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Chapter 5

LIFE FORMS AND PHENOLOGY

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INTRODUCTION

One of the most enlightening approaches to the study of terrestrial ecosystems is that focused on the careful consideration of the morphological features and the phenological behavior of their member species, as expressed both by peculiar traits of external morphology and overall organization, and by sequential development of structures during each annual cycle. In ecosystems evolving in extreme environments, the external constraints to plant survival are so strong that just a few possibilities of morphological and phenological expression remain available, narrowing the range of possible plant responses to such unfavorable conditions; in these cases, then, species follow only a few different behavioral patterns. Warm humid tropical eco-systems, on the other hand, occupy the other extreme of the range of natural environments; here the external constraints are much more gentle and less varied, imposing only some broad limitations, mainly as a need to overcome some kind of seasonal water stress. Under such circumstances the possi-bilities open to the flora are so numerous that a wide range of life-cycle and life-form strategies becomes compatible with the successful perfor-mance of plant species.

According to this reasoning, warm humid tropi-cal ecosystems such as rain forests and savannas will exhibit a diversity of specific solutions to overcome the obstacles set by the biotic and physi-cal environment. A critical analysis of these plant responses may accomplish in this case a dual purpose: first, to penetrate into the very essence of the functioning of the ecosystems by recognizing patterns of spatial and temporal division in the allocation of resources among their populations;

and, second, to grasp the fantastic evolutionary skill displayed by plant life that led to successful survival under such a set of external constraints, including among the restrictive factors both abiotic strains and the biotic pressures derived from competition and coevolution.

The rich and taxonomically diversified floristic stocks of tropical savannas have evolved under environmental pressures that, though not ex-tremely harsh, represent a serious handicap to the performance of flowering plants. Species with a long evolutive acquaintance with these ecosystems have found adaptive answers to these challenges through different architectural designs and developmental patterns. Furthermore, the type of seasonal stress imposed by the humidity regime in savanna ecosystems has allowed a wider spectrum of plant responses than in the case of temperate ecosystems synchronized mainly with thermal seasonality, where low temperatures permit only a few strategies of survival through a cold season dormancy.

Within the whole tropical life world, savannas appear to be one of the most marked examples of seasonal ecosystems, the changes during each an-nual cycle being perhaps one of their most striking observable features. The woody and the herbaceous savanna species have to overcome the same major environmental risks: seasonal drought and/or flood, and periodic burning; they attain these goals by means of a precise synchronization of their successive phases with the rhythmically changing environment. The allocation of resources to the various plant structures must become compatible with the periodic consumption of almost the whole aerial standing crop by fire, and this sole drastic restriction has necessarily imposed certain architec-

tural patterns, while other solutions have had to be discarded as less efficient. The same may be said about the filtering effect of an extended dry season, operating as a strong selective sieve against plant forms and developmental strategies not suited to avoid, resist or escape this major environmental stress.

Besides the intrinsic importance of knowing the forms and rhythms of savanna species, this knowledge also appears as a necessary precondition to implement efficient procedures of ecosystem management, particularly in those ecosystems whose main role in the near future seem to be as natural rangelands. The desirability of improving the quality of this resource makes still more urgent an understanding of every aspect related to biomass allocation and to the seasonality of the species.

After the pioneer work of some of the founders of plant ecology (Warming, 1909; Clements, 1920; Braun-Blanquet, 1932; Du Rietz, 1931; Raunkiaer, 1934), the morphophenological approach to the study of plant populations and ecosystems fell into relative disregard, overwhelmed by an avalanche of floristic works of an increasingly quantitative nature. A more balanced treatment of the various aspects of plant ecology has been attained many decades later, following the ambitious projects of the International Biological Programme between 1968 and 1974, partly because of the obvious implications of growth forms and rhythms for an understanding of primary production processes. Furthermore, evolutionary plant ecology regained its lost position as an important biological subject, highly deserving recognition in its own right as a growing and powerful field of inquiry. The few far-sighted publications arguing for a more Darwinian approach to plant ecological problems (Harper, 1967) bore fruit in several convergent research lines which tackled the problems of plant populations within their respective ecosystems (Harper, 1977). One of these new research lines leads to a more dynamic approach to plant form and organization, viewed not just as ready-made structures, but as the accomplishment of an architectural design, coded in the genotype, but permitting varied phenotypic expression in accordance with the hazards of life cycles under the influences of diverse external modelling agents (Hallé and Oldeman, 1970). This integrated approach contributed to the renewed interest in plant form and in developmental pat-terns, not only by linking together both kinds of phenomena, but by putting them within a common frame of the natural ecosystems in which these structures and patterns have evolved (Oldeman, 1974).

However, in spite of all these recent advances in the ecology of plant populations, it is still too early to see them reflected in ecological studies of savanna species. Thus, for example, the architectural approach to plant form as defined by Hallé and Oldeman (1970) implies a detailed knowledge of the successive phases of plant development that is still far from being reached in savanna species, which by the very nature of the external stresses to which they are subjected, have a twisted appearance of quite difficult interpretation. Furthermore, the dis-entangling of architectural patterns in herbaceous plants is still only in its very beginning (Jeannoda-Robinson, 1977) and almost nothing is known about the architecture of perennial grasses. Neither has knowledge of the demography of perennial grasses advanced beyond its first steps, although one may hope for a vigorous development of these subjects during the next decade. We will be obliged, then, to restrict our treatment to a more classic approach, but on any possible occasion we will risk discussion of implications concerning architectural models and considerations regarding the evolutionary advantages of plant forms and developmental patterns.

The present situation concerning the knowledge of phenological strategies in savanna species seems to be somewhat better, since relevant information is already available at least for a few well-known ecosystems, such as the Lamto savannas in the Ivory Coast and the *llanos* savannas in Venezuela. Here, our task has mostly been limited to an analysis of this information in order to point out the main phenological patterns found so far in tropical savannas, and afterwards to discuss their possible significance as responses to the major environmental impulses and competitive pressures characteristic of these ecosystems.

Though both aspects of form and development cannot be isolated from each other if they are to provide a basis for the comprehension of adaptive strategies, in order to attain a clearer picture of these two aspects in our limited space we will proceed first to discuss life forms afterwards to enter into the consideration of seasonal cycles, and

to end the chapter with a joint treatment of the evolutionary implications of forms and rhythms, as well as of their relevance to understanding of the major characteristics of tropical savanna ecosystems.

LIFE FORMS

The Raunkiaer system of life forms and biological spectra (Raunkiaer, 1934), with various later improvements, has been widely employed to compare numerous floras from everywhere in the world. Table 5.1 shows some results for the floras of several savannas from different tropical regions.

Compared with Raunkiaer's normal spectrum, it is clear from Table 5.1 that phanerophytes are very much under-represented in the savanna flora, while therophytes appear in a much greater proportion than in the average world flora. The ensemble of chamaephytes, hemicryptophytes and geophytes is over-represented, though the participation of each group varies among the different savannas — perhaps partly because of differences in criteria among the authors about what life form should be ascribed to some species of subshrubs and perennial herbs. In general, hemicryptophytes and geophytes together seem to be the dominant group of life forms in the savanna flora. But, according to Raunkiaer's principles and conclusions, a "hemicryptophtic–geophytic phytoclimate" corresponds to a cool- or cold-humid climate proper to high latitudes or altitudes, quite unrelated ecologically to the tropical savanna environment.

This sort of result has led to the almost unanimous opinion among tropical ecologists that the applicability of Raunkiaer's life form system to savannas in particular, and to the whole tropical plant world in general, provides information of very dubious interpretation. On the one hand, this system classifies life forms primarily according to the position of buds during the unfavorable season, on the supposition that the limiting factor for plant growth was the low winter temperature. In tropical lowlands, obviously, low temperatures do not represent an ecological factor to be taken into account, the crucial environmental limitations being quite different, such as an extended drought as well as periodic burnings in seasonal savannas, plus a period of waterlogging in hyperseasonal savannas.[1] Bud height above ground level does not

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[1] The phrase "hyperseasonal savannas" was introduced by the authors (Sarmiento and Monasterio, 1975) to describe savannas subject to both seasonal drought and seasonal waterlogging.

TABLE 5.1

Life-form spectra for several savannas, according to the Raunkiaer system

Locality	Phanero-phytes	Chamae-phytes	Hemicrypto-phytes	Geophytes	Thero-phytes	Reference
Zaire, Lake Edward plains; mean of 2 savannas	5	38	22	5	29	Lebrun (1947)
Nigeria, Olokemeji savanna site	30	0	23	21	25	Hopkins (1962)
Ivory Coast, Lamto; mean of 8 savannas	9	1	62	9	19	César (1971)
Southwest Madagascar: mean of 11 savannas	21	18	26	3	32	Morat (1973)
Northern Surinam; total savanna flora	8	3	38[1]	28	23	Van Donselaar-Ten Bokkel Huinink (1966)
Central Venezuelan llanos, savanna flora of Calabozo	28	7	31	5	29	Aristeguieta (1966)
Western Venezuelan llanos, savannas of Barinas	11	3	18	40	28	Sarmiento (unpubl.)

[1] Including Geophyta geopodiosa.

influence the response of plants to these factors as it does to cold, which therefore renders the Raunkiaer system of low interpretative value in comparing tropical with extratropical plant communities.

On the other hand, a feature often noticed in tropical savannas is the occurrence of many species which are difficult to classify into one or another life form, since they behave as phanerophytes under certain conditions, and as hemicryptophytes under another environmental stress; there are even certain species that pass through three or even four different life forms during their development. In many tropical savannas, particularly those subjected to a severe dry season and to frequent fires, the growth patterns of certain perennial herbs and subshrubs show features that make their classification as geophytes, hemicryptophytes or chamaephytes so arbitrary as to lack any ecological significance; examples of this phenomenon will be mentioned later.

Due then to these inherent limitations of the Raunkiaer life form system, we thought it more fruitful to consider the most conspicuous forms occurring in savanna ecosystems without pretending to follow any formal system, focusing our attention on those morphological features that seemed to us to be of adaptive and evolutionary significance for plant fitness under the environmental conditions where these populations have been successful.

To start with, savanna species will be divided into three morphofunctional groups according to the degree of perennation of their vegetative structures. The first group comprises those species that have certain permanent above-ground structures, that is, some organs that live more than one year and receive therefore the full impact of a whole cycle of environmental stresses. The aerial plant parts living more than one year may, in a few cases, be the entire shoot including leaves and young branches, such as in palms for instance, more commonly the single persistent structure is the trunk together with old branches. This group includes all woody species, such as trees and shrubs, as well as caulescent palms and a few succulent rosettes, like the aloes in African savannas and the bromeliads in America. In Raunkiaer terminology all phanerophytes and chamaephytes, and certain hemicryptophytes are assembled here.

Our second group is formed by perennial species in which all above-ground parts are entirely seasonal — the aerial organs do not survive from one annual cycle to the next, but the plants have perennating underground structures of different types. To this group belong the geoxyles or hemixyles, that is, species with woody underground organs, as well as perennial herbs with non-woody rhizomes or bulbs. All geophytes, most hemicryptophytes and a group of species hard to classify into one or another category, have been assembled into this group.

A third type of growth form includes annuals, all of them lacking any perennating vegetative structure, of which only the seed bank persists during the unfavourable season. It corresponds to the therophytes of the Raunkiaer system.

We consider that this primary differentiation of three growth forms is more meaningful from an ecological viewpoint that the traditional division between woody and herbaceous species — firstly because it gives a clearer idea of the structural behavior of each species in face of the environmental constraints, and secondly because the strict anatomical differentiation of herbaceous and woody plants is not so straightforward as it might appear at first sight. Separation of primary and secondary tissues and structures is often difficult since in dicotyledons there are varying degrees of lignification (Esau, 1953), besides the great dissimilarities between "woody" monocotyledons and dicotyledons.

However, there is a difficulty with our proposed system: often enough, the ground level is not a sharp boundary for the separation of perennating structures, since in many species a woody organ may persist almost at ground level or immediately above or below it. Under other circumstances, the ground level may change a few centimeters either by sheet erosion, deposition or some biological artifacts, without affecting the survival of these species. Our criterion in these cases has been to consider a given structure as aerial or subterranean according to where most of its living biomass is located.

SPECIES WITH PERENNIAL ABOVE-GROUND ORGANS

In savannas, the tree form constitutes the major architectural type within this group, while palms,

shrubs, woody vines, succulents, caulescent rosettes, epiphytes and so forth are much less frequent types. We consider first, then, the main morphological features of savanna trees.

It is convenient to keep in mind that there has not been unanimity as to whether woody savanna species should be considered as trees or as shrubs, therefore we will regard as trees all woody plants with a well-defined trunk, and also those forms branching close to the ground or even bifurcating from the ground level itself. In fact, the branching patterns and the existence of a well-defined bole, or of several suckers sprouting from the stem base or from roots, are dependent on the past events acting upon any particular population; hence, the distinction between forms with one or with two or three main axes does not seem very important. Trees branching from ground level represent less frequent forms originated by suckering after fire damage, but under suitable circumstances these suckers will be able to become trees.

Once having stated what we call a tree, the first feature of savanna trees to note is the relatively modest development attained by their aerial biomass. In fact, in most savanna communities an overwhelming proportion of the tree flora have a mean height ranging from 2 to 6 m, the tallest individuals rarely exceed 12 m. When they reach their maximum development, most trees are just microphanerophytes or at the best some of them slightly surpass the upper limit of this class (8 m). This most obvious trait neatly separates the forest canopy species (in rain forests or in tropical deciduous forests) from the tallest savanna trees.

In accordance with their limited height, the arboreal savanna species also have rather small stem diameters; in any species, when an individual has already formed a single main bole and attained its maximum development, its diameter will usually be well below 40 or 50 cm, the average for mature trees being of the order of 20 to 30 cm. Lawson et al. (1968) gave the girth class distribution of all tree species (34 species) in four sample plots (50 × 50 m) in the Guinean savanna of northern Ghana. Their figures show a modal class at 20 to 30 cm, and a sharp decline in frequency above 70 cm, with just a few trees reaching maximum girth values slightly surpassing 100 cm. Menaut (1971) sampled the woody populations in the Lamto savannas with five 50 × 50 m quadrats, measuring tree height and stem girth at the base. His diagrams show that all trees were lower than 10 m, except the palm *Borassus aethiopum* which might attain 20 m; stem girths very rarely surpassed 150 cm, with the mean in the classes from 20 to 40 cm, while the histograms of frequency sharply declined above 50 cm. Ataroff (1975) gave figures for 200 randomly chosen individuals of the two most frequent tree species (*Curatella americana* and *Byrsonima crassifolia*) in the seasonal savannas of the western Venezuelan llanos. The mean stem girth at ground level calculated on her data are 26 and 23 cm, respectively; the largest girth recorded was 125 cm. These modest dimensions, both in height and trunk girth, together with a typically tortuous branching pattern, make the gnarled shape[1] the dominant tree form in most savannas. As a natural corollary of these facts, one may suppose that these low trees will show much less longevity than forest species. Through counts of annual rings, Warming (1892) found ages of about 30 to 40 years for the oldest individuals of several species of cerrado trees.

Taller trees, well above 12 m, occur in ecosystems transitional between savannas and deciduous forests as well as in small forest outliers within a more or less continuous savanna matrix, as has been reported for the central Venezuelan llanos by Sarmiento and Monasterio (1971). The same may be said about the "derived savannas" of the Guinean zone, where mesophanerophytes dominate the savanna tree layer (Hopkins, 1962; Menaut, 1971). These cases have to be considered rather as ecotones, mosaics or seral stages, where certain pioneering forest species may become established. Likewise the *miombo* woodlands in the Zambezian region have a taller tree canopy up to 20 or 25 m high; but most authors consider these ecosystems rather as open forests than as savannas, though when they have been cleared the resulting open woodlands have been often referred to as savannas.

Other morphological features shared by a high proportion of the arboreal savanna flora relate to leaf size, shape, texture and life span. The leaves may be either single or compound, but in any case their sizes fall most frequently within Raunkiaer's

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[1] Many authors have compared the shape of savanna trees to that of an orchard apple or of a fruit tree in temperate regions.

mesophyllous class. Microphyllous leaves are less common, while tree species with smaller leaves are almost absent. But generally the large, compound leaves of certain trees have numerous fairly small leaflets. Most species have flat leaves with entire margins, or if compound, with entire leaflets. The *Pinus* species of some Central American and West Indian savannas, however, constitute a conspicuous exception. In these features of leaf size and form, woody savanna species differ sharply from xeromorphic species characteristic of arid climates.

But the most noteworthy feature of the leaves of savanna trees is the scleromorphism that results from several characteristics, such as the superabundance of mechanical tissues and the deposition of silica. The anatomy of some of these leaves has been discussed by several authors (Morretes and Ferri, 1959; Beiguelman, 1962; Morretes, 1966, 1969; Mérida and Medina, 1967). Many species have leathery leaves that in some cases, such as in *Curatella americana* and *Palicourea rigida*, reach a consistency as stiff as pasteboard. A quantification of this scleromorphism is provided by the leaf area/dry weight ratio (Table 5.2). Other anatomical features frequently found in the leaves of savanna trees are: thick cuticle and cuticular layers; stomata

in the bottom of deep depressions; and great development of hypodermis and colorless parenchyma. These morphological traits are often accompanied by a high total ash content and slow stomatal reactions.

Leaves of savanna trees live for about one year, hence most species appear as evergreen or as brevideciduous. In these cases, leaf fall proceeds simultaneously with the development of a new leaf crop, in such a way that the total green biomass on the plant decreases during that period, but the trees never remain entirely leafless. Truly deciduous species — that is, those remaining leafless for several months — are less frequent and they often represent pioneering forest species colonizing certain savannas. This seems to be the case with *Cochlospermum vitifolium*, *Genipa americana* and *Godmania macrocarpa*, and other deciduous trees in certain areas of the Venezuelan llanos, as well as with several tall forest trees in the Ivory Coast savannas (Lamotte, 1978). The Brazilian cerrados, with a woody flora richer than any other tropical savanna area, have a larger number of deciduous species, but nevertheless they are far less numerous than the brevideciduous and evergreen species (Rizzini, 1965). Most woody species change their

TABLE 5.2

Area/weight ratios of mature leaves (in cm^2 g^{-1} dry weight) for several species of trees occurring either in the tropical deciduous forest or in the savannas of the Venezuelan llanos

Species	Area/weight ratio		
	Montes and Medina (1975)	Mérida and Medina (1967)	Sarmiento (unpubl.)
Deciduous forest tree			
Luehea candida	$317 + 39$		
Deciduous forest and savannas			
Godmania macrocarpa	113 ± 15		
Genipa americana	107 ± 18		
Savanna species			
Curatella americana	$69 + 6$	96	86
Byrsonima crassifolia	57 ± 7	84	81
Byrsonima coccolobaefolia			86
Bowdichia virgilioides		116	92
Casearia sylvestris		144	125
Palicourea rigida			76
Roupala complicata			62

leaves during the dry season. Towards the first weeks of the rainy season, apical meristems close further activity, and the plants enter then into a period without morphogenetic activities that extends throughout the whole rainy season.

Another characteristic shared by many savanna trees is the development of thick, hard, often corky barks — a trait of obvious value for the protection of the cambium against burning injury. Ferri (1962) illustrates several striking examples of these barks in cerrado trees, such as *Erythroxylon suberosum* and *Connarus suberosus*. Hopkins (1962) measured bark thickness in thirteen species of a Nigerian savanna, finding a mean of 15.2 mm and a maximum of 31.6 mm in *Cussonia kirkii*.

Concerning the behavior of woody species in response to fire damage or any other mechanical injury, one of the most general responses is sprouting from stumps, or suckering from rootstocks or from deep lateral roots. In this way, the shoots are reconstituted more or less rapidly after a traumatic destruction, this process leading to the coppice appearance of many tree populations. Lawson et al. (1968) illustrated various examples of this behaviour in the Guinean savanna. These responses to injury by sprouting and suckering are almost universal, too, in all Neotropical savanna ecosystems.

The tortuous and irregular branching patterns of savanna trees, as well as their open crowns, seem to be more a consequence of certain endogenous rhythms of meristematic activity than a phenetic response to external agents, whether drought or fire. In fact, many species may develop these features even under irrigation and fire protection, thus suggesting that this growth pattern derives from the death of apical meristems after each period of leaf formation and a subsequent development of adventitious buds during the next growth season. In some species like *Curatella americana* and *Bowdichia virgilioides*, under a regime of annual burning, the whole annual shoot growth dies back and the next season growth starts from adventitious buds that develop from the vascular cambium of older branches. In this way, a tree behaves merely as a mechanical structure supporting a crop of annual branches. In other species, or even in these same species under different environmental conditions, some annual branches develop profusely, giving rise to adventitious buds that will originate the next crop of leaves and branches, and

so develop the permanent aerial structures of the tree. Apparently, in many tree species the vascular cambium assumes the role of apical meristems as the main replacement tissue, since it will be responsible for any subsequent aerial development, either vegetative or reproductive; this is clearly shown in *C. americana* and *B. virgilioides*. Furthermore, numerous woody species are able to maintain themselves almost indefinitely as hemixyles — that is with annual shoots and woody underground structures — and even to complete the reproductive process in this growth form. Obviously, this is a behavior of high adaptive value in ecosystems subjected to seasonal drought and recurrent fires.

Many authors referring to African and American savannas have remarked that woody species which elsewhere are tree-like occur in savannas as shrubs with several stems sprouting from a xylopodium or from rootstocks, and that they are able to regenerate from these structures following the destruction of aerial parts. All these facts are in accordance with the statement above about the crucial role played by adventitious buds arising from the vascular cambium of stems and roots in the regeneration of the aerial shoots after a traumatic destruction.

But besides maintaining a tree population in a coppice state by sprouting and suckering, fire injury has also been thought of as responsible for the gnarled tree habit characteristic of woody savanna species. However, this does not seem to be the case, since in typical savannas the apical meristems of most trees cease their annual cycle of activity according to an endogenous rhythm, and any further growth has to depend on the development of new meristems in the form of adventitious buds arising from the cambium. This type of growth, with seasonally active apical meristems and the replacement of shoots through adventitious budding may explain the tortuous branching pattern of these trees.

The response of trees to fire damage during their active phase of leaf and flower production is the immediate development of a new crop of leaves and flowers through the fire-induced formation of numerous adventitious buds in the cambium of old branches uninjured by fire. Even when the whole aerial structures have been damaged, as is frequently the case with small individuals and low suckers, renewal is ensured by sprouting from

underground rootstocks or lateral thick roots. But if fire occurs during the wet season, when the trees are morphogenetically inactive, a new leaf crop is seldom produced. Many individuals die, and the surviving trees will not form a new leaf crop until the following dry season.

Another major consequence of fire and drought on the woody species is their maintenance as half-shrubs or hemixyles. In effect, many individuals may be maintained in this subshrubby stage for many years, so that in some species the tree form becomes almost exceptional, as occurs with *Casearia sylvestris*, *Byrsonima verbascifolia* and *Andira humilis*, for instance.

An interesting experiment has been reported by Labouriau et al. (1964) concerning the behavior of *Caryocar brasiliense*, a typical tree species of the Brazilian cerrados. This tree was cultivated from seeds; some young plants were kept under normal field conditions, others were irrigated during their first two dry seasons. In most saplings under the normal water regime, the shoot died back during the dry season and new growth started during the following rainy season from buds located at the base of the stem. Repetition of this behavior in successive years led to a geophytic habit, the plants gradually acquiring a large underground woody structure. By contrast, those plants which were irrigated during their first two dry seasons continued their development. Their branches remained alive throughout the year, sprouting again each wet season to form after five years a tree ten times higher than the subshrubby unirrigated individuals. This experiment clearly shows the influence of the dry season in the acquisition and persistence of the half-woody habit in what would otherwise be a potential tree. Some species under favorable conditions — such as when irrigated — maintain their branches which will give rise to further growth during the next cycle, acquiring then, more or less rapidly, the tree habit. The above experiment also indicates that fire reinforces the action of drought, but that its action is not crucial for acquiring either the subshrubby or the gnarled habit.

Another polemic point clarified by Laboriau et al. (1964) concerns the type of multiplication of cerrado trees. Some authors have supported the idea that seed establishment was extremely unlikely in savanna trees, and hence that most species relied on some form of vegetative propagation to maintain their populations. Through an extensive survey of the cerrado region, Labouriau et al. found 50 species of trees germinating under natural conditions, while 32 additional species were found as young plants probably originating through seed germination. These results suggest that germination may not be a major filtering process during the life cycle of a savanna tree, probably the fate of the young seedlings may be more important.

Besides trees, palms constitute another woody form of frequent and widespread occurrence in tropical savannas. There are two growth forms among savanna palms: the normal, monocaulous, tree-like rosette; and the acaulescent, dwarf palm habit. The first type is represented for instance by species of *Acrocomia*, *Butia* and *Syagrus* in the Neotropical seasonal savannas, by *Copernicia tectorum* in the hyperseasonal savannas of Venezuela, and by *Mauritia flexuosa* in *esteros* and other waterlogged communities throughout tropical South America. In Africa, *Borassus aethiopum* is a tall palm of wide geographical range, mostly occurring in wet soils. Several acaulescent palms of genera such as *Attalea*, *Acanthococos* and *Diplothemium* are common in the Brazilian cerrados (Fig. 5.1). They are a part of the herb layer of these seasonal savannas, and must really be considered as geophytes, since even their hard, large leaves dry out during the dry season. Another architectural type related to palms is the low, few-branched rosette of some Velloziaceae; they occur mostly in rocky habitats, but also become frequent in some areas of cerrados.

Woody vines and epiphytes are rather exceptional in savannas, among this latter form we may include a few bromeliads and cacti in South America. The aphyllous-succulent form is also not characteristic of savannas, the columnar cactus *Cereus jamacaru* is one of the few exceptions. Some bromeliads of the genera *Bromelia*, *Dyckia* and *Ananas* represent the succulent rosette form in the Neotropical area, while the same growth form in Africa is exemplified by the aloes. Succulent trees also appear to be exceptional, some Bombacaceae may be among the few examples of this life form.

In hyperseasonal savannas, a different woody form may predominate, represented by spiny legumes with deciduous, compound leaves, such as the species of *Acacia* in alluvial communities

25 cm

140 cm

10 cm

Craniolaria integrifolia

35 cm

45 cm

Attalea exigua
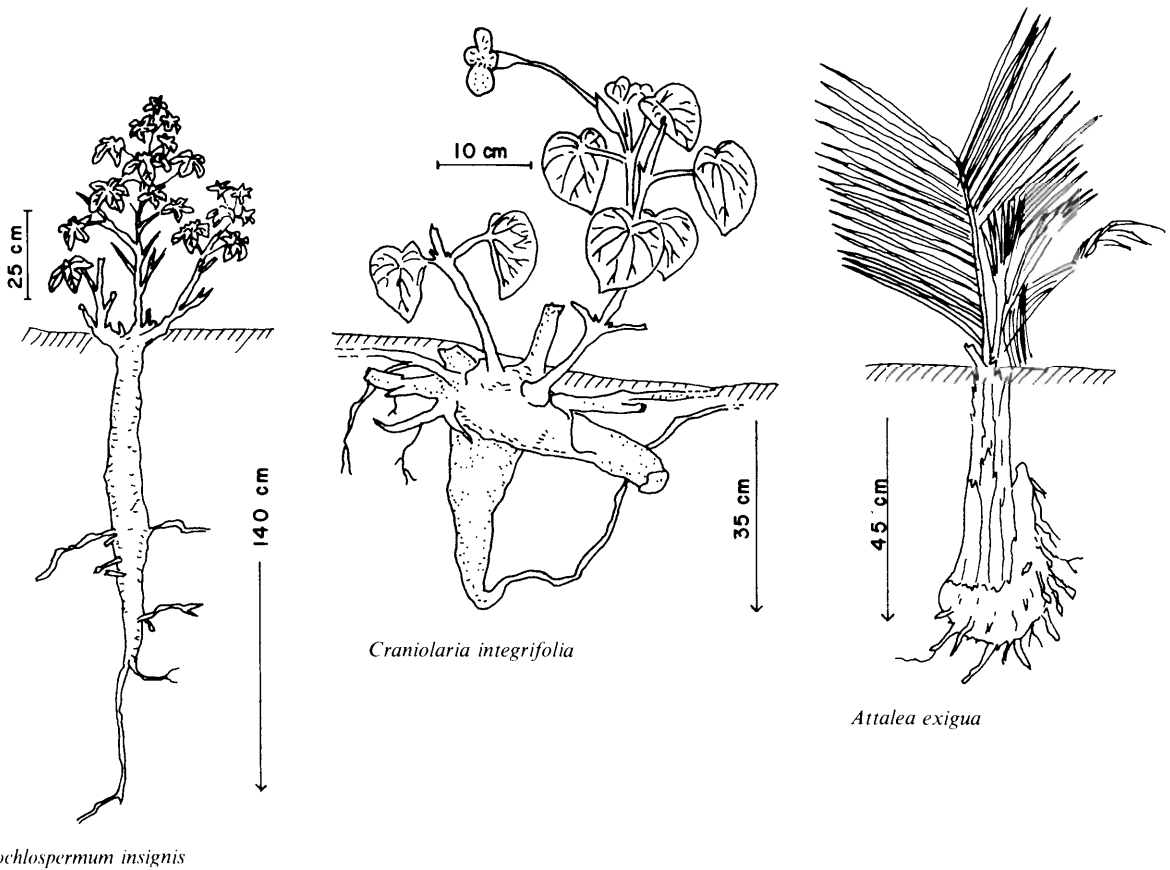
Cochlospermum insignis

Fig. 5.1. Some growth forms characteristic of the cerrado savannas. *Cochlospermum insignis* has a deep and prominent xylopodium; *Craniolaria integrifolia* has a branched, more superficial underground structure; the dwarf palm *Attalea exigua* shows a deep, corm-like organ. (After Rawitscher and Rachid, 1946; and Rachid, 1947.)

throughout tropical Africa, and species of *Acacia*, *Mimosa* and *Prosopis* in America. In many cases, these species may be considered rather as shrubs than as trees. When compared with the trees characteristic of well-drained soils, the differences sharply point out the enormous ecological dissimilarities between these two types of savanna ecosystems.

A last point, but by no means the least important, refers to the extensive nature of root systems in savanna trees, which apparently enable them to exploit the water and mineral resources of a great volume of soil. There are many references on the remarkable development of vertical roots in deep soils, particularly when the water table remains deep all year and there are no physical barriers to root penetration. According to Rawitscher et al. (1943) cerrado trees can develop enormous root

systems when growing in deep soils. They report the example of *Andira humilis*, a "subterranean tree" whose roots have been found to a depth of 18 m. Foldats and Rutkiss (1969) showed how the most widespread trees in the Venezuelan savannas have thick superficial roots that may reach twenty or more meters in length. Likewise, Van Donselaar-Ten Bokkel Huinink (1966) reported a similar type of root development in many of the trees of the Surinam savannas. Lebrun (1947), Lawson et al. (1968), and Menaut (1971) reported similarly on the vertical and horizontal root development of tree species in various African savannas.

The general picture emerging from these observations is that many trees have a double-purpose root system, with a main tap root able to reach great depths under favorable circumstances, and a very extensive crown of thick lateral roots

emerging at various depths from the main root. In shallow soils only this latter system may develop.

In several species, like the widespread African species *Parinari curatellifolia* and *Daniellia oliveri*, root suckers develop after mechanical destruction of aerial parts; other species, like *Burkea africana* and many other savanna trees, have a remarkable capacity to regenerate by repeated sprouting of coppice shoots from the underground stump that gradually develops after successive shoot regenerations.

A final characteristic to notice in tree species is their capacity for rapid root elongation from the young seedling stages, a feature that obviously will greatly increase the chances of survival when the upper soil layers progressively dry out.

HALF-WOODY LIFE FORMS

Among the species without perennial aboveground structures, we have further distinguished those forms having woody underground organs from the perennial herbs having only fleshy rhizomes, bulbs or other non-lignified perennating organs. Plants with woody underground organs, but with all shoots annual, constitute one of the most characteristic life forms in American as well as in African savannas, either considering the number of species having this growth habit, or taking into account that they seem to be almost peculiar to these ecosystems. This life form has been variously called subshrubby, half-shrubby, suffrutescent, geofrutescent, geoxyle, hemixyle, half-woody, etc.

Two cases of different ecological and evolutionary significance have to be distinguished within this growth form: the permanent geoxyles, that will conserve this growth habit under any circumstance; and the traumatic geoxyles, in which this habit results from external injury, but which will revert to their normal tree habit when circumstances are favorable.

Seasonal savannas, particularly those ecosystems occurring on deep and well-drained soils, may show a rich diversity of subshrubs; but this life form appears more rarely or is completely absent in hyperseasonal savannas or waterlogged sites. To attain an evolutionary interpretation of this plant strategy, it may be important to point out that often the subshrub species of the savanna belong to genera mostly composed of forest trees or less commonly of forest woody vines. This is the case of *Anacardium pumilum*, *Andira humilis*, *Cochlospermum insignis*, *Jacaranda decurrens* and many other vicariant species that have acquired the suffrutescent growth habit. Other subshrubs belong to genera whose species include both herbs and subshrubs, like the genera *Cissus*, *Eriosema*, *Galactia*, *Indigofera*, *Tephrosia* and many others.

Warming (1892), in his unsurpassed study of the cerrado at Lagoa Santa, already called attention to this peculiar growth form, remarking how it was difficult to decide whether these species should be considered as perennial herbs, as subshrubs, or as shrubs. Rawitscher et al. (1943) and Rawitscher and Rachid (1946) described large woody, underground systems as quite frequent among cerrado species, analyzing the case of the extensive underground systems of *Anacardium pumilum* and *Andira humilis* that led them to the concept of "subterranean trees"; likewise they illustrated the conspicuous xylopodia of *Cochlosperum insignis* and *Craniolaria integrifolia* (Fig. 5.1) as typical of many cerrado subshrubs. All these species, as mentioned above, are vicariants of forest trees.

Rizzini and Heringer (1966) differentiated, among the cerrado species with this growth form, trees maintained in this suffrutescent habit on the one hand, and true subshrubs, either with xylopodia or with an extensive woody system, on the other. This latter case, which they called **diffuse underground systems**, may be either of caulinar or of radical nature, but only careful anatomical observation may distinguish between them. This functional convergence between organs of different nature is striking, since both types have the same key function in regeneration and clonal growth. Rizzini and Heringer listed among subshrubs with an extensive underground system of radical nature, the species *Anemopaegma arvense*, *Peschiera affinis* and *Coccoloba cereifera*, while *Annona pygmaea*, *Esenbeckia pumila*, *Chrysophyllum soboliferum* and others have caulinar underground structures.

In the flora of the Surinam savannas, the hemixyles are the best represented group. Van Donselaar-Ten Bokkel Huinink (1966) reported that, among 23 species of subshrubs, 19 have a conspicuous xylopodium, while 16 species of perennial "herbs" also have a woody stem base. The author proposed to name these forms *Geophyta*

geopodiosa. In the seasonal savannas of the Venezuelan llanos, the geoxyles with large woody xylopodia are well represented, among them being, for instance, several species of *Galactia, Indigofera, Pavonia* and *Ichtyothere.* Extensive underground systems are less common than in the cerrados, some examples being species of *Psidium, Clitoria* and *Tephrosia.* On the other hand, species like *Byrsonima verbascifolia* and *Casearia sylvestris* which under some circumstances are low, gnarled trees, appear in this region almost exclusively as geoxyles.

Most African savannas also have a rich flora of half-shrubs. Lebrun (1947) gives several examples from the Lake Edward plain, such as *Vigna friesiorum* and *Cissus mildbraedii,* both with conspicuous xylopodia. In these savannas the suffrutescent species form 35% of the flora. Duvigneaud (1949) distinguished "steppes" from savannas in the lower Congo. His concept of "steppe" is equivalent to the type we have called savanna grassland, while his savannas comprise both hyperseasonal ecosystems and degraded forests. Duvigneaud considered that the two growth forms most characteristic of the "steppes" were perennial bunch grasses, and shrubs with xylopodia, this latter form frequently represented by vicariant species of rain-forest trees; on the other hand, the subshrub form is almost completely lacking in his savannas. In further papers he considered rhizomatous subshrubs with annual shoots that dry out completely during the rainless season as the ecological group characteristic of the Zambezian "steppes" and "steppic savannas" (Duvigneaud, 1955, 1958). Thus this growth form is characteristic of grasslands on the high plateaus covered by the Kalahari sands. Malaisse (1975) in his study of the Upper Shaba (Zaire) vegetation, followed the nomenclature of Duvigneaud for the plant formations, indicating, as a distinctive feature of the "dry steppes" on the sandy plateaus, the abundance of geofrutices, among which he listed *Syzygium guineense, Parinari capense* and *Eugenia malangensis.* In a similar way, the "tree steppes" are rich in subshrubby species, while the "humid steppes", with a high water table, only show one species with this growth habit: *Syzygium guineense.*

Schnell (1976–77) in his monograph on tropical African vegetation indicated that dwarf-woody species constitute one of the peculiar growth forms of the plateau savannas in the whole Congo area.

Referring to a paper by Makany (1970), he listed as the more frequent geophytic subshrubs *Parinari pumila, Anisophyllea poggei* and *Landolphia thollonii,* all three vicariants of rain-forest trees.

In West Africa, on the other hand, there are relatively few species with a well-developed woody underground system in comparison with the Zambezian savannas, except traumatic forms of trees. In the Lamto savannas, César (1971) remarked on the abundance of suffrutescent forms in the herb layer, listing among them some species of *Cissus, Galactia, Rhynchosia* and *Eriosema.* However, these species do not seem to reach the huge underground development of other geoxyles. As these species are difficult to classify according to the system of Raunkiaer, César proposed for them the term **geochamaephytes**. In the same area of the Ivory Coast, Menaut (1971) discussed the case of the commonest tree components of the ecosystem which are able to maintain themselves for a long time in a subshrubby form, and even to complete their sexual reproduction in this state. Menaut considered that both drought and fire could be responsible for the subshrubby form of these otherwise normal trees, since only in some favorable years may the annual aerial growth develop further to form perennial above-ground structures.

After reviewing the variety of woody and half-woody growth forms occurring in most savannas, one could hypothesize an entire sequence of evolutive changes leading from species of "normal" trees to temporary hemixyles by the replacement of apical meristems by the vascular cambium as the main organogenetic tissue, and by the development of the capability to sprout from the stem base or from roots after a fire or drought injury. These temporary hemixyles possibly acquired later the capacity to flower in this stage, thus opening the way for a later evolutive change to permanent hemixyles; thus the original trees have been transformed by successive adaptive changes to geoxyle well suited to cope with the savanna environment, but unable to recover their ancestral tree habit. Obviously, this model only applies to those subshrubs which are vicariant of forest trees. It is interesting to notice that in the oldest savanna areas, such as the cerrados, which have evolved for a long time in close contact with tropical forests, this type of hemixyles predominates over the suffrutescent genera, while in younger ecosystems, such

as the Orinoco llanos or the derived savannas of the Guinean zone, the reserve situation is true: almost all subshrubby species belong to genera without obvious ancestral tree forms.

THE HERBACEOUS PERENNIAL LIFE FORMS

To this group, devoid of woody structures of any kind, belong the dominant species in the herb layer of all types of tropical savannas, those that contribute most to the structure and primary production of the ecosystems and that control the possibilities and frequency of fires. Within this rich and diversified group, we will first discuss the major morphoecological features of the dominant growth form in any tropical savanna: the tussock grasses and sedges.

The tussock form is represented in the savannas by species that have perennating underground structures relatively close to ground level, while all aerial parts are entirely seasonal. The perennial organs are rather thin rhizomes that survive more than one year, characterized morphologically by their short internodes and scaly leaves. Through various branching patterns, the rhizomes give rise to the typical tuft or bunch of tussock species. The compactness of the tussock will depend on the length of the internodes and on the branching pattern of rhizomes. Tillers may be exclusively formed by the rhizome's apical meristem, or by the development of buds in the axils of the scales. Thus, a great variation of architectural models may be found within the same basic type of growth habit, such as: tussocks with or without aerial culms; culms that may or may not branch; rhizomes forming short internodes only, or changing periodically from short to long internodes; monopodial or sympodial branching; plants with or without runners or stolons; and so forth.

The architecture of two common Neotropical tussock grasses may illustrate the variability of developmental patterns within this life form. *Leptocoryphium lanatum* shows a modular structure where the basic modular unit is an upright shoot or tiller formed by a much reduced underground rhizome with short internodes and nodes with normal leaves. At a particular period of the annual cycle, the apical meristem of the rhizome changes to a reproductive stage, producing the single aerial

culm of each module: an inflorescence axis bearing reduced leaves. After that, some axillary buds start to develop and reproduce the module in a sympodial fashion. This proliferation of axillary buds on short vertical rhizomes gives rise to the compact corm-like underground structure of this plant (Fig. 5.2). Each module has definite growth and lives only one year, the perennation of the tussock is ensured by sympodial growth through several additional modules formed by the axillary buds of rhizomes.
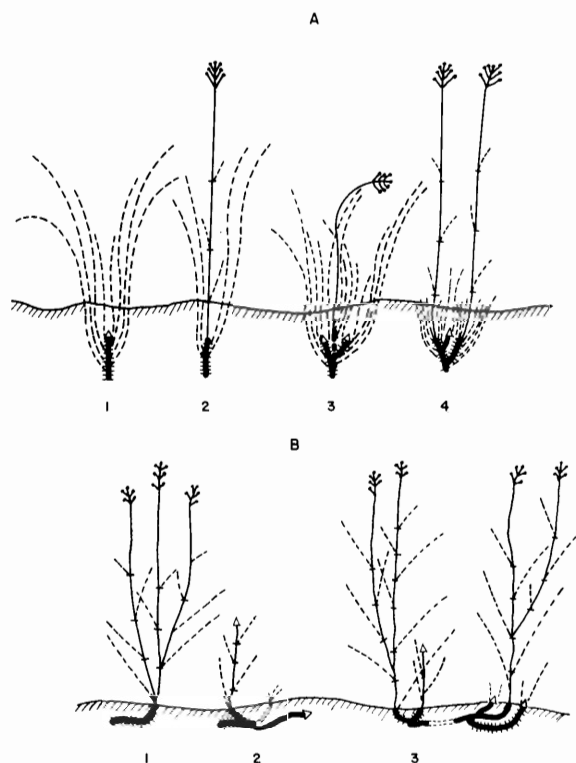

Fig. 5.2. Architectural patterns of two tussock grasses. A. *Leptocoryphium lanatum*: 1, the vertical rhizome with its apical bud, short internodes and leafy nodes; 2, the apical bud has changed to the reproductive phase forming the inflorescence, sole aerial axis of the plant; 3, after decay of the reproductive structures, axillary buds on the rhizome give rise to lateral branches; 4, the old rhizome and the aerial tiller it produced have decayed and new rhizomes repeat the growth process. B. *Trachypogon plumosus*: 1, a young tussock formed by a horizontal rhizome with short internodes that gives rise to a branched aerial tiller with long internodes and terminal inflorescences; 2, after the old tiller dies back, axillary buds on the rhizome form various lateral branches, some with short, others with long internodes; 3, by fragmentation of the old rhizome a loose tussock is composed of more or less independent tillers.

A different architectural design is shown by another widespread savanna grass: *Trachypogon plumosus*. This species has horizontally spreading rhizomes bearing scaly leaves, that may form either short or long internodes. Apical meristems give rise to the aerial tillers, which consist of long, branching culms, bearing normal leaves. When these meristems change to a reproductive stage, the inflorescences are formed and the development of a given tiller comes to the end. Buds in the axils of scale leaves give rise to branches of the original rhizome, thus originating a compact underground structure in which the branched rhizomes produce further rhizomes through the development of lateral buds and produce tillers from their apical meristems (Fig. 5.2).

These two examples illustrate the possibilities of obtaining different modular patterns through rhythmical functioning of meristems or through functional differentiation between apical and axillary buds, but in any case it is worthwhile to emphasize that the disentangling of these architectural designs remains yet at its very beginning.

Most tussock grasses and sedges have hard, scleromorphic leaves, either flat or revolute, glabrous or densely pubescent, with abundance of silica bodies that may be utilized to recognize the species. In fact, a series of contributions have built a catalogue for the identification of soil phytoliths in the cerrados for use as an auxiliary character in grass taxonomy (Sendulsky and Labouriau, 1966; Campos and Labouriau, 1969; Teixeira da Silva and Laboriau, 1971; Figueiredo and Handro, 1971).

Another morphological feature characteristic of many perennial savanna grasses is the protection of the apical bud from fire and dessiccation by a thick tunic formed by the old leaf sheaths; Rachid (1956) described this structure in several cerrado grasses, such as *Aristida pallens*, *Tristachya leiostachya*, and *Paspalum carinatum*. Tunicate species having their buds well protected at ground level are able to regrow rapidly after fire, the buds not only remain totally unharmed but revert to an active phase.

A majority of the species of tussock grasses belongs to the tribe Andropogoneae and are C_4 plants, but C_3 species are also well represented in tropical savannas, particularly on ill-drained, wetter habitats. Concerning tussock height, most species fall into the class Beard (1953) named as

"tall bunches" (50–220 cm in vegetative stage), but some Paleotropical grasses are "high grasses" (120–240 cm tall); this is the case, for instance, in *Hyparrhenia* species, as well as in several species of *Pennisetum*, *Panicum* and other genera. In tropical American savannas, on the other hand, native high grasses are rather exceptional, only a few species of *Paspalum* and *Panicum* in hyperseasonal savannas reaching these heights. But one may recall here that some Old World bunch grasses, such as *Hyparrhenia rufa* and *Panicum maximum*, have become widely established in tropical America, colonizing modified habitats produced by forest clearing; nowadays, these alien grasses extend even over areas of disturbed savannas.

Bunch grasses and sedges may have their renewal buds immediately above the ground, in which case they have to be considered as hemicryptophytes; these buds stay well protected against desiccation and burning by a thick cover of old leaf sheaths. Other species are geophytes, the buds lie in the soil at depths down to ten or more centimeters.

In respect of allocation of energy and resources, the two major features that characterize tussock grasses are: first, a relatively weak reproductive effort during each annual cycle, since only some tillers in each bunch reach the flowering stage; and, second, a biomass allocation to the underground organs leading to a high ratio of below-ground to above-ground biomass Table 5.3 gives some data from dominant bunch grasses of the seasonal Venezuelan savannas.

Besides the tussock growth form, other architectural patterns found among the herbaceous savanna species include perennial grasses with isolated tillers. César (1971) remarked that in the Lamto savannas only two grasses belong to this type: *Imperata cylindrica*, with long rhizomes, and *Schyzachirium platyphyllum*, which extends by aerial stolons. In Neotropical savannas, particularly in hyperseasonal ecosystems, rhizomatous and stoloniferous grasses and sedges are not uncommon; sometimes they become the dominants of the herb layer. This is the case, for instance, with *Imperata brasiliensis*, *Paspalum chaffanjohnii* and *Leersia hexandra*, as well as several sedges of the genera *Cyperus*, *Kyllinga*, *Rhynchospora* and others. These species spread more rapidly than the slow-moving bunch grasses, thus becoming efficient colonizers on disturbed habitats; their extensive

TABLE 5.3

Some data concerning biomass allocation, reproductive effort and growth rates of five dominant species of perennial tussock grasses in Venezuelan savannas (H/E=ratio of below-ground to above-ground biomass, six months after fire; R/E=ratio of maximum reproductive biomass to maximum above-ground biomass)

Species	H/E	R/E	Average growth rates (mg dry weight per plant per day)		
			30 days after fire	132 days after fire	178 days after fire
Trachypogon vestitus	0.9	0.10	60	166	303
Axonopus canescens	1.1	0.05	27	63	98
Leptocoryphium lanatum	4.7	0.14	223	133	237
Sporobolus cubensis	1.9	0.11	690	172	161
Elyonurus adustus	1.8	0.08	367	272	284

Growth rates are minimum estimates assuming no decomposition, and are averages over the whole period considered. (from Sarmiento, unpublished data).

rhizomes give rise to new tillers, more or less apart from one another, that may in turn become centers for further spreading during the following season.

Finally, with regard to the growth forms of other perennial herbs, it may be stated that the most common life form of these species in tropical savannas is the bulbous geophyte, represented by numerous species of Amaryllidaceae, Iridaceae, Liliaceae, Orchidaceae and some other families. As will be shown later, these species have only a short active period, and remain most of the year as underground latent structures. Less frequent are rhizomatous geophytes and hemicryptophytes with aerial perennating structures at ground level, such as some orchids of the genus *Cyrtopodium*.

THE ANNUAL PLANTS

The representation of annuals in the savannas is highly variable, although their contribution to the biomass of the herb layer may be considered as generally inconspicuous. In the cerrados of the Lagoa Santa area in central Brazil, Warming (1892) remarked on the scarcity of annuals, since, of a total of about 730 species, the annuals hardly amounted to 30, forming thus less than 5% of this flora. Almost every author dealing with the cerrado

vegetation has noted the under-representation of annuals.

In the Venezuelan llanos, the importance of therophytes varies according to the habitat. They become more common in the driest sites, such as sand dunes and lateritic outcrops, and on the other hand, they colonize the unstable habitats created by seasonal fluctuations in swamps and other water-logged sites; likewise, they are well represented among the flora colonizing disturbed habitats. Ramia (1974) lists, for the whole area of the Venezuelan llanos, 55 species of annual grasses as against 145 perennial species in this family. In the llanos, the more widespread annual grasses belong to the genera *Andropogon*, *Aristida*, *Diectomis*, *Eragrostis* and *Gymnopogon*, while some frequent annual sedges belong to the genera *Cyperus*, *Fimbristylis* and *Scleria*. Among other families, some genera with a good representation of annual species in the savannas are *Borreria*, *Cassia*, *Euphorbia*, *Heliotropium*, *Hyptis*, *Polygala* and *Stylosanthes*.

In Lamto, César (1971) found only one annual grass, *Sorghastrum bipennatum*, while the proportion of therophytes varied among the different savanna communities in that area from less than 5% in the *Loudetia* grass savanna to more than 30% in the Andropogoneae shrub savanna. In the following section we will further discuss the behavior of annuals during the different seasons.

PHENOLOGY

In spite of the unquestionable interest that knowledge of annual cycles and seasonal rhythms of plant species represent for a deeper understanding of the behavior of the whole ecosystem, as well as to provide a sound basis for any type of management practice, systematical phenological observations on tropical savanna ecosystems have been till now astonishingly scarce.

In this field, as in many others related to tropical ecology, Warming (1892) was the pioneer. Almost seventy years later, this approach to Neotropical savannas was followed by Van Donselaar-Ten Bokkel Huinink (1966) in Surinam and by Monasterio (1968) in Venezuela. Hoock (1971) in his study of the savanna vegetation of French Guiana, presented some relevant data on the phenological cycles of the most frequent species. More recently, Coutinho (1976) reported the changes in phenological behavior of some cerrado species as a response to fire; Monasterio and Sarmiento (1976) presented a view of the main phenological strategies of plant species in the Venezuelan seasonal savannas; Ramia (1977, 1978) followed plant behavior along topographic gradients in the southern Venezuelan savannas; and Sarmiento (1978) discussed the general picture of plant rhythms related to other major ecological aspects of Neotropical savannas. In Africa, several early papers dealing with vegetation types and classification included phenological observations (Lebrun, 1947; Duvigneaud, 1949; Sillans, 1958; Koechlin, 1961), as do those of Morat (1973) for Madagascar, Perera (1969) for Sri Lanka (Ceylon), and Moore (1973) for the Australian grasslands. The first quantitative data on seasonal growth were presented by Hopkins (1970), who analyzed the growth patterns of several species in the derived savannas of Nigeria. More recently, the phenology of the Lamto savanna in the Ivory Coast has been considered by César (1971) in respect of herbs and by Menaut (1971) for woody species.

The basic phenological concepts that will be employed hereafter have been discussed in our previous paper (Monasterio and Sarmiento, 1976), together with certain methodological problems involved in sampling and measuring phenophases in natural populations; we refer to that paper for these two basic points. Our approach to the phenological behavior of a certain species in a given ecosystem is to consider this as simply a partial component of its global evolutionary strategy (Monasterio, 1982). This means that the adaptive mechanisms of any population may operate on every response relating the individuals, in each of their developmental phases and life-cycle stages, to the outside impulses and constraints of the biological and physical environment; hence their results may be expressed in an interplay of features and processes, including growth form, architecture, life cycle, annual and circadian rhythms, reproductive strategies, demographic structure, and so on, each response constituting a partial element of the global strategy of that population in that ecosystem.

The species that show similar patterns in their phenodynamics may be assembled into phenological groups, each one representing a major phenological strategy which allows its species to cope successfully with the cyclic fluctuations of the environment, and of the ecosystem as a whole, through the perception of some periodic signals and impulses coming from the outside. We consider in the following pages the main strategies as they have been described in the various tropical savannas, leaving for a final section a general discussion on the significance of these rhythms to the functioning of the whole ecosystems. Hopkins (1968) emphasized that no two savanna species show exactly the same annual rhythm; but, although this observation may be correct, our groups seem to disclose roughly similar phenological patterns within species that otherwise may diverge from each other in many important aspects.

The phenological groups were established by taking into account certain crucial rhythmic activities of the species (Table 5.4 and Fig. 5.3). A first major division sets apart species with assimilation all year from species with seasonal carbon gain, which consequently have a rest period devoid of any above-ground activity. Within this last group we differentiate the perennials, with latent underground structures, from the annuals which are present only as a seed bank during a certain period of the year. In turn, both groups are further subdivided — according to the reproductive phenodynamics — into species having precocious flowering (at the beginning of the rainy season); delayed flowering (from the middle to the last part of the rainy season); tardy flowering (during the dry

TABLE 5.4

The major phenological groups of savanna species and the features utilized for their characterization; the species are those after which the groups in question are named

			Perennials	Annuals
Carbon assimilation all year	Growth continuous or nearly so	flowering — precocious	A1. *Leptocoryphium lanatum*	
		delayed	A2. *Trachypogon plumosus*	
		tardy	A3. *Cassia moschata*	
		continuous	A4. *Evolvulus sericeus*	
		opportunistic	A5. *Imperata brasiliensis*	
	Growth seasonal	flowering — precocious	A6. *Jacaranda decurrens*	
		delayed	A7. *Piliostigma thonningii*	
		tardy	A8. *Curatella americana*	
Carbon assimilation seasonal (resting phase)		flowering — precocious	B1. *Curculigo scorzonaerifolia*	B2. *Spilanthes barinensis*
		delayed	B3. *Bulbostylis junciformis*	B4. *Aristida capillacea*
		tardy	B5. *Cochlospermum vitifolium*	B6. *Egletes florida*
		opportunistic		B7. *Phyllanthus sublanatus*

season); and opportunists, able to bloom in any period if suitable conditions occur.

Among the species with continuous carbon assimilation, all of which obviously are perennials, we distinguish a group that has continuous or nearly continuous growth from another group with strictly seasonal growth. Both groups are further sub-divided on the basis of their reproductive dynamics, thus giving groups with precocious, delayed, tardy, continuous and opportunistic flowering behavior. The terms "precocious", "delayed" and "tardy" imply that one takes as the starting point for each annual cycle the onset of rains, but this is pure convention, since it might be argued that the "tardy" flowering species are in fact the most precocious, and vice versa.

By application of the above criteria, one may obtain phenological groups that combine species with comparable behavior in respect of some of their chief dynamic features, such as the duration of life cycle (perennials vs annuals), the seasonality of the assimilatory structures, the rhythm of meri-stematic activities (apical meristems of the shoot), and the timing of flowering. Within each group the species may differ in other important character-istics of their phenodynamics, but the groups are homogeneous enough to give us a glimpse of the wide possibilities of phenological expression pro-vided by the savanna ecosystems to their com-ponent species. To each phenological group we give the name of a typical savanna species showing that phenological behavior; we will briefly consider now the major characteristics of each of these groups.

PRINCIPAL PHENOLOGICAL GROUPS IN THE SAVANNA FLORA

A. Species with carbon assimilation all year

A.1. Species with continuous growth and precocious flowering. The *Leptocoryphium lanatum* group

The phenodynamics of these species may be summarized as follows (Fig. 5.4). A phase of vigo-rous shoot growth starts with the onset of rains after the long dry season, or even before that if the savanna has burnt during the last weeks of drought. Leafing and blooming, as well as tillering in the grasses, proceed simultaneously, or in some species inflorescence elongation precedes leafing. The growth rates during this early period of flush activity reach the highest annual values, they are in fact high by any standard of comparison (Table 5.3).
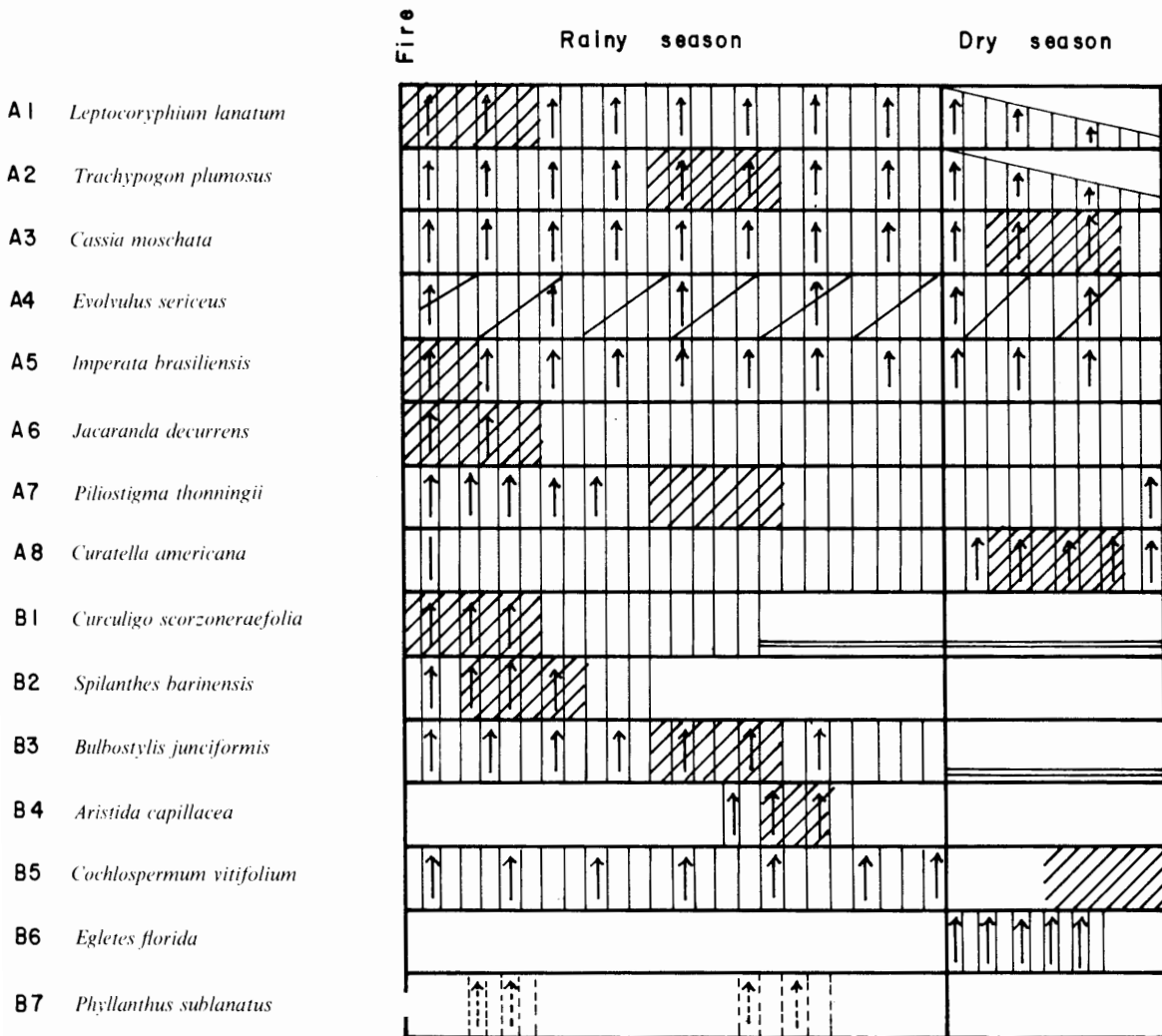
Fig. 5.3. Diagrammatic representation of the phenodynamics of the different phenological groups in the savannas. Arrows indicate leafing; vertical hatching refers to the presence of active green biomass; diagonal hatching indicates the flowering periods; horizontal hatching represents the persistence of perennating below-ground structures; white areas indicate the period when the species remain as a seed bank in the soil.

In a few weeks all the reproductive phenophases are over, including seed dispersal, so that during the rest of the rainy season the plants remain vegetative but actively growing. When drought becomes severe, the half-woody species belonging to this phenological group shed part of their leaves, while the grasses and sedges become increasingly yellowish, and end the season with a standing aboveground biomass almost totally formed of dead shoots. However, even during this unfavorable period, the plants continue to grow, producing new tillers and leaves, though at much slower rates and

with low efficiency, since this late growth does not proceed beyond the youngest stages and most of it dries out. This is what we consider as a semi-resting stage, since all plant activities sharply decrease, though the capability of these species to continue their growth is shown, even if the severe environmental stress hinders any further development of the newly formed organs.

In Neotropical savannas, this phenological group is represented by certain dominant tussock grasses such as *Leptocoryphium lanatum* and *Sporobolus cubensis*, by the common sedge *Bulbostylis*
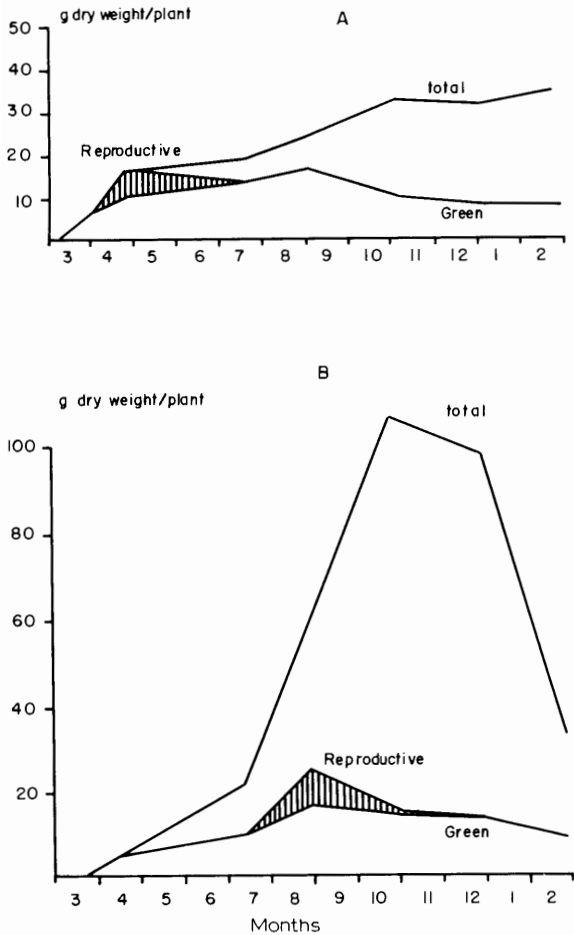
Fig. 5.4. Phenodynamics of two perennial grasses in the savannas of the western Venezuelan llanos when annual fire occurs at the beginning of March. A. *Leptocoryphium lanatum*. B. *Trachypogon vestitus*. The lines represent the development of the green, reproductive and total above-ground biomass during an annual cycle.

paradoxa, and by many half-shrubs such as *Clitoria guianensis*, *Stylosanthes capitata*, etc. In the Guinean savannas this behavior is shown by *Brachiaria brachylopha* and some half-woody species (César, 1971). César applied to these plants the name of long-cycled, early flowering species.

In the coastal savannas of the Guianas, under an ever-wet climate, *Leptocoryphium lanatum*, as well as many other species, flowers immediately after burning, during a short period of reduced rainfall in September (Hoock, 1971). The flowering process in this species appears thus as fire-induced, but in each area it blooms just once a year, differing thus

from the group of opportunistic species we consider later.

A.2. Species with continuous growth and delayed flowering. The *Trachypogon plumosus* group

These species start their vegetative growth once the rainy season is under way, or even before the first rains if the savannas have burnt late in the dry season. Their annual cycle resembles that of the preceding group of precocious evergrowing species, but with two main differences: first, the vegetative development starts smoothly with the rainy season, the highest growth rates only being attained several months afterward; and, second, sexual reproduction occurs towards the middle of the rainy season (Fig. 5.4).

A further distinction can be made among the species of this group according to their seasonal growth rates and the precise timing of flowering; some species are early-growing plants, developing rapidly from the beginning of the rainy season; while others are more slowly developing species, which start a phase of rapid shoot growth a couple of months later, to bloom towards the end of the rainy season. On this basis, César (1971) separated these species into two groups, one with immediate or early emergence and the other with late emergence; but we consider it is more a matter of continuous variation, from certain species emerging as soon as the rains come, to other species whose development is retarded till the last weeks of the rainy period.

After seed dispersal, these plants generally show further vegetative growth, but sooner or later they enter into a declining semi-resting phase that extends throughout the dry season; during this phase new tillers are formed but the mortality rate of the aerial biomass surpasses the assimilatory rates thus leading to an accumulation of standing straw at the end of the dry season.

This type of annual rhythm is shown by many dominant grasses and sedges, such as the common Neotropical grasses *Trachypogon plumosus*, *Axonopus canescens*, *Andropogon semiberbis*, and many others; the African grasses *Hyparrhenia diplandra*, *Andropogon schirensis* and *Loudetia simplex* behave in a similar way. Many sedges have the same phenological pattern, as for instance *Bulbosylis capillaris* in American savannas and *B. aphyllanthoides* in the Guinean communities.

A.3. Species with continuous growth and tardy flowering. The *Cassia moschata* group

This is a rather uncommon type of phenological behavior shown by some savanna trees. These species have continuous growth all the year, but they flower during the dry season; or in some cases they may flower twice a year, once during the dry season, and again some months afterwards. Monasterio (1968) reported this type of phenodynamics in several species of evergreen trees growing both in the gallery forests and the savannas of the central Venezuelan llanos, such as *Cassia moschata*, *Vochysia venezuelana* and *Copaifera officinalis*. In *Cassia moschata*, for instance (Fig. 5.3), leaf production and leaf fall occur simultaneously during the whole year, while flowering occurs early in the dry season, followed by a second peak during the change from the dry to the wet season. In other species, such as *Copaifera officinalis*, leaf production is rather aberrant, with small flushes at several periods of the year,and a single peak of flower production during the dry season. The same pattern, either with one or with two flowering periods, is found in several trees of the cerrado region.

A.4. Evergrowing and everflowering species. The *Evolvulus sericeus* group

This group includes a few perennial subshrubs and some rhizomatous herbs that have continuous growth and flowering all year. They occur in seasonal savannas with deep soils, where their extensive root systems reach water resources probably not available to other herbs and grasses. Some of these appear as completely arhythmical, with continuous leaf and flower production, while others, even if they grow and flower for a quite extended period, decrease their activities during the dry season.

This peculiar phenodynamics may surprise one in a highly seasonal ecosystem as most tropical savannas certainly are; however, the continuous development of the species may be understood on the basis of their life form and architectural design. In fact, from a more or less conspicuous underground xylopodium, successive crops of seasonal branches emerge and develop for a certain time, giving rise to new leaves and to flowers from axillary buds. When each shoot dries out after attaining a certain size and age, new branches appear, thus giving the plant its evergrowing and everflowering characteristic.

Some widespread half-woody species of Neotropical savannas may exemplify this behavior, such as *Evolvulus sericeus* and *Pavonia speciosa*, while the same phenodynamics is shown by some perennial herbs in the Lamto savannas (César, 1971), such as *Aneilema setiferum* and *Afromomum latifolium*.

A.5. Continuously growing, opportunistic species. The *Imperata brasiliensis* group

Some perennial grasses and many subshrubs apparently show the same phenological behavior of Group A.1 — that is, they grow continuously all the year and bloom at the beginning of the rainy season or even before, if a late fire burns the savanna. However, they have an important distinctive feature compared with those species, since these plants are able to bloom after any fire at whatever season. Therefore, we consider these species as opportunistic strategists that may profit from any favorable circumstance (a reduced competition in this case) to reproduce by rapid induction of flowering.

Coutinho (1976) thoroughly discussed this kind of behavior in the cerrados, giving a long list of species able to bloom after any fire, and another list with species that only bloom if the fire occurs during the dry season; these species would bloom at that time anyway, even without having been burnt. *Imperata brasiliensis* and *Elyonurus adustus*, two quite common savanna grasses, exemplify the first group of entirely pyrophilous (fire-tolerant) species blooming after any fire. Though not yet precisely reported, it seems quite possible that this same response may be found among the African savanna species. Meguro (1969) analyzed the flowering behavior of *Imperata brasiliensis* in southern Brazil under various experimental conditions, including fire, leaf-cutting and application of gibberellic acid. This grass does not bloom unless it is burned; a plant unburned during one growth season or more will flower after any fire during the next year, but once it blooms, a new flower induction by fire can only be obtained a year later. Mechanical removal of all leaves also induced flowering, but the response was much less intense than that induced by fire. The application of gibberellic acid enhanced flowering in those plants whose leaves were removed, but had no effects either on intact or on burned individuals. Meguro concluded that at least two different processes are involved in the in-

duction of flowering in this species, one triggered by any kind of leaf removal, the other promoted by some other effect of fire, perhaps the temperature shock. In any case the behavior of *Imperata brasiliensis* exemplifies the phenological strategy of opportunistic perennials able to bloom after fire when they have remained in a vegetative phase for a certain minimum period.

A.6. Species with seasonal growth and precocious flowering. The *Jacaranda decurrens* group

This group consists of the evergreen species capable of photosynthetic assimilation all year, but showing seasonal growth and precocious flowering. Their active period of growth and flowering starts with the onset of rains or after the consumption of above-ground biomass by fire if burning has occurred late in the dry season. In a period ranging from a few weeks to a couple of months, the leaves are fully developed and all the reproductive phases accomplished, in such a way that during the remainder of the wet season the plants are green but without any further growth, the meristems seeming to degenerate or to die. During the dry season, the leaves may become partly senescent but nevertheless the plants remain photosynthetically active, though with a reduced green area.

This phenological behavior is shown by many half-woody species in Neotropical savannas, such as *Jacaranda decurrens*, *Cochlospermum regium* and *Psidium salutare*. They differ from group A.1 because leaf production is restricted to a short period of the year, and from group B.1 because the species in this latter group, as will be seen later, have a rest period of underground life.

A.7. Species with seasonal growth and delayed flowering. The *Piliostigma thonningii* group

Apparently a few woody evergreen species have seasonal growth and delayed flowering, thus uncoupling the processes of leaf formation and flower initiation. As an example, one may consider the phenodynamics of *Piliostigma thonningii*, a common low tree in the Lamto savannas, as reported by Menaut (1971). The period of active growth begins before the first rains, when the buds start to open. A late fire may destroy this early growth, but in any case leaf formation proceeds rapidly after fire and continues for two or three months. The first flowers open in June, four to five months after the start of

leafing, the flowering process and the ripening of fruits continuing for several months. The old leaves fall gradually as the new ones are formed at the start of a new growth cycle.

This phenodynamics is not very common among savanna woody species, since most evergreens with seasonal growth bloom at about the same time that they produce their new leaf crop, either during the dry season or immediately after the onset of rains. Only some deciduous species have the same reproductive rhythm as this group, flowering several months after leafing (Group B.2).

In Neotropical savannas *Roupala complicata* and *Kielmeyera coriacea* may be mentioned among the common trees having this behavior.

A.8. Evergreen trees with seasonal growth and tardy flowering. The *Curatella americana* group

To this phenological group belong the evergreen woody species that produce their leaves and flowers during the dry season (Fig. 5.5). It is in this apparently unfavorable period that these species change their leaves through the almost simultaneous progress of the two opposite processes of leaf fall and new leafing. Consequently, the individuals never remain leafless, there is nothing comparable to a rest phase, though the green area diminishes during these phenophases of leaf renewal. Due to this fact, the species in this group can be considered either as evergreens or brevideciduous, since they remain with a smaller leaf area during a short period of time.

Foldats and Rutkiss (1975) gave quantitative data on the phenology of *Curatella americana* in the Venezuelan llanos; we take it as a typical example of this type of behavior and will consider therefore its phenodynamics in more detail.

The reproductive phenophases start during the dry season concurrently with sprouting to produce new shoots. After several weeks, the flowering process is completed, but fructification and seed dispersal may continue for a short time during the rainy season. Some species sprout leaves before flowers; in others, as in *Curatella*, both processes go on simultaneously, while a third group blooms before leafing. Once a new leaf crop has been formed, the shoots remain unchanged for several months without any further growth; apical meristems cease functioning irreversibly, thus ending all morphogenetic activity for the rest of the rainy
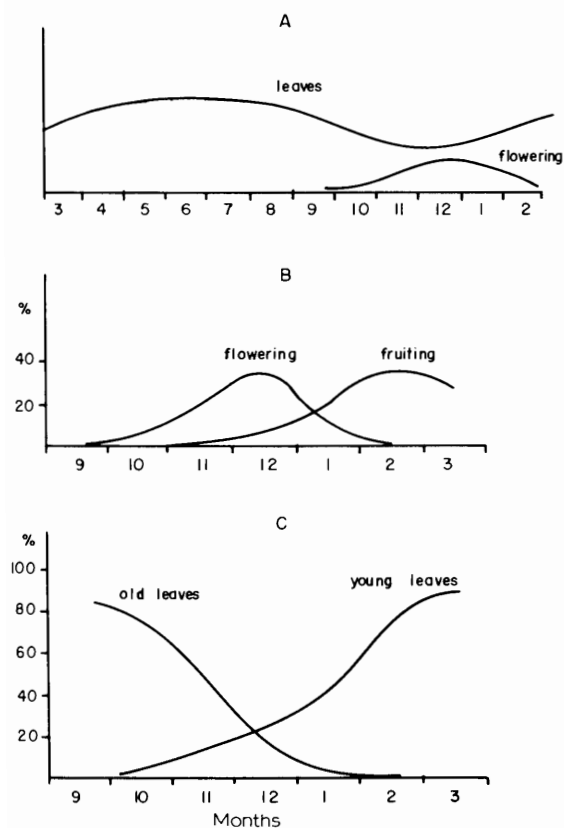
Fig. 5.5. Phenodynamics of *Curatella americana* in the Venezuelan llanos. A. A semi-quantitative representation of the annual cycle of leaf and reproductive biomass. B. Flowering and fruiting. C. Leaf production and leaf fall. In B and C the vertical axis indicates the percentage of the population at a given phenophase. (After Foldats and Rutkiss, 1975.)

season. Towards the end of this season, some leaves begin to yellow, and soon the entire foliage enters into a period of senescence preceding leaf fall. As we already remarked, a fire during the dry season does not hinder the normal cycle of phenological events; most old leaves simply fall and a flush of new leaves and flowers appears after a few days.

A peculiar feature apparent in many of these species, already noticed by Warming (1892) among the Lagoa Santa woody flora, is that in some cases, a second period of leafing and blooming occurs during the wet season, but this is much more irregular and occasional than the main active phase during the dry season.

In the cerrados as well as in the llanos, a fairly important proportion of the total tree flora shows this kind of phenodynamics. Some representative

examples besides *Curatella americana* are *Bowdichia virgilioides*, *Casearia sylvestris*, *Caryocar brasiliense*, *Salvertia convallariodora*, various species of *Byrsonima*, and many others. In the Lamto savannas, according to Menaut's observations, a few of the common trees, like *Crossopterix febrifuga* and *Bridelia ferruginea*, show this behavior, but in these savannas the woody species seem to show a greater variation in phenological patterns than does the Neotropical woody savanna flora.

B. Species with seasonal carbon assimilation

B.1. Perennial with precocious flowering. The *Curculigo scorzoneraefolia* group

The species with this phenological pattern start their development with the rainy season (Fig. 5.6); they give rise simultaneously to shoots and inflorescences, accomplishing all phases of sexual reproduction in a few weeks; thereafter the leaves persist for a while but soon they enter into a declining phase, to disappear entirely from the ground either towards the middle or at the end of the rainy season; only the perennating underground structures remain alive, together with the seed bank, during a long resting phase of dormancy.

This behavior characterizes many geophytes either in seasonal or in hyperseasonal savannas, particularly sedges and bulbous species of Amaryllidaceae, Liliaceae, Iridaceae and other monocotyledon families. *Curculigo scorzoneraefolia* in Neotropical savannas and *Curculigo pilosa* in the African savannas are good examples of this group. Some subshrubs show this same phenodynamics, such as *Vernonia guineensis* and *Rhynchosia sublanata* in Africa. *Ruellia geminiflora* and *Desmodium pachyrrhizum* in America.

As these species disappear from the ground during the dry season and their perennating organs remain more or less deeply buried in the soil, fire cannot have any direct effect on their phenology, therefore their cycle has necessarily to be synchronized with other environmental signals.

B.2. Annuals with precocious flowering. The *Spilanthes barinensis* group

Apparently, a few annuals show essentially the same phenological rhythms as the preceding group of perennials, with precocious growth and flowering, but of course during the rest phase only the
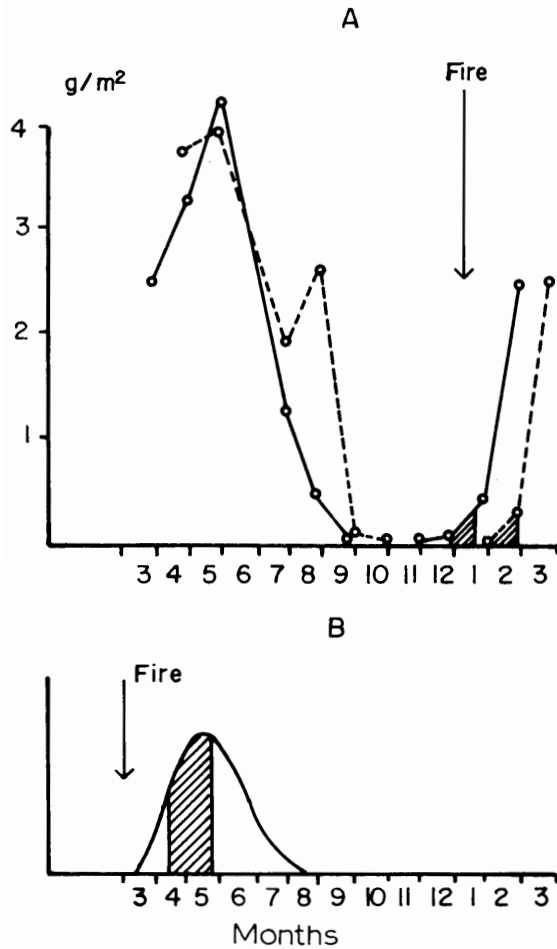
A

B

Fig. 5.6. Phenodynamics of two perennial species with seasonal carbon assimilation and precocious flowering. A. *Curculigo pilosa* as it behaves in two different savanna communities at Lamto, Ivory Coast (after César, 1971). B. *Curculigo scorzoneraefolia* in the savannas of the western Venezuelan llanos. In A the biomass data were obtained by random sampling; in B the curve only represents a subjective estimate of the development of the biomass; in both cases diagonal hatching indicates the flowering period.

seed bank persists in the soil. Their entire annual cycle occurs during the first months of the rainy season, they germinate after the first rains and bloom and disperse the seeds within a couple of months.

Most of these species have a more or less weedy ecological behavior. *Brachiaria plantaginea*, a widespread grass in wet savannas, constitutes a typical example, as well as the small Neotropical composite *Spilanthes barinensis*. Other species in the group are weeds of such genera as *Amaranthus* and

Croton, that differ from the two forementioned species by having a longer period of blooming. We could not find any example of African species belonging to this phenological group.

B.3. Perennials with delayed flowering. The *Bulbostylis junciformis* group

In this group are included all perennial species which have a definite rest phase, and which flower several months after their emergence, in the case of herbs and subshrubs, or several months after leafing, in the case of deciduous trees.

The active phase starts with the rains (Fig. 5.7), they produce the annual crop of leaves, and towards the middle of the wet season their reproductive phenophases begin. When the dry season becomes severe, the deciduous trees shed their leaves, while the whole aerial parts of herbs and subshrubs die back, only the perennating underground organs remaining alive.

In this phenological group are included many sedges, some other geophytic monocotyledons, a variety of subshrubs and a few deciduous trees. *Bulbostylis junciformis* and the bulbous *Cypella linearis* (Iridaceae) may typify this phenodynamics within the Neotropical herbaceous flora, while in the Guinean savannas the best examples are two widespread sedges, *Cyperus schweinfurthianus* and *Scleria canaliculato-triquetra* (César, 1971). Many half-shrubs also behave in this way, like *Tephrosia bracteolata* and *T. elegans* in Lamto and *Zornia*
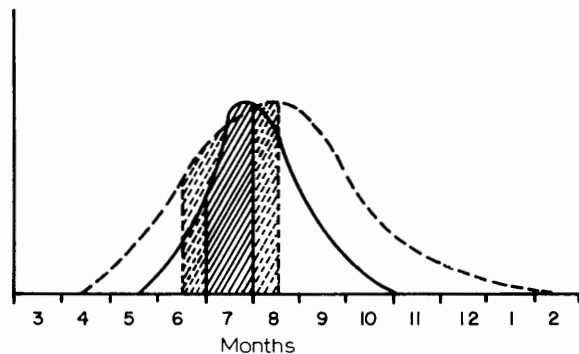

Fig. 5.7. Phenodynamics of *Bulbostylis junciformis*, a perennial sedge with seasonal assimilation and delayed flowering. The curves give a subjective estimate of the development of the green biomass and indicate the flowering period. The continuous curve corresponds to a savanna normally burnt in March, while the discontinuous lines indicate the behavior of this species when protected from fire.

reticulata and *Aeschynomene brasiliana* in Venezuela. Examples of deciduous trees flowering several months after leafing are *Genipa americana* in the Neotropics and *Terminalia glaucescens* in Africa.

B.4. Annuals with delayed flowering. The *Aristida capillacea* group

The life cycle of these species lasts between two and seven months, entirely within the rainy season, except in a few species whose reproductive activities extend to the first part of the dry period. From one to six months after the onset of rains, they germinate, rapidly develop the vegetative structures, and enter into the sexual reproductive phases. Even before completing seed dispersal, many of these annuals die back completely.

In order to obtain phenologically homogeneous groups it is necessary to distinguish between two sets of annuals with delayed flowering: the "long-cycled" species, whose life cycle spans three or more months; and the "ephemerals" that accomplish all their active phenophases in an exceptionally short time.

All long-cycle annuals have in common that they start their development at the middle, even toward the end of the rainy season (Fig. 5.8). This fact has been remarked both in African savannas (César, 1971) and in American communities (Monasterio, 1968). This means that germination takes place at least two months after the onset of rains; in some cases four months elapse between the start of the rainy season and the development of these annuals. Another distinctive functional trait shared by most annuals is their extended period of blooming, since the production of new leaves and new flowers proceed during almost their entire active cycle. As was noted in the section on life forms, the number of annual species varies greatly among the various savanna ecosystems, but in any case a large part of the annual flora shows this kind of phenodynamics. *Hyptis suaveolens*, a widespread weedy forb in northern South American savannas may typify this behavior as may do most annuals in Paleotropical savannas.

The ephemerals constitute a highly interesting group of species within the floras of the savannas, if not by their number or their importance in vegetation, at least by the very fact that this strategy occurs in savanna ecosystems. Their activities start
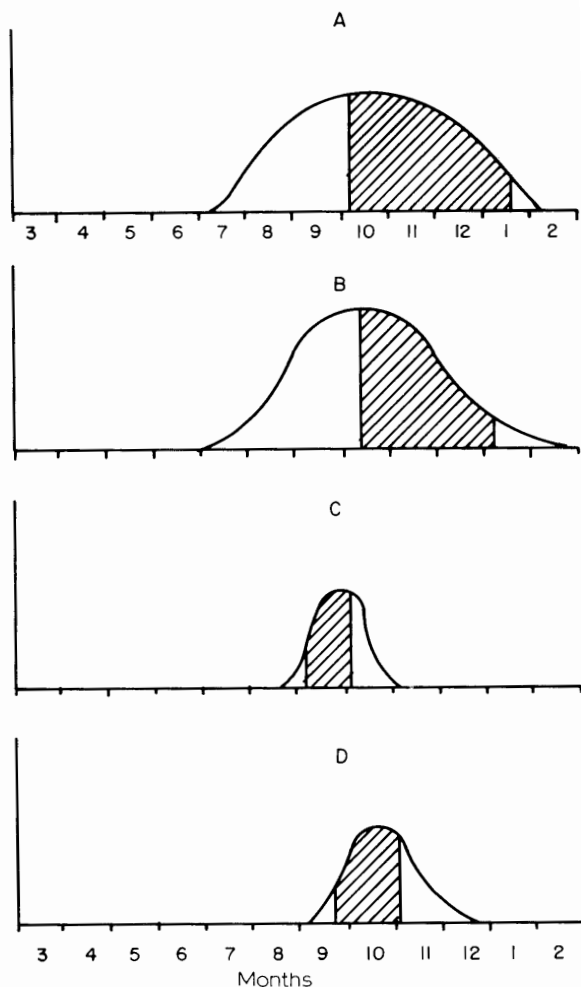

Fig. 5.8. Phenodynamics of four species of annuals in the savannas of the Venezuelan llanos. It is a subjective estimate of the development of the green and flowering biomass. A. *Cassia desvauxii*. B. *Hyptis suaveolens*. A and B represent two long-cycled annuals with delayed flowering. C. *Aristida capillacea*. D. *Gymnopogon foliosus*, C and D. are two ephemeral grasses.

very late (Fig. 5.8) in the last half of the rainy season; after germination they have an extremely rapid development, with immediate blooming, since they show practically no exclusively vegetative phase of growth, but begin to bloom from the very early stages of shoot development. Their decay is as fast as their previous development; they rapidly disappear from the ground, to remain just as a seed bank in or on the soil for a large part of the year.

Considering a whole local population, an ephemeral species may complete its active life cycle in about two months, but if one follows individuals,

they may be found to pass through all developmental phases in no more than four or six weeks.

In Venezuelan savannas, some characteristic ephemerals are the grasses *Aristida capillacea*, *Digitaria fragilis*, *Gymnopogon foliosus* and *Microchloa indica* (this latter species also occurs in Zambezian "steppes"); as well as many forbs like *Borreria ocimoides*, *Polycarpaea corymbosa* and several species of *Polygala*. Outside tropical America, this phenological pattern has not been reported, though the occurrence of the same or of very similar species makes its existence quite probable.

B.5. Tardy flowering perennials. The *Cochlospermum vitifolium* group

This group includes all the deciduous woody species that flower during the dry season. This behavior is much more frequent among the canopy trees of the tropical deciduous forest than among savanna species, where, as already pointed out, most trees are evergreen or brevideciduous. In fact, among the deciduous trees growing in savannas, there are many species that also occur in the neighbouring forests, and they could be considered as pioneer forest species colonizing some unstable savannas. This seems to be the case, for instance, with most trees invading the derived savannas in Nigeria (Hopkins, 1962).

After the vegetative rest period when they remain leafless for a part or the whole of the dry season, the trees generally start to grow a few days before the onset of rains (Fig. 5.9), developing their new leaf crop in a couple of weeks to complete this process of leaf renewal at the very beginning of the rainy season. Other species may have their leaf flush after the onset of rains instead.

Once the new leaf crop has been produced, the phenodynamics of these species may show some slight variations among different species, some of them, like *Spondias mombim*, cease all vegetative development, while others, like *Cochlospermum vitifolium*, continue to produce new leaves throughout the wet season. In any case, shortly after the rains cease, the abscission process starts and more or less suddenly the whole foliage is shed. Flowering occurs during the leafless period in the dry season; this is thus a resting phase for vegetative activities only, and not for reproduction, except for the short period of complete rest after leaf fall and before blooming.
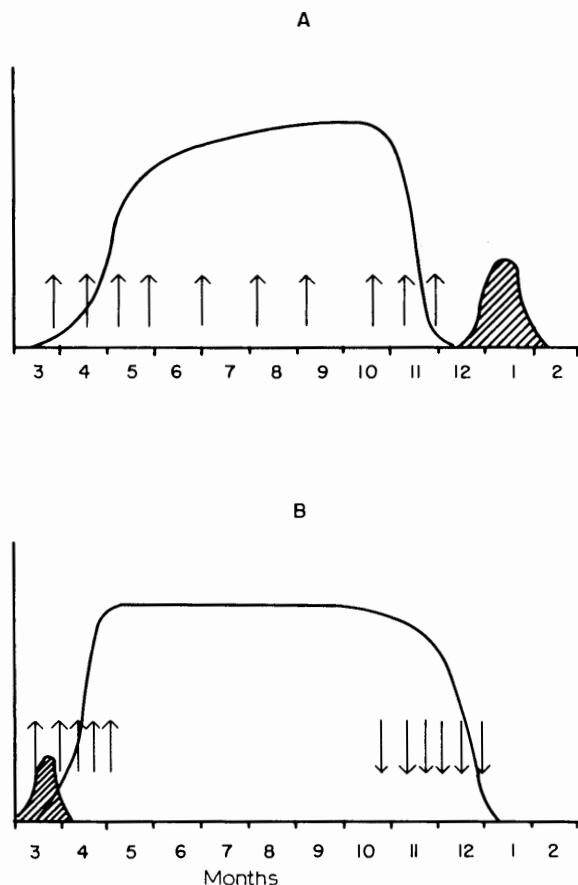
Fig. 5.9. Phenological behavior of two deciduous trees in the savannas of the Venezuelan llanos. A. *Cochlospermum vitifolium*. B. *Spondias mombim*. Upward arrows indicate leafing; downward arrows refer to leaf fall; diagonal hatching refers to flowering and the continuous curves indicate the annual cycle of leaf biomass. Notice that *C. vitifolium* shows continuous leafing throughout the rainy season, while *S. mombim* produces its foliage in a limited period during the change from the dry to the rainy season.

This phenological strategy of deciduous trees flowering during the leafless stage is more common among the rich arboreal flora of the Brazilian cerrados than in any other savanna area; in this region, this strategy is represented by many Bombacaceae, such as several species of *Bombax*, as well as by common species of other families, such as *Cochlospermum insignis*, *Terminalia argentea*, *Sterculia striata*, and many others. According to Hopkins (1968), *Annona senegalensis* and *Butyrospermum parkii* show the same behavior in the Nigerian savannas.

B.6. Tardy flowering annuals. The *Egletes florida* group

In most savannas, almost all annuals belong to a "wet season annual flora", which accomplish the whole active cycle during the favorable season of the year, when there are fewer probabilities of water shortage for these shallow-rooted species. But in *esteros* and similar seasonally waterlogged habitats, a "dry season annual flora" may occur, since its species may take advantage of the short period left between the drainage of surface water and the exhaustion of water reserves in the upper soil layers.

These species germinate as soon as soil humidity becomes favorable, after the excess water has been drained off — that is, some time after the last rains (Fig. 5.3); they rapidly develop to complete their active phenophases, either vegetative or reproductive, before the soil becomes too dry; seed dispersal, however, may continue until the end of the rainless season.

Among the annuals behaving this way, a few species may be listed which occur in seasonally waterlogged areas of the Venezuelan llanos (Ramia, 1977, 1978), such as *Egletes florida*, *Trichospira verticillata* and *Heliotropium filiforme*.

B.7. Opportunistic annuals. The *Phyllanthus sublanatus* group

The developmental strategy of opportunistic annuals that may profit from any short favorable period to become active seems to be peculiar to a few species living under highly unreliable environments, such as extreme deserts. It is striking, therefore, that the same strategy may be found in tropical savannas under entirely different humidity conditions. César (1971) noted that *Phyllanthus sublanatus*, a small annual occurring in the Lamto savannas, shows this opportunistic behavior. This plant accomplishes its cycle in a few weeks whenever humidity conditions become favorable. We do not know yet of any similar case in other savannas.

A somewhat comparable phenological strategy is displayed by some annuals that can grow and reproduce at any time of the year because almost always they can find suitable environmental conditions. They occur, for instance, in habitats where, due to a permanently high water table, water shortage never becomes acute, but where the ground does not become waterlogged either. This is the case in wet savannas in northern Surinam, where Van Donselaar-Ten Bokkel Huinink (1966) reported that three species of annuals become active whenever conditions are favorable in any season of the year. These plants, which accomplish their cycle in a few months, could hardly be considered as annuals since it is obvious that they do not have any annual rhythmicity, therefore it seems better to consider them simply as short-cycled plants.

PHENOLOGICAL STRATEGIES AND THE DYNAMICS OF SAVANNA ECOSYSTEMS

Considering the whole spectrum of annual rhythms found in the savanna flora, the first fact to emphasize is the wide range of phenological strategies apparent among the species of these tropical ecosystems. In spite of the sharp seasonality of the vegetation that seems to reflect an acute water shortage during the long rainless season, every period in the year appears to be favorable at least to the accomplishment of certain phenophases in one or another group of plant species. Thus all perennial herbs, as well as a majority of the annuals, grow and flower during the wet season; but there are some species that are able to flower during the dry season, as occurs with the dry season annuals and the everflowering perennials.

In contrast with herbs, a majority of woody and half-woody species renew their leaves and bloom during the dry season, giving thus a clear indication that there are then certain water resources remaining available to these deep-rooted plants.

Among the species showing active growth during the wet season, it is quite interesting to notice that they behave as if a certain temporal division of the niche exists (Fig. 5.10), since some species start to grow with the first rains or soon after a late fire, entering immediately into their reproductive phenophases (precocious species); other populations instead emerge only gradually, develop their shoots slowly, and enter into their reproductive phases towards the middle of the rainy season or even during its last weeks. The annuals too show a differentiation between precocious and delayed species, with a small group that is able to develop even during the rainless period.
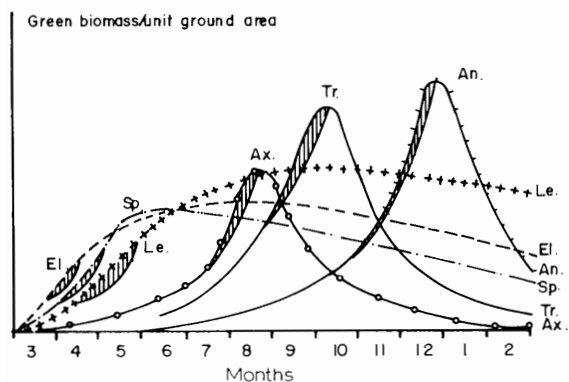
Green biomass/unit ground area

Fig. 5.10. The temporal division of the niche in the herb layer of a seasonal savanna in the Venezuelan llanos. This savanna is normally burnt in March. The annual cycle of the six dominant grasses is indicated by the development of the green biomass and by the flowering periods (vertical hatching). Notice the temporal displacement of flowering periods and the non overlapping of the periods of maximum growth-rates in each species. $El = Elyonurus$ $adustus$; $Sp = Sporobolus$ $cubensis$; $Le = Leptocoryphium$ $lanatum$; $AX = Axonopus$ $canescens$; $Tr = Trachypogon$ $vestitus$; $An = Andropogon$ $semiberbis$.

If the phenodynamics of each group is now considered against the background of seasonal changes at the whole ecosystem level, one may realize that, through their rapid response to fire or to drastic changes in soil humidity, the early growing species, either annuals or perennials, develop when the ground is practically devoid of any plant cover, since it has either been consumed by fire or, in unburnt savannas, it is mainly formed of dead leaves. Under these conditions they do not face any competitive pressure from other species, either for light, water or nutrients. Besides that, the less common species, either wind-or insect-pollinated, have the best conditions for effective pollination shortly after a fire, since their visibility and accessibility become maximum at this moment.

Some of these early growing and precocious flowering species, such as the annuals and the perennials with a resting phase, will disappear from the ground surface when the dominant grasses and other species with late emergence and delayed flowering reach their maximum ground cover, while the precocious perennial grasses will slow down their growth rates as the late-emergence grasses increase theirs.

The annuals with late emergence and delayed flowering have a strategy that at first sight does not

seem to give them many chances to compete with the perennial grasses and subshrubs. In effect, when these annuals germinate and start their fast developmental cycle, most savannas already have a closed herbaceous canopy. Under these circumstances, one can understand why these annuals have adopted one of two following divergent strategies. On the one hand, they tend to occupy the less favorable sites, where the herbaceous matrix becomes discontinuous, leaving open places where annuals may establish more easily. On the other hand, shade-tolerant plants may survive under a herb canopy that seldom is closed enough to prevent the filtering of a certain amount of light; in this case, these annuals prosper in a microenvironment that, if it is poorer in radiant energy, seems to compensate by being more humid and cooler.

If the phenodynamics of woody species is now examined, it can be seen that a majority of them belong to the *Curatella americana* group (A.8) with continuous photosynthetic assimilation, seasonal growth and tardy flowering (during the dry season). At this time, an overwhelming proportion of the herb layer has already changed to a standing dead cover, annuals have disappeared, and perennials with a semi-resting phase are reduced to their annual minimum. Under these circumstances, active trees do not find any competition from the herbaceous plants. Furthermore, the occurrence of natural fires greatly increases during this season, both because of climatic drought and because there is a continuous blanket of standing straw; if a fire does occur, it will consume only old decaying leaves, or, at the worst, a part of the new leaf crop, but it will not do irreparable harm to the trees. Besides these advantages, a change of foliage during the relatively less favorable season makes it possible to display a fully developed photosynthetic apparatus functioning at full rates when more favorable conditions arrive. This group also shows a phenodynamics perfectly coupled with the major environmental changes, providing that water availability during the dry season make possible the maintenance of a certain green area. If through the development of an extensive and deep root system these trees are able to exploit the water held in deeper soil layers out of reach of herbs, then there is an obvious advantage in changing leaves and reproducing during the period of relative water

shortage and of greater fire risks, leaving to the rainy season the function of active assimilation permitting a storage of energy to support the dry season's activities.

The deciduous trees, instead, must be able to reconstitute their foliage as soon as possible when the wet season arrives, in order to take advantage of its favorable conditions to re-establish a positive carbon balance after the long period of zero assimilation; moreover, they neglect the growth possibilities offered during the rainless season, as if this period were totally unfavorable for any assimilation, being therefore at a net disadvantage with respect to evergreens which, through a strategy of profiting from deep water resources, may maintain a positive carbon balance throughout the year.

The phenological strategy of continuously growing perennials that flower tardily in the rainy season (the *Trachypogon plumosus* group, A.2) appears as the most successful, since a majority of the dominant grasses and sedges in different savanna ecosystems all over the tropical area belong to this group. This good ecological performance may be easily understood on the basis of the perfect coupling between the phenorhythms of these species and rainfall seasonality. In effect, during the period of water shortage, their aerial biomass rapidly decays, while as the rainy season progresses they gradually develop their shoots and reproductive structures, to reach the maximum growth rates during the reproductive phenophases that occur in the safest period of the year in respect of water availability. Moreover, these perennials effectively occupy the ground during most of the annual cycle, holding the space and depending much less than annuals on seed establishment. When perennial grasses with this developmental pattern reach their full size, they overtop all other species in the herb layer, being then the most competitive for light. The semi-resting phase during the dry season means that they retain the capability of growth; although this late growth does not contribute greatly to a better carbon balance, it represents a plastic response to adverse conditions, giving the possibility of finer adjustments to the particular humidity conditions actually met with each year. In this sense, they surpass species with a complete resting phase, since these are absolutely unable to respond in such a plastic way. The semi-resting period of perennial grasses and sedges implies that during the less

extreme years a greater green area could be maintained for a longer time, enhancing thus the possibilities of early growth when water becomes again available.

Another successful strategy in most savannas has been that of the *Leptocoryphium lanatum* group (A.1) — that of continuously growing perennials with precocious flowering. These species, through a rapid early growth at the beginning of the rainy season, may occupy a niche left temporarily void by the dominant grasses, that have slower emergence and delayed flowering. These two strategies may also be seen as successful adaptations to recurrent fires, since, when the savannas are burnt late in the dry season, the flames just consume the annual shoots, mostly dry at that moment, leaving intact and unharmed the perennial underground structures.

While the hydroperiodicity of the savanna environment seems to be the major external compulsion regulating plant development and rhythmicity, in many cases the direct signals triggering the physiological mechanisms responsible for the successive phenophases seem to be different from soil or atmospheric humidity. This fact is most obvious in woody species sprouting before the onset of rains, when the soil and the atmosphere still remain quite dry. This is the case of a majority of woody species, as already discussed; it is necessary then to consider other external signals of high constancy from year to year, that could be received by these plants. There are two such rhythmical environmental impulses, namely photo- and thermoperiodicity. Flowering of trees during the dry season starts after the shortest days and in a period of maximum daily fluctuations of temperature as well as of minimum night temperatures. Quite the opposite situation occurs in species blooming during the peak of the rainy season after the longest days and during the narrowest daily temperature fluctuations. Monasterio and Sarmiento (1976) discussed thoroughly the possible relations between rhythmicity and environmental impulses in the seasonal savannas and semideciduous forests of the Venezuelan llanos, we refer to that paper for further details concerning this point.

A last point worthy of further consideration relates to the influence of fire on the phenological behavior of savanna species. One may take for

granted that fire has always been a natural eco-logical factor inducing different adaptive responses from the savanna populations. Most savanna species must have had a long evolutionary interplay with recurrent fires. Natural burnings have more probabilities of occurring during the last part of the dry season, precisely in the period when nowadays ranchers set fire to the savannas, for different practical purposes.

Our main argument concerning fire action is that a late burning (that is, a fire during the last weeks of the dry season or at the very beginning of the rainy season) does not alter drastically the normal course of phenological events in the savannas. In fact, its direct action on annuals will be nil, since the seed banks may lie well protected in the soil. Herbaceous perennials with a resting phase have already dis-appeared from the ground, and the semi-resting species have at that time a great proportion of dead biomass. Half-woody species and low trees may lose a part or even the whole of their leaves and annual branches, but in any case these are short-lived structures that were passing through decaying phases. Adult trees, taller than a certain minimum threshold height normally attained by the flames, remain fairly unharmed. The most obvious conse-quences of a late fire will be then: first, the main-tenance of tree species in a half-shrubby habit; second, slight damage to young trees by partial or complete loss of their new leaf crop; and, third, a triggering effect on perennial herbs, grasses, half-shrubs and trees, promoting immediate leafing and/or flowering. These two effects could hardly be considered as deleterious.

When the savannas do not burn, these species show essentially the same rhythmicity as when burned, but the different species appear as less synchronized with each other, and in some cases their development is slower and less intense. A late fire acts then as a synchronizing agent among the species having similar phenological responses.

Furthermore, there are particular cases where savanna species show some kind of fire-dependency. Coutinho (1977) reported that fire promotes fruit dehiscence in some subshrubs of the cerrados, such as *Anemopaegma arvense* and *Jacaranda decurrens*; afterwards the seeds will find favorable conditions for anemochoric dispersal. But the main dependence is shown by savanna species that do not flower unless fire or other destructive agents have eliminated the entire above-ground biomass. Coutinho (1976) found that 150 species of half-shrubs and perennial herbs have fire-induced flowering, some of them blooming after fire when-ever in the year it may occur (opportunistic strate-gists), other species responding only to a dry season burning. Only in this last case it seems possible to evoke a dependency on photoperiodicity.

Finally, Coutinho (1976) reported that in some half-shrubs with a xylopodium, dormant buds were structurally changed by the action of fire, to repro-ductive buds resulting in reproductive organs, which he called a "pyro-morphogenetic effect". One may see, then, how a number of characteristic species belonging to the savanna flora have evolved phenological patterns not only adequate to cope with frequent fires, but that even take advantage of burning to improve their performance in the eco-system.

To conclude this chapter on life forms and phenology of savanna species, we want to summa-rize our main arguments as follows. Apparently, during a long evolutionary interaction between plant populations and the environmental con-straints characteristic of savanna ecosystems, cer-tain forms and rhythms were originated as success-ful responses to the selective pressures which oper-ate nowadays, as if natural selection had been acting with similar selective pressures for a rather long time. Most populations have optimized their fitness through architectural and phenological adaptations that produced plant forms, develop-mental patterns and annual rhythms leading to good performance under the prevailing set of outside challenges.

We may advance the hypothesis that hydro-periodicity on the one hand and recurrent fires during the dry season on the other, have been the principal environmental factors selectively filter-ing out inadequate responses, and allowing the plant populations that evolved in a certain direction a better reproductive efficiency. There are also some reasons to suppose that the interplay between plant populations with different growth forms — annuals, perennial tussocks, half-shrubs, trees — and with different phenodynamics — continuous assimilation or rest phase; seasonal or continuous growth; early or late emergence; precocious, de-layed or tardy flowering — have led to a spatial and temporal division of the niche, as suggested by the

division of soil water resources between herbaceous and woody species, or the sequential development of the various phenological groups during each annual cycle, as if they were replacing each other in the use of some critical resource.

The major morphological and developmental strategies of successful plant species have been either to shorten the life cycle and to synchronize its active phenophases with the most favorable season, thus escaping the filtering action of drought and fire, as annuals and resting perennials have done; or to resist these stresses through, first, a precise synchronization of the developmental processes with favorable periods, and, second, a type of resource allocation among the various plant structures favoring resistance and survival under these stresses, as most perennials have done. Sometimes, these adaptations involved original solutions, such as the substitution of the shoot apical meristems by the vascular cambium as the main replacement tissue; or the exceptional degree of subterranization of the biomass and of certain key functions attained by half-woody plants, where even the function of producing and restoring vegetative and reproductive organs relies on underground meristems.

Other types of phenological behavior seem rather to be a result of selective pressures no longer operative under the conditions where these species live nowadays in the savannas; this may be the case, for instance, for the ephemerals and the opportunistic strategists, since it may be reasonable to suppose that these strategies have evolved as responses to stronger environmental stresses.

To accept or reject these hypotheses much more observational and experimental work is needed; but in any case we think they may be useful as research guidelines, suggesting some profitable ways to get further insight into these very interesting populations and ecosystems.

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