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CHAPTER 2 - WATER.

WATER RELATIONS OF TREES AND GRASSES AND THEIR CONSEQUENCES FOR THE STRUCTURE OF SAVANNA VEGETATION

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1. INTRODUCTION

The balance between a continuous grass cover and a discontinuous layer of woody plants is mainly determined in tropical savannas by soil moisture availability and nutrient content (Walker et al., 1981; Walker and Noy-Meir, 1982; Sarmiento et al., 1985; Knoop and Walker, 1985). Other determinants such as herbivore pressure and fire frequency may also have important evolutionary and short term consequences for savanna structure and functioning.

Although mean annual rainfall in tropical savannas may be as high as 1800 mm and even exceed annual potential evapotranspiration, most of the rain falls during one well-defined wet season (Fig. 2.1). The occurrence of distinctly wet and dry seasons coupled with constantly high temperatures appear to be two of the most important environmental prerequisites of savannas (Sarmiento et al., 1985). Figure 2.2 shows typical climatic patterns of a Venezuelan seasonal savanna. Mean monthly temperatures along the year differ only by 2.5°C. Precipitation, on the other hand, is strongly concentrated in only one season. Air humidity is also subjected to seasonal changes. Evaporation rates during the dry season may be twice as high as in the wet season. Figure 2.2 also shows changes in soil water availability (measured in terms of soil water potential) at different soil depths. Soil water potential decreases during the dry season mainly in the topsoil while deeper soil layers exhibit a much higher degree of water constancy.

The combination of alternating wet and dry seasons with well-drained soils, characteristic of seasonal savannas (Sarmiento, 1984), produces a series of ecological consequences that influence both the morphofunctional responses of plants and the structure and functioning of the whole ecosystem. During the non-rainy season the soil begins to dry out from the surface downwards, and therefore the soil water potentials in these upper levels may become quite negative (Fig. 2.2). Among the shallow-rooted herbaceous species only those able to obtain water under low soil-water potentials may continue to exchange water vapor and CO₂ during the dry season. The deeper soil layers decrease their water levels more slowly due to the lower root density of woody plants, and the buffering effect of

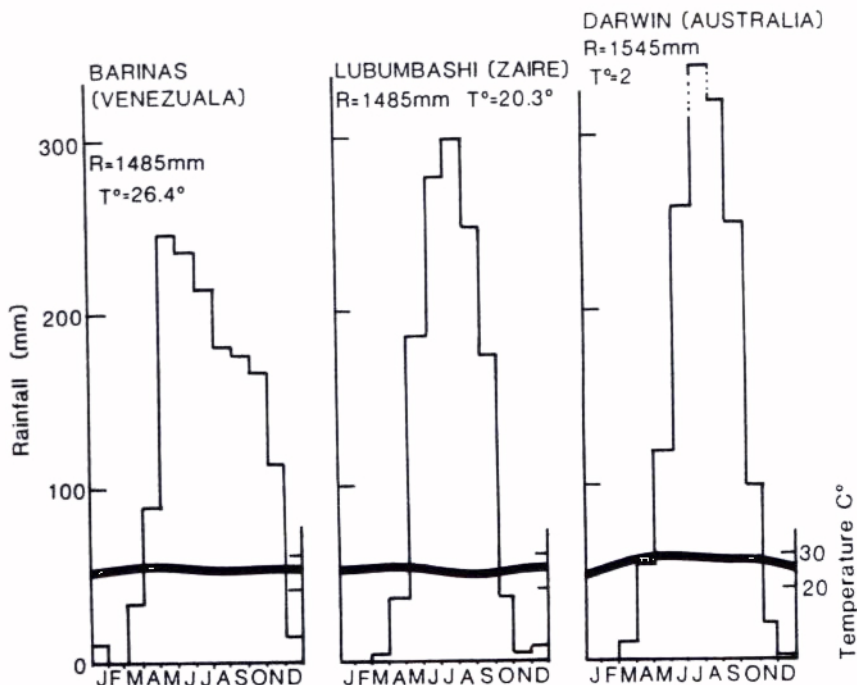


Fig. 2.1. Climadiagrams for South American, African and Australian localities with typical wet and dry tropical climates. In spite of the peculiarities of each climate, there is a basic similarity in the pronounced dry season (4 to 7 months long) followed by several consecutive months with heavy rainfall. Annual precipitation (R) and mean annual temperature (T) are also indicated. (From Sarmiento et al., 1985).

the topsoil. Physical characteristics of soils that influence permeability and moisture retention should have a profound impact on seasonal patterns of moisture availability at different soil depths.

A second major consequence of the savanna climate is the gradual leaching of the soil profile in well-drained soils. In effect, the large water surplus during the rainy season, together with a free water movement through the soil, promotes a downward transport of ions and clay that results in a rapid impoverishment of the soil nutrient content.

A third ecological consequence of the seasonal savanna climate derives from the combination of an extended

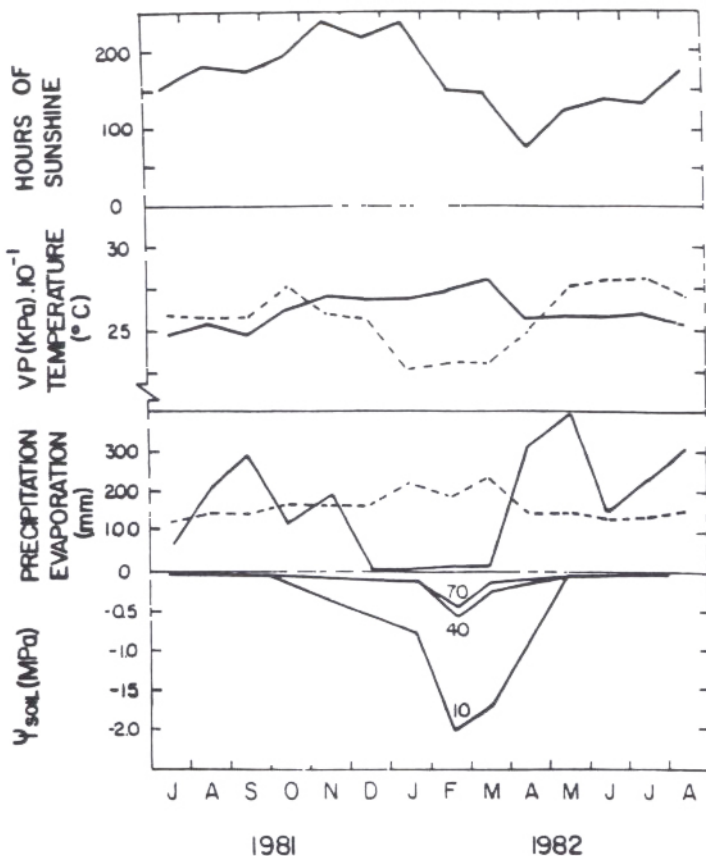


Fig 2.2. Seasonal pattern of sunshine hours during the month, vapor pressure at the corresponding mean monthly temperature, temperature and relative humidity (VP, —), mean monthly temperatures (-----), pan evaporation (-----), total monthly precipitation (—), and soil water potential (Ψ_{soil}) at 10, 40 and 70 cm depth. (From Goldstein et al., 1996).

dry season with a continuous grass cover that dries out during the non-rainy period. This large amount of standing dead biomass greatly increases the likelihood of fire. Burning is responsible for the loss of volatile elements, such as nitrogen and sulphur, reinforcing in this way the nutrient deficient characteristic of the ecosystem (Medina, 1982; Gillon, 1983).

The most intriguing and extended savanna types in South America are the humid seasonal savannas (also called

trees and grasses, we must discuss to some extent the related nutrient and carbon effects.

The second problem deals with differences between types of savannas. The high diversity of savanna types has been sometimes overlooked, although it is an inherent characteristic of the savanna ecosystem as a whole. We will constrain the analysis of the water relations of savanna plants to the well drained, seasonal savannas that do not suffer extended periods with an excess of water that could lead to water saturation, anaerobiosis or reductive soil environments.

2. WATER DEFICIT, OSMOTIC ADJUSTMENT AND WATER USE EFFICIENCY OF TREES AND GRASSES

In this section we compare savanna woody and grass species in terms of mechanisms that each growth form utilizes to maintain an adequate water and carbon balance.

There are important differences between grasses and trees concerning seasonality in water consumption. Midday leaf water potential (ψ_L) of two woody species (Fig. 2.3) remain practically constant throughout the year, while two grass species exhibit strong fluctuations that parallel the changes in water availability of the upper part of the soil profile. This difference in seasonal changes of ψ_L suggests that these trees and grasses explore two distinct layers of soil in terms of water dynamics. An upper layer that dries out during the rainless season and a lower soil layer to which the deep-rooted woody plants have access.

A similar difference in the degree of seasonal constancy of trees and grasses occurs in transpiration rates (Fig. 2.4). Transpiration levels of trees may be as high during the dry season as they are during the wet season. Transpirational fluxes of grasses, on the other hand, are very low during the unfavorable period. Not only the transpirational flux density (water loss per unit leaf area) decreases, but also the total amount of the green leaf surface.

Savanna grasses generally exhibit strong osmotic adjustments, a mechanism whereby plants maintain positive turgor despite low (negative) water potential (Ferreles et al., 1978; Turner and Jones, 1980). While this extends the period of physiological activity, it may also promote a more rapid depletion of soil moisture in the rooting zone of the grasses and eventually leads to a strong water deficit, desiccation and death of a large part of the green biomass. Maintenance of leaf turgor in the face of decreasing soil moisture availability has been emphasized as

cerrados in Brazil) that occupy oligotrophic and well-drained soils (Sarmiento, 1983). In contrast to hyperseasonal savannas, seasonal savannas do not suffer extended periods with an excess of water in the upper soil levels. These savannas are normally burnt once a year, towards the end of the dry season. The trees are largely evergreen and exhibit a quite distinctive morphology. They have low, twisted trunks, deep and extensive root systems, relatively high root/shoot biomass ratios and large, highly scleromorphic leaves. Evergreen tree species renew their leaves in the dry season when conditions seem least favourable for leaf expansion. This is a mechanism that helps to conserve nutrients (Sarmiento et al., 1985).

The previous combination of adaptive features does not prevail in all African savanna woody species. At least in East Africa, the trees tend to have smaller and/or less scleromorphic, leaves, and tend to be deciduous. These differences in functional and morphological adaptations suggest that savanna trees of the new world have been subjected to a different combination of selective pressures.

Perennial C4 grasses are the dominant herbaceous plants. Grass species diversity is quite high. These species, however, differ in several aspects including shoot/root biomass ratios, plant form, degree of leaf pubescence, seasonal growth rhythms and phenology. Some species start to grow with the first rains or soon after a fire early in the wet season. Other grass species develop their shoots slowly and enter into their reproductive phases towards the middle of the rainy season or even during its last weeks (late growing species) (Sarmiento and Monasterio, 1983).

The grass component of the savanna ecosystem has a very different growth seasonality than evergreen trees. Grasses have a pronounced annual variation in the amount of living biomass. They reach their peak above ground biomass during the wet season, and maintain a low but significant green leaf area during the dry period.

The objective of this chapter is to describe some of the consequences of a seasonal climate, with a well defined dry season, on tree and grass growth, and some of the adaptations and mechanisms that have evolved in savanna plants to cope with water deficits. In order to fulfill this goal we will have to overcome two problems. The first is related to the nature of many tropical savanna ecosystems in which water dynamics are tightly coupled to the nutrient and carbon economy of the individual components. Although the focus of this analysis will be on the water economy of

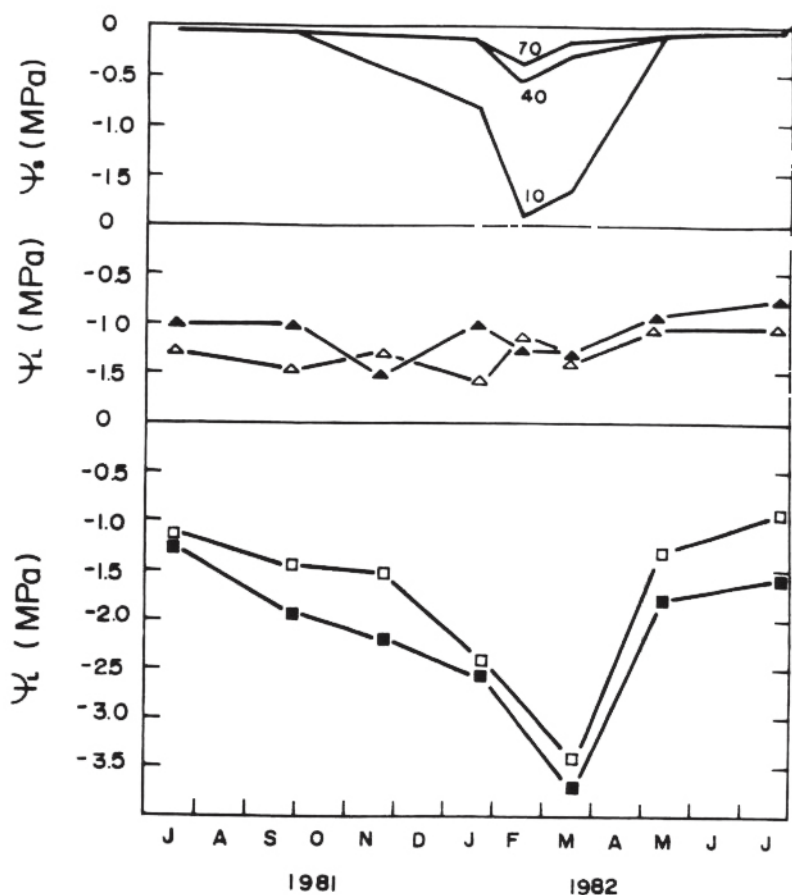


Fig. 2.3. Seasonal courses of soil water potential (ψ_{soil}) at 10, 40 and 70 cm depth, and minimum leaf water potential (ψ_l) for *Curatella americana* (Δ), *Byrsonima crassifolia* (\blacktriangle), *Sporobolus subensis* (\square), and *Trachypogon vestitus* (\blacksquare). The first two species are evergreen trees and the last two are perennial grasses. From Goldstein et al., 1988, and unpublished data.

an important adaptation for preventing stomatal closure and cessation of growth and other physiological activities (Hsiao et al., 1976; Bradford and Hsiao, 1982). Mature leaves of evergreen savanna trees, on the other hand, do not adjust osmotically during the rainless period. On the contrary, water potentials at zero turgor (determined by means of pressure-volume methods) tend to increase

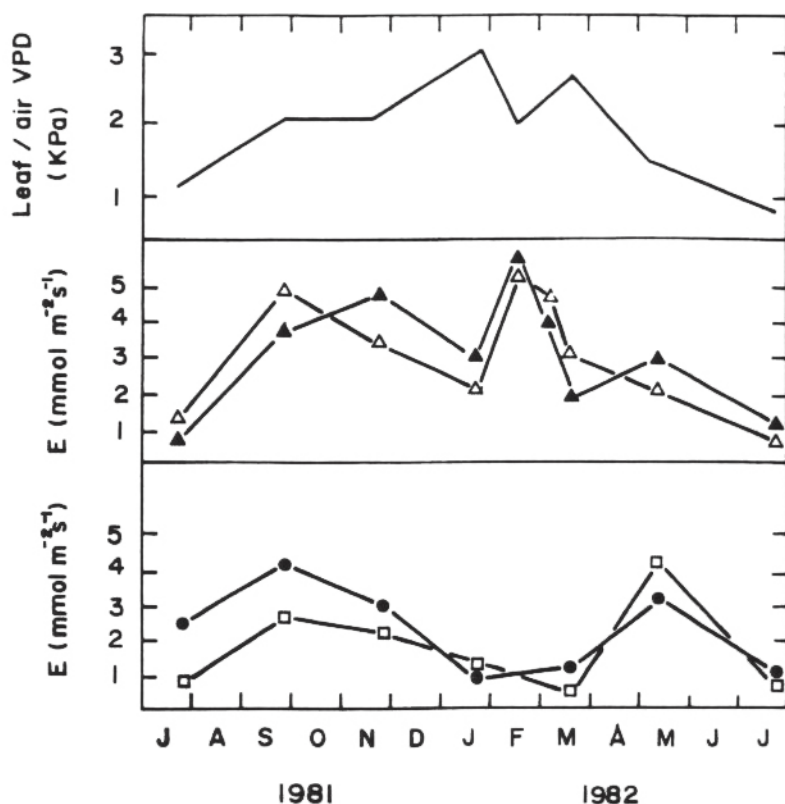


Fig. 2.4. Seasonal courses of leaf to air vapor pressure deficit (Leaf/air VPD), and transpiration rates (E) for *Curatella americana* (Δ), *Byrsonima crassifolia* (\blacktriangle), *Sporobolus cubensis* (\square), and *Andropogon semiberbis* (\bullet). The first two species are evergreen trees and the last two are perennial C4 grasses. (From Goldstein et al., 1986, and unpublished data).

paralleling the decrease of osmotically active solutes before leaf senescence (Goldstein, Catalan and Meinzer, unpublished). The amount of change in the leaf water potential at zero turgor (ψ_{π}^0) during stress is one of the methods used to evaluate the degree of osmotic adjustment in plant tissues. The evergreen savanna trees instead of exhibiting a decrease in ψ_{π}^0 , typical of plants that osmotically adjust, exhibit a reverse trend.

Trees and grasses also differ markedly in their water use efficiency (the ratio of carbon uptake to water loss). Grass species are subjected to water stress during the rainless season and therefore are expected to have a higher

water use efficiency than trees, which usually have an adequate water supply throughout the year. C4 grasses also usually have much higher photosynthetic capacities than savanna trees. The initial differences, furthermore, are augmented by contrasting stomatal aperture effects on CO₂ and water vapor exchange. Leaf conductance to water vapor (g) is closely correlated (at low g 's) with carbon assimilation (Fig. 2.5) but the slope of the relationship is different between grasses and trees. Since for a given value of net photosynthesis, g and therefore transpiration are less in grasses than in evergreen savanna trees, grasses will have higher water use efficiencies. This is clearly shown in Figure 2.5 where the relationships between photosynthesis, transpiration, and leaf conductance are contrasted for Curatella americana and three widespread C4 savanna grasses.

Figure 2.6 summarizes the main traits of water and carbon budgets of selected grasses and trees of neotropical savannas.

3. WATER AND CARBON BALANCE OF EVERGREEN SAVANNA TREES

In addition to their more uniform water supply levels, leaves of mature reproductive trees are also exposed to a more constant temperature regime than grass plants that grow near the soil surface, where higher temperatures can be observed during the daytime. Tree species from different savanna types and different continents seem to have a wide array of morphological and physiological characteristics.

The flow diagram in Figure 2.7 illustrates a few interrelationships between some selective forces of neotropical savanna woody species and adaptive features and mechanisms. The arrows may be considered either as plant responses or as ecophysiological mechanisms. Leaf conductance (a measure of the degree of stomatal aperture) may remain high all day and partial closure of stomata at midday may be considered as a safety valve under very high evaporative demand conditions. Conductance and transpirational fluxes of evergreen savanna trees are generally high even during the dry season. Conductances higher than $0.4 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ have been measured on a few occasions (Goldstein et al., 1986). Only a small proportion of species are known to have conductances over $0.4 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Korner et al., 1979) and only a few cultivated C4 plants and two tropical cultivated trees are reported to approach the extreme value of $1.2 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Grace et al., 1982). In the latter case, however, large leaf size, and therefore a thick boundary layer, seems to partially offset

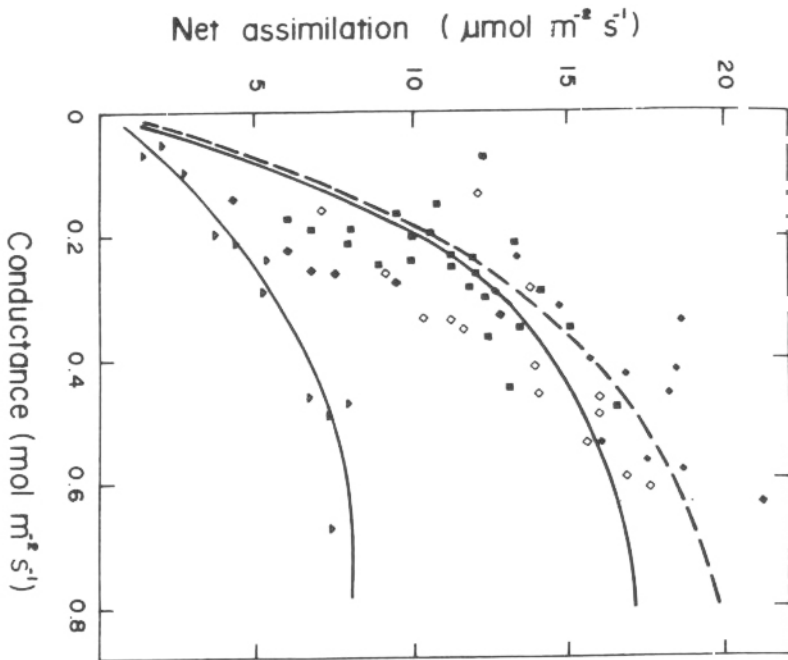
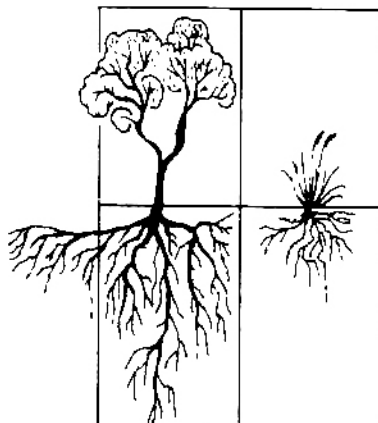


Fig. 2.5. Relationship between photosynthesis, transpiration and stomatal conductance to water vapor for three grass species; *Hypharrenia rufa* (\diamond), *Leptocoriphium lanatum* (\blacklozenge), *Trachypogon vestitus* (\blacksquare), and one woody species, *Muratella americana* (\triangle), measured under constant VDP, leaf temperature and photosynthetic active radiation conditions. Asymptotic lines are mathematical functions fitted to the data. The relationship between stomatal conductance and transpiration is linear and the same for all species. Transpiration must linearly increase with increasing conductance to water vapor at constant VDP. The transpiration axis does not have a scale since the relative differences in water use efficiency do not depend on the exact transpiration values. Adapted from Torres, 1951.

the high stomatal conductance. The adaptive significance of high stomatal conductance and transpiration rates in the

Fig. 2.6. Summary of main traits related to water and carbon budgets of selected savanna grass and tree species.



Seasonal fluctuations in ψ leaves	none	strong
Degree of osmotic adjustment	none	strong
Maximum E ($\text{mmol m}^{-2}\text{sec}^{-1}$)	8-12	8-12
Stomatal sensitivity to VPD	moderate	moderate
Maximum CO_2 uptake ($\mu\text{mol m}^{-2}\text{sec}^{-1}$)	10-12	25-35
Water Use Efficiency ($\mu\text{mol CO}_2/\text{mmol H}_2\text{O}$)	0.8	1-5

sclerophyllous evergreen savanna trees is not readily apparent. Meinzer et al. (1983) and Sarmiento et al. (1985) have suggested that high stomatal conductances may help to maintain a favorable carbon balance, and promote the mass flow of nutrients, particularly the highly mobile cations such as calcium and magnesium. Only in young leaves may partial stomatal closure be important in maintaining an adequate water status (Meinzer et al., 1983).

Under the high evaporative demand conditions prevailing in the savannas, transpirational fluxes do not induce major drops in leaf water potential to below the turgor loss point. In this way CO_2 can be continuously assimilated through partially open stomata. The hydraulic properties of the vascular system contribute to the slow decrease of leaf water potential as transpiration increases

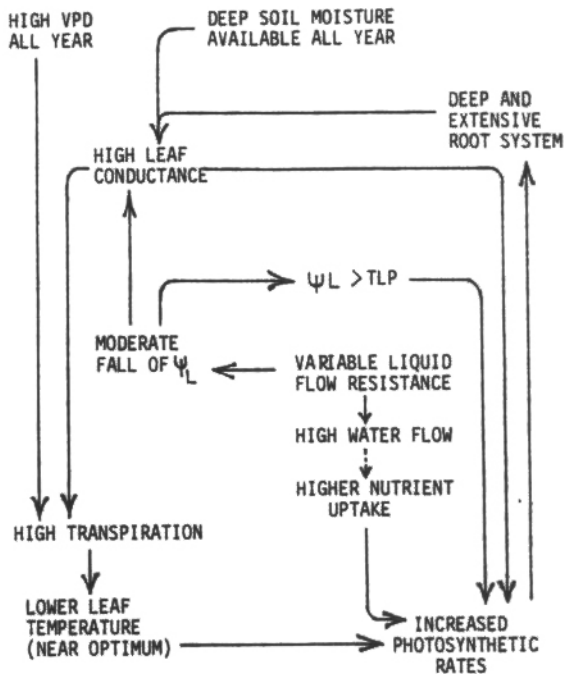


Fig. 2.7. Mechanism contributing to maintain a favorable water balance in woody species of seasonal savannas, and some of their consequences and costs for the carbon and nutrient economy. (Adapted from Sarmiento et al., 1985).

during the day (Meinzer et al., 1983; Goldstein et al., 1986).

High transpiration rates also help to maintain leaf temperature of evergreen savanna trees near the temperature optimum for photosynthesis. Figure 2.8 shows the response of CO₂ uptake to leaf temperature variations of two important savanna woody species. The temperature optimum for photosynthesis is approximately 25°C in Curatella americana and 28°C in Byrsonima crassifolia. These temperatures are several degrees below the 31–33°C average midday air temperature measured in the field. The photosynthetic temperature optima are very narrow in both species. The difference between the temperature optimum and the upper or lower compensation point is about 15°C. Above the optimum, net photosynthesis decreases very rapidly and at 35°C carbon uptake is 50% of the maximum in both tree species. Given that the leaves of these two species are large and that the air temperatures and radiation loads are

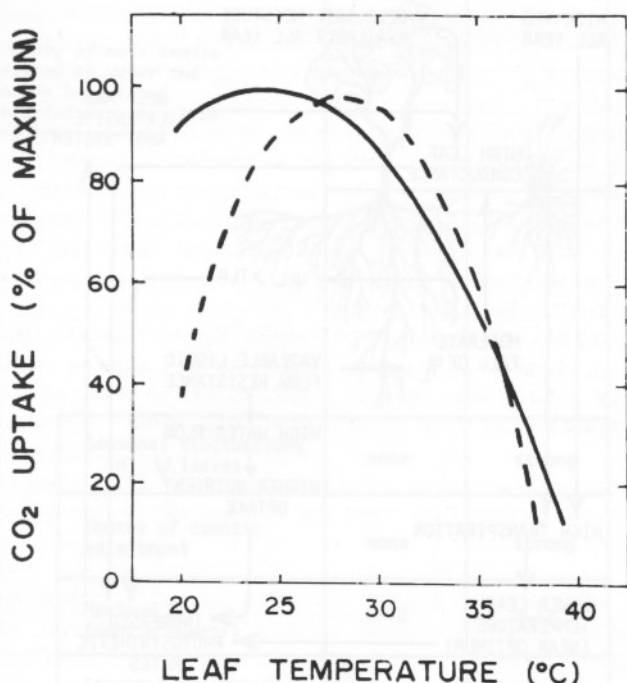


Fig. 2.3. Relationship between carbon uptake and leaf temperature for *Curatella americana* (—) and *Byrsonima crassifolia* (----). Each curve represents second degree polynomials fitted to the data of 8 experiments. (From Goldstein et al., 1986).

usually high under the prevailing savanna conditions, high evaporative cooling is necessary to maintain carbon uptake near the maximum for each species.

The maintenance of an adequate water and carbon balance in evergreen savanna trees implies two costs. One is the investment necessary to develop and maintain extensive root systems in order to have access to available water in deep soil layers during the dry season. The other is a consequence of the permanent access and use of water resources. These tree species do not have the ability to osmotically adjust, by increasing levels of solutes in leaves, when exposed experimentally to water deficits.

What morphological and physiological adaptation could we predict to be the most successful in response to the lengthening of the dry period? While water is continuously available in the subsoil we may predict the occurrence of evergreen trees producing deep and extensive root systems.

Extended dry periods in consecutive years may deplete subsoil water. In this case leaf water potential of trees could decrease below the turgor loss point causing stomatal closure, leaf overheating and reduced growth rates. If the conditions that lead to a decrease of available water in the lower soil layers, such as a decrease in total annual precipitation or an extension of the dry season length, persist, the investment in deep roots may not be profitable. In this case other trait combinations such as deciduous trees or more drought tolerant trees with smaller leaf sizes, might be favored.

To formalize these hypotheses on the most successful strategies of trees under variable water stress conditions we can try to design an exercise where for given morphofunctional traits we predict the environmental conditions in which they may best compete. The above/belowground biomass ratio, leaf size and the temporal pattern of leaf production are key tree characteristics that surely reflect important environmental conditions of savanna ecosystems. If we assume that evergreenness is associated with high root/shoot biomass ratios four regions can be defined in the model depicted in Figure 2.9. Trees with

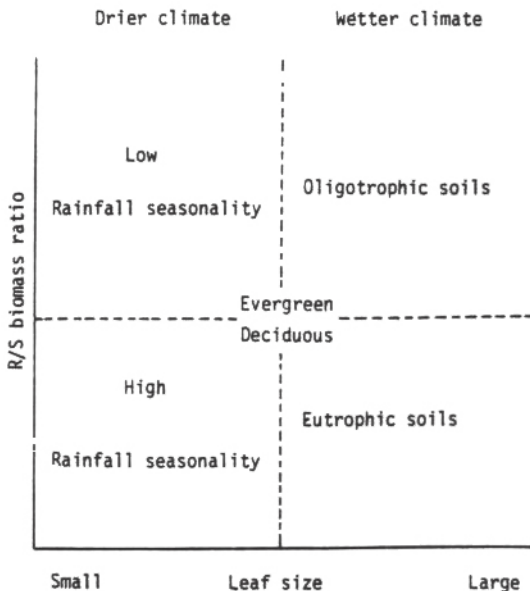


Fig. 2.9. Model depicting environmental conditions in which trees with different combinations of root/shoot biomass ratio, leaf size and temporal patterns of leaf production (evergreen and deciduous) are able to compete.

large leaves and high belowground biomass would be favoured in very well drained, oligotrophic soils where water is continuously available. We are also proposing that deciduous large leafed trees with a relatively small and superficial root system will be selected in environments with a relatively extended wet season and richer soils. Trees with predominantly small leaves would dominate the vegetation in semi-arid climates. In dry sites with a short but very distinct wet season, deciduous trees would be favoured. If precipitation is more evenly distributed, evergreen, drought-resistant woody species would be favored.

Undoubtedly not all the evergreen seasonal savanna trees share the same morphological and physiological traits. Although most of the evergreen tree species have deep root systems and large scleromorphic leaves, there are other tree species that tend to have smaller leaves or leaflets and less extensive root systems. Lower allocation of energy to roots should affect the seasonal behaviour of trees. In this case more drought tolerant syndromes are expected. This is illustrated in Figure 2.10 where daily courses of vapor pressure deficit, leaf temperature, stomatal conductance and leaf water potential of 4 coexisting tree species are depicted for one wet and one dry season day. Casearia sylvestris is the species that exhibits the most negative leaf water potentials at midday, even though conductance values (and therefore transpiration rates) are significantly lower than those of the other tree species, particularly during the dry season day. Two factors account for the lowest water potentials occurring at midday in C. sylvestris. First, the root system does not extend as much into the deep soil layers as do the roots of the other species (the root/shoot ratio is relatively low). Thus available soil water decreases during the rainless period. Second, the leaf-turgor loss point of C. sylvestris is more negative than the turgor-loss point of the other coexisting species. Low ψ_{π} reflects the ability of a species to continue extracting water from a drying soil while maintaining turgor.

4. WATER RELATIONS OF C4 GRASSES WITH DIFFERENT GROWTH PATTERNS

Grasses are the dominant species in the herb layer of all types of tropical savannas. They are also the plants that contribute most to the primary production of these ecosystems and control the possibilities and frequency of fires (Sarmiento and Monasterio, 1983). The diversity of perennial C4 grass species in savanna ecosystems is usually

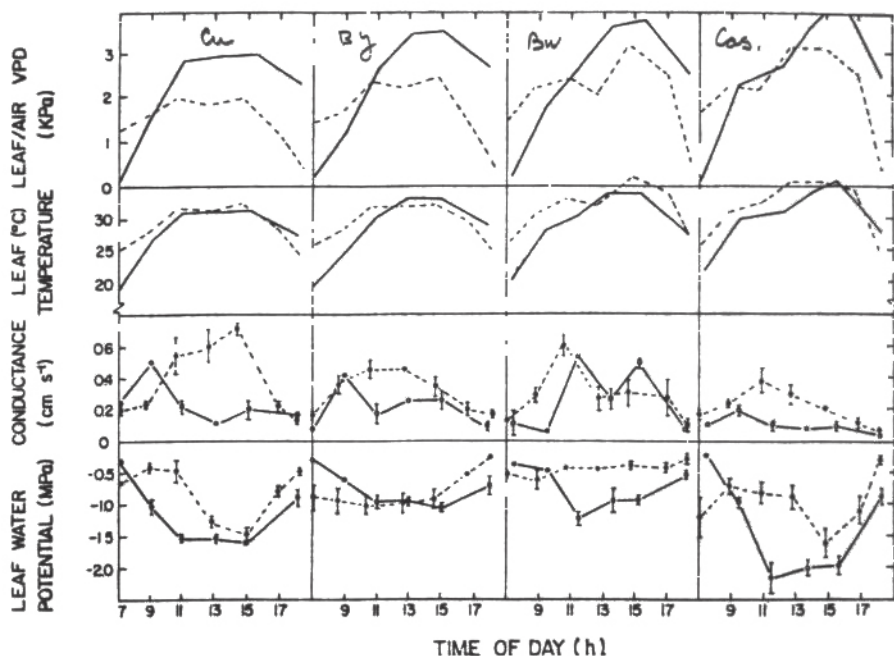


Fig. 2.10. Daily courses of leaf-to-air vapor pressure deficit (VPD), leaf temperature, stomatal conductance and leaf water potential for four woody species during a wet season day (-----) and a dry season day (—). From Goldstein et al., 1986).

very high. Many different species with apparently similar characteristics can coexist in the same community. The patterns of growth and reproduction during the wet season, however, are different. Sarmiento and Monasterio (1983) have suggested that they behave as if a certain temporal division of the niche exists, since some species start to grow with the first rains or soon after a late fire, entering immediately into their reproductive stages. Other species, instead, grow only gradually, develop their shoots slowly, and enter into their reproductive phases towards the middle and end of the rainy season. This apparent temporal displacement in the peaks of growth and reproduction may explain partially the ability of similar grass species to escape competition and coexist in a similar environment. However, this model of growth patterns of perennial savanna grasses does not completely explain all that is known (Silva, this book).

A predictive understanding of the ways in which savanna grasses respond to natural stresses and man-made disturbances should take into account the existence of the great diversity in life history characteristics among grass species. Precocious and early growing species rapidly increase their green biomass when soil water potential may still be low and therefore should be adapted to withstand water deficits. On the other hand "intermediate and late growers" increase their aboveground biomass more gradually during the wet season, when soil water availability is high. We want to consider the relationships between drought resistance mechanisms and growth patterns in perennial grasses, in particular the ecophysiological traits allowing grass species to withstand different drought conditions.

Our results indicate that each phenological group has different ecophysiological attributes, and suggest that these attributes possess an adaptive value. Precocious species tend to maintain lower transpiration rates and higher turgor pressure than intermediate and late growing species (Fig. 2.11). Maintenance of positive turgor pressures should allow the precocious species a continuous growth under high water-stress conditions.

Precocious grasses seem to have higher water use efficiencies probably by limiting water loss through partial stomatal closure (Fig. 2.12). The leaf photosynthetic characteristics of these species are typical of tropical C4 grasses (Torres, 1985). Maximum photosynthetic rates at high photon flux densities and low vapour pressure densities are between 25 and 32 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and do not differ significantly among species. The stomata of these species also exhibit similar sensitivity to external air humidity variations. In general, plants using the C4 photosynthetic pathway have high photosynthetic rates owing, in part, to their lack of photorespiration. Furthermore, since photosynthesis is saturated at a relatively low internal carbon dioxide concentration, partial stomatal closure may not result in decreased CO₂ uptake, although transpiration is reduced. Mooney and Gulmon (1979) have found that for many desert plants closure of stomata may not result in an increase in water-use efficiency, since leaf temperature may rise, as a consequence of lower evaporative cooling, above the optimum for photosynthesis. Small differences in stomatal conductances, however, are not expected to produce significant differences in leaf temperatures among savanna grasses.

The observed differences in gas exchange characteristics would help explain the higher growth rates

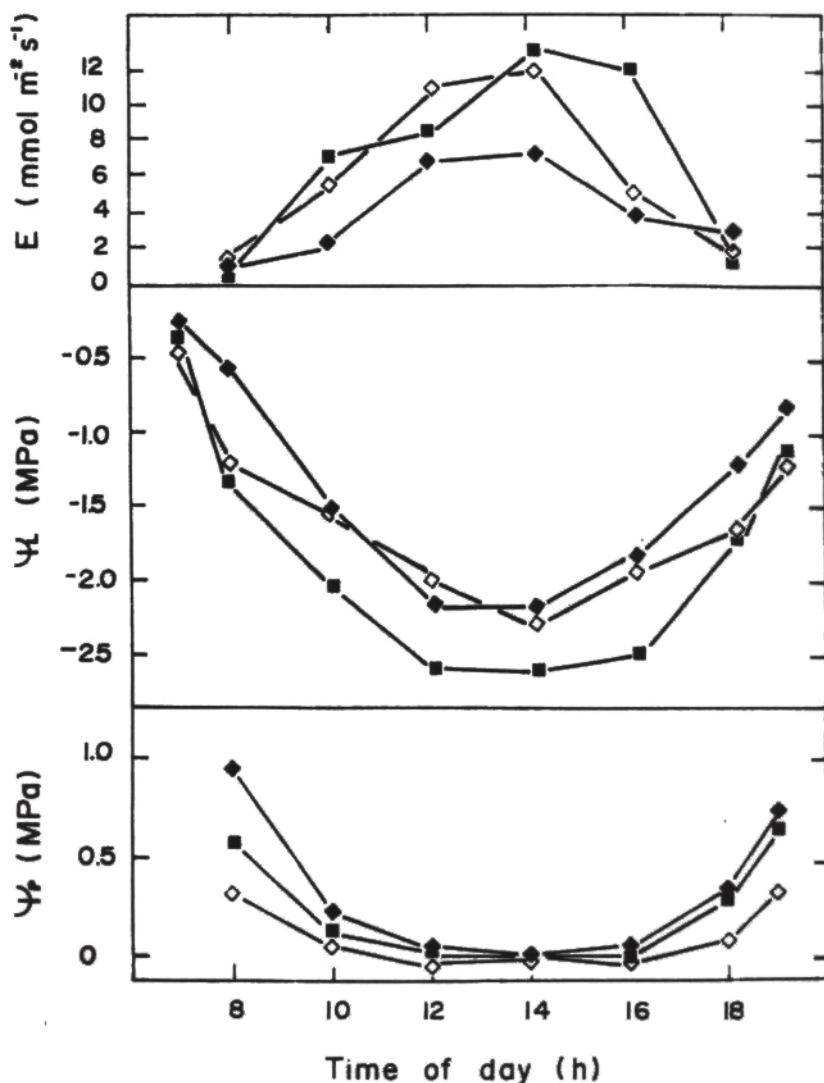


Fig. 2.11. Daily courses of transpiration rates (E), leaf water potential (Ψ_L) and turgor pressure (Ψ_t) for *Hypharrena rufa* (◇), *Trachypogon vestitus* (■) and *Leptocoriphium lanatum* (◆), three perennial C4 grass species. *Leptocoriphium lanatum* is a precocious species. (Adapted from Torres, 1985).

of the precocious species during the dry to wet season transition period. Even small but significantly higher

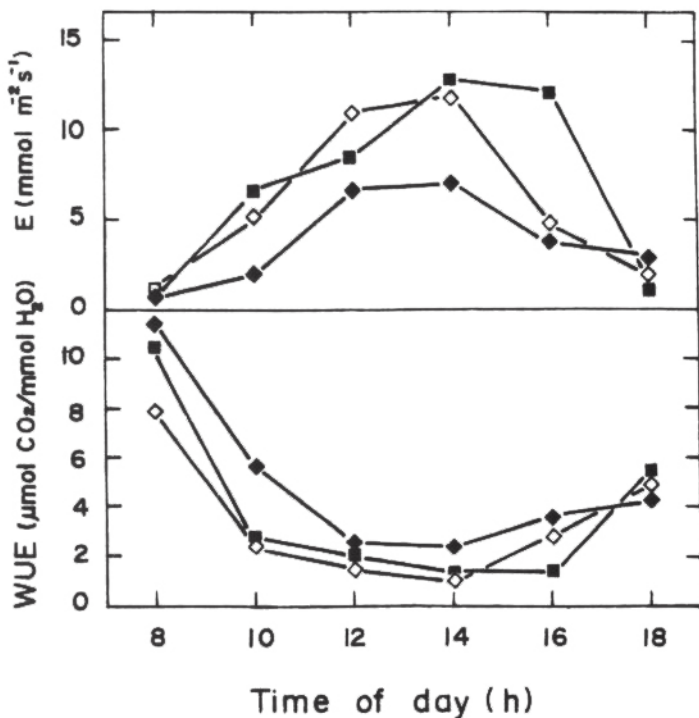


Fig. 2.12. Daily courses of transpiration (E) and Water Use Efficiency (WUE) for *Hypharrenia rufa* (◇), *Trachypogon vestitus* (■) and *Leptocoryphium lanatum* (◆). Adapted from Torres, 1985.

water use efficiencies would partially explain the ability of the precocious species to sustain active growth under stronger water stress conditions than these other species. We agree with Baruch et al. (1985), however, that the differences in ecological behaviour among perennial C4 savanna grasses may also be determined by the proportion of photosynthates allocated to leaves and underground organs, and hence by differences in architectural patterns. The higher growth rates of the precocious species at the beginning of the wet season may also be associated with the higher proportion of photosynthates allocated to roots and storage belowground organs (Fig. 2.13). Underground reserves in precocious grass species are used in leaf construction and plant development during the initial burst of growth (Maldonado, 1983). Precocious grass species such as *Elyonurus adustus*, *Sporobolus cubensis*, and *Leptocoryphium lanatum* have relatively high root/shoot

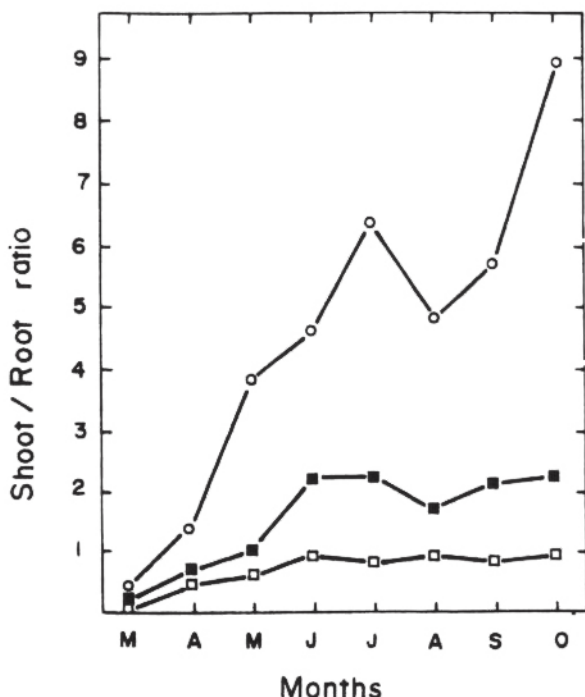


Fig. 2.10 Shoot/Root biomass ratios of *Hypharrena rufa* (○), *Trachypogon vestitus* (■) and *Sporobolus cubensis* (□) during the wet season months. Plants were grown in pots. (From Maldonado, 1985).

biomass ratios and conspicuous underground storage organs while intermediate and late growing species allocate a higher proportion of photosynthates to the aerial portions of the plant.

5. A MODEL OF SAVANNA STRUCTURE BASED ON WATER RELATIONS OF GRASSES AND TREES

The sharp delimitation of contrasting seasons characteristic of the water regime of seasonal savannas arises primarily from rainfall distribution. Most seasonal savannas occur under a tropical wet and dry climate where the year appears clearly divided into two more or less equally extended seasons: one almost rainless, the other with high peaks of monthly rainfall frequently reaching (in South American savannas) 300 mm or more (Fig. 2.1). With an annual precipitation between 1000 and 1800 mm falling with this distribution pattern, water fills in the whole soil reservoir during the rainy season leaving a surplus that

drains and feeds the water table. This annual refilling of the entire soil profile is one of the prerequisites for the occurrence of tree savannas.

Besides rainfall, the water budget in seasonal savannas depends on several environmental and biotic factors that regulate rainfall interception, evaporation, run off and infiltration. Furthermore, the fate of the infiltration water depends on the capacity of the soil reservoir and on the rate of water consumption by the vegetation. Since few continuous field measures of these parameters during several annual cycles exist, detailed water budgets of seasonal savannas rely on very scanty information. Table 2.1 shows the annual water budget in a tree savanna site of the Sudan type, at Korhogo, Ivory Coast, where annual rainfall attains 1353 mm (Roose, 1979, 1981). The two points we want to emphasize concerning this budget are: a) about 95% of the total rainfall enters the soil, (the precise percentage being strongly dependant on slope and plant cover); b) about 80% of the annual precipitation is recycled through the vegetation, that is, the real evapotranspiration has a 29 year mean of 1064 mm and varies only slightly with total annual rainfall.

Table 2.1 *water balance of a savanna site at korhogo, Ivory Coast. After Roose 1979*

Rainfall	mm	1353
Potential	mm	1660
Evapotranspiration	%	(123)
Run off	mm	40.6
	%	(3)
Real	mm	1064
Evapotranspiration	%	(78.7)
Deep drainage	mm	248
	%	(18.3)

One of the most fundamental hypotheses concerning the behavior of plant species in seasonal savannas postulates the spatial division of water resources between shallow-rooted perennial grasses and deep-rooted evergreen trees (Sarmiento, 1984; Knoop and Walker, 1985; Sarmiento et al., 1985). This two layer model considers that even if there is a partial overlapping in the water resources used by trees and grasses, each vegetation component is the superior competitor in a different layer: grasses in the topsoil, woody species in the subsoil (Knoop and Walker, 1985). The phenological behavior of the two growth forms,

particularly the long semi-rest phase of perennial grasses during the dry season when evergreen trees are producing their annual leaf crop (Sarmiento and Monasterio, 1983), together with the relatively constant transpiration rates of trees throughout the year (we have already discussed) seem to support the model.

Taking into account the available soil water together with the transpiration fluxes in grasses and woody species, a more quantitative model may be obtained, depicting the relative role of each vegetation layer and predicting tree densities under various water regimes. To this controlling factor of water availability, other influences may be added to obtain a more satisfactory picture of the overall balance between grasses and trees.

The first assumption is that available water stored in the soil throughout the year amounts to about 80% of annual rainfall. This figure starts from data already discussed. The second assumption relates to tree transpiration. Although it differs according to species and weather conditions, a good average obtained from our data on tropical American evergreen savanna trees (Sarmiento et al., 1985; Goldstein et al., 1986) is $200 \text{ mg H}_2\text{O} \cdot \text{cm}^{-2} \cdot \text{day}^{-1}$. This daily rate represents a total amount of 730 mm of water transpired per cm^2 leaf surface per year. Taking as a starting point the assumption that soil water is equally distributed between the two life forms, that is that woody vegetation consumes half the available water, this represents from 400 to 700 mm for a total rainfall varying from 1000 to 1800 mm. With this volume of water, under the transpiration rate just considered, a mean leaf area of $400/730$ to $720/730$ could be supported, that is an average LAI throughout the year roughly between 0.5 and 1. To translate these figures to physiognomic terms, we may consider that the dominant low trees in seasonal savannas have leaf area indexes of 4 to 6. With the obtained mean leaf area, a total cover of the tree layer between 8% and 25% is obtained, which in fact represents a range frequently found in seasonal savannas. Changing the ratio of soil water used by trees and grasses, the whole range of physiognomies occurring in seasonal savannas may be obtained, but even utilizing all the soil water reservoir, leaving none to the grasses, the tree cover does not surpass 40 or 50%, pointing out that under the environmental conditions where seasonal savannas occur it is not possible to reach a continuous forest cover of savanna evergreen trees. Their transpiration rates hinder the possibility of a closed woody vegetation.

Few data are available concerning transpiration rates of savanna grasses under field conditions. For our model we take a figure of $130 \text{ mg H}_2\text{O cm}^{-2} \text{ day}^{-1}$ as a representative average (Cresswell et al., 1982; Goldstein and Sarmiento, in prep.). This rate corresponds to 475 mm transpired per unit grass leaf area per year. Spending half the available water, the mean green leaf surface that could be sustained throughout the year varies from 400/475 to 720/475, that is roughly from almost 1 to 1.5. We know that the maximum LAI attained by the herb layer in seasonal savannas stands around 4 to 5, while the minimum LAI for burned savannas is almost zero. Hence the obtained yearly average may represent a realistic mean for this layer in seasonal savanna ecosystems.

The figures produced by the model suggest that the division of water resources between trees and grasses will allow a continuous cover of living grasses, at least during the wet season when the aboveground living grass biomass reaches its peak, but will permit just a rather sparse tree cover. Both features characterize seasonal savannas all over the tropics.

Besides the limitation imposed by water availability, other factors such as fire, grazing and competition certainly operate to regulate tree density. Long term observations of fire-protected savannas show that the density of evergreen woody species increases (San Jose and Farinas, 1983). According to their data in the Calabozo savanna in Venezuela, after 16 years of fire exclusion evergreen trees had a ten-fold increase in density. Furthermore, the density of deciduous trees, rarely found on burnt savannas, increased rather explosively reaching values similar to those of evergreens. It may be suggested then that evergreen trees are handicapped by recurrent burning while deciduous species are unable to grow under fire conditions. Overgrazing by cattle strongly reduces grass cover while, according to our observations, seems to favor tree expansion. However systematic data are necessary to confirm or reject this preliminary observation.

Competition for topsoil water between herbs and tree seedlings may be a factor negatively affecting the survival of tree species and maintaining a permanent pressure against the establishment of new individuals. The positive effect of heavy grazing on the survival of tree seedlings is therefore a logical consequence.

To summarize, our model of savanna structure tries to explain the balance between woody and herbaceous species emphasizing the limiting character of water availability,

even considering that the soil water resources are spatially divided between the two plant strategies. The water factor imposes an upper threshold to the total standing biomass of green leaves and hence to tree density. Fire and competition contribute to maintain these populations below this threshold, and overgrazing may have an opposite effect.

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