

Phenological strategies of plant species in the tropical savanna and the semi-deciduous forest of the Venezuelan Llanos

MAXIMINA MONASTERIO

GUILLERMO SARMIENTO

Facultad de Ciencias, Universidad de Los Andes,
Mérida, Venezuela

Abstract

Six phenological patterns are recognized in the flora of a tropical savanna in the Venezuelan Llanos. The dominant perennial grasses and sedges have an alternation between a period of intensive tiller production, shoot growth and sexual reproduction during the rainy season, and a phase of semirest during the dry season, when shoots decline and tiller development decreases to a minimum. An opposite strategy is displayed by the tree species; they have a phase of full leaf development and maximum assimilation during the rainy season, but without any shoot growth or leaf formation, while in the dry season they renew the foliage and flower.

Annuals constitute a numerically-significant part of the savanna flora, and have been ascribed to two different phenological groups. The long-cycle annuals form one group and these have an active life cycle of 6 to 7 months, coincident with the rainy season; the other group is formed by the short-cycle annuals or ephemerals, which complete their cycle in only 2 to 4 months during the latter part of the rainy season.

Another phenological strategy is displayed by those species which enter into a dormancy phase during drought, when all their above-ground organs dry out; their active phenophases occur during the rainy period. The sixth phenological group is formed by the evergrowing and everflowering plants, i.e. those savanna species without a manifest seasonality.

In the semi-deciduous tropical forest which occurs in the same area, two phenological strategies were discerned. The first is displayed by deciduous trees which stay leafless for a part of or for the entire dry season, and which put out a new crop of leaves either

just before the onset of rains, or at the beginning of the rainy season. Different reproductive patterns are found in this group, with various species flowering at different times, either during the wet or the dry season. The second strategy in this forest is comprised of evergreen and brevideciduous species which renew their foliage during drought, when both opposite phenophases (leaf flush and leaf drop) proceed simultaneously. Flowering also takes place during the dry season, but only in the brevideciduous species is it directly related to leaf renewal.

Considering the total flora of both communities, a major peak of flowering in the middle of the rainy season characterizes the savanna, while the forest has two equally important flowering peaks, one in each season.

A discussion of the possible role of various environmental impulses in plant phenology in this region is attempted, considering all seasonal factors, such as daylength, rainfall seasonality, thermoperiodism, extreme temperatures, insolation and radiation. Finally, the conditions favouring the existence and success of each phenological strategy are considered, together with a critical examination of the seasonal characteristics of the two ecosystems.

Introduction

Until quite recently the phenological approach was generally overlooked in most ecosystemic studies. A renewed vigour in this branch of ecological research only arose when it was included within the IBP Biome Programme as one of the major parameters used to characterize ecosystems (US/IBP Phenology Committee, 1972; Lieth, 1970, 1971, 1974). In this Programme, phenological information was obtained from intensive study sites, in order to relate facts concerning species establishment, growing periods, reproduction, etc. with other biomass and turn-over results, with the ultimate aim of obtaining an integrated picture of productive processes.

Using this same approach, the annual rhythms of growth and reproduction of various species characteristic of seasonal savannas and semi-deciduous forests, two of the most widespread biomes in tropical America, are to be examined. Phenological information about these biomes, either in tropical America or in other regions of the tropical world, are somewhat fragmentary; programmes such as that in the Miombo ecosystem in tropical Africa (Malaisse *et al.*, 1972, 1975) have not been paralleled in related biomes of the seasonal wet-and-dry tropical belt.

In the case of the seasonal savanna, it may be expected that a more precise knowledge of the times and periods of shoot development and leaf activity, as well as the successive phases of sexual reproduction of species belonging to the main growth forms will, in addition to providing information of direct use to the management of these grazing lands, also clarify the adaptive and evolutionary behaviour of species in the flora of this still poorly-understood ecosystem. Furthermore, a comparison of the phenological patterns of herbaceous and woody savanna species with those of trees of the semi-deciduous forest occurring in the same area should show how a variety of phenological strategies have

evolved to cope with similar cycles of environmental stress in these contrasting ecosystems.

Phenological observations on the species of both ecosystems were made at the Los Llanos biological station, located in the central part of the Venezuelan Llanos a few kilometres southeast of Calabozo (8° 56' N and 67° 25' W, 100 m a.s.l.; Fig. 1). Due to the facilities provided by the station and to the total protection from grazing and burning of its 300 ha field, various floristic and ecologic aspects of the savannas and forests of this area already have been intensively analysed, resulting in an adequate basis of knowledge in which to frame the phenological observations (Medina, 1966, 1967; Medina, Silva & Castellano, 1969; Monasterio, 1968, 1971; San Jose & Medina, 1975; Sarmiento & Monasterio, 1969, 1971; Vareschi & Huber, 1971).

Phenological studies on similar ecosystems in tropical America are scarce. Croat (1969, 1975) has presented detailed records on flowering and fruiting patterns for the whole flora of Barro Colorado Island in Panama. At this site, in spite of a very rainy climate, a seasonal rain forest occurs, probably as a result of three consecutive months having a lower rainfall. Croat (1975) grouped all species on this island into twenty-seven seasonality types,

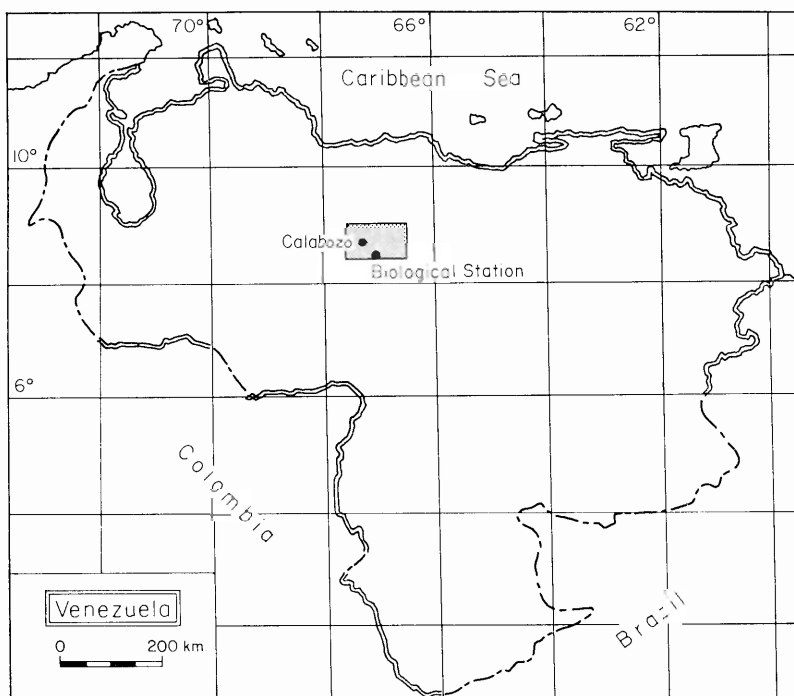


Fig. 1. Map of Venezuela showing the locality of Los Llanos biological station.

according to their reproductive seasonal patterns. The most numerous groups were those in which species flowered and fruited during the wet season, and those in which species flowered and fruited all year with no annual peak, but several other modalities were also found in this slightly seasonal biome.

The phenology of trees in the semi-deciduous forest of Costa Rica has been analysed by Daubenmire (1972) and Frankie, Baker & Opler (1974). For a year, Daubenmire (1972) charted the foliage and reproductive activities of fourteen tree species in the Guanacaste region of northwestern Costa Rica. In that area, rainfall, though higher, is equally as seasonal as in the Calabozo region of Venezuela, and the forest community has many affinities with the semi-deciduous forest of the Venezuelan Llanos. Frankie *et al.* (1974) studied the phenological patterns of 113 species of trees in the same area. They listed the periods of leaf drop and flushing, flowering and maturation of fruits, and compared the resulting data with the behaviour of trees in the Wet Forest type of eastern Costa Rica.

The seasonality of plant species in tropical American savannas was considered for the first time in the now classic work of Warming (1892) in the Brazilian campos cerrados at Lagoa Santa. Warming (1892) carefully described the growth forms and functional features of the main species of herbs, shrubs and trees in this plant formation, which is so similar in many respects to the seasonal savannas of northern South America. He produced a sound description of the seasonal aspects of the herbaceous vegetation, giving details as to which species appear or flower in each season. Today, the only systematic phenological observations on the cerrados remain those of Warming (1892) (Labouriau, 1966), and this seems to be the situation also for all major savanna areas in tropical America.

In Surinam, Van Donselaar-Ten Bokkel Huinink (1966) has made systematic observations on the growth habits and seasonal rhythms of many savanna species, grouping them according to the seasons in which vegetative structures remained functional. She also has presented much valuable information on root form and distribution in different savanna communities.

In the extensive savannas of the Orinoco Llanos in Colombia and Venezuela, the only systematic observations on the phenology of several species belonging to various growth forms have been presented by Monasterio (1968). She has analysed

forest and savanna species in the Calabozo region, and has established groups of species of similar phenological behaviour, based both on vegetative and reproductive rhythms. This present paper completes the previous work of the senior author, and discusses the relative advantages that each phenological strategy may have had for plant survival in this hard seasonal environment. In the following pages, the environmental characteristics of the site will be considered first, as well as the major structural and floristic features of the two plant formations which are present. Following this, some morphological and ecological features of the component species will be briefly summarized. Then, methodological details and basic phenological concepts will be discussed, before reaching the main part of the work, in which seasonal rhythms will be presented, along with a consideration of each phenological strategy from a broad ecological and evolutionary perspective.

The study area

Main climatic and soil features

A detailed climatic analysis of the Calabozo area has been presented elsewhere (Monasterio, 1971), and accordingly only the main features of the climate will be summarized here, paying particular attention to those parameters which are more significant in a phenological context.

Air temperature in the Calabozo area always remains within an optimum range for growth and assimilation of tropical plant species; the annual mean temperature is 27.5°C, and the variation of mean monthly temperatures throughout the year is no more than 2.3°C (Fig. 2a, b). In spite of this relative constancy, there are two temperature pulsations which may certainly have wide ecological and phenological implications—first, the daily thermoperiodism, and secondly, the yearly path of these daily oscillations. A variation of 11–13°C between day and night occurs most frequently, but these cyclical oscillations show a clear pattern of variation throughout the year. During the limpid nights of the dry season, temperature minima reach their lowest annual figures of about 18°C, and as diurnal maxima are also the highest at this time, daily ranges become wider, with a mean of 14°C for the month of April. In contrast, narrower oscillations occur during the cloudy weather of the rainy season, particularly in September (the month

of maximum rainfall), when the mean difference between day and night is only 10.6°C .

Of all seasonal climatic events, rainfall appears to be the one with the most obvious impact on the annual cycles of plant species in the Calabozo area. Almost 90% of the annual rainfall (1312 mm) occurs during the 6 months of the rainy season (May–October); two transitional months (April and November) separate the rainy season from the four-month dry period, when only about 2% of the annual rainfall occurs (Fig. 2c). Interannual variability of rainfall is very high, with an absolute minimum of 581 mm in the 38 years of meteorological records. In dry years, the rainless season may extend to six consecutive months. The highest recorded annual rainfall is 1998 mm, but even in this rainy year the dry season consisted of four consecutive months in which there was no rain.

In general, daylength is obviously another sharply seasonal environmental factor, but at this latitude variations of photoperiodism throughout the year scarcely reach 64 min. (Fig. 2d). Insolation and total

incoming radiation have their annual peaks during the dry season, from December to March.

Soils at the biological station are developed on alluvial deposits of the Mesa formation (Sarmiento & Monasterio, 1969, 1971). In this area, this Plio-Pleistocene formation is mostly composed of sandy loams and sandy clays with a few interspersed gravelly layers. The gently-rolling relief shows on the higher parts indurated layers of lateritic concretions, the relicts of earlier iron-accumulation processes, that nowadays appear as discontinuous outcrops of more-or-less disintegrated rocky blocks. On fine sediments, the soil profile is very mature and most soils then approach the latosolic stage of evolution. However, on lateritic outcrops, the profile is lithosolic and the habitat appears to be much drier.

Soil water content has been measured in the biological station's savanna over a period of 1 year (San Jose & Medina, 1975), and the data obtained indicate that the entire upper 700 mm of soil dries out completely for at least a 4-month period, from

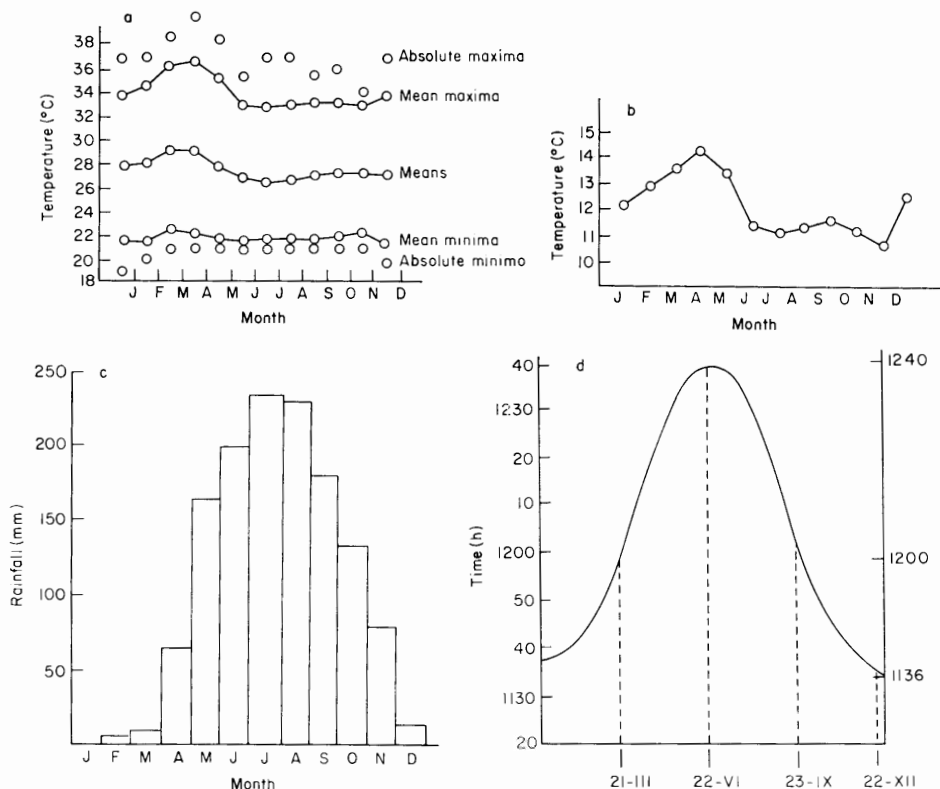


Fig. 2. Main climatic features of the Calabozo area: (a) monthly temperatures; (b) mean monthly oscillation of temperature; (c) rainfall; (d) daylength. After Monasterio (1971).

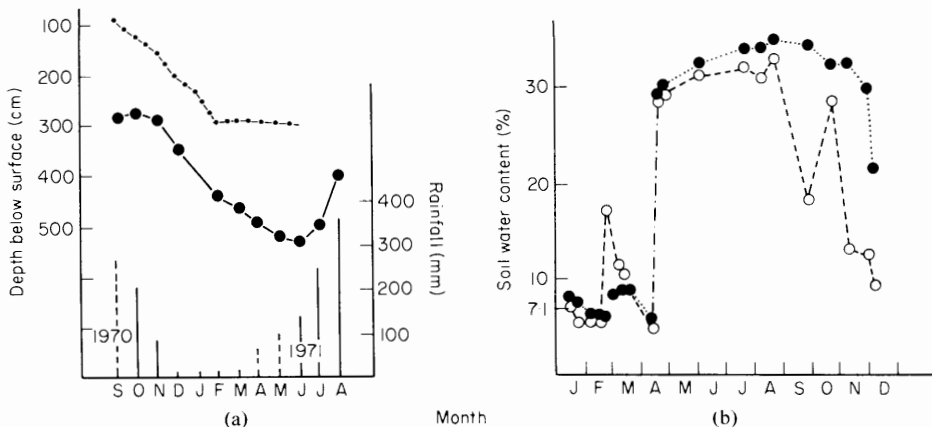


Fig. 3. Annual variation in soil water at Los Llanos biological station. (a) Oscillation of the water table at two points, one under savanna and the other under forest. Rainfall for the period is also indicated (After Foldats & Rutkis, 1975. --- savanna; ●— forest. (b) Per cent of soil water content in a protected savanna site during 1969, an extremely moist year (1839 mm rainfall). Soil water content at -15 bars was 7.1% (After San Jose & Medina, 1975). Depth: ○ 20 cm; ● 40 cm.

January to the end of April (Fig. 3). But at 700 mm, the soil water content remains close to the wilting point (-15 bars) for most of this period, which suggests that in deeper soil layers water may be available for deep-rooted species for the whole of the rainless period. According to Foldats & Rutkis (1975), the water table at various points in the biological station reaches its shallowest values around September (0.8–2 m), and then falls steadily until May–June, when its level ranges from between depths of 3 and 7 m (Fig. 3).

Vegetation

The savanna and forest vegetation in the Calabozo area has been described in previous papers (Sarmiento & Monasterio, 1969, 1971). The gross pattern is one of a continuous tree savanna interrupted by gallery forests along water courses, and with frequent patches of semi-deciduous forest, each of no more than a couple of hectares in size, and scattered within the savanna to give a parkland appearance to the landscape. Phenological observations of forest trees have been undertaken in these forest patches.

The savanna at the biological station corresponds to what has been defined (Sarmiento & Monasterio, 1975) as a seasonal savanna ecosystem, which differs from both non-seasonal savannas in equatorial climates, and hyperseasonal savannas occurring on

seasonally-waterlogged soils. The grass layer in seasonal savannas alternates between a period of development, when its component species are green and grow steadily, and a rest or semirest phase during the dry season, when the dominant species gradually dry out to become, at the end of this season, a standing dead biomass. The dominant grasses are species of *Trachypogon*, *Axonopus* and *Andropogon*, together with sedges of the genus *Bulbostylis*. Many forbs and subshrubs appear among the grasses, the most frequent in the study area being species of *Borreria*, *Cassia*, *Desmodium*, *Galactia*, *Indigofera*, *Hyptis* and *Zornia*. This seasonal savanna is a rich ecosystem floristically in that the total savanna flora in the biological station is comprised of about 200 species (Aristeguieta, 1966), with a mean number of twelve species in 4 m² quadrats. Many of the dominant grasses have the C₄ photosynthetic pathway and therefore they may have a better assimilation rate than others, at the prevailing high temperatures (Mooney, 1972).

The trees scattered in the herbaceous savanna layer constitute a very open storey formed by a few species of low trees, with tortuous trunks, open crowns and scleromorphic, evergreen leaves. The most frequent tree species in the Calabozo savannas are *Curatella americana*, *Byrsonima crassifolia* and *Bowdichia virgilioides*.

This tree savanna is rather uniform throughout the area except for some changes in tree density, but in spite of this physiognomical homogeneity,

important floristic changes reflect the variations in soil conditions. We have distinguished at the biological station three main floristic types. On lateritic outcrops, a community occurs which consists of an open grass layer (maximum cover not exceeding 40%), with the lowest tree density; here the dominants are *Trachypogon plumosus* var. *montufarii*, *Bulbostylis capillaris* and *Bulbostylis conifera*. Because of the open cover of perennial grasses and sedges, many annuals appear on the seasonally bare soil, as for example *Diectomis fastigiata*, *Gymnopogon foliosus*, *Polycarpaea corymbosa*, *Tephrosia tenella* and several others.

A second floristic type is located on deep, well drained, red soils. In this instance, the herb layer may reach a cover of 100%, with *Trachypogon plumosus*, *Axonopus canescens* and *Andropogon semiberbis* being the dominant species. A third type occurs on deep, yellow soils, with poorer drainage and a higher water table. The closed herb layer is dominated in this case by *Trachypogon vestitus*, *Axonopus canescens*, *Axonopus chryso-blepharis* and *Bulbostylis junciformis*. We made phenological observations on all three of these communities.

The forest community in which forest trees were sampled may be considered to be a tropical semi-deciduous forest, from its mixture of evergreen, brevideciduous and deciduous species. The main evergreen trees are *Copaifera officinalis*, *Cassia moschata* and *Vochysia venezuelana*, whereas *Pterocarpus podocarpus* and *Lonchocarpus ernestii* together with *Spondias mombin*, *Acacia glomerosa* and *Luehea candida* are the most frequent brevideciduous and deciduous trees respectively. The forest understorey is rich in low trees, shrubs and vines; it has one species of palm (*Bactris* sp.) and two tree cacti (*Cereus jacamaru* and *Pereskia guamacho*). The total forest flora at the biological station includes fifty species of trees, sixty-five shrubs and vines, and twenty-one herbs (Aristeguieta, 1966).

Characteristics of the species

Table 1 indicates in summary some relevant features of the forty-one species whose phenology was observed. Each species' family, the ecosystem to which it belongs, and the precise vegetation layer in which it occurs are pointed out. The relative abundance of species in the communities of the area is considered in a rough scale of four categories:

dominant, subdominant, frequent and infrequent. Life form and leaf size follow Raunkiaers' system; leaf periodicity refers to the functionality of foliage, in which a species is considered seasonal when the dry leaves persist on the plant as a dead standing crop; when the leaves fall, we indicate whether the plant behaves as a deciduous, brevideciduous or evergreen species. Under 'perennating organs', we considered the plant parts that remained alive all year, while the phenological groupings refer to the classification of species according to their phenological strategies; these latter are discussed in the following pages.

Table 1 shows that, of a total of eleven forest trees whose rhythms were analysed, seven belonged to the forest canopy and four to the understorey layer. The canopy trees were either evergreen, brevideciduous or deciduous, whereas the lower trees were all deciduous. Leaf size in forest trees varied from leptophyll to mesophyll. Of the thirty savanna species, three were evergreen microphanerophytes, fourteen were hemicryptophytes, eleven of them with seasonal foliage, and three were evergreens with xylopod that may also behave as chamaephytes. Finally, there were thirteen species of annuals, many of them of a very small size and with a quite short life cycle.

Methods

Some basic phenological concepts

It seems convenient at this point to attempt a short summary of a few basic concepts which have stimulated the development of modern phenological research and its application to ecosystem analysis. In doing so, we wish to clarify both our methodological procedures and the whole approach of this study.

As stated previously, phenological parameters are to be focused on the rhythmic features of plant functioning, which are useful in the characterization of the evolutionary strategy of species. In other words, we are to consider the phenological variables as pieces of information which, together with the architectural features of plant organization, the modalities of resource allocation, the seasonal carbon and water balances, and the prevailing reproductive and genetic systems, will provide an overall picture of the evolutionary strategy of the species. These characteristics have evolved as adaptive adjustments of populations to the en-

Table 1. Some characteristics of the species observed

Species	Family	Ecosystem and layer	Abundance	Life form (Raunkiaer)	Plant height (m)	Leaf size (Raunkiaer)	Leaf periodicity	Perennating organs	Phenological group
<i>Acacia glomerosa</i> Benth.	Leg.	Forest canopy	Freq.	MePh	15	Lepto	Deciduous	Woody parts	7
<i>Aeschynomene brasiliana</i> DC.	Leg.	Savanna herb	Infreq.	H	0.4	Nano	Seasonal	Xylopod	5
<i>Aeschynomene hystrix</i> Poir.	Leg.	Savanna herb	Infreq.	Th	0.1	Nano	Seasonal	Seeds	4
<i>Andropogon brevifolius</i> Sw.	Gram.	Savanna herb	Freq.	Th	0.3	Nano	Seasonal	Seeds	3
<i>Andropogon semiberbis</i> (Nees) Kunth	Gram.	Savanna herb	Subdom.	H	1.2	Meso	Seasonal	Rhizome	1
<i>Aristida capillacea</i> Lam.	Gram.	Savanna herb	Freq.	Th	0.2	Nano	Seasonal	Seeds	3
<i>Axonopus canescens</i> (Trin) Pilger	Gram.	Savanna herb	Dominant	H	0.8	Micro	Seasonal	Rhizome	1
<i>Axonopus chrysocephalus</i> (Lag) Chase	Gram.	Savanna herb	Dominant	H	0.8	Micro	Seasonal	Rhizome	1
<i>Axonopus purpusii</i> (Mez) Chase	Gram.	Savanna herb	Dominant	H	0.5	Micro	Seasonal	Rhizome	1
<i>Borreria suaveolens</i> Mey.	Rubiaceae	Savanna herb	Freq.	Th	0.4	Nano	Seasonal	Seeds	4
<i>Bowditchia virgilioides</i> H.B.K.	Leg.	Savanna herb	Dominant	MiPh	6	Micro	Evergreen	Woody parts	2
<i>Bulbostylis capillaris</i> Kunth	Cyperaceae	Savanna herb	Subdom.	H	0.4	Micro	Seasonal	Rhizome	1
<i>Bulbostylis confertifera</i> Kunth	Cyperaceae	Savanna herb	Subdom.	H	0.3	Micro	Seasonal	Rhizome	1
<i>Bulbostylis junceiformis</i> (H.B.K.) Kunth	Cyperaceae	Savanna herb	Subdom.	H	0.8	Micro	Seasonal	Rhizome	1
<i>Byrsonima crassifolia</i> (L.) H.B.K.	Malpighiac.	Savanna tree	Dominant	MiPh	6	Meso	Evergreen	Woody parts	2
<i>Cassia moschata</i> H.B.K.	Leg.	Forest canopy	Dominant	MePh	15	Micro	Evergreen	Woody parts	8
<i>Chomelia spinosa</i> Jacq.	Rubiaceae	Forest underst.	Freq.	MiPh	6	Micro	Deciduous	Woody parts	7
<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	Cuculsp.erm.	Forest underst.	Freq.	MiPh	10	Meso	Deciduous	Woody parts	8
<i>Copaifera officinalis</i> H.B.K.	Leg.	Forest canopy	Dominant	MePh	20	Micro	Evergreen	Woody parts	7
<i>Curatella americana</i> L.	Dilleniaceae	Savanna tree	Dominant	MiPh	6	Meso	Evergreen	Woody parts	2
<i>Diectomis fastigiata</i> (Swartz) H.B.K.	Gram.	Savanna herb	Subdom.	Th	0.8	Micro	Seasonal	Seeds	3
<i>Digitaria fragilis</i> (Steud) Luces	Gram.	Savanna herb	Infreq.	Th	0.3	Micro	Seasonal	Seeds	3
<i>Eragrostis maypurensis</i> (H.B.K.) Steud.	Gram.	Savanna herb	Freq.	Th	0.15	Nano	Seasonal	Seeds	3
<i>Evolvulus sericeus</i> Sw.	Convolvulac.	Savanna herb	Freq.	H	0.15	Nano	Evergreen	Xylopod	6
<i>Galactia jussieana</i> H.B.K.	Leg.	Savanna herb	Freq.	H-Ch	0.5	Micro	Evergreen	Woody parts	6
<i>Godmania macrocarpa</i> Hensley	Bignoniac.	Forest underst.	Freq.	MiPh	0.1	Meso	Deciduous	Woody parts	7
<i>Gymnopogon foliosus</i> (Willd.) Nees	Gram.	Savanna herb	Infreq.	Th	0.15	Nano	Seasonal	Seeds	3
<i>Indigofera pascuorum</i> Benth	Leg.	Savanna herb	Freq.	H-Ch	0.8	Nano	Evergreen	Woody parts	6
<i>Lonchocarpus ernestii</i> Harms	Leg.	Forest canopy	Freq.	MePh	15	Micro	Brevidec.	Woody parts	8
<i>Luehea candida</i> (DC) Mart.	Tiliaceae	Forest canopy	Freq.	MePh	15	Meso	Deciduous	Woody parts	7
<i>Microchloa indica</i> (L.F.) Kuntze	Gram.	Savanna herb	Infreq.	Th	0.1	Nano	Seasonal	Seeds	3
<i>Pectis carthasianorum</i> Less.	Compositae	Savanna herb	Freq.	Th	0.1	Nano	Seasonal	Seeds	4
<i>Pectis ciliaris</i> L.	Compositae	Savanna herb	Infreq.	Th	0.1	Nano	Seasonal	Seeds	4
<i>Pereskia guamacho</i> Weber	Cactaceae	Forest underst.	Freq.	MiPh	6	Micro	Deciduous	Woody parts	7
<i>Polycarpa corymbosa</i> (L.) Lam.	Caryophyll.	Savanna herb	Infreq.	Th	0.1	Lepto	Seasonal	Seeds	3
<i>Pterocarpus podocarpus</i> Blake	Leg.	Forest canopy	Dominant	MePh	0.15	Micro	Brevidec.	Woody parts	8
<i>Spodias mombin</i> L.	Anacardiace.	Forest canopy	Dominant	MePh	15	Micro	Deciduous	Woody parts	7
<i>Tephrosia tenella</i> Gray	Leg.	Savanna herb	Infreq.	Th	0.1	Lepto	Seasonal	Seeds	4
<i>Trachypogon plumosus</i> (H.B.K.) Nees	Gram.	Savanna herb	Dominant	H	0.8	Meso	Seasonal	Rhizome	1
<i>Trachypogon vestitus</i> Anders	Gram.	Savanna herb	Dominant	H	0.8	Meso	Seasonal	Rhizome	1
<i>Zornia reticulata</i> Sw.	Leg.	Savanna herb	Freq.	H	0.4	Nano	Seasonal	Xylopod	5

vironments which they have met throughout their history, and they allow species to cope successfully with various environmental hazards and to survive under the competitive conditions of any given ecosystem. By following this approach, we want to consider together the phenological patterns of coexisting species in an ecosystem, to obtain a further understanding of their functional and productive processes, as well as aiming to reach a deeper insight into the constrictions which plant species need to overcome in any particular constellation of those interacting forces which we call an ecosystem.

The most basic phenologic concept is that of phenophase, which is defined as an observable stage of plant development, clearly circumscribed in time, that is accomplished by an individual in a given site and ecosystem during a precise period of observation. Although phenophases are by definition phenomena of direct observation with the unaided eye, the recording of phenological data presents inherent difficulties. An initial problem arises from the fact that each individual, or each discrete plant unit that might be considered functionally as an individual, might also be treated as a subpopulation of more-or-less repetitive morphofunctional units (Harper & White, 1974). These units, as for example a leaf and its axillary bud, though submitted to a certain coordination given by regulatory processes at the whole plant level, and though endowed with a similar genetic information (population of ramets belonging to the same genet, Kays & Harper, 1974), may nevertheless behave independently from one another, particularly in respect of the timing of rhythmic phenomena. Considering phenological processes at this subpopulation level, phenophases may occur more or less asynchronously across a given individual and consequently the characterization of each phenophase even at this level may need a statistical approach, as would be the case with any other population feature. Most phenophases, such as shoot growth, leafing, bud formation and eclosion, blooming, etc., have to be treated as statistical variables inside each single individual, and in many cases architectural patterns can be discerned in phenophases at this individual level of analysis. Only some kinds of phenophases, such as seedling development, can be considered as punctual processes and treated as qualitative, all-or-none phenomena.

A second difficulty is related to the fact that phenophases have to be referred not only to a single individual but also to the entire local population,

if this information is to be useful at the level of the ecosystem. Hence, the characterization of phenophases in a plant population within an ecosystem needs a double statistical treatment that renders arduous the design of phenological observations.

A further difficulty arises from the fact that many phenophases really are developmental processes which are able to be quantified as cases of growth analysis, and then the proper acquisition of phenometric data implies additional decisions concerning sampling and measuring procedures.

A plant may be accomplishing several phenophases simultaneously, as for example leaf drop with leafing and flowering, or blooming with dispersal of old fruits etc. This fact adds a further complication to analysis, and renders uneasy the representation of phenological events in a simple form.

The annual cycle of phenological events for one species, given by the succession or the overlapping of its phenophases, constitutes the phenodynamics of that population in that site and ecosystem, whereas the annual rhythms of phenophases constitutes its phenorhythm for that period of observation. Except in annuals, the phenodynamics of one species does not correspond to its life cycle, since in most growth forms the life cycle extends for more than one year, giving to the phenodynamics a new component related to the developmental stages of the individuals composing a population. But in a first approximation, these life cycle features fall far beyond a strictly phenological analysis.

If several species show the same phenorhythm, a particular phenological pattern may be identified. The degree of concordance among the various species will be judged according to the aspects that might be emphasized in the phenological interpretation of the ecosystem. Frequently, several species in a community show similarities in their vegetative phenorhythms, but they differ in their reproductive phenodynamics, allowing then the characterization of phenological patterns at various levels of similarity.

Phenological patterns have also to be viewed from the three scales of analysis which have been previously mentioned: those of the functional, the individual, and the local population. The first of these is qualitative in occurrence and quantitative in development (phenology and phenometry), while the second and third give rise to architectural and demographic phenological variability, and call for a statistical approach. We may take as an example of the application of these concepts the classification

of Alvim (1964), who recognized four flowering patterns in tropical trees: (a) everflowering trees, which bloom all year; (b) nonseasonal flowering trees, which flower aperiodically in any season; (c) gregarious flowering trees, when each tree is aperiodic but many neighbour individuals show the same rhythmicity; and (d) seasonal flowering trees, when blooming occurs at a fixed period of the year. If these flowering patterns of tropical trees are analysed, the similarity in phenological behaviour may represent phenomena occurring at different scales. In the case of everflowering trees, three types of behaviour can produce the same overall pattern: (1) each developing shoot gives rise continuously to flowering buds and blooms throughout its life (everflowering and evergrowing species); (2) each branch of a tree flowers in a given season, but different branches are not synchronized with one another, in which case the individual may be continuously in flower (architectural or subpopulation pattern) in spite of the fact that their developing units are strictly seasonal; and (3) each tree flowers in a precise season, but the local population has no synchronization among its various biotypes or individuals. The everflowering pattern then is a feature that only appears at the local population level. Along similar lines of reasoning, different scales of patterning among the other flowering or phenological types may be discerned.

The concept of phenological strategy refers to the relationship between the phenodynamics of a species and the environmental and competitive conditions under which it accomplishes its annual cycle. The phenological strategy, together with such aspects as plant organization, allocation of nutrients and energy etc., conforms to the evolutionary strategy of the species. A phenological strategy is only meaningful when it is referred to a particular ecosystem and its environment, and though this strategy has to be explained in ecological terms it gives support to evolutive generalizations concerning both the species and the entire ecosystem.

The whole set of phenological patterns occurring in a community constitutes its phenological spectrum, in the same way that life forms characterize a life form spectrum of the plant community. The phenological spectrum can be represented by phenograms that plot the number of species having each pattern within an ecosystem, or phenograms may give a qualitative representation of the various patterns on the basis of the annual rhythms of its phenophases.

Field procedures

Systematic phenological observations were undertaken at Los Llanos biological station (Fig. 1), where well preserved and protected stands of seasonal savannas and semi-deciduous forests occur. The savanna species were sampled in their respective communities, the *Trachypogon plumosus* savanna on lateritic concretions, the *T. plumosus* community on deep, well drained red soils and the *Trachypogon vestitus* savanna on deep, yellow soils. The three sites were located a few hundreds of metres apart from one another. Forest species were recorded in two isolated forest patches within the continuous savanna, the five sites being located within the 300 ha field of the biological station. During the period of observation, the savannas remained ungrazed and unburned, as they have been for the previous 6 years (the forest patches are not subject to fire as is usually the case).

Observations were taken at 1-month intervals during a 20-month period, in 1967 and 1968. This period comprises two rainy seasons and one dry season. For each species, the following phenophases were observed: germination; shoot growth and leaf formation; leaf colouring and fall; tillering in grasses; flower initiation and blooming; maturation of fruits; and seed dispersal. For each species, the overall pattern of the local population was also considered, by means of a rough estimate of the percentage of the population attaining a given phenophase, as well as through the record of erratic (early or late) occurrences of the phenophases. These estimates were obtained from throughout the biological station.

Besides observations of local populations, ten individuals of each savanna species were chosen at random during each period of observation, so as to obtain a phenometric estimate of the development attained by various phenophases. As the number of trees of certain forest species were rather limited, these observations were restricted on each occasion to the same individuals. These systematic records provided our basic phenological data, and they are complemented with further observations taken during frequent field trips through the Llanos over a period of 10 years. These field observations provided a broader regional picture of the variability in phenological behaviour, especially in respect of leafing, leaf drop, flowering and fruiting patterns for many species, at different sites, and during years with varying rainfall conditions.

Phenological strategies in the savanna*Group 1. Perennials with a semirest phase*

To this phenological group belong the dominant grasses and sedges of the savanna, the 'builders' of the ecosystem. The annual dynamics of these species indicate an apogee stage during the wet season and a semirest phase during the dry season. All species in this group are bunch grasses or sedges, whose only perennial part is a short rhizome that produces tillers and roots.

The typical phenorhythm of the group may be summarized as follows (Fig. 4). After the onset of rains (if the savanna has not been burned), or after the consumption of the previous year's standing crop by fire, an explosive phenophase of intensive tiller production and shoot growth reconstitutes the assimilatory biomass in a few months leading to apogee when the plants reach their maximum vegetative development. After this, towards the middle of the rainy season, vegetative growth sharply decreases, at the same time that the reproductive

phase starts. In a month or so, the inflorescences elongate, following which the population blooms, and fruits begin to mature. After seed dispersal, a short period of full leaf development may persist in some species, until the increasing drought results in severe limitations to tiller survival. As soils become increasingly water-depleted, shoots gradually yellow and dry out. However, new tillers continue to appear, but they either remain incipient without further growth, or they die after forming a few leaves. This is the semirest phenophase, characterized by a generalized plant decline and a persistent formation of new tillers which, under the unfavourable water balance, do not progress beyond the initial stages of development.

Figure 5 presents a more quantitative picture of the annual behaviour of one of these species, and clearly shows the short period of intensive shoot development, the seasonal variations in green biomass, the constancy of total aboveground biomass, and the reproduction after the maximum development of vegetative organs.

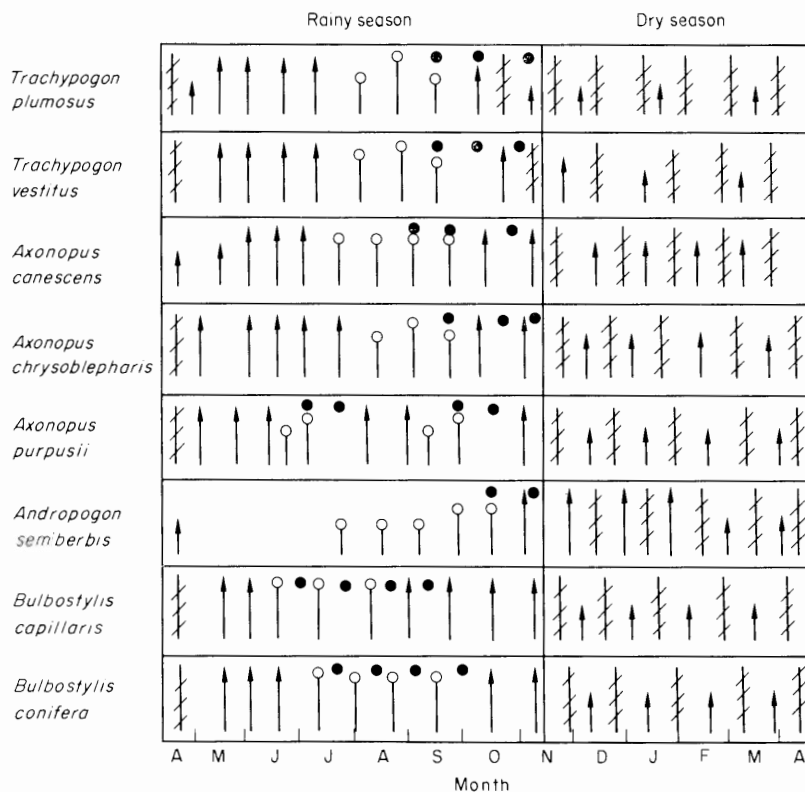


Fig. 4. Phenogram of Group 1. The ↑ indicate tiller and leaf development, crosshatched verticals refer to tiller dry-out; their sizes represent the intensity of each process. ○ flowering and ● fruiting.

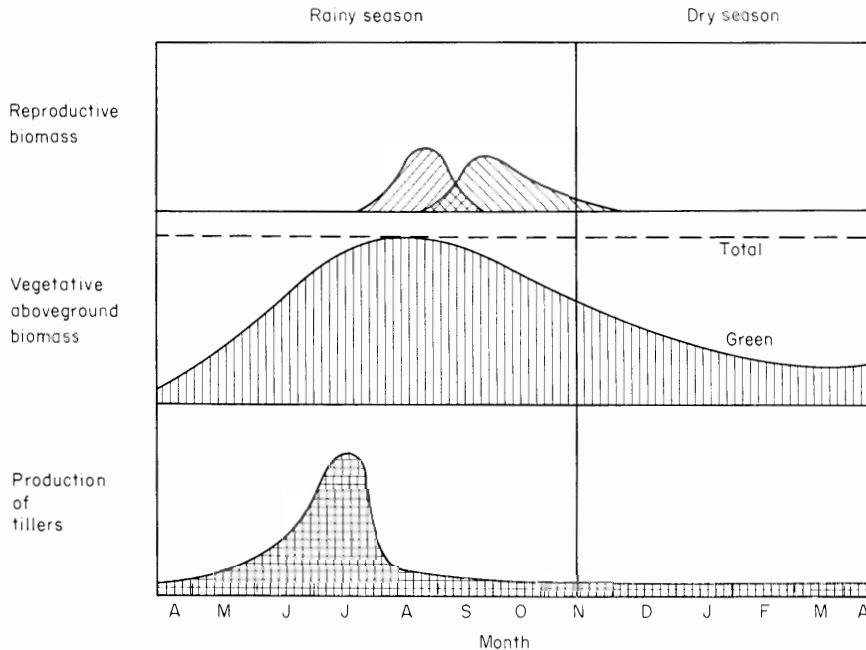


Fig. 5. A semiquantitative phenogram of *Trachypogon plumosus*, a perennial grass belonging to Group I. The diagram only attempts to give an indication of phenometrics variation; therefore, the vertical scales are relative and they do not have numerical values. The lower curve represents the biomass of tillers produced each month; the middle curve depicts variation in vegetative aboveground biomass (total and green); and the top curve indicates changes in reproductive biomass.

Other grasses and sedges, which are dominant in some seasonal savannas in the Llanos, show the same alternation of active and semirest phases, although their phenodynamics during the wet season is different. Thus *Leptocoryphium lanatum*, *Elyonurus adustus* and *Bulbostylis paradoxa*, three widespread savanna species, start intensive growth by first developing their reproductive organs and delaying the reconstitution of the shoot system until fruiting is over (Sarmiento & Vera, 1976).

When the savanna is not burned, the dry standing crop, comprised mainly of old shoots of the dominant species, decomposes slowly during the next rainy season. For this reason, the total plant biomass does not vary in quantity between the seasons, although the state of that biomass does change. But the green biomass is entirely seasonal and is renewed each year; this layer of the ecosystem does not increase in growth from one year to the next. The only plant parts that really increase in size in consecutive years are the underground rhizomes.

Although we have no data on the seasonality of underground organs in these species, available figures which relate to similar ecosystems in tropical

Africa (Lamotte, 1975) suggest that underground development follows a rhythm which is opposite to that of the aboveground shoots. It seems that once full shoot development has been reached, reserves are stored in rhizomes in the remainder of the growing season, and most of the nutrients accumulated in shoots during the previous growth phase are translocated to the aboveground organs.

The phenological strategy shown by this group of species seems to have a clear adaptive value under the environmental conditions of the seasonal savanna ecosystem, and it may be one of the major reasons for their ecological success. Indeed, it appears to be a direct response to the cyclic drought stress. These species overpass the drought by maximizing assimilation and securing reproduction during the favourable period, to decline afterwards to a minimum of activity when environmental stress becomes limiting. However, the semirest phase does not seem to be genetically incorporated: it appears to be just a flexible adaptation which enables genotypes to survive in this environment, even though they may not have been programmed to do so.

The species within this group comprise most of

the biomass of the herb layer, and have a major proportion of their underground biomass in the topsoil. Sarmiento & Vera (1976) have shown that in the western Venezuelan Llanos, in similar tree savannas, 74% of the underground biomass of herbs was concentrated in the upper 0.2 m of soil, and 92% in the upper 0.6 m. This soil layer obviously comprises the most seasonal part of the ecosystem, wetting and drying in strict accord with the seasonal rhythm of rainfall (Fig. 3). The intensive exploitation of the topsoil by these species allows them to start development as soon as this layer is moistened by the first rains of the rainy season, but they also dry out equally quickly as soil water is depleted once the rains have ended.

The slow decomposition of old leaves allows a good utilization of nutrients through internal recycling, a quite important feature in ecosystems such as these which operate under severe nutrient limitations. Likewise, the permanent presence of a grass standing crop, either green or dead, leads to an effective occupation of the ground all year, and thus reinforces the competitive ability of these builder species.

Considering the impact of burning on the species of this group, it should be noted that fires normally occur towards the end of the dry season, when they consume the dry standing crop, which has been already depleted of a substantial proportion of its nutrients by translocation to underground organs, and when the seed bank, produced several months before, lies in the soil protected from the flames. The destructive effect of fire is minimized; moreover, burning also produces the same direct effect on vegetation as do the first rains, which is that it triggers a new annual growth cycle. However, if fire occurs a long time before the onset of rains, it will have a more deleterious action on these species.

It is interesting to note the high degree of synchronization among the various species of this phenological group (Fig. 4). In each species, either vegetative development, or the successive reproductive stages, occur within the same short period. There is also a relationship between the total cover of the herb layer in a particular savanna community, and the degree of phenological synchronization. The more closed the herb layer of a savanna community appears, the more synchronized are the activities of the different dominant species. It seems that those habitats in which a more closed savanna occurs favour a given phenological strategy, with the almost complete exclusion of other possible

alternatives, whereas less favourable habitats, occupied by more open communities, allow a wider spectrum of phenological strategies, leading to a temporal partition of habitat resources.

To summarize, the phenological characteristics of these species which render them highly competitive are (a) their capacity to withstand a long dry season by means of entering into a semirest phase; (b) their ability to surmount the effects of annual burning; (c) their efficiency in the use of seasonal water resources by a rapid development of their assimilatory organs as soon as water becomes unlimited; (d) their ability to recycle essential elements which are scarce within the ecosystem; and (e) their effective occupation of space throughout the whole year. It is also clear that these features will result in the same species losing their adaptive advantages in less seasonal environments, and in fact in the non-seasonal savannas of northern South America this group of species is not as important in the vegetation.

Group 2. Evergreen trees with seasonal growth

This group includes the tree species of this savanna community, since all of them have similar phenorhythms (Fig. 6). They produce their leaves and flowers during the dry season, whereas in the rainy period buds become dormant and every apparent morphogenetic activity ceases completely.

At the beginning of the dry season, leaves start to fall in a gradual process that is prolonged throughout the entire rainless period, and at the same time new leaves begin to expand. As both opposing processes progress simultaneously, the total leaf area and biomass decrease during this season. When the rains arrive all further growth ceases; no new leaves are formed, and the immature leaves do not continue to expand to adult size. Throughout the rainy season, the foliage remains green and its chlorophyll content reaches a maximum (Medina *et al.*, 1969), although towards the end of the season, some leaves take on a brown colour, indicating senescence.

Reproductive phenophases also occur during the dry season, except for fruit maturing and seed dispersal, which may extend to the first few weeks of the rainy season. Germination seems to be quite uncommon in these species, and only a few seedlings of *Curatella americana* were observed at the end of the rainy season.

Although the phenophases are mostly synchronical in the three tree species, *Byrsonima crassifolia* displays a longer flowering period, in that it has two

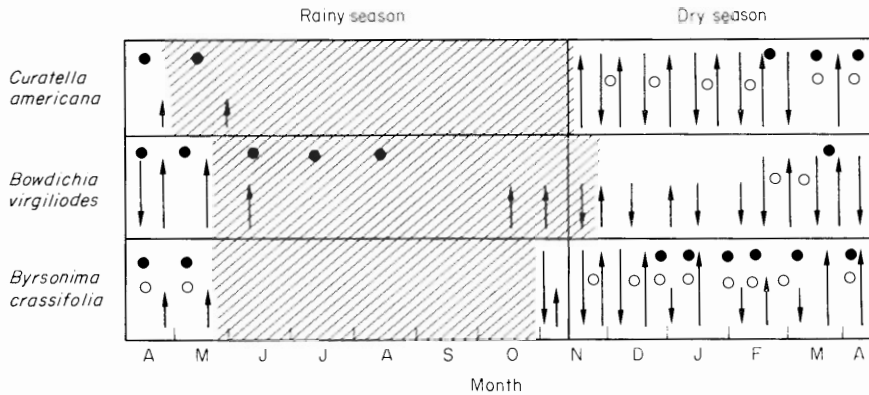


Fig. 6. Phenogram of Group 2. The \uparrow refer to leafing, \downarrow to leaf drop; their sizes indicate the intensity of the processes. \circ and \bullet refer to flowering and fruiting respectively. The cross-hatched area is the period of full leaf development without further growth.

peaks of blooming, one when the apical bud in each branch, after producing several pairs of leaves, changes to the reproductive stage, giving rise to a terminal raceme, and the other being produced by the later development of axillary buds at the base of the older leaves.

In spite of this overall synchronization in their main phenophases, local populations of each species show great plasticity, varying their phenorhythms according to the age of individuals. In *Curatella americana*, for example, younger trees produce leaves and flowers some days before older trees. Figure 7 is a representation of the phenological development of this species, showing the peak of shoot growth during the dry season, when the lowest green biomass is attained and sexual reproduction occurs.

At first sight, the phenological strategy of these species may appear surprising, since they accomplish their main developmental activities, such as shoot growth, leaf production and expansion, flowering and fruiting, during the most unfavourable season of the year, i.e. during the long rainless period. What could be the relative advantages of such behaviour? It has been shown how leaf fall, which leads to a drastic reduction of total leaf area per tree, occurs as drought increases, so favouring a better-balanced water budget. Furthermore, since savanna trees obviously have the ability to grow and develop during the dry season, they must therefore have a secure source of water for this, even though growth could be limited by high energy requirements. In fact, the root system of these trees is quite extensive, and a medium-sized individual may have a lateral root system extending 20 m or more from the tree foot

at an average depth of 0.5 m (Foldats & Rutkis, 1975). Moreover, from these lateral roots, vertical roots can develop to 6 m and deeper. With the large water surplus attained during the rainy season, the lower soil layers can store enough water to maintain deep-rooted trees all year. In some cases, the roots of these species may reach the water table, but this is not necessary for their survival. Foldats & Rutkis (1975), in their analysis of the phenology of *Curatella americana* and *Byrsonima crassifolia*, maintain that these species may drop their leaves as a response to unfavourable aeration due to a high water table; however, their data at the biological station (Fig. 3) show that during the dry season the water table is not too high and it could be supposed that a thick soil layer would remain unsaturated during this period.

Since the plants can use the entire wet season for maximum carbon gain because of their then well developed assimilatory system, the renewal of the system thus is left to a less favourable period when, in any case, photosynthetic rates will be lowest due to the increased difficulty in obtaining water.

The contrast between the phenological strategies of the dominant herbs and trees accordingly can be explained along these lines. When grasses enter their semirest phase, as the topsoil becomes water-depleted, trees continue to grow actively because of their exploitation of deeper water resources. It may thus be seen that a partition of the underground niche occurs as between the two dominant growth-forms, in a way which is similar to their partition of the aboveground space.

Fire may kill some of the old leaves on trees,

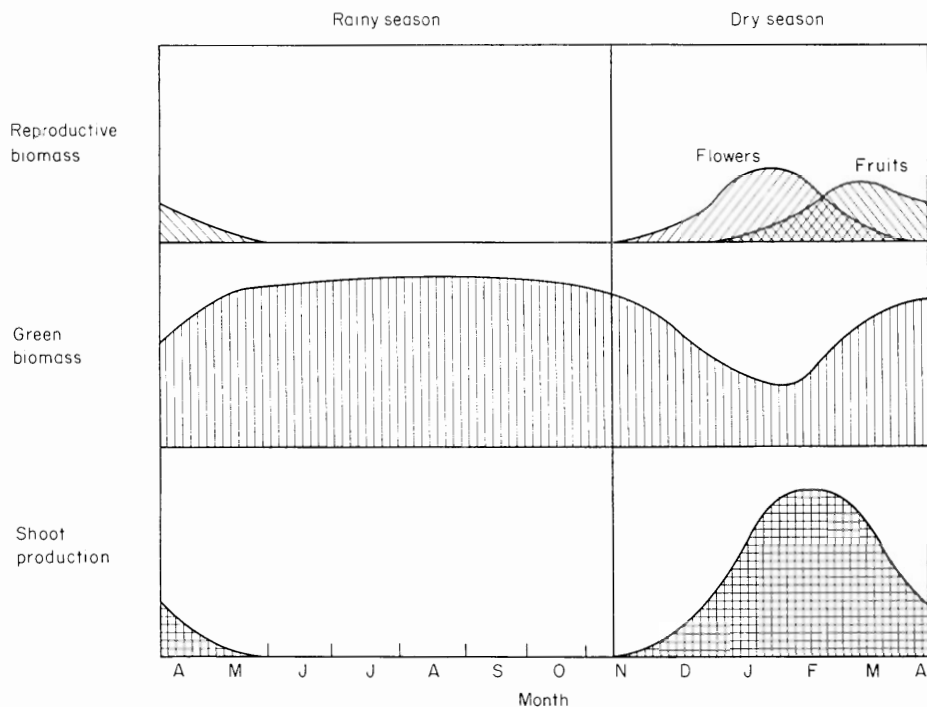


Fig. 7. A semiquantitative phenogram of *Curatella americana*, an evergreen tree belonging to Group 2. The lower curve represents the biomass of shoots produced each month; the middle curve gives variation in green biomass; the top curves refer to reproductive biomass. Since the curves only illustrate seasonal tendencies, the vertical axes do not have numerical values.

and trigger the development of a new foliage. But this effect is conspicuous only on low trees and juveniles, while adult trees beyond a certain critical height remain unaffected. We do not know the impact of fire on the seed bank, but when fire passes through, most seeds are still on the trees. However, as we will discuss later, it seems that the survival of these species in the savanna environment relies more on vegetative propagation, which is promoted by fire damage, than on sexual reproduction.

Group 3. Ephemeral species

While the two preceding groups comprise the dominant species of the savanna ecosystem, the remaining four include species of the herb layer which are of only minor quantitative importance in the vegetation. However, their occurrence illustrates some interesting points concerning the adaptive modalities of plant species to the savanna environment.

In the flora of the biological station, there are about eighteen species of short-cycle annuals, eight

of which have been analysed herein. These include seven grasses and one *Caryophyllaceae* (*Polycarpaea corymbosa*). Most of the grasses are minute herbs, such as *Microchloa indica*, *Gynopogon foliosus* and *Eragrostis maypurensis*, although some species like *Diectomis fastigiata* and *Andropogon brevifolius* may reach a greater size; but whatever their size, all these annuals are ephemerals, which complete their life cycle in a couple of months.

Their activity begins from the middle of July to the end of August (Fig. 8), i.e. towards the middle of the rainy season. There is a notable synchronization between the phenorhythms of the eight species, and the group as a whole is the last to become active in the savanna, since its species persist as seeds for a good part of the wet season (from May to August). Their phenodynamics may be divided into three developmental stages, which succeed each other very quickly.

- (1) Germination, vegetative development and flower formation. These three phenophases proceed so quickly that it has been said that these species 'germinate in flower'. In other

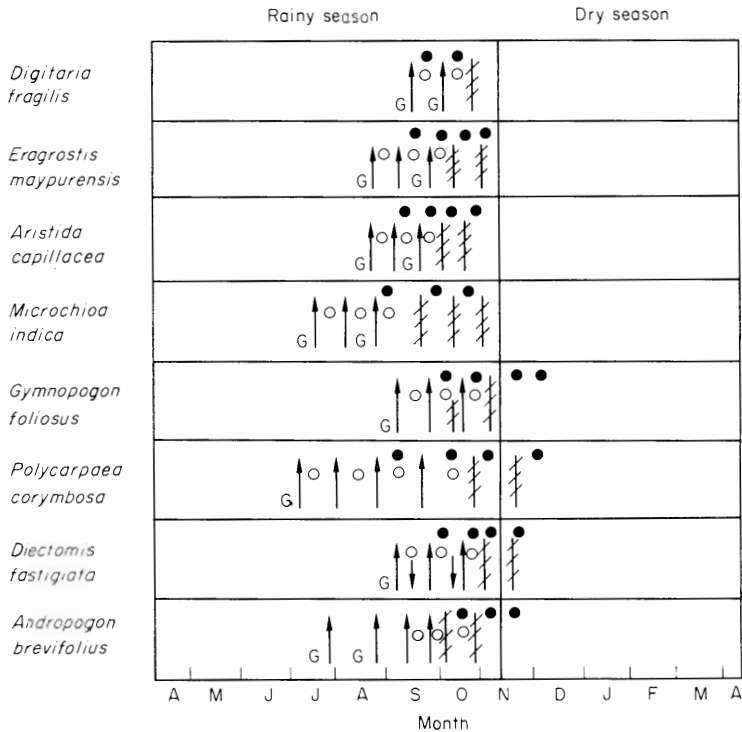


Fig. 8. Phenogram of Group 3. Symbols as in Fig. 4. G refers to germination.

words, they reach almost instantaneously their reproductive maturity, or they already have the capability of flowering from the seedling stage.

- (2) In a second stage, the vegetative part of the plant begins to decline and dries out in a few days; fruit and seed-ripening continue on the drying plants.
- (3) In the third stage, seeds complete their maturity and persist for a while on the plants, eventually to be dispersed. The seed bank may lie in the soil for eight or ten months, until a new active cycle commences.

In each population, the germination period extends to between 20 and 30 days; after this, the lifecycle of each plant is completed rapidly. Therefore, individuals are even more short lived than the total plant population of these species.

The morpho-ecologic features that characterize these ephemerals may be summarized as follows. They are very shallow-rooted plants, which exploit the resources of a thin soil layer. Their vegetative structures are restricted, with few and small leaves

which live for only a few days and then die, in spite of the fact that the entire lifecycle of the plants elapses at the peak of the wet season. Apparently, these species represent extreme examples of r-strategists which maximize seed production to form a great number of small seeds. Their allocation of energy for sexual reproduction seems to be exceptionally high.

After their brief lifespan, seeds remain for a long time in the soil. The possibilities of germination during the next rainy season seem very dependent on the presence of the right niche, since they grow in empty places unoccupied by competitors. Such favourable sites are not available every year. Plants with this strategy prosper in open places, where perennials become sparser, as on disturbed sites or on drier sites with gravelly soils, lateritic outcrops or sand dunes. The exception to this pattern of behaviour is represented by *Digitaria fragilis* and *Andropogon brevifolius*, both of which prosper under the shade of perennial plants, so forming a group of shade ephemerals in contrast to the other sun-loving annuals.

The ephemerals seem to have a low degree of

competitive ability, which is a well known feature of most annuals. Each species germinates massively, where appropriate conditions are found, forming almost pure colonies. As happens in the case of most annuals, when a seed does germinate it develops through until seed production, the major environmental filter operating at the germination phase. In that their short active cycle spans the wettest period of the year, the ephemerals are both drought- and fire-escaping species. The fact that seeds germinate after 3 months of heavy rainfall suggests either that germination could be regulated by an hydrosoluble inhibitor, or that it is dependent on maximum photoperiodicity, in June and July.

The existence of this phenological strategy in a rather humid environment may indicate these species represent a relict group from drier grasslands which have been present in the area in the near past. The sun-loving ephemerals in particular are species with several precise adaptations which allow their survival under desert-like climates. Even if we take into consideration the dry sites on which these species live, their adaptations to a very short growing season do not appear to be justified in this environment. As these species do not occur in arid ecosystems in tropical America, they are also not desert plants, which later colonized open habitats within the savanna. The hypothesis that they are a relict group is supported by the former dramatic oscillations of

lowland climates present in northern South America during the Quaternary (Veillemier, 1971; Van der Hammen, 1974), in which the drier phases corresponded with the recession of tropical forests and the maximum spreading of savannas. This explanation implies that the phenological strategy of these ephemerals represents a paleorhythm which has allowed them to survive today in particular habitats within the savanna region.

Group 4. Annuals with a long cycle

The flora of the Los Llanos station has sixty-three annual species, excluding the ephemerals. Twenty-six of them grow in the savanna, twenty-eight occur either in the forest-savanna border or under trees in the savanna, and nine are exclusive to the forest floor. We followed the phenology of five long-cycle annuals which seemed representative of the seasonal behaviour of these therophytes. In spite of the rather high number of annuals in the savanna (about 15% of its flora), their role in the vegetation is quite modest, except in disturbed places or in those open communities occurring in less favourable habitats.

The lifecycle of these species lasts between 6 and 7 months and elapses entirely during the rainy season (Fig. 9). Their phenodynamics may be summarized as follows. (1) Germination occurs one

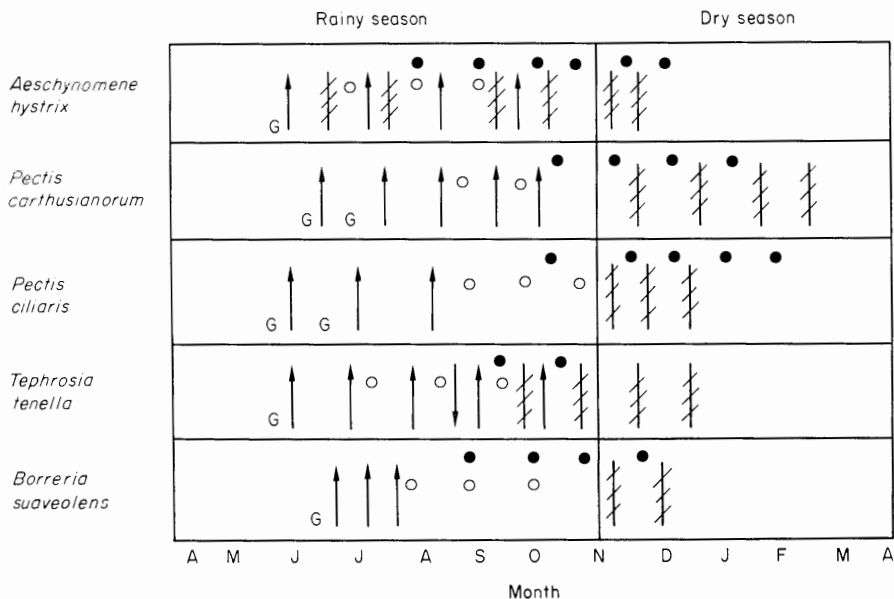


Fig. 9. Phenogram of Group 4. Symbols as in Fig. 4. G refers to germination.

or two months after the onset of rains. Following a short phase of vegetative development, which varies from a few weeks to 3 months according to the species, flowering processes start. (2) The rest of the lifecycle appears to be dominated by re-productive activities. Flowering may extend to 4 months of continuous flower production. After the initiation of the reproductive phases, further vegetative development occurs, with simultaneous formation of leaves, flowers and fruits. (3) When the rainy season is over, these plants are already rapidly declining, but mature fruits may persist for a long time on the dry standing plant. Finally, all seeds become dispersed, in such way that the seed bank rests in the soil for 5 to 6 months, until the start of a new cycle.

As can be seen, the strategy of these annuals seems to be directed towards the maximization of the reproductive effort; they behave as r-strategists which devote most of their active cycle of growth to seed production. This active period coincides with the rainy season, and therefore these species may be considered, *sensu* Levitt (1972), as drought-escaping and fire-escaping plants. Vegetative development is restricted to a minimum, and each leaf has a surprisingly short life in view of the fact that they form during a very wet season.

Some of these annuals, such as *Borreria suaveolens* and *Tephrosia tenella*, are able to develop a new basal growth from the apparently dry plant after completing an annual cycle, and when burning has not occurred. In this way, they behave either as perennials or as annuals, according to fire frequency.

From an ecological viewpoint, long-cycled annuals may be divided into two contrasting groups. Several species are weeds that prosper in disturbed places, such as patches of overgrazed land or in abandoned fields, but other annuals are an integral part of the savanna ecosystem where they occupy specific habitats and persist for many years. The five species analysed belong to this latter category.

The presence of this phenological group in the seasonal savanna may be explained by three factors: (a) the natural and widespread occurrence of open places (gravels, cuirasses, dunes), in which these species are common; (b) the variability of rainfall which is typical of savanna areas, and particularly the periodic droughts which result in the climate then becoming truly semi-arid, in which case the development of perennials is handicapped, and more niches become available for annuals; and (c) the former existence of arid phases in this area in the

near past, which may have left these species, as well as the ephemerals, as present day relicts of a formerly more widespread flora.

Group 5. Perennials with seasonal dormancy

The main phenological characteristic of this group of perennial herbs is the existence of a long phase of complete rest or dormancy. These species are either hemicryptophytes or geophytes, whose seasonal aerial organs are renewed each year; their underground perennating parts (bulbs, rhizomes or xylo-pods) persist in a latent stage until the onset of a new active cycle in the ensuing rainy season. Their aboveground biomass is strictly seasonal, and they approach the phenological behaviour of annuals; however, they differ from them in the permanence of their perennating underground parts.

In the study area, fourteen species show this strategy, ten of which occur in the savanna and four in the forest. We followed the phenorhythms of three of these species (Fig. 10). *Bulbostylis junciformis* is a medium-tall bunch sedge with a perennial rhizome, and shoots that dry out towards the end of the rainy season, though they persist until they are either fire-consumed or decomposed during the next rainy season. The other two species (*Aeschynomene brasiliana* and *Zornia reticulata*) are legumes, whose aerial biomass disappears entirely after the reproductive phenophases have been completed.

The active stage in these species lasts from 5 to 8 months, beginning with the rainy season and perhaps extending to a part of the dry period. In *Bulbostylis junciformis*, the activity begins in May, the plant reaching its full shoot development in about a month; then the inflorescences start to elongate. By July, the flowering phases already have been completed, and the plants immediately show signs of decline, which leads to shoot death in a few weeks. In *Aeschynomene brasiliana* and *Zornia reticulata*, growth persists during the entire rainy season, resulting first in the development of stems and leaves, and then transferring to the reproductive phase. In November, the leaves of these two species drop more or less suddenly, but their green assimilatory stems remain alive for a further period. In some instances, after the almost complete death of the plant, some basal buds may become active, but this late growth does not prosper, and eventually all shoots die.

Most geophytes (*Iridaceae* and *Araceae*) show an

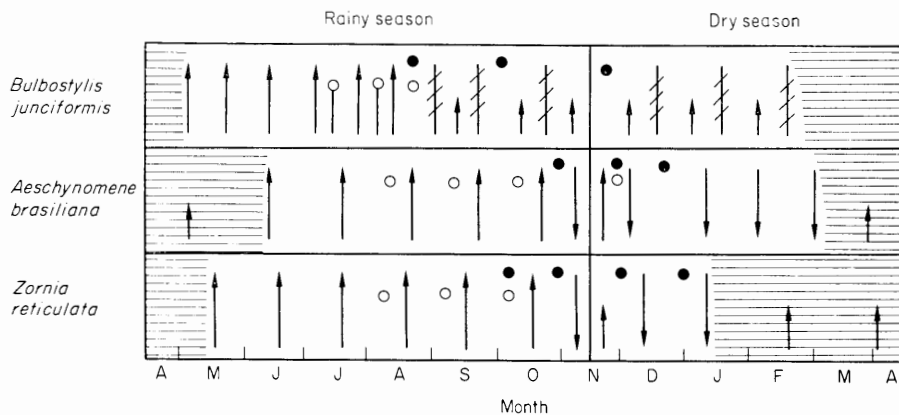


Fig. 10. Phenogram of Group 5. Symbols as in Fig. 4. Horizontal hatching indicates the dormancy period.

even greater seasonal pattern of behaviour, starting their development suddenly with the rains, to complete their cycle in 3 or 4 months, and then disappearing for the remaining 8 or 9 months, except for the perennial bulbs deeply buried in the soil.

The several species which have this pattern of seasonal dormancy are not as synchronized with each other as in the case of the previously described phenological groups. Neither the start of development, nor the end of their active phase occurs synchronically; in the case of *Bulbostylis junciformis*, for example, the rest phase has already begun before the end of the rainy season, as if in obedience to an endogenous rhythm, while the other species seem to resist the drought as long as possible before entering into their dormancy phase. The behaviour of *Bulbostylis junciformis* seems to be an extreme form of the semirest strategy of the other dominant species in the savanna.

As in the case of the annuals, this is a group of drought-evaders which probably evolved as a response to both the long rainless season and the periodic occurrence of fires during the dry period, and their presence further emphasizes the sharp seasonality of this savanna ecosystem.

Group 6. Evergrowing and everflowering species

This group is comprised of perennial, evergreen subshrubs that have continuous growth all year. We followed the phenology of three of these (Fig. 11), all of which have a similar plant organization, with a gross underground xylopod as a perennating organ which acts as a reservoir of nutrients and minerals. From the woody xylopod, the roots extend to a depth of 1 m or more, while from its neck a series of branches develop successively throughout the year.

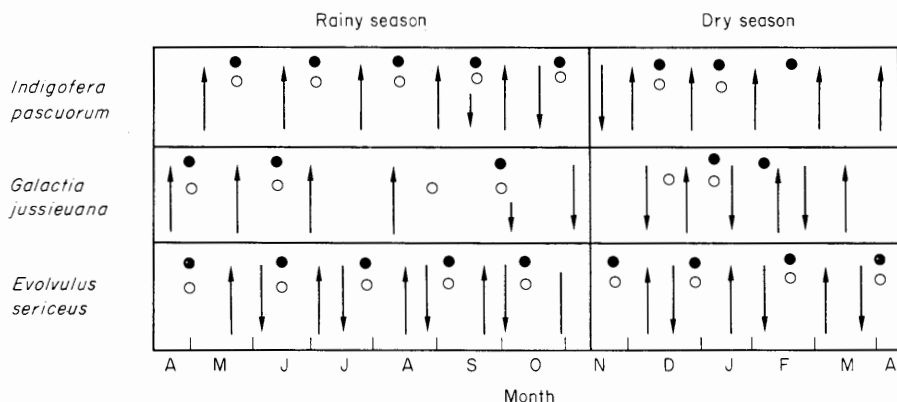


Fig. 11. Phenogram of Group 6. Symbols as in Fig. 4.

Of the three species studied, *Evolvulus sericeus*, a low halfshrub of decumbent habit, high frequency and wide distribution in neotropical savannas, is the only absolutely arrhythmical species. In effect, it shows continuous leaf and flower production all year. Each branch, after emerging from the upper part of the xylopod quite close to the ground, grows for a time, giving a shoot 0.15–0.30 m in length covered with small, densely pubescent leaves. As the branch grows, axillary buds give rise to small flowers. When the shoots reach a certain size, they dry out. As they grow and die, new shoots appear continuously in such a way that the plant remains evergreen without any apparent reduction of its green biomass at any time. Each plant continues to grow and flower throughout the unfavourable period, and it is therefore an evergrowing and everflowering species. The continuous activity manifests itself at the individual level, but it is really an architectural pattern, since each branch behaves as an independent growing unit.

The two other species studied, *Indigofera pascuorum* and *Galactia jussieana*, although exhibiting continuous activity, show some different phenophases associated with the hydroperiodism; thus, for example, the foliage is reduced by a partial leaf drop. Their phenorhythms may be summarized as follows (Fig. 11). During the rainy season, the plants are always in full leaf and form new leaves continuously, though at low rates. At the end of this season and during most of the dry period, the leaves drop and shoots dry out, but at the same time new branches start to grow. Because of this simultaneous drop of old leaves and the development of new shoots, these species are evergreen in spite of the seasonal reduction of the green foliage. From March to May, leaf development is completed and the plants enter again into their less active phase, characteristic of the wet season. In contrast, flowering occurs at any season, but not synchronically in the entire local population, or in every shoot of the individual plants.

The real developmental unit in these species seems to be the individual branch which grows from the perennial xylopod to complete all its vegetative and reproductive phases in less than one year. In *Evolvulus sericeus*, branches are produced continuously, whereas in the other two species a certain incipient seasonality is already apparent. It is interesting to note that, according to Van Donselaar-Ten Bokkel Huinink (1966), these same species show a divergent phenological pattern, in northern

Surinam's savannas, under a different pattern of climatic seasonality.

This phenological strategy persists in the seasonal savanna because a deep root system and a thick, conspicuous xylopod allow these species to grow even during the rainless season. Furthermore, the strategy of independent branch development seems to be quite adapted to periodic burning, since fire destroys those plant parts which will in any case be seasonal. The only additive growth occurs in the woody xylopod, whereas the aerial biomass, though ever present, has a strictly seasonal development of individual branches. The recurrence of fires makes the chamaephytic growth form uncompetitive because burning consumes the whole standing crop from a few centimetres to 1.5 m above the ground, but fire is harmless to underground organs, to above-ground protected structures (thick-barked trees), and to those plant parts located above about 1.5 m. Below this height, only thickbarked trees are undamaged by burning.

Another feature of this group of species is the arrhythmicity in the production of reproductive structures, in which flowers and fruits are formed in any season. Although we have not observed germination in any of these species, we know that seeds are produced and dispersed almost continuously, and the reproductive effort seems to be stepped along the year in a series of small successive impulses.

Phenological strategies in the forest

Group 7. Deciduous trees

Of approximately fifty species which form the total tree flora of this forest, fifteen are most frequent, though no single species can be considered the exclusive dominant of the community. We followed the phenology of eleven of these tree species, seven of which were deciduous. In every case, leaf fall is associated with the dry season; in other words, they are drought-deciduous trees, as opposed to the cold-deciduousness of temperate trees. Their leaves are microphyllous or mesophyllous, and they do not have a scleromorphic nature; this may be seen in the leaf weight per unit area, which is much lower than in the case of savanna trees (Montes & Medina, 1976).

Two sharply contrasted functional stages are evident in the annual cycle of deciduous trees: the full leaf stage during the rainy season, and the

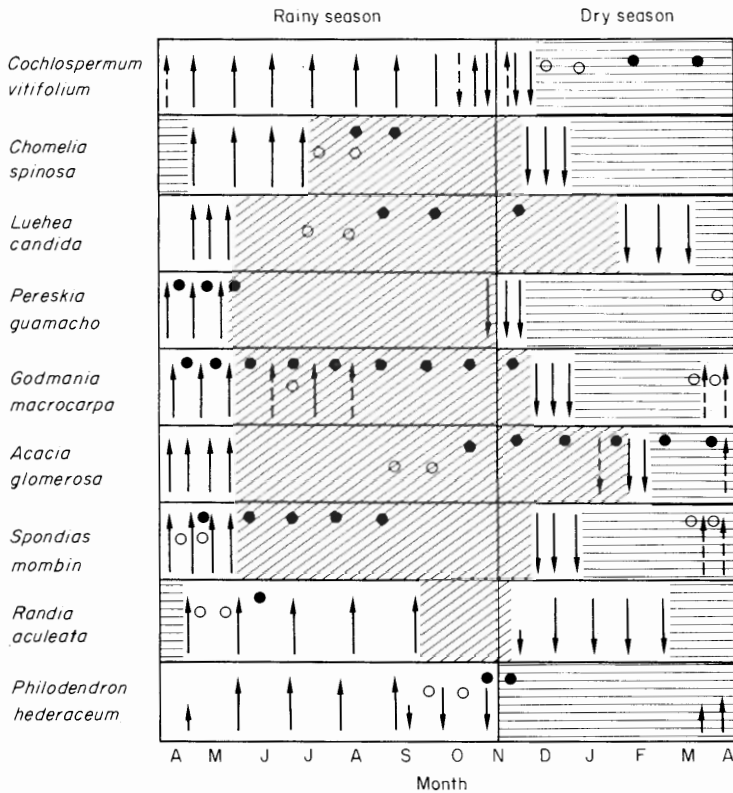


Fig. 12. Phenogram of Group 7. Symbols as in Fig. 4. Horizontal hatching corresponds to the leafless period, crosshatching to the full leaf phase.

leafless phase during a part of, or the whole dry season. These two contrasting aspects are separated by transitional periods of great phenological significance: one of these corresponds to the change from wet to dry weather, when these species drop their leaves; and the other is the transition from dry to wet, when leaf flushing occurs. Most deciduous trees drop their leaves either at the end of the wet season or during the ensuing first weeks of the dry period (Fig. 12), though in some instances, such as *Luehea candida* and *Acacia glomerosa*, old leaves are not shed until the middle of the dry season. Accordingly, the leafless period ranges from 2 to 5 months. As a general rule, in each species leaf fall occurs suddenly, a tree becoming bare in about 2 weeks and the local population in about 1 month. The only exception to this seems to be *Cochlospermum vitifolium*, which colours and loses its leaves over a longer period. This species also has some further anomalies in respect of the general behaviour of other components of this group; for example, it

is the only deciduous species which flowers in the middle of the dry season, and the only one to continue to grow during most of the rainy season.

As regards the onset of leafing in these deciduous trees, two patterns can be recognized. Some species, such as *Chomelia spinosa* and *Luehea candida*, start their leaf development after the arrival of the rains, whereas other species, such as *Spondias mombin* and *Godmania macrocarpa*, begin to develop their new foliage some time before the first rains fall. In the first case, the hydroperiodicity itself seems to be the external impulse which triggers leafing, while in the latter a different environmental signal is indicated. In those cases in which the beginning of leaf growth is dependent on the rains, the plant response can be more precisely matched with the rainfall conditions of each place and year.

Leafing occurs suddenly. When the onset of plant activity precedes the rainy season, it manifests itself in the appearance of flower buds, at which time the leaves do not develop, or they develop

slowly until the first rains. Then the young leaves begin an explosive development, forming the normal foliage in a few days. Once this full leaf phase is reached, most species do not display any further growth or leaf formation.

Various phenological patterns of reproduction may be discerned in this group (Fig. 12). In some cases, reproduction occurs during the dry season while the plants are leafless and do not display any sign of vegetative activity. Among the species studied, *Cochlospermum vitifolium*, as well as several species of *Tabebuia*, show this pattern. In communities in which these species are abundant, their flowering peaks give a spectacular aspect to the leafless forest. The seeds of these trees mature during the dry season, germination taking place as soon as the rains come. A second pattern is one in which flowering occurs towards the end of the dry season, preceding the onset of leafing. Both phenophases seem to be physiologically connected. In *Spondias mombin*, for example, leaf and flower buds differ from each other in location, the reproductive bud being apical and the leaf buds axillary, but leafing does not begin until anthesis is over. This pattern is displayed by many other trees. In these cases, fruit ripening proceeds during the wet season, over 3 to 4 months. A third phenological pattern is characterized by flowering in the rainy season, as soon as leaf development has been completed. Such is the case of *Chomelia spinosa* and *Luehea candida*. Finally, in other species such as *Godmania macrocarpa*, more than one peak of flowering occurs, so that these trees always have fruits at different stages of ripening.

As opposed to savanna trees, in which vegetative propagation is of great importance, these forest trees propagate exclusively by seeds, and except in the case of those species which flower during drought, their fruits may persist on the tree for a long time, so that germination can take place during the following rainy season.

Accordingly, deciduous trees have a drought-escaping strategy, entering into a long vegetative dormancy as the unfavourable season comes in. Monsi (1960) has pointed out that trees seem to be the most efficient architectural growth form for storing assimilates and nutrients; thus one may suppose that the deciduous trees in this forest may use their stocks to start growth even before the arrival of a favourable period. Their extensive and shallow root system also allows these tree species a rapid utilization of soil water as soon as it becomes

available after the first rains. Their ability for intensive carbon gain during the season in which water is unlimiting further makes possible the storage of reserves in the woody parts, which will be used for a rapid leaf flush as soon as the water stress is over, or even before this occurs. One should also remember that savanna fires never enter into the forest spontaneously, and therefore these trees do not have to be fire-resistant in order to survive, as is the case with savanna trees.

The questions as to which environmental impulses trigger the mechanisms of leaf abscission and leaf eclosion, and how these mechanisms came to be established evolutionarily in tropical deciduous trees cannot yet be properly answered. Daubenmire (1972) pointed out that in the semi-deciduous forest of Costa Rica, leaf senescence and abscission seem to be attuned more closely to dryness than to daylength, an opposing pattern of behaviour to most known temperate deciduous trees. Axelrod (1966) has put forward the hypothesis of the random appearance of deciduousness in tropical rain forests, which pre-adapted the species acquiring this to compete successfully in seasonal environments. Although this suggestion may explain the evolutionary origin of deciduousness, one has further to understand the nature of the two most critical phenophases of tropical deciduous species: leaf abscission, and leaf flushing. In some cases, these appear as endogenous rhythms which are not attuned to environmental pulsations of direct ecological consequence, but rather with such signals as photoperiod or temperature oscillations. In other species, these same processes seem to be plastic responses more closely associated with climatic events, and directly related to major environmental stresses. These points will be considered more thoroughly in the final discussion.

Group 8. Evergreen and brevideciduous trees

We grouped together evergreen and brevideciduous trees because their phenological strategies differ only in minor aspects related to the lapse between leaf formation and leaf drop. The four species studied which have this phenological pattern are all canopy trees, whose microphyllous, slightly coriaceous leaves live for somewhat less than a year. As compared with deciduous trees, these leaves are smaller and more scleromorphic.

Figure 13 indicates that three out of the four species studied in this group renewed their leaves during

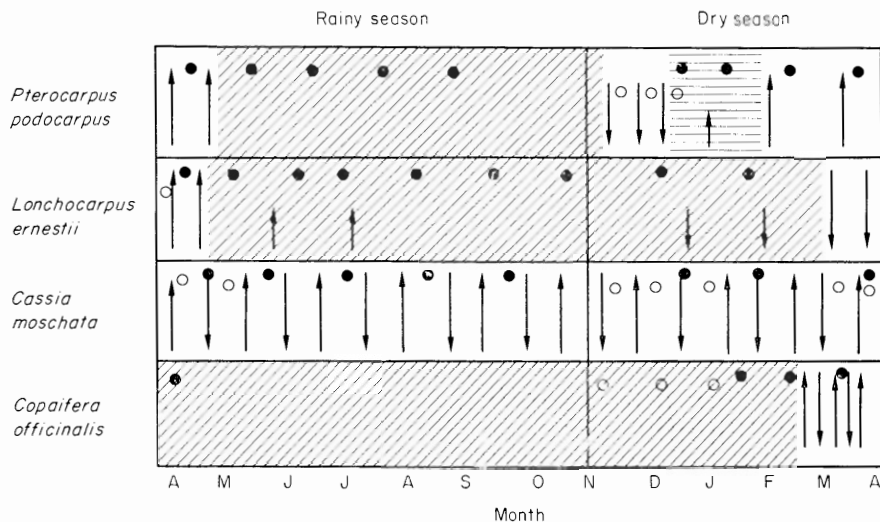


Fig. 13. Phenogram of Group 8. Symbols as in Fig. 12.

the dry season, or in the first few days of the rainy period. In the latter spell, both opposing processes (leaf fall and leaf production) proceeded in the evergreens more or less simultaneously, whereas they are not attuned entirely in the brevideciduous species, so that during the phenophase of leaf renewal, these species may be partly or totally leafless for a period of not longer than a couple of weeks. The evergreens always conserve part of their foliage, but their total green biomass decreases during this phase of change.

As a rule, the brevideciduous trees seem to be quite sensitive to water conditions, since they remain leafless for longer periods in drier habitats or in drier years. In this sense, they behave as facultative or occasional deciduous species, their deciduousness being a rather flexible response to the drought stress.

Except for *Cassia moschata*, the other three species studied do not display any growth during most of the rainy season and also for a part of the dry season; their leaf development starts towards the end of the dry season, a few weeks before the onset of rains, and is accomplished rapidly. In *Cassia moschata*, however, leafing is aperiodic, leaves developing and falling throughout the year. These two processes occur asynchronously in different trees of the same local population and on different branches of the same tree. This species can be considered as an evergrowing species at the population level, a tree with non-periodic growth at the

individual level (subpopulation of ramets), and one with seasonal growth at the ramet level.

The four species studied in this group reproduce during the dry season. In the two brevideciduous trees (*Pterocarpus podocarpus* and *Lonchocarpus ernestii*) flowering and leaf renewal occur simultaneously, the peak of blooming following the drop of old leaves. *Copaifera officinalis* flowers at the beginning of the dry season before changing leaves, and the seeds have already been dispersed at the onset of the rainy season. *Cassia moschata* has a wider flowering lapse, with two peaks of blooming, one at the beginning and the other at the end of the dry season. Most other evergreen and brevideciduous trees in this forest, such as *Vochysia venezuelana*, *Hymenaea courbaril*, *Licania pyrifolia* and *Lecythis ollaria*, have the same reproductive pattern: they flower during the dry season. But whatever the details of flowering phenology might be in each individual species, the general fact is that evergreens differ from brevideciduous species in that they do not show any synchronization between flowering and leaf fall.

This group of species has a continuous carbon gain all year, but they can show either an evergrowing pattern of activity, as in *Cassia moschata*, or a seasonal growth, as in the three other species studied. The dry season does not represent a dormancy period for these trees, since during this time they not only display their foliage, but flowering and leafing also take place. Apparently, these

species avoid drought by using the water stored in the lower soil layers, or by reaching the water table when it does not descend too deep in the rainless period.

Finally we want to emphasize the fact that many possible phenological patterns are found among the evergreen and brevideciduous trees of this forest, as if the environment allowed the simultaneous occurrence of different plant strategies within this same growth form. It seems that neither dryness nor any other environmental constriction is strong enough to induce a unanimous response of the tree flora; on the contrary, almost every species can develop an individual phenological pattern to cope successfully with external limitations and selective pressures.

Discussion

Strategies of savanna species

Our observations on the behaviour of forest and savanna species emphasize the wide range of phenological strategies found in the floras of these two ecosystems. Figure 14 summarizes this information, and frames it within the major environmental restriction: rainfall seasonality. One may see from this that all the herbaceous species in the savanna (groups 1, 3, 4 and 5) show an annual alternation between a phase of minimum activity and another of maximum development. During the apogee stage they have intensive assimilation and growth, and accomplish their reproductive phases; their minimum activity phase, always within the dry season, corresponds either to a period of semirest, with a drastic reduction of the aerial live biomass (group 1), or to a phase of total rest or dormancy with complete decomposition of all aboveground organs (group 5) or to the seed-bank stage (groups 3 and 4).

The phenological strategy of the herbaceous species included in group 1 has many features which not only explain their adaptation to the seasonal savanna environment, but also suggest the key to their ecological success, which has led them to play a dominant role in the community and become the builders of the whole ecosystem structure. In the first place, their rhythms seem to be perfectly coupled with the hydroperiodism, since the species sharply decline during the period of water shortage and grow explosively as soon as soil water becomes available. This dramatic growth is possible because these perennials, with their permanent underground biomass, intensively exploit the upper soil layers.

Furthermore, they occupy the ground during the whole year, maintaining either an actively-developing biomass or a standing-dead crop. As a result, they are far more competitive than either annuals or totally drought-dormant plants, such as those of group 5. The coupling of vegetative phenophases with the hydroperiodism also allows a plastic response, which is adequate for the interannual variability of this climate; whatever the amount and periodicity of rainfall in a certain year, plant growth and decline will follow them strictly. In contrast, the reproductive phases of these species seem to be coupled with constant environmental signals, such as those of the photoperiod, and in fact most bloom in July and August, i.e. after the longest day. This strategy also represents a good adaptation to the prevailing fire conditions in the seasonal savanna, since when fire occurs the aboveground biomass is dry in about 90% of cases, and the perennating organs lie well protected below ground. Furthermore, fire can act as a trigger of new growth and if burning occurs in the proper period, that is just a few days before the start of the rainy season, it may favour further plant development. San Jose & Medina (1975) have confirmed previous data which shows that this ecosystem increases its primary production when burned at the right time.

In respect of the carbon and nutrient balance, which is important for competitive success in this nutrient-poor ecosystem, these species have three morphofunctional features of undoubted adaptive value: they do not maintain passive structures as do woody species; they can recycle critical nutrients within the plant by translocation from shoots to underground organs, while drying or before burning (Medina, unpublished); and they have an optimal assimilation rate when water is unlimited, since most are C_4 plants with unrestricted transpiration, high efficiency in water use and a high temperature optimum for photosynthesis (Mooney, 1972).

Most of the component bunch grasses and sedges are formed by local populations of a few genets that originate from the extension of underground rhizomes. As the rhizomes grow, they contribute to an increase in the number of plant individuals by mechanical fractioning. In this manner, the competitive importance of sexual reproduction becomes greatly reduced in the short term and with it the selective filters against seedling establishment in these closed herbaceous communities. This reproduction pattern serves as a K-strategy, a point which is to be discussed further below.

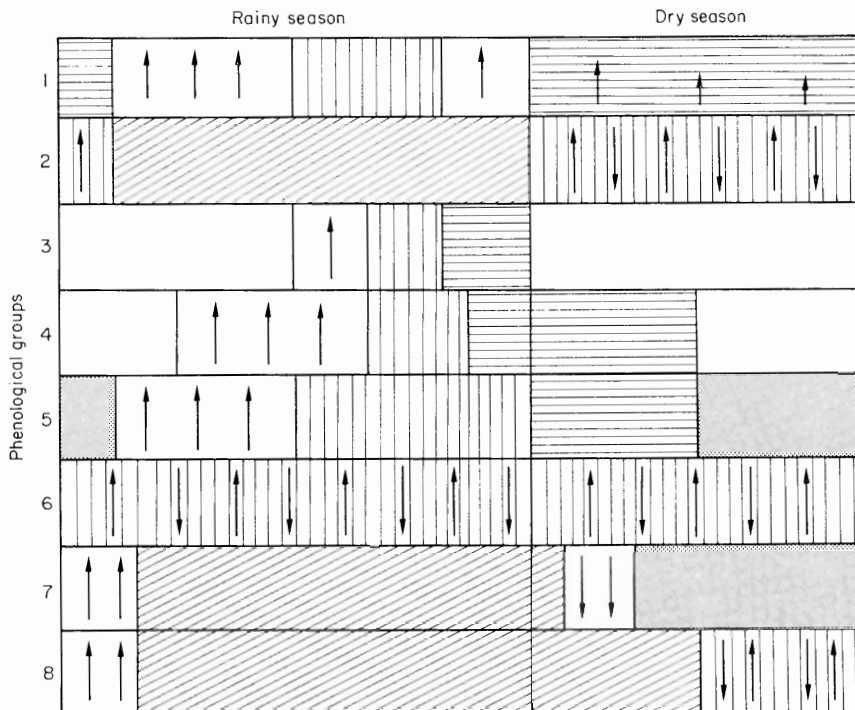


Fig. 14. Phenological strategies present in seasonal savanna and semi-deciduous forest. Each numbered line corresponds to the respective phenological group (see text: particular cases within each group have been ignored). \uparrow indicate leafing; \downarrow refer to leaf drop; horizontal hatching indicates the phase of drying out of aerial biomass; vertical hatching indicates the reproductive phases; diagonal hatching indicates the period of vegetative development; dotted hatching refers to the dormancy phase; white areas represent the period in which species remain as seeds in the soil.

The phenological patterns of annuals (groups 3 and 4) appear also to be well adapted to this seasonal environment, with its extended dry period, but although annuals are well represented in the savanna flora, they play a minor role in vegetation structure, except on open sites and in disturbed places. Under normal conditions, these annuals cannot compete with the perennial species of group 1, but there are enough empty niches available for them to persist under present day conditions as possible relicts from drier periods.

The perennial species with a rest phase (group 5) are neither as competitive nor as successful as the dominants, since they have a shorter growth period and must reestablish themselves each year in the face of competition from the semirest, ever-present species. They show the same plastic response to the hydroperiodic stimulus as do the dominants, in that their phenological patterns are strictly attuned to soil water conditions.

The phenological characteristics of the woody

and half-woody savanna species (groups 2 and 6) display many features which contrast with those of the herbaceous plants. In the first place, they have a continuous growth activity all year: in the case of savanna trees (group 2), the rainy season is their main period of carbon gain while they renew their foliage and flower during the dry season; and the half-shrubs (group 6) have an evergrowing and everflowering pattern. To survive the adverse dry season, both groups rely on two types of morpho-functional features: first, an extensive and deep root system which apparently behaves as a nutrient and water sink during the unfavourable period; and secondly, the evergreen scleromorphic features of their leaves, which restrict water losses. Consequently they behave simultaneously as drought-avoiders, through seeking deep water resources, and as drought-resisters, in their restriction of water losses.

Other features which may explain the ecological success of these evergreen trees are: (a) they maximize carbon gain during the season of unrestricted

water availability by exposing their maximum leaf area and attaining at that moment their highest chlorophyll content; (b) they renew their leaves during the season in which water is restricted to the deeper soil layers and is held by higher water potentials, so that a synchronization is established between the phase of minimum leaf area and the period of maximum water shortage; (c) the requirement of forming and maintaining an escleromorphic photosynthetic apparatus may be compensated by its functioning all year; (d) before leaf shedding, critical nutrients are translocated to permanent organs; (e) the synchronization of leaf renewal with the period of most probable fire occurrence makes it easier for a new leaf crop to form immediately after burning; (f) young trees affected by fire also react immediately by developing new shoots from basal or underground buds, this forming a very effective means of propagation, in that each shoot may give rise to several new ramets, in some cases quite distant from one another, which will soon become independent individuals; and (g) apparently many plant populations are maintained by vegetative propagation, and seedling establishment seems to be very uncommon (Ataroff, 1975), an additional ecological advantage is that this strategy avoids competition between tree seedlings and perennial grasses.

Although the perennial half-shrubs (group 6) have been far less successful than savanna trees, they nevertheless persist as minor components of the savanna ecosystem because their adaptive features allow them to overpass both major environmental constrictions, drought and fire. These adaptations are centred around the possibilities of exploiting deep soil water resources and the allocation of most of their biomass to an underground xylopod, protected from fires, which constantly develops new shoots.

If we try to ordinate all phenological groups of the savanna along an axis representing the degree to which each phenological pattern approaches ideal *r* and *K* strategies, we will obtain as the extreme *r*-strategists, the ephemerals, followed by the long cycle annuals, the perennials with a rest phase, the evergrowing perennials, the evergreen trees and finally, as the closest to typical *K*-strategists, the group of perennial grasses and sedges with a semirest phase (group 1). Indeed, the latter group attain a leading role in conditions of heavy competition in the grass layer, and their species are the most constant in the occupation of space throughout the year.

Stanyukovich (1970) has presented a most interesting classification of world plant formations,

according to their rhythms and seasonal aspects. He considered tropical savannas as being comprised of two facies communities, with alternating growth and rest (or semirest) phases, the latter corresponding to a xeropause. But according to our data, the rest or semirest phase is an exclusive feature of the herbaceous layer, and in particular of its main growth form, the perennial grasses and sedges, whereas trees have uninterrupted growth activities throughout the year.

There is accordingly no rest phase or even a semirest phase at the level of the two dominant growth forms of the ecosystem. It does not seem possible in this case to accept the generalized existence of a xeropause in savannas. Nevertheless, we might treat this savanna as a two-facies community by considering the ecological dominance of each growth form throughout the year. If the species or growth form which effectively uses a maximum of the available resources in the ecosystem at any given period is defined as the ecological dominant, then the perennial herbs are dominant during the rainy season, while trees become dominant during the dry season, when they are the major users of light, water and other resources. However, the overall picture which emerges from our phenological analysis of this savanna ecosystem is more complex than that implied by Stanyukovich's (1970) classification.

Strategies of forest species

It is clear that this ecosystem has only one dominant growth form, the mesophanerophytic tree; however, this growth form presents three different alternative strategies in respect of leaf longevity, assimilation period and rest phase. One is represented by deciduousness, in which leaves live less than 10 months, carbon gain is restricted to the leafy phase, and a period of negative carbon balance extends from leaf fall to new leafing. The opposite case is an evergreen pattern, in which leaves live approximately 12 months, assimilation occurs all year, and there is no rest phase. A third, intermediate case is presented by brevideciduous species, whose leaves live for somewhat less than a year; assimilation proceeds nearly continuously, except for a very short semirest phase occurring between leaf drop and new leafing.

This simple picture of one dominant growth form and three alternative assimilatory patterns becomes more complicated if the other major phenophases are also taken into consideration. In effect, the

seasonal patterns of growth and reproduction, and their relationships to leafing and leaf fall, indicate a wide spectrum of phenological strategies within the trees of this semideciduous tropical forest. On the basis of our previously discussed data, we suggested the existence of two main phenological groups, one with deciduous trees only (group 7) and the other being comprised of evergreen and brevideciduous species (group 8); however, it was also clear in our presentation that these two groups are heterogeneous in many aspects and they include many phenological strategies which, apart from leaf periodicity, differed from one another in various aspects.

In the case of deciduous trees, it was indicated that leaf fall proceeded from the end of the rainy season to the middle of the dry season (Figs 12, 14), whereas leafing varied from leaf eclosion immediately before the onset of rains to its occurrence some weeks after the beginning of the rainy season. In four of seven deciduous tree species analysed, the growth of shoots was restricted to a short period; in two other species (*Godmania macrocarpa* and *Chomelia spinosa*) the growth period was somewhat longer, and in the remaining species (*Cochlospermum vitifolium*) it extended to the whole rainy season.

Flowering patterns also were varied. In *Godmania macrocarpa*, we found a two-peak flowering pattern; in *Spondias mombin* and *Pereskia guamacho*, leafing and blooming were simultaneous; *Cochlospermum vitifolium* flowered at the beginning of the dry season, after total leaf drop; and *Luehea candida*, *Chomelia spinosa* and *Acacia glomerosa* flowered at the middle of the rainy season.

The group of evergreen and brevideciduous trees (group 8) displayed two main phenological patterns, that of evergrowing species with seasonal flowering, as exemplified by *Cassia moschata* (Fig. 13), and a pattern of seasonal growth (end of dry season and first two weeks of rainy season) and seasonal flowering (dry season) such as occurs in the case of the three remaining species in this group.

There are no observations on the phenology of other growth forms in this forest, although data on two understorey species are available. Castellano (1968) has studied the annual cycle of *Philodendron hederaceum* (Jacq.) Schott., a common vine growing to the top of the upper tree storey. This species begins to form its leaves before the onset of rains (Fig. 12), and this phenophase continues during the rainy season up to the end of September, when further shoot elongation and leaf production stop

totally. At this time, 6 weeks before the end of the wet season, the leaves start to colour, and from then to the end of November leaf fall occurs, simultaneously with flowering. During the 4 months of the dry season, *Philodendron hederaceum* remains leafless in a rest phase. This Araceae accordingly has a phenological strategy which closely corresponds to the pattern of the deciduous trees of group 7. It is notable that this herbaceous vine starts its growth before the wet period begins, and after 4 months of rest; this behaviour is perhaps possible due to its succulent stems, which act as reservoirs of water and nutrients. This same phenological pattern persists even when the species grows in gallery forests, where most trees are evergreen.

Silva (1968) has observed the phenology of *Randia aculeata* L. in the same forest stand at the biological station. This Rubiaceae is the dominant shrub in the forest understorey; it is a microphyllous plant that drops its leaves during the dry season (Fig. 12). After the onset of rains, it flushes and flowers, continuing its growth until September, when leaf formation stops. But the most interesting data on this shrub is respect of its behaviour as a facultative deciduous species. Silva (1968) kept the plants in full leaf during the dry season by irrigating them under natural conditions in the forest, or in pots in the laboratory. Those shrubs which were irrigated in February (after leaf drop) produced a new leaf crop in March, about 2 months before the non-irrigated plants. It thus became evident that deciduousness in this case was not a fixed rhythm, but a flexible response to the environment, and one which is subject to change according to water availability. *Philodendron hederaceum* instead behaved as an obligatory deciduous species, in which leaf drop was controlled by some signal different from hydroperiodism.

If we compare the aspects and rhythms of this semideciduous forest with the types established in Stanyukovich's (1970) classification it is clear that this particular forest does not fit easily into that system. This is probably due to the heterogeneous nature of the Semideciduous Tropical forest type, since its deciduous species characterize the Deciduous Tropical forest type which occurs in drier habitats, and its evergreen and quasi-evergreen components are typical of gallery forests which occur on wetter sites. Both kinds of floristic elements and their corresponding phenological strategies converge in this intermediary forest type, which occupies a transitional habitat. This renders difficult

its classification, since according to Stanyukovich (1970) deciduous trees represent the dominant form in a two-facies community with xeropause, whereas the other strategy characterises a one-facies community, with slightly varying seasonal aspects.

Environmental impulses and phenological patterns

It is difficult everywhere to establish casual relationships between observed plant rhythms and external factors. However, this is perhaps even more the case under tropical conditions, in which many environmental pulsations show subtle seasonal variations. Furthermore, many climatic impulses are attuned to each other, rendering it almost impossible, without the help of experimental work, to individualize the factor which triggers one particular phenological event.

Alvim (1964) has established a relationship between several phenophases of tropical trees and such environmental factors as thermoperiodism, maximum temperatures and the number of hours of insolation. He also assumed that the high incoming radiation synchronical with these factors might be the key controlling agent. The environmental pulsations which might affect the phenorhythms of species in the ecosystems which we studied are: (a) the annual hydroperiodism (Figs 2c, 3b), which seems to be the main direct stress acting on savanna and forest species, the two key periods being those of rapidly changing soil water conditions, i.e. the period of abrupt change from wet to dry (November–December) and the similar change from dry to wet in April–May; (b) the daily thermoperiodicity (Fig. 2b), in which greater amplitudes occur from March to May, with a peak in April; (c) the extremes of temperature (means and absolute), the annual maxima being reached from March to May, with a peak in April (Fig. 2a), and minima from December to February, with a peak in January; (d) insolation and incoming radiation, whose maxima occur from December to March; (e) the photoperiod, in which the longest days occur in June–July and the shortest in December–January (Fig. 2d).

Taking the period of initiation of the three major phenophases (leaf formation, leaf drop and flowering) and excluding the non-seasonal phenological patterns, these may be related to the major environmental pulsations as follows (Fig. 15).

First, in respect of leafing and shoot growth, three groups of savanna species (the annuals, and

the perennials with a rest phase—groups 3 to 5) start to grow at consecutive times during the rainy season. Species in group 5 appear attuned to hydro- and thermo-periodicity, as well as to the temperature maxima, while the two groups of annuals start their growth during or after the longest days. Savanna trees start leafing at a time when none of the five environmental stimuli appear to be important, and in this case a chain of physiological processes which begins well before leafing may be significant. The same may be true of the processes of leaf drop and flowering, at least for some of these species. Forest trees (groups 7 and 8) start leafing before the onset of rains, being tuned to maximum temperature fluctuation and to the occurrence of the highest temperatures. Secondly, in respect of leaf fall, the only species in the herb layer of the savanna which shed their leaves (some species of group 5) do this immediately before the dry weather, emphasizing the lack of association between leaf drop and hydroperiodicity. The other herbaceous savanna species decline as a response to water shortage (group 1), or because of an endogenous rhythm not attuned to drought (groups 3, 4 and 5). We suppose that these species have been preadapted to withstand this environment, in that they previously evolved under still harsher conditions. The various forest trees begin to drop their leaves over such a long period that it does not always seem possible to consider leaf fall as an hydroperiodic response; rather, this appears to be synchronized with the occurrence of minimum temperatures, maximum insolation, and partly with the shortest days.

Thirdly, in respect of flowering, all seasonal groups in the herbaceous layer of the savanna ecosystem bloom during the rainy season, during or after the longest days. Woody savanna species, as well as most forest trees, flower in the dry season, while a few deciduous forest trees bloom in the rainy period. The flowering pattern of savanna trees, as already mentioned, does not appear to be synchronized with external stimuli; forest trees which flower in the dry season are attuned to hydroperiodism (group 8) or thermoperiodism (group 7), whereas those trees which flower during the wet season bloom after the longest days.

Comparison of phenological patterns of savanna and forest species

In both communities, there are dominant growth forms with contrasting phenological patterns. While

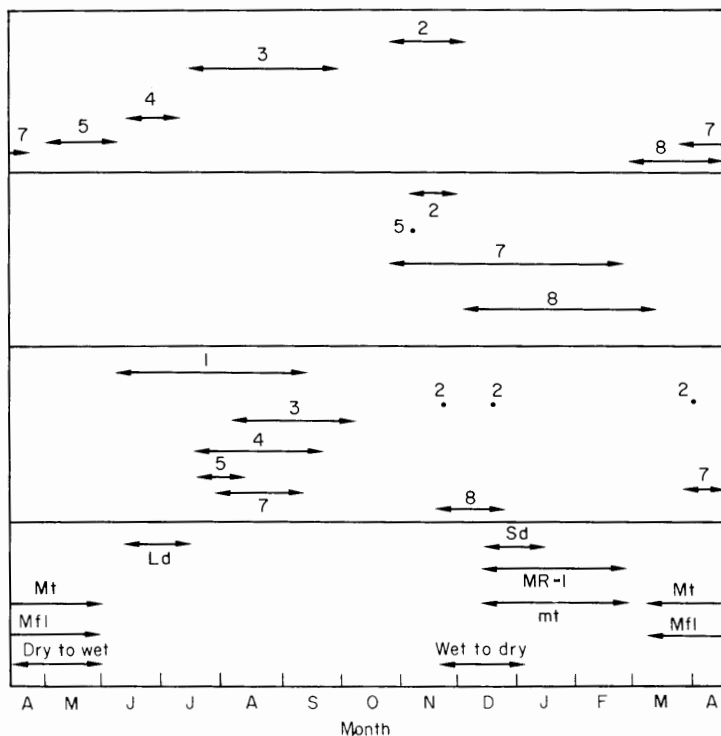


Fig. 15. Correspondence between the beginning of phenophases in each group and major environmental pulsations. The bottom diagram depicts environmental pulsations (Ld, longest days; Sd, shortest days; MR-I, maximum incoming radiation and insolation; Mt, maximum temperatures; mt, minimum temperatures; Mfl, maximum temperature fluctuation; dry to wet and wet to dry, periods of rapid weather change). The top diagram represents the start of leafing and shoot growth in each group (the lines depict the range found in the species of the respective group). The upper middle diagram indicates the start of leaf fall; the lower middle diagram the start of flowering.

one group of dominants is active in each community during drought (savanna trees, and evergreen forest trees), the other enters into a rest or semirest phase (perennial savanna grasses, and deciduous trees in the forest). Thus it is clear that neither of the two ecosystems shows a complete xeropause. This is even more true if the other, non-dominant phenological strategies present are considered, such as those of the evergrowing half-shrubs in the savanna, and the evergreen species of the forest understorey.

The two communities show some particularly conspicuous differences in their flowering patterns (Fig. 16). For the total flora, it is clear that the savanna is more seasonal than the forest in this respect, since a majority of its species flowers during the wet season, with a sharp peak towards the middle of that period (August), while only a couple of species flower at the onset of drought and a few more (all of them woody species) bloom in the

middle of the dry period. The forest flora shows contrasting behaviour, with about one half of its species blooming during the drought period, and the other half during the rains. In the dry season, two flowering peaks are apparent, one at the beginning, and the other, more important peak, towards the end of this season.

The fact that most herb species in the savanna flower during the wet season, whereas the woody species, as well as half the flora of the forest, flower during the dry season, calls for further comment. From an ecological viewpoint, flowering in the middle of the wet period, when water is unlimited and the assimilatory apparatus has reached its full development, does have obvious advantages for herbaceous species. From an evolutive viewpoint, there also will be a positive selective pressure to maintain the flowering process as far as possible away from the burning period, which is of course the dry period. An herbaceous plant cannot allow

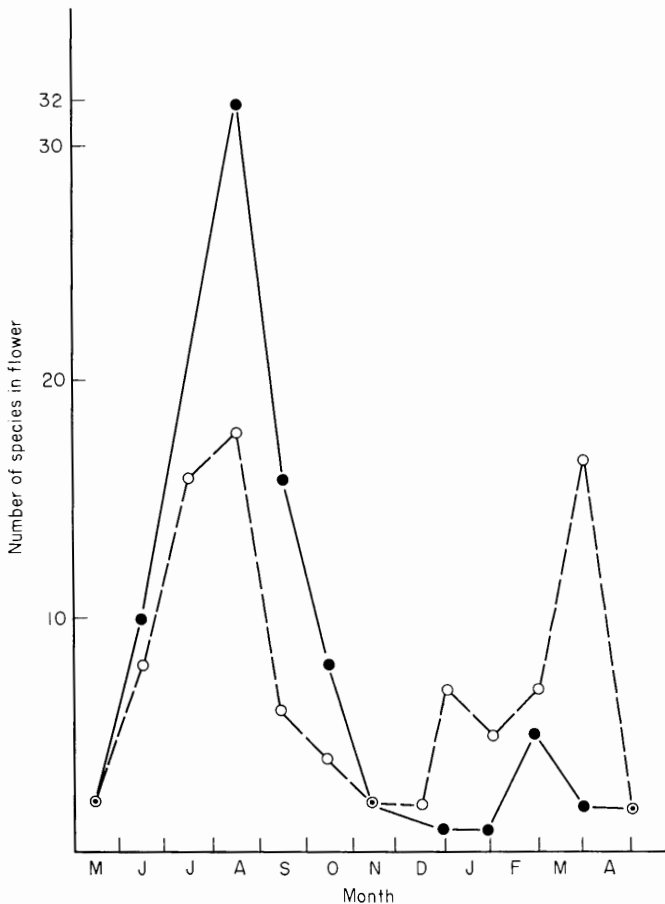


Fig. 16. Monthly variations in the number of species in flower in savanna and forest. ●—● savanna species; ○--○ forest species.

the whole reproductive effort of one growth season to fail due to burning. Further evidence to support this lies in the fact that in savanna communities with an open grass layer, several dominant species, such as *Elyonurus adustus*, *Leptocoryphium lanatum* and *Bulbostylis paradoxa*, as well as some legumes and orchids, do flower in the dry season, but only after burning; that is, fire acts as the trigger to flowering. This appears to be the perfect adaptive response necessary to avoid fire damage, and at the same time to profit from a period in which most species are just beginning to develop. The strategy also favours pollination, since the plants in flower can be identified from great distances. In closed communities, however, the strategy of first forming the vegetative structures, and then flowering may be more competitive.

In the case of those tree species which flower during the dry season, Janzen (1967) has discussed the adaptive advantages that this behaviour has in terms of increasing the efficiency of insect pollination and seed dispersal. It is also evident that trees, as compared to herbs and grasses, have a wider general spectrum of possibilities in their flowering strategies, reflecting fewer environmental restrictions.

We would like to emphasize the similarities between the various phenological strategies of plants and the ecosystems in which they occur. The correspondence between the behaviour of deciduous trees in the forest and of perennial grasses and sedges in the savanna, has already been noted. From an ecological viewpoint, both groups of species exploit the resources of the upper soil layers, and when water becomes limiting they

enter into a rest phase. In this way, perennial grasses and sedges, and deciduous trees, show the same alternation between a phase of intensive assimilation and a phase of rest or semi-rest, when a negative carbon balance prevails. Through extrapolation of these features to the respective ecosystems, one may say that a grass savanna (without trees) and a tropical deciduous forest are basically equivalent in their overall response to environmental stresses. In fact, both ecosystems can occupy drier habitats than those of the Calabozo region, where there is less rainfall, or where the water budget is less favourable.

Evergreen trees in savanna and forest also have many similarities in phenology and ecology. Both have continuous assimilation all year, which is made possible by the use of permanent water resources in deeper soil layers. Through extrapolation to the ecosystem level, a correspondence thus can be established between savanna woodland, with a canopy of low scleromorphic trees, and dry evergreen forest, whose trees also have many scleromorphic traits. In both cases, scleromorphism does not seem to be an exclusive response to a seasonal water shortage, but also to a sharp limitation in nutrient supply. These two types of ecosystem appear side by side in many tropical areas, and one such example has been analysed in detail in the Matto Grosso region of Brazil (Ratter *et al.*, 1973; Askew *et al.*, 1970, 1971).

Finally, the open tree savanna and the semi-deciduous forest which we studied at Los Llanos biological station are clearly similar to each other in their mixed character, both in terms of their use of scarce resources in the ecosystem, as well as in their phenological strategies. The two ecosystems exploit simultaneously all soil layers through the spatial and temporal partitioning of resources among different growth forms and by means of different phenological strategies.

The existence of a pool of phenological patterns in these two tropical ecosystems emphasizes that, in spite of the many external limitations to plant life therein, a full range of adaptive alternatives for survival do exist. The entire pool of adaptive possibilities forms the reserves of each ecosystem's capacity to face continuously changing conditions. If the recent history of this area, and of most continental regions in general are considered with their recent changes in climate, and consequently in soils and geomorphology, it may be supposed that this inherent instability forms the ultimate

key to any explanation of the existing diversity of growth forms and of phenological behaviour. This same diversity will also be a guarantee that the ecosystem will be able to cope successfully with the inevitable future environmental changes which will occur therein.

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References

- ALVIM, P. DE T. (1964) Tree growth periodicity in tropical climates. In: *The Formation of Wood in Forest Trees* (Ed. by M.H. Zimmerman), pp. 479-495. Academic Press, New York & London.
- ARISTEGUIETA, L. (1966) Flórida de la Estación Biológica de Los Llanos. *Bol. Soc. Venez. Cienc. Nat.* **110**, 228-307.
- ASKEW, G.P., MOFFATT, D.J., MONTGOMERY, R.F. & SEARL, P.L. (1970) Interrelationships of soils and vegetation in the savanna-forest boundary zone of north-eastern Mato Grosso. *Geogr. J.* **136**, 370-376.
- ASKEW, G.P., MOFFATT, D.J., MONTGOMERY, R.F. & SEARL, P.L. (1971) Soils and soil moisture as factors influencing the distribution of the vegetation of the Serra do Roncador, Mato Grosso. *III Simposio sobre o Cerrado*, pp. 150-160. Universidade de Sao Paulo, Brazil.
- ATAROFF, M. (1975) *Estudios ecologico poblacionales en dos especies de árboles de las sabanas de los Llanos*, pp. 51. Thesis, U.L.A., Facultad de Ciencias, Mérida, Venezuela.
- AXELROD, D. (1966) Origin of deciduous and evergreen habits in temperate forests. *Evolution* **20**, 1-15.
- CASTELLANO, E. (1968) *Aspectos fisio-ecológicos de Philodendron hederaceum (Jacq.) Schott*, pp. 28. Thesis, U.C.V., Facultad de Ciencias, Caracas, Venezuela.
- CROAT, T.B. (1969) Seasonal flowering behaviour in Central Panama. *Ann. Mo. Bot. Gdn.* **56**, 295-307.
- CROAT, T.B. (1975) Phenological behaviour of habit and habitat classes in Barro Colorado Island (Panama Canal Zone). *Biotropica*, **7**, 270-277.
- DAUBENMIRE, R. (1972) Phenology and other characteristics of tropical semideciduous forest in north-western Costa Rica. *J. Ecol.* **60**, 147-170.
- FOLDATS, E. & RUTKIS, E. (1975) Ecological studies of chaparral (*Curatella americana* L.) and manteco (*Byrsonima crassifolia* H.B.K.) in Venezuela. *J. Biogeogr.* **2**, 159-178.
- FRANKIE, G.W., BAKER, H.G. & OPLER, P.A. (1974) Comparative phenological studies of trees in tropical Wet and Dry forests in the lowlands of Costa Rica. *J. Ecol.* **62**, 881-913.
- HARPER, J.L. & WHITE, J. (1974) The demography of plants. *Ann. Rev. Ecol. Syst.* **5**, 419-463.
- JANZEN, D. (1967) Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution*, **21**, 620-637.
- KAYS, S. & HARPER, J.L. (1974) The regulation of plant and tiller density in a grass sward. *J. Ecol.* **62**, 97-105.
- LABOURIAU, L.G. (1966) Revisao da situacao da ecologia vegetal nos Cerrados. *An. Acad. Brasil. Cienc.* **38** (Supl.), 5-38.

- LAMOTTE, M. (1975) The structure and function of a tropical savanna ecosystem. In: *Tropical Ecological Systems* (Ed. by F.B. Golley & E. Medina), pp. 179–222. Springer Verlag, New York.
- LEVIIT, J. (1972) *Responses of plants to environmental stresses*, pp. 697. Academic Press, New York, U.S.A.
- LIETH, H. (1970) Phenology in productivity studies. In: *Analysis of Temperate Forest Ecosystems* (Ed. by D. Reichle), pp. 29–46. Springer Verlag, New York, U.S.A.
- LIETH, H. (1971) The phenological viewpoint in productivity studies. In: *Productivity of Forest Ecosystems* (Ed. by P. Duvigneaud), pp. 71–84. UNESCO, Paris, France.
- LIETH, H. (Ed.) (1974) *Phenology and Seasonality Modelling*, pp. 444. Springer Verlag, Berlin, Heidelberg, New York.
- MALAISSÉ, F., ALEXANDRE, Y., FRESON, R., GOFFINET, G. & MALAISSÉ-MOUSSET, M. (1972) The Miombo ecosystem: a preliminary study. In: *Tropical Ecology* (Ed. by F. Golley), pp. 363–403. Athens, Georgia, U.S.A.
- MALAISSÉ, F., ALEXANDRE, Y., FRESON, G., GOFFINET, G. & MALAISSÉ-MOUSSET, M. (1975) Litter-fall and litter breakdown in Miombo. In: *Tropical Ecological Systems* (Ed. by F. Golley & E. Medina), pp. 137–152. Springer Verlag, New York, U.S.A.
- MEDINA, E. (1966) Producción de hojarasca, respiración edáfica y productividad vegetal en bosques deciduos de los Llanos Centrales de Venezuela. *Progresos en Biología del Suelo*, 97–108. Centro de Cooperación Científica de UNESCO para América Latina, Montevideo, Uruguay.
- MEDINA, E. (1967) Intercambio gaseoso de árboles de las sabanas de *Trachypogon* en Venezuela. *Bol. Soc. Venez. Cienc. Nat.* **111**, 56–69.
- MEDINA, E., SILVA, J. & CASTELLANO, E. (1969) Variaciones estacionales del crecimiento y la respiración foliar de algunas plantas leñosas de las sabanas de *Trachypogon*. *Bol. Soc. Venez. Cienc. Nat.* 115–116, 67–82.
- MONASTERIO, M. (1968) *Observations sur les rythmes annuels de la savane tropicale des 'Llanos' du Venezuela*, pp. 108. Thesis, Université Montpellier, France.
- MONASTERIO, M. (1971) Ecología de las sabanas de América tropical. II. Caracterización ecológica del clima en los Llanos de Calabozo, Venezuela. *Rev. Geogr.* **21**, 5–38.
- MONSI, M. (1960) Dry-matter reproduction in plants. I. Schemata of dry-matter reproduction. *Bot. Mag. Tokyo*, **73**, 81–90.
- MONTES, R. & MEDINA, E. (1976) Seasonal changes in nutrient content of leaves of savanna trees with different ecological behaviour. (*Unpublished*).
- MOONEY, H.A. (1972) The carbon balance of plants. *Ann. Rev. Ecol. Syst.* **3**, 315–346.
- RATTER, J.A., RICHARDS, P.W., ARGENT, G. & GIFFORD, D.R. (1973) Observations on the vegetation of north-eastern Mato Grosso. I. The woody vegetation types of the Xavantina-Cachimbo Expedition area. *Phil. Trans. R. Soc. B. Biol. Sci.* **266**, 449–492.
- SAN JOSE, J.J. & MEDINA, E. (1975) Effect of fire on organic matter production and water balance in a tropical savanna. In: *Tropical Ecological Systems* (Ed. by F.B. Golley & E. Medina), pp. 251–264. Springer Verlag, New York, U.S.A.
- SARMIENTO, G. & MONASTERIO, M. (1969) Studies on the savanna vegetation of the Venezuelan Llanos. I. The use of association-analysis. *J. Ecol.* **57**, 579–598.
- SARMIENTO, G. & MONASTERIO, M. (1971) Ecología de las sabanas de América tropical. I. Análisis macroecológico de los Llanos de Calabozo, Venezuela. *Cuad. Geogr.* **4**, 1–127.
- SARMIENTO, G. & MONASTERIO, M. (1975) A critical consideration of environmental conditions associated with the occurrence of savanna ecosystems in tropical America. In: *Tropical Ecological Systems* (Ed. by F.B. Golley & E. Medina), pp. 223–250. Springer Verlag, New York, U.S.A.
- SARMIENTO, G. & VERA, M. (1976) Composición, estructura, biomasa y producción primaria de diferentes sabanas en los Llanos Occidentales de Venezuela. *Bol. Soc. Venez. Cienc. Nat.* (*In press*).
- SILVA, J. (1968) *Aspectos fisiocológicos de un arbusto de las matas llaneras* (*Randia aculeata L.*), pp. 37. Thesis, U.C.V., Facultad de Ciencias, Caracas, Venezuela.
- STANYUKOVICH, K.V. (1970) An attempt to classify world plant communities on the basis of their ecological rhythm. Translated from *Ekologiya*, **1**, 18–26. Consultants Bureau, New York, U.S.A.
- US/IBP PHENOLOGY COMMITTEE (1972) *Report, July 1972*, pp. 54. Environmental Programs Coordination Office, Austin, Texas, U.S.A.
- VAN DONSELAAR-TEN BOKKEL HUIJINK, W.A.E. (1966) Structure, root systems and periodicity of savanna plants and vegetations in northern Suirnam. *Wentia*, **17**, 1–162.
- VAN DER HAMMEN, TH. (1974) The Pleistocene changes of vegetation and climate in tropical South America. *J. Biogeogr.* **1**, 3–26.
- VARESCHI, V. & HUBER, O. (1971) La radiación solar y las estaciones anuales en los Llanos de Venezuela. *Bol. Soc. Ven. Cienc. Nat.* 119–120, 50–135.
- VEUILLEMIER, B.S. (1971) Pleistocene changes in the fauna and flora of South America. *Science*, **173**, 771–780.
- WARMING, E. (1892) *Lagoa Santa*. Branco Lunos Kgl. Hof-Bogtrykkeri, Kjobenhavn, pp. 386. (Portuguese translation: E. Warming, *Lagoa Santa*. 1973. Editora da Universidade de Sao Paulo, Brazil).