

Reproductive phenology of Atlantic forest tree species in Brazil: an eleven year study

VERA LEX ENGEL^{1*} & FERNANDO ROBERTO MARTINS^{**}

**UNESP- São Paulo State University, Agronomic Sciences Faculty, Department of Natural Resources, P.O. Box 237, 18.603-970 Botucatu, SP, Brazil; **UNICAMP-State University of Campinas, Institute of Biology, Department of Botany, P.O. Box 6109, 13083-970 CAMPINAS, SP, Brazil*

Abstract: This paper describes the reproductive phenorhythms of tree species in a tropical seasonal lowland forest in Southeastern Brazil. Every two weeks, five individuals of 41 species were observed for the occurrence of flowering and fruiting, from May 1982 to December 1992. All phenophases showed high seasonality, when considering the whole set of species, but the amplitude of the cycles was much more variable between years; only 13 species had regular flowering. Infra-annual flowering and fruiting were found in 11 and four species, respectively, while only one species flowered and fruited continually. Supra-annual cycles were observed in four (flowering) and seven (fruiting) species. An increase was observed in number of species and individuals flowering and fruiting from 1990 to 1992, following mainly an elevation in the absolute minimum air temperature. These data suggest a relationship between reproductive phenology and major climatic phenomena like “El Niño” events and solar activity cycles.

Resumen: El objetivo de este trabajo fue describir los fenorritmos reproductivos de algunas especies arbóreas en un bosque tropical estacional semidecíduo en el sudeste de Brasil. La presencia de floración y fructificación fue observada en cinco individuos de 41 especies con una frecuencia quincenal, desde mayo de 1982 hasta diciembre de 1992. Considerando al conjunto total de especies todas las fenofases mostraron una fuerte estacionalidad, pero la amplitud de los ciclos fue mucho más variable entre años, y solamente 13 especies tuvieron una floración regular. Se observaron ciclos infra-anales de floración y fructificación en 11 y 4 especies, respectivamente, mientras que solamente una especie floreció y fructificó de manera continua. Se observaron ciclos supra-anales en cuatro (floración) y siete (fructificación) especies. Se observó un incremento en el número de especies e individuos en floración y fructificación entre 1990 y 1992, siguiendo principalmente un incremento en la temperatura absoluta mínima del aire. Estos datos sugieren que existe una relación entre la fenología reproductiva y eventos climáticos de gran escala como “El Niño” y ciclos de actividad solar.

Resumo: Este estudo descreve os fenorritmos reprodutivos das espécies arbóreas numa floresta tropical estacional das terras baixas no sudeste do Brasil. De Maio de 1982 a Dezembro de 1992, em cada duas semanas, foram observados cinco indivíduos, de 41 espécies, quanto à ocorrência da floração e frutificação. Quando considerado o conjunto das espécies, todas as fenofases mostraram elevada sazonalidade, mas a amplitude dos ciclos foram muito mais variáveis entre anos e só 13 espécies apresentaram uma floração regular. A floração e frutificação

¹Corresponding author

infra-annual apareceram em 11 e quatro espécies, respectivamente, enquanto só uma espécie floresceu e frutificou continuamente. Os ciclos supra-anuais foram observados em quatro (floração) e sete espécies (frutificação). Entre 1990 a 1992 foi observado um aumento no número de espécies e indivíduos florescendo e frutificando, seguindo, principalmente, um aumento na temperatura mínima absoluta do ar. Estes dados sugerem uma relação entre a fonologia reprodutiva e os principais eventos climáticos como o “El Niño” e os ciclos de actividade solar.

Key words: Atlantic forest, El Niño, reproductive phenology, seasonality, tropical tree species.

Introduction

The diversity and complexity of phenological patterns is greater in tropical than in temperate forest ecosystems (Borchert 1983; Rathcke & Lacey 1985). Also, the seasonality of reproduction, leaf senescence and leaf production in tropical wet and moist forests generally show a higher geographical and temporal variation than in any other biome (Bullock & Sollis-Magallanes 1990; Morellato *et al.* 1990; Wright 1996). This diversity is considered important to maintain the great species richness in these communities (Gentry 1974, 1976; Wright 1996).

In tropical and subtropical forest ecosystems, the phenological rhythms may be very variable among years, mainly for flowering and fruiting. Often, these variations, like the “gregarious flowering” phenomenon in Southeast Asia’s forests (Appanah 1985; Ashton *et al.* 1988; Medway 1972) are not revealed in short-term studies, or when only the average patterns for the community among years are described. Irregular reproduction has been reported in median- and long-term studies in Mexico (Carabias-Lillo & Guevara-Sada 1985) and Costa Rica (Wheelwright 1986). In Brazil, studies done in Amazonian forests by Alencar *et al.* (1979), Pires-O’Brien (1993) and Knowles & Parrotta (1997) also demonstrated very irregular flowering and fruiting patterns between years in the tree community.

According to Newstrom *et al.* (1994), at least a five-year period is needed to recognize and describe the great diversity of reproductive phenological patterns in tropical trees, due to many differences in frequency and regularity within time series between species. In spite of this, long term phenological studies are scarce in the

literature, the majority of them referring to a period of up to two to four years (Engel 2001). Studies for a 10-year period or more in tropical and subtropical ecosystems are known only for Malaysia (Ashton *et al.* 1988; Medway 1972; Yap & Chan 1990); Panama (Wright *et al.* 1999); Australia (Law *et al.* 2000) and for the Brazilian Amazon (Alencar *et al.* 1979; Alencar 1990, 1994; Knowles & Parrotta 1997).

The region of Linhares, in northern Espírito Santo state, Southeastern Brazil, has one of the largest continuous remnants of lowland Atlantic Forest in Brazil. This vegetation is classified, according to IBGE (1992), as being in the domain of dense tropical wet forest. Nevertheless, this region does not correspond to a wet climate, as it combines a peculiar set of relatively low rainfall annual averages with mild dry seasons. Rainfall patterns are among the reasons pointed out by Peixoto & Gentry (1990) that may contribute to the very high species richness in this area. Also, the climate is irregular among years: the annual rainfall may vary as much as 100% in cycles from 7 to 10 years, mainly during the rainy season. During the drier years, average air temperature may also increase as much as 1.6 °C. These rainfall and temperature fluctuations may be attributable to the “El Niño” southern oscillation phenomenon. Phenological responses are expected in the vegetation by direct or indirect influence of these climatic disturbances.

The aim of this paper is to describe the phenorhythms and phenological patterns of the major tree species at Linhares, ES, during an eleven-year period, in relation to climatic variations. The main question is: does climatic irregularity cause changes in the phenological

behavior of tree species in lowland Atlantic forests in Brazil?

Materials and methods

Site description

The study was done at Linhares Natural Reserve, which belongs to the Vale do Rio Doce Mining Company, in Linhares municipality, Espírito Santo state, southeastern Brazil. The geographical coordinates are 19° 06' - 19° 18' S and 39° 45' - 40° 19' W. The reserve has a total area of 21,787.00 ha, and 72% of it is covered by forests (Jesus 1987). The topography is characterized by tertiary sedimentary plains, with elevations varying from 28 to 65 m, which are dissected by "V"-shaped valleys; the predominant soils are dystrophic alic yellow-red podzols (Jesus *et al.* 1992).

The climate is hot and humid with summer rainfalls and dry winters and is classified as Aw according to Köppen's system (Jesus 1987). The annual average air temperature is 23 °C, varying from 25.6 °C (February) to 19.9 °C (July). The annual average maximum temperature is 33.5 and

the minimum is 15.0 °C. The absolute maximum temperature (39.8 °C) was recorded in 1990 and the absolute minimum (8.3 °C) in 1988. The annual averages for relative air humidity, total evaporation and total insolation are 83.4%, 916.5 cm³ and 2,145.9 hours, respectively. Precipitation seasonality is high; 83.3% of the total falls from October to March, with monthly averages from 196.6 (January) to 32.2 mm (June). Annual average precipitation is 1,249.0 mm and varies from 1,595.4 (1981) to 816.6 mm (1990). From 1986 until 1990, a period drier than average was observed, with rainfall mean of 905 mm. In spite of relatively low rainfall, water deficit is small when considering the normal averages for the site. The water balance permits the distinction of a wet season, a dry season and two transitional seasons (Fig. 1).

Forest vegetation of the region is known as "tablelands forests" and is classified as lowland dense wet forest (IBGE 1992). According to Jesus (1987), the forest at the reserve is semideciduous with a very short period of deciduousness. Peixoto & Gentry (1990) included this forest in the domain of "Bahia Hilea".

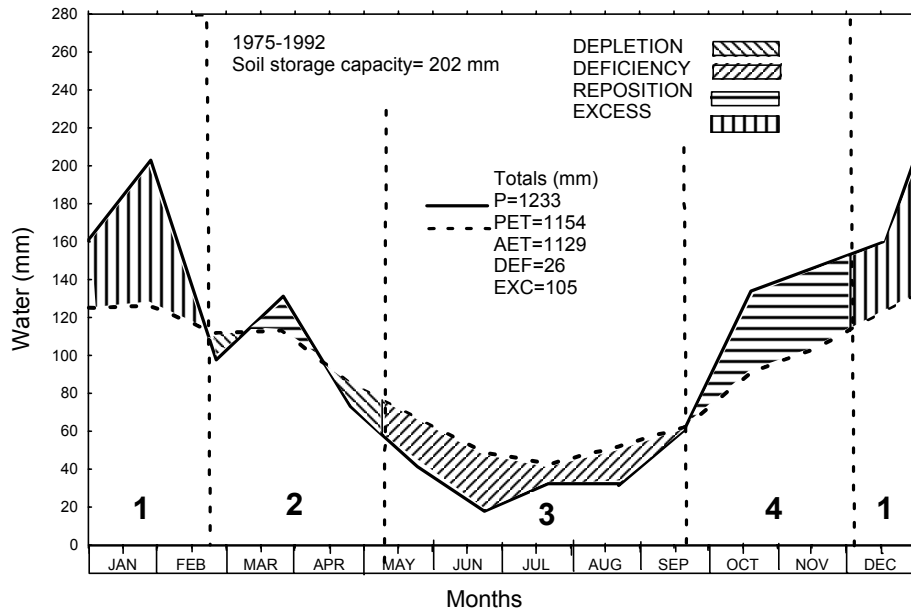


Fig. 1. Annual water balance of Linhares Natural Reserve (Thorntwaite 1948). Data for calculations obtained at Class "A" Meteorological Station in the Reserve (1975 - 1992). Periods signalized with number on the abscissas correspond to: 1- wet season; 2- wet to dry transitional season; 3-dry season; 4- dry to wet transitional season. P= precipitation; PET= potential evapotranspiration; AET= actual evapotranspiration; DEF=deficiency; EXC= excess.

Data collection and analysis

We studied 41 species from 28 botanical families (Table 1); the species selection criteria were basically their economic and silvicultural importance, frequency in the forest and taxonomic representation, based on Alencar *et al.* (1979). For each species, five reproductively mature and healthy individuals (totaling 205) were marked along trails previously opened in old-growth forest

patches, starting from the main roads of the reserve. Every fortnight, from May 1982 to December 1992, all individuals were observed for the occurrence of flowers (anthesis) and fruits (mature fruits), by means of binoculars when possible, and using canopy access techniques if necessary. Trees were also observed for the presence of flower buds, immature fruits and propagule dispersion, although these phenophases are not being considered in this paper.

Table 1. List of species included in the phenological study in Linhares, ES, Brazil.

Local name	Species	Family
Aderne	<i>Astronium graveolens</i> Jacq.	Anacardiaceae
Araçá-branco	<i>Myrcia lineata</i> (Berg.) Barroso	Myrtaceae
Batinga-branca	<i>Eugenia microcarpa</i> Berg.	Myrtaceae
Bicuíba	<i>Virola gardneri</i> (A.DC.) Warb.	Myristicaceae
Boleira	<i>Joannesia princeps</i> Vell.	Euphorbiaceae
Bomba-d'água	<i>Hidrogaster trinervis</i> Kuhlman	Tiliaceae
Braúna-preta	<i>Melanoxylon brauna</i> Schott.	Caesalpiniaceae
Canela-amarela	<i>Ocotea conferta</i> Coe-teixeira	Lauraceae
Canela-preta	<i>Ocotea organensis</i> Mez.	Lauraceae
Caxeta	<i>Simarouba amara</i> Aubl.	Simaroubaceae
Cedro-rosa	<i>Cedrela odorata</i> L.	Meliaceae
Faia	<i>Emmotum nitens</i> (Benth) Miers	Icacinaceae
Farinha-seca	<i>Pterygota brasiliensis</i> Fr. Al.	Sterculiaceae
Garapa	<i>Apuleia leiocarpa</i> (Vog.) Macbr.	Caesalpiniaceae
Gonçalo-alves	<i>Astronium concinum</i> Schott.	Anacardiaceae
Guaiti	<i>Licania salzmanni</i> (Hookf.) Fritsch	Chrysobalanaceae
Imbaubão	<i>Schefflera morototoni</i> (Aubl.) Naguirre, Steymark, Frodin	Araliaceae
Imbiruçú	<i>Eriotheca macrophylla</i> (Schum.) A. Robyns	Bombacaceae
Ipê-amarelo	<i>Tabebuia riococensis</i> A.Gentry	Bignoniaceae
Jacarandá-caviúna	<i>Dalbergia nigra</i> (Vell.) Fr.All. Ex Benth.	Fabaceae
Jequitibá-rosa	<i>Cariniana legalis</i> (Mart.) O.Ktze	Lecythidaceae
Jueirana-vermelha	<i>Parkia pendula</i> (Willd) Bent.ex Walp.	Mimosaceae
Louro-pardo	<i>Cordia trichotoma</i> Vell.	Boraginaceae
Macanaíba-marreta	<i>Diploptropis incexis</i> Rizz et Mattos F.	Fabaceae
Macanaíba-pele-de- sapo	<i>Bowdichia virgilioides</i> HBK.	Fabaceae
Maçaranduba	<i>Manilkara salzmanni</i> (A.DC.) Lam.	Sapotaceae
Nagib	<i>Kielmeyera albopunctata</i> Sadd.	Guttiferae
Oiticica	<i>Clarisia racemosa</i> Ruiz et Pav.	Moraceae
Orelha-de-onça	<i>Zollernia ilicifolia</i> Vog.	Caesalpiniaceae
Parajú	<i>Manilkara bella</i> Monach.	Sapotaceae
Pelada	<i>Terminalia Kuhlmanii</i> Aiwan & Stace	Combretaceae
Pequi-liso	<i>Qualea multiflora</i> Mart.	Vochysiaceae
Pequi-vinagreiro	<i>Caryocar edule</i> Casar.	Caryocariaceae
Peroba-amarela	<i>Paratecoma peroba</i> (Record.) Kuhlm.	Bignoniaceae
Peroba-osso	<i>Aspidosperma cylindrocarpon</i> M. Arg.	Apocynaceae
Pitomba-amarela	<i>Talisia intermedia</i> Radlk.	Sapindaceae
Quina-preta	<i>Ziziphus platyphylla</i> Reissek	Rhamnaceae
Quina-rosa	<i>Simira rubescens</i> Schum.	Rubiaceae
Roxinho	<i>Peltogyne angustifolia</i> Ducke	Caesalpiniaceae
Sapucaia-vermelha	<i>Lecythis pisonis</i> Carmb.	Lecythidaceae
Vermelhinha	<i>Qualea magna</i> Kuhlmann	Vochysiaceae

The species were classified by their reproductive phenological patterns, according to the system of Newstrom *et al.* (1994), considering the population as the reference. Even considering that five individuals per species are not sufficient to represent a population, the term population was used in this paper due to the necessity of explicitly defining the approach level. The primary classification criterion adopted was the frequency, or number of phenological cycles per solar year, which defined the classes: continuous, sub-annual; annual and supra-annual. The frequency classes were then subdivided according to their regularity (regular and irregular), duration (short- less or equal to one month; intermediate-one to four months, and long- more than five month long) and time of calendar year. In this study, a phenophase was considered irregular when it was not observed during two or more years during the period of study. To describe the phenorhythms we also considered the amplitude (quantity of activity, or response intensity, showed by the population), here expressed by the proportion of individuals showing a particular phenophase in each fortnight during the study period, as well as the synchronism degree in the population (defined as low, medium and high).

During the study period, data on air temperatures and relative humidity, evaporation (from a "Class A" pool), precipitation and insolation were taken daily at a meteorological station located inside the Reserve. Fortnight averages and totals, depending on the variable, were computed. Potential evapotranspiration was estimated by the Thornthwaite-Camargo's normogram and the actual evapotranspiration and water deficit of the soil for each fortnight during the study period were estimated by calculating the water balance according to Thornthwaite's method (Tubelis & Nascimento 1988). In the water balance computation, soil water storage capacity was estimated according to Arruda *et al.* (1987) to be 202 mm. Meteorological variables were compared between years using multivariate analysis of variance and when necessary data were transformed as $x' = \ln x$ (Zar 1984). Rainfall monthly averages of drier (April to September) and wet periods (October to March) of the year were also compared separately between years.

The phenological data were analyzed by descriptive simple time series analysis techniques,

according to Chatfield (1992) and Statsoft (1995), using the computer pack Statistica® for Windows V. 5.0. The response variables analyzed were, respectively, the proportion of species and the proportion of individuals showing a particular phenophase in each one of the 260 fortnights during the study period (May 1982 to December 1992).

Periodicity of flowering and fruiting for the whole set of trees among years was studied by means of seasonality analysis (autocorrelation function), according to Chatfield (1992). In phenology, the term seasonality is defined as the temporal association of a phenological event with a recognizable time of the calendar year (Morellato 1991; Newstrom *et al.* 1994). In time series analysis, the term seasonality refers to a variable's property of assuming certain values periodically in a given time interval, and hence it has not the same sense as used in phenology. In this paper, we used the term seasonality in its phenological meaning, and the term rhythm or periodicity was used instead of seasonality as in the sense of time series analysis meaning. The autocorrelation function, which represents the correlation coefficient of a variable with itself, considering different time lags (Appendix 1), was obtained using time lags from 1 to 50, to encompass time intervals smaller than one, up to two years.

Average proportions (considering the average of each single fortnight during the 11-year period) of individuals and species bearing flowers and/or fruits during the calendar year was plotted, as well as the observed values in every fortnight during the complete time series. In the former case, the models were adjusted by weighted minimum least squares. The phenological data [transformed as $x' = \arcsin(\sqrt{x})$] were analyzed against meteorological data using multiple regression models.

Results

Seasonality and phenorhythms of tree species at Linhares Natural Reserve

When considering the whole set of tree species, autocorrelation functions showed a high periodicity for flowering and fruiting (Fig. 2). Because results of the proportion of species or individuals were similar, the results considered here are only those for the proportion of species.

High autocorrelation coefficients were obtained for time lags varying from 1 to 5 fortnights, due to a high serial correlation. Nevertheless, the highest correlations were obtained for a time lag equal to 24, corresponding to a significant annual rhythm both for flowering and fruiting (Fig. 2).

Besides the annual flowering rhythm detected, a high positive autocorrelation with “k”=12 (6-month cycle) and negative correlations with “k” around 6 and 18, respectively, were also observed (Fig. 2A). This pattern agrees with the bimodal

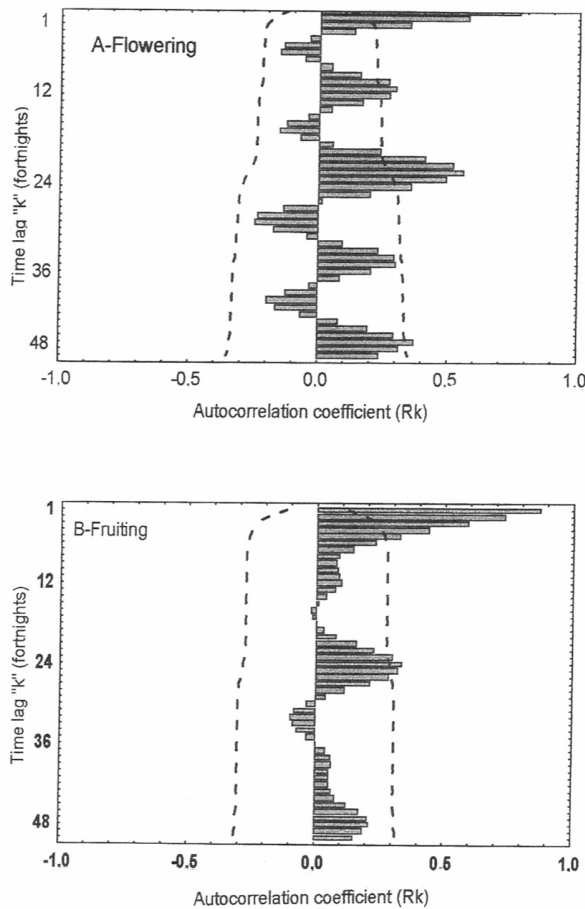


Fig. 2. Autocorrelograms for the variables flowering and fruiting, considering the whole set of trees. The bars represent the autocorrelation coefficient for each time lag considered. Positive values correspond to episodes of the phenophase; negative values their absence, for a given time lag. The traced lines represent, in each graphic, a pair of standard deviations for the respective time lags. All autocorrelations are statistically significant at 1% probability level, but the ones out of the limits of the traced lines are the most significant ones.

flowering curves shown in Fig. 3, which represents the average values for each fortnight during the 11-year period, both for proportion of species (3A) and individuals (3B). This was due to the fact that part of the species flowered at the end of the wet and in the transition to the dry season, while another large proportion flowered at the beginning of the wet season. The negative correlations of Fig. 2A correspond to periods of low flowering activity during the year, in the middle of wet and dry seasons (Fig. 3A). There was a significant autocorrelation for “k”=48, may be due to some species with supra-annual cycles.

The autocorrelation analysis indicated that fruiting was also rhythmic (Fig. 2B). Nevertheless, there was a higher serial correlation for fruiting than for flowering, and a lower correlation when considering “k”= 24. This is also coherent with the unimodal fruiting curves in Fig. 3A, which shows also that the fruiting is less seasonal than flowering and at least 12% of species bear fruits at any time of the year.

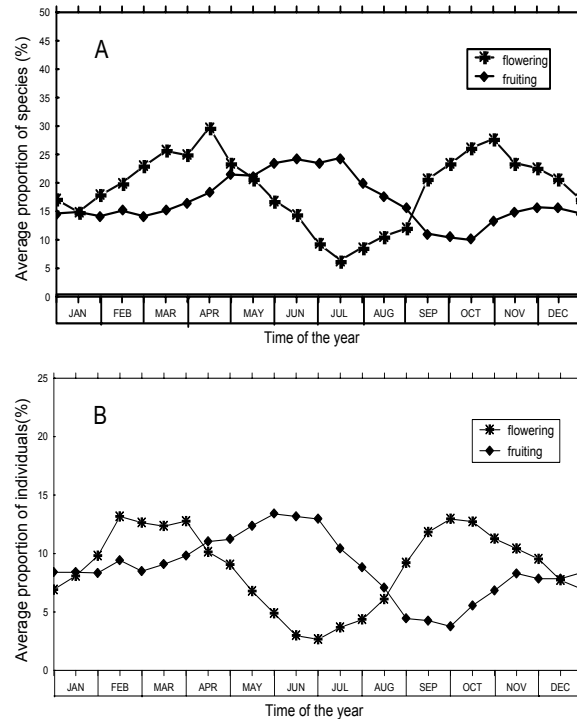


Fig. 3. Seasonality and the annual variation of reproductive phenophases amplitude for the whole set of trees, in Linhares, ES, Brazil. Data plotted are the average proportion, in each fortnight, of species (A) and individuals (B) observed in flower or fruiting, considering the 11-year period.

Reproductive phenological patterns of tree species

Based on the criteria frequency, duration and intensity of the phenological cycles, it was possible to recognize 12 different patterns of flowering and fruiting (Table 2) in the tree species studied. The majority of species (25, or 61%) flowered annually, but the cycles were regular in only 11 of them, with a well defined timing. Irregular flowering patterns were found in 71% of the tree species. Continuous flowering and fruiting were observed only in *Emmotum nitens* (Table 3). Among the species with supra-annual cycles, *Schefflera morototoni* flowered and fruited biannually, very regularly; and other three species were observed in flowers only twice (*Diploptropis incexis*) or three times (*Eriotheca macrophylla*) and *Peltogyne angustifolia* during the 11-year period.

The fruiting activity in these species was even lower than flowering. Four of six species (14.7%) that flowered in sub-annual irregular cycles fruited annually. Only *Apuleia leiocarpa* and *Parkia pendula* fruited sub-annually at the population level. Considering the duration, the majority of the species had short flowering and intermediate fruiting (Table 2). Fifty-six percent of

the species fruited annually, and irregular patterns predominated for fruiting. In general, the amplitude of fruiting cycles was lower than that of the flowering cycles. Some species were dioecious, thus, part of the observed individuals were males, e.g. *Astronium* species; this was unknown at the beginning of the research. In some species, some individuals in the population flowered but did not fruit. Eight species fruited only four-five times during the study (Table 3).

Reproductive phenophase cycles and climatic variability

When analyzing the whole set of trees, in spite of well-defined flowering and fruiting annual rhythms (Figs. 2 & 3), there was considerable variation between years in the amplitude of the cycles (Fig. 4). After 1988, the amplitude of flowering increased and there was a greater proportion of reproducing species and individuals from 1990 to 1992. Analyses of the time series for meteorological variables within the period (Fig. 5) revealed a slight increase in the rainfall, actual evapotranspiration and air relative humidity, as well as a decrease in the evaporation, insolation and soil water deficit after 1990. Nevertheless, the

Table 2. Number and proportion (percentage, inside parenthesis) of tree species with different flowering and fruiting patterns.

	Duration and Regularity	Long 4 (9.8)		Intermediate 13 (31.7)		Short 24 (58.5)	
		Reg. 2 (4.9)	Irreg. 2 (4.9)	Reg. 2 (4.9)	Irreg. 11 (26.8)	Reg. 8 (19.5)	Irreg. 16 (39.0)
Flowering	Annual 25 (61)	2 (4.9)	1 (2.4)	2 (4.9)	6 (14.6)	7 (17.1)	7 (17.1)
	Sub-Annual 6 (14.7)	----	----	----	4 (9.8)	----	2 (4.9)
	Supra-Annual 9 (21.9)	----	----	----	1 (2.4)	1 (2.4)	7 (17.1)
	Continuous 1 (2.4)	----	1 (2.4)	----	----	----	----
Fruiting	Annual 23 (56.1)	5 (12.2)	6 (14.6)	5 (12.2)	1 (2.4)	3 (7.3)	2 (4.9)
	Sub-Annual 2 (4.9)	----	----	----	----	----	2 (4.9)
	Supra-Annual 15 (36.)	----	1 (2.4)	1 (2.4)	8 (19.5)	----	5 (12.2)
	Continuous (2.4)	----	1 (2.4)	----	----	----	----

largest environmental variation was reported for the minimum air temperature, which increased 3-4°C after 1988. This pattern occurred independently from the average and maximum air temperatures variation (Fig. 5). Of the variables studied, only evaporation, air relative humidity,

air minimum temperature, dry season rainfall and average water deficit of the dry season showed statistically significant differences among years (Table 4).

Multiple regression analysis for flowering indicated significant positive correlations with

Table 3. Flowering and fruiting patterns of tree species at Linhares Natural Reserve, according to Newstrom *et al.* (1994) classification system. The registered times are the ones when the phenophase were most frequently observed, from 1982 to 1992. The numbers 1 and 2 after the month initials are correspondent to the respective fortnight. Numbers between parentheses indicate the time of highest amplitude of the correspondent phenophase.

Phenophases		Flowering				Fruiting			
Species	Frequency	Duration	Regular	Time (month)	Frequency	Duration	Regular	Time (Month)	
<i>Apuleia leiocarpa</i>	sub-annual	interm.	irreg.	(Oct - Dec); Jan - Mar 1	sub-annual	short	irreg.	(Nov - Dec); Jun - Jul	
<i>Aspidosperma cylindrocarpon</i>	annual	interm.	irreg.	Aug 2 - Nov 2 (Sep)	annual	long	irreg.	Dec - May	
<i>Astronium concinum</i>	annual	short	irreg.	Aug 2 - Oct 2 (Sep 2)	supra-annual	short	irreg.	Oct 2 - Nov 1	
<i>Astronium graveolens</i>	annual	short	irreg.	Aug 2 - Oct 1 (Sep 2)	annual	short	irreg.	Sep 2 - Oct 1	
<i>Bowdichia virgilioides</i>	annual	short	irreg.	Oct 1 - Dec 2 (Nov 2)	supra-annual	short	irreg.	Dec	
<i>Cariniana legalis</i>	supra-annual	interm.	irreg.	Jan 2 - May 1 (Mar 1)	supra-annual	interm.	irreg.	Apr 1 - Aug 1 (Apr 2)	
<i>Caryocar edule</i>	annual	short	reg.	Dec 2 - Feb 2 (Jan 1)	annual	short	reg.	Feb 1 - Apr 1 (Feb 2 - Mar 1)	
<i>Cedrela odorata</i>	sub-annual	interm.	irreg.	Feb 2 - May (Apr 2), Aug 2 - Sep 1	annual	long	reg.	Mar 1 - Aug 2 (Jun)	
<i>Clarisia racemosa</i>	annual	short	irreg.	Oct 2 - Dec 2 (Nov 2)	supra-annual	interm.	irreg.	Dec 1 - Mar 2 (Jan 1 - Feb 1)	
<i>Cordia trichotoma</i>	annual	interm.	irreg.	Feb - May (Mar)	annual	short	irreg.	Apr 2 - Jul 1 (May 2 - Jun 1)	
<i>Dalbergia nigra</i>	supra-annual	short	irreg.	Nov 2 - Dec 2 (Dec 1)	supra-annual	long	irreg.	Jan 1 - Sep 1 (Jan 1)	
<i>Diptotropis incexis</i>	supra-annual	short	irreg.*	Dec	supra-annual	short	irreg.*	Jan	
<i>Emmotum nitens</i>	continuous	long	irreg.	(Mar - Apr)	continuous	long	irreg.	(Apr 2 - Sep 2)	
<i>Eriotheca macrophylla</i>	supra-annual	short	irreg.*	Dec - Jan	supra-annual	short	irreg.*	Jan - Feb 1	
<i>Eugenia microcarpa</i>	annual	short	reg.	Feb - Apr (Mar)	annual	interm.	reg.	Mar 2 - Aug 2 (Apr 1)	
<i>Hidrogaster trinervis</i>	annual	long	reg.	Feb 2 - May 2 (Apr)	annual	interm.	reg.	Apr 2 - Aug 1 (Jun 2)	
<i>Joannesia princeps</i>	sub-annual	interm.	irreg..	Aug - Nov 1 (Sep); Apr	annual	interm.	reg.	Aug 2 - Feb 2 (Nov 1 - Dec 2)	
<i>Kielmeyera albopunctata</i>	annual	interm.	reg.	Feb - May (Mar)	annual	long	reg.	Apr 2 - Sep 1 (Jun 2 - Jul 1)	
<i>Lecythis pisonis</i>	annual	short	reg.	Oct 2 - Dec (Dec 1)	annual	long	reg.	Dec 2 - Jul (Jan - Mar)	
<i>Licania salzmannii</i>	supra-annual	short	irreg.	Sep 2 - Nov 2	supra-annual	interm.	irreg.**	Nov 1 - Apr 2 (Dec)	
<i>Manilkara bella</i>	annual	interm.	irreg.	Aug 2 - Oct 2 (Sep 2)	annual	long	irreg.	Aug 1 - Dec 2 (Jul 2 - Aug 1)	
<i>Manilkara salzmannii</i>	annual	interm.	irreg.	Apr - Sep (Jul)	annual	long	irreg.	Aug - Dec 2 (Oct)	
<i>Melanoxylon brauna</i>	annual	interm.	regular	Feb 2 - May (Mar 2)	annual	interm.	reg.	May 2 - Sep 2 (Jul)	
<i>Myrcia lineata</i>	supra-annual	short	irreg..	Apr 2 - Jun 1 (May 2)	supra-annual	interm.	irreg.	May 2 - Sep 2 (Jun 1 - Jul 2)	
<i>Ocotea conferta</i>	supra-annual	short	irreg.	Oct - Dec (Oct 2)	supra-annual	interm.	irreg.	Nov 2 - Feb 2 (Jan 1)	
<i>Ocotea organensis</i>	annual	short	irreg.	Sep - Dec 1 (Oct 2 - Nov 1)	supra-annual	interm.	irreg.**	Jan 1 - Mar 2 (Jan 1)	
<i>Paratecoma peroba</i>	annual	short	irreg.	Oct 2 - Dec 2	annual	long	irreg.	Jan 1 - Aug 2 (Mar 2 - Apr)	
<i>Parkia pendula</i>	sub-annual	short	irreg.	Jan 2 - Mar; Sep - Dec (Sep 2)	sub-annual	short	irreg.	(Oct 2 - Dec); Mar - May	
<i>Peltogyne angustifolia</i>	supra-annual	short	irreg.**	Oct 2 - Feb	supra-annual	interm.	irreg.**	Jun - Jul	
<i>Pterygota brasiliensis</i>	annual	short	regular	Sep 1 - Dec 2 (Sep 2 - Oct 1)	annual	long	reg.	Nov 2 - Jul 2 (Feb - Mar)	
<i>Qualea magna</i>	annual	interm.	irreg..	Jan 2 - May (Mar)	annual	long	irreg.	Apr 2 - Sep 2 (Jul 2)	
<i>Qualea multiflora</i>	sub-annual	short	irreg.	Nov 2 - May 1 (Jan 2 - Feb 1)	annual	long	irreg.	Feb 2 - Sep 1 (May - Jun)	
<i>Schefflera morototoni</i>	supra-annual	short	reg.	Aug 2 - Oct (Aug)	supra-annual	interm.	reg.	Nov 1 - Feb 1 (Nov 2)	
<i>Simarouba amara</i>	annual	short	reg.	Aug 2 - Nov 2 (Sep)	annual	long	reg.	Nov - Dec (Nov)	
<i>Simira rubescens</i>	annual	long	reg.	Nov 2 - May 2 (Mar)	annual	short	reg.	Mar - Aug (Jun)	
<i>Tabebuia riodecensis</i>	annual	short	irreg.	Sep 2 - Oct 1 (Oct 1)	supra-annual	short	irreg.**	Oct 2	
<i>Talisia intermedia</i>	annual	short	regular	Aug 2 - Oct 2 (Sep 2)	annual	short	reg.	Oct - Nov 2	
<i>Terminalia Kuhlmanii</i>	sub-annual	interm.	irreg..	Aug 2 - Nov 2 (Sep 2 - Oct 1)	annual	interm.	irreg.	Oct 2 - Feb 1 (Dec)	
<i>Virola gardneri</i>	annual	long	irreg.	(Jan 1 - May 1)	annual	interm.	irreg.	Mar 1 - Jul 2 (May 2 - Jun 1)	
<i>Ziziphus platyphylla</i>	annual	short	regular	Jan 2 - Apr 1 (Feb 2)	annual	interm.	regular	Mar 1 - Jul 1 (May - Jun 1)	
<i>Zollernia ilicifolia</i>	annual	interm.	irreg.	Feb 1 - Jun 2 (Mar 2)	supra-annual	interm.	irreg.	Apr - Aug (Jul - Aug)	

*observed only once or twice; ** observed only tree to four times.

minimum and average air temperature, and negative correlations with actual evapotranspiration and water deficit (Table 5). The minimum temperature explained the greater part of total variance ($r^2=0.34$ and 0.38 , respectively, for proportion of species and individuals) and was the

less redundant one. Considering that only the former variable as well as the water deficit varied significantly between years, the other significant correlations are due to the flowering and climatic seasonality within the year and not between years (Fig. 2).

Table 4. Annual averages of meteorological variables from 1982 to 1992 at Linhares Natural Reserve, Brazil. Comparisons between years made by LSD test. Averages of the same variable followed by the same letter do not differ at 5% probability level.

Year	Evaporation (cm ³) F _(10, 55) = 5.69 P < 0.000	Minimum temperature (°C) F _(10, 55) = 8.16 P < 0.000	Relative air humidity (%) F _(10, 55) = 4.12 P < 0.000	Average rainfall of the dry season (mm) ^{(1) (2)} F _(10, 55) = 1.10 P < 0.378	Average water deficit of the dry season (mm) ⁽²⁾ F _(10, 55) = 3.63 P < 0.000
1982	70.6 ac	16.4 a	84.9 a	53.9 ab	00.0 a
1983	69.9 ac	16.8 a	84.7 a	54.7 ab	36.1 b
1984	70.8 ac	16.7 a	84.8 a	64.9 a	21.7 ab
1985	66.5 c	16.1 a	84.6 a	48.7 ab	01.9 a
1986	78.8 a	16.0 a	82.1 b	52.5 a	29.5 b
1987	78.9 a	16.7 b	82.4 b	33.4 b	39.2 b
1988	83.8 b	20.7 b	81.7 b	38.6 ab	43.9 b
1989	87.8 b	20.8 b	81.0 b	38.6 ab	43.2 b
1990	87.3 b	20.3 b	82.3 b	42.2 ab	38.2 b
1991	64.4 c	21.3 b	85.1 a	40.9 ab	18.8 ab
1992	58.4 c	19.6 b	86.2 a	66.4 a	00.0 a

April to September; (2) Data transformed as $x' = \ln(x)$

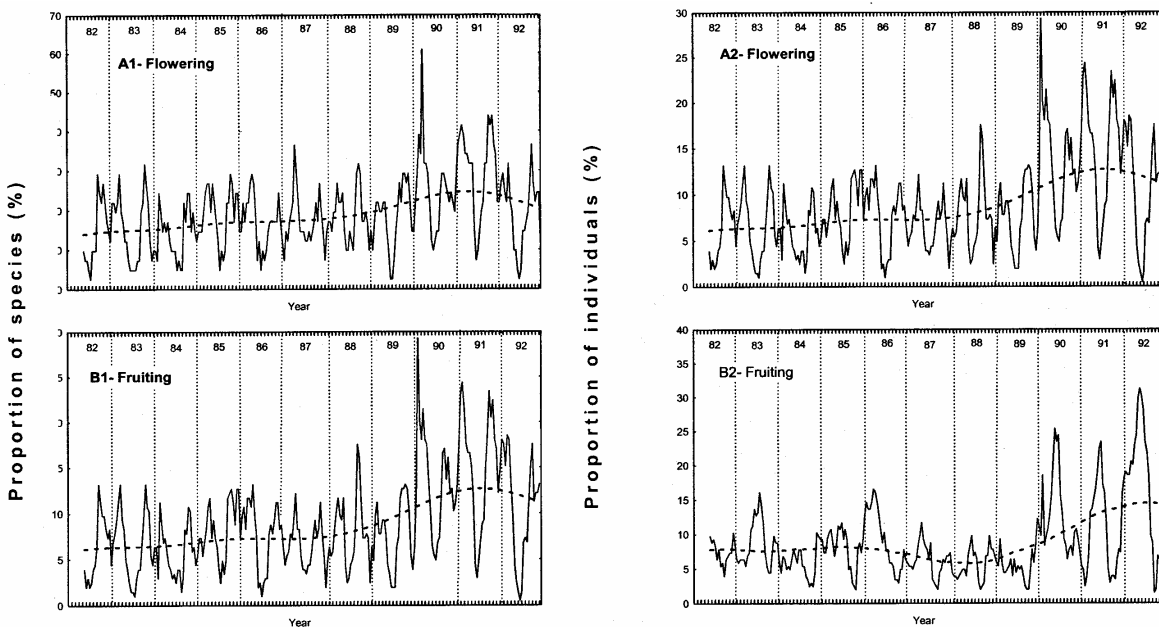


Fig. 4. Time series for reproductive phenophases of tree species in Linhares, ES, Brazil, from May 1982 to December 1992. Traced lines adjusted by weighted minimal least squares method.

Table 5. Results from the analysis of multiple regressions. The dependent variables are the proportion of individuals flowering and fruiting in every fortnight of observation, from May 1982 to December 1992; independent variables are the meteorological ones (see text for details). Phenological data transformed in $x^2 = \arcsin(x)$. Only the significant partial correlations are shown.

Independent Variables	Beta	B (parameter estimate)	$t_{(256)}$ and significance	Partial Correlation	Redundancy ⁽¹⁾
Percentage of Flowering Individuals (N=256) ⁽²⁾					
Minimum Temperature (°C)	0.43	0.0114	6.477**	0.39	0.35
Actual Evapotranspiration (mm)	-0.41	-0.0015	-2.799**	-0.18	0.86
Average Temperature (°C)	0.33	0.0124	2.458**	0.15	0.84
H ₂ O Deficiency (mm)	-0.30	-0.0016	-2.63185**	-0.15	0.76
Percentage of Fruiting Individuals (N=256) ⁽³⁾					
Evaporation (cm ³)	-0.48	-0.0048	-5.2903 **	-0.32	0.66
Insolation (hours)	0.49	0.0016	6.7719 **	0.40	0.43
Minimal Temperature (°C)	0.37	0.0071	3.9424 **	0.24	0.35
Average Temperature (°C)	-0.36	-0.0139	-2.7020 **	-0.17	0.84
Actual Evapotransp	0.32	0.0011	2.0738*	0.13	0.86

(1) r^2 between the independent variable and the others in the model; (2) Regression Summary: $R = 0.53$; $R^2 = 0.30$; $F_{(9,249)} = 11.55$; $P < 0.00000$; Standard error of estimate = 0.07; (3) Regression Summary: $R = 0.54$; $R^2 = 0.29$; $F_{(8,247)} = 12.24$; $P < 0.00000$; Standard error of estimate = 4.83.

The negative correlation with water deficit seems also to be because of seasonality within years, considering that the period of maximum flowering amplitude observed (January to March 1990) was coincident with a “veranico”, (an abnormal drought during summer with a period of water depletion in the soil). At the end of summer 1987, there was a less pronounced increase in the proportion of species bearing flowers (Fig. 5). This increase in proportion of species flowering also coincided with an abnormal water deficit in January and February (Fig. 5), followed by showers in the beginning of March, what may have stimulated the bud dormancy break, at least, in some of the species.

Besides the increase in flowering and fruiting after 1990, there was a decrease in fruiting amplitude in 1984 and 1987-1989 (Fig. 4B). The former period coincided with increase in evaporation and water deficit and decreased relative air humidity (Fig. 5 & Table 4). Although variable, the rainfall exhibited decreasing trend from 1987 to 1989 (Table 4), with very strong winter drought periods. In 1987, there was a long

drought from April to August, with almost no rain. Besides the positive correlation with the minimum temperature, the variables correlated to fruiting that had significant differences between years were evaporation (negative) and air relative humidity (positive); the other significant correlations (average temperature, negative; actual evapotranspiration and insolation, positives) were also attributable to their variation within the year and not between years (Tables 4 & 5).

Discussion

Seasonality and phenorhythms of trees

Our results indicate that regularity of reproductive phenological events for the whole set of trees was greater than that for individual species. In Linhares, there was a regular flowering and fruiting rhythm as a whole, although irregular rhythms predominated in the individual species phenorhythms. The sub-annual and annual predominant rhythms for flowering and fruiting may be conditioned by climatic seasonality.

Many other studies in Brazil showed that flowering predominates in the dry season and at the beginning of the rainy season, varying from August to December, like in Amazonian forests (Alencar *et al.* 1979; Knowles & Parrotta 1997; Pires-O'Brien 1993); south of Bahia state (Mori *et al.* 1982) or southeastern region of Brazil (Jackson 1978; Morellato *et al.* 1989; Morellato 1991). Only in a wet forest is flowering concentrated in the rainy season (Talora & Morellato 2000). But some other studies in

southeastern Brazil showed also a bimodal flowering curve (Fonseca 1998; Matthes 1980; Morellato 1991), similar to the present study. In the forest we studied, maximum flowering intensity during the calendar year may be related to different environmental stimuli, since the two flowering peaks occur in different times of the year; this deserves further investigation. Nevertheless, an increase at the rainfall after a period drier than normal seems to be associated with two peaks (Fig. 1).

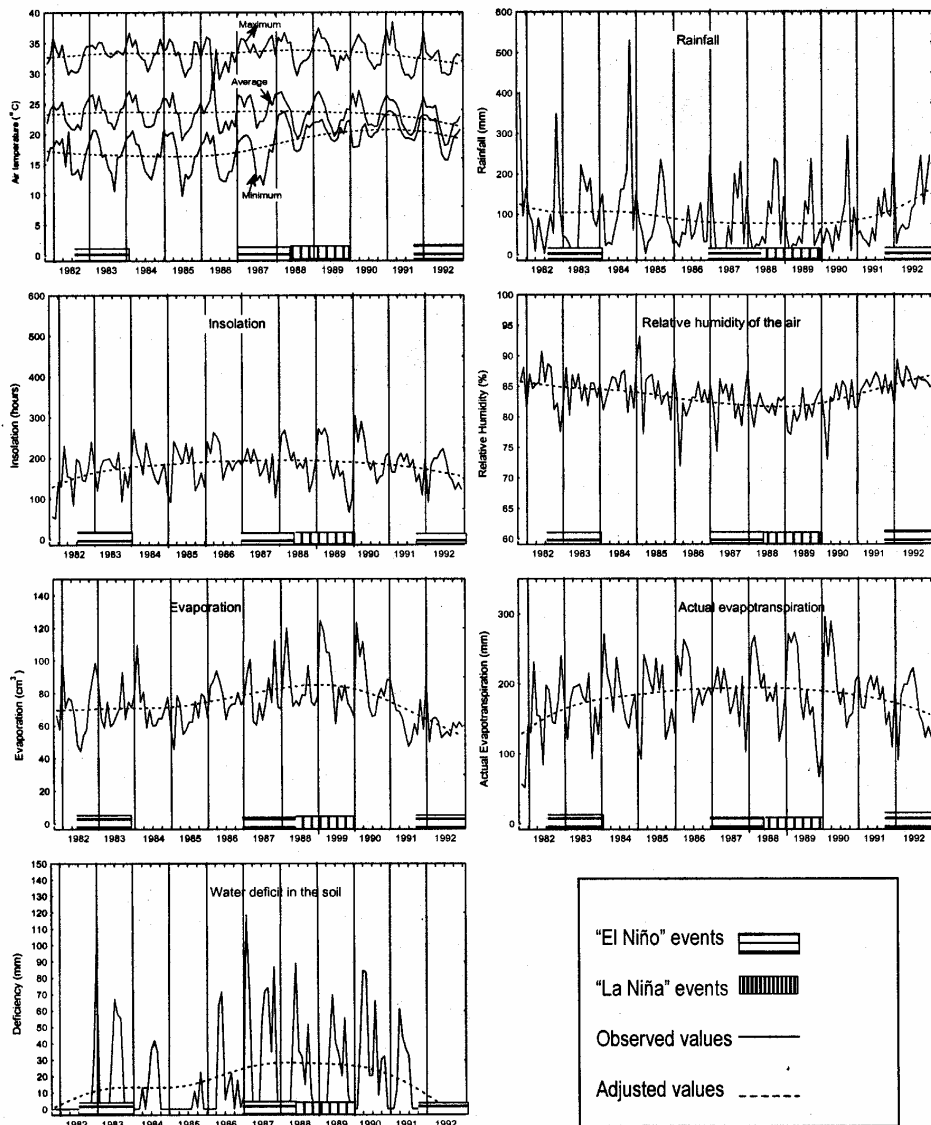


Fig. 5. Time series trends for meteorological variables at Linhares Natural Reserve, Brazil. The air temperatures and relative humidity represent monthly averages; the other data represent monthly totals. Soil water deficit estimated by the water balance computations (see text for further details).

The fruiting curve showed a period of highest intensity in the dry season. Our results agree with some other studies done in more seasonal forests (Frankie *et al.* 1974; Foster 1982a; Ibarra-Manríquez *et al.* 1991). Other studies relate the canopy position of the tress with the fruiting seasonality. In our paper, the dry season maximum was due to the predominance of upper canopy species, what agrees with results obtained by Matthes (1980), Foster (1982a), Morellato (1991) and Fonseca (1998).

Reproductive phenological patterns of individual species

The great diversity of phenological patterns found at Linhares Natural Reserve agreed with the literature (Morellato *et al.* 1990; Morellato 1991; Newstrom *et al.* 1993, 1994). In the present study, annual irregular patterns are predominant, followed by supra-annual irregular ones. In a seasonal semideciduous forest in Campinas, Brazil, Morellato (1991) found that the majority of trees had regular annual patterns. At La Selva Biological Station, Costa Rica, where the rainfall is well distributed, Newstrom *et al.* (1994) encountered a predominance of irregular infra-annual patterns, with the supra-annual and continuous patterns being the rarest. A diversity of patterns in a community has been interpreted to be a result of selection pressures by factors like pollination systems and pollinator foraging behavior (Morellato 1991; Newstrom *et al.* 1993, 1994; Rathcke & Lacey 1985).

Reproductive irregularity has been reported in all long-term phenological studies, but the causes are still open to discussion. Medway (1972), studying a tropical rainforest in Malaysia during a 10-year period, verified that annually only 10 and six of 45 tree species flowered and fruited, respectively, although for the community as a whole the patterns were regular between years. It was also reported that during drier years reproductive activity was more intense, involving a larger number of species with a higher intrapopulation synchronism; the author called this "gregarious flowering". Appanah (1985) described the gregarious flowering in a tropical rain forest in Southeastern India as a phenomenon involving a large number of tree species from different families which flowered synchronically and massively within irregular time intervals from 2 to

10 years. The same phenomenon was related to the entrance of dry air masses into the region during "El Niño" events (Ashton *et al.* 1988). In a tropical evergreen forest in Mexico, Carabias-Lillo & Guevara-Sada (1985) observed that only 44% of the tree species studied flowered and fruited every year. In a tropical cloud forest (Costa Rica), Wheelwright (1986) has verified that the fruiting rhythms in 22 tree species of Lauraceae were very irregular between years, without any relationship to the rainfall and air temperatures nor the previous reproductive history of individual trees. In Australia, the flowering patterns of 12 Myrtaceae tree species varied from annual to no flowering during a 10-year period (Law *et al.* 2000). In Panama, Wright *et al.* (1999) reported cycles of high fruit production followed by equal periods of low fructification. In Central Amazon, 9 out of 27 species reproduced annually in a 10-year period (Alencar *et al.* 1979). In other sites in Brazilian Amazon, species that flowered but did not fruit in the same year, or ones that fruited irregularly, were also reported by Pires-O'Brien (1993) and Knowles & Parrota (1997). The majority of papers cited related the phenological irregularities to the proximate factors, mainly climate abnormalities. In Linhares, climatic abnormalities influenced the phenological behavior of species, but evolutionary causes must also be considered.

Our study revealed a high proportion of supra-annual flowering and fruiting species. According to Foster (1982 b), supra-annual reproduction may be due to depletion and restorage of energy and nutrient stocks, which are modulated by irregular climatic events. According to Janzen (1978), the abundance of species with supra-annual irregular fruiting cycles would be a response to a seasonal environmental stimulus, provided there was a minimal resource stocking by the plants. These energy resources have to be partitioned between growing and reproduction functions, resulting in variations in the number of flowers, pollen quantity, number and size of seeds.

Schefflera morototoni is a supra-annual species and has alternated reproduction years with vegetative activity, showing a regular bi-annual regular flowering and fruiting. Wheelwright (1986) found evidence that fruiting irregularities in Lauraceae trees in a cloud forest (Costa Rica) were negatively correlated with vegetative growth in the same year. In the case of *S. morototoni*

reproduction seems to be reduced from the influence of vegetative growth of the former year.

Some papers have stressed the influence of anthropogenic disturbances on flowering and fruiting rhythms of tropical tree species (Bawa & Krugman 1991; Janzen & Vázquez-Yanes 1991). In spite of the large forest cover area and good protection efforts in present time, we do not discharge the hypothesis that past and present disturbances could be contributing to microclimatic changes and a decrease in pollen flux between individuals in the population. Present-time disturbances include, for instance, a dense trail system inside the reserve and high perimeter/area relationship of the forest, and resulting edge effects. The reproductive rhythms of Linhares reserve's tree species deserve further studies, especially for the poorly reproducing and dioecious species.

Interannual variability of phenorhythms and climate at Linhares Natural Reserve

Considering the tree set as a whole, the meteorological variable that seemed to be the major proximate factor influencing the increase in flowering and fruiting was the minimum air temperature, especially after 1988. The positive correlation between minimum air temperature and flowering has not been reported in the literature and the possible physiological causes are still open to discussion. Possibly it involves some other factor influencing the time of flower bud differentiation, but we do not know. On the contrary, studies done in tropical forests have revealed a negative correlation between minimum air temperature and flowering. Ashton *et al.* (1988) concluded that a decrease at 2 °C in the minimum night temperature was enough to trigger gregarious flowering in the dipterocarpaceous forest of southeastern Asia. This decrease was associated with the penetration of dry air masses associated to "El Niño" events. Law *et al.* (2000) reported that a decrease in air temperature in the period preceding the appearance of flower buds influenced nine out of 20 myrtaceous species in Australia.

The decrease in fruiting in 1984 was due to lack of fructification in species such *Astronium graveolens*, *Astronium concinum*, *Bowdichia virgilioides* and *Cariniana legalis*. In other species only two or three individuals fruited in this year,

like *Caryocar edule*, *Hidrogaster trinervis*, *Qualea magna* and *Qualea multiflora*. In 1984, we reported a decrease in precipitation, an increase in evaporation and decrease in air relative humidity, from January to March, which may have affected the subsequent fruiting. In 1987 and 1988, several species with regular annual fruiting did not bear any fruits, in spite of having flowered before (*Apuleia leiocarpa*, *Kyelmeiera albopunctata*, *Paratecoma peroba* and *Melanoxylon brauna*, *B. virgilioides*, *C. edule*, *H. trinervis*, *Ocotea conferta*, *Q. magna* and *Q. multiflora*). The long 1987 dry season that provoked an increase in evaporation and a decrease in air relative humidity was responsible for low fruiting; this effect persisted until mid-1989. On the other hand, the increase in fruiting activity after 1990 seems to be a consequence of an increase in flowering.

The decrease in fruiting in 1984 and in 1987-1988 occurred during and after strong "El Niño" episodes. At Barro Colorado Island, Panama, Wright *et al.* (1999) verified that the fruiting of a tropical rainforest increased during "El Niño" years, due to a higher flowering synchronization, provoked by the drier weather condition, a decrease in cloud cover and an increase in insolation. As a consequence, this led to the depletion of stored energy and a decrease in the fruiting activity during the following years.

In southeastern Brazil, particularly in the Linhares region, the "El Niño" phenomenon does not provoke a predictable effect in rainfall distribution, as in other parts of the country. Usually, there is a tendency for increased average winter temperatures, while during "La Niña" years there is a tendency for cooler summers (CPTEC 2004). During the study period, there were strong El Niño episodes in 1982-1983 and 1986-1987, and another less intense but longer one from mid-1990 to 1995. Only one La Niña event was registered in 1988-1989. It is not possible to identify a characteristic pattern of climatic abnormalities that could be directly associated to these events. The "El Niño" event in 1983 provoked only a slight drought that seems to have stimulated fructification and led to a decrease in fruiting the following year. Nevertheless, the strong 1987-1988 "El Niño" event provoked a 5 month-long drought, the most severe in the site's history that, instead of stimulating, seemed to limit the fruiting of the majority of species studied. The 1990-1992 event

resulted in a gradual increase in rainfall and water deficit decrease that was not correlated to the increase in reproductive activity after 1988.

The existence of drier periods at Linhares climate must have an effect not only in the phenological rhythms but also in forest dynamics as a whole. Rolim (1997) reported that the 1987 dry season influenced significantly the mortality rates of trees in this forest, and canopy species were the most affected. Fifty percent of the total tree mortality from 1975 to 1995 corresponded to the period between 1987 and 1989. The same author concluded that after 1992 the forest had recovered, and that this could reflect the adaptability of the community to periodical droughts.

The reproductive phenology patterns showed by the tree species in Linhares Natural Reserve during the 11-year study suggests that we sampled a small proportion of a longer cycle, not yet known or reported in the literature. One explanation could be a possible influence of solar activity cycles. Landscheidt (2000) described the solar activity cycles as having an average duration of 11 years, characterized by an ascendant phase, a peak and a descendant one, the former longer than the first one. According to this author, from 1982 to 1986 the solar activity cycle was in the descendant phase. In 1986-1987, there was a period of minimal solar activity and minimal solar constant "S", while from 1987 to 1991 the sun was in the ascendant phase reaching its maximum activity. Data from satellite measurements indicated an increase in the Earth's temperatures from 1989 to 1992, corresponding exactly to the time of increasing solar activity and a decrease in global cloud cover. Our hypothesis is that this major cycle could be influencing the phenological behavior of tropical trees, by means of mechanisms not completely understood. Unfortunately there is no comparable data set that could help in identifying similar patterns in other parts of the planet.

The results presented here stress that data from short-term studies do not represent adequately the phenological behavior of tropical forest communities, mainly when the objective is to investigate the relation between phenorhythms and abiotic factors in tropical forests. Also, due to the great diversity of phenological patterns in these communities, detailed population studies are

still needed, aiming to give a better understanding of the species responses to the environmental and biotic factors.

Acknowledgements

We are grateful to Companhia Vale to Rio Doce (CVRD), especially to Drs. Renato Moraes de Jesus and Marcos de Souza Menandro for supporting this research and assigning the data set; our sincere thankfulness to the field work staff of Linhares Natural Reserve, coordinated by Domingos Folli, for assistance in data collection. S. de C. do Império, M. L. Lyra and O. Herrera kindly assisted in data processing. J. A. Parrotta, L. P. Morellato, W. Mantovani and F. Poggiani made useful suggestions in previous versions of this paper.

References

- Alencar, J. da C. 1990. Interpretação fenológica de espécies lenhosas de campina na Reserva Biológica de Campina do INPA ao norte de Manaus. *Acta Amazonica* **20**: 145-183.
- Alencar, J. da C. 1994. Fenologia de cinco espécies arbóreas tropicais de Sapotaceae correlacionada a variáveis climáticas na Reserva Ducke, Manaus, AM. *Acta Amazonica* **24**: 161-182.
- Alencar, J. da C., R.A. de Almeida & N.P. Fernandes. 1979. Fenologia de espécies florestais em floresta tropical úmida de terra firme na amazônia central. *Acta Amazonica* **9**: 163-198.
- Appanah, S. 1985. General flowering in the climax rain forests of south-east India. *Journal of Tropical Ecology* **1**: 225-240.
- Arruda, F.B., J. Zullo Jr. & J.B. Oliveira. 1987. Parâmetros de solo para o cálculo da água disponível com base na textura do solo. *Revista Brasileira de Ciência do Solo* **11**: 11-15.
- Ashton, P.S., T.J. Givinish & S. Appanah. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *The American Naturalist* **132**: 44-66.
- Bawa, K.S. & S.L. Krugman. 1991. Reproductive biology and genetics of tropical trees in relation to conservation and management. pp. 119-136. In: A. Gómez-Pompa, T.C. Whitmore & M. Hadley (eds.) *Rain Forest Regeneration and Management*. UNESCO, The Parthenon Publishing Group, Paris.

- Borchert, R. 1983. Phenology and control of flowering in tropical trees. *Biotropica* **15**: 81-89.
- Bullock, S.H. & J.A. Solis-Magallanes. 1985. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* **22**: 22-35.
- Carabias-Lillo, J. & S.Guevara-Sada. 1985. Fenologia en una selva tropical humeda y en una comunidad derivada: Los Tuxtlas, Veracruz. pp. 27-66. In: A. Gomez-Pompa & S. del Amo-Rodríguez (eds.) *Investigaciones sobre la regeneracion de selvas altas en Veracruz, México: Tomo II*. Instituto Nacional de Investigaciones sobre Recursos Bioticos, Editorial Alhambra Mexicana, México.
- Chatfield, C. 1992. *The Analysis of Time Series: An Introduction*. Chapman & Hall, London.
- CPTEC. 2004. Centro de Previsão do Tempo e Estudos Climáticos (CPTEC), Instituto Nacional de Pesquisas Espaciais (INPE)-<http://www.cptec.inpe.br/products/elinho/>
- Engel, V.L. 2001. *Estudo fenológico de espécies arbóreas de uma floresta tropical em Linhares, ES*. Ph.D. Thesis, Universidade Estadual de Campinas, Campinas, Brazil.
- Fonseca, R.C.B. 1998. *Fenologia e estrutura de uma floresta semidecídua em Botucatu, SP: relação com as fases de desenvolvimento sucessional*. Ms. Dissertation, Universidade de São Paulo, Piracicaba, Brazil.
- Foster, R. 1982a. The seasonal rhythm of fruitfall on Barro Colorado Island. pp. 151-172. In: E.G. Leigh Jr., A.S. Rand & D.M. Windsor (eds.) *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Smithsonian Institution Press, Washington.
- Foster, R. 1982b. Famine on Barro Colorado Island. pp. 201-212. In: Jr, E.G. Leigh, A.S. Rand & D.M. Windsor (eds.) *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Smithsonian Institution Press, Washington.
- Frankie, G.N., H.G. Baker & P.A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* **62**: 881-913.
- Gentry, A. H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica* **6**: 64-68.
- Gentry, A. H. 1976. Bignoniaceae of southern central America: distribution and ecological specificity. *Biotropica* **8**: 117-131.
- Ibarra-Manríquez, G., B. Sánchez-Garcías & L. Gonzáles-García. 1991. Fenologia de lianas y arboles anemócoros en una selva calido-humeda de México. *Biotropica* **23**: 242-254.
- IBGE. 1992. *Manual Técnico da Vegetação Brasileira*. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.
- Jackson, J.J. 1978. Seasonality of flowering and leaf-fall in a Brazilian subtropical lower montane moist forest. *Biotropica* **10**: 38-42.
- Janzen, D.H. 1978. Seeding patterns of tropical trees. pp. 83-127. In: P.B. Tomlinson & M.H. Zimmermann (eds.) *Tropical Trees as Living Systems*, Cambridge University Press, Cambridge.
- Janzen, D.H. & C. Vázquez-Yanes. 1991. Aspects of tropical seed ecology of relevance to management of tropical forested wildlands. pp. 137-156. In: A. Gómez-Pompa, T.C. Whitmore & M. Hadley (eds.) *Rain Forest Regeneration and Management*. UNESCO, The Parthenon Publishing Group, Paris.
- Jesus, R. M. de. 1987. Mata atlântica de Linhares: aspectos florestais. pp. 35-71. In: *1º Seminário sobre Desenvolvimento Econômico e Impacto Ambiental em Áreas do Trópico Úmido Brasileiro*. Companhia Vale do Rio Doce, Rio de Janeiro.
- Jesus, R.M., A.L Souza & A. García. 1992. Produção sustentável de floresta atlântica. Sociedade de Investigações Florestais, Viçosa (*Documento SIF 7*).
- Knowles, O. H. & J.A. Parrotta. 1997. Phenological observations and tree seed characteristics in an equatorial moist forest at Trombetas, Para State, Brazil. pp. 67-84. In: H. Lieth & M.D. Schwartz (eds.) *Phenology in Seasonal Climates*. Backhuys Publishers, Leiden.
- Landscheidt, T. 2000. Solar forcing of El Niño and La Niña. pp. 135-140. In: *European Space Agency (ESA) Special Publication 463*. <http://www.john-daly.com/solar/solar.htm>.
- Law, B., C. Mackowski, L. Schoer & T. Tweedie. 2000. Flowering phenology of myrtaceous trees and their relation to climatic, environmental and disturbance variables in Northern New South Wales. *Australian Ecology* **25**: 160-178.
- Matthes, L.A.F. 1980. *Composição florística, estrutura e fenologia de uma floresta residual do planalto paulista: Bosque dos Jequitibás (Campinas, SP)*. M.Sc. Dissertation, Universidade Estadual de Campinas, Campinas, Brazil.
- Medway, L. 1972. Phenology of a tropical rain forest in Malaya. *Biological Journal of the Linnean Society* **4**: 117-146.
- Morellato, L.P.C. 1991. *Estudo da fenologia de árvores, arbustos e lianas de uma floresta semidecídua no Sudeste do Brasil*. Ph.D. Thesis. Universidade Estadual de Campinas, Campinas, Brazil.
- Morellato, L.P.C., H.F. Leitão-Filho, R.R. Rodrigues & C.A. Joly. 1990. Estratégias fenológicas de espécies arbóreas em floresta de altitude na serra do Japi, Jundiá, São Paulo. *Revista Brasileira de Biologia* **50**: 149-162.

- Morellato, L.P.C., R.R. Rodrigues, H.F. Leitão-Filho & C.A. Joly. 1989. Estudo comparativo da fenologia de espécies arbóreas de floresta de altitude e floresta mesófila semidecídua na Serra do Japi, Jundiá, São Paulo. *Revista Brasileira de Botânica* **12**: 85-98.
- Mori, S.A.; G. Lisboa & J.A. Kallunki. 1982. Fenologia de uma mata higrófila sub-bahiana. *Theobroma* **12**: 217-230,
- Newstrom, L.E., G.W. Frankie, H.G. Baker & R.K. Colwell. 1993. Diversity of long-term flowering patterns. pp. 142-160. *In*: L.A. Mc Dade (ed.) *La Selva: Ecology and Natural History of a Lowland Tropical Rainforest*. University of Chicago Press, Chicago.
- Newstrom, L.E., G.W. Frankie & H.G. Baker. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* **2**: 141-159.
- Peixoto, A. L. & A. Gentry. 1990. Diversidade e composição florística da mata de tabuleiros na reserva florestal de Linhares. (Espírito Santo, Brasil). *Revista Brasileira de Botânica* **13**: 19-25.
- Pires-O'Brien, M.J. 1993. Phenology of tropical trees from Jari, lower Amazon, I: Phenology of eight forest communities. *Boletim Museu Paraense Emílio Goeldi, Série Botânica* **9**: 67-92.
- Rathcke, B. & E. Lacey. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**: 179- 214.
- Rolim, S.G. 1997. *Dinâmica da Floresta Atlântica em Linhares (ES) (1980-1995)*. M.Sc. Dissertation. Universidade de São Paulo, Piracicaba, Brazil.
- Statsoft. 1995. *Statistica for Windows [Computer program manual]*. StatSoft, Inc, Tulsa.
- Talora, D.C. & L.P. Morellato. 2000. Fenologia de espécies arbóreas em florestas de planície litorânea do sudeste do Brasil. *Revista Brasileira de Botânica* **23**: 13-26.
- Thornthwaite, C.W. 1948. An approach towards a rational classification of climate. *Geographical Review* **38**: 55-94.
- Tubelis, A. & F.J.L. Nascimento. 1988. *Meteorologia Descritiva: Fundamentos e Aplicações Brasileiras*. Nobel, São Paulo.
- Wheelwright, N.T. 1986. A seven-year study of individual variation in fruit production in tropical bird dispersed tree species in the family lauraceae. pp. 19-35. *In*: A. Estrada & T.H. Fleming (eds.) *Frugivores and Seed Dispersal*. Dr. W. Junk Publishers, Dordrecht.
- Wright, S.J. 1996. Phenological responses to seasonality in tropical forest plants. pp. 440-460. *In*: S.S. Mulkey, R.L. Chazdon & A.P. Smith (eds.) *Tropical Forest Plant Ecophysiology*. Chapman & Hall, New York.
- Wright, S.J., C. Carrasco, O. Calderon & S. Paton. 1999. The "El Niño southern oscillation variable fruit production, and famine in a tropical forest. *Ecology* **80**: 1632-1647.
- Yap, S.K. & H.T. Chan. 1990. Phenological behavior of some shorea species in peninsular Malaysia. pp. 21-35. *In*: K.S. Bawa & M. Hadley (eds.) *Reproductive Ecology of Tropical Forest Plants*. Unesco, The Patheron Publishing Group, Paris. (MAB Series, 7).
- Zar, J. H. 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliff, 2nd ed.

Appendix

In this paper, the autocorrelation dependence of the phenophases and hence its periodicity in the time series was determined by the coefficient "R_k", according to the Equation 1 below (Chatfield, 1992)

$$R_k = \frac{\sum_{i=1}^{N-k} (X_i - \bar{X})(X_{i+k} - \bar{X})}{\sum_{i=1}^N (X_i - \bar{X})^2}$$

where:

R = autocorrelation coefficient; k = time lag (1 to 50 fortnights); N = number of elements in time series; X = variable considered (\bar{X} = average).

