

Adaptive strategies of perennial grasses in South American savannas

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Abstract. Morpho-functional features of perennial grasses in South American savannas are considered as adaptive strategies to cope with stress and disturbance factors of savanna environments. The tussock growth form, annual patterns of vegetative growth and reproductive phenology, allocation of carbon and nutrients, and accumulation of standing dead phytomass at the end of the dry season, are discussed in relation to water economy, resistance to drought, photosynthetic rates, growth rhythms, regrowth after drought and fire, seasonal translocation of critical nutrients and carbohydrates, and the total nutrient budget of the grass layer. Different strategies combining various morphological patterns, phenological alternatives and mechanisms for resisting drought and fire exist within the grass flora of each savanna community. The lack of adaptive responses to grazing by large herbivores is a major distinction from African savanna grasses. Many African grasses, either introduced in pastures or colonizing disturbed savannas, do show positive responses to defoliation, including compensatory growth and enhanced photosynthetic rates. Some guidelines for further research are suggested in order to disclose the mechanisms underlying this different behaviour of native and introduced savanna grasses.

Keywords: Defoliation; Drought; Fire; Growth pattern; Phenology; Photosynthetic rate.

Nomenclature: Pohl (1980).

Introduction

The most distinctive feature of tropical savannas is a nearly continuous herb layer dominated by perennial grasses and sedges. This feature is shared with various temperate ecosystems, (e.g. prairies and steppes) and with tropical high-altitude vegetation (paramos), but here other life forms, such as shrubs, cushion plants, herbaceous and woody rosettes are usually co-dominant. The grass flora of tropical-American savannas is quite distinctive and consists of many species which are both almost exclusive of savanna ecosystems and widespread in most savanna areas of Central and South America.

This paper will focus on external constraints and

plant responses leading to the dominance of perennial grasses in savannas, with tropical-American seasonal savannas as an example. These ecosystems have evolved for millions of years under stressful conditions (Fig. 1). Grasses show a wide array of morphological and physiological attributes that may contribute to their ecological success in grasslands and savannas (see McNaughton, Coughenour & Wallace 1981; Risser 1985); a comprehensive model applicable to all perennial grasses in a given ecosystem has not yet been proposed. Large herbivores do not seem to have played a key role in South American savannas, as contrasted with palaeotropical savannas. Only a small part of the ecosystem's energy flows through the grazing food web. Instead, fire takes away the above-ground herbaceous biomass. Another difference is that American savanna soils are less fertile.

Tropical savannas and their environment

The common distinction between wet savannas, occurring in alternating wet and dry climates, and dry savannas, typical of semi-arid tropical climates, referring to Africa and Australia, does not apply to tropical America. Here no formation is found that is physiognomically, floristically or ecologically related to the dry savannas of other continents. In semi-arid climates in tropical America thorn-forests, woodlands or shrublands occur, which do not present a more or less continuous layer of perennial graminoids.

Three types of savanna ecosystems can be distinguished on the basis of differences in seasonal variation in soil water availability (Sarmiento 1984, 1990): seasonal, hyperseasonal and semiseasonal savannas (Fig. 2). Seasonal savannas have a dry season (3 to 7 months) when soil-water potential in the surface layers is below the permanent wilting point, frequently down to -3.0 or -4.0 MPa. In hyperseasonal savannas, mostly occurring on bottomlands and other imperfectly-drained sites, periods of water shortage, water availability and water excess alternate in an annual cycle; during water excess the topsoil becomes water-saturated. Hence, grasses are

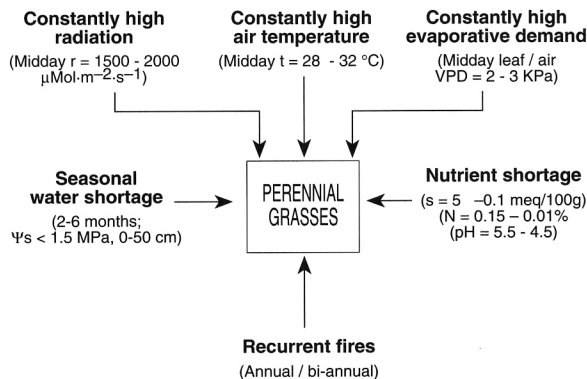


Fig. 1. Major environmental factors influencing the behaviour of perennial grasses in tropical savannas.

subjected to two contrasting forms of stress: drought and water excess. In semi-seasonal savannas, extended periods of water shortage do not occur; on the other hand the soil remains water-saturated for several months.

The savanna types are dominated by perennial graminoids and are physiognomically similar; differences occur in floristic composition and morpho-functional characteristics of the grasses. The three types frequently occur separated along topographic and humidity gradients. In seasonal savannas, medium-tall tussock grasses and sedges dominate both in biomass and in total species number. In hyper-seasonal formations, other growth forms normally form a lower and more continuous grass layer, though bunch grasses may be important. In semi-seasonal savannas several growth forms may be dominant or co-dominant. Tussock grasses are dominant only when drought is a constraint; they decrease in importance and diversity from seasonal to semi-seasonal savannas.

The photosynthetic pathway is different as well: in seasonal savannas all important species have the C4-pathway, in hyper-seasonal savannas both C3- and C4-species occur, and in semi-seasonal savannas perennial C3-grasses predominate (Medina & Motta 1990).

The adaptive syndrome of perennial grasses in seasonal savannas

Growth form

Perennial tussock grasses dominate in seasonal savannas; species with other architecture are restricted to

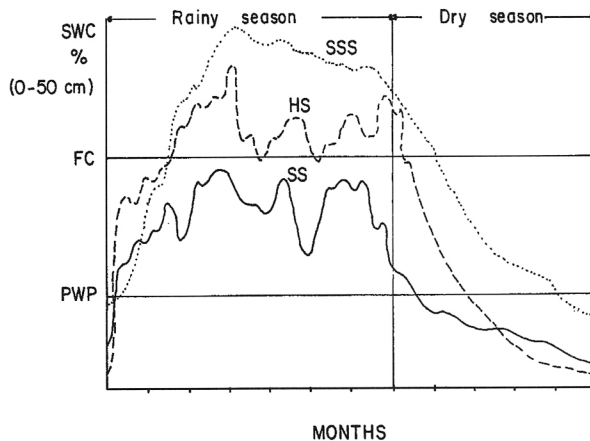


Fig. 2. Seasonal patterns of soil water content (SWC) in the topsoil (0-50 cm) in three types of tropical American savanna ecosystems: seasonal (SS), hyperseasonal (HS) and semi-seasonal savannas (SSS). FC = Field capacity; PWP = Permanent wilting point.

particular habitats. Many species of the widespread genera *Andropogon*, *Axonopus*, *Trachypogon*, *Paspalum* and *Elyonurus* are bunch grasses. In contrast, most grasses in disturbed habitats (ruderals and invaders), as well as cultivated forage grasses, are decumbent stoloniferous: *Brachiaria decumbens*, *Cynodon plectostachum*, *Digitaria decumbens* and *Echinochloa polystachya*. Two important exceptions are: *Panicum maximum* and *Hyparrhenia rufa*, highly competitive African tussock grasses, which are also cultivated in managed pastures.

Within the tussock growth form, two architectural types (Hyder 1972) are important in seasonal savannas. In species with culmless vegetative shoots, such as *Leptocoryphium lanatum*, *Sporobolus cubensis* and *Elyonurus adustus*, the below-ground position of meristems assures plant regrowth after defoliation. In species with culmed vegetative shoots, such as *Trachypogon plumosus* and *Andropogon semiberbis*, culm elongation proceeds before floral induction, with the auxiliary buds well above ground level. Culmless species tend to be early-growing and early-blooming, while culmed plants are late-growing and late-flowering.

Dynamics of growth, tillering and leafing

In most perennial graminoids in seasonal savannas most of the above-ground plant parts die off during the dry season, but some green leaf area is maintained and photosynthesis and transpiration continue. This period of decreased activity or *semi-rest* phase (Monasterio & Sarmiento 1976) differs from the true dormancy or rest phase shown by grasses in high latitude grasslands

during the cold season. Only a few savanna graminoids have a real rest phase and start a new growth cycle at the onset of rains or after burning.

Although all grasses attain the highest above-ground biomass during the rainy season, they differ in growth pattern. Some start growing immediately after the first rains, or even earlier, if they are burned, while others attain their highest growth rate after a lag of some months. Fig. 3 shows changes in biomass in *Sporobolus cubensis* and the negative effect of fire.

When *Sporobolus cubensis* is grown in pots without interspecific competition it continues growing during the last months of the humid season (Fig. 4). Tillering reaches its peak 2 or 3 months after the start of growth. Fire does not affect time of tillering, but it affects tillering rate. The late-growing *Trachypogon plumosus* (Fig. 4), starts growing slowly at the onset of rains and persists at reduced rates for several months, to accelerate and bloom during the last months of the rainy season. Apparently, late-growing species do not change their growth pattern when competition with early growing grasses is excluded (Raventos & Silva 1988).

Reproductive phenology

In seasonal savannas perennial grasses bloom in the rainy season, but vary in precise reproductive timing (Sarmiento & Monasterio 1983). Most species bloom once a year, but some have two or more peaks of growth and flowering. The reproductive behaviour of some grasses changes after burning or defoliation.

Perennial grasses in the Venezuelan savannas were classified into four phenological groups according to period of flowering and maximal growth (Sarmiento 1983). The first group accomplishes all reproductive phenophases at the start of rains, or even earlier if the savanna burns late in the dry season. These *precocious* species are highly dependent on fire, since very few tussocks will flower when the savanna does not burn. In a population of the precocious *Sporobolus cubensis* 7% of the shoots flowered after burning, while in a fire-protected population only 0.05% bloomed (Canales & Silva 1987). *Leptocoryphium lanatum* and *Elyonurus adustus* show the same behaviour. A similar response to fire was reported for some West African savanna graminoids (Adam & Jaeger 1976).

Some precocious grasses bloom immediately after a fire, even in the rainy season, but only once a year. Other species, like *Imperata brasiliensis*, will flower after any fire, being totally fire-dependent for blooming. The same effect, but less intense, may be caused by clipping (Meguro 1969). Even under a regular fire-regime, the proportion of reproducing plants varies widely from year to year.

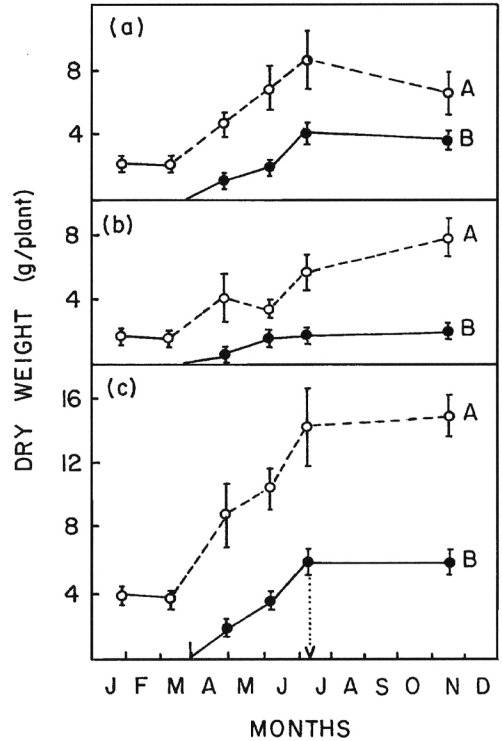


Fig. 3. Seasonal patterns of above-ground biomass in the precocious grass (*Sporobolus cubensis*), in a seasonal savanna in the Venezuelan llanos. (a) green biomass per plant; (b) standing dead; (c) total standing crop; A. unburned; B. burned at the end of the dry season (March). From Canales & Silva (1987).

The second phenological group includes the *early* grasses, which bloom after 2 or 3 months of vegetative growth, during the first half of the rainy season. The *intermediate* grasses (group 3) bloom during the second half of the rainy season, after 5 or 6 months of growth. Finally, the *late* grasses (group 4) bloom during the final weeks of the rainy season and complete seed dispersion in the dry season. Like the precocious grasses, grasses in these groups reduce blooming when not burned, but apparently the mechanisms involved are different, i.e. related to the shading effect of dead leaves (Silva, Raventos & Caswell 1991).

There is a close relationship between growth form and reproductive behaviour. Precocious grasses are culmless; early and intermediate grasses are culmed and medium-tall; late species are culmed and tend to be the tallest grasses in each community.

Cesar (1971, 1990) and Menaut & Cesar (1979) reported a similar spreading of growth and blooming over the entire rainy season in the savannas of the Ivory Coast, where they distinguish precocious from late-growing grasses. Apparently, this is a general character-

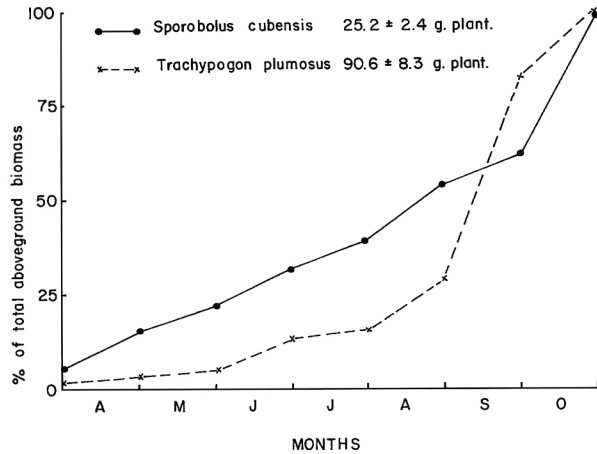


Fig. 4. Biomass accumulated as a proportion of peak above-ground biomass in the precocious grass *Sporobolus cubensis* and the intermediate-growing grass *Trachypogon plumosus*, cultivated in pots in the western Venezuelan llanos. Data from Gallardo de Maldonado (1983).

istic of graminoids in seasonal savannas. In Venezuelan savannas, 3-12 (7 on average) perennial grasses coexist in each community (Sarmiento 1983). Most communities appeared to be an even mixture of precocious, early, intermediate and late-flowering grasses. We suggested that this pattern favours a temporal differentiation among perennial grasses in the uptake of scarce resources, such as water and nutrients (Sarmiento & Monasterio 1983). A similar pattern has been reported for the short-grass prairie (Dickinson & Dodd 1976).

According to Silva & Ataroff (1985), in the precocious *Leptocoryphium lanatum*, *Sporobolus cubensis* and *Elyonurus adustus*, co-existing in a savanna in western Venezuela, germination occurs immediately after seed dispersal. Seeds of the intermediate grass *Trachypogon plumosus* germinate after the start of the rains the following year. The late-blooming species are subjected to seed predation and mortality in the soil, and therefore have higher reproductive outputs than the early ones. Some grasses, e.g. *Axonopus affinis*, *A. compressus* and *A. purpusii*, show two peaks of blooming, one when the early species bloom, the other when the intermediate species flower. In other species such as *Paspalum virgatum* unclipped plants bloom early, while clipping induces an extension of the reproductive period almost over the entire rainy season. This behaviour favours these species in grazed or clipped grasslands.

Biomass allocation

A distinctive feature of savanna plants, perennial herbs, graminoids and half-woody and woody species,

is the high proportion of below-ground biomass (Sarmiento 1984). Fig. 5 shows the distribution of live and dead biomass in a precocious (*Leptocoryphium lanatum*), and an intermediate grass (*Trachypogon vestitus*), towards the end of the rainy season. The below-ground to above-ground biomass ratios (B/A) are ca. 2 in *L. lanatum* and 0.4 in *T. vestitus*. Sarmiento & Monasterio (1983) found B/A ratios of 0.9 to 4.7 in five dominant tussock grasses in the Venezuelan savannas, six months after fire and the initiation of regrowth. For West African savannas, several authors (Cesar 1971; Fournier 1982, 1987; Abbadie 1983) reported B/A values for whole communities in the range of 1.1 to 4.5, the higher figures in savanna grasslands.

Grasses with culmless vegetative shoots present higher B/A ratios as leaf bases remain below-ground. Carbohydrates are mainly stored in below-ground organs: rhizomes, roots and leaf bases, allowing a rapid regrowth when the rains start. There is a close relationship between growth form (tussock grass with culmless vegetative growth), biomass allocation (high B/A ratio), pattern of vegetative growth (early-growing) and pattern of reproduction (precocious-blooming). This is one of the most common adaptive syndromes of savanna grasses.

There are few data on the consequences of burning upon biomass allocation. Canales & Silva (1987) reported that in two populations of *Sporobolus cubensis*, one burned and one unburned, the B/A ratio did not differ 4 months after burning, but thereafter it was higher in the burned savanna. Consequently, less carbon was allocated to above-ground parts in burned plants. Fire reduces above-ground growth rather than below-ground and thus increases the B/A ratio.

Leaf texture

Most neotropical savanna grasses are highly sclerophyllous, which is partly due to the development of mechanical and vascular tissues that make their leaves thick and rigid, and hence less palatable to grazers. Specific leaf weight (SLW) is probably relatively high, as in evergreen woody species, whose SLW-values are among the highest reported (Medina 1982; Sarmiento & Monasterio 1983). American savanna grasses seem to be more sclerophyllous than their African counterparts. *Trachypogon plumosus* has a SLW of 47-49 g/m², contrasting with 29 g/m² in *Hyparrhenia rufa* and 26 g/m² in *Melinis minutiflora* (Baruch, Ludlow & Davis 1985).

Other features related to leaf roughness and unpalatability are high total ash, silica and aluminium contents. Georgiadis & McNaughton (1990), give element contents in the leaves of grasses growing in three Serengeti savannas sites, in the middle of the growing season. Total ash (15-16%), silica (3-8%) and aluminium (>1%)

contents are very high. We may assume that neotropical grasses growing on soils with still higher concentrations of silica and aluminium will show higher concentrations of these elements and of total ash as well.

Responses to stress

Water stress

In seasonal savannas, soil water potential attains relatively high values during the whole rainy season, but it falls sharply after this season is over (San José & Medina 1975; Sarmiento & Vera 1977; Goldstein, Sarmiento & Meinzer 1986). As the soil dries out from the surface downwards, water potentials in the upper levels become more negative than in deeper soil horizons, reaching values of the order of -2.0 MPa or less towards the end of the dry season. From 50 to 120 cm, where an important proportion of tree roots are found, water potential does not fall below -0.5 or 1.0 MPa (Sarmiento & Acevedo in press).

The effects of these seasonal differences in water availability for the water budget of trees and grasses have been discussed by Goldstein & Sarmiento (1987). Savanna grasses exhibit seasonal fluctuations in leaf water potential (Ψ_L), which follow the changes in water content in the upper soil horizons where their roots are concentrated. During the rainy season, minimum Ψ_L is -1.2 to -1.8 MPa, while at the annual peak of drought, minimum diurnal Ψ_L is -3.8 MPa in *Trachypogon plumosus* and -2.4 MPa in *Sporobolus cubensis*. However, even at these low Ψ_L values grasses continue to transpire and assimilate, though at low net photosynthetic rates. Baruch, Ludlow & Davis (1985) found positive carbon gains in *T. plumosus* leaves even at a Ψ_L value of -6.0 MPa. During a day in the dry season, when minimum Ψ_L in *T. plumosus* decreased to -2.4 MPa, transpiration losses did not decrease even at midday, remaining at moderate levels, ca. $20 \mu\text{g cm}^{-2} \text{sec}^{-1}$. As savanna grasses show quite low stomatal conductance, transportation flux and green area during the dry season, their water demands should be quite moderate.

In the dry season, leaf water potentials drop less in the precocious *Sporobolus cubensis* than in the late-growing *Trachypogon plumosus*. Minimum leaf conductances and daily transpiration losses are also lower in *S. cubensis* than in *T. plumosus*. Thus, precocious species behave rather as drought avoiders, whereas later growing grasses are more drought-tolerant. In deep soil layers (below 100 cm) water must be available to grass roots, and as this zone is also exploited by trees, grasses and trees compete here for water during the dry season.

The total amount of water transpired by the whole

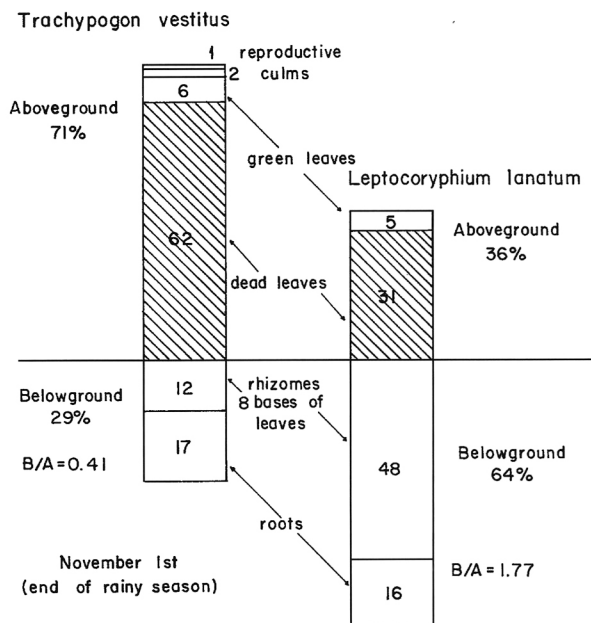


Fig. 5. Biomass allocation (g dw/plant) in the precocious *Leptocoryphium lanatum* and the intermediate *Trachypogon vestitus* in a seasonal savanna of the Venezuelan llanos towards the end of the rainy season.

grass layer of a seasonal savanna during the dry season, calculated on the basis of mean LAI and average rates in *S. cubensis* and *T. plumosus*, is ca. 100 mm. The woody layer would transpire at about the same level, since transpiration losses by trees are higher but, on the other hand, tree densities in most seasonal savannas are low. For both savanna components, soil water, which accumulates in deep layers during the period of water surplus, provides their requirements during the dry season.

Nutrient stress

Soils in seasonal savannas are among the most infertile of the lowland tropics, and this is particularly true in tropical America. Scarcity of plant-available nutrients has been postulated as one of the principal environmental constraints acting upon these ecosystems. Recent reviews of factors determining savanna responses emphasize the all-important role of plant available moisture (PAM) and plant-available nutrients (PAN) (Frost et al. 1986; Walker & Menaut 1988).

Several processes related to the evolution of soils and landscapes have been suggested as being responsible for the dystrophic character of savannas (Sarmiento 1984). Inputs and outputs of nutrients and the internal turn-over rate are important. Sarmiento (1990) took as a simple indicator of soil fertility the amount of exchangeable bases in the topsoil ($S = \text{Ca} + \text{Mg} + \text{K} + \text{Na}$). When

S ranges between 1 and 5 meq/100 g soil, the savanna is considered *dystrophic* and when $S < 1$ meq/100 g, it is considered *hyperdystrophic*, i.e. extremely nutrient-deficient. The topsoil in South American seasonal savannas falls within these two categories, and S may be as low as 0.12 meq/100g here. These low values are linked to low values of pH, carbon and nitrogen content, cation exchange capacity, base saturation and total phosphorus, but high values of exchangeable aluminium.

A first response by savanna plants to the scarcity of soil nutrients is the low concentration of N, P, K and Ca in all plant parts. (Table 1). This is also the case in West African grasses (Cesar 1990). In comparison with cultivated grasses like corn, rice and sugar cane, or with East African grasses (Georgiades & McNaughton 1990) the nutrient content of American savanna grasses is very low throughout the year. Certain spore elements, like copper and zinc, may also be scarce and below the requirements of large herbivores for most of the time (Cesar 1990; Gonzalez Jimenez 1979).

A second response to nutrient shortage is the re-allocation of nutrients between various plant parts following a precise yearly schedule. In North American prairie grasses nitrogen accumulates in rhizomes during the peak of growth and is depleted during early growth (McKendrick, Owensby & Hyde 1975; Clark 1977). In savanna species such re-allocation has not been documented, but may be inferred from observations of mature leaves, which drop their nitrogen content by 80 % and their potassium content by 120 % (Sarmiento 1984).

Little is known about rhizospheric nitrogen fixation and VA-mycorrhizal infection in native neotropical species, but there is some evidence of their significance in tropical grasses and grasslands (Balandreau 1975; Balandreau et al. 1976; Döbereiner & Day 1974; Döbereiner 1979; Sylvester-Bradley et al. 1980; Wallace 1981).

Constraints on carbon gains

Maximum photosynthetic rates may be very high with high leaf temperature and high levels of light and available water and nutrients. Torres (1984) reported maximum rates of the order of 16-20 $\mu\text{mol m}^{-2}\text{s}^{-1}$ CO_2 in the two native grasses *Trachypogon plumosus* and *Leptocoryphium lanatum* and Baruch et al. (1985) reported rates as high as 28 $\mu\text{mol m}^{-2}\text{s}^{-1}$ in *T. plumosus*; this is about the same rate as found in two highly productive African grasses *Hyparrhenia rufa* and *Melinis minutiflora*. High optimum leaf temperatures, 30-40 °C, and high light saturation intensities also characterize the photosynthetic behaviour of C4 savanna grasses. However, under field conditions net photosynthesis depends on leaf conductance and leaf water potential. Frequently

both parameters are quite low in seasonal savanna grasses. Therefore assimilation rates are lower during the dry season, due to water stress.

As net carbon assimilation rate decreases with decreasing leaf conductance and leaf water potential (Torres 1984; Baruch, Ludlow & Davis 1985), with k_s -values during the dry season in a grass such as *Trachypogon plumosus* (k_s 0.1 - 0.2 cm/s), net photosynthesis may reach 30 - 50% of rates under unrestricted CO_2 exchange ($k_s > 0.6 \text{ cm s}^{-1}$, $\Psi_L > -1.0 \text{ MPa}$) (Fig. 6).

Photosynthetic rates depend on leaf nitrogen concentration, which decreases with leaf age. Consequently, assimilation rates are highest in recently expanded leaves, intermediate in young leaves and lowest in senescent leaves (Ludlow & Wilson 1971; Parsons et al. 1983). Chacón, Rada & Sarmiento (1991) determined midday assimilation rates of 34, 28 and 22 $\mu\text{mol m}^{-2}\text{s}^{-1}$ respectively, in the three categories of leaf blades in *Panicum maximum*, the dominant species in many secondary grasslands. Water was not a limiting factor during the rainy season (Fig. 7). Under these favourable circumstances, field rates in young expanded leaves may approach the maximum rates obtained under optimum laboratory conditions.

Responses to disturbance

Fire

Consequences of fire for nutrient availability

In unburned savannas large amounts of standing dead material accumulate (Sarmiento 1984). Such an accumulation of fuel leads, sooner or later, to a natural fire much more severe than the annual fires. In savannas, almost all standing crop and litter are consumed, leaving a thin, irregular layer of ashes on the ground. How much of the above-ground primary production is consumed depends on the season. Savannas generally burn towards the end of the dry season, when a large proportion of the above-ground standing crop is already dead (ca. 90% of the aerial phytomass in different savanna communities in Venezuela). At this time most mineral nutrients are translocated underground. Considering that fire consumes about 90% of the standing crop (500 - 700 g/m²), the amounts of nutrients liberated are in g/m²: 1.3 - 1.9 for N, 1.1 - 1.6 for K, 0.9 - 1.3 for Ca and 0.4 - 0.6 for P. In savannas outside tropical America nitrogen losses are within this same range (Frost & Robertson 1987).

If ashes are not carried away by rains or wind, they may be recycled and taken up again by the vegetation. However, a small amount of potassium and phosphorus, and almost all the nitrogen and sulphur are lost by volatilization. The amount of nitrogen lost, which is

Table 1. Concentration of mineral elements in leaves of seasonal savanna grasses during the peak of the rainy season (% dry weight) and in leaves of a cultivated grass (rice).

Species	N	P	K	Ca
<i>Trachypogon vestitus</i> ¹	0.74	0.07	0.40	0.17
<i>Axonopus canescens</i> ¹	1.00	0.08	0.73	0.17
<i>Axonopus purpusii</i> ²	0.71	0.14	1.37	0.18
<i>Sporobolus indicus</i> ²	0.71	0.18	1.06	0.19
<i>Oriza sativa</i> (rice) ³	2.69	0.30	2.20	0.37

¹Medina, Mendoza & Montes 1977; ²González Jiménez 1979; ³Ahmad & Jones 1969.

quite significant in the nitrogen budget of the ecosystem, seems to be about the same as is gained through symbiotic and free fixation (Sarmiento 1984).

Effects of fire on plant growth

Well-established tussocks are not affected by burning, as their buds are protected inside the basal leaf sheaths, or underground. They will sprout again, reconstitute their photosynthetic surfaces and flower. Many species seem to be fire-dependent in their reproductive outputs. However, a more detailed analysis of plant growth shows that these grasses are adversely affected by burning. Canales & Silva (1987) showed how burning decreases above-ground biomass accumulation in *Sporobolus cubensis* (Fig. 3), and also has a reducing effect on roots and rhizomes. Shoot mortality increases after fire and the total number of tillers per tussock is reduced. The precocious *S. cubensis*, whose blooming is clearly promoted by late dry-season fires, experiences nevertheless reduced vegetative growth and plant survival.

Plant mortality

Silva & Castro (1989) followed seedlings of *Andropogon semiberbis*, which is late-flowering and germinates early in the rainy season. They concluded that the highest mortality rate is found during the dry season, and that this is due to fire, while during the wet season other mortality factors seem to be important. Silva et al. (1991), using matrix population models under contrasting fire regimes, concluded that to stabilize a population of *A. semiberbis*, burning frequency has to be at least 0.85, that is 5 burns in 6 yr, below which its population starts to decline.

Thus, fire may have different effects on different phenological phases of savanna grasses. On the one hand it reduces vigour and growth rates, and is responsible for high seedling mortality. On the other hand, it increases reproductive output, and the long-term persistence of a species may be dependent on rather a high fire frequency.

Plant quality

Most savannas are burned by ranchers with the aim of improving forage quality. This may be true because the youngest tissues are richest in nitrogen and proteins. Or, there is a direct effect of the liberated nutrients on plant regrowth. Christensen (1977) concluded that both effects may occur in a regularly burnt pine savanna in North Carolina. Increased concentrations of phosphorus and potassium are a consequence of younger leaf age, while higher concentrations of nitrogen, calcium and magnesium may depend on increased nutrient availability induced by burning.

Long-terms trends

A few experiments have been made in tropical America concerning long-term changes induced by protection from fire. The first one started in 1946, a second one in 1961 in Calabozo, Venezuela, and a third more recently in Minas Gerais, Brazil. In all three the same general pattern of change resulted. In the experiment started in 1946 in Emas, São Paulo, Brazil, a sequence of changes in savanna structure and composition occurred (Coutinho 1982), starting with a decreased vigour of savanna grasses and an increasing density of quick-growing trees and shrubs. Later on, the alien grass *Melinis minutiflora* became dominant and replaced native species, which was followed by the gradual disappearance of the grass layer due to increasing shading. Finally, a cerrado with a forest physiognomy had

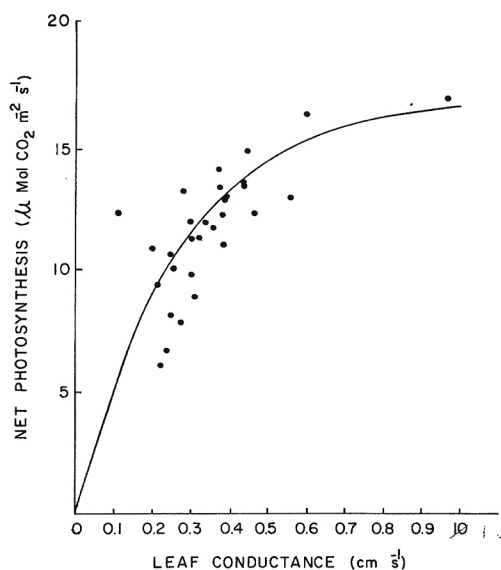


Fig. 6. Net photosynthesis as a function of leaf conductance in *Trachypogon vestitus*, under laboratory conditions. PAR = 1000 Em⁻²s⁻¹; leaf temperature = 30.1 ± 1.5 °C; VPD varies from -1.0 to -3.5 KPa. From Torres (1984).

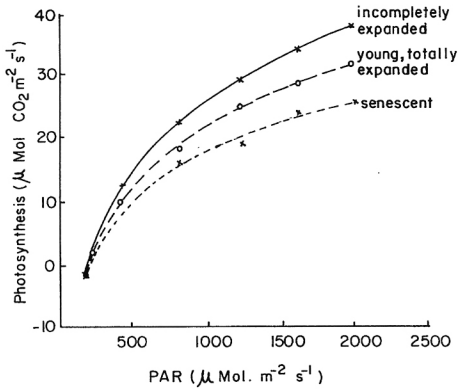


Fig. 7. Photosynthetic rates in leaves of *Panicum maximum* at different developmental stages, under field conditions in the Venezuelan western llanos, during the rainy season. From Chacón, Rada & Sarmiento (in press).

replaced the original open savanna. A similar pattern was observed in an experiment started recently in the Minas Gerais area (Coutinho 1982).

San José & Fariñas (1983) and Fariñas & San José (1987) followed the changes in composition in a Venezuelan savanna after fire protection. Tree density increased much in only a few years, while the vigour and diversity of the grass layer sharply decreased. The African grass *Hyparrhenia rufa* gradually displaced the native grasses. However, after almost 30 yr of fire protection, and of exclusion of domestic herbivores as well, still no forest had developed. The vegetation continued to be a seasonal savanna, but with a denser woody layer.

Grazing and clipping

Forage quality and grazing

Gonzalez Jiménez (1979) analysed the nutritive value of grasses and the diet of the largest native herbivores (capybara and deer) in the hyperseasonal and semi-seasonal savannas of the southern Venezuelan llanos, and included cattle and horses in the comparison. In the middle of the wet season C3-grasses in flooded savannas are richer in crude proteins (6–15%) and phosphorus (0.18–0.24%) than C4-grasses in seasonal savannas (4–6% CP; 0.12–0.18% P). Other elements vary within the same range in grasses from the three types of savannas. Not surprisingly, flooded savannas are preferentially grazed by domestic herbivores. The four grasses most frequently consumed by cattle in any season are *Hymenachme amplexicaulis*, *Leersia hexandra*, *Panicum laxum* and *Paratheria prostrata*, being the dominant grasses in flooded communities. Dominant grasses in

seasonal savannas, in this case *Sporobolus indicus* and *Axonopus purpusii* become common in the diet of cattle only during the dry season, when available forage is at its annual minimum in amount and quality. Tejos (1987) and Tejos, Schargel & Berrade (1990) found in the same area that the nutritive value of dominant grasses in hyperseasonal and semi-seasonal savannas sharply decreases during the dry season, reaching an average crude protein content of 5.2% and a phosphorus content of 0.15%, well below the requirements of cattle. Gonzalez Jiménez (1979) showed that only at the end of the dry season do capybara, deer, cattle and horses compete for the same grass species, while their alimentary niches diverge during the rest of the year.

Seasonal savannas, in spite of the rather high primary production of the grass layer, have a low carrying capacity for domestic herbivores, because the quality of the grass becomes less than the grazers require during at least six months, from the last part of the wet season until the following growing season. Burning has been the traditional tool for improving forage quality and palatability. However, it does not provide adequate animal feed throughout the entire dry season, but it somewhat extends the period when acceptable forage may be available. Both hyperseasonal and semi-seasonal savannas offer better forage over a longer period, but flooding hinders grazing. Actually, optimal management is reached by having the herds utilize each type of savanna alternately.

Apparently, neotropical seasonal savannas have never supported a rich fauna of large native herbivores. It is difficult to indicate the primary cause and the consequences of this situation, but as a matter of fact seasonal savannas do not offer an adequate diet to grazers. As large native grazers are absent, co-evolutionary mechanisms never evolved.

The possibility for improving cattle raising and carrying capacities in seasonal savanna areas seems to depend on an extra source of proteins. Here, we need a better knowledge of the possibilities of improving grass quality through management of native species.

Grass response to grazing

Information on the responses of native grasses to intensive grazing is rather scanty, since stocking rates are maintained at very low levels. Probably, the most valid generalization is that the grasses of neotropical seasonal savannas do not tolerate frequent defoliation. In a field experiment in the savannas of the western Venezuelan llanos, a seasonal savanna was managed as a mown lawn and clipped nearly bimonthly for more than 15 yr. This regime simulated severe grazing (though the clipped plant material was left on the ground). As a result, not a single perennial grass from the original

savanna community persisted. Some of the species that totally replaced native grasses, such as *Panicum maximum* and *Hyparrhenia rufa*, are aggressive colonisers of African origin; other now common species are annuals, and the two native perennials, *Paspalum virgatum* and *Axonopus compressus*, which became dominant, are widespread neotropical grasses occurring in disturbed sites or as pioneers in abandoned fields. This mown grassland is of acceptable productivity and palatability, but like the original savanna, it almost stops growing during the dry season.

The dynamics of the growth and production of *P. maximum* in the western Venezuelan llanos is under study. *P. maximum* was introduced early from Africa, and is one of the most wide-spread species in secondary grasslands all over the neotropics. It is a species of wide tolerance and high productivity, reaching an annual production of 60 to 70 tons/ha under grazing. *P. maximum* is a tussock grass that may be easily compared with the native tussock grasses.

In contrast with native savanna grasses, *P. maximum* tolerates severe clipping regimes; defoliation promotes its growth and improves its palatability (Chacón & Sarmiento in press; Chacón, Rada & Sarmiento in press). Two clipping treatments (monthly and bimonthly clipping frequencies at 15 cm) showed that total leaf biomass produced in four months is highest in the bimonthly clipped population and lowest in the control plants (Table 2). In the control plants the largest proportion of the above-ground biomass is stored in the culms, in the two clipped populations the largest proportion is found in the leaves.

Photosynthetic rates in young, fully developed leaves

Table 2. Responses of *Panicum maximum* to different clipping treatments. Plants were clipped at 15 cm. Results after 132 days. From Chacón & Sarmiento (in press).

		Control	Clipped monthly	Clipped bimonthly
Total above-ground biomass (g/plant)	Live	1493	208	294
	Dead	93	62	82
	Total	1586	270	376
Culms (g/plant)		1209	8.5	40.8
Leaf biomass (g/plant)	Live	219	278	278
	Dead	72	20	25
	Total	291	298	303
Green leaf area (m ² /plant)		1.5	3.6	3.9
Above-ground production (g/plant in 132 days)	Leaves	574	792	542
	Total	3023	811	869
Relative growth rate 14 - 132 days (mg g ⁻¹ d ⁻¹)		36.1	80.1	40.1

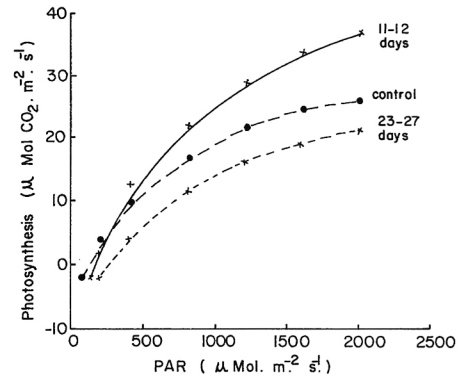


Fig. 8. Photosynthetic rates of young leaves of *Panicum maximum*, 11-12 and 23-27 days after clipping; • = control plants. From Chacón, Rada & Sarmiento (in press).

in the field (Fig. 8), were highest in plants that had been cut 11 to 12 days before measurements, and lowest in plants after 22 to 27 days of regrowth, and intermediate in the control plants. That is, independent of absolute leaf age, clipping promotes higher assimilation rates almost at any light intensity, being thus a compensatory assimilation in the sense of McNaughton (1979) promoted by defoliation and probably induced by processes internal to the defoliated plant.

After some time, in this case in the order of 20 days after clipping, the rates were already somewhat lower than in unclipped plants, probably because the leaves in the control plants had shorter life spans due to shading and, when the photosynthesis was measured, these leaves appeared to be younger than the 23 to 27 day-old leaves of the clipped treatment. In any case, the increase in photosynthetic rate following partial defoliation extends for a period long enough to contribute significantly to the rapid reconstitution of the assimilatory processes.

Thus, *Panicum maximum* is supported by frequent and severe defoliation, providing large amounts of good forage. The frequently clipped *P. maximum* population survived for 3 yr even under the more severe defoliation treatment (cutting at 15 cm each 15 days). Compensatory photosynthesis after clipping surely plays a key role in recomposing leaf area and increasing leaf production.

Conclusions and some questions for further research

Morphological and functional features that may help perennial grasses in seasonal savannas to overcome severe environmental constraints during each annual cycle are summarized in Table 3. Among these constraints are constantly high atmospheric evaporation demands coupled with an extended season of soil water shortage, as well as almost yearly fires.

Table 3. Some major morphological and functional features of tropical savanna grasses and consequences for their survival and ecological success.

Tussock growth form	
Bud bank close to ground level. (protected by old leaves, or below-ground)	Low mortality (drought, fire)
Roots concentrated in the topsoil	Intensive use of water in wet season, water shortage during dry season
High B/A	Accumulation of below-ground reserves, carbon and nitrogen costs
Evergreen, semi-rest phase	
Carbon assimilation all year	Positive carbon budget
Minimum green leaf area during the dry season	Minimum water losses, Accumulation of standing dead crop
Low concentration of nutrients	
Low concentration of leaf nitrogen and mineral nutrients	Low Pn rates
High C/N, sclerophylly, high specific leaf weight	Low palatability, slow decomposition
Recuperation of nutrients	
Decrease in concentration with leaf age	Decrease in Pn rate
Accumulation in below-ground organs	Rapid regrowth after fire, drought
C4 photosynthetic pathway	
High potential Pn rates	High assimilation when water and nutrients are not limiting
Gradual fall in conductance with decreasing ψ_L	Gas exchange at high water stress, high TFD, low water loss during dry season (low green leaf area)
Gradual fall in Pn with decreasing ψ_L	Positive carbon budget even at very low ψ_L
Annual fires	
Consumption of standing dead crop	Liberation / loss of nutrients
Improved light conditions at ground level	Increase in Pn rate
Decreased tillering, plant production	Increase in plant mortality
Induced blooming	Increase in reproductive output

Besides the C4-photosynthetic syndrome as an adaptation to high temperature, irradiation and water stress, the tussock growth form is important. In tussocks, buds and most carbon and mineral reserves are protected from fires. Thus rapid reallocation to above-ground organs is possible at the onset of rains or after a fire, meeting the demands of shoot regrowth.

Maintaining a considerable amount of standing biomass during the whole year, either green or mainly dead, without any period of total dormancy may contribute to the persistence of plant populations in any given site, once the ground becomes occupied. Furthermore, the lack of dormancy contributes to continued carbon gains, even under high water stress. This behaviour also characterizes evergreen savanna trees (Sarmiento, Goldstein & Meinzer 1985). Finally, a positive response to burning that promotes blooming and increases reproductive

output contributes to the stability of grass populations in savannas burned regularly.

Seasonal savannas exhibit a diversity of perennial grasses and phenological strategies, leading to a better use of scarce resources through a temporal division of the niche. Phenological behaviour is related to architectural pattern, ecophysiological attributes and resistance to defoliation. The richness of the grass flora and its phenological diversity have to be taken into account if the carrying capacity of savannas and the forage value of their grasses have to be improved.

Evidently, these grasses do not tolerate frequent and severe defoliation, as if such kind of disturbance were totally alien to them. Annual burnings that may consume up to 90% of the above-ground standing crop, together with occasional consumption by small animals (ants, grasshoppers), seem to be the strongest pressure on their shoots that species may tolerate. This apparent lack of adaptability to large grazers, leads to the incapacity of seasonal savannas to support economically interesting grazing pressures by domestic herbivores. High stocking rates are impossible due to the rather low quality of the forage produced during most of the year. Only the early regrowth after fire or at the onset of rains meets the nutritional requirements of domestic animals.

African grasses introduced into tropical America in managed pastures, or colonizing disturbed habitats, do tolerate both burning and heavy and frequent defoliation. As was shown for *P. maximum*, compensatory growth allows a high production of new leaves after partial defoliation.

Knowledge of the characteristics of ecophysiological and population ecology of tropical American native grasses and of the ecology of seasonal savanna ecosystems is still quite fragmentary. Comparisons with other tropical systems have just started. Crucial aspects in need of further analysis are:

- responses of native savanna grasses to defoliation (grazing, clipping);
- responses of native savanna grasses to water stress;
- role of nutrients on plant response to defoliation and on the competitive ability of savanna grasses;
- comparison of native and introduced species;
- scanning of native species tolerant to higher grazing pressures;
- population and competition studies.

A better knowledge of these aspects will enable a sounder utilization of savannas for animal production.

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