ADAPTIVE STRATEGIES OF WOODY SPECIES IN NEOTROPICAL SAVANNAS

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CONTENTS

I. INTRODUCTION

Few tropical species have to overcome such diversity of external constraints in each annual cycle as do perennial species in tropical savannas. Among these constraints one may list: permanently high air and soil temperatures, alternating periods of high and low water availability, very poor soils, recurrent burnings and continuous predation. Members of two contrasting life forms, tussock grasses and woody evergreens, have been the most successful under these pressures, becoming dominant in the two distinct structural layers that characterize these formations. Perennial bunch grasses dominate

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the continuous herb layer while evergreen trees constitute the major life form in the more or less sparse stratum of woody plants. We wish to discuss here the major morphological, phenological and functional features that characterize as a whole one of these groups: the woody evergreens. We consider on the one hand the various selective pressures possibly contributing to model these responses, and on the other hand the ecological and evolutionary meaning of these characteristics as significant components of their overall strategy.

Plant adaptations may be based on any aspect of the life cycle and on whatever functional process, for example, the architectural model, patterns of allocation of nutrients and reserves, phenological strategies, assimilatory and biochemical pathways. Each mechanism or process may contribute to the optimization of resource utilization. In this paper we discuss characteristics of savanna trees with regard to water economy, nutrient budget and carbon gain.

Although the concept of tropical savanna includes a wide array of related ecosystems, the woody species characteristic of them might well be considered as representatives of the stress-resistant strategy in the sense of Grime (1977). Given the sparse nature of the woody layer and the exploitation of different spatial niches by herbs and trees (Sarmiento, 1984; Walker & Noy-Meir, 1982), competitive selection seems to be negligible in most savannas. At least in extensively grazed communities, the major disturbance is periodic burning, although this disturbance may also be considered as a particular case of recurrent environmental stress. Savanna trees, thus, may be considered as comprising a wide group of stress-adapted species modelled by a complex array of interacting environmental strains.

Increasing knowledge of the ecological behaviour of a few savanna woody species permits some generalizations on how they may maintain favourable water, nutrient and annual carbon budgets. Although our knowledge is far from being satisfactory and many gaps still remain, we think it of value to construct an integrated model that might link selective pressures with adaptive strategies. We hope that such an approach contributes to a further understanding of both the functioning of the savanna ecosystem and the ecological rationale for the adaptive syndrome of attributes that distinguish its woody species.

General models on these principles have already been worked out by Mooney & Dunn (1970) for woody plants under Mediterranean climates, and a cost–income model for desert species has been discussed by Orians & Solbrig (1977). The contrasting features of competitive–ruderal vs nutrient–stress strategies as determined by nutrient availability were considered by Chapin (1980), while Gray (1983) gives two models of nutrient use representing the strategies of two of the dominant shrubs in the Californian chaparral and in the coastal sage scrub respectively. In tropical savannas either very general interactions have hitherto been suggested (Bourlière & Hadley, 1983), or some specific ecological processes have been analysed through simulation or quantitative models, such as those produced for the Nylsvley savannas in South Africa (e.g. energy budget (Jager & Harrison, 1982), nitrogen flow (Bate & Gunton, 1982), litter decomposition and trophic ecology (Gandar, 1982; Morris, Bezuidenhout & Furniss, 1982)). In a comparable study, Walker & Noy-Meir (1982) modelled the conditions of resiliency and stability of savanna ecosystems with particular reference to plant–herbivore interactions. Our aim is more akin to the aforementioned models on nutrient economy and to the cost–benefit

analysis of Orians & Solbrig than to the more quantitative approach of the Nylsvley project workers.

Our generalized model of adaptive strategies in seasonal savannas corresponds to the commonest type of morphofunctional adaptation found in the woody species of this ecosystem. It is based primarily on data from four of the most widespread and abundant tropical American savanna trees: *Curatella americana* L., *Byrsonima crassifolia* (L) HBK, *Bowdichia virgilioides* HBK and *Casearia sylvestris* Sw., together with the available information on other savanna woody species. It is obvious, however, that many departures from this model could be found within the whole of the woody flora of tropical savannas, and that ultimately each species must be considered as representing a peculiar and unique evolutionary history and response. However, the model presented here try to account for and synthesize many of the known facts regarding tropical savanna trees and thus may be useful both as an explanation of the existing evidence and as a guide to further research.

There seems to be general agreement on the relative advantages of woody evergreens compared with deciduous species in ecosystems subjected to strong climatic or soil constraints (e.g. peat bogs, swamps, mediterranean scrubs, and subtropical woodlands) (Small, 1972, 1973; Schlesinger & Chabot, 1977; Mooney & Rundel, 1979; Chapin, 1980; Goldberg, 1982; Gray, 1983). Chabot & Hicks (1982) provide an excellent discussion on adaptive values of various leaf-span strategies. The selective advantages of evergreenness may be understood in terms of a cost–benefit analysis either of carbon gains or of nutrient-use efficiency. Tropical savannas afford an additional system, quite divergent in many aspects from those hitherto studied, where the competitive ability of evergreens over deciduous may be further analysed.

II. TROPICAL SAVANNA ECOSYSTEMS

Savanna ecosystems, characterized by a continuous grass layer dotted with low trees or shrubs, occupy a significant proportion of the world's tropical belt (UNESCO, 1979; Bourlière, 1983; Huntley & Walker, 1982). In Brazil the vernacular terms *cerrado* and *campo* are commonly used. Likewise, when referring to open vegetation in East Africa, Pratt, Greenway & Gwynne (1965) avoid the term savanna and replace it with a series of physiognomic types such as woodland, bushland, bushed grassland and wooded grassland. All of these types are currently included within the concept of tropical savanna ecosystem.

(1) *Savanna types*

A prime distinction among tropical savannas sets apart dry and humid formations, the dry types under semi-arid climates (BS climates of Koeppen, 1932), the humid types under wet seasonal climates (mostly AW climates of Koeppen). There are many crucial differences between these two contrasting types of ecosystem. With regard to the woody flora the most conspicuous difference lies in the fact that trees and shrubs in humid savannas are mostly evergreen, with medium-sized sclerophyllous leaves, while spines and succulence are almost unknown. Woody species in the dry formations are either deciduous or small-leaved evergreens, where many xerophyllous features, such as spines, aphylly, or succulence, are well represented.

A further distinction recognizes divergent ecological types within humid savannas,

on the basis of annual water availability or seasonality (Sarmiento & Monasterio, 1975; Sarmiento, 1983). *Seasonal savannas* are defined as the savanna ecosystem where, in each annual cycle, an extended period (3–6 months) with low soil–water potentials in the upper soil layers alternates with another where water is continuously available to herbaceous and woody plants. This seasonality in the amount and, as we will see later, in the spatial distribution of water resources, is marked by the dominance of certain life forms and plant strategies able to withstand such seasonal stress. Furthermore, in contrast to the hyperseasonal savannas, seasonal savannas do not suffer extended periods with an excess of water in the upper soil levels that could lead to water saturation, anaerobiosis, or reductive microenvironments.

(2) *Seasonal savannas*

The structure and function of the seasonal savanna ecosystem have been analysed in few tropical areas. The Lamto savannas in the Ivory Coast constitute perhaps the world's best-known tropical savannas (Lamotte, 1978, 1979, 1982; Menaut & Cesar, 1979), but other sites where ecological research is actively in progress include the Nylsvley savanna in South Africa (Huntley & Walker, 1982), the Brazilian *cerrados* (Ferri, 1963; Eiten, 1972; Coutinho, 1982), and the Venezuelan plains or *llanos* (Medina & Sarmiento, 1979; Medina, 1982; Sarmiento, 1984). Although we will often refer to these results during our discussion of adaptive responses of seasonal savanna trees, we will give particular emphasis to tropical American species and ecosystems because from an ecological viewpoint neither of the best-known African ecosystems, Lamto and Nylsyley is strictly comparable with the seasonal neotropical formations. Lamto is located so close to the rain forest border that it has been considered not as a primitive but as a forest-derived savanna, while the South African site at Nylsvley lies at the very border of the tropical area and in this case other environmental factors, such as low winter temperatures, begin to operate as selective forces against savanna species.

Several environmental conditions must co-exist to give rise to the soil–water regime characteristic of seasonal savannas. The occurrence of a distinctly seasonal wet and dry tropical climate appears to be one of the two prerequisites favouring this ecosystem, since it does not normally occur either under dry climates in the sense of Koeppen (1932) or in ever-wet regions (Sarmiento & Monasterio, 1975; Nix, 1983). Fig. 1 shows three climatic diagrams for savanna localities in tropical America, Africa and Australia. Notice the basic similarities in rainfall regimes, temperatures, and therefore in soil–water regimes. The second necessary condition for the occurrence of seasonal savannas relates to soil drainage. Because of heavy rainfall occurring during several consecutive months, this system could exist only on well- or moderately well-drained soils. Seasonal savannas, thus, are found either on slopes with good drainage or, more frequently, on higher topographic positions in plains, where relief together with a gentle slope favour rapid infiltration and the percolation of excessive rainfall. In this way, seasonal savannas are not found either in bottomlands where rains may accumulate or on heavy soils that may retard or impede the evacuation of excess water.

The combination of an alternating wet and dry climate with well-drained soils produces a series of ecological consequences that influence both the morphofunctional responses of plants and the structure and functioning of the whole ecosystem. In the first place, heavy rainfall during the wet months induces rather high soil–water
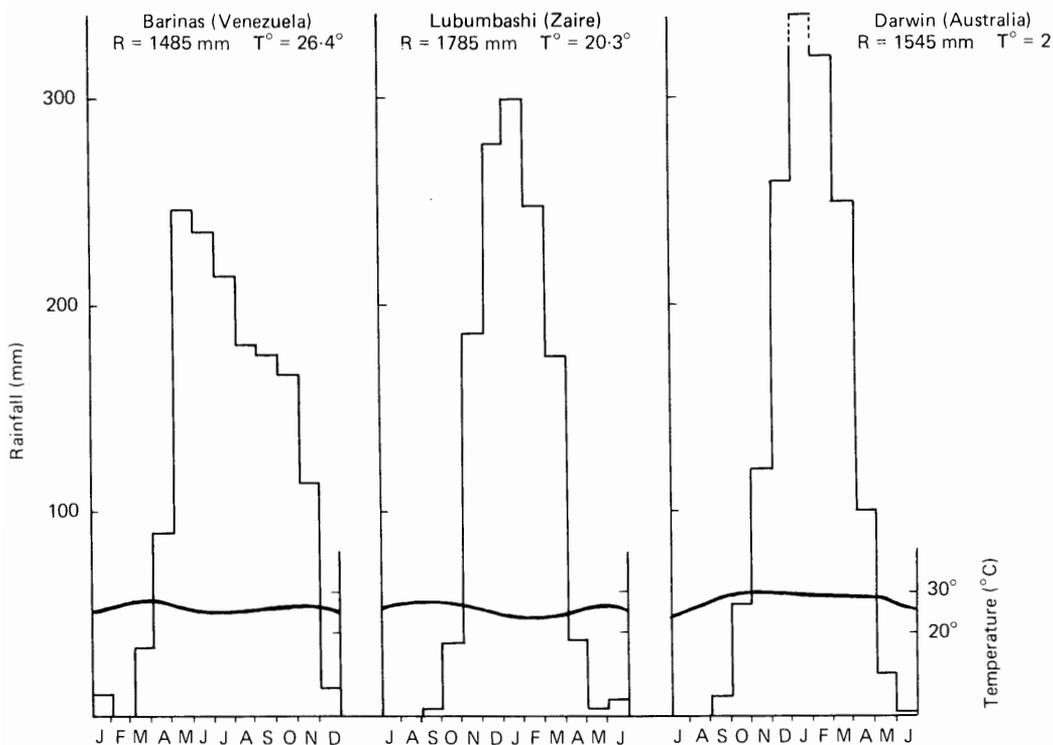
Fig. 1. Climadiagrams for a South American, an African and an Australian locality with typical wet and dry tropical climate. In spite of the peculiarities of each climate, notice their basic similarity in having a quite pronounced dry season (4 to 7 months long) followed by several consecutive months with heavy rainfall. Notice also the slight variation in monthly temperature during the year. Annual precipitation (R) and mean annual temperature (T°) are also indicated in each locality.

potentials throughout the rainy season. Fig. 2 shows the seasonal changes in soil–water content and soil–water potential in a tree savanna in the Veneuelan llanos. These data confirm the conclusions of previous studies on water economy of savanna ecosystems that although these soils dry out when the rains end, at a certain depth, depending on the particular conditions of climate, topography and soil, available water persists throughout the climatically dry season (Eden, 1964; San José & Medina, 1975; Sarmiento & Vera, 1977; Alvim & Silva, 1980; Sarmiento, 1984). In the case shown in Fig. 2, already at 70 cm soil–water potential remains above −14 bars, when the upper layers reach water potentials well below −15 bars.

Water surplus above the field capacity of the soil percolates more or less rapidly, to become stored in deep layers or to feed the water table, according to the topography and to the geomorphology of the land surface. During the rainless season the soil begins to dry out from the top downwards, since the root biomass of herbs and grasses is chiefly concentrated in the uppermost 20 or 30 cm (Sarmiento & Vera, 1977; Menaut & Cesar, 1982; Sarmiento, 1984). Soil water potentials in these upper levels may become quite negative. This fact implies that only those shallow-rooted species able to extract water under low soil–water potentials can continue to transpire actively during the dry season.
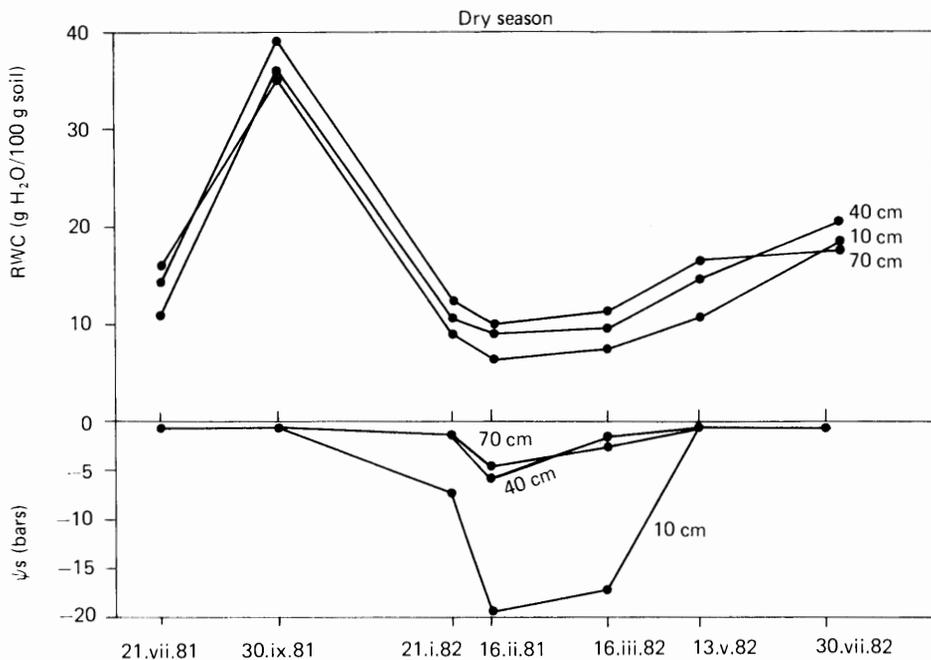
Fig. 2. Seasonal variations of relative soil water content (RWC) and soil water potential (Ψ_L) in a seasonal savanna of the Venezuelan llanos (Hato Palma Sola). Each data point is the mean of five measurements.

The deeper soil levels lose their water more slowly due to the lower root density of woody species, spaced in a larger soil volume, allowing thus the persistence of less negative soil–water potentials in the root zone of deep-rooted woody species.

Another distinguishing feature of the seasonal savanna environment is consistently high evaporative demands. Under a warm tropical climate with daily air temperatures ranging from 22° to more than 35 °C (Fig. 3), daily evaporation is high throughout the year, but still higher under the clear skies and the high radiation of dry-weather days (Fig. 4). To confront this evaporative demand during the rainless season, savanna plants must rely on some permanent water resource, since otherwise only annuals or perennials with a rest phase might survive such water stress (Monasterio & Sarmiento, 1976). Our hypothesis then is that woody perennials of seasonal savannas, which actively transpire throughout the year, exploit water resources stored in deeper soil layers, beyond the level reached by herbs and grasses.

A second major consequence of the tropical seasonal 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 decalcification, followed by desaturation, acidification and argillation. If these processes proceed for a long time, ferralization or latosolization will occur, leading to the complete weathering of primary minerals with formation of kaolinitic clays and sesquioxides (Buring, 1970). Depending on total rainfall, infiltration, soil temperature, type of parent material, plant cover and time, soils will become progressively impoverished with age due to the simultaneous destruction
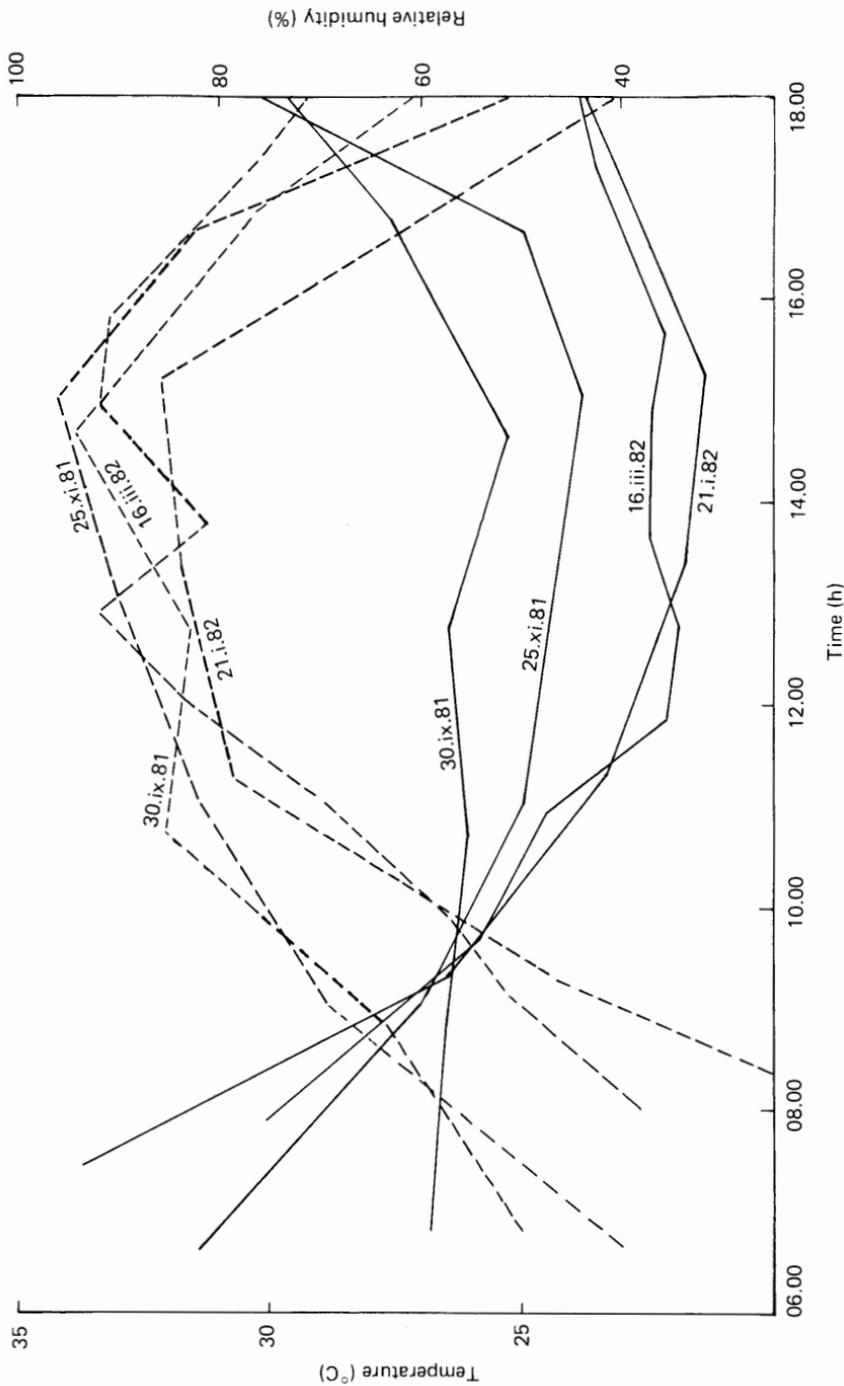
Fig. 3. Daily cycles of temperature and humidity in days of the wet and dry seasons in a savanna site of the Venezuelan llanos (Hato Palma Sola).
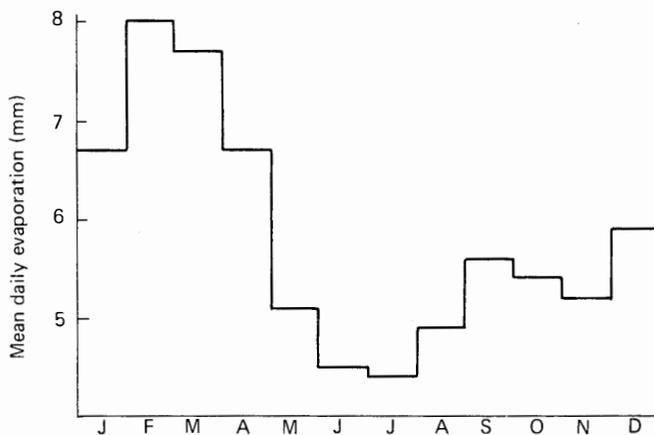
Fig. 4. Mean daily pan evaporation in Barinas, a savanna site of the Venezuelan llanos. Although evaporation remains high all year, maximal values are attained during the dry season (December–April).

of the cation exchange complex and to its accentuated desaturation. In old soils, whether ferruginous (*Ultisols*) or ferralitic (*Oxisols*), the mineral fraction retains very few nutrients, with most of the cation exchange sites becoming occupied by aluminium. In this case the soil nutrient status depends almost exclusively on the amount of organic matter. Table 1 gives some figures indicative of the nutrient status of seasonal savanna soils. As we may see, the available cations, as well as phosphorus and nitrogen, are about two orders of magnitude below their values for normal agricultural soil. To grow under these conditions, plant species must be able to tolerate high acidity, high concentration of exchangeable aluminium and very low pools of most nutrients. This oligotrophic or dystrophic nature of tropical savanna soils is considered to be one of the key environmental features determining the occurrence of savannas, particularly on very old surfaces dating from the Tertiary or the Early Quaternary where soils have reached their most advanced stages of evolution (Alvim & Araujo, 1952; Arens, 1958; Hills, 1969; Cole, 1968, 1982; Askew *et al.* 1971, Sarmiento, 1984).

A third ecological consequence of the seasonal savanna climate derives from the combination of an extended dry season with a continuous grass cover that dries out during this rainless period. This large amount of standing dead phytomass greatly increases the possibilities of combustion. Thus, for instance, in a Venezuelan savanna at the end of the dry season, we determined that standing dead phytomass represents 70% of total above-ground plant material, or an accumulation of straw of about 500 g m^{-2}. Hence it may be suggested that seasonal savannas have evolved under the influence of recurrent fires which generally occur towards the end of the dry season, when the accumulation of fuel is greatest, the standing dead biomass drier and electric storms perhaps more frequent. Fire consumes the above-ground biomass of herbs and half-woody species, as well as that of tree saplings and juveniles. It also produces several morphological and functional effects on mature trees. Thus periodic burning represents a strong disturbance that savanna populations have to overcome in order to persist. Moreover, burning is also responsible for the loss of volatile elements, such as nitrogen and sulphur, reinforcing in this way the nutrient stress characteristic of the ecosystem (Medina, 1982; Gillon, 1983).

Table 1. *Some physical and chemical characteristics of the soil under a seasonal savanna in the Venezuelan llanos (Hato Palma Sola). Figures are means for ten soil profiles*

Soil layer (cm)	pH	Organic matter (%)	Clay (%)	P (ppm)	c.e.c. meq/100 g	Ca	Mg meq/100 g	K	Base saturation (%)
0–10	4·9	1·98	27	2·2	3·50	0·06	0·05	0·06	4·5
10–50	5·1	1·33	32	1·6	2·98	0·01	0·02	0·04	2·5
50–80	5·1	0·86	34	1·3	2·87	0·01	0·02	0·03	2·5
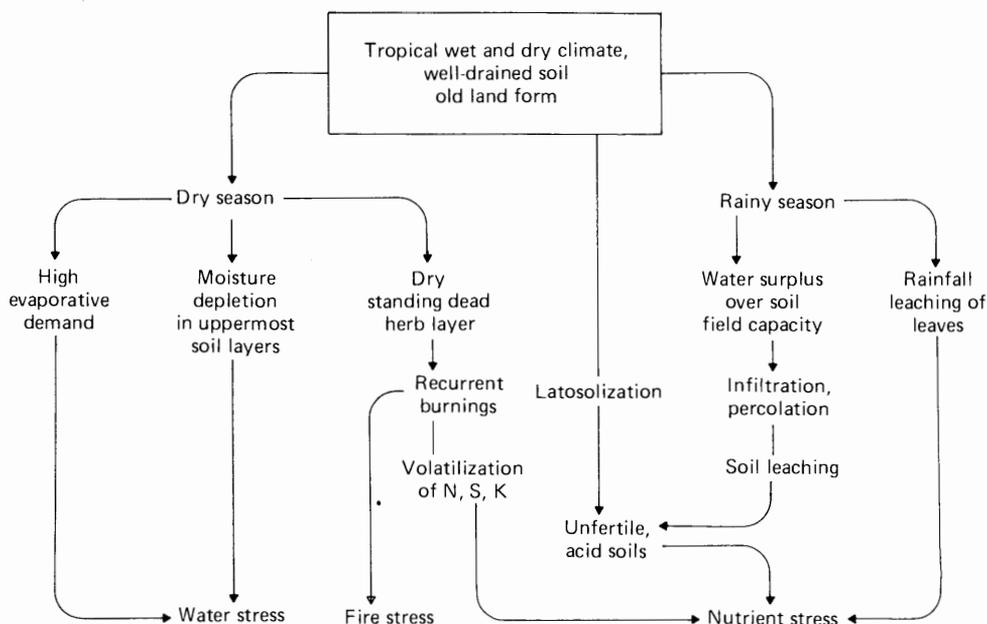
Fig. 5. Major ecological consequences arising from climate, soil and site characteristics in seasonal savannas.

We see then how, due to the combination of certain climatic and soil features, the strong environmental constraints which characterize the seasonal savanna ecosystem originate. Seasonal variation in water availability, high evaporative demand throughout the year, low nutrient content of soils and recurrent fires, all contribute to the formation of these environmental pressures. Fig. 5 summarizes the causal chains leading from major environmental characteristics to the selective pressures acting upon perennial savanna species. We shall now consider the various morphological mechanisms by which savanna species may resist these environmental constraints. Considered together, these characteristics surely constitute a peculiar resistance syndrome forming a significant part of the adaptive strategy that has allowed woody taxa to evolve and persist, with great evolutionary and ecological success, as one of the dominant life forms in this ecosystem.

III. THE ADAPTIVE SYNDROME OF SAVANNA WOODY SPECIES

(1) *Plant size and form*

Both from the viewpoint of their gross morphology and the anatomical features of trunks and leaves, savanna woody species show peculiar traits that set them apart from the woody flora of any other major tropical ecosystem (Eiten, 1972; Menaut, 1983; Sarmiento & Monasterio, 1983). First, savanna trees rarely grow more than 8 or 10 m high, being most frequently within the height range of 3–8 m. Thus, compared with canopy trees in every forest type, savanna species have a much lower total phytomass, maybe in the same range of low, understorey forest trees. On the basis of some data available for the Nylsvley savanna in South Africa (Huntley & Morris, 1982; Rutherford, 1982), the average dry weight per tree ranges from 1 to less than 100 kg. It seems that very seldom do these trees attain a dry weight of more than a few hundred kilograms. This seems logical since, due to the lack of competition for light in the savanna open canopies, there is no selective pressure to increase tree height above a certain minimum threshold determined probably by the height of the herb layer and by the height normally reached by fire.

Greater bark thickness of savanna trees as opposed to forest trees has been noticed in both American and African savannas. Ferri (1961, 1969) showed some striking illustrations of thick-barked trees in the Brazilian cerrados, with most of the species showing a corky bark. Similarly, three out of four of the species we are studying intensively: *Curatella americana*, *Bowdichia virgilioides* and *Casearia sylvestris*, have a remarkably thick bark. This morphological trait has been considered as promoting resistance to fire (Ferri, 1961; Brockman-Amissah *et al.*, 1980; Menaut, 1983), although those savanna trees lacking this protection are none the less fire-resistant.

A third morphological feature apparently shared by many of these trees, though unfortunately one not easily observed nor quantified, is the remarkable development of the below-ground organs, a feature which sharply contrasts with the low aerial biomass. Early observations on the tree species in the Brazilian cerrados pointed out this remarkable below-ground development, noting roots at depths of 12 m and more (Rawitscher & Rachid, 1946; Rawitscher, 1948). In Venezuela, Foldats & Rutkis (1965, 1975) reported quite extensive root systems in various trees, e.g. *Curatella americana*, *Byrsonima crassifolia* and *Bowdichia virgilioides*, for both horizontal and vertical growth. They show, for instance, how a *C. americana* tree less than 5 m high had roots that reached more than 20 m laterally from the trunk. A bimorphic type of root system, with a superficial system concentrated in the upper 30 or 40 cm, in addition to a deep-ranging root system proceeding down to bedrock, has been reported for various woody plant species in African and South American savannas (Van Donselaar-Ten Bokkel Huinink, 1966; Lawson, Jenik & Armstrong-Mensah, 1968; Rutherford, 1982). Lawson *et al.* (1968) studied the root systems of five woody species in a Guinea savanna, where the development of this bimorphic type of root system is also readily apparent. Vertical stratification of root biomass, however, shows that the greatest concentration of tree roots occurs in the 20–30 cm soil layer. *Ochna pulchra*, a common tree of the Nylsvley savanna, apparently behaves in a similar manner (Cresswell *et al.*, 1982).

(2) *Biomass allocation*

Root/shoot biomass ratio (R/S) may give a more precise indication of the relative development of below-ground parts (Table 2). Menaut & Cesar (1979) report root/shoot biomass ratios between 0·45 and 0·49 for the lower woody layer of the Lamto savanna (2–3 m). In a previous, more detailed paper (Cesar & Menaut, 1974) they reported that R/S for the four commonest tree species in the Lamto savanna varied according to the development of aerial parts, which in turn was determined primarily by fire frequency. Thus in *Crossopteryx febrifuga* the ratio is about 1 when the tree attains 4–5 m high, but it reaches between 0·5 and 0·25 in the tallest individuals. In *Bridelia ferruginea* low trees have a ratio of 3, while mature individuals show an R/S of about 0·5. In *Cussonia barteri* they estimate the average ratio to be 0·4, while it is 0·8 in *Piliostigma thonningii*. In South Africa the first quantitative data on below-ground biomass allocation in one savanna tree, *Ochna pulchra* (Rutherford, 1982), indicate an R/S ratio of approximately one, with a maximum lateral extent in the root system reaching up to seven times the extent of the canopy. Rutherford also remarks on the relation between R/S and shoot biomass. With a ratio of 1 attained by trees of about 1 to 10 kg of shoot mass.

Although the root/shoot ratio varies both with the species and with tree height, it is in general quite high, particularly in comparison with forest trees. For instance, in the Central Amazonian rain forest, the below-ground/above-ground ratio for the whole forest is 0·07 (Fittkau & Klinge, 1973), while Bernhard-Reversat, Huttel & Lemée (1970) give a value for the Banco forest in the Ivory Coast of only 0·09. Analysing R/S ratios in different height classes, Fittkau & Klinge find an R/S of 0·21 for the 1·5–5 m height class; the ratio decreases to 0·15 in the 5–10 m height-class, and it drops to 0·06 in the highest trees (35–38 m). Thus, even low, understorey forest trees show significantly lower R/S ratios than savanna trees of similar size.

These few figures may serve to illustrate the relatively high root/shoot biomass ratio in savanna trees. Sarmiento (1984) already emphasized the general trend among seasonal savanna species towards an increasingly higher below-ground biomass allocation. At the level of the whole ecosystem, this characteristic is also found in arid or cold climates, where there is a conspicuous development of roots and other below-ground organs; however, the seasonal savanna is apparently the only reported ecosystem where even trees show this trend towards an increased biomass allocation into below-ground parts. Apart from the many advantages of allocating a substantial part of the resources in below-ground organs located well beyond reach of fire, Mooney & Gulman (1979) point out that in habitats where water or nutrients are limited, there will be a greater return in carbon by investing in roots for gathering more of the limiting resource than in making more resource-limited leaves. Thus in savanna ecosystems fire, water and nutrient regimes seem to favour a strategy of stress tolerance through the increased development of underground parts.

(3) *Leaf biomass*

A third characteristic of savanna trees refers to their total leaf biomass. The scarcity of foliage and the low leaf density in the crowns are readily observable features of these species, but it is quite interesting to note that in spite of this fact, their leaf/shoot biomass ratios (L/S) are surprisingly high. Thus for several species of trees in the Nylsvley

Table 2. *Root/shoot and leaf/shoot ratios in savanna and in forest trees*

		R/S (°/oo) Tree height		L/S (%)	Source
		4-5 m	> 5 m		
	Seasonal savannas				
Lamto (Ivory Coast)	*Crossopteryx febrifuga*	1	0·5-0·25	—	Cesar & Menaut, 1974
	Bridelia ferruginea	3	0·5	—	Menaut & Cesar, 1979
	Cussonia barteri	0·4		—	
	Pilostigma thonningii	0·8		—	
	Trees 2 m			33-50	
	Trees 2–8 m			8	
	Trees 8 m			3·6	
Nylsvley (South Africa)	*Ochna pulchra*	1		13·5	Rutherford, 1979 and 1982
	Grewia flavescens			18·4	
	Mean, all tree species			5·3	
	Mean, all shrubs			17·4	
Western llanos (Venezuela)	*Byrsonima crassifolia*			48·0	Vera, 1979
	Bowdichia virgilioides			28·7	
	Curatella americana			19·2	
	Tropical rain forests				
Central Amazonian (Brazil)	Trees 1·5–5 m	0·21		—	Fittkau & Klinge, 1973
	Trees 5–10 m	0·15		8·8	
	Trees 35–38 m	0·06		1·2	
	Whole forest	0·07		—	
Banco Forest (Ivory Coast)	Whole forest	0·09		1·5	Bernhard-Reversat et al., 1978
	Temperate forests				
Quercus ilex evergreen forest (France)	Whole forest	0·15		2·6	Lossaint & Rapp, 1978
	Whole forest	0·18		—	
Quercus petraea–Fagus silvatica deciduous forest (France)	Whole forest	0·17		1·1	Lemée et al., 1978

savanna (Rutherford, 1979), a mean leaf/shoot ratio of 6·8 % was obtained, with figures as high as 18·4 % in *Grewia flavescens* and 13·5 % in *Ochna pulchra*, two of the most common trees. Menaut & Cesar (1979) give, for the Lamto savannas, L/S values between 33 % and 50 % for the lowest trees (2 m), an average of about 8 % for the 2–8 m tall layer, and 3·6 % as a mean for the 8 m trees. Interestingly, with higher tree densities, leaf/shoot ratios also increased. Vera (1979), working in a seasonal savanna of the Venezuelan llanos, obtained L/S ratios for 3–4 m high trees of 19·2 % in *C. americana*, 28·7 % in *B. virgilioides* and 48 % in *B. crassifolia*. Values for rain forest trees averaged 1·5 % in three tropical forests of the Ivory Coast (Bernhard-Reversat *et al.*, 1978) and, in a Central Amazonian rain forest (Fittkau & Klinge, 1973), L/S increased from 1·2 % in the canopy trees to 8·8 % in the 5–10 m tree layer (Table 2). In temperate ecosystems, evergreen trees seem to attain higher ratios than deciduous species. *Quercus ilex* in a Mediterranean evergreen forest in southern France has an L/S of 2·6 % (Lossaint & Rapp, 1978), while for canopy trees of a deciduous *Fagus sylvatica–Quercus petraea* forest in northern France L/S averaged 1·1 % (Lemée *et al.*, 1978). Savanna trees thus have relatively high leaf/shoot ratios, maybe higher than in canopy or upper-storey trees found in either tropical or temperate forests. This relatively high proportion of leaf biomass with repect to total above-ground biomass may be a consequence not only of their lower height, but also of higher specific leaf weight and of different crown geometries. Since these trees grow more or less isolated from each other, they may maintain a greater leaf area, and thus higher L/S ratios, with less leaf overlap between neighbours.

(4) *Leaf types*

A wide diversity in leaf forms, size and anatomy can be found in seasonal savanna trees. However, if we had to refer to a 'typical' tree, it might be described as having quite sclerophyllous leaves, either simple or compound, pubescent or glabrous, rather thick, and of the mesophyll size-class area (20·25–182·25 cm²). Toledo Rizzini (1976) gives a list of leaf sizes in 23 woody species of the Brazilian cerrados. His list includes 15 mesophylls, 5 microphylls and 3 macrophylls. Medina (1982) for 10 evergreen species of northern South American savannas gives leaf areas ranging from 13 to 200 cm², while van Donselaar-Ten Bokkel Huinink (1966) reports for the northern Surinam savannas that 11 out of 16 tree species growing in various soil types have mesophyll leaves, 4 microphyll and 1 macrophyll. We see then that savanna trees show a clear trend to develop moderate or large leaves, while the smallest leaf-size classes are almost totally absent.

The sclerophyllous nature of leaves in savanna trees may be quantified through the specific leaf weight ratio (SLW) (dry weight per unit leaf area). In the Toledo Rizzini list, this ratio ranged from 11·4 to 39·8 mg cm⁻², with a mean of 19·6 mg cm⁻², while in the Medina list SLW ranged from 9·1 to 18·9 mg cm⁻², with a mean of 13·4 mg cm⁻². In various types of temperate vegetation evergreen leaves also show high SLW, at least twice as high as those of deciduous leaves in the same ecosystem. Thus in 73 evergreen broadleaved trees in Japan the average SLW was 6·9 mg cm⁻², the mean for six bog shrubs in Canada was 13·6 mg cm⁻², while five heath shrubs in Tennessee gave an average of 8·4 mg cm⁻² (Chabot & Hicks, 1982). We may say that, comparatively, savanna evergreen trees attain high specific leaf weights, even higher than the mean of

evergreen species in other ecosystems, and of course well above deciduous species in any ecosystem.

Several ecologists have related scleromorphy of evergreen leaves in various vegetation types to poor, nutrient-deficient soils (Beadle, 1966; Loveless, 1961; Monk, 1966; Small, 1972). Extremely poor soils have been hypothesized as the direct cause of certain morphological and physiological features of tropical savanna trees (Arens, 1958, 1963). Mineral deficiencies, particularly for nitrogen, phosphorus, calcium and sulphur, would limit growth and would produce an accumulation of carbohydrates that could be deposited either as cellulose in cell walls, or as thick cuticles, sclerenchyma and other mechanical structures.

To end this discussion of leaf characteristics we have to mention a few anatomical features of possible ecological interest. Morretes & Ferri (1959) studied the anatomy of leaves in 12 common cerrado trees, concluding that several sclerophyllous features do occur in most of these species, such as thick cuticle, deep stomatal chambers, varied pubescence, abundance of mechanical elements in the mesophyll and pronounced development of colourless parenchyma or hypodermis. Merida & Medina (1977) showed further anatomical details in four woody species: *Curatella americana*, *Bowdichia virgilioides*, *Byrsonima crassifolia* and *Casearia sylvestris*. In these species leaf thickness ranges from 150 to 315 μm and number of stomata mm^{-2} from 145 to 642, with a total stomatal area, in the abaxial face, between 2·1 and 10·4 % of total leaf surface. These seem to be rather high numbers of stomata, above the average of herbs and deciduous trees, and within the same order of those reported for other evergreen trees (Curtis & Clark, 1950). The anatomical structure of the leaf mesophyll in all four species also shows typical scleromorphic features, such as small intercellular spaces, large vascular bundles, colourless parenchyma, trichomes, and very thick cuticle.

(5) *Phenology*

Three main features must be emphasized in the annual phenodynamics of savanna woody species (Monasterio & Sarmiento, 1976; Sarmiento & Monasterio, 1983). First, an overwhelming majority of these species are evergreen, that is, the old foliage persists on the tree until the emergence of new leaves. Some minor variants may be distinguished, from those species that shed their leaves a few days after the flushing of the new foliage (mean leaf life span somewhat more than 12 months) to the trees that shed old leaves some days or even a few weeks before the flush of new foliage (average leaf life span less than 12 months). In this latter case, the plants may remain for a short time with a reduced leaf area, and might therefore be considered as brevi-deciduous species. However, from a functional and ecological viewpoint, both types of behaviour are similar and will be treated here as variants of evergreenness. Secondly, most species renew their foliage during the dry season, either at its beginning, the middle or towards its final days, but in any case almost the entire process of leaf renewal takes place during what appears to be the least favourable part of the annual cycle, when environmental strains due to the quite reduced or even non-existent rainfall are strongest. Finally, the process of leaf flush and expansion, together with shoot elongation, is restricted to a period of about 3 or 4 months (Fig. 6). At the beginning of the rainy season all leaf growth ceases completely. During most of the rainy season leaf area remains stable: towards the end of this season leaf senescence is already apparent and leaf fall starts with the dry season. As blooming and leaf flushing occur in these species either simultaneously

	Rainy season						Dry season					
	A	M	J	J	A	S	O	N	D	J	F	M
Curatella americana							D	D	D	D		
							L	L	L	L	L	
	F						F	F	F	F	F	
Byrsonima crassifolia							D	D	D			
	L						L	L	L	L	L	
	F	F					F	F	F	F	F	
Bowdichia virgilioides	D								D	D	D	
	L	L							L	L	L	
	F								F	F	F	
Casearia sylvestris								D	D			
									L	L		
	F									F	F	

Fig. 6. Annual phenodynamics of four woody species in the seasonal savannas of the Venezuelan llanos. D = leaf drop; L = leafing; F = flowering.

or successively, bud activity, at least in the above-ground parts, appears as a strictly seasonal process entirely synchronized with the dry season.

Radial growth in stem and branches appears, on the contrary, to occur almost exclusively during the rainy season. Alvim & Silva (1980) followed diameter increment in trunks of 10 cerrado trees near Brasilia, and in all cases growth was restricted to the rainy season and ceased completely during the dry months, when stem diameter may even decrease somewhat.

It is also interesting to note that many savanna trees may persist for many years in a suffruticose or half-woody habit, with several stems sprouting each year from a xylopodium or from rootstocks. Sarmiento & Monasterio (1983) discuss the ecological significance of these temporary hemixyles as a traumatic growth form induced by fire injury. Tree seeds and seedlings also show some features that might be related to fire and drought avoidance. Although some seeds are able to germinate after being subjected to high temperatures (60–90 °C) for a few minutes (Toledo Rizzini, 1967), a majority of savanna trees seem to germinate after the start of rains, that is, in a relatively fire-free period of high water potential in the topsoil. In his studies of fire action on cerrado plants, Coutinho (1976, 1982) points out that about 150 species have the capacity to flower a short time after fire. Furthermore, in some woody species with fruits that take a full year to ripen, fire may promote fruit dehiscence and seed dispersal. Both mechanisms appear as adaptations promoting the escape of seedlings and juveniles from fire injury. Coutinho in Brazil, as well as Cesar & Menaut (1974) in the Ivory Coast, noticed that not only do adult savanna plants respond to fire damage by a profuse sprouting from underground parts, but even seedlings show this capacity to sprout when damaged. All these features suggest a long-term adaptation of savanna plants to recurrent fires.

From the viewpoint of their phenodynamics, savanna trees are completely opposed to grasses and herbs, since they are actively growing and expanding leaves just when the grass layer appears as an accumulation of dead standing crop. This relative phenological independence of the two main vegetation layers is one of the most striking features of seasonal savannas. We shall consider now the physiological responses of savanna trees that allow them to maintain positive water, nutrient and carbon budgets.

IV. WATER BUDGET

(1) *Transpiration and leaf conductance*

The first studies on transpiration of cerrado trees showed that, in spite of the apparent xeromorphism of their leaves, most species scarcely control water losses, even during the peak of the dry season (Ferri, 1944, 1955; Rawitscher, 1948; Ferri & Coutinho, 1958; Coutinho & Ferri, 1960). A similar result was found in trees of the Venezuelan savannas (Vareschi, 1960; Foldats & Rutkis, 1975). Ferri distinguished three basic types of stomatal behaviour in cerrado trees: (*a*) species without any restriction, even during the dry season, for example *Kielmeyera coriacea* and *Hymenaea stigonocarpa*; (*b*) trees restricting water loss towards the end of the dry season through partial stomatal closure at midday hours, such as *Byrsonima coccolobaefolia* and *Terminalia argentea*; (*c*) a few species, like *Anona coriacea*, that restrict transpiration during all the dry season, with somewhat greater control in its last part.

All the aforementioned results were obtained in isolated leaves with a torsion balance (the Stocker method). Few data are available on porometer determinations of leaf conductance and transpiration in intact shoots of savanna trees (Medina, 1982), but they mostly confirm previous results. We measured leaf conductance and calculated transpiration flux density (TFD) hourly, during 5 days of the rainy season and 4 days in the dry season (Goldstein, Sarmiento & Meinzer, 1985 *b*). Fig. 7 summarizes some of our results. As we may see, none of the four species shows marked differences in stomatal behaviour between seasons. In either season, stomata may be partially closed at midday hours or they may remain fully open. Similarly, TFD shows small interseasonal changes. Thus, for instance, in *Bowdichia virgilioides* daily water loss per unit leaf area on a clear, dry-season day may be 3 or 4 times greater than the amount transpired on a cloudy day of the rainy season (Fig. 8). That is, transpiration seems to depend more on atmospheric or radiation conditions than on topsoil water. Measurements by Lange & Schulze (1971) for *Fagus sylvatica* suggest that total amount of water transpired per unit leaf area in savanna trees may be comparable with the amount lost by temperate forest trees on clear summer days. Our totals in savanna trees often reached 200 or even 300 mg H_2O cm^{-1} day^{-1}, corresponding to 20 g or more of water per gram of leaf dry weight.

We see then that savanna trees scarcely exercise stomatal control, and hence transpirational losses may be high even during the rainless season. This high transpiration maintains leaf temperature near air temperature in spite of the large size of the leaves (Goldstein, Meinzer & Sarmiento, 1985 *a*). Meinzer, Seymour & Goldstein (1983) also show that when some of these species, like *Curatella americana* and *Byrsonima crassifolia*, change foliage, and both old and new leaves coexist on each tree, the young expanding leaves have significantly lower conductances to water vapour than the more mature ones. This tighter control of water loss may contribute to maintain a favourable water budget in young leaves, making possible their growth and expansion in the less favourable period of the year.

(2) *Leaf water potential*

Until very recently, determinations of leaf water potential (Ψ) in savanna trees with the pressure bomb were not available. Medina (1983), in his review of the physiological
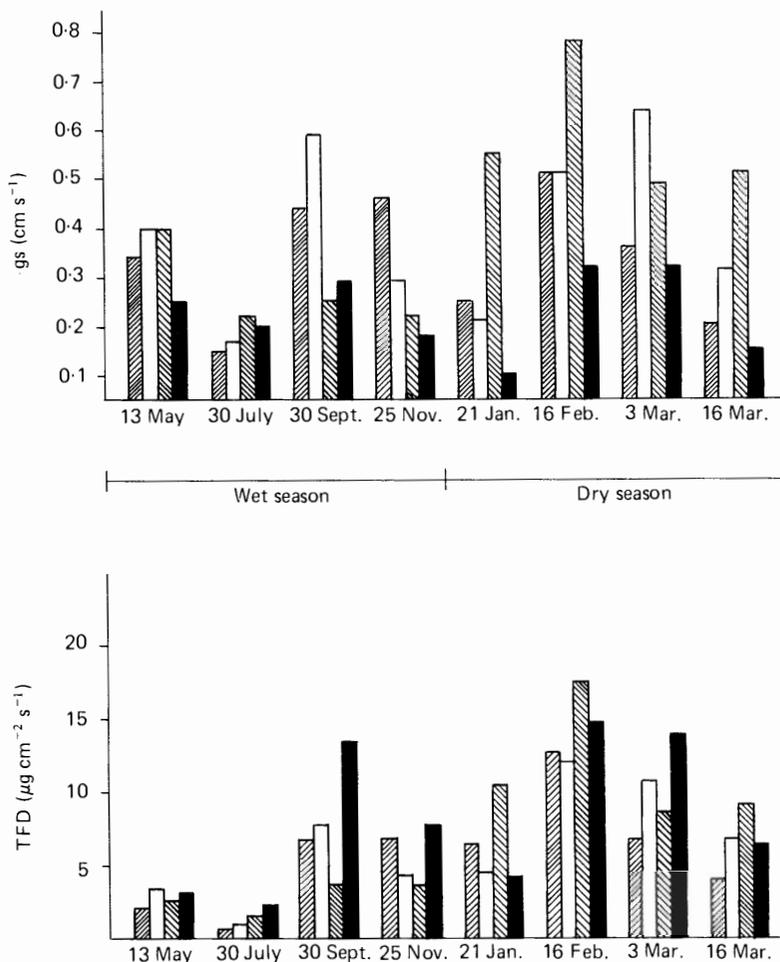
Fig. 7. Leaf conductance (gs, cm s^{-1}) and transpirational flux density (TFD, μg cm^{-2} s^{-1}) at noon, in four woody species in a seasonal savanna of the Venezuelan llanos (Hato Palma Sola): *Byrsonima crassifolia* ▨; *Curatella americana* □; *Bowdichia virgilioides* ▧; *Casearia siylvestris* ■.

ecology of neotropical savanna plants, does not cite any values of leaf water potentials. Apparently the first daily cycles of this potential in neotropical savanna trees are those presented by us (Meinzer *et al.*, 1983) and by Goldstein *et al.* (1985a, b). Cresswell *et al.* (1982) have some comparable data for tree species in the much drier Nylsvley savannas of South Africa.

Figure 9 shows the lowest and the highest (base or pre-dawn) leaf water potentials reached by four tree species in a savanna of the Venezuelan llanos. In eight daily cycles during the year, the minimum does not change much. In *C. americana* and *B. crassifolia* minimum daily Ψ attained about -15 bars in clear days, in either the dry or the rainy season. Likewise, *Casearia sylvestris* may attain somewhat more negative values: -20 bars, in either season. *Bowdichia virgilioides*, however, does seem to have a seasonal response, with lower Ψ in the dry season (-14 bars) than in the rainy season (minimum $\Psi = -8$ bars).
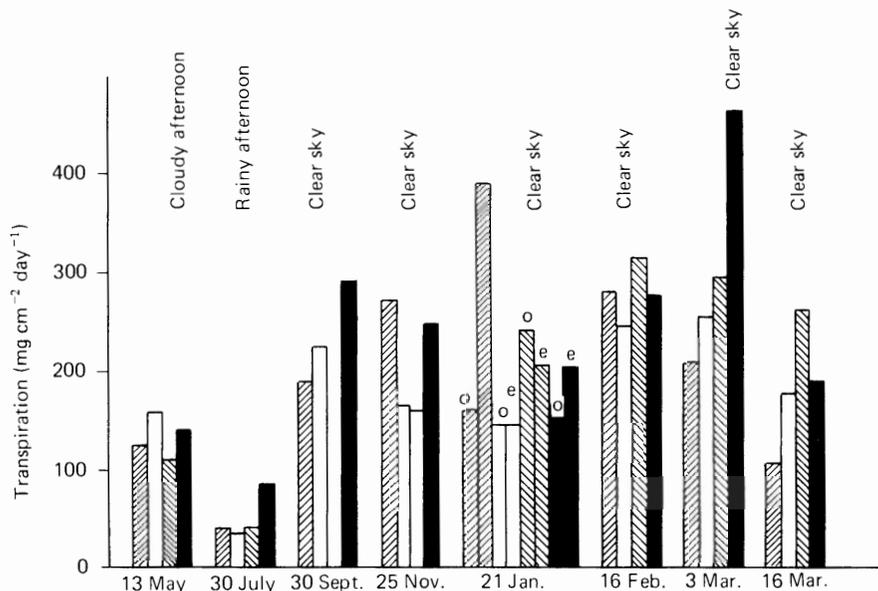
Fig. 8. Total daily transpiration (mg H_2O cm^{-2} day^{-1}) in savanna trees, during several days of the dry and rainy seasons under different weather conditions. In January, figures for old mature (o) and expanding (e) leaves are given. *Byrsonima crassifolia* ▨; *Curatella americana* ☐; *Bowdichia virgilioides* ▨; *Casearia sylvestris* ■.

Meinzer *et al.* (1983) determined leaf osmotic potential at the turgor loss point (TLP) in new mature leaves of these same four species. It is interesting to realize that the minimum almost always remains above this critical threshold (Fig. 9), thus allowing leaf expansion during the dry season. Base or pre-dawn leaf water potential gives further support to the hypothesis that the root zone of these trees always has enough available water. In fact, pre-dawn Ψ values, when Ψ supposedly has reached an equilibrium with soil water potential, remain rather high not only in the rainy season but also during the entire dry season, when these values are slightly more negative (-5 to -8 bars, Fig. 9). In this respect it is worth pointing out that the least deeply rooted of the four species, *Casearia sylvestris*, is the one that reached the lowest pre-dawn Ψ on a dry season day: -12 bars, suggesting a relatively dry soil, but still with available water. Notice also that low pre-dawn Ψ may occur even during the rainy season – -6.7 or -6.8 bars, in days in May and September, the rainiest months of the year in this area – confirming again the relative irrelevance of seasonal variations for the water budget of these trees.

Considering daily cycles of transpiration and water potential we showed (Goldstein *et al.*, 1985b) that leaf water potential in *C. americana* and *B. crassifolia* is nearly independent of transpiration under high transpiration rates. Thus in both species, when transpiration rate exceeds 8 g cm^{-2} s^{-1}, Ψ stabilizes around -10 to -12 bars. These results suggest that liquid flow resistance in the two species decreases as transpiration flux is increased.
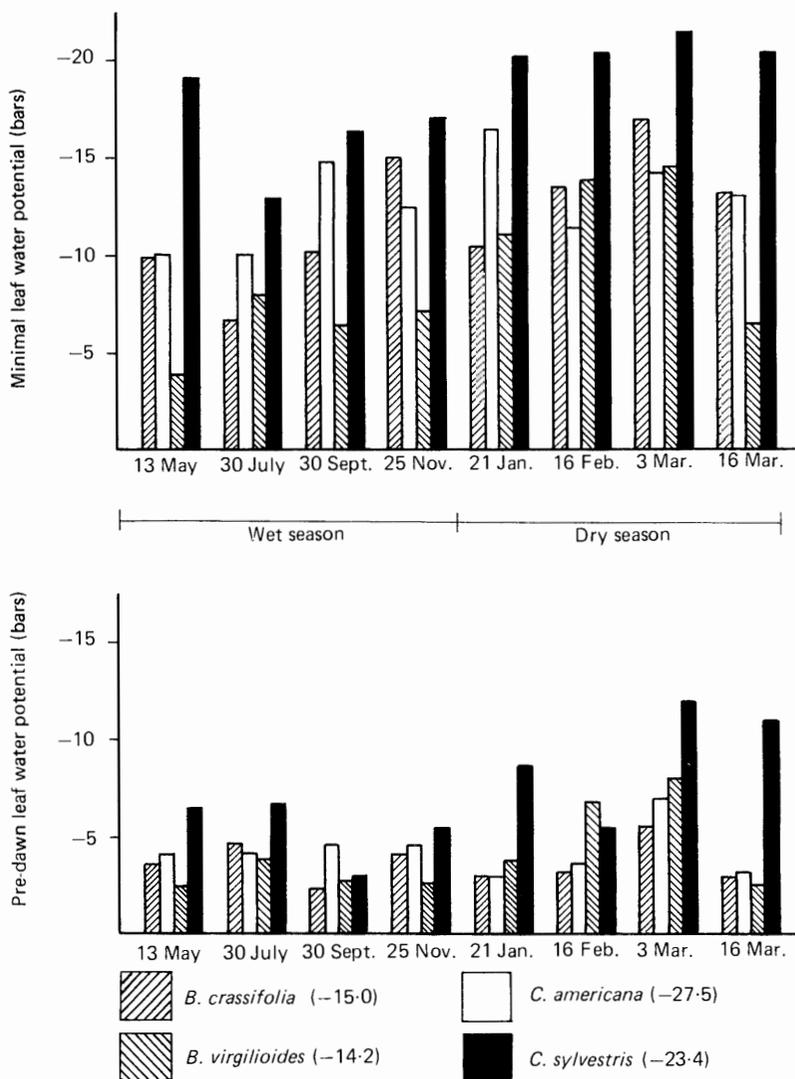
Fig. 9. Minimal and maximal or pre-dawn leaf-water potential reached by woody species in the seasonal savanna of Hato Palma Sola, Venezuela. Leaf osmotic potential at the turgor loss point (TLP) determined for new, mature leaves in bars is indicated in parentheses (according to Meinzer *et al.*, 1983).

(3) *Hydraulic conductivity*

Another mechanism that may contribute to maintain a high water flux through the plant is an efficient system of water transport able to keep pace with increasing transpiratory demands. Catalan (1983) measured specific hydraulic conductivity in two evergreen savanna trees and in two drought-deciduous forest species, according to concepts and methods proposed by Zimmermann (1978). His data show (Table 3) that the two savanna species *Curatella americana* and *Byrsonima crassifolia* have specific hydraulic conductivities per leaf supplied from 5 to 10 times greater than those measured

Table 3. *Specific hydraulic conductivity per unit leaf dry weight* ($ml\ h^{-1}\ g^{-1}$) *and per unit leaf area* ($ml\ h^{-1}\ cm^{-2}$) *in two evergreen savanna trees and two deciduous forest species. Means and standard error for replicates. From Catalan* (1983)

	Specific hydraulic conductivity	
Species	Per unit leaf dry weight	Per unit leaf area
Byrsonima crassifolia	170·17 + 27·13	1·47 + 0·24
Curatella americana	84·47 + 21·32	0·47 + 0·14
Genipa americana	18·20 + 1·39	0·20 + 0·02
Cochlospermum vitifolium	16·04 + 1·04	0·10 + 0·00

in the two deciduous trees (*Genipa caruto* and *Cochlospermum vitifolium*). The respective transpirational rates were twice as high in the savanna as in the forest species. These two savanna trees showed a higher efficiency in their conductive tissues than temperate-climate trees. Catalan also found that hydraulic resistance, determined by heat flow velocity, increased as soil water availability decreased, but in the savanna trees hydraulic resistance was flow-dependent, while the forest trees showed a constant resistance to liquid flow when transpiration rate increased. It is suggested that in contrast to drought-deciduous trees, savanna evergreens have vascular systems well adapted to maintain high hydraulic conductivities that could keep pace with the equally high transpiration rates, without resulting in an excessive drop in leaf water potential. However, even this moderate fall in leaf water potential gives rise to a hydraulic gradient through the plant that, coupled with the low internal resistance to water flow, allows a relatively high soil water uptake.

V. ECONOMY OF NUTRIENTS

(1) Soil resources

Most savanna soils, particularly those of seasonal and semi-seasonal formations, are strikingly deficient in all major plant nutrients (Montgomery & Askew, 1983; Sarmiento, 1984). Thus 90 % of 112 topsoil samples of the Brazilian cerrados had cation exchange capacities below 10 meq/100 g soil and a total of exchangeable bases below 1·0 meq/100 g soil (Ranzani, 1971). Comparising 182 topsoil samples from the savannas in the Venezuelan llanos with 85 samples from forest soils in the same area, savanna soils contained on the average only 70 % of the nitrogen and 40 % of the base content of forest soils (Sarmiento, 1984). These few data (see also Table 1) may confirm nutrient deficiency as a quite general feature of tropical American savanna soils. In the well-drained soils of seasonal savannas this low fertility is still more conspicuous, due to the low organic matter content and to the predominance of kaolinitic clays in the mineral exchange complex.

(2) Nutrient concentration in plants

In considering the possible action of nutrient deficiency on plant growth under the natural conditions of tropical savannas, the first point to notice is that the concentrations of such elements as N, K and P in the leaves of savanna trees are relatively low. Ernst

Table 4. *Leaf nutrient concentration (mg/g dry weight) in evergreen savanna trees, tropical deciduous forest trees, temperate evergreen and deciduous trees. Data from Montes & Medina (1977); Medina (1982) and Chabot & Hicks (1982)*

	Mature leaves					Recently fallen leaves				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg
Curatella americana	9·3	0·75	8·3	4·9	2·7	4·6	0·14	4·1	8·6	3·1
Byrsonima crassifolia	8·0	0·35	5·4	8·0	3·0	5·7	0·20	1·4	11·3	2·2
Xylopia aromatica	10·6	0·61	4·7	5·3	1·6					
Vochysia venezuelana	6·5	0·33	2·1	6·0	2·6					
Copaifera pubiflora	13·6	0·70	5·8	3·9	1·3					
Mean savanna trees	9·6	0·55	5·3	5·6	2·2					
Mean of three species of deciduous trees	17·4	1·10	21·6	8·9	4·9					
Mean Eurasian evergreen trees	11·2	1·10	4·3	7·0	2·0					
Mean Eurasian deciduous trees	20·9	2·10	11·5	16·6	3·3					

(1975) gives the mineral content of leaves in 17 species of trees in the Zimbabwe woodlands (*miombo*), in the middle of the rainy season. Montes & Medina (1977) and Medina (1982) present comparative data for evergreen savanna trees and deciduous and evergreen forest species (Table 4). Although there are important differences within morphologically similar species in the same ecosystem, as a general trend these data show that leaves of evergreens have a lower peak nutrient content than deciduous species, and among the evergreens, savanna species are poorer than forest trees. This is particularly true for N, P, K and Ca. A first response of savanna trees to the poverty of soils seems to be, then, a lower accumulation of these nutrients. This is a common physiological response to a nutrient-deficient medium, but one which is even more apparent in evergreen woody species (Chapin, 1980; Chabot & Hicks, 1982).

Another conservative mechanism in the use of critical nutrients by savanna trees is their translocation from senescent leaves before leaf fall. Ernst (1975) and Montes & Medina (1977) show that the leaf concentration of N, P and K reaches a peak in young leaves, followed by a steady decrease during the wet season, reaching minimum levels just before abscission. Other elements, like Ca, Na, Mn, Al and Fe, have a reverse trend, increasing their concentrations with leaf age. Bate & Gunton (1982) report that in the Nylsvley savanna tree species decrease the concentration of nitrogen during the dry season to less than half the peak content of the rainy season. Some of this drop in leaf nutrient content during the rainy season may be caused by leaching, but most of this diminution cannot be an effect of leaching because the concentration of other readily leached ions, as sodium, increases during this time.

The amount of nutrients reabsorbed before abscission may constitute a high proportion of the peak annual nutrient content of leaves. Notwithstanding the ecological and physiological relevance of such conservative mechanisms for species submitted to severe soil deficiencies, it is important to point out that most perennial species, either evergreen or deciduous, in any type of ecosystem, show high redistribution rates (Woodwell, 1974; Chapin, 1980; Gray, 1983). We may only say that in seasonal savanna trees these recuperation rates are among the highest reported in the literature.

(3) *Nutrient losses*

Besides the adaptation to low internal nutrient concentrations and the high internal recycling of absorbed elements, other conservative mechanisms may operate to minimize nutrient losses in throughfall, since the heavy rainfall of the wet season might induce high losses through leaching of leaves. A possible way to decrease these losses may be the relative impermeabilization of the leaf surface by means of increased water repellency governed by cuticular factors (Martin & Juniper, 1970). A measure of the possibility of leaching may be obtained with wettability tests. Table 5 gives some results for leaves at different developmental stages in the four tree species that we have been using as system models of savanna trees. The leaf surface wettability is lowest in young leaves. Since certain nutrients reach their highest concentrations in developing leaves, a low wettability affords them a certain protection against rain leaching. Arens (1958) held that the hydrophobia of young leaves is an adaptive mechanism that has arisen through evolutionary processes. In the case of seasonal savannas dew may also be important as a leaching agent, as it is in other regions where rainfall is low (Tukey, 1970), given that it occurs almost daily during the dry season. Thus a low wettability would still be critical to prevent nutrient loss caused by dew on young leaves expanded during the rainless period.

An artificial leaching experiment was performed to simulate the possible loss of potassium from leaves of different ages in the same four species. The results presented in Table 6 show that potassium might be significantly leached from these leaves. Wide interspecific variation per unit leaf area is also apparent. *Casearia sylvestris*, for instance, lost at least ten times less potassium in this experiment than the other three species, but aside from these differences the youngest leaves appear as the most susceptible. The experiment suggests, then, that throughfall might be a significant mechanism for nutrient losses in these trees, particularly from young, developing leaves. Changing foliage during the dry season minimizes this potential loss, since in that period of the year rainfall is almost non-existent, and only dew is present to effect leaching.

Cuticular conductance to water vapour represents another factor variable with leaf age, that might further illustrate the susceptibility of leaves to leaching, since a direct relation seems to exist between permeability to water and ions. Table 7 shows the figures we obtained with leaves of different ages. Though all cuticular conductances are relatively low, they are significantly higher in the youngest leaves. The greater potential leachability of expanding leaves also reinforces the adaptive advantage of changing leaves during the dry season.

To summarize the main points on nutrient economy of savanna trees, we have shown first that infertile soils may have induced as an adaptive response relatively low concentrations of some nutrients in plant tissues and particularly in leaves. In the case of nitrogen and phosphorus, these low concentrations may in turn be responsible for certain genetically fixed metabolic changes that directly led to the expression of several sclerophyllous traits. But a further consequence of leaf scleromorphism and of its low content of nitrogen and phosphorus is the increased resistance to CO_2 uptake, that is, a greater participation of the so-called mesophyll resistance in the total diffusive resistance on these leaves, not just by structural obstacles to CO_2 diffusion, but chiefly by the limiting role of the carboxylation enzyme in photosynthesis (Mooney & Gulman, 1979). In this way, sclerophyllous species show a lower photosynthetic capacity.

Table 5. *Leaf wettability obtained by measuring the diameter of water drops of standard volume allowed to fall from a standard height on to the leaf surface. Diameter units are arbitrary units of a microscope ocular scale. Averages for twelve determinations (three replicates in four leaves). From Goldstein, Meinzer & Sarmiento (unpublished data)*

	Expanding leaves	Expanded soft leaves	Expanded sclerophyll leaves	Senescent leaves
Curatella americana				
Adaxial surface	26·9	27·6	28·1	37·6
Abaxial surface	28·4	29·5	29·3	31·1
Byrsonima crassifolia				
Adaxial surface	25·0	27·0	29·6	31·2
Casearia sylvestris				
Adaxial surface	—	39·0	39·8	—
Bowdichia virgilioides				
Adaxial surface	—	29·4	35·1	—

Table 6. *Losses of potassium from leaf samples submerged in a known volume of distilled deionized water for three minutes. Amount of K (ppm × 10^{-4} cm^{-2} leaf area) determined by atomic emission spectrophotometry. From Goldstein, Meinzer & Sarmiento, unpublished data*

	Expanding Leaves	Expanded soft leaves	Expanded sclerophyll leaves
Curatella americana	4	2	9
Byrsonima crassifolia	39	22	16
Casearia sylvestris	—	4	3·5
Bowdichia virgilioides	—	18	22

Table 7. *Leaf cuticular conductance to water vapour expressed on a single-surface basis (cm s^{-1})*

They were estimated by measuring rates of water loss from leaves connected to photometers and maintained in a controlled environment chamber. To ensure stomatal closure, leaves were kept in darkness and the chamber was flooded with CO_2 from a dry-ice source. From Goldstein, Meinzer & Sarmiento (unpublished data).)

	Expanding leaves	Expanded soft leaves	Expanded sclerophyll leaves
Curatella americana	0·027	0·014	0·006
Byrsonima crassifolia	0·050	0·016	0·006
Casearia sylvestris	—	0·006	0·006
Bowdichia virgilioides	—	0·006	0·005

VI. CARBON BUDGET

(1) *Photosynthetic rates*

Information about photosynthetic capacity (photosynthesis-conductance relationships) of *C. americana* and *B. crassifolia* appears in Fig. 10. We see that with leaf conductances above 0·6 cm s^{-1} net assimilation becomes constant and independent of leaf conductance under optimal laboratory conditions. The values attained range from
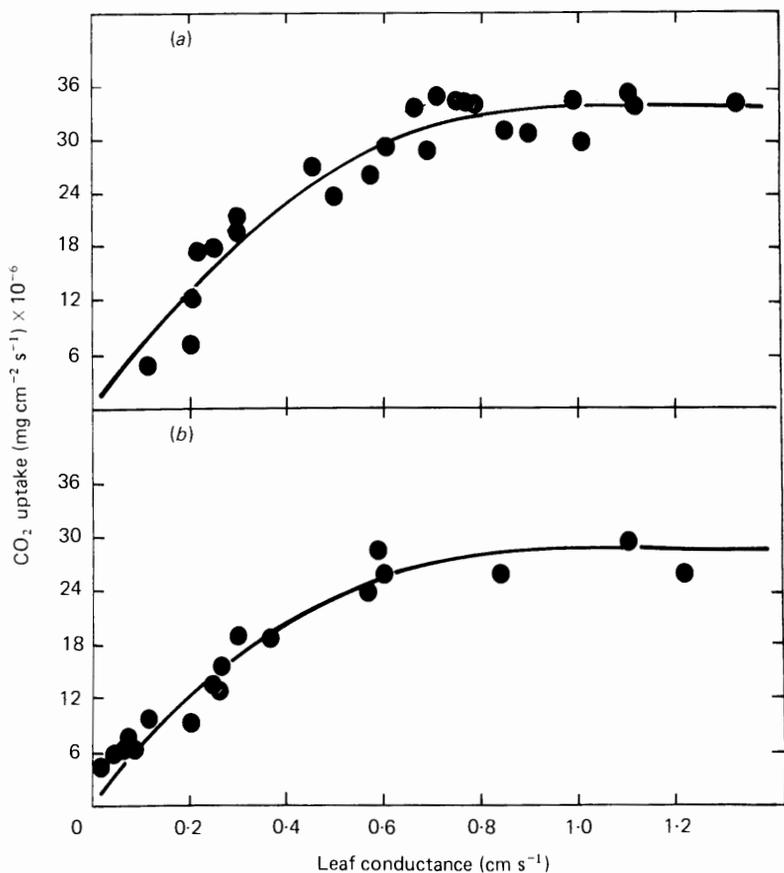
Fig. 10. Relationship between CO_2 uptake and leaf conductance (gs) for two savanna species: *Curatella americana* (a) and *Byrsonima crassifolia* (b). From Goldstein *et al.* (1983).

24 to 30 ng cm^{-2} s^{-1} in *B. crassifolia* and between 30 and 36 ng cm^{-2} s^{-1} in *C. americana*. Medina (1967) measured colorimetrically CO_2 exchange in four savanna species including *B. virgilioides* and *C. sylvestris* under field conditions during the dry season. In the early morning, with leaf temperatures between 26 and 36 °C, photosynthetic rates ranged from 2·5 to 5·0 mg CO_2 dm^{-2} h^{-1} (7–14 ng cm^{-2} s^{-1}). As these values represent non-optimal field conditions, they may be considered in agreement with our own laboratory data. Medina (1982) reports a figure of 26·8 ng cm^{-2} s^{-1} for detached leaves of *C. americana* under some water stress conditions, also in agreement with our values.

Data from the Nylsvley savanna (Cresswell *et al.*, 1982), however, indicate a fairly wide range of interspecific variation among savanna trees. They report values of 15 ng cm^{-2} s^{-1} in *O. pulchra*, 25 ng cm^{-2} s^{-1} in *T. sericea*, 30–35 ng cm^{-2} s^{-1} in *G. flavescens*, and somewhat more than 40 ng cm^{-2} s^{-1} in *B. africana*. A rather wide range of interspecific variation among savanna trees is thus apparent.

A first conclusion from these data is that maximal rates in savanna trees, under optimal laboratory conditions, are comparatively low, in general less than half the maximal reported rates for C_3 plants (about 30 mg CO_2 dm^{-2} h^{-1} (19·8 mol m^{-2} s^{-1})). Low

photosynthetic capacity is also characteristic of evergreen woody species in various temperate ecosystems (Mooney & Dunn, 1970; Small, 1972; Dunn, 1975; Strain, 1975), perhaps due to their scleromorphic, nutrient-poor leaves, that both contain less photosynthetic machinery and conduct CO_2 less rapidly (Mooney, 1972).

(2) *Seasonal trends in carbon gain*

Actual assimilation rates in savanna trees probably decrease with leaf age, in correlation with the decreasing concentration of nitrogen and other nutrients. This decline in photosynthetic rate is suggested by the high positive correlation found by Mooney, Ferrar & Slatyer (1979) between nitrogen content of leaves and photosynthesis in evergreen species of *Eucalyptus*. There is no reason to suppose that this relation does not apply to other woody evergreens. Unfortunately, the only available data on seasonal trends in photosynthesis in savanna trees (Cresswell *et al.*, 1982) are ambiguous, possibly because of the abnormal occurrence in that year of a dry period in the middle of the rainy season and also because their data only cover six months, from September to March. They report that all four tree species exhibited increased rates with leaf expansion towards the end of the dry season or first weeks of the rainy period, followed by a decreasing trend for two or three months, then a new increase, finally declining towards the end of the growing season.

However inconclusive these seasonal trends may appear, we want to emphasize that they seem to confirm that newly expanded leaves have maximum assimilation rates, and hence that near-peak assimilation rates do occur during the dry season or in the transition between the dry and the rainy season, when evaporative demand is highest and soil water content lowest. Leaf resistance to CO_2 uptake would seem to be then at a minimum, given that it is chiefly determined by the internal resistance derived from the low concentrations of certain enzymes, such as RuDP-carboxylase, because of low leaf nitrogen concentration (Medina, 1982). However, developing leaves are both the least sclerophyllous and have the highest concentrations of nitrogen, phosphorus and potassium. We may therefore postulate that photosynthetic rates are correlated with leaf age, with a yearly maximum in young, recently matured leaves, followed by declining values thereafter. Such a decline in photosynthetic rate along the rainy season, when there is no problem of water supply, implies a trade-off between maximization of carbon gain and optimization of nutrient use. Apparently the availability of these nutrients constitutes a major bottleneck, and therefore their translocation from leaves to stems has been more crucial to these species than keeping higher photosynthetic rates for a longer period of the year. If relevant data on the dependence of photosynthesis on leaf nitrogen content were available, the cost of nitrogen recuperation in terms of loss of carbon gain could be quantified. Anyway, the internal translocation of nutrients seems to be a part of a genetically programmed reallocation of resources within the plant, since neither known stress leads to the gradual leaf senescence characteristic of these trees.

(3) *Temperature response and leaf size*

Data on the response of photosynthesis to temperature for two savanna species are presented in Fig. 11. According to these results (Goldstein *et al.*, 1985a), the optimum for photosynthesis in *Curatella americana* is about 24 °C, while it reaches 28 °C in *Byrsonima crassifolia*, with a sharp fall below 22 °C in *B. crassifolia* and above 33 °C
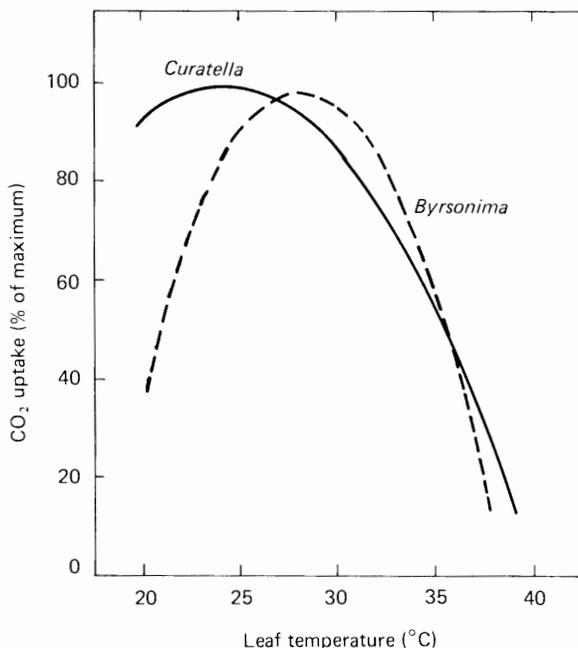
Fig. 11. Net photosynthesis response to leaf temperature for *Curatella americana* and *Byrsonima crassifolia*. From Goldstein *et al.* (1983).

in both species. The range between 22 and 33 °C encompasses the most frequent air temperature during the sunlight hours in the Venezuelan savannas (Fig. 3). It should thus be highly advantageous for savanna trees to maintain leaf temperatures close to or even below air temperatures. As sensible heat dissipation is inversely related to leaf width (Gates, 1963), large leaves have to dissipate relatively more latent heat in order to maintain their temperature near air temperature.

According to Parkhurst & Loucks (1972), construction cost per unit leaf surface is inversely related to leaf size. Large leaves would seem to have a lesser energy demand than small ones, on a per-unit leaf-area basis. Then, if selective pressures towards a decrease in leaf size arising from considerations of water or heat balances did not exist, leaves might be large. Transpirational rates in savanna trees are high enough to cool even large leaves. These broadleaved species may improve their annual carbon budget through both a reduction in the energy cost of leaf construction and the maintenance of leaf temperature near the photosynthetic optimum.

(4) *Leaf conductance, water potential and assimilation*

For an interpretation of the seasonal behaviour of these species and their strategies of water use and carbon gain, it is also important to discuss the relationships between stomatal conductance (gs), leaf water potential (Ψ), and net assimilation (A). Two interesting points arise from the data of Cresswell *et al.* (1982). First, for the two species studied under controlled conditions, *Grewia flavescens* and *Terminalia sericea*, a negative correlation was obtained between photosynthetic rate and leaf water potential, with a sharp decline in A with Ψ below −15 bars. In *G. flavescens* net photosynthesis attains

about 50 % of maximum at about -15 bars, while in *T. sericea* the 50 % point was reached at -10 bars. Photosynthesis ceases when Ψ falls below -27 and -40 bars, respectively. Secondly, both trees may be hardened by subjecting them to low water-supply levels. Such conditioned trees have a less marked fall-off in A with more negative Ψ values. This hardening capacity undoubtedly represents a valuable mechanism to maintain higher photosynthetic rates under field conditions, given the rather low water potentials normally found in savanna soils.

Our results in *C. americana* and *B. crassifolia* under controlled conditions (Goldstein *et al.*, 1985*a*) clearly show a sharp decrease in carbon gain with low *gs* (Fig. 10), since with leaf conductances below 0·4 cm s^{-1} CO$_2$ uptake rapidly drops off. However, our field data also show that leaf conductance tends to be maintained above 0·4 cm s^{-1} in mature expanded leaves. In this way, even under the high VPD frequently met with in the field, the stomata remain at least partially open and carbon gain does not suffer a dramatic fall. Apparently, in these species leaf water potential does not drop appreciably due to a mechanism of variable liquid flow resistance. That is, with high transpiration rates hydraulic resistance decreases, allowing the maintenance of high water flux through the plant with only a small decline in leaf water potential (Meinzer *et al.*, 1983). Clearly, reduced hydraulic resistance at high flux rates is of adaptive value in the high-evaporative-demand savanna environment, as it permits maintenance of high stomatal conductance without excessive water potential drop and consequent turgor loss. Such turgor loss might promote stomatal closure, decreasing carbon uptake.

To conclude with the consideration of carbon-gain strategies, we may state that savanna trees probably show a positive carbon balance throughout the year, independent of sharp seasonality in rainfall seasons. Their strategy maximizes photosynthetic rates through a stomatal control that might maintain less negative leaf water potentials during the sunlight hours, but instead they keep their leaves freely transpiring as long as possible. In this way, two goals may be attained: first, lower leaf temperatures, closer to optimal for photosynthesis, and second, a greater flux of water and probably of nutrients through the soil–plant system. Carbon gain is thus subjected to a trade-off between the negative effects of lower leaf water potentials and the positive effects of lower leaf temperatures. Stomatal closure under high evaporative demand would allow the maintenance of less negative and hence of higher assimilation rates, since CO$_2$ diffusion is scarcely hindered by a partial closure of the stomata down to 0·4 cm s^{-1}, but in this case leaf temperatures would be too high, becoming thus the limiting factor for carbon gain. Therefore the adaptive strategy of these species has been to maintain a high water flux as long as possible, as a way of simultaneously solving the problems of maintaining a favourable carbon budget and an improved nutrient economy.

VII. UNIFYING MODELS RELATING SELECTIVE FORCES, ADAPTIVE MECHANISMS AND PLANT STRATEGIES

Figs. 12–15 use flow diagrams to illustrate the interrelationships between the selective forces that might have modelled the evolutionary changes of savanna woody species and the adaptive features and mechanisms present. We centre the models on three major ecological processes: carbon gain, water balance and nutrient economy. The arrows may be considered either as plant responses or as ecophysiological mechanisms contributing to the overall adaptive syndrome responsible for the fitness of these populations. For

simplicity of presentation we depict separately water use (Fig. 12), nutrient economy (Fig. 13), and phenological behaviour relationships (Fig. 14), and then illustrate the major aspects related to overall carbon budget (Fig. 15). In Table 8 we present a brief overview of all the aforementioned processes.

We have already considered the chain of environmental events that arises from the major features of climate and soils in seasonal savannas (Fig. 5). One of these consequences is the gradual downwards drying of the soil profile during the rainless season. Continuous water storage occurs only in relatively deep soil layers during part or most of the dry season, and thus only those species with deep and extensive root systems can remain active throughout the year. For adult, deep-rooted individuals we may consider that the soil water resource does not show significant seasonal changes. Several consequences of this continuous availability of soil moisture and of its vertical distribution are indicated in Fig. 12.

First, a high energy cost and nutrient investment is necessary to develop and maintain these extensive root systems and the corresponding high R/S biomass ratios. Secondly, since water is available to deep-rooted species throughout the year, tight stomatal control of transpiration is not a priority in spite of the high vapour pressure deficits prevailing most days of the year. Thus leaf conductance may remain high all day and partial closure of stomata at midday hours may be considered more as a safety valve than as a normal regulator of water flux. Only in young leaves may partial closure be important in maintaining an adequate water status. Under the high VPD prevailing in the savanna warm tropical climate, and with the rather high stomatal densities in the leaves of savanna trees, transpiration rates attain high daily values, however, this transpirational flow does not induce major drops in leaf water potential, which are maintained most of the time above the turgor loss point (TLP). The variable liquid flow resistance of these plants contributes to this moderation of the drops in Ψ_L.

Under such conditions of rather free gas exchange between leaves and air CO_2 uptake may proceed at rates limited by internal leaf resistance. That is, the maintenance of an acceptable leaf water status does not imply limitations in carbon uptake. On the other hand, a continuously high flux of water through the soil–plant–atmosphere system in all seasons allows a higher concentration of soil nutrients near the roots and possibly a larger passive uptake with water flux. The high hydraulic conductivity of stems and branches also favour this high water flux.

Another set of adaptive responses may be related to nutrient stress (Fig. 13), given not only that savanna soils are infertile, but that roots of woody species exploit the relatively deep and hence poorest soil layers. A primary response to the low concentration of the soil solution may be an increased allocation of energy and resources to further root development and the exploitation of a larger soil volume. Higher R/S biomass ratios would allow increased relative water and nutrient uptake. In general, it has been shown that in nutrient-deficient habitats roots tend to remain active longer, grow more slowly, and function in a more conservative way through the maintenance of low rates of nutrient uptake per unit root length and the utilization of each root for a longer period (Nye & Tinker, 1977; Chapin, 1980).

The effect of water flux on the uptake of nutrients has not been analysed in savanna woody species. However, it seems quite possible that increased water flux may improve the movement of nutrients through the soil towards the root zone and increase their

Table 8. *Some relations between environmental factors, plant responses and ecological behaviour in woody species of the seasonal savanna*

| Environmental factors	Water	Light, temperature	Nutrients
External constraints	Available only in deep soil during the dry season	High radiation, high air and soil temperatures all the year	Small nutrient-pool in the soil
Plant responses morphological	Deep root system, high R/S ratio	Large, sclerophyllous leaves, high L/S ratio	Deep root system, high R/S ratio
phenological	Evergreens, leaf renewal in the dry season	Evergreens, continuous assimilation, asynchrony between stem growth and leaf renewal, low photosynthetic capacity	Slow, continuous uptake of nutrients
Ecological consequences	Low water-use efficiency	Maximization of photosynthetic rates within the inherent limitations of the assimilatory machinery	Low concentration of nutrients in plant tissues, optimization of nutrient-use efficiency by maximizing total annual uptake and internal redistribution
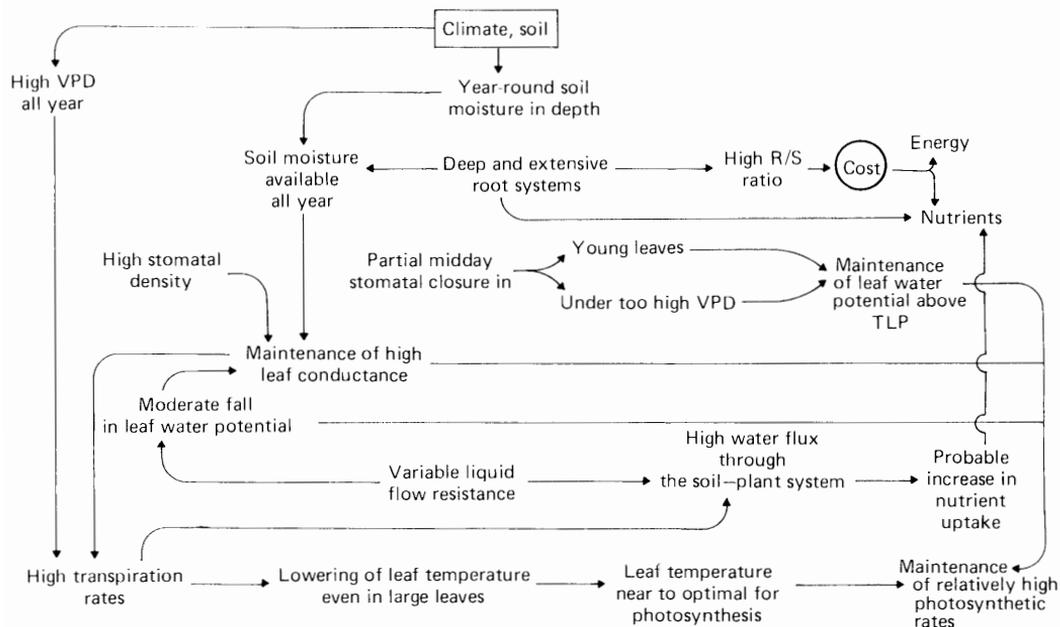
Fig. 12. Mechanisms contributing to maintain a favourable water balance in woody species of seasonal savannas, and some of their consequences for the economy of nutrients and the carbon budget.

uptake by roots (Nye & Tinker, 1977). The experimental data reported by Hooymans (1969) show, however, that a high transpiration rate with low external solution concentrations has only a small effect on uptake by roots. But even a small effect, in the order of a 10–20 % increase, may be quite important for the nutrient budget of those species growing on dystrophic soils.

Another adaptive mechanism to cope with low nutrient availability seems to be lower concentrations of scarce elements, such as nitrogen, phosphorus, sulphur and potassium, in all plant tissues including roots and leaves. This tolerance to nutrient shortages, however, may be paid for with important metabolic and structural changes that lead on the one hand to the relative metabolic inactivity of roots and on the other to an accentuated scleromorphism of leaves. Sclerophyllous plants have relatively low photosynthetic capacity, and thus the potential carbon gain of these leaves is handicapped by considerations of nutrient stress.

Sclerophylly may also function as a positive feedback mechanism on the nutrient budget of these plants. First, scleromorphic, low-nutrient leaves have low leachability, not only because of the small concentration of leachable ions, but also due to the reduced leaf-surface permeability caused by such scleromorphic features as thick cuticles, thick cells walls, a closer cell packing in the mesophyll, etc. In this manner rainfall leaching is reduced (Vera, 1979). Secondly, scleromorphic leaves that have a high energetic cost tend to be long-lived. In savanna trees, leaf life span is approximately one year. As we have seen, shortly after leaf expansion the concentration of mobile elements starts to decrease, most probably because of a significant translocation to storage nutrient pools in the only tissues actively growing during the moist season, i.e. the vascular cambium
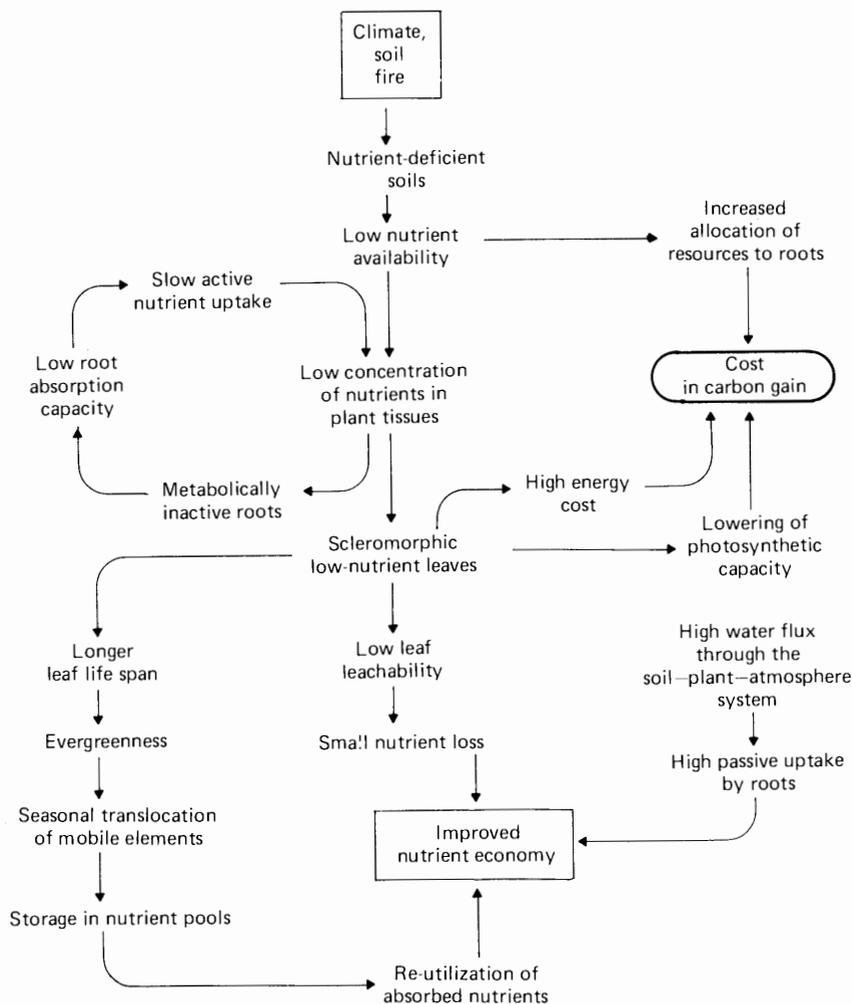
Fig. 13. Processes influencing the nutrient economy of seasonal savanna trees and some of their consequences for carbon gain.

in stems (Alvim & Silva, 1980). These elements may later be re-utilized when a new cycle of leafing begins in the following dry season. This within-plant nutrient recycling must certainly contribute to make these species less dependent on external supplies.

Before referring to carbon gain, we want to consider the various consequences arising from the annual phenodynamics of savanna trees (Fig. 14). The central point to emphasize is the simultaneous occurrence of leafing and leaf fall during the dry season (Fig. 6). Growth is thus effectively partitioned between the two climatic seasons: stem increment during the rainy period and leaf flush and flowering during the rainless season. The ecological consequences of such partitioning are manifold. First, the internal recycling of critical nutrients becomes feasible, as nutrients are alternatively used to supply the most active and nutrient-demanding tissues. Rapid leaf growth becomes possible, supported more by stored nutrients than by absorption. Following the
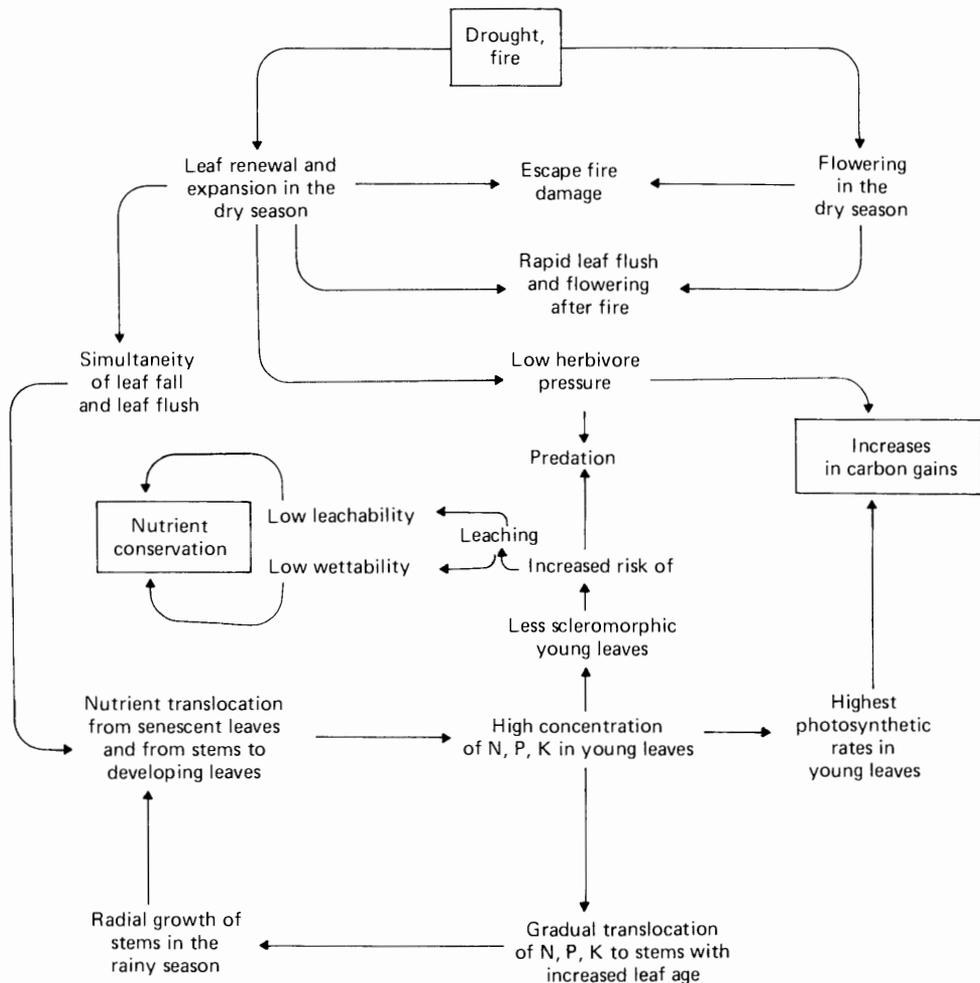
Fig. 14. The impact of the annual phenodynamics on nutrient conservation, carbon gain and water economy, in seasonal savanna trees.

formation and expansion of leaves and inflorecences, the meristems die, perhaps because the nutrient capital of the plant is insufficient to maintain continued meristematic growth for a long period. Stem nutrient capital is gradually replenished throughout the wet season by translocation from senescing leaves and also by absorption from the soil, since mobile nutrients, like nitrogen, phosphorus and potassium, move preferentially to sites of greatest meristematic activity or 'sink strength' (Chapin, 1980). Thus the processes of leaf change and sexual reproduction become entirely restricted to a period of a few months. Furthermore, gradual uptake of minerals during the long season without leaf production may be very important for the nutrient economy of these trees, as it is for other sclerophyllous evergreens like the dominant shrubs of the Californian chaparral (Mooney & Rundel, 1979).

A second consideration is that young leaves are the least scleromorphic and the richest in nitrogen, phosphorous and potassium by unit leaf weight. The high leaf nutrient

content, at least in these three elements, makes these leaves more efficient in carbon assimilation, since they do not show inherent limitations to CO_2 fixing because of either structural features or deficient enzymic machinery. In this way, it seems certain that young leaves contribute to the annual carbon budget of the plant in a proportion unrelated to their short duration in this developing phase, or to the total leaf surface they might represent.

Another point related to the advantages of changing leaves during the dry season is that the risks of predation by leaf and flower eaters are minimized. Insect populations in most savannas show striking seasonal fluctuations, but always their minima, either in species diversity or in numbers, correspond to the dry season (Huntley & Morris, 1982; Gillon, Y., 1983). Thus the richest plant tissues, with highest protein and nutrient content (N, P, K), and hence the most attractive to predators, are exposed to the lowest herbivore pressure. This fact has been repeatedly observed in the Venezuelan savannas, where insect damage to the leaves of trees increases noticeably with leaf age, even though mature leaves become rather unpalatable due to structural defences and low protein content.

Young leaves are also the least protected against nutrient losses by rainfall leaching, since leaching occurs most readily when there are high inorganic nutrient concentrations in the intercellular spaces of leaves, as in periods of rapid growth and high nutrient accumulation. We have shown that young leaves present significantly lower wettability and leachability than adult, mature leaves, but even so, nutrient losses might be important. Expanding leaves during the rainless season greatly reduces any possible risk of nutrient loss. Lastly, leaf renewal and flowering in the dry season, when fires are most likely to occur, imply either that the buds develop after burning, and therefore the flames consume only a part of the old, senescent leaves, or that if a fire swept the savanna after leaf flush the damage could be repaired by a new growth since the shoots are in their active phase. We see then that in terms of both carbon gain and nutrient conservation, the annual phenodynamic cycle seems to be one of the masterpieces in the overall strategy of savanna trees.

Centring now on the various processes that affect the annual carbon budget of savanna trees, we indicate in Fig. 15A those features promoting near-maximum assimilation rates. Thus the maintenance of large, constantly active leaves, with open stomata, relatively high leaf water potential and leaf temperatures near to the optimum for photosynthesis, are all factors favouring high assimilation rates. Two additional features contributing to improve carbon gain are the maintenance of full foliage throughout the year (i.e. in opposition to deciduous species) without a rest period, and secondly, the rapid recycling of critical nutrients from stems and roots to developing leaves which allows, regardless of the limited external supplies, the use of nutrients when and where they are required: in leaves and buds at leaf flush and flowering, in the vascular cambium when growth is taking place.

The above characteristics notwithstanding, the inherent photosynthetic capacity of these trees is quite limited, thus setting a ceiling to maximum carbon gains. This innate limitation of the assimilatory apparatus is probably due primarily to morphological and functional traits imposed by nutrient limitations (Fig. 15B). Thus scleromorphic, low-nutrient leaves offer high internal resistance to CO_2 uptake. Furthermore, the high investment and energy cost of below-ground organs drains a significant part of carbon

A

Leaf temperatures
near to the optimum ____   Relatively high
for photosynthesis   leaf water potential
                                                           even under high VPD

High transpiration
rates

Stomata open   Relatively high photosynthetic rates
all day   ———→ All day   All year ◄———

                                                                    Evergreens,
                                                               leaf area relatively
                                                                 constant all year
        Rapid translocation ———
        of critical nutrients to   ——— Large leaves
        developing leaves

B

High mesophyll   Sclerophyllous   High investment
resistance to   low-nutrient leaves   and high energy cost
CO_2 uptake   of below-ground organs

                        ——→ Low photosynthetic
                              capacity

                            Higher costs, ◄———
                            lower incomes

C

Slow root turnover ———
                            Improves
                          annual carbon budget

High L/S ratio   Evergreens
                                                 continuous assimilation

        Low herbivore pressure ———   ——— High photosynthetic
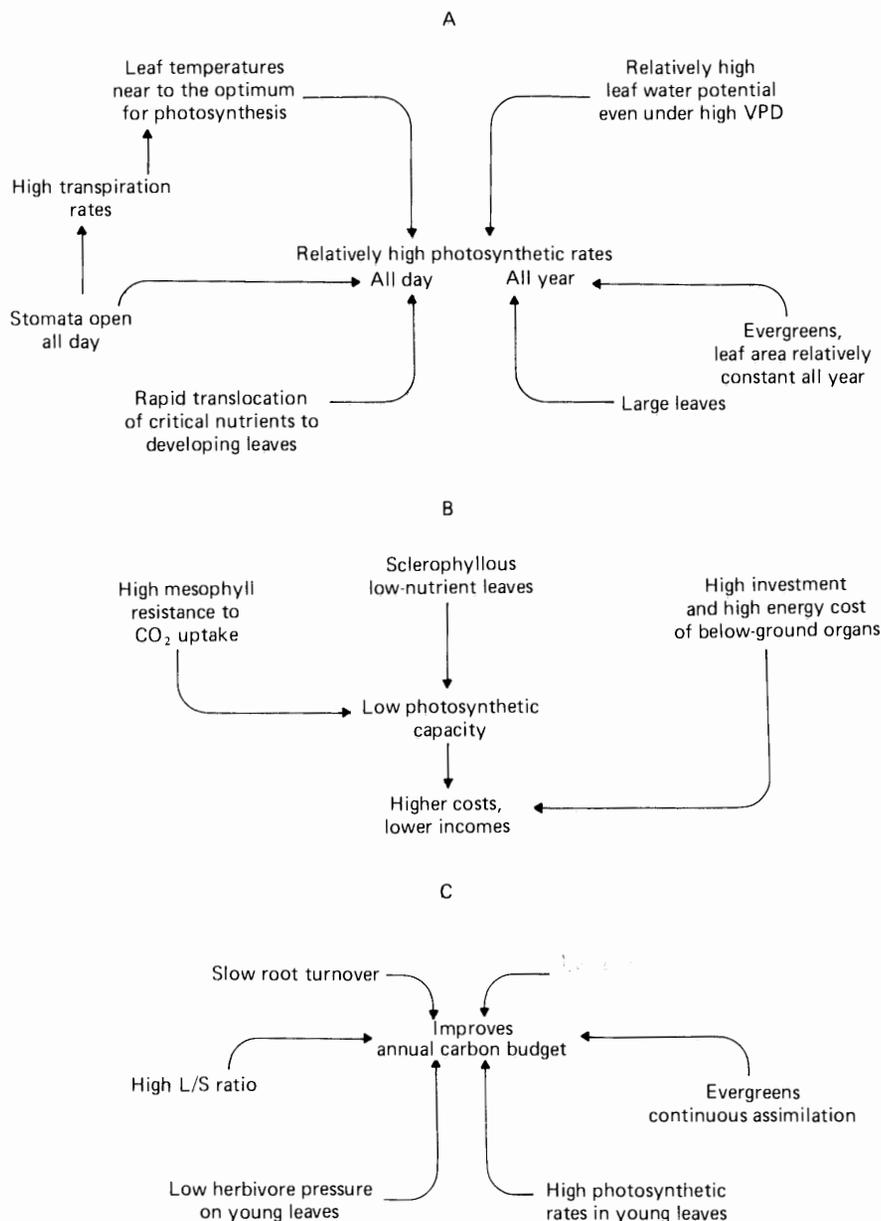   on young leaves   rates in young leaves

Fig. 15. Processes affecting the annual carbon budget of seasonal savanna trees. (A) Features and mechanisms contributing to maintain high photosynthetic rates under field conditions. (B) Processes affecting the carbon cost/income ratio. (C) Some characteristics that tend to improve the annual carbon budget.

gain to roots. Given the warm temperatures prevailing in the soil throughout the entire year, this cost must represent an important proportion of the total yearly carbon gain if root maintenance, growth and uptake of nutrients are taken into account (Caldwell, 1979). However, evergreen species growing in nutrient-poor habitats possess several attributes that may lower these costs. Among them we should mention the slow turnover

rate of below-ground organs, low root absorption capacity and hence lower expenditure per unit time in nutrient uptake, and the frequent occurrence of mycorrhizal associations that improve uptake of nutrients by roots with only minor energy cost to the plant (Chapin, 1980). Although these attributes have not been demonstrated in savanna trees, their normal association with evergreen woody species in conditions of nutrient stress leads us to think that in seasonal savannas they might also represent adaptations minimizing the investment in roots.

Figure 15C summarizes the aforementioned mechanisms, which contribute to the attainment of a positive annual carbon budget. To conclude, we present a synthesis in Table 8 showing the major plant responses and their interdependent physiological characteristics, which together constitute the stress-tolerant adaptive strategy of savanna trees.

VIII. CONCLUSIONS

Woody species in seasonal savannas show only slight seasonal variation despite the two contrasting humidity seasons characteristic of tropical savanna climate. These evergreen trees are able to match the high atmospheric evaporative demand while maintaining open stomata, given that the soil water resources are permanent. In this way they behave as water spenders. The year-round physiological activity puts them in sharp contrast with the perennial grasses of the herb layer, which significantly decrease their green biomass during the dry, unfavourable season (Sarmiento, 1984).

The adaptive advantage of maintaining almost unrestricted transpiration on both a daily and an annual level is obvious. Despite strong insolation, leaf temperatures remain closely coupled to the surrounding air temperatures even on the warmest days. Latent heat loss ensures that even at midday leaf temperatures do not greatly exceed the optimal range for photosynthesis. Furthermore, a continuously high water flow through the plant may have the additional consequence of increasing nutrient uptake by roots, by promoting ion movement through the bulk soil to the rhizosphere and by favouring pasive ion uptake in the incoming water flow.

On the other hand, it seems clear that nutrient limitations operate as the major stress on these species. Nutrients are scarce and thus photosynthetic machinery becomes relatively inefficient, as shown by the low photosynthetic capacity under optimal laboratory conditions. If carbon gain is intrinsically limited, this handicap has to be counterbalanced by improving other conditions tending to increase actual photosynthetic rates under field conditions. High leaf conductances, leaf water potentials that are always above the turgor loss point, besides continuous assimilation all year under near-optimum leaf temperatures, may all contribute to balance the annual carbon budget and may afford the relatively high investment directed to underground plant parts. We see then that the high water expenditure may be compensated by higher carbon gains and further nutrient uptake. But to have this strategy inevitably leads to low water-use efficiency.

If nutrient limitation is the crucial challenge to savanna trees, every mechanism promoting a better nutrient economy will be positively selected. Reallocation of the same absorbed nutrients, cutting down possible rainwash losses, and maintaining a continuous water-flow through the soil–plant–atmosphere continuum, seem to be some of the plant responses to nutrient shortage.

Perhaps a 'cost' these species have to pay as water spenders is the possibility of just maintaining quite low population densities, giving rise to the open woody cover

characteristic of savanna ecosystems. In this way the limited soil water resource is partitioned between fewer individuals that may thus use it unrestrictedly according to the atmospheric demands.

As a final observation we must point out that although throughout this review the basic similarities between savanna woody species were emphasized, a further analysis will undoubtedly show the particular adaptive pattern individualizing each species. We suggest (Goldstein *et al.*, 1985*b*) that adaptive patterns constitute a continuous gradient of plant responses going from species with a more or less clear avoidance strategy to those with a conspicuous tolerance syndrome, but maybe the most typical adaptive syndrome corresponds to species showing a combination of the two basic types, with a mixture of stress-avoiding and stress-toierant strategies.

IX. SUMMARY

1. In this review we discuss the adaptive strategy of woody species in tropical savannas. The low, evergreen, broadleaved, sclerophyllous tree is considered as the typical woody representative in these ecosystems. The discussion is largely based on data concerning four widespread neotropical species: *Curatella americana*, *Byrsonima crassifolia*, *Bowdichia virgilioides* and *Casearia sylvestris*, together with more fragmentary information available on other American and African savanna woody species.

2. Several types of savanna ecosystems with contrasting ecological features have to be distinguished. Our discussion refers to tree species in one of these types: seasonal savannas, that occur in a tropical wet and dry climate, with constantly high temperature, and on well-drained soils. Most of these savannas are normally burned once a year, towards the end of the dry season.

3. Woody species in seasonal savannas exhibit a quite distinctive morphology. They have low, tortuous trunks, deep and extensive root systems, relatively high R/S and L/S ratios, and large, highly scleromorphic leaves. Their annual phenodynamics appears somewhat puzzling since leaf renewal and expansion, as well as blooming, take place during the dry, apparently less favourable, part of the year.

4. Savanna trees maintain high leaf conductance throughout the year. Some species show a moderate midday decrease in leaf conductance suggesting partial stomatal closure, particularly under very high atmospheric water demands, or in young, developing leaves. However, given the steep vapour density gradient, transpiration flux density tends to be high, especially on clear dry-season days.

5. There is no drastic drop in leaf water potential, as might be expected with a high transpiration rate. The most negative values attained in either season only rarely exceed the leaf turgor loss point. This moderate fall in Ψ permits leaf expansion in the dry season. Variable hydraulic resistance contributes to maintain high water flow when steep Ψ gradients between soil and leaves are produced.

6. When all factors are taken into account, it seems that savanna trees maintain a favourable water budget all the year, thanks to their extensive root systems that may extract soil water from deep layers, thus allowing the maintenance of a high water flux through the soil–plant–atmosphere system even during the dry season. In this way, these trees have the least seasonal behaviour of all plant components in the seasonal savanna ecosystem.

7. Seasonal savannas occur on extremely poor, nutrient-deficient soils. As an

apparent consequence of this nutrient stress, the concentration of nitrogen, phosphorus, potassium, calcium and magnesium in leaves tends to be significantly lower than in forest trees or in drought-deciduous species.

8. Two mechanisms contribute to improve the nutrient economy. One is the reallocation of absorbed nutrients between old and young tissues; the other, the minimization of nutrient losses due to low leaf wettability, low leaf cuticular conductance, and leaf renewal in the rainless season.

9. Savanna trees have low photosynthetic capacity. This is probably due to high internal resistance of leaves induced by their low nitrogen concentration. However, under field conditions rates of CO_2 uptake may be maintained near their optimum because leaf conductance is high all day, and leaf temperature closely matches air temperature, remaining therefore within the optimal range for photosynthesis.

10. All in all, it appears that the physiological behaviour of savanna trees favours a continuously high water flux through the plant that, even if it lowers water-use efficiency, maintains leaf temperatures near optimum for CO_2 uptake, prevents sharp drops in leaf water potential, and induces a high passive uptake of soil nutrients. In this way, the close interaction between water, carbon and nutrient economies leads to the increased fitness of these populations in the seasonal savanna environment.

X. ACKNOWLEDGEMENTS

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