

Productivity of Tropical Savannas and Grasslands

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I. Introduction

The savanna biome is diverse, including formations ranging from almost treeless grasslands to more or less closed-canopy woodlands with considerable variation in plant composition, biomass, and net primary productivity (NPP). Savannas cover an extensive area in the tropics, inhabited by a fifth of the human population and supporting the majority of the world's livestock and large mammals. Population pressure and land use changes are high and are likely to increase in the foreseeable future. Savanna areas are increasing due to deforestation and abandoned agriculture, and decreasing due to cultivation and degradation, the balance is probably a decrease. These changes often occur in remote areas and are poorly documented.

Pollen records show that savanna systems are very old, natural systems, characterized by huge heterogeneity, and experiencing rapid changes in plant and animal composition (Menaut *et al.*, 1985). Within this highly dynamic biome, the proportion of trees and grasses can vary enormously, sometimes leading to degradation. Savanna ecosystems and dynamics are currently poorly understood because little attention has been paid to these areas in the past compared to tropical forests or temperate grasslands. Yet it is emerging that savannas have a higher biodiversity (Solbrig *et al.*, 1996a),

greater productivity (Long *et al.*, 1989, 1992; Scholes and Hall, 1996) and larger impact on global carbon cycles (ORNL, 1998; Hall *et al.*, 1995; Ojima *et al.*, 1993; Scholes and Hall, 1996) than previously realized.

Most research carried out in savanna ecosystems to date has been in the form of short-term site studies of one or two ecological aspects. Some sites have been studied in more detail or over long periods of time, with different emphases, e.g., structure and determinants in Nylsvley, South Africa (Scholes and Walker, 1993), nutrient cycles, fire, and biophysical properties in Lamto, Côte d'Ivoire (Menaut *et al.*, 1999), determinants, fire, and biophysical properties in the Orinoco Llanos, Venezuela (San Jose and Montes, 1997), and hydrology and energy balances in HAPEX-Sahel, Niger (Goutorbe *et al.*, 1997). Due to the great heterogeneity of the savanna biome from site to site, and even from year to year, individual studies cannot provide a representative picture of the whole biome.

More recently there has been a shift from individual studies to syntheses under specifically designed collaborative research programs such as the "Responses of Savannas to Stress and Disturbance" (RSSD) 10-year program set up in 1983 (Frost *et al.*, 1986; Walker, 1987; Walker and Menaut, 1988; Solbrig, 1990); "The Primary Productivity and Photosynthesis of Semi-Natural Ecosystems of the Tropics and Sub-Tropics" program, UNEP 1984 (Long *et al.*, 1989, 1992); the International Geosphere-Biosphere Programme (IGBP) terrestrial transects, which include the Kalahari Transect, the North Australian Terrestrial Transect (NATT), and SALT (Savanna in the Long Term) Ivory Coast to Mali (Koch *et al.*, 1995); The Miombo Network (<http://miombo.gecp.virginia.edu>); SAFARI 2000 (Southern African Fire-Atmosphere Research Initiative, <http://safari.gecp.virginia.edu>); and the SCOPE tree-grass modeling group (<http://www.nceas.ucsb.edu>, search under projects, tree-grass). Over the years, several good synthesis reviews have been published on savannas (Bourlière and Hadley, 1970; Huntley and Walker, 1982; Bourlière, 1983; Sarmiento, 1984; Tothill and Mott, 1985; Cole, 1986; Werner, 1991; Young and Solbrig, 1993; Scholes and Hall, 1996; Solbrig *et al.*, 1996a; Scholes and Archer, 1997).

II. Definition

The classification of "savanna" is inexact and has been based on different, often subjective, criteria. Savannas are most commonly defined as tropical seasonal ecosystems with a more or less continuous herbaceous cover and a discontinuous cover of trees or shrubs in varying proportions (Frost *et al.*, 1986). It is this coexistence and close interaction of herbaceous and woody species that makes savannas unique and complex. The proportions of

woody:grass biomass are highly variable and subject to environmental and management changes within broad climatic and edaphic constraints (Scholes and Archer, 1997).

The one constant and defining characteristic of savannas is the seasonality of rainfall: "Tropical savannas, woodlands and grasslands can be defined as those formations constrained by water rather than temperature with an annual dry season of sufficient duration and intensity to cause woody plants to shed their leaves and grasses to dry out, thus providing dry fuel for periodic fires" (Huntley and Walker, 1982). Authors often distinguish between "humid" and "arid" savannas based on a rainfall amount—typically of 600 mm (Walker, 1985), or length of dry season whereby 2.5–5 months is classified as "humid" and 5–7.5 months is "arid"; in some areas the dry season may even last 9 months (Solbrig *et al.*, 1996b). Seasonality may be bimodal with long and short rainy seasons. Fire and grazing are also integral elements in natural and managed savannas.

Savannas form a continuum between tropical forests and grasslands and have often been classified as either one or the other in the past. The distinction between what is forest, grassland, and different structural savanna types can only be set with arbitrary limits and descriptions such as those defined by Scholes and Hall (1996):

- Forests:** Complete tree canopy cover and three or more overlapping vegetation strata
- Woodlands:** 50–100% tree canopy cover, and a graminaceous layer
- Savannas:** 10–50% cover by woody plants and well-developed grass
- Grasslands:** Less than 10% tree cover

Different authors and classification systems vary as to whether "savanna" includes dense woodlands or treeless tropical grasslands. Some authors use the term "tropical grasslands" to include "the mixed grass and tree communities of the savanna and savanna forest" (Long *et al.*, 1992), and others use "rangelands" in the same context. In this chapter we use the term "savanna" to include the whole range from treeless grasslands to closed-canopy woodlands (with a graminaceous layer) unless otherwise stated.

Savanna Formations

A number of distinctive savanna formations exist, and some common definitions (scientific and vernacular) are listed below (Menaut, 1983; Sarmiento, 1984).

- Grass savannas or grasslands: Without woody species taller than the herbaceous stratum
- Bushlands/shrublands: Low-statured trees (<3 m), <2% = shrub, 2–15% = bush savanna
- Dwarf shrubland: Woody plants <1 or 3 m tall (depending on author)
- Wooded grasslands, savanna grasslands, savanna woodland: 2–15% tree cover

- Savanna parkland: Mosaic patches of trees
- Thicket/scrub forest: Low-statured, multistemmed woodlands or forests, often impenetrable and clumped, with absent or discontinuous grass layer
- Tiger savanna: Tree patches in linear bands parallel to slope contours
- Bushveld, lowveld, thornveld: Different savanna formations in Southern Africa
- Steppes: Savanna grasslands, sometimes with woody component

III. Extent

Savannas occupy a wide range of environments. Rainfall can vary from 200 to 2000 mm, and tends to be more erratic at the arid end of the scale, often occurring as short storm events (Walker 1985; Solbrig *et al.*, 1996b). Temperatures vary from hot tropical temperatures with little seasonality to subtropical temperatures that can approach frost in the winter. Soils vary from fertile to infertile. Typically, savannas in high rainfall areas have poor soils because wet areas with good soils tend to tropical rainforests. Similarly, arid savanna areas tend to have nutrient-rich soils, because low rainfall plus poor soils leads to desert vegetation. However, there are exceptions to these rules.

The extent of savanna is uncertain due to the variation in classification of this biome and the sparsity of data in these areas. Table 16-1 shows a range of estimates. Whittaker and Likens (1973, 1975) estimated savanna cover in 1950 to be 15 Mkm² using a modified UNESCO scheme. Atjay *et al.* (1979) used the same classification as Whittaker and Likens for their estimate of 22.5 Mkm², which incorporates updated reports and vegetation maps as well as a consideration of human interference such as the cutting of forest areas and subsequent formation of secondary or derived savannas. The Olson *et al.* (1983) map reflects better knowledge of classification, mapping, and ecosystem change, and the tropical and temperate tree-grass classes included in Table 16-1 represent a quarter of the global land surface. Scholes and Hall (1996) used the digitized version of this map published by the United States Environmental Protection Agency (U.S. EPA) for their estimate of 16.1 Mkm² using the four savanna classes they considered tropical. However, 74.5% of the “warm or hot grasslands” class is within the tropics giving a total of 27.6 Mkm³ (almost a fifth of the global land surface). Temperate tree-grass mixes occur in the warmer areas of North America (5 Mkm²) (McPherson, 1997) Mediterranean Europe, and parts of Russia and Asia.

A. Africa

Savannas form a semicircle around the western central rainforest areas, bordered by the desert zones to the north and south, across a variety of soil conditions with rainfall ranging from 200 to 1800 mm. *Broadleaved savannas* are found in the subhumid interior plateau on old, highly weathered, infertile soils. *Fineleaved savannas* are typical of the low-lying, semiarid regions. The

Table 16-1 Previous Estimates of Area, Biomass, and NPP of Tropical Savannas and Grasslands^a

Source	Vegetation type	Area (Mkm ²)	Biomass (Pg DM)	Biomass (kg DM m ⁻²)	NPP (Pg DM yr ⁻¹)	NPP (g DM m ⁻² yr ⁻¹)
Whittaker and Likens (1973, 1975)	Savannas (includes tropical grasslands)	15	60	4 (0.2–15)	13.5	900 (200–2000)
Atjay <i>et al.</i> (1979)	Dry savanna thorn forest	3.50	52.5	15.0	4.55	1300
	Low tree/shrub savanna	6.00	45	7.5	12.60	2100
	Dry thorny shrubs	7.00	35	5.0	8.40	1200
	Grass-dominated savanna	6.00	13.2	2.2	13.80	2300
	Total	22.50	145.7	6.5	39.35	1749
Olson <i>et al.</i> (1983)	Tropical dry forest and woodland (32)	4.7	73.3	15.6	6.00	1271
	Tropical savanna and woodland (43)	6.7	44.9	6.7	7.33	1091
	Succulent and thorn woods (59)	4.0	35.6	8.9	3.56	889
	Semi-arid woodland or low forest (48)	0.9	11.1	11.1	0.89	977
	Warm or hot shrub and grasslands (41)	17.3	50.2	2.9	15.56	899
	Total (temperate and tropical)	37.3	247.1	6.6	36.22	972
Scholes and Hall (1996)	Drought-deciduous woodlands	4.6 (4.2)	34.4	8.3	5.2	1263 (462–1789)
	Savanna	6.7 (6.0)	15.1	2.5	8.6	1426 (681–1941)
	Succulent and thorn woods	3.9 (3.1)	1.4	2.5	2.7	856 (289–1370)
	<i>Eucalyptus</i> and <i>Acacia</i> woodlands	0.9 (0.5)	7.8	2.5	0.4	733 (186–1242)
	Total (tropical)	16.1 (13.9)	58.7	3.6 (0.9–21)	16.9	1216 (440–4135)
This study	Tropical dry forest and woodland	4.7	64.7	13.7	6.0	1263
	Tropical savanna and woodland	6.7	31.8	4.7	9.6	1426
	Succulent and thorn woods	4.0	23.4	5.8	3.4	856
	Semi-arid woodland or low forest	0.9	6.3	7.0	0.7	733
	Warm or hot shrub and grasslands	11.2	32.4	2.9	10.1	899
	Total (tropical)	27.6	158.5	5.75	29.7	1078

^aDM, Dry matter; Mg = 10¹⁶ g; Pg = 10¹⁵ g. Used carbon content of dry matter of 0.45. Olsen *et al.* (1983) categories include tropical at temperate tree-grass mixes (not montane) Scholes and Hall areas, based on Olsen *et al.* (1983) classes 32, 43, 48, and 59, estimated undisturbed area (i.e., still under natural vegetation, not urban/agricultural/degraded) shown in brackets and used for biomass and NPP calculations, although corrected totals shown here due to inconsistency in use of land areas in original paper. NPP calculated using the relationship between WAI and total NPP shown in Fig. 16-3 and discussed in text. This study land areas from Olson *et al.* (1983), tropical portion of “warm or hot shrub and grassland” (between 30°N and 30°S) calculated by Dale Kaiser, ORNL, USA. Biomass average of Table 16-3 based on Scholes and Hall (1996) and Olson *et al.* (1983).

northern *Sudan-type* savannas are open xerophytic grasslands with scattered deciduous trees forming a transition with the Saharan desert vegetation. The *Guinea-type* savanna woodlands form the transition with the evergreen moist forests. The eastern African savannas, with bimodal rainfall typically totalling less than 700 mm, are dominated by herbaceous vegetation with some shrubs or scattered trees. The southern savanna area is known as “*Miombo*” woodland due to its distinctive tree species. (Menaut *et al.*, 1985; Backéus, 1992; Scholes and Walker, 1993; Solbrig, 1996).

B. Australia

Australian savannas occur in two distinctive climatological areas—the cooler, wetter east coast and the warmer, drier north coast. Rainfall is mostly below 1000 mm, soils tend to be poor, fires frequent, and diversity high. Australian savannas include monsoon, tropical, and subtropical tallgrass communities along coastal areas with *Eucalyptus* woodlands; the midgrass savannas on clay soils with *Acacia harpophylla* (Brigalow) and associated *Eucalyptus* woodlands; tussock and hummock grasslands (Mitchell grass); and *Acacia* shrublands (mulga and gidgee pastures) (Mott *et al.*, 1985; Braithwaite, 1990; Burrows *et al.*, 1990; McKeon *et al.*, 1990; Solbrig, 1996).

C. South America

The South American savannas tend to be wetter, with less contrasting seasonal variation, and very nutrient-poor soils, often high in aluminum. The largest savanna type, the cerrado, covers 1.8 Mkm² within Brazil and includes the pure grassland campo limpo, through the low open woodland of the true *cerrado*, to the closed dry-forest formations of the *cerradao*. In Colombia/Venezuela the llanos del Orinoco area is grassland with scattered trees (San Jose and Montes, 1989). Flooded savannas occur in Brazil and Bolivia. The *caatinga* region of Brazil and the *chaco* region of Paraguay/Bolivia/Argentina (which can suffer frost) are often not considered savannas but do fall into the descriptions used by African ecologists. Other smaller areas of distinct savanna types are scattered through South America, Central America, and Cuba (Sarmiento, 1983; Medina and Silva 1990; Solbrig, 1996).

D. Asia

Savannas are mostly “secondary” or “derived” and are formed by deforestation, abandoned cultivation, and burning, being maintained by repeated grazing, harvesting, and burning. Savannas are fairly extensive in India and Sri Lanka, with continued forest clearing increasing their extent, although many areas are under threat from agriculture (Misra, 1983; Yadava, 1990; Backéus, 1992; Pandey and Singh, 1992). Savannas are not so common in South East Asia. Thailand, Laos, Cambodia, and Vietnam have an open de-

ciduous dipterocarp forest with the ground covered by grasses, similar to some vegetation types in Africa, which form a transition between dense forest and shrub savanna. Treeless savannas occur in many places but occupy only a small area (Blasco, 1983; Stott, 1990).

IV. Plant Composition: Structural and Functional Variability

A. Savanna Structure: Tree–Grass Mix

The relative abundance of woody and herbaceous species is highly dependent on environmental conditions and seasonal and interannual variations. Plant available moisture (a function of climate, soil type, and topography) seems to be the key determinant of the tree–grass balance, but structure, function, and species composition are also altered by available nutrients, fire, and herbivory, and these are all discussed later (Walker and Noy-Meir, 1982; Menaut *et al.*, 1985; Solbrig, 1990; Scholes and Hall, 1996; Solbrig *et al.*, 1996b; Scholes and Archer, 1997; Scholes *et al.*, 1997).

Within this naturally dynamic ecosystem, small environmental/management changes may be buffered in the short term, but in the long term can lead to shifts in species and even functional types. Larger changes can lead to rapid transformations in vegetation structure, which may go beyond certain thresholds into a new structural domain, from which it is hard to return (Menaut *et al.*, 1985). For example, fire exclusion and heavy grazing promote increases in tree cover, grasses are suppressed, and there is no fire, thereby leading to dense thickets resistant to fire. Conversely, beyond a certain high fire and low grazing threshold large amounts of grass lead to regular hot fires, destroying all seedlings eventually excluding trees.

B. Plant Function

Functionally, arid and humid savannas are very different (Walker, 1985). Arid savannas have more affinity with semidesert vegetation in their adaptation to water limitation, and growth is less predictable and responds closely to rainfall events. Humid savanna vegetation has more adaptations for fire and low nutrients and trees are functionally more similar to forest vegetation. Savanna vegetation also shows adaptations for herbivory (particularly thorns) and light/shade. Many plants have underground stems and complex root systems to cope with high environmental stresses. Table 16-2 captures the main functional attributes that reflect current environmental conditions for southern Africa (Scholes *et al.*, 1997).

Grasses with a C_4 photosynthetic pathway tend to be dominant, particularly in hotter environments (Huntley, 1982; Menaut *et al.*, 1985). Grasses in wetter African sites tend to be perennial and tufted, with fewer larger seeds, whereas in more arid sites they are rhizomatous or stoloniferous, producing

Table 16-2 Broad Plant Functional Types Found in African Savannas^a

Plant type	Phenology	Water	Herbivory	Nutrients	Plant functional type common name
Woody plants Long lived (>5 years); high fraction of secondary growth	Drought deciduous	(Mostly fine-leaved)	Thorny (hydrolyzable tannins)	Fast growth and nutrient uptake; may be N-fixing	Thorn shrub/tree
		(Mostly broad-leaved)	Indigestible (condensed tannins)	Inherently slow growth and uptake capacity	Broadleaved shrub/tree
	Evergreen	Sclerophyllous	Indigestible (fiber and tannins)	Inherently slow growth and uptake capacity	Evergreen shrub/tree
		Succulent	Often palatable, sometimes tannins, resins, or alkaloids		Succulent shrub/tree
	Wet season deciduous	Phreatophytic Water storage organ	Tall, or unpalatable Toxic	Inherently slow growth	Phreatophyte Geoxylic suffrutex
Graminoids Short lived (<2 yr per tiller); monocots, buds basal; mainly vegetative reproduction		Xerophytes	High fiber	Roots sheaths common on sandy soil	Wire grasses
		Mesophytes	Low digestibility Lawn-forming	Seasonally low N Continuously adequate N	Tuft grasses Creeping grasses
Forbs As above, but dicots with terminal buds; mainly sexually reproducing	Ephemeral/ annual	Avoid drought as seeds	Toxic (alkaloids, etc.)		Ephemeral forbs
	Perennial	Drought deciduous	Often palatable but hairy	N-fixing Non-N-fixing	N-fixing forbs Perennial non-N-fixers
Geophytes	Antiseasonal	Water storage bulb	Toxic		Geophytes

^aFrom Scholes *et al.* (1997).

many small seeds (Scholes *et al.*, 1997). Some may be fairly deep rooted with some roots even approaching 2 m. Annual grasses tend to have shorter roots compared to perennials and are more competitive in upper soil layers, responding faster to low and erratic rainfall patterns where there is not so much deep percolation. On the other hand, perennials can respond more quickly to the first rains, mobilizing root stores before annuals start their growth from seed. On the whole, grasses are able to respond quickly to rainfall events with rapid leaf flush and high productivity, but leaf loss during dry periods reduces losses due to respiration.

Trees have access to deep water, enabling prerain leaf growth by up to 3 months before the first rains (Tybirk *et al.*, 1992), and late leaf shedding, which enables a longer growing season compared to grasses (Scholes and Walker, 1993). It was initially thought that trees essentially used deeper soil water than grasses, and this resource partitioning allowed the coexistence of these two life forms (Walter, 1971). However, it is now known that some trees, particularly in more arid areas, have shallow roots that extend laterally (particularly on clay soils where percolation is low) and may not have many deep roots (e.g., Menaut, 1983; Knoop and Walker, 1985; Belsky *et al.*, 1989; Coughenour *et al.*, 1990; Le Roux and Bariac, 1998). Besides water, this takes advantage of nutrient concentration in upper soil layers, including that washed out from fire ash in the early rains before grasses become established. In arid areas, deciduous trees are more common because leaf loss reduces water stress. Deciduous trees in humid savannas are thought to have most of their roots in the upper soil layers, thus they shed their leaves in the dry season. Evergreen trees have extensive root systems, enabling them to use water from deep soil layers, thus maintaining relatively high transpiration and photosynthetic rates during the dry season (Vareschi, 1960).

There are few empirical data on allocation of primary production in savanna plants. Herbaceous plants are short lived and almost all aerial parts die back after reaching maturity, to be replaced at the start of the next growing season. Perennials allocate more primary production to belowground structures, dropping their leaves and increasing root production at the onset of the dry season. Annuals, on the other hand, have much higher seed production and may produce seed several times throughout the growing season to avoid drought, fire, and herbivory. Woody plants invest more production in long-lived structures (the bole, branches, and coarse roots). They also use a higher proportion of primary production for maintenance respiration (Illius *et al.*, 1996). The fraction of NPP allocated belowground for all plants is affected by nutrient and water availability, fire, herbivory, and competition, increasing with stress and disturbance. Belowground allocation is typically 40–80% in grasses compared with 20–60% in trees (Scholes and Hall, 1996).

C. Tree–Grass Interactions

Interactions, both competitive and facilitatory, between tree and grass components are very complex, variable, and poorly understood (Scholes and Archer, 1997). Trees and grasses both compete for limited resources, and grass biomass/NPP typically decreases as tree biomass/density increases. Several studies show a concave curvilinear change (Donaldson and Kelk, 1970; Walker *et al.*, 1972; Beale, 1973; Dye and Spear, 1982; Scanlan and Burrows, 1990; Teague and Smit, 1992). The inverse relationship between an index of “treeness” and grass production shows the steepest decline when woody biomass is low (Fig. 16-1). It has been shown at one site that the degree of curvature decreases as the productive potential of the site (i.e., water and nutrient availability) increases, suggesting that it is related to the degree of resource competition (Scanlan and Burrows, 1990). Convex relationships also occur (Aucamp *et al.*, 1983). Trees can create a more suitable microhabitat for grass species, and low tree densities have been seen to increase grass production in arid areas by providing shade (reducing evaporation) and nutrient concentration due to leaf litter and root decay and feces of sheltering animals and birds (Weltzin and Coughenour, 1990; Belsky *et al.*, 1989, 1993; Pugnaire *et al.*, 1996).

In most situations, mature trees out-compete grasses for light, water and nutrients, yet grasses out-compete small shrubs and tree seedlings (reducing establishment) and they increase the likelihood of fires, which kill small trees (Knoop and Walker, 1985; Scholes and Archer, 1997). This competitive asymmetry can lead to structural instability (Scholes and Hall, 1996). Often some degree of tree clumping takes place, adding further complexity, with conditions often very different between the undercanopy and intercanopy areas (Weltzin and Coughenour, 1990; Belsky, 1989, 1993; Veetas, 1992; Mordelet and Menaut, 1995).

D. Plant Composition and Ecosystem Productivity

This structural diversity raises the question of how the mixture of trees and grasses, and changes in this mixture, will affect overall ecosystem productivity. The theory that the total NPP of a site remains fixed as the vegetation mix changes (an assumption in some top-down NPP models) seems unlikely, but because most studies measure only the NPP of one component, it is difficult to draw conclusions. It seems probable that some combination of woody and herbaceous biomass leads to higher ecosystem productivity, compared to having one component alone, as is the assumption of some multi-species agroforestry studies. This is partly because of facilitation, and also that trees and grasses can take advantage of different resources spatially and temporally (seasonally).

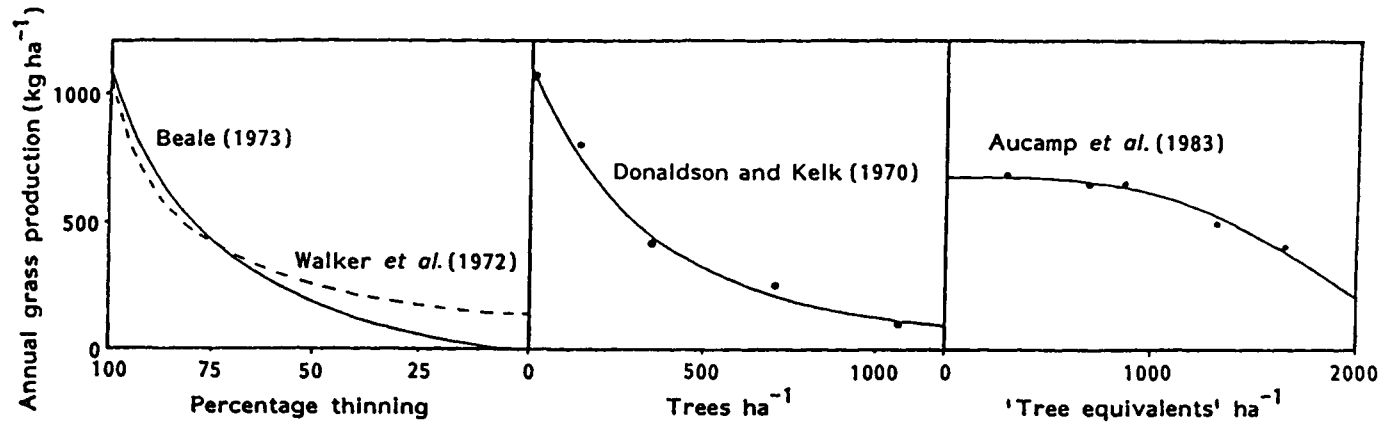


Figure 16-1 Some published relationships between the quantity of trees in a savanna and the annual grass aboveground NPP. Almost all the studies show concave inverse relations; the inverse convex relationship is unusual (reproduced from Scholes and Hall, 1996).

V. Estimates of Biomass and Productivity

There is a paucity of data on the biomass and productivity of different types of savannas and grasslands under the considerable range of climatic and soil conditions they experience. Of the studies that have measured savanna biomass and/or productivity, very few have been sufficiently long term to capture the interannual variations (which can be considerable), few have measured both tree and grass components, even fewer have measured roots, and almost none have looked at insectivorous and microbial production, although herbivorous production is sometimes considered. Thus there are no estimates for total ecosystem biomass/productivity. This chapter considers plants only.

Table 16-1 presents several estimates of biomass each based on different published data. Biomass values reported for individual savanna sites and compiled in Scholes and Hall (1996) are shown in Table 16-3, with the original class names and groupings, although the calculations have been redone and totals differ slightly from the original paper. Due to the paucity of root data, total biomass was calculated from average aboveground biomass using estimates belowground biomass percentage, ranging between 20% and 30% in different savanna types. Jackson *et al.* (1996, 1997) reported a higher average belowground biomass of 40% for tropical savannas and grasslands in their compilation and analysis of root data for all global biomes.

It is difficult to match up the biomass classes given by Scholes and Hall (1996) in Table 16-3 with the land use classes of Olsen *et al.* (1983) in Table 16-1. Scholes and Hall (1996) assigned their *woodlands* biomass class (originally 83 t/ha) to the land class *drought-deciduous woodlands*. In fact, the original Olson *et al.* (1983) description of *tropical dry forest and woodland* class includes drought deciduous forest types such as Australian Brigalow as well as the Miombo woodlands, therefore it seems more reasonable to combine these two classes in Table 16-3. Scholes and Hall (1986) assigned their *savannas* biomass class value (originally 25 t/ha) to all other land classes as it included examples from all of them. The Scholes and Hall (1996) biomass values are all lower than the Olson *et al.* (1983) values which were also based on reported data. For the purposes of this chapter it seems reasonable to take an average of the two sets of estimates, using the re-calculated Scholes and Hall (1996) values in Table 16-3. This gives an average biomass value for the savanna biome of 5.75 kg DM m⁻², or a total biomass of 158.5 Pg (DM). Assuming 30% of biomass in roots, the average belowground biomass is therefore 1.73 kg DM m⁻², and aboveground is 4.02 kg DM m⁻². The Jackson *et al.* (1996, 1997) analysis of root data calculated a total (tree and grass) root biomass of 1.4 kg m⁻² (of which fine roots account for 0.99 kg m⁻²). Using his value of 40% root biomass this would equal a total biomass of 3.5 kg m⁻², much lower than the other estimates.

Table 16-3 Biomass Reported for Tropical Grasslands and Savannas^a

Site	Source	Aboveground biomass (t/ha)			Roots (t/ha)	Aboveground biomass Total (t/ha)	Belowground biomass (%)	Total biomass (t/ha)
		Wood	Tree leaf	Grass				
Drought-deciduous forests								
Kurukshutra, India	Rajvanshi & Gupta (1985)	53.12	3.29	1.33		57.74		
Brigalow, Australia								
<i>Dalbergia sissoo</i>	Moore <i>et al.</i> (1967)	158.1	11	0	40.7	169.1		
Oro Forest, Nigeria								
<i>Acacia harpephylla</i>	Fatubarin (1984)	132				132		
Mean total aboveground biomass						119.6	20	149.5
Woodlands (all <i>Brachystegia</i> spp.) = Miombo woodlands								
Kasapa, Zaire	Malaisse <i>et al.</i> (1975)	101.7	4.82			106.52		
Makaholi, Zimbabwe	Ward & Cleghorn (1964)	44.6	2.29			46.89		
Zambia		40				40		
Marondera, Zimbabwe	Frost (in Scholes & Hall, 1996)	39.73	2.74	0.1		42.57		
Dukwe, Botswana	Tietema (1993)	81.9				81.9		
Mean total aboveground biomass						63.9	25	84.8
Average of above two classes = Olson <i>et al.</i> (1983) "tropical dry forest and woodland" class					117.1			
Savannas								
Sengwa, Zimbabwe	Guy (1981)	22.5	0.53			23.3		
Cobar, Australia	Harrington & Johns (1982)	36	3.2	1		40.2		
Nylsvley, S. Africa <i>Burkea africana</i>	Scholes & Walker (1983)	15.54	0.748	1.5	7.1	17.788		
Waterberg, Namibia <i>B. africana</i>	Rutherford (1982)	22.3				22.3		
Klaserie, S. Africa								
<i>Colophospermum Mopane</i>	Scholes (1988)	20.84	0.8	0.5		22.14		

(continues)

Table 16-3 (Continued)

Site	Source	Aboveground biomass (t/ha)			Roots (t/ha)	Aboveground biomass Total (t/ha)	Belowground biomass (%)	Total biomass (t/ha)
		Wood	Tree leaf	Grass				
Klaserie, S. Africa <i>Acacia nigrescens</i>	Scholes (1988)	5.05	0.664	1		6.714		
Klaserie, S. Africa <i>Combretum apic.</i>	Scholes (1988)	10.5	0.759	0.5		11.759		
Kruger, S. Africa <i>Combretum apiculatum</i>	Dayton (1978)	15.4	1.5	0.5		17.4		
SE Zimbabwe <i>Colophospermum mopane</i>	Kelly & Walker (1976)	19.7				19.7		
Hwange, Zimbabwe <i>Terminalia sericea</i>	Rushworth (1978)	3.65	3.21	1.23	34.4	8.09		
Khakhea, Botswana <i>Acacia/Combretum</i>	Tietema (1993)	8.05				8.05		
Kang, Botswana	Tietema (1993)	18.02				18.02		
Morwa Forest, Botswana <i>A. tortilis</i>	Tietema (1993)	17.5				17.5		
Morwa Hill, Botswana <i>Croton/Combretum</i>	Tietema (1993)	30.87				30.87		
Dikeletsane, Botswana <i>Acacia/Combretum</i>	Tietema (1993)	32.97				32.97		
Mean total aboveground biomass (incorporates several Olsen <i>et al.</i> savanna classes)						19.8	30	28.2

"Table re-compiled from Scholes & Hall (1996) Table 4.4, totals, re-calculated, hence values differ slightly. Categories and groupings assigned by Scholes & Hall (1996) according to their judgement.

Woody biomass production is nonlinear, declining with maturity (which can be in the range of 30 to 100 yr) (Scholes and van der Merwe, 1996). It is not possible to estimate average annual production from tree rings because growth may be negligible in drought years, and certain regions experience two growing seasons in some years. Therefore production is typically estimated from change in biomass alone, which is an underestimation because it does not take account of death, removals, and turnover. Litter traps fail to account for dead branches. Removals for fuelwood, building materials, browsing, etc. are common but are poorly recorded in these largely “unmanaged” areas.

Estimates of tropical grassland production vary by almost fivefold, depending on the techniques employed (Long *et al.*, 1989). Herbaceous NPP has generally been estimated using annual maximum standing crop (aboveground), usually at the end of the growing season [see Bourlière and Hadley (1970)—figures for 22 tropical grasslands, and Rutherford (1978)]. Importantly, this method does not account for belowground productivity, the effects of grazing and trampling, mortality before or growth after peak standing crop has been attained, the differences in time at which species attain their peak standing crop (especially mixtures of perennials and annuals), or litter turnover (Rutherford, 1978; Solbrig, 1996). Milner and Hughes (1968) proposed a method for the International Biological Programme (IBP) that measures positive increments in aboveground live biomass [see Singh and Joshi (1979) for a review of 21 studies in tropical grasslands in India and Africa], but this still leads to underestimates.

A more robust methodology was developed under a United Nations Environment Program (UNEP) project for measuring NPP in tropical grasslands (Long *et al.*, 1989, 1992). This measured monthly increments in aboveground live and dead biomass, roots, and monthly decomposition rates for standing dead material, litter, and roots. NPP was defined as the sum of net monthly increases in live biomass plus losses due to death and decomposition. NPP at three of these grassland sites was two to five times higher than that obtained using the standard IBP procedure, which ignores mortality, and two to ten times higher than previous methods, which ignore belowground NPP (Long *et al.*, 1989, 1992).

Measurements of worldwide “grassland” NPP have been incorporated into an Internet database site managed by the U.S. Oak Ridge National Laboratory (ORNL) Distributed Active Archive Center (<http://www-eosdis.ornl.gov/npp/npp—home.html>) (Scurlock *et al.*, 1999; see Chapter 18, this volume). The sites are often mixed tree–grass systems, although for many of the studies only grass NPP was measured.

Belowground production can be as high as or higher than aboveground production, but it is difficult to measure because it is hard to distinguish between live and dead roots and different species, thus assumed root:shoot ra-

tios are often used. However, the ratio is highly variable, depending on the vegetation formation, maturity, prevailing environmental conditions, and disturbances. For example, in the UNEP study, belowground NPP varied from 40 to 70% of total NPP in different years at some sites (Long *et al.*, 1992). Although root:shoot ratios tend to increase with stress, severe drought or frequent fire can lead to negative belowground NPP (Long *et al.*, 1992). Root turnover and exudates are rarely considered. Menaut and Cesar (1979) observed root turnover up to 100% in an open humid savanna and 70% in wooded savannas.

Some estimates of NPP in the savanna biome as a whole can be found in Table 16-1. Whittaker and Likens (1973, 1975) used measured production and phytomass values and extrapolated them by their estimated area. Atjay *et al.* (1979) used this as a basis for their own study, but they evaluated more recent data on NPP and took account of the role of organic matter. They cite improved root production data as the main factor accounting for their much higher NPP value. In the assessment of Atjay *et al.*, savanna has the second highest share of total production after forest systems. Lieth (1973) suggested mean production of $800 \text{ g m}^{-2} \text{ yr}^{-1}$, which Long *et al.* (1992) multiplied by 3.5 to take account of methodological underestimates to give a value of $2800 \text{ g m}^{-2} \text{ yr}^{-1}$. Both Olson *et al.* (1983) and Scholes and Hall (1996) give much lower estimated rates of productivity. It is not clear where Olson *et al.* obtained their figures, but the Scholes and Hall values were derived as follows: Rather than apply one estimate of NPP (based on studies at a small number of sites) to an entire vegetation class that incorporates a range of environmental conditions, Scholes and Hall (1996) used data from individual studies to develop a relationship between water availability and NPP, and then applied this to a number of points in each class. Table 16-4, compiled by Scholes and Hall (1996), lists a series of NPPs reported for tropical savannas and grasslands. To be included, studies must have measured NPP over a period of at least a year, and used the sum-of-positive-increments method plus some assessment of losses.

Several studies reported belowground NPP for tree and/or grass components, enabling the calculation of a relationship between total NPP and aboveground NPP for the trees and grasses:

$$\text{total NPP} = 1.01(\text{aboveground NPP}) + 853.$$

This equation predicts that belowground production accounts for between 5 and 70% of the total NPP, the proportion decreasing with increasing productive potential of the site (Scholes and Hall, 1996). However, this equation would seem to have an unrealistic intercept and is driven by an outlier—the floodplain site Manaus in Brazil, which can be considered an exception due to high water and nutrient availability, although it does show the potential of grassland vegetation. This relationship is redrawn in Fig. 16-2 with-

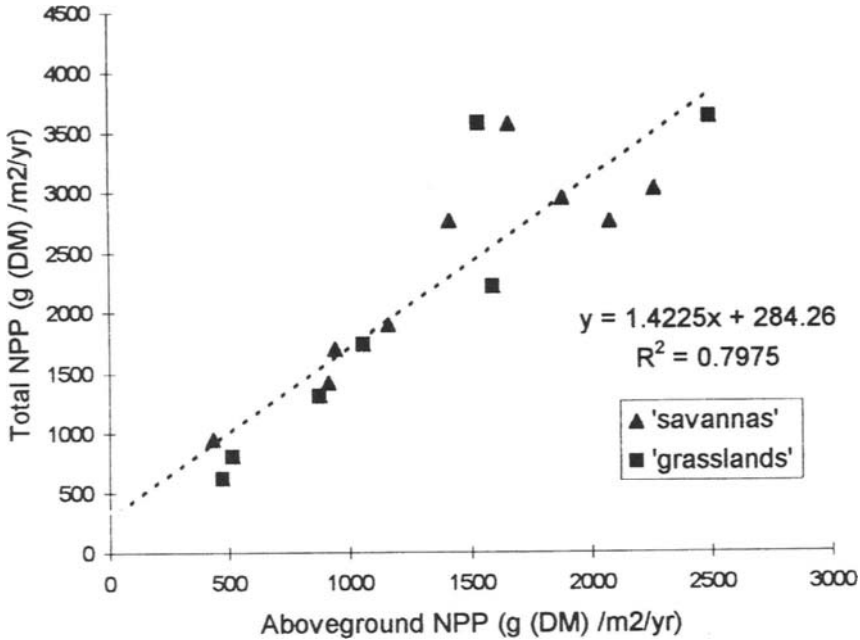


Figure 16-2 The relationship between total NPP and aboveground NPP. [Based on Scholes and Hall (1996, Table 4.2), recompiled in this chapter as Table 16-3]. Excluding “plantations” and outlier site Manaus, Brazil; DM, dry matter

out the outlier, and, sticking to the simple linear relationship, the equation becomes

$$\text{total NPP} = 1.42(\text{aboveground NPP}) + 284.$$

Scholes and Hall used this equation to calculate total NPP for all the sites, then plotted total NPP (tree and grass, above- and belowground) against a calculated water availability index (WAI) based on the monthly ratio of rainfall to evaporation at each site (equivalent to the number of days per year without water stress), presented in Fig. 16-3. The derived relationship was then applied to a large number of randomly selected locations in each of the vegetation classes to calculate a more representative average NPP, which is presented in Table 16-1. Although water and nutrient limitations do constrain savanna productivity, the inherent capacity for production by savanna plants is comparable to forest systems, i.e., they can produce just as much or more biomass per unit of water available. Referring to Fig. 16-3, if the upper range of data is projected to a water availability of 365 days (i.e., no water limitation), the predicted annual NPP is 4000 g m^{-2} , which is well within the average-to-high range for other natural ecosystems (Scholes and Hall, 1996).

Table 16-4 Primary Production Reported for Tropical Grasslands and Savannas^a

Site	Latitude	Longitude	Aboveground NPP (g DM m ⁻² yr ⁻¹)			Belowground NPP (g DM m ⁻² yr ⁻¹)			Total NPP (g DM m ⁻² yr ⁻¹)	Source
			Trees	Grass	Total	Trees	Grass	Total		
Savannas										
Lamto, Côte d'Ivoire	6°13'N	5°02'W	633	1450	2083	37	633	670	2753	Menaut and Cesar (1979)
			277	1610	1887	23	1040	1063	2950	
			137	1280	1417	13	1330	1343	2760	
			55	1610	1665	5	1900	1905	3570	
Mokwa, Nigeria	9°18'N	5°04'E	378	—	—	—	—	—	Collins (1977)	
Nylsvley, South Africa	24°42'S	28°42'E	282	157	439	187	325	512	951	Scholes and Walker (1993)
Niona, Senegal	14°18'N	6°0'W	—	225	—	—	—	—	—	De Ridder <i>et al.</i> (1982)
Uttar Pradesh	24°18'N	83°0'E	520	645	1165	60	675	735	1900	Pandey and Singh (1992)
			230	715	945	30	720	750	1695	(estimates for area
			430	490	920	40	460	500	1420	protected from grazing)
Grasslands										
Towoomba, South Africa	24°50'S	28°15'E	—	141	—	—	—	—	—	Donaldson <i>et al.</i> (1984)
Makaholi, Zimbabwe	19°48'S	30°48'E	—	146	—	—	—	—	—	Ward and Cleghorn (1964)
Nuanetsi, Zimbabwe	21°24'S	30°48'E	—	261	—	—	—	—	—	Kelly <i>et al.</i> (undated)
Klong Hoi Kong, Thailand	6°0'N	100°56'E	—	1595	—	—	625	—	2220	Long <i>et al.</i> (1992)
Charleville, Australia	26°24'S	146°12'E	—	520	—	—	290	—	810	Christie (1978)

Nairobi, Kenya	1°0'N	36°49'E	—	881	—	—	431	—	1312	Long <i>et al.</i> (1989)
Udaipur, India	25°30'N	72°24'E	—	180	—	—	—	—	—	Vyas <i>et al.</i> (1972)
Jodhpur, India	26°18'N	73°06'E	—	108	—	—	—	—	—	Gupta <i>et al.</i> (1972)
Delhi, India	28°54'N	77°12'E	—	798	—	—	—	—	—	Vashney (1972)
Ejura, Ghana	7°30'N	3°30'E	—	870	—	—	—	—	—	Greenland and Nye (1959)
Kurukshetra, India	9°58'N	76°51'E	—	2500	—	—	1131	—	3631	Rajvanshi and Gupta (1985)
Calaboza, Venezuela	8°48'N	67°27'W	—	478	—	—	146	—	624	Sarmiento (1984)
Manaus, Brazil	3°20'S	60°0'W	—	9418	—	—	507	—	9925	Long <i>et al.</i> (1989)
Montecillos, Mexico	19°28'N	92°28'W	—	1063	—	—	678	—	1741	Long <i>et al.</i> (1989)
Lamto, Cote d'Ivoire	6°13'N	5°02'W	—	1540	—	—	2040	—	3580	Menaut and Cesar (1979)
Plantations (mostly exotic trees)										
Kurukshetra, India	29°58'N	76°51'E	1547	248	—	—	—	—	—	Rajvanshi and Gupta (1985)
Gandi Nagar, India	23°12'N	77°06'E	2270	—	—	757	—	—	3027	Gurumurti <i>et al.</i> (1986)
Mudigere, India	13°12'N	75°36'E	1872	—	—	—	—	—	—	Swaminath (1988)
Nigeria	10°30'N	7°18'E	1337	—	—	—	—	—	—	Kadeba and Aduavi (1985, 1986)

^aTable recompiled from Scholes and Hall (1996; Table 4.2). Terms "savannas" and "grasslands" refer to categories originally separated by Scholes and Hall (1996); DM, dry matter. To be included, studies must have measured NPP over a period of at least a year, and used the sum-of-positive-increments method plus some assessment of losses (it was not always possible to determine from the sources whether losses included turnover or herbivory, or litterfall only). Long *et al.* (1989, 1992) figures used sum-of-positive-increment results rather than UNEP method results (see text), because this fits better with the rest of the data quoted.

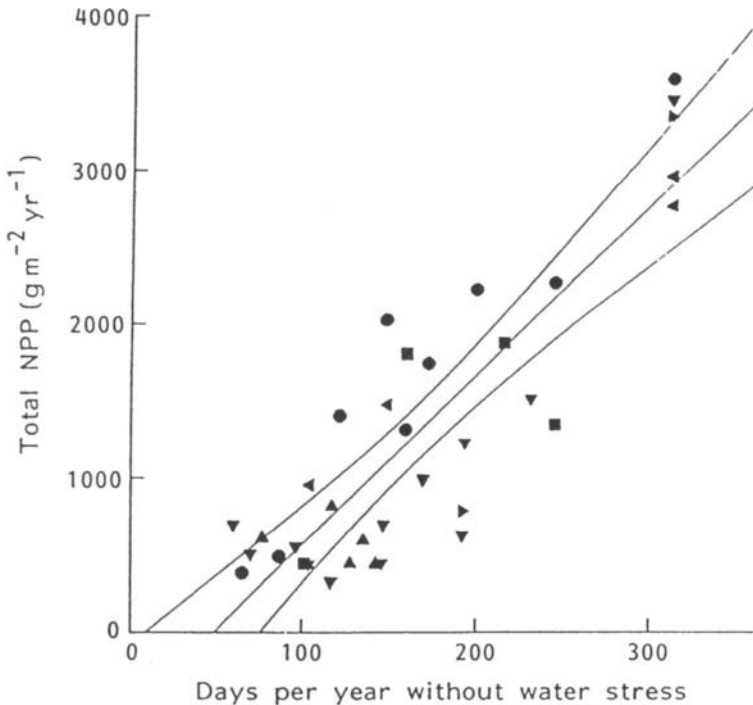


Figure 16-3 The relationship between total NPP and an index of water availability for tropical grasslands and tree-grass mixtures, with 95% confidence limits. The water availability index (WAI) can be thought of as the number of days per year on which growth is not water limited. The derivation of WAI is discussed in the text. The least-squares best-fit line has the equation $\text{NPP} = 11 \times \text{WAI} - 539$ ($n = 37$, $F = 108.6$, $p < 0.001$, $r^2 = 0.75$). The data are from Scholes and Hall (1996), and a number of other studies that did not satisfy the criteria for inclusion, for instance, because they refer to regions rather than sites. The symbols denote different structural types: (●) grasslands; (▲) derived grasslands; (▼) grassy savannas; (◄) savannas; (►) woodlands; (■) plantations of exotic trees in savanna areas (reproduced from Scholes and Hall, 1996).

VI. Biophysical Properties, Fluxes, and Efficiencies

Biophysical properties, fluxes, and efficiencies vary enormously and are radically affected by the high seasonality of savannas and fire. The few sites where such measurements have been made in any detail are highlighted in Table 16-5.

A. Leaf Area Indices

The leaf area index (LAI) is highly seasonal, e.g., in Lamto the LAI increases from 0 after fire in January to a peak of 4.0 in November (Le Roux *et al.*,

1997). Values for Venezuela and the UNEP sites also represent the complete seasonal ranges, whereas the Niger study captured part of the wet and dry seasons. The Nylsvley study incorporated trees with measured LAI under canopies (tree + grass, 2.25) and between canopies (grass only, 0.6), giving an overall LAI of 1.2 (Scholes and Walker, 1993). The Brazil study also measured tree LAI but figures seem relatively low (Miranda *et al.*, 1997). Thus, according to this limited data set, the range in arid savannas is 0 to 1.7 (or 2.3 if trees are included), and the range in humid savannas is 0 to 4.8 (and could be higher with the inclusion of trees).

B. Albedo and Radiation

Albedo is a function of underlying soil as well as vegetation, and fires can darken the soil surface and affect its spectral qualities. Albedo in Lamto was 0.07 over bare black soil, and increased over open areas with low shrub coverage from 0.08 to a peak of 0.23, with an overall mean annual albedo of 0.194 (albedo in more shrubby areas was similar) (Le Roux *et al.*, 1994). In contrast, bare soil albedo at Niger was 0.4, greater than the average vegetation albedo of 0.2 (Braud *et al.*, 1997). Similarly in Nylsvley, with a light soil, albedo was at its lowest value of 0.11 over peak biomass, and rose to 0.15 at the end of the dry season, with an annual average of 0.12. San Jose (1992) found that dry season albedo was lower in recently burned areas 0.08 compared to unburned areas 0.12, because the smoother burned surfaces trapped radiation more efficiently (vegetation scattered it). In spite of this, net radiation was also lower due to higher emission of long-wave radiation as a consequence of higher daytime mean temperature in the surface of the bare soil.

C. Roughness, Conductance, and Resistance

Spatial heterogeneity between different patches of savanna vegetation causes a discontinuity in aerodynamic, radiative, thermal, and moisture features. This is exacerbated by fire because air flows from the smooth and hot recently burned savanna (bare soil) to a rougher and cooler unburned savanna (vegetative surface). San Jose (1992) showed that the roughness length and aerodynamic conductance were far lower in burned patches (Table 16-5), and that mixing due to thermal turbulence in the burned savanna was three times greater than that due to roughness-generated turbulence in the unburned savanna. In Brazil and Venezuela (site 2) surface conductance was higher with more leaves in the canopy, and the degree of coupling (Ω) was higher, indicating less coupling between canopy and atmosphere (San Jose *et al.*, 1998; Miranda *et al.*, 1997) (Ω approaches 1 in well-watered and aerodynamically smooth canopies, where the transpiration rate is driven by radiation, and approaches 0 over aerodynamically rough

Table 16-5 Biophysical Properties,

	Lamto, Ivory Coast (humid, open shrubby)				Venezuela, site 1 (humid, grasslands)		Venezuela, site 2 ⁶ (humid, grasslands)	
	Start wet season ¹			Other ^{2,3}	Dry season ⁴		Wet season ⁵	
	Feb	Mar	Apr		Burned	Unburned	Cultivated	Natural
Rainfall (annual mm)			1210			1257	1050	
Total production (gm/m ² /yr)			2700					
Herbaceous biomass only (g/m ²)						600–1000	675	433
LAI site average								
Herbaceous layer	0.8	1.5	1.9	4.0		0.08–0.68	4.4	1.7
Trees								
Radiation balance								
Incoming solar radiation (MJ/m ² /y)								
(MJ/m ² /d)					20.6	20.6	15.8	15.7
max (W/m ²)					720	720	762	
Net radiation, daily (MJ/m ² /d)					11.2	11.9	12.0	8.4
max (W/m ²)					630	550	550	410
Mean daytime albedo α	0.08–0.23, av. 0.19, burnt soil 0.0				0.08	0.12	0.3	0.3
Roughness and conductance								
Vegetation height (m)		Shrubs 2–6, grass 1				Grass max 1.8	0.6	1.2
Roughness length Z ₀ (m)					0.0013	0.039		
Zero displacement d (m)					0.0070	0.196		
Aerodynamic cond. (mol/m ² /s) max					0.068 ^b	1.8 ^b	4.0 ^b	3.2 ^b
Canopy conductance (mol/m ² /s) max						0.039 ^b		
Surface conductance (mol/m ² /s) max							1.0 ^b	0.6 ^b
Coupling coefficient Ω						0.17	0.29	0.17
CO ₂ fluxes ^c								
Leaf assimilation (μmol CO ₂ /m ² /s)				19–33				
Canopy assimilation A _c (MJ/m ² /day)							0.138	
max (μmol CO ₂ /m ² /s)	19.0	23.3	24.7					
Soil respiration (MJ/m ² /day)							–0.036	
max (μmol CO ₂ /m ² /s)	–6.6	–8.9	–9.6					
Net ecosystem flux F _c (MJ/m ² /day)							0.102	
Daytime peak (μmol CO ₂ /m ² /s)	19.0	23.3	24.7					
Nighttime peak (μmol CO ₂ /m ² /s)								
Efficiencies (g/MJ) ^d	Early	Mature	Annual ²					
Net prod (g)/incident rad (g/MJ)	1.58	1.06	0.85					
Net prod (J)/incident rad (%)							0.7	
NPP/IPAR total	3.38	2.28	1.82					
NPP/APAR total = RUE	3.84	2.56	2.04					

References: ¹Le Roux and Mordelet (1995); ²Le Roux *et al.* (1997); ³Le Roux *et al.* (1994); ⁴San Jose (1992); ⁵San Jose *et al.* (1991); ⁶San Jose *et al.* (1998); ⁷Miranda *et al.* (1997); ⁸assorted papers in Goutorbe *et al.* (1997). Hansan *et al.* (1998); ⁹Scholes and Wlaker (1993); ¹⁰chapters in Long *et al.* (1992). Where possible original values have been converted to standard format/units.

^aValues here for grass and dicotyledons.

^bCalculated from the original data as inverse of resistances in s/m; and at sea level and 25°C, g mol/m²/s = 0.04 g mm/s (Jones, 1992).

^cCO₂ flux notes: Venezuela values calculated from original table for 30th July.

^dEfficiency notes: Lamto original values converted AG biomass, and OPAR = 0.467 R_i from values in paper. For other sites used IPAR = 0.45 Rs. RUE = radiation use efficiency, IPAR and APAR incident and absorbed photosynthetically active radiation. Kenya and Mexico values recalculated from original data; Thailand and Amazon figures from graphs of cumulative NPP of cumulative NPP against cumulative.

canopies, where transpiration is driven by canopy to air saturation deficit). Although roughness values in Niger were similar to those for the unburned Venezuelan grassland site (Braud *et al.*, 1997), the sparse tree crowns of the Brazilian cerrado vegetation form a more aerodynamically rough surface.

Fluxes, and Efficiencies

UNEP sites¹⁰

Brazil ⁷ (humid, dense scrub)		Niger ⁸ (arid, regen. shrub) Wet/dry 8 weeks	Nylsvley ⁹ (semiarid, mixed S. Africa annual)	Kenya (arid, grassland)	Mexico (arid, grassland)	Thailand (humid, grassland, unburned)	Amazon (wet, grassland, floodplain)
Dry	Wet						
1500			623	800	580	2000	2100
			951	1292	1803	2036	9930
474 ^a	503 ^a						
0.3 ^a	0.5 ^a	1–1.25	1.2	0–3.1	0–1.7	0.7–2.0	2.3–4.75
0.4	1.0		0.6				
			2.25				
			7316	7190	6741		4400
700	950		20	19.7	18.5	9.9–20.6	12.0
650	950		11.3				
		0.2 (0.4 soil)	0.11–0.15, av. 0.12				
Trees 9		Shrub 1–3	Tree 6; grass 0.75				
1.2		0.07					
6.3		0.38					
0.15	0.4						
0.17	0.32						
			25	27	23		31
4	15	15					
–2	–5	–5					
		0.99	0.13	0.18	0.27	0.66	2.30
				0.32	0.80		
		2.21	0.29	0.40	0.60	1.47	5.11

D. Carbon Dioxide Fluxes

Several studies have been carried out on leaf photosynthetic rate (or CO₂ flux) of savanna grass species, showing a range of 15 to 33 μmol CO₂ m^{–2} s^{–1} across a range of dry and humid sites, with results showing a high variability (Le Roux and Mordelet, 1995; and see Table 16-5). In Nylsvley alone, measurements for one grass species varied by 13-fold, dependent partly on techniques used and local conditions, although for further calculations Scholes and Walker (1993) used an overall average of 25 μmol CO₂ m^{–2} s^{–1}. Some measurements were also made of tree leaf photosynthesis at Nylsvley and, on average, the C₃ woody plants had 18% lower rates than the C₄ grasses, which are better adapted to high irradiation and heat and water stress.

Primary productivity is much more closely linked to canopy CO_2 flux than to leaf flux, yet there are even fewer savanna studies on this. At Lamto, Le Roux and Mordelet (1995) measured CO_2 canopy fluxes at the beginning of the wet season after a January fire. Despite low N at this site, the peak net canopy CO_2 flux/assimilation F (measured above the canopy) was high at $24 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for a LAI of only 1.9 not long after the fire. They compare this to net canopy fluxes of $27 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for LAIs of 7 and 8 in Amazonian and Malaysian rainforests (Fan *et al.*, 1990; Aoki *et al.*, 1975), sustaining the emerging opinion that the primary productivity of tropical savannas could be close to that of tropical forests (Atjay *et al.*, 1979; Gifford, 1980; Long *et al.*, 1989). Net canopy fluxes measured in Niger (LAI 1–1.25) (Hannan *et al.*, 1998) were similar to those found in the wet season in Brazil (LAI 0.5) (Miranda *et al.*, 1997) at $15 \mu\text{mol m}^{-2} \text{ s}^{-1}$ into the canopy during the day and $-5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ out at night. During the wet season in Brazil, the fluxes were higher and although vegetation was found to be a CO_2 sink in the wet season of up to $0.15 \text{ mol m}^{-2} \text{ d}^{-1}$, it was a source of CO_2 for a brief period at the height of the dry season (Miranda *et al.*, 1997). San Jose *et al.* (1991) measured CO_2 fluxes in the wet season in Venezuela and found that the net community assimilation ranged from 6.6 to $7.9 \text{ g (DM) m}^{-2} \text{ d}^{-1}$, which was similar to the mean community growth rate they calculated from biomass measurements (2.8 – $6.9 \text{ g (DM) m}^{-2} \text{ d}^{-1}$).

E. Production Efficiency

Several different methods are used to calculate efficiency, and some of these are represented in Table 16-5. Radiation use efficiency (RUE) is calculated as total NPP/IPAR (incident photosynthetically active radiation) and we have tried to convert all values to this. IPAR can be assumed to be a fixed proportion of incident radiation (R_s), usually between 45 and 50%. The range of RUE is 0.4 to 1.8 taking the annual results only (i.e., not Niger) and ignoring the outlier Brazil. RUE is partly related to rainfall, with the average across the three semiarid sites being 0.43, and the two humid sites 1.65. Many arid species have a lower conversion efficiency because lower stomatal conductance is an adaptation to water stress. The Lamto results show how efficiency declines as the stand matures. In Thailand, one year of fire reduced RUE from 1.47 to 1.35 and a second year of fire caused it to drop further to only 0.17 (assuming $\text{IPAR} = 0.45R_s$).

VII. Environmental Determinants

As noted earlier, the amounts of moisture and nutrients available to savanna plants determine the structure of savannas and their NPP. The primary determinants of both of these factors are climate and soil type, rainfall and soil

texture being particularly important. In low-rainfall areas, deep, sandy soils allow more water to infiltrate to greater depths, reducing runoff and evaporation and increasing moisture availability. However, where rainfall is high, sandy soils can lose water through drainage and runoff, often leaching nutrients. Clay soils have a higher water-holding capacity and nutrient retention, leading to a higher NPP in moist and mesic systems, but are less advantageous in arid areas due to low infiltration (Dodd and Lauenroth, 1997).

Moisture and nutrient availability in turn influence the occurrence and intensity of fire and herbivory, which are secondary determinants modifying savanna vegetation (Walker and Noy-Meir, 1982; Frost *et al.*, 1986; Solbrig, 1990; Scholes and Hall, 1996). At a more local scale, differences in topography, geomorphology, and management lead to further differences in structure and floristic composition (Solbrig, 1996). Many of the factors controlling savannas are interdependent, interacting positively or negatively on each other either simultaneously or sequentially. The relative importance of individual factors shifts with time and location, leading to the dynamic mosaic of savanna types and NPP. Light is generally sufficient in the tropical savannas except when canopies become dense.

A. Water Availability

Water availability is widely considered the most important controlling factor. Rainfall determines the supply of water, but the amount that is subsequently available to plants (its *effectiveness*) depends on drainage and storage (soil texture, depth, and topography) and losses due to evaporation and evapotranspiration (climatic conditions, vegetation cover, etc.). Annual potential evaporation substantially exceeds annual rainfall, therefore rainfall is, in a sense, less effective than in temperate climates. Rainfall and evapotranspiration are highly seasonal and therefore annual means can be misleading.

Rainfall mostly occurs as short-duration, high-intensity convectional storms. Variability is high, increasing with aridity, and is a primary cause of compositional change. Rainfall may be bimodally distributed and the timing affects the species mix, survivability, extent, and overall growth (Pandey and Singh, 1992; Veenendaal *et al.*, 1996). Many areas regularly experience drought and have developed a range of adapted and tolerant species. Plants close their stomata to reduce water loss during dry periods, which also restricts CO₂ uptake and hence productivity. In some savanna areas flooding is common and can lead to a long-term reduction in production due to soil erosion (Rutherford, 1978).

Many studies in arid areas have shown a high correlation between productivity and rainfall. However, NPP can often be more closely related to the length of the wet and dry seasons than to annual rainfall, because this is a better indicator of water availability. Scholes and Hall (1996) calculated that semiarid savannas, where the duration of the growing season is about 100

days, have a total (above- and belowground tree and grass) NPP of around 500 g (DM) m⁻² yr⁻¹, whereas very moist savannas (300 growing days per year) have an NPP of around 3000 g (DM) m⁻² yr⁻¹ (Fig. 16-3).

B. Nutrient Availability

Savanna soils tend to have low cation-exchange capacity (CEC), very low phosphorous and nitrogen contents, and high aluminium and iron contents (Solbrig, 1996). More than half of the tropical savanna soils are derived from old, highly weathered acid crystalline igneous rock, leading to leached sandy soils with low fertility and CEC. There are also extensive areas of basic igneous rock forming base-rich clays with more favorable nutrient content and retention (Solbrig, 1996). Local conditions, age, and history lead to a complex regional distribution. Soil catenas are common with dense woodlands on sandy upper areas, through mixed scrub on shallow midslope soils, to open tall-tree savanna on deep fine-textured soils at slope bottoms (Walker, 1985). Iron pans often occur in arid areas (Menaut *et al.*, 1985).

Nutrient mineralization, transport, and root uptake are all dependent on soil water content. Thus it has been suggested that water availability may actually be controlling plant growth by its influence on nutrient availability, and that, certainly in some areas, nutrients rather than water may be the major production constraint. This is borne out by the high carbon:nutrient ratio of many savanna plants, various fertilization experiments, and comparisons of NPP on adjacent soils with different fertility status (Scholes and Hall, 1996).

High rainfall can leach soils, causing a gradient from arid/eutrophic to moist/dystrophic savannas, seen clearly in Africa (Huntley, 1982). Arid, sandy savannas have a slow-release, low-nutrient stock favoring perennials with low growth rate over a long period. Clay soils release nutrients in pulses after rain, favoring annuals with rapid regrowth for short periods. In arid savannas, litter production plays a major role in nutrient cycling whereas moist savannas tend to have a short, closed nutrient cycle bound closely to root decomposition, so the amount of nutrients in the soil at any instant may be misleading (Abbadie *et al.* 1992). Nutrients are released steadily throughout the year in humid areas, favoring perennials, although there is still a nutrient pulse at the beginning of the rainy season as rain washes the nutrients from litter decomposition and fire ash into the soil (Menaut *et al.*, 1985).

Low nitrogen and phosphorous availability constrain many savanna ecosystems, yet little is known in detail of the nutrient dynamics of tropical savannas (Bremner and De Wit, 1983; Medina, 1987; Menaut *et al.*, 1985; Solbrig *et al.*, 1996a). Most nitrogen is lost through pyrodenitrification with frequent fires and an accumulation of decomposition-resistant charcoal. Leguminous plants are common, but may fix little nitrogen on low-fertility soils, possibly due to a deficiency of cofactors (Zieman *et al.*, 1988). Nitrogen reallocation from leaves can be high, thereby retaining nitrogen stocks before leaf fall and fire.

Earthworms can process up to 70% of soil organic matter in upper horizons (Lavelle *et al.*, 1983; Menaut *et al.*, 1985). Termites are more dominant in drier climates and are very efficient secondary consumers, probably more important than the herbivores, generally consuming around 30% of litter biomass, but this can reach 70%. Termite biomass often averages 10 g m^{-2} of fresh weight with maximums up to 50 g m^{-2} , which is comparable to large herbivores (Wood and Sands, 1978). Nutrients (and seeds) become concentrated in large termite mounds. Herbivory also transforms and concentrates nutrients (Scholes and Walker, 1993).

C. Fires

Fires are inevitable with the buildup of dead grass during the dry season. "Natural" (lightning-induced) fires occur every 1 to 3 years in humid savannas and perhaps 1 in 20 years in arid savannas (Frost, 1985; Walker, 1985). Fires are deliberately set or restricted by humans as part of vegetation management, which has a history of at least $50,000 \text{ yr}^{-1}$ in Africa (Menaut *et al.*, 1985). In Africa, 25–50% of the total land surface is burned annually in the "Sudan Zone" (arid) and 60–80% in the "Guinea Zone" (humid) (Menaut *et al.*, 1991). Fire is considered necessary to the functioning of savannas, which have evolved with it, preventing bush encroachment, removing dead material, and recycling nutrients (Trollope, 1982; Walker and Noy-Meir, 1982). Fire prevention leads to organic matter and litter accumulation and increased tree density, often resulting in the long term in a forested area without grasses. Although fire leads to local and short-term heterogeneity, creating a mosaic structure of open grassland that carries fire, and clumps of trees that lack the herbaceous fuel load to do so, it also maintains regional and long-term homogeneity and stability (e.g., maintaining a sharp boundary between savanna and forest) (Menaut *et al.*, 1985, 1990).

The incidence, intensity, and impact of fire depends on the amount of fuel (grass) present, the prevailing environmental conditions, and thus the time (season) of burning (Trollope, 1982, 1984; Menaut *et al.*, 1993, 1995). Fire removes aboveground herbaceous vegetation and small/immature woody plants, and changes the microclimate and nutrient status. This creates opportunities for seedling development, enhanced reproduction, and fresh growth. Mature trees are not usually affected but total woody biomass is controlled in the long term by reducing recruitment. Underground plant parts are only affected by very hot fires, although the root:shoot ratio increases in regularly burnt areas (Trollope, 1984). Humid plants show many fire adaptations such as withdrawal of plant parts underground, increased (fire-resistant) seed production, and fire-induced phenology.

Fire-induced mortality of plant populations is often extremely low (0–10%) (Frost, 1985). Early-season fires burn 20–25% of the aboveground herbaceous biomass, and late fires burn 60–95% (Menaut *et al.*, 1991). Because much of the total system NPP is belowground or in tree leaves, less

than 20% of the total NPP is lost in annually burnt savannas (Scholes and Walker, 1993), and only 5% in triennially burned savannas (Scholes and Hall, 1996). In the long term, frequent burning tends to increase herbaceous production in humid regions by perhaps 20–50% while decreasing it in arid regions (San Jose and Medina, 1975; Menaut *et al.*, 1993). In fact, the NPP of annually burnt humid savannas is comparable to that of rain forests under similar climatic and edaphic conditions (Scholes and Hall, 1996).

Fire releases carbon, nitrogen, and other elements, which are partly returned to the soil as ash. The long-term effect on nutrient budgets is unclear. It is suggested that savannas that have experienced frequent fires for thousands of years may have been driven to a low-equilibrium nutrient status, but on an annual basis losses of N and C are balanced by annual inputs. Incorporation of charcoal residues in the soil may lead to carbon accumulation in the long term (Menaut *et al.*, 1993).

D. Herbivory

Savannas support large numbers of herbivores, both grazers and browsers. Browsers consume various parts of woody plants and grazers prefer herbaceous biomass, although diets are often mixed and depend on food availability. Insects account for an equal, or even greater, proportion of herbivory compared to mammals, yet they are infrequently studied (Lamotte, 1982; Anderson and Lonsdale, 1990); mammals have greater impact on savanna structure because they trample, urinate, defecate, and trash plants (Skarpe, 1991). Large herbivores, such as elephants, kill trees, thus opening up woodlands and turning savanna into grasslands; giraffes keep trees at a lower, fire-sensitive height (Pellew, 1983). Large concentrations of grazers can cause degradation and erosion of grasslands by severe, long-term removal of the herbaceous cover. Grazing favors tree seedlings, removing competition from grasses and reducing fuel available for fire (Skarpe, 1990).

At the species level, herbivory changes composition and physiognomy, favors annual grasses and increases annual and perennial forbs (Illius *et al.*, 1996). At the individual plant level, changes in quantity, chemical composition, and physiognomy either promote or deter different herbivores. Infertile soils support vegetation with a nitrogen content less than 1%, which is below the threshold for ruminant consumption for most of the year, and less than 10% of NPP is typically consumed compared to 80% on fertile soils (Drent and Prins, 1987; Scholes and Walker, 1993). Some trees can be entirely defoliated by browsing and produce a new crop of leaves in the same season, almost doubling leaf production (Rutherford, 1978).

Grazing has contradictory effects, depending on intensity and local conditions. Moderate grazing removes dead plant material, reduces shade, recycles nutrients, and improves seed dispersal and germination, promoting palatable species, NPP, and high vegetation cover. For example, Pandey and

Singh (1992) found that prevention of grazing in a dry savanna resulted in a decline of NPP (and species diversity), whereas moderate grazing stimulated aboveground NPP by 4–45% and reduced belowground NPP by 25–65%. Intense grazing and trampling result in low plant cover, high mortality, low soil nutrients, low infiltration, decline in water availability, and higher erosion, reducing NPP, particularly in arid and infertile areas (McNaughton, 1983). As the number of humans living in savanna areas has increased, so has the number of domestic livestock, putting pressure on savanna systems (Skarpe, 1991).

VIII. Human Influence

Human-induced land use change has a greater effect on savanna structure and NPP than any other environmental changes. Savannas generally have low human population density because their capacity to support intensive agriculture and livestock grazing is poor; however, population pressure and land use changes are likely to be greater here than in other biomes over the coming decades. The agropastoral communities in savannas are highly dependent on the natural vegetation, which is vulnerable to degradation. Strong social and economic forces will continue to force the conversion of forests to savannas and grasslands to pasture or agriculture fields, although tourism is supporting conservation of large areas of savannas in Africa.

Cattle rearing has been occurring for more than 6000 yr in India and Africa and was sustainable before more recent increases in population, changing social practices, colonialization, war, extensive commercial ranching, etc. Shifting cultivation has also been practiced for thousands of years, generally in areas with rainfall greater than 700 mm, but this is being affected by reduced fallow periods, larger commercial operations, and increased use of fertilizer and irrigation, which increases short-term productivity but can lead to long-term depletion of resources and environmental degradation. South American savannas are rapidly being transformed for soybean cultivation and cattle raising. Australian savannas are likely to remain as grazing lands as alternative economic land uses are limited (Young and Solbrig, 1993; Solbrig, 1996, J. S. Scanlan, personal communication).

Humans influence savannas by managing fire, wildlife, domestic livestock, and wood and grass removals. Intensive livestock grazing, exclusion of indigenous browsers, and fire prevention lead to rapid bush encroachment. In areas of high population and charcoal production, intensive wood harvesting leads to decreased woody biomass, which, combined with high grazing, leads to erosion. The same happens when fire frequency is increased and the animal load is too high (Young and Solbrig, 1993).

IX. Climate Change

Changes in CO₂ concentration, rainfall, and temperature will all affect NPP, fire frequency, etc. Few studies have been carried out on the effects of climate change on savanna ecosystems, there are no true free-air / carbon dioxide enrichment experiments, and few CO₂ studies are as yet complete (R. J. Scholes, personal communication). In tropical savannas the woody biomass is C₃ and most of the herbaceous biomass is C₄. C₃ plants have a greater response to CO₂ enrichment in terms of increased productivity, thus it has been postulated that trees will have an advantage, and, in fact, woody species have been seen to increase in savanna areas although more local changes may be the cause (Polley *et al.*, 1996). However, this is only part of the story. Partial stomatal closure in CO₂-rich environments allows better water and nitrogen use efficiency, which is very important in certain savanna areas constrained in either or both resources (Gifford *et al.*, 1990); Owensby *et al.* (1999) have shown an increase in production in C₄ grasslands due to this effect, and some preliminary results from trials in grasslands in the United States show C₄ grasses actually doing better than C₃. Increased temperatures will lead to increased respiration; however, CENTURY model simulations suggest that increased photosynthesis will exceed increased respiration, resulting in a net carbon sink (Hall *et al.*, 1995). All of the above changes will modify soil carbon storage, which accounts for 80% of the total ecosystem organic carbon in tropical savannas (Scholes and Hall, 1996).

Savannas already have a great impact on carbon cycles due to fires, fuelwood, and land use changes. Amthor *et al.* (1998) found the savanna biome to have the highest potential for carbon gain and among the highest potential for carbon loss. Scurlock and Hall (1998) cautiously propose that this biome may already constitute an annual sink of about 0.5 Pg C, as supported by recent eddy covariance measurements over Brazilian *cerrado* (Miranda *et al.*, 1997) (Table 16-5). Savanna burning releases between 0.87 Pg C yr⁻¹ (Scholes and Hall, 1996; extrapolation of Menaut *et al.*, 1991) and 1.66 Pg C yr⁻¹ (Scholes and Hall, 1996; extrapolation of Hao *et al.*, 1990). Fire suppression and the resultant increase in tree density could store an extra 30 g C m⁻² annually in soils (Scholes and Van der Merwe, 1996).

Introducing deep-rooted African grasses and legumes to South American grasslands has increased soil carbon storage, mostly in the form of dead roots, which, if applied throughout Latin America's savanna areas could store 0.1–0.3 Pg C per annum (Fisher *et al.*, 1994). In Venezuela (San Jose *et al.*, 1998) maximum aboveground yield was four times higher for African grasses than native savanna. However, the continuing pressure on these lands and their subsequent degradation are likely to lead to an increase of carbon loss in the future. These human-induced changes will far outweigh any impacts due to climate change.

X. Summary

Tropical savannas (including grasslands) form one of the world's most extensive biomes, covering 27.6 Mkm². These areas are experiencing significant population pressure and land use changes, and are vulnerable to rapid land degradation. This will have large impacts on global NPP predictions and climate change, thus it is important to improve our understanding of them. The proportion of trees and grasses is highly variable in space and time, yet very little is understood about the complex dynamic processes and interactions controlling them. There is a great paucity of even basic data for these highly heterogeneous ecosystems because relatively few studies have been carried out in this biome in the past. Additionally there is a need for large-scale syntheses of existing data to improve knowledge and understanding. Some are now underway, and it is becoming increasingly clear that these areas have a greater productivity, higher biodiversity, and larger impact on global carbon cycles than previously realized (Long *et al.*, 1989; Solbrig *et al.*, 1996; Scholes and Hall, 1996). The current best estimate for productivity ranges from 733 to 1426 g (DM) m⁻² yr⁻¹ for different savanna formations, average 1078 g (DM) m⁻² yr⁻¹ (Scholes and Hall, 1996), with total annual production in savannas and grasslands at 29.7 Pg (DM) yr⁻¹ (about a quarter of global NPP), although the data these calculations are based on are underestimates (e.g., Long *et al.*, 1989, 1992).

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