

## ASSESSING TROPICAL VEGETATION SEASONALITY

### Expression de la saisonnalité de la végétation tropicale

J. DEGREEF\*, M. VANOVERSTRAETEN\*\* & F. MALAISSE \*

#### RESUME

*Les auteurs rappellent les définitions des termes "saisonnier", "saisonnalité" et "phénologie". Ils passent en revue l'impact des facteurs physiques (radiation, précipitation, humidité de l'air et du sol, photopériodisme) sur la végétation en régions tropicales. Ils envisagent ensuite l'objet des observations (synusies chlorophylliennes, floraison, fructification, variations diamétrales) et leur approche méthodologique. Les modes d'expression sont passés en revue et illustrés. Enfin, les lacunes de nos connaissances sont soulignées.*

#### ABSTRACT

*The authors remind the reader of the definitions of "seasonal", "seasonality" and "phenology". The impact of physical factors (radiation, rainfall, air and soil moisture, photoperiodism) on vegetation is reviewed with regard to tropical regions. The object of observations (chlorophyllous synusia, flowering, fruiting, girth changes) as well as their measuring are discussed. Various ways of expressing results are listed and illustrated. Finally gaps in our present knowledge are underlined.*

#### INTRODUCTION

Many studies concerning seasonality were carried out in the past but few allowed to know with certainty factor or factors responsible of any particular behaviour of vegetation. This can be noted in the temperate regions but is especially noteworthy for vegetation phenology in the intertropical belt. Actually, under tropical climates alternation of seasons is often summarized at a regular episodical emergence of rainfall in alternance with shorter or greater dry periods and other factors like air or soil

---

\* Laboratoire d'Ecologie, Faculté des Sciences agronomiques, 2 Passage des Déportés, 5030, Gembloux.

\*\* U.E.R. Science du sol, Faculté des Sciences agronomiques, 5030, Gembloux.

temperature, air or soil moisture, photoperiodism are not taken into account to characterize tropical climates. Such environmental data are rarely recorded but their importance is sometimes pinpointed by various authors. This study consists in a preliminary synthesis of actual knowledge about phenological inducers and the various ways that have been followed to assess seasonality.

## DEFINITION

In the temperate regions, the vegetation varies in its aspects with seasonal changes in the climate. The succession of very contrasted seasons at regular periods of the year is characterized by temperature variations, the amplitude of which is a function of latitude. On the other hand, tropical or subtropical forests or savannas show more or less regular seasonal rhythms which seem much more difficult to analyze and appear to be often a function of a combination of many environmental factors.

LIETH (1974) quoted seasonal to mean events, objectives, state variables, that are "pertaining to, dependent on, or accompanying the seasons of the year or some particular season", a special case of "periodical" events. He proposed as definition for the term "seasonality" the following: "Seasonality is the occurrence of certain obvious biotic and abiotic events or groups of events within a definite limited period or periods of the astronomic (solar,calendar) year".

A consequence of seasonality is the recurrence of biological events, the study of which is also called "phenology". The first scientist interested by phenology was LINNE (1751) who outlined methods for compiling annual plant calendars of leaf opening, flowering, fruiting, and leaf fall, together with climatological observations. Nevertheless, the term "phenology" was first proposed by the Belgian botanist MORREN in 1853.

A definition of phenology was proposed by the US/IBP Phenology Committee (LIETH, 1974) and suggested that "Phenology is the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species".

## TROPICAL VEGETATION SEASONALITY

### WHY SEASONALITY ?

Seasonality is primarily related to abiotic physical factors. These include radiation and precipitations.

Radiation has to be considered in connection with insolation, day length, cloudiness. This bilan is partly expressed in air and soil temperature. Temperature changes may constitute an effective stimulus for the renewed bud activity (NJOKU, 1963) but may also explain the difference in behaviour between lower sheltered and upper exposed branches of the same tree. Some plants are known to respond to cold periods by flowering, the most celebrated example being *Dendrobium crumenatum*, an orchid from

Malaysia which flowers 9 days after a cold snap (MABBERLEY, 1992). *Bromheadia finlaysoniana* flowers in mass 7 days after a markedly cool day (HOLTUM, 1949). Flowering of *Oxytenanthera abyssinica*, the small zambesian bamboo, takes place on a cycle varying from 7 to 21 years, after that the entire plant often dies; this flowering appears to be triggered by extreme low temperature or severe frosts (FANSHAW, 1972). Some Malayan epiphytic orchids flower 8-11 days after a thunder-shower following a dry spell. In this case, the effect of showers is not directly that of rain but is due to the sudden temperature fall (COSTER, 1926).

As related in tropical deciduous forest in Mexico (BULLOCK & SOLIS-MAGALLANES, 1990) or in Zaire (MALAISSE, 1974), there is no evident indication that soil temperature should be an important limitation or cue involved in flushing. Daily changes in soil temperature are highly dependent on the season they occur and also vary with the type of vegetation.

The effect of radiation may also explain the relatively earlier leaf flushing occurring in sloping stations where the amount of direct sunlight is greater (PUIG & DELOBELLE, 1988).

As far as ecosystems are concerned precipitation has to be included in a general approach on water balance, thus including air and soil humidity, a result of interception, evapotranspiration, percolation, water table position, ... But precipitation is not the only source of moisture in the Tropics where relatively important dew, fog and clouds sometimes also influence the water balance (MABBERLEY, 1992).

In many parts of the Tropics where moisture appears to be the main seasonally variable factor, attempts have often been made to fit crop growth data to rainfall data and to infer a causal relationship. Causal relations inferred from such correlations may, however, be misleading since the effective cause may be some other factor of the environment which is correlated with rainfall. The period of seasonal drought in the Tropics is generally also the period of changes in day length, air temperature, air humidity and number of bright sunshine hours. In many cases lack of synchronisation of the phenology with the seasonality of a precise environmental factor suggests that periodicity in the vegetation must be controlled either by an internal factor either by an interaction of several external factors. Nevertheless some major trends could be pinpointed.

Several strategies exist according to vegetation types but may also coexist in a unique ecosystem. The restriction of leaf flushing to periods of favourable moisture status appears to be a general adaptive feature of tropical trees (REICH & BORCHERT, 1984). In dry forest of Ghana, flushing patterns varied somewhat between tree species and between individuals within species, although all flushing activity was restricted to wet periods while relatively drier periods within wet season brought about a cessation of flushing activity. For instance, leaf production in the oil palm is well correlated with rainfall (BROEKMANS, 1957). In a seasonal evergreen forest in Costa Rica, the majority of tree species produce new leaves at the beginning of rainy season but leaf-flushing of some others appears at the beginning of the dry season (ROCKWOOD, 1975). In most species, an increase in leaf fall preceding dry season is marked and explained logically as the result of increasing age and senescent condition of the leaves put on the previous year. This leaf fall peak occurs when leaves are dislodged by the first hard rain after several drier days (HAINES & FOSTER, 1977). Flushing generally begins just at the time leaf-shedding ceases. This can be explained by the improvement of moisture balance of the tree resulting from the drought-induced leaf shedding (KOZLOWSKI, 1973). The so-called pre-rain flushing seems to be in relation with the triggering effect of rising

temperatures and with the annual variation in length of day even when leaf abscission peaks are attuned to peaks of dryness (DAUBENMIRE, 1972, FRANKIE *et al.*, 1974).

Generally, leaf fall of most deciduous trees is associated with the dry season and considered as an adaptive feature to avoid excessive transpiration but a few exceptions are quoted. Some species like *Jacquinia pungens* (JANZEN, 1970), *Cordia alliodora* (CROAT, 1975) or *Acacia albida* however lose their leaves in the wet season. *Acacia albida* has the peculiarity of shedding its leaves at the approach of the rains and putting them forth at the first sign of the dry season in Nigeria (LELY, 1925) or dropping its leaves and growing new ones during wet season in Zimbabwe (DUNHAM, 1989). Regarding evergreen species, in many cases leaf fall occurs throughout the year but peaks are observed for some species. For example, some evergreen tree species lose their old leaves soon after new leaves production at the onset of wet season (ALVIM, 1964, MORI & KALLUNKI, 1976).

Greater or lesser amounts of rainfall modify soil moisture status during a wet season and are accompanied by proportionate responses in the number of species and individuals flushing (LIEBERMAN & LIEBERMAN, 1984). Yet, in wet areas, soils' rehydration and flushing may proceed in the absence of rainfall, while in dry areas, flushing will not occur until after an adequate amount of rainfall has been received. In a tropical forest on Barro Colorado Island (Panama), understory trees and shrubs species have different seasonal patterns of vegetative phenology according to water relations (RUNDEL & BECKER, 1987). *Hirtella triandra* maintained high turgor pressures throughout the dry season, probably because its deep root system, and thereby exhibited active vegetative growth at this time. In contrast, *Hybanthus prunifolius* had a single period of synchronized leaf flushing at this same transition time, and showed a strong pattern of seasonal osmotic adjustment. Some authors showed the non-relation between leaf production or abscission and soil moisture variations. In the tropical semi-deciduous forest in Costa Rica, a considerable number of species put out new leaves well in advance of rainy season (DAUBENMIRE, 1972, FRANKIE *et al.*, 1974).

The flowering pattern of many species consists first in an accumulation of flower buds which achieve a certain stage of development and then remain dormant waiting for a stimulus to flower all together. Rainfall is often considered as an effective stimulus but whether it is water, or the associated low temperature, or the rapid drop in temperature which is really effective is unresolved (REES, 1964).

Flowering in the majority of tropical woody plants appears to be initiated after a critical dry period. In more seasonal forests, most flowering occurs at the end of the dry season so that water stress is invoked as a stimulus to flowering (MABBERLEY, 1992). But on the other hand, the end of the dry season coincides with a warmer period in some regions and may also provoke the stimulus to flowering. More rarely, flowering induction seems to be directly produced by rainfall. It is the case of *Clerodendron incisum* (REES, 1964). In a dry tropical forest in Ghana, a significant correlation between the number of species in flower and the amount of rain fallen over the preceding 21 days is outlined (LIEBERMAN, 1982). Some shared species are present both in dry and wet forest of Costa Rica and then show different phenological patterns which appear to be no more than a simple response to local rainfall and soil moisture regimes (OPLER *et al.*, 1980). Several ecosystems of the Zambezian region are subjected to seasonal conditions notably by the alternance of 5 to 6 dry months and 5 to 6 rainy months but like cupricolous flora, they may however present a saturation of flowering all year round (BROOKS & MALAISSE, 1985).

It has been demonstrated that photoperiodism can induce dormancy in the case of temperate trees and also be responsible of the passage from vegetative to flowering condition (LAWTON & AKPAN, 1968). A similar study for tropical trees showed the consequence of short days in the reduction of vegetative growth to a very slow rate (DOWNS, 1958). ALVIM (1964) pointed out that in tropical trees these photoperiodic responses are often complicated by simultaneous or superseding responses to other physical environmental factors. Studies on tropical species like *Coffea arabica*, *Theobroma cacao* or *Plumeria acuminata* highlight the effect of short days on the flowering induction (PIRINGER & BORTHWICK, 1955, PIRINGER & DOWNS, 1960, LAWTON & AKPAN, 1968) or the flowering of *Hibiscus siriacus* under long days (ALLARD, 1935). In the Amazon basin some trees flush during relatively dry season just prior to flowering. Some authors suggest that photoperiod could be a controlling factor in this response (LANGENHEIM *et al.*, 1973). Leguminous trees in Central America often initiate flushing during early dry season at time corresponding with increasing daylength after winter solstice (STUBBLEBINE *et al.*, 1978). The onset of dormancy of *Hildegardia barteri* in dry forest of Nigeria is influenced by the small seasonal changes in natural day length; bud dormancy being induced in 11 hours 1/2 days and prevented in 12 hours 1/2 days (NJOKU, 1964).

Even though phenological patterns are principally considered as dependent on abiotic factors, they might also be modulated by various biotic factors, especially interactions with animal species in terms of pollination, seed dispersal or consumption and be in some cases a coevolution result (JANZEN, 1967; HLADIK, 1980).

#### WHAT TO OBSERVE ?

Seasonality and phenological patterns are world-wide observed and pinpointed at least for some species in all vegetation formations. Nevertheless some exceptions are reported for species that seem to possess non evident phenological behaviours. It is the case of the Dipterocarp species of lowland rain forest in West Malaysia where no strong seasonality is observable. Some 85% of the species there do not flower or produce new leaves at regular intervals and, within species, there is a lack of synchrony (PUTZ, 1979).

Observations can be directed on

- a.- *chlorophyllous synusia*;
- b.- *flowering*;
- c.- *fruiting*;
- d.- *girth changes*.

According to our purpose, we will mainly detail the first item.

#### a.- *Chlorophyllous synusia*.

Chlorophyllous roots from epiphytic orchids and green stems from several Euphorbiaceae and Asclepiadaceae notably are minor in regard of the importance of foliage and should be neglected for our purpose.

Species are generally characterized by their evergreen, semi-deciduous or deciduous behaviour but some with a large extension area may have a great behaviour

variability. It is the case of *Prosopis juliflora* which behaves as an evergreen in arid formations of tropical South America and may be completely leafless during subtropical South American winter (SARMIENTO, 1972).

Some species are called early deciduous because they are totally leafless at the beginning of the dry period. At the opposite late deciduous species are only bare for a short period and are somewhat similar to evergreen species. Intermediate patterns of progressive leaf shedding are shown by slow deciduous species (HLADIK, 1980).

Foliar organs may be characterized through:

- biomass;
- leaf area index (L.A.I.);
- leaf area density (L.A.D.);
- leaf inclination;
- chlorophyll content;
- mineral composition;
- leaf surface structure;
- leaf anatomy;
- for which seasonal changes exist.

In deciduous tropophyllous vegetation, leaf biomass is generally approached through leaf fall. For evergreen and semi-evergreen vegetation yearly leaf fall values do not inform on biomass as lifetime of leaves according to species is generally unknown. In moist evergreen forest of Ivory Coast, annual production of leaves was however estimated to about  $8.1 \text{ t ha}^{-1} \text{ year}^{-1}$  (BERNHARD, 1970) and to about  $4.7 \text{ t ha}^{-1} \text{ year}^{-1}$  in a dry semi-deciduous forest in Nigeria (HOPKINS, 1966).

Leaf Area Index (L.A.I.) which is the ratio of total leaves surface - one side - of plants of a plot to the plot's surface depends on the vegetation type but seems fairly constant in a given environment. In tropical rain forests where L.A.I. can be assigned a maximal annual value of 8.2, structural heterogeneity and seasonality are however important sources of variability (ALEXANDRE, 1981). The variation of specific leaf surface according to their position in crown is also pinpointed (KATO *et al.*, 1978).

Studies about the seasonal variation of L.A.I. are presented for a subtropical dry forest in Porto Rico where it varies from 1.2 to 4.2 (LUGO *et al.*, 1978), for a tropical moist forest in Panama where L.A.I. reaches 10.6 in the dry season and 22.4 in the rainy season (GOLLEY *et al.*, 1975) or in a dry evergreen forest of Zaire where it varies from 2.6 to 5.0 (Fig. 1, MALAISSE, 1993).

In subtropical rainforests of South America, understorey layers always show a greater inter-species variability in foliage periodicity than the corresponding upper strata (SARMIENTO, 1972). Differences may even exist which depend upon the age of the individuals. Long period of leaf production for seedlings in a mixed deciduous forest of Nigeria are in marked contrast to the behaviour of mature trees in which the period of leaf production is restricted to 2 or 3 months and sometimes to only 1 month of the year (Njoku, 1963, 1964).

Leaf Area Density (L.A.D.) takes into account the distribution of leaf area in space within the canopy and represents the area of leaf per unit volume of canopy (RUSSEL *et al.*, 1989).

Leaf inclination is extremely rarely evaluated. In dry evergreen forest in Zaire, the horizontal and vertical angulations were measured for about 20 woody species and revealed a great variability between species which is function of the period of measurement. In dry period in Porto Rico, leaves of many species turn yellow and hang

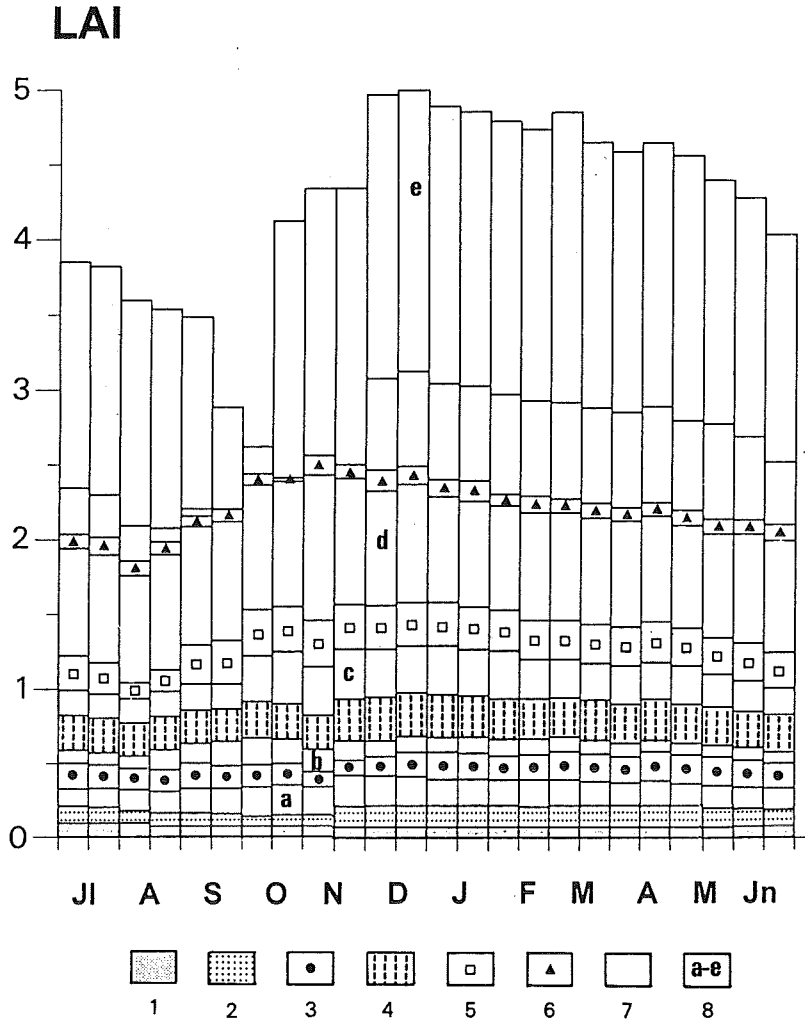


Fig.1. - Fortnightly L.A.I. in a Zambezan dry evergreen forest. (1 : *Apodytes dimidiata* subsp. *dimidiata*, 2: *Diospyros hoyleana* subsp. *hoyleana*, 3: *Tabernaemontana pachysiphon*, 4: Other species, 5: *Entandrophragma delevoiyi*, 6: *Brachystegia taxifolia*, 7: *Combretum acutifolium*, 8(a): *Parinari excelsa*, 9(b): *Combretum gossweileri*, 10(c): *Syzygium guineense* subsp. *afromontanum*, 11(d): *Aidia micrantha* var. *msonju*, 12(e): *Brachystegia spiciformis* var. *schmitzii*) (after MALAISSE, 1993)

vertically along branches (MURPHY & LUGO, 1986). Compound leaves are considered to represent a preadaptation for rapid changes of leaf angle at midday (EHLERINGER & FORSETH, 1989). This feature may explain the increase in the number of canopy species with compound leaves as you move along an environmental gradient from wet, evergreen tropical forests to seasonally dry, deciduous tropical forests (GIVNISH, 1978).

In an investigation of the seasonal variation of mineral composition in miombo trees of Zimbabwe, levels of K, Mg, N and P are highest in young leaves and these elements are reabsorbed to some degree prior to abscission. Al, Ca, Fe and Mn increase with maturation of the leaves, while Cu and Zn show no regular trend of change (ERNST, 1975). For a dry evergreen forest in Zaire, the P, Mn, Mg, K, Ca and N compositions of leaves show more or less important decrease in the dry season (DIKUMBWA, 1990).

Changes in chlorophyll content are function of the age of leaves and may vary seasonally too. In a tropical rain forest of Porto Rico, the amount of chlorophyll A extracted from the dominant tree *Dacryodes excelsa* is about 16% greater in January than in May (ODUM *et al.*, 1970).

#### *b. - Flowering.*

Flowering may be assessed

- 1) in a general pattern of sexual reproduction which allows to recognize the sequence buds - blossoming - faded flowers;
- 2) as its owns:
  - number of flowers per individual;
  - differentiation between buds and mature flowers;

According to their flowering patterns, species may be separated in "mass flowering" species and "steady state" ones. The "mass flowering" are species the individuals of which produce large numbers of flowers each day over a week or even less. The "steady state" species are characterized by the production of small numbers of flowers but almost daily for many weeks. In addition variability among individuals affects population synchrony and flower abundance throughout the population's flowering period ( Fig. 2, AUGSPURGER, 1983). Nevertheless it is possible to distinguish many intermediate flowering mechanisms between these two types for example flowering waves patterns.

#### *c. - Fruiting.*

In a dry tropical forest in Ghana, fruiting occurs throughout the year but different patterns occur in relation with the type of fruit produced. Dry-fruited species fruit principally in dry seasons and fleshy-fruited ones in either wet or dry seasons, although fruits are most abundant in wet seasons (LIEBERMAN, 1982). When comparing individuals within each species, the individual's flower number appears to be the best predictor of fruit set even if some may abort. In view of more detailed studies, those characteristics or items could be studied :

- to count up the number of fruits;
- to distinguish fruits from swollen unpolinated ovaries;
- to distinguish immature fruits from mature fruits.

#### *d. -Girth changes.*

Vegetation seasonality is perceptible too through the annual increment of woody trees corresponding to more or less favourable growth conditions. In rain evergreen forests, the girth increase is continuous and no age ring is noticed but under more seasonal climate, the correlation between age rings and seasons' succession is really clear.



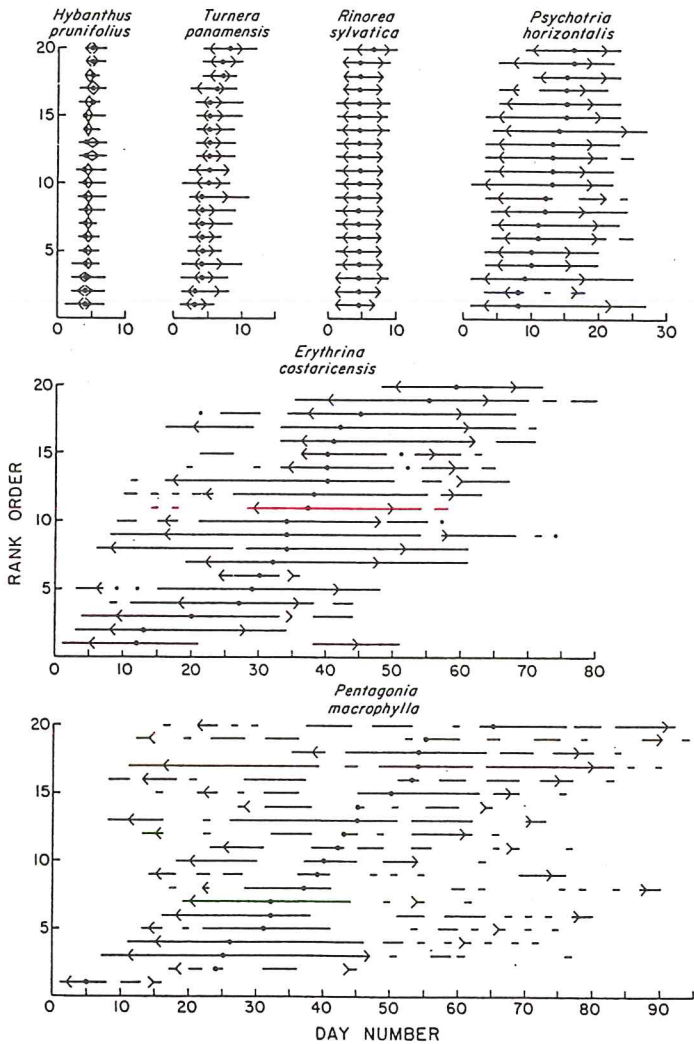


Fig.2 - Timing of flowering of individuals arranged in rank order of the day the median flower was open (N=20 for each of six species). Each horizontal line represents the total duration of flowering by an individual. A broken line indicates discontinuous flower production. The brackets enclose the period around the median flower day during which 90 % of individual's flower were open. The heavy dot indicates the day the median flower was open; this day corresponds to the peak day (maximum number of flowers) for mass-flowering individuals of the first three species (after AUGSPURGER, 1983)

In addition, dry seasonal shrinkage which consists in a temporary decrease of girth was observed in semi-deciduous forest in Costa Rica (DAUBENMIRE, 1972). In a dry tropical forest of Ghana, girth changes which were also influenced by shrinkage appear to be closely linked to foliage condition. Flushing occurs when the girth is at a relative maximum and is accompanied by a marked decrease in girth; this is most probably due to a high rate of transpiratory water loss from young leaves (LIEBERMAN, 1982).

#### HOW TO MEASURE ?

Phenological observations in a forest are sometimes limited to upper-layer individuals the seasonality of which is then considered to characterize the forest phenology. Generally, understorey tree species are not taken into account. However, the leaf amount they represent may influence the phenological behaviour of the forest studied. In Costa Rica, seasonality of flowering by wet forest trees seems more pronounced than that of understorey shrubs. Continuous leaf production is shown by 28% of overstorey trees, 40% of understorey trees and 49% of shrubs and appears to be an inverse function of the strata involved (OPLER *et al.*, 1980). A comparison of fruiting phenology in wet and dry forests clearly shows the markedly seasonal pattern of trees in both forests but shrubs fruiting is aseasonal in wet forest and exhibits a double peak in dry forest (FRANKIE *et al.*, 1974, OPLER *et al.*, 1980).

The biomass of epiphytes in dry forest may be about  $0.15 \text{ t ha}^{-1} \text{ yr}^{-1}$  corresponding to three times that in moist forest (MURPHY & LUGO, 1986). Lianas are frequently neglected. Nevertheless average L.A.I. of them may reach about 20% of the total rain forest leaf area as well in Venezuela (PUTZ, 1983), in Australia (HEGARTY, 1990) and in Gabon (HLADIK, 1974).

Phenological observations are carried out either on (1) one or two individual plants clearly labelled, (2) on a variable sampling of plants with or without repetition, (3) following transects along which individuals are tagged, finally (4) on parcels where some individuals are regularly observed. Some more original technics allow to observe such phenomenon from above the canopy. For instance, in lowland rain forest in West Malaysia, a suspended transect walkway was used over a 4-year period (PUTZ, 1979). A phenological state of the individual may be evaluated based upon the general observation of its crown but also by choosing a few labelled shoots of each tree and keeping regular records of leaf-fall, flowering, (NJOKU, 1963).

Due to the seasonal changes from year to year, which might be important in spite of regular climatic pattern, the yearly variation in plant phenology must be considered (GACHET, 1971).

Periodicity of observations varies according to the studies involved. Nevertheless the period of observation is often of one year. For the Low-Ruzizi region in Burundi, six periods have been selected and defined in regard to the onset or end of the dry and rainy seasons : (1) end of dry season, (2) two weeks after the onset of rains, (3) six weeks after rain onset, (4) four months after rain onset, (5) end of rains and (6) dry season (REEKMANS, 1980). For other studies, observations are conducted according to a rigid calendar based on monthly or weekly frequency. Several studies run on a longer period with a higher observation frequency: 3 years with reproductive and foliage status assessments every 10 days in Ghana (LIEBERMAN, 1982), 3 years too in Costa Rica but with 4 to 6 weeks intervals between observations (OPLER *et al.*, 1980) and even 6 years in Madagascar ( Fig. 3, ROHNER & SORG, 1986). Those studies indicate the great interest



of such an approach: (1) sensitive lag of the period (date, length) of a phenophase according to year (some correlated with the amount of rains), (2) non yearly periodicity (2-year, ..., even more complicated). A few mature treelets and shrubs, particularly among the Rubiaceae, for example do not flower every year in the wet forest of Costa Rica (OPLER *et al.*, 1980).

For estimating leaf biomass, litter trays floored with nylon mesh are usually placed at a variable height above ground level to avoid excessive decomposition. Litter which falls into these trays includes leaves but also flowers, fruits and twigs. A selective classifying allows to separate different components of litterfall. Litterfall estimations may be affected by overhanging subcanopy branches and by closeness to tree trunks but do not vary neither under different sides of one tree, at sufficient distances from the trunk, nor among individuals of the same canopy species (LOWMAN, 1988). So collected litter samples are then air dried on the field before being oven dried, generally at 65°C, to constant weight to estimate dry weight (DANTAS & PHILLIPSON, 1989). But the ununiformity of the methods employed to collect data by different authors rarely allows to compare all the results available.

As shown above, Leaf Area Index (L.A.I.) may be a useful indicator of the vegetation cover at an appointed time. The results obtained by estimation methods of L.A.I. are controversial because of the necessarily tedious fieldwork they require or the relative reliability of optical or spectral techniques used. Photoplanimetry consists in establishing linear regression equations based on the product of the lamina's length by width and to compare with standard leaf images (VAN SEVEREN, 1969, HELLER, 1971). Either planimetry, in the case of irregularly shaped leaves, or assimilation (with, in general, a correction factor) for simply geometric forms (mainly an ellipse) were used to study the time and space L.A.I. variation of woody and grass layers in a Zambezi miombo forest (MALAISSE, 1988). Sampling was earlier used to evaluate L.A.I. in Porto Rico (ODUM *et al.*, 1963), Panama (GOLLEY *et al.*, 1975) and Malaysia (KATO *et al.*, 1978) among others. For grass layer, the use of a needle permits in pricking through the leaves to determine both leaf inclination and L.A.I. (WARREN-WILSON, 1963). A derived method is also employed for tree canopies by counting leaf contacts with a vertical weighted string suspended from a 10 meters telescoping pole (MURPHY & LUGO, 1986). Litter fall can be used to derive L.A.I. but it supposes knowledge about leaf life span (ALEXANDRE 1981). Results obtained by this approach are notably distorted by leaf-eaters consumption and by rapid decomposition rates in tropical regions (BRAY & GORHAM, 1964, EWEL, 1976, LEIGH & SMYTHE, 1978, PUIG, 1979). Ideally, square collecting baskets used to intercept litterfall are raised to avoid excessive decomposition of the litter between harvests and bottoms are mesh plastic made (EWEL, 1976). Correlation between dry foliage biomass on the ground and L.A.I. is proposed for cropping species and allows to reduce the numerous area measures in the determination of L.A.I. (LEMASTER *et al.*, 1980). Allometric methods seem to yield good results when appropriate factors are used. Estimation of L.A.I. from D.B.H. (diameter breast height) measurements was practised in Thailand where leaf amount tended to approach a certain asymptotic value with the increase in size of the trunk (OGAWA *et al.*, 1965). More accurate is the estimation of L.A.I. from D.B.H. and total height of the trees (HOZUMI *et al.*, 1969, JORDAN & UHL, 1978). The rate of light crossing a vegetation canopy is estimated from the ground by hemispherical photographs (fish-eye) (BONHOMME, 1976), or by optoelectronic sensors (DAUZAT *et al.*, 1981) to determine leaf angle and L.A.I. But optical means altogether cannot distinguish between leaves and other aerial parts like branches or trunks. Portable spectrometers are also used either under the canopy

(JORDAN, 1969) or above it (BRACH *et al.*, 1981) to measure transmittance or reflectivity and to give an estimation of L.A.I.

Because of the extended activity or the extreme asynchrony between individuals, it sometimes appears impossible to state when a species is in flower or fruit. In Ethiopia, a tree species was considered in flower if 10% or more of the plants of the species observed were in anthesis (BURGER, 1974). A subjective assessment is sometimes practiced monthly and for each numbered individual of the species taking into account the number of flower buds, open flowers, immature and mature fruits. These monthly values are summed separately and divided by the number of individuals to obtain a monthly mean value for each reproductive characteristic of each species (OPLER *et al.*, 1980). Another method to study the canopy trees in Mexico consisted in rating each individual on scales of 0 to 4 for the presence of leaves, flower buds or flowers, and fruits (BULLOCK & SOLIS-MAGALLANES, 1990).

#### HOW TO EXPRESS ?

Observations and/or results may be expressed in several ways.

An horizontal line materializes the period during which a phenological stage, mainly flowering or fruiting but also leaf presence, has been observed; this line is sometimes prolonged at its ends by an interrupted line in order to differentiate periods of initiation and end of stage from the maximal period. For six woody shrubs in Panama, timing of flowering is presented for twenty individuals per species and shows then the phenological variability among them. Each line representing the total duration of flowering by an individual is ended by a broken line indicating discontinuous flower production. Brackets enclose the period around the median flower day during which 90% of an individual's flowers were open. Dots indicate days the median flowers were open corresponding to peak days (maximum number of flowers) for mass flowering individuals (AUGSPURGER, 1983).

Frequency curves may also be used to represent flushing activity by the number of trees flushing. In addition, horizontal lines may represent flushing episodes for observed individual trees during a given period and are a useful complementation to show the intra-species variability (LIEBERMAN & LIEBERMAN, 1984). Girth change may also be represented as a function of time by a curve and in relation with reproductive and vegetative phenology symbolized under the curve by particular signs (LIEBERMAN, 1982). Another nearby representation, consists in the use of a lenticular form, authorizing by its thickness to express the relative importance of the phenophase. In some cases, only foliation is represented by a lenticular form and signs are placed under to symbolize flowering or fruiting periods (HLADIK, 1980). Phenological spectrum for 22 species of a miombo in Zaïre shows the evolution and duration of foliation, presence of flowers and inflorescence buds, blossoming, presence of faded flowers, of unripe or ripe fruits and scattering ( Fig.4, MALAISSE, 1974).

Diagrams are also used. They allow to follow temporal differences according to the time scale choosed (season or month generally, week more rarely). The intensity of the phenological stage is sometimes expressed through an approximative scale and called phenogram (REEKMANS, 1980). They are also frequently used for litterfall expression with differentiation between leaves, fruits, twigs... (MALAISSE *et al.*, 1975). Some diagrams present the monthly rainfall amounts in parallelism with phenological observations.

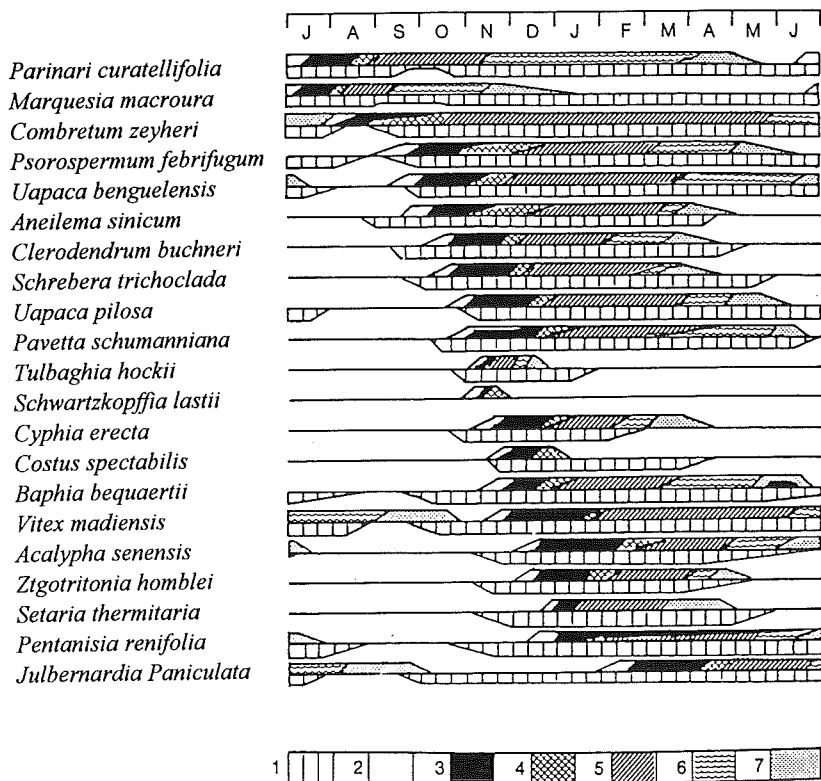


Fig. 4 - Phenological spectrum for 21 selected species of a Zambeian open forest of the wet miombo type, in the vicinity of Lubumbashi. The phenophase key is (1) foliation, (2) flower and inflorescence buds, (3) blossoming, (4) faded flowers, (5) unrip fruits, (6) ripe fruits, (7) scattering (after MALAISSE 1974, modified).

"System phenology", expressed as the percentage of all individuals irrespective of species is sometimes presented in addition of "community phenology" based on the number of species showing different phenological states (BULLOCK & SOLIS-MAGALLANES, 1990).

Leaf area index evolution is rarely presented. In a deciduous forest of Porto Rico, an insufficient sampling of six data for a 2-year period was used to express the seasonal variation of L.A.I. on a frequency curve (LUGO *et al.*, 1978). For open forest and dry evergreen forest of Zaïre, fortnightly data were collected and a histogram shows the L.A.I. changes for some woody species during one year (MALAISSE, 1988, MALAISSE, 1993).

Phenological characteristics may be presented in table with particular signs corresponding to phenological stages (REEKMANS, 1980).

HOW TO ANALYSE ?

As seasonal cold or drought stress is usually present, and leaves must be shed to minimize the effects of this seasonal stress, adaptative strategies of leaf replacement as a function of seasonality of temperature and moisture are observed ( Fig.5, JACKSON, 1978). Where seasonality of temperature is great, the leaf replacement strategy will emphasize avoidance of cold stress by cold season leaf fall and warm season flushing regardless of the seasonality of moisture. Where the temperature differential through the year is small, the strategy depends on the seasonality of moisture. This allows also to predict the phenology pattern of a vegetation type based on physical constraints. But as shown above, meso-climatic constraints may be a very important source of variability like is intra or inter-species sampling.

Fig.5. Adaptive strategies (types A-E) of leaf replacement as a function of seasonality of temperature and moisture ( after JACKSON 1978).

		SEASONALITY OF TEMPERATURE		
		LARGE	MODERATE	SMALL
SEASONALITY OF MOISTURE	LARGE	A cold season leaf-fall warm season flushing	B dry season leaf-fall wet season flushing	B dry season leaf-fall wet season flushing
		MODERATE	A cold season leaf-fall warm season flushing	
	SMALL		A cold season leaf-fall warm season flushing	C warm season leaf-fall warm season flushing

CONCLUSION

The study of vegetation dynamics has acquired new concerns with the recent obviousness of the consequences of tropical deforestation on the global environment. Actually, seasonal changes in the functioning of ecosystems are affecting gas fluxes and energy balance and thereby influence the carbon cycle and, ultimately, climate characteristics. Seasonality and the consequent vegetation phenology appear very hazardous to synthesize and to express at a global scale. Many studies all around the world and particularly in the Tropics do not allow to pinpoint general phenological patterns according to a vegetation type and even no more according to a given latitude. Each case must be approached at a local scale and until now no clear expectation about the phenology seems to be reasonable at a large scale.

Correlations between environmental data and phenological changes are not clear nor are the link between some vegetation behaviour and other biotic agents supposed having evolved together. Any climatic change seems responsible for a particular phenological behaviour directly and independently from other stimulus. In most cases global and local factors interact and are supposed to explain the extreme complexity of phenological behaviour patterns encountered.

As we saw, phenological observations should not be limited to the forest canopy alone. Understorey layers must also be taken into account to characterize the temporal evolution of the vegetation. Yet observations are complicated by great inter-species variability and by great variability between individuals of a same species. Discordances appear also between phenological behaviour observed a year and the next ones and consequently the importance of a followed study of phenology is fundamental.

## REFERENCES

- ALEXANDRE, D.Y., 1981. L'indice foliaire des forêts tropicales. Analyse bibliographique. *Acta Oecol., Oecol. Gener.*, 2, 4, 299-312.
- ALLARD, H.A., 1935. Response of the woody plants *Hibiscus syriacus*, *Malvaviscus concanensis*, and *Buginvillea glabra* to length of day. *J. Agric. Res.*, 51, 27-34.
- ALVIM, P. de T., 1964. Tree growth and periodicity in tropical climates. In: ZIMMERMANN M.H. (Ed.). *The formation of wood in tropical trees*. Academic Press, New York. pp.
- AUGSPURGER, C.K., 1983. Phenology, flowering synchrony, and fruit set of six Neotropical shrubs. *Biotropica*, 15, 4, 257-267.
- BERNHARD, F., 1970. Etude de la litière et de sa contribution au cycle des éléments minéraux en forêt ombrophile de Côte- d'Ivoire. *Oecol. Plant.*, 5, 247-266.
- BONJOMME, R., 1976. Détermination des profils d'indice foliaire et de rayonnement dans un couvert végétal à l'aide de photographies hémisphériques faites *in situ*. *Ann. Agron.*, 27, 1, 33-59.
- BRACH, E.J., DESJARDINS, R.L., LORD, D. & DUBE, P.A., 1981. Field spectrometer to measure percent ground coverage and leaf area index of agricultural crops. In: Signatures Spectrales en Télédétection. Colloque International. Avignon, 8-11 septembre, pp. 323-330.
- BRAY, J.R. & GORHAM, E., 1964. Litter production in forests of the world. *Adv. Ecol. Res.*, 2, 101-157.
- BROEKMANS, A.F.M., 1957. Growth, flowering and yield of the oil palm in Nigeria. *J. W. Afr. Inst. Oil Palm*, 2, 187-220.
- BROOKS, R.R. & MALAISSE, F., 1985. *The heavy metal-tolerant flora of Southcentral Africa. A multidisciplinary approach*. Balkema Press, Rotterdam, 199 p.
- BULLOCK, S.H. & SOLIS-MAGALLANES, J.A., 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica*, 22, 1, 22-35.
- BURGER, W.C., 1974. Flowering periodicity at four altitudinal levels in Eastern Ethiopia. *Biotropica*, 6, 1, 38-42.
- COSTER, C., 1926. Periodische Bluteerscheinungen in den Tropen. *Ann. Jard. Bot. Buitenz.*, 35, 125-162.
- CROAT, T.B., 1975. Phenological behaviour of habit and habitat classes on Barro Colorado Island (Panama Canal Zone). *Biotropica*, 7, 4, 270-277.



- DANTAS, M. & PHILLIPSON, J., 1989. Litterfall and litter nutrient content in primary and secondary amazonian terra firma rain forest. *J. Trop. Ecol.*, 5, 27-36.
- DAUBENMIRE, R., 1972. Phenology and other characteristics of tropical semi-deciduous forest in North-Western Costa Rica. *J. Ecol.*, 60, 1, 147-170.
- DAUZAT, J., METHY, M. & LACAZE, B., 1981. Modélisation de la réflectance directionnelle de couverts végétaux herbacés à partir de leur caractérisation architecturale par une technique automatisée de points quadrats. In: Signatures Spectrales d'objets en Télédétection. Colloque International, Avignon, 8-11 septembre, pp. 351-361.
- DIKUMBWA, N., 1990. Facteurs écoclimatiques et cycles biogéochimiques en forêt dense sèche zambézienne ( Muhulu ) du Shaba méridional. *Geo-Eco-Trop*, 14,1-4, 159 p.
- DOWNES, R.J., 1958. Photoperiodic control of growth and dormancy in woody plants. In: THIMANN K.V., CRITCHFIELD W.B. & ZIMMERMAN M.H. (Eds.). *The physiology of forest trees*. Ronald Press, New-York, pp. 529-537.
- DUNHAM, K.M., 1989. Litterfall, nutrient fall and production in an *Acacia albida* woodland in Zimbabwe. *J. Trop. Ecol.*, 5, 227-238.
- EHLERINGER, J.R. & FORSETH, I.N., 1989. Diurnal leaf movements and productivity in canopies. In: RUSSEL G., MARSHALL B. & JARVIS P.G. (Eds.). *Plant canopies : their growth, form and function*. Cambridge Univ. Press, London, pp.129-142.
- ERNST, W., 1975. Variation in the mineral contents of leaves of trees in miombo woodland in south central Africa. *J.Ecol.*, 63, 801-807.
- EWEL, J.J., 1976. Litterfall and leaf decomposition in tropical forest succession in Eastern Guatemala. *J. Ecol.*, 64, 293-308.
- FANSHAWE, D.B., 1972. The Bamboo, *Oxytenanthera abyssinica* its Ecology, Silviculture and Utilization. *Kirkia*, 8, 2, 157-166.
- 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, 881-919.
- GACHET, C., 1971. Premiers résultats d'une période d'observations phénologiques à Morofandilla-Morondava. C.T.F.T. Madagascar, *Sol Forêt*, 51.
- GIVNISH, T.J., 1978. On the adaptive significance of compound leaves, with particular reference to tropical trees. In: TOMLINSON P.B. & ZIMMERMAN M.H. (Eds.). *Tropical Trees as Living Systems*. Cambridge Univ. Press, London, pp 351-380.
- GOLLEY, F., MCGINNIS, J., CLEMENTS, R., CHILD, G. & DUEVER, M., 1975. *Mineral cycling in a tropical moist forest ecosystem*. Univ. Georgia Press, Athens, 248 p.
- HAINES, B. & FOSTER, R.B., 1977. Energy flow through litter in a Panamanian forest. *J. Ecol.*, 65, 147-155.
- HEGARTY, E.E., 1990. Leaf life-span and leafing phenology of lianes and associated trees during a rainforest succession. *J. Ecol.*, 78, 300-312.
- HELLER, H., 1971. Estimation of photosynthetically active leaf area in forests. In: ELLENBERG H. (Ed.) *Integrated experimental ecology*, Springer Verlag, Berlin, Ecological studies, 2, pp. 29-31.
- HLADICK, A., 1974. Importance des lianes dans la production foliaire de la forêt équatoriale du nord-est du Gabon. *C.R. Acad. Sciences de Paris, Série D*, 278, 2610-2617.
- HLADICK, A., 1980. The Dry Forest of the West Coast of Madagascar: Climate, Phenology, and Food available for Prosimians. In: CHARLES-DOMINIQUE P. *et al.* (Eds.). *Nocturnal Malagasy Primates*. Academic Press, New-York, pp. 3-40.

- HOLTTUM, R.E., 1949. Gregarious flowering of the terrestrial orchid *Bromheadia finlaysonianae*. *Gardens Bull. Singapore*, 12, 295-302.
- HOPKINS, B., 1966. Vegetation of the Olokemeji forest reserve, Nigeria. Part IV. The litter and soil with special reference to their seasonal changes. *J. Ecol.*, 54, 3, 687-703.
- HOZULI, K., YODA, K., KOKAWA, S. & KIRA, T., 1969. Production ecology of tropical rain forests in south-western Cambodia. I. Plant biomass. *Nature & Life in South-East Asia*, 6, 1- 51.
- JACKSON, J.F., 1978. Seasonality of flowering and leaf-fall in a Brazilian subtropical lower montane moist forest. *Biotropica*, 10, 1, 38-42.
- JANZEN, D.H., 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution*, 21, 620-637.
- JANZEN, D.H., 1970. *Jacquinia pungens*, a Heliophile from the understorey of tropical deciduous forest. *Biotropica*, 2, 112-119.
- JORDAN, C.F., 1969. Derivation of leaf area index from quality of light on the forest floor. *Ecol.*, 50, 663-666.
- JORDAN, C. & UHL, C., 1978. Biomass of a "tierra firme" forest of the Amazon basin. *Oecol. Plant.*, 13, 387-400.
- KATO, R., TADAKI, Y. & OGAWA, H., 1978. Plant biomass and growth increment studies in Pasoh forest. *Malay. Nat. J.*, 30, 2, 211-224.
- KOZLOWSKI, T.T., 1973. Extent and significance of shedding plant parts. In: KOZLOWSKI T.T. (Ed.). *Shedding of plant parts*. Academic Press, New York.
- LANGENHEIM, J.H., LEE, Y.T. & MARTIN, S.S., 1973. An evolutionary and ecological perspective of the Amazonian hylaea species of *Hymenaea* (Leguminosae, Caesalpinioideae). *Acta Amazonica*, 3, 3-57.
- LAWTON, J.R.S. & AKPAN, E.E.J., 1968. Periodicity in *Plumeria*. *Nature*, 281, 384-386.
- LEIGH, E.G.Jr. & SMYTHE, N., 1978. Leaf production, leaf consumption and the regulation of folivory on Barro Colorado Island. In: MONTGOMERY G.G. (Eds.). *Ecology of arboreal folivores*. Smithsonian Inst. Press., Washington, pp. 33-50.
- LELY, H.V., 1925. *The useful trees of Northern Nigeria*. London.
- LEMASTER, E.W., CHANCE, J.E. & WIEGAND, C.L., 1980. A seasonal verification of the SUITS spectral reflectance model for wheat. *Photogramm. Engin. and Remote Sensing*, 46, 1, 107-114.
- LIEBERMAN, D., 1982. Seasonality and phenology in a dry tropical forest in Ghana. *J. Ecol.*, 70, 791-806.
- LIEBERMAN, D. & LIEBERMAN, M., 1984. The causes and consequences of synchronous flushing in a dry tropical forest. *Biotropica*, 16, 3, 193-201.
- LIETH, H., 1974. Purposes of a Phenology Book. In: LIETH H.(Ed.). *Phenology and Seasonality Modeling, Introduction to Phenology and the Modeling of Seasonality*. Springer-Verlag, New-York, pp. 3-19.
- LINNE, C., 1751. *Philosophia Botanica*. Kisesewetter, Stockholm.
- LOWMAN, M.D., 1988. Litter fall and leaf decay in three Australian rain forest formations. *J. Ecol.*, 76, 451-465.
- LUGO, A.E., GONZALES-LIBOY, J.A., CINTRON, B. & DUGGER, K., 1978. Structure, productivity and transpiration of a subtropical dry forest in Puerto Rico. *Biotropica*, 10, 4, 278-291.
- MABBERLEY, D.J., 1992. *Tropical Rain Forest Ecology*. Chapman & Hall, New York, 300 p.

- MALAISSÉ, F., 1974. Phenology of the Zambesian woodland area with emphasis on the Miombo ecosystem. In: LIETH H.(Ed.) *Phenology and Seasonality Modeling*, Springer-Verlag, Berlin, pp. 269-286
- MALAISSÉ, F., 1988. Variation in time and space of leaf area index in a Zambesian open forest of wetter miombo type (Lubumbashi, Zaïre). *Geo-Eco-Trop*, 12, 1-4, 143-163.
- MALAISSÉ, F., 1993. The ecology of Zambesian dry evergreen forest with recommendations for conservation management. In: LIETH H. & LOHMANN M. (Eds.). *Restoration of Tropical Forest Ecosystems*. Kluwer Academic Publishers, Amsterdam, pp. 75-90.
- MALAISSÉ, F., FRESON, R., GOFFINET, G. & MALAISSÉ-MOUSSET M., 1975. Litter fall and litter breakdown in miombo. In: GOLLEY F. & MEDINA E. (Eds.), *Tropical Ecological Systems. Trend in terrestrial and aquatic research*. Springer Verlag, Ecological Studies, 11, pp. 131-152.
- MORI, S.A. & KALLUNKI, J.A., 1976. Phenology and floral biology of *Gustavia superba* (Lecythidaceae) in Central Panama. *Biotropica*, 8, 3, 184-192.
- MURPHY, P.G. & LUGO, A.E., 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica*, 18, 2, 89-96.
- NJOKU, E., 1963. Seasonal periodicity in the growth and development of some forest trees in Nigeria. I. Observations on mature trees. *J. Ecol.*, 51, 3, 617-624.
- NJOKU, E., 1964. Seasonal periodicity in the growth and development of some forest trees in Nigeria. II. Observations on seedlings. *J. Ecol.*, 52, 1, 19-26.
- ODUM, H.T., COPELAND, B.J. & BROWN, R.Z., 1963. Direct and optical assay of leaf mass of the lower montane rain forest of Puerto Rico. *Proc. nat. Acad. Sci. Wash.*, 49, 429-434.
- ODUM, H.T., ABBOTT, R.K., SELANDER, R.K., GOLLEY, F.B. & WILSON, R.F., 1970. Estimates of chlorophyll and biomass of the Tabonuco Forest of Puerto Rico. In: ODUM H.T. (Ed.) *A Tropical Rain Forest*. U.S. Atomic Energy Commission, pp.13-18.
- OGAWA, H., YODA, K., OGINO, K. & KIRA, T., 1965. Comparative ecological studies of three main types of forest vegetation in Thailand. Plant biomass. *Nature & Life in S-E Asia*, 4, II, 49-80.
- OPLER, P.A., FRANKIE, G.W. & BAKER, H.G., 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.*, 68, 167-188.
- PIRINGER, A.A. & BORTHWICK, H.A., 1955. Photoperiodic responses of coffee. *Turrialba*, 5, 72-77.
- PIRINGER, A.A. & DOWNS, R.J., 1960. Effects of photoperiod and kind of supplemental light on the growth of *Theobroma cacao*. Proc. 8th Inter-Amer. Cacao Conf., Trinidad, 82-90.
- PUIG, H., 1979. Production de litière en forêt guyanaise résultats préliminaires. *Bull. Soc. Hist. Nat. Toulouse*, 115, 3-4, 338-346.
- PUIG, H. & DELIBELLE, J.-P., 1988. Production de litière, nécromasse, apports minéraux au sol par la litière en forêt guyanaise. *Rev. Ecol. (Terre et Vie)*, 43, 3-22.
- PUTZ, F.E., 1979. Aseasonality in Malaysian tree phenology. *Malay. For.*, 42, 1-28.
- PUTZ, F.E., 1983. Liana biomass and leaf area of a "Tierra Firme" forest in the Rio Negro Basin, Venezuela. *Biotropica*, 15, 3, 185-189.
- REEKMANS, M., 1980. La flore vasculaire de l'Imbo (Burundi) et sa phénologie. *Lejeunia*, 100, 1-51.

- REES, A.R., 1964. The flowering behaviour of *Clerodendron incisum* in southern Nigeria. *J. Ecol.*, 52, 9-17.
- REICH, P.B. & BORCHERT, R., 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *J. Ecol.*, 72, 61-74.
- ROCKWOOD, L.L., 1975. The effects of seasonality on foraging in two species of leaf cutting ants (*Atta*) in Guanacaste Province, Costa Rica. *Biotropica*, 7, 3, 176-193.
- ROHNER, U. & SORG, J.-P., 1986. *Observations phénologiques en forêt dense sèche*. Tome I, C.F.P.F. Morondava, Madagascar, 129 p.
- RUNDEL, P.W. & BECKER, P.F., 1987. Seasonal changes in plant water relations and vegetative phenology in understory plants of a tropical forest on Barro Colorado Island, Panama. *Revista de Biología Tropical*, 35, 1, 71-84.
- RUSSEL G., JARVIS P.G. & MONTEITH J.L., 1989. Absorption of radiation by canopies and stand growth. In: RUSSEL G., MARSHALL B. & JARVIS P.G. (Eds.). *Plant canopies their growth, form and function*. Cambridge Univ. Press, London, pp. 21-39.
- SARMIENTO, G., 1972. Ecological and floristic convergences between seasonal plant formations of tropical and subtropical South America. *J. Ecol.*, 60, 367-410.
- STUBBLEBINE, W., LANGENHEIM, J.L. & LINCOLN, D., 1978. Vegetative response to photoperiod in the tropical leguminous tree *Hymenaea courbaril* L. *Biotropica*, 10, 1, 18-29.
- VAN SEVEREN, J.P., 1969. L'index foliaire et sa mesure par photoplanimétrie. *Bull. Soc. roy. Bot. Belg.*, 102, 2, 373-385.
- WARREN-WILSON S., 1963. Estimation of foliage denseness and foliage angle by inclined point quadrats. *Austr. J. Bot.*, 11, 95-105.