. 1984; Poiani and Johnson 1989; Oliff et al. 1988). In Venezuela, flood-intolerant C_4 species are most common on elevated areas, whereas commonly inundated swales are dominated by flood-tolerant C_3 plants (Medina and Motta 1990). This pattern is reversed in the more temperate flooding pampa where elevated communities are dominated by C_3 species and neighboring lower patches are dominated by C_4 species (Sala et al. 1986). These regional differences may be explained by ecophysiological and climatic differences. Pampean C_4 species have lower reductions in leaf water potential than C_3 species in response to flooding (Sala et al. 1982).

Grasses from the flooding pampa and from flooded regions of Africa's Serengeti ecosystem exhibit a variety of common responses to flooding (Oesterheld 1990). Greater flooding tolerance in both floras is associated with greater plant height, lack of roots above the soil surface, higher root porosity, and the ability to maintain higher stomatal conductance and photosynthesis when flooded.

Large grazing mammals, whether livestock in South America (Sala et al. 1986) or native grazers in Africa (McNaughton 1984), have a pronounced effect upon vertical structure of savanna grasslands. Grazing compresses the canopy into a shallow layer within about 5 cm of the soil surface that is inaccessible to large grazers. In ungrazed grasslands, the major green canopy layer is substantially above the ground surface, and many short-statured species or ecotypes are eliminated from the ground layer by shading in the absence of grazing (McNaughton 1983; Sala et al. 1986).

When grazing pressure is not intense, grass swards develop a lateral structure of bimodal height classes partitioned between tall, ungrazed patches and short, grazed patches (Vesey-Fitzgerald 1974). Grazed patches are returned to repeatedly by grazers, but the tall patches are ignored. The high quality of the grazed patches makes them preferred foraging areas, whereas the patches that escaped grazing decline in quality and in yield per bite as growth proceeds (McNaughton 1984).

Africa's abundant browsers also have significant influences upon the tree-grass balance (Laws 1970; McNaughton and Sabuni 1988). Elephants (*Loxodonta africana*) can severely deplete the tree layer by direct destruction and bark-stripping, browsers suppress the height growth of seedings and saplings, keeping them in the fire-susceptible height range, and fire burns potential recruitment classes back to ground level (Norton-Griffiths 1979). These interacting factors often lead to tree size-frequency distributions that are decidedly bimodal (McNaughton and Sabuni 1988), with many small trees in the browser- and fire-susceptible class and a very few quite large trees that managed to surpass this bottleneck at some time in their life.

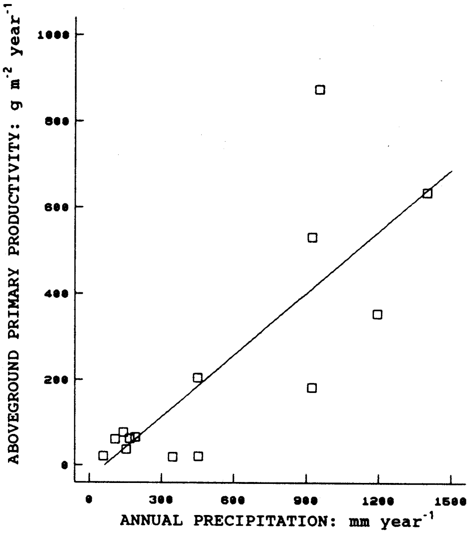

Figure 18.2. Relationship between annual precipitation and net aboveground primary productivity for South American arid to subhumid ecosystems.

IV. Primary Production

Primary productivity, the rate at which plants accumulate biomass, is a fundamental ecosystem variable that acts as a major indicative integrator of many other ecosystem properties (McNaughton et al. 1989). A comparison of correlations between primary productivity and precipitation for African and South American data sets reveals essentially identical relationships between the two variables. For 14 South American ecosystems collated for this chapter (San José and Medina 1975; Fonseca et al. 1976; Bulla et al. 1981; Sala et al. 1982; Bertiller 1984; Distel and Fernandez 1986; Oesterheld and Léon 1987; Defosse et al. 1990; Fernandez et al. 1991), the relationship was (see figure 18.2)

$$\text{ANPP} = 0.48 \text{ mm} - 30,$$

for 20 locations in the Serengeti ecosystem in East Africa (McNaughton 1985),

$$\text{ANPP} = 0.69 \text{ mm} - 102,$$

for 33 combinations of locations and years in East and southern Africa (Deshmukh 1984),

$$\text{ANPP} = 0.85 \text{ mm} - 20,$$

and for 45 North African ecosystems (Le Houérou and Hoste 1977),

$$\text{ANPP} = 0.26 \text{ mm} - 11,$$

where ANPP is aboveground net primary productivity in g m^{-2} $year^{-1}$ and mm is annual precipitation (figure 18.3). Although a wide variety of investigators and methods were involved in data collection in all data sets except the Serengeti ecosystem, these relationships suggest a remarkable uniformity of production-precipitation relationships. For 100 locations across the North American Great Plains (Sala, Parton, et al. 1988),

$$\text{ANPP} = 0.6\ \text{mm} - 34.$$

Therefore, the relationship between primary productivity and precipitation in arid to subhumid ecosystems is widely similar across many different geographic regions, with an increment of between one-half and three-fourths of a gram of production per square meter annually for each millimeter of precipitation (figure 18.3).

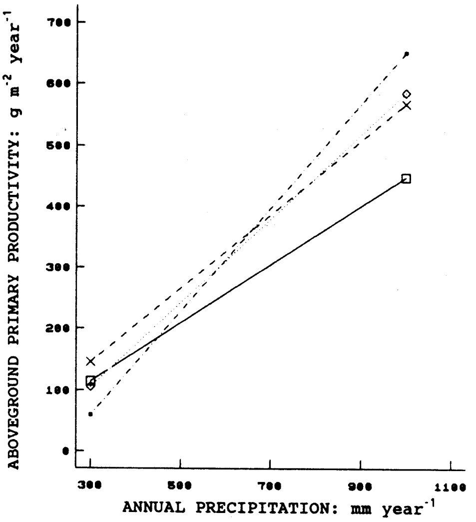

Figure 18.3. Best fit lines relating annual precipitation to net aboveground primary productivity from several geographic compilations for arid to subhumid ecosystems in Africa and South America.

Using the X-intercept as an index of the lower limit of these ecosystems (where potential productivity equals zero), values of rainfall limit are 63 mm for South America, 148 mm for the Serengeti ecosystem, 23 mm for Africa, 42 mm in the Sahel, and 57 mm for North America. Of course, the ecosystems considered here merge into desert past their lower limits, so these data suggest that semi-arid ecosystems become desert at rainfalls of less than approximately 100 mm annually, near our initially defined limit of around 200 mm annually.

Although the similarity of these general trends is of major ecological significance, substantial deviation does occur due to finer-scale ecosystem differentiation. In the Serengeti ecosystem, for example, productivity of vegetation growing in locations with high rainfall on old, leached sands derived from Precambrian deposits that contain little organic matter and nitrogen falls substantially below the regression line (McNaughton 1985). ANPP at five locations in the Orinoco Llanos in Venezuela with a rainfall of 1257 mm ranged from 123 to 482 g m^{-2} yr^{-1} (San José et al. 1985), whereas values predicted from the above equations range from 559 to 1022 g m^{-2} yr^{-1}. The exploitable soil volume and soil nutritional factors seemed important across these localities. Similarly, Sarmiento's (1984) tabulation of 23 savanna ANPP values in Venezuela over a rainfall range from 1017 to 1350 mm revealed a productivity range from 229 to 731 g m^{-2} yr^{-1}, and no evident association with precipitation.

Sala, Parton, and co-workers (1988) demonstrated for the North American Great Plains that the factors controlling primary productivity changed with spatial scale considered. At a coarse scale, broad regional patterns of primary productivity were explained principally by annual precipitation. At finer spatial scales, however, additional environmental properties had to be incorporated, particularly soil properties. At fine scales they confirmed an inverse-texture hypothesis: below an annual rainfall threshold of 370 mm, production is greater on coarse-textured soils (sands with low water-holding capacities), but above this threshold, production is greater on finer-textured soils (clays with greater water-holding capacities).

Therefore, although there are broad regional patterns of association between primary productivity and precipitation, fine-scale differentiation within narrow precipitation ranges reveals considerable heterogeneity in the productive process. Localized edaphic factors are particularly important causes of such deviations in both South America and Africa.

Recent comparative studies of tropical grasslands at four locations, one each in Central America, South America, Africa, and Asia, indicate that many estimates of ANPP, including most of those discussed above, undercalculate ANPP by 5 to 39 percent compared to estimates that include tissue turnover (Long et al. 1989). Total productivity estimates, including the productivity of belowground organs, were 37 to 80 percent below values including estimated tissue turnover. In contrast, recent analyses of the methods commonly used to calculate above- and belowground production indicate that most estimates represent overestimates of the true production value (Singh et al. 1984; Sala, Biondini, et al. 1988). Random errors associated with the estimates of plant biomass, which are then used to calculate net production, always result in a positive bias in estimating primary production. Although methods that include tissue turnover may be closer to actual values, they are also likely to be positively biased by small random errors. Therefore, more information on productivity that incorporates tissue turnover is desirable, but we think this information is unlikely to modify the fundamental trends presented here.

V. Herbivory

The most conspicuous difference between native South American and African semiarid to subhumid ecosystems is the prevalence of leaf-harvesting ants as principal herbivores in the former (Bucher 1982) and large mammals as major herbivores in the latter (McNaughton and Georgiadis 1986). Large mammals, of course, have been reintroduced as livestock throughout the arid to subhumid ecosystems of South America, where they currently constitute the major herbivore class.

The forage-harvesting attine ants are now categorized as major "pests" of Neotropical agriculture, and most estimates of their importance are related to this status (Fowler et al. 1986). This status, therefore, may lead to overestimates of their importance compared to natural ecosystems, since there may be a tendency to concentrate measurements where the influence is most pronounced. Nevertheless, studies in pastures indicate that they can be formidable competitors with livestock (Robinson and Fowler 1982). Ants have a direct inhibitory effect on cattle grazing. Cattle avoid areas where ants are foraging and, when confined to those areas by staking, graze less and walk more than when staked in control areas (Fowler and Saes 1986). In addition, confined cattle fed forage with ants on it consume significantly less than if they are absent, suggesting that thoracic spines or other properties of the ants act as direct feeding deterrents to large mammals.

Estimates of the level of herbivory by ants are indirect and conspicuously variable but, nonetheless, indicate that they are major herbivores in Neotropical arid to subhumid ecosystems (Fowler et al. 1986). Methods of estimating consumption include (a) multiplying counts of foraging workers by weights of loads carried, (b) calculating the weight ratio of fresh to spent fungal substrate, and (c) comparing exclusion plots, where ants are poisoned, with untreated plots. In pastures in Paraguay, exclusion indicated that ants consumed from 2 to 37 percent of the standing crop, compared to cattle consumption of 20 to 65 percent; in all cases, consumption was conspicuously lower in plots where both ants and cattle had access, suggesting mutual interference (Robinson and Fowler 1982). A compilation of consumption values from subtropical South American grasslands indicates that ants consume up to 900 g m^{-2} yr^{-1} (Fowler et al. 1986). Therefore, leaf-harvesting ants appear to be the natural herbivores in South America occupying the grazing niche that is occupied by large mammals in Africa. In fact, the fragmentary data on herbivory indicate that they may sometimes attain levels of consumption comparable to the large mammals. We believe that one of the great gaps in a comparative understanding of South American and African arid to subhumid ecosystems is the paucity of data on consumption by leaf-harvesting ants in South America.

Excluding primates, more than 90 species of large (weighing more than 5 kg) mammalian herbivore species occur on the African continent (Maglio and Cooke 1978). More than 10 species coexist in most game areas, and large reserves commonly have more than 20 species of large mammalian herbivores (Cumming 1982). The highest levels of sustained herbivory in natural ecosystems have been consistently recorded in Africa, with estimates commonly in the range of 33 to 66 percent of aboveground productivity consumed, although some values range up to 95 percent (McNaughton and Georgiadis 1986). For 28 study sites spread across the Serengeti ecosystem (McNaughton 1985), the proportion of ANPP consumed annually ranged from a minimum of 17 percent to a maximum of 94 percent, with a mean value of 66 percent and a median of 71 percent (figure 18.4). These data were from studies employing temporary exclosures and unfenced plots to estimate both

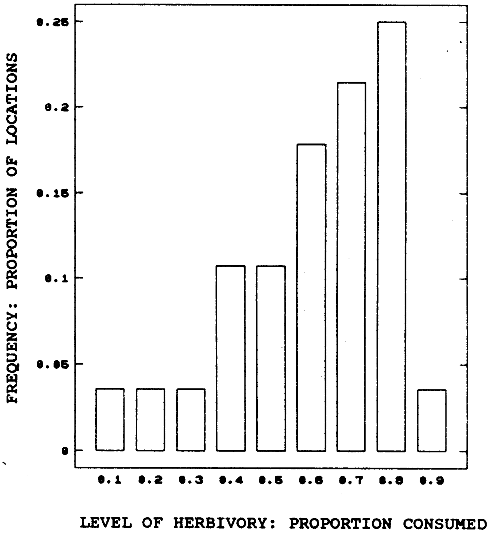

Figure 18.4. Frequency of proportion of net aboveground primary productivity consumed at different locations in the Serengeti ecosystem (after McNaughton 1985).

ANPP and herbivory. Using the common comparison of peak standing crop with minimum standing crop indicated that 92 percent of aboveground production in the Serengeti ecosystem disappeared by the end of the growing season due to herbivory (including both mammals and termites), fire, and trampling into the soil. Therefore, the residual standing crop in African ecosystems is extremely low by comparison with most other systems, where the bulk of primary production enters detritus food webs. In African ecosystems where herbivores are abundant, there is virtually no sustained accumulation of residual standing dead plant material, and turnover time of standing crop is very short compared to plots that are fenced and unburned (McNaughton et al. 1988). The vast majority of primary productivity each year is consumed by herbivores or termites, burned, or trampled into the soil where it is rapidly decomposed.

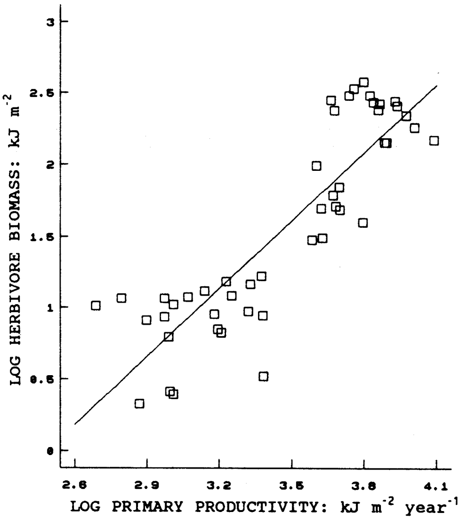

Figure 18.5. Relationship between large herbivore (livestock) biomass and net aboveground primary productivity of South American ecosystems.

VI. Primary Productivity and Large Herbivore Biomass

All significant ecosystem properties of the herbivore tropic level, biomass, consumption, and productivity are significantly correlated with primary productivity in terrestrial ecosystems ranging from desert and tundra to tropical forest and salt marsh (McNaughton et al. 1989). However, tropical grasslands depart from the general trend by having higher levels of consumption and lower levels of biomass per unit of primary productivity than comparable ecosystems with invertebrates as the major consumer class (McNaughton et al. 1991).

A compilation of livestock biomass (*B*) across Argentina (Mininsterio de Economia 1974), with primary productivity estimated from the ANPP/precipitation relationship documented above, reveals a similar association (figure 18.5):

$$\log B = 1.64 \log \mathrm{ANPP} - 3.75,$$

where B is expressed in kJ m^{-2} and ANPP in kJ m^{-2} yr^{-1}. However, a comparison of this pattern with the best fit line from natural ecosystems reveals a major difference (figure 18.6). The biomass of livestock supported per unit of primary production is about an order of magnitude above the level of natural herbivores. This indicates that agricultural management practices, including dietary supplementation, veterinary practices, and elimination of predators, significantly increases the carrying capacity of ecosystems for herbivores. To our knowledge, this is the first quantitative documentation of

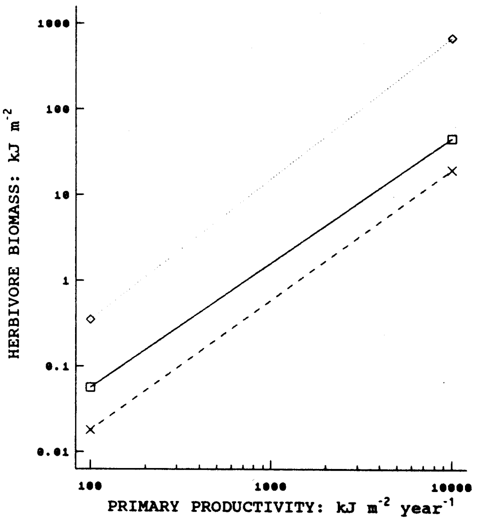

Figure 18.6. Best fit lines relating herbivore biomass to net aboveground productivity. Diamond: South American livestock; box: African ungulates; x: all native herbivores.

this phenomenon over a broad range of primary productivities (Oesterheld et al. 1992).

In addition to the positive association between total mammal herbivore biomass and vegetation productivity, data from African game reserves indicate that the biomass of 19 of 23 individual species is also positively associated with rainfall (East 1984). At the highest rainfall levels, however, there were tendencies both for the biomass of many species to decline and for some species to disappear altogether. Moreover, the trends were accompanied by a pattern of change in average body size of major herbivores. At progressively higher rainfall levels and, therefore, higher levels of net primary production, larger species (e.g., elephant and buffalo, *Sycerus caffer*) become increasingly important elements of the herbivore trophic level.

A similar pattern of variation in livestock size with net primary productivity was evident in South American livestock (figure 18.7). The proportion of sheep, compared to cattle, present in livestock herds declined with increasing ANPP from near 100 percent sheep at the lowest productivity levels in Patagonian areas receiving less than 200 mm of precipitation annually to near zero at the highest productivities in subtropical regions with annual precipitation levels near 1500 mm. Small-bodied livestock predominate at low levels of rainfall and, therefore, primary productivity, whereas large-bodied livestock predominate at higher rainfalls, just as in African wildlife communities.

Gut volume of mammals is a constant proportion of body weight, but maintenance metabolism is a fractional power of that weight (Demment and Van Soest 1985). Thus, the metabolic requirement per unit of gut capacity decreases as body weight in-

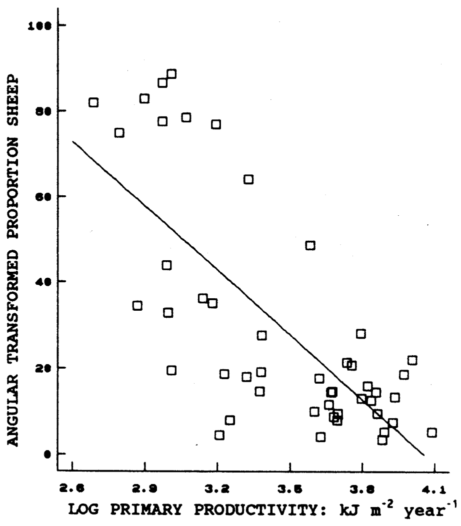

Figure 18.7. Proportion of sheep in South American livestock biomass in relation to net aboveground primary productivity.

creases and the fiber content of an herbivore diet increases with body size. Since a positive relationship probably exists between fiber content of the vegetation and primary production (Demment and Van Soest 1985), herbivores of larger body size, whether wild or domesticated, are more capable of using the more abundant but lower-quality forage produced at higher levels of rainfall.

VII. Plant Nutrition

It has long been known that the savanna vegetation of the Neotropics is often associated with extraordinarily infertile soils (Beard 1953; Lopes and Cox 1977). However, this is not true of all arid to subhumid ecosystems there, and the Argentinean pampas occur on soils that are among earth's most fertile (Scobie 1964; Hall et al. 1991). African arid to subhumid ecosystems are commonly characterized by a gradient from arid-eutrophic to moist-dystrophic systems (MacVicar 1977; Huntley 1982). This seems most applicable to eastern and southern Africa, less so to northern and western Africa.

The Malian-Dutch Sahel Primary Production project, spanning rainfall levels near and at the lower limits considered here, concluded that low nutrient availability, particularly of phosphorus and nitrogen, was a more serious limitation on productivity than low rainfall (Bremen and de Wit 1983). Experimental fertilization in the Sahel produced increases in ANPP of three- to fivefold (De Vries et al. 1980). These increases were attained on a wide range of soil types and with vegetation varying from dominance of the grass layer by annuals to dominance by perennials. In some instances, the vegetation response to nitrogen appeared linear to application levels nearing 250 kg N ha^{-1}. At nearer the humid-dystrophic end of the African nutritional continuum, fertilization of *Hyparrhenia* grasslands in Kenya resulted in linear increases in production up to application levels of 300 kg N ha^{-1}, and additional increments of production due to the addition of phosphorus at higher levels of nitrogen fertilization (Keya 1973).

Fertilization of Venezuelan llanos dominated by *Trachypogon* with 67 kg N ha^{-1} or 79 kg P ha^{-1} produced aboveground yield increases of 30 percent and 18 percent, respectively (Medina et al. 1977). An array of grassland fertilization experiments distributed throughout Argentina serve to characterize the fertility features of the region at a coarse scale (Berardo and Darwich 1969; Bruno et al. 1982; Marchegiani et al. 1982; Mendoza et al. 1983; Ginzo et al. 1986). The sites encompassed a variety of climates from subtropical to temperate. Nitrogen fertilization at levels between 80 and 360 kg N ha^{-1} resulted in primary productivity increases up to 87 percent. The response to phosphorus fertilization was larger than the response to nitrogen. Additions of phosphorus ranging between 20 and 140 kg P ha^{-1} resulted in production increases up to 135 percent.

For each site, there was a linear increase in yield that corresponded to the level of nitrogen or phosphorus fertilization. However, when all sites are pooled together, the large variability in soils and climates masks a clear relationship between yield and fertilization dose. Again, as in the case of the pattern and controls of primary production associated with climate, soil features vary at a scale finer than the regional patterns.

In general, the larger response to phosphorus than to nitrogen fertilization can be considered a regional characteristic of South American arid to subhumid ecosystems. Phosphorus is primarily stored in the soil and its availability is mainly controlled by properties of the parent material. In contrast, the largest nitrogen pool is located in the atmosphere and the parent material controls its availability primarily through the effects of soil particle size (Parton et al. 1988).

Much of the Kalahari ecosystem in Botswana and southwest Africa occurs on sandy soils of extremely low fertility, perhaps an extreme of the dystrophic status, and also at lower levels of rainfall (Cole 1986), that is, it is an arid-dystrophic ecosystem. However, the sands are often covered with cyanobacterial crusts and acetylene-reduction assays indicate that these crusts have a substantial nitrogen-fixing capacity shortly after being moistened (Skarpe and Henriksson 1987). In addition, important grasses in the Kalahari have rhizosphere sheaths containing *Azospirillum* with acetylene-reducing capacity. Thus, much of the nitrogen flow in this arid-dystrophic ecosystem on deep, porous (95 percent sand) soils may be derived from direct fixation fluxes rather than from recycling of residual soil pools.

VIII. Animal Nutrition

Forages of South American ecosystems are commonly so nutrient-deficient for livestock that complete mineral supplementation is advocated as a standard husbandry practice (McDowell et al. 1983). In fact, it is unlikely that there would be a substantial livestock industry in South America without such supplementation. For instance, 80 to 90 percent of the ranches in the Brazilian cerrado supply common salt to livestock and 5 to 30 percent also supplement ground bone (Saturino et al. 1977). Since South America did have a diverse large mammal fauna until the Pleistocene, however, it seems implausible to argue that their historical absence was due to soil-related nutritional deficiency (Sanchez and Buol 1975). Moreover, many areas of Africa require mineral supplementation for livestock, particularly higher rainfall areas supporting moist-dystrophic ecosystems (McDowell et al. 1983), where native animal biomass is lower than in arid-eutrophic systems and consists principally of large-bodied species (Bell 1982).

Bell's (1982) tabulation of animal biomass, rainfall, and geological substrate in African game parks and wildlife areas provides a means of examining the role of nutritional factors, as indexed by soil parent material, in ecosystem carrying capacity for large mammals. Data in his table 3 characterize parent material as (1) volcanic, (2) rift sediments washed from highlands associated with faulting, (3) marine sediments, and (4) basement rocks, largely granite of Precambrian age (he also included single examples of Kalahari sands and floodplains, which we excluded). The geographic range was from Sudan to Zaire to South Africa, and we utilized the rainfall span from a minimum mean annual value of 165 mm to a maximum of 1550 mm.

Animal biomass carrying capacity per unit of rainfall, expressed as kg km^{-2} mm^{-1}, varies substantially in African ecosystems ($F_{3,39} = 5.40$, $p < 0.01$) with geometric means of: basement = 2.74^{a}, rift sediments = $4.14^{a,b}$, marine sediments = $7.50^{a,b}$, and volcanic = 9.41^{b} (values with different superscripts differ significantly from one another by Sheffé's test, at least at $p = .05$). Therefore, the large mammal carrying capacities per unit of rainfall in African arid to subhumid ecosystems vary more than threefold from minima in regions where soils are derived from old, heavily weathered and leached basement rocks to maxima in regions where soils are of volcanic derivation associated with tectonic activity and the continental rifting system.

African ecosystems contain mammalian herbivore populations that exploit the environment in two different ways: resident herds occupy spatially fixed home ranges and migratory herds move between distinct seasonal ranges (McNaughton and Georgiadis 1986). Resident herds are heterogeneously distributed: some areas contain concentrations of several species, whereas nearby areas are only sparsely occupied (McNaughton 1988). Some migrants congregate around permanent surface water in the dry season and disperse to more arid locations in the wet season; others move along rainfall gradients, concentrating in more arid areas in the wet season and moving to wetter areas in the dry season (McNaughton 1990). Migratory animals typically dominate community biomass wherever they occur (Fryxell et al. 1988).

Both the distribution of resident animals (McNaughton 1988) and the seasonal movements of migratory herds (McNaughton 1990) are related to forage mineral nutrient concentrations in the Serengeti ecosystem. The nutritional requirements of pregnant and lactating females and of young, growing animals appear particularly important to resident herd distribution and the seasonal utilization patterns of migrants. Resident herds are concentrated in areas supporting forages of high magnesium, phosphorus, and sodium content (McNaughton 1988). Migratory herds spend the period of major lactation demand for females and growth demand for young animals in areas supporting forages of higher calcium, copper, magnesium, nitrogen, phosphorus, sodium, and zinc levels (McNaughton 1990).

These results indicate that areas of Africa supporting dense herds of native herbivores contain critical habitats supporting forages with nutritional properties capable of meeting animal demands during critical life stages. They also suggest that the sparser populations of large-bodied species in humid-dystrophic ecosystems may be due to a paucity of such habitats, which forces the animals to forage over larger areas and to be more selective in balancing their diets.

Although the movements of migrants in the Serengeti are related to regional soil fertility gradients (McNaughton 1985), there was no evidence that the soils supporting resident herds are intrinsically more fertile than soils in adjacent areas lacking resident concentrations (McNaughton 1988). However, since the activity of animals can facilitate nutrient recycling (McNaughton et al. 1988) and create localized areas of high nutritional status (Georgiadis and McNaughton 1990), it is possible that certain areas predisposed to animal occupance by the presence of permanent water or mineral licks could, through the activities of the animals themselves, develop nutritional sufficiency.

An explanation for the scarcity of large mammalian herbivores in South American compared to African ecosystems still remains enigmatic, although lack of suitable recolonization routes following the more pronounced Pleistocene extinctions in South

America seems a plausible explanation (see Chapter 13). Nevertheless, a diverse and locally abundant fauna of Camelidae does occur in South America. Given the apparent importance of isolated high nutritional areas in African wildlife distribution and abundance, it would be interesting to determine whether this camelid fauna is restricted to similar areas of nutritional sufficiency and whether such areas are lacking throughout much of the South American arid to subhumid zone.

IX. Concluding Comparisons

South American and African arid to subhumid ecosystems share many structural and functional similarities at broad regional levels, but differentiation in properties at finer scales is also evident on both continents. Vegetation structural properties are similar and there is strong evidence for belowground partitioning of soil resources due to different rooting depths of the herbaceous and arborescent layers. Grasses can take advantage of rain due to their shallow rooting, but woody plants have a refuge from competition when heavy rainfall results in soil water percolation into deeper soil layers. Relationships between primary productivity and precipitation are almost identical over broad precipitation ranges, but on both continents local edaphic constraints result in departures from the regional patterns, particularly due to low fertility or flooding. Native large mammals are much more important herbivores in Africa than in South America, where attine ants have evolved to fill the primary grazer niche. Mammalian herbivore biomass is closely correlated with primary productivity on both continents, and there is a transition from dominance by smaller-bodied species at low precipitation levels to larger-bodied species at higher levels, with a decline in biomass at the highest levels of rainfall on both continents. However, livestock biomass in South American ecosystems is about an order of magnitude above the level of biomass in natural ecosystems due to husbandry practices. Localized areas containing forages of high nutritional content are important determinants of animal distribution and abundance in Africa, but nothing is known of these in South America. Mineral supplementation of livestock suggests, however, that such habitats are rare in South America. The post-Pleistocene differences between the abundances of large, mammalian herbivores on the two continents may have been related to different frequencies of nutritionally sufficient habitats.

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