Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests

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ABSTRACT. To study the impact of the annual long-term flooding (flood-pulse) on seasonal tree development in Amazonian floodplains, the phenology and growth in stem diameter of various tree species with different leaf-change patterns were observed over a period of 2 y. The trees of the functional ecotypes, evergreen, brevi-deciduous, deciduous and stem-succulent showed a periodic behaviour mainly triggered by the flood-pulse. Trees have high increment during the terrestrial phase. Flooding causes a shedding of some or all leaves leading to a cambial dormancy of about 2 mo and the formation of an annual ring. Studies carried out in tropical dry forests verify a strong relationship between the phenological development and the water status of the trees, strongly affected by seasonal drought. The comparison of the phenology and the diameter growth of the corresponding ecotypes in floodplain forest and a semi-deciduous forest in Venezuela shows a displacement of at least 2 mo in the periodicity, except for stem-succulent tree species. For stem-succulent trees it remains unclear which factors influence phenology and stem diameter growth.

KEY WORDS: Amazon, annual rings, dendrometer, ecotypes, floodplain forest, phenology, semi-deciduous forest, várzea, Venezuela

INTRODUCTION

Water-level fluctuation of 16 m of the Amazon River and its tributaries causes a periodic annual flooding over a wide floodplain naturally covered with forests.

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Floodplain ecosystems in the Amazon Basin influenced by nutrient-rich, sediment-carrying whitewater rivers, are called várzea (Prance 1979). The predictable long-term annual flooding, defined by Junk *et al.* (1989) as flood-pulse, results in phenological, morphological and physiological responses of tree species (Parolin 1997, Schlüter 1989, Schlüter & Furch 1992, Waldhoff *et al.* 1998, Worbes 1985, 1997). Flooding causes anaerobic conditions for the roots (Worbes 1986), leading to a reduction of root activity (Meyer 1991), a water deficit in the crown (Worbes 1997) and leaf shedding by many species (Adis *et al.* 1979, Ayres 1993, Franken *et al.* 1979, Parolin 1997, Wittmann & Parolin 1999). This finally results in a cambial dormancy and the formation of annual rings in the wood (Worbes 1985, 1986). Despite the unfavourable growth conditions, several studies show that flooding does not completely impede physiological processes, as some evergreen tree species are photosynthetically active (Maia 1997, Parolin 1997), while others flush new leaves during the flood period or produce flowers and fruits (Ayres 1993, Worbes 1997, Ziburski 1991).

Most phenological studies in the Amazonian floodplain forests have focused on flowering and fruit production (Piedade 1985, Ziburski 1991). Leaf phenology was studied either unspecifically and quantitatively to determine litter production (Adis *et al.* 1979, Franken *et al.* 1979), for a small number of species (Worbes 1997) or for species during periods of less than one year (Wittmann & Parolin 1999).

Since the beginning of the 20th century the question of the triggering factor for phenological processes in tropical tree species (on non-flooded sites) has been debated (Klebs 1915, Geiger 1915). Reports of isolated observations or plantation trials of tropical species in the temperate zones and vice versa (Coster 1926) have not helped clarify the subject. Few investigations considered vegetative parts of the plants (Coster 1927–1928, Medway 1972). The development of leaves, however, is more closely connected to changing conditions in water availability than to flowering or fruit production. Borchert (1994) hypothesized physiological causes of differing leaf-fall behaviour in species of the dry forest in Costa Rica. He classified different strategies of responses to a distinct dry period for tree species as:

– Evergreen species which flush new leaves constantly or on shoots while senescent leaves are shed. They never appear leafless during the entire year. This ecotype is probably characteristic of the humid tropics (Tomlinson & Longman 1981), but also occurs in tropical dry forests on sites with good soil water storage which allows rehydration during the leaf shedding in the early or mid dry season.
– Brevi-deciduous (leaf-exchanging) tree species which shed their leaves synchronously and after remaining bare for a short period of some days or weeks, leaf flush follows immediately.
– Deciduous species are widely distributed in tropical regions with a severe dry season. Leaves are shed early in the dry season followed by a strong

dehydration of the stem. The trees remain bare until the rehydration of the stem after the first rainfalls induce a synchronous leaf flushing in the first weeks of the rainy season.

– Stem-succulent tree species store water in the wood of their bulbous stems. Leaves are shed at the end of the rainy or in the early dry season and trunks rehydrate. Stem water allows flowering and fruiting during the dry period. These species never react to irrigation or rainfall within the dry period by flushing (Borchert & Rivera 2001).

The early studies of phenology in the floodplains and our own observations show that Borchert's ecotypes of the dry forest are also found in the Amazonian floodplain forest, despite the apparently contrasting stress factor. Some species, such as *Cedrela odorata* L. (Meliaceae), *Hura crepitans* L. (Euphorbiaceae) and others, occur in both habitats. In this study we test this classification and relate the leaf exchange behaviour to changes in stem diameter during the annual cycle. We explain the results through the seasonal changes in flooding and precipitation. Growth reactions to seasonal variations in triggering factors are discussed in a comparison with a tropical semi-deciduous forest of the northern hemisphere.

METHODS

Study area

The study was carried out on the Ilha da Marchanteria (3°15′S, 59°58′W) located in the Solimões River near its confluence with the Rio Negro (Figure 1). The study area was a forest stand next to the Lake Camaleão located in the middle of the island. The elevations of the chosen stand were between 21.9 and 24.5 m (mean elevation of 23.3 m) above sea-level (asl). In the study year of 1999 the stand was flooded between 206 and 243 d from February until September. The mean water-level above the forest floor reached a height of 6.05 m in late June and was much higher than the average of 4.88 m of the last 30 y. According to Junk (1989), the chosen stand belongs to the mid-level forest community, equivalent to the restinga baixa (Ayres 1993).

The climate in Central Amazonia shows a mean temperature of 26.5 °C and annual precipitation of 2100 mm. A distinct seasonal dry period occurs between June and November with rainfall below 100 mm or even 50 mm mo^{-1}. A comparison between the seasonal variations of water-level and precipitation patterns shows a displacement in the recurrent periodicity of about 2 mo between flooding and drought (Figure 2). The difference between maximum and minimum daylength in this low latitude is only 21 min.

Species

For the study, 66 trees from 23 species comprising 19 families were chosen for phenological observations and classified into ecotypes. In Table 1 all species
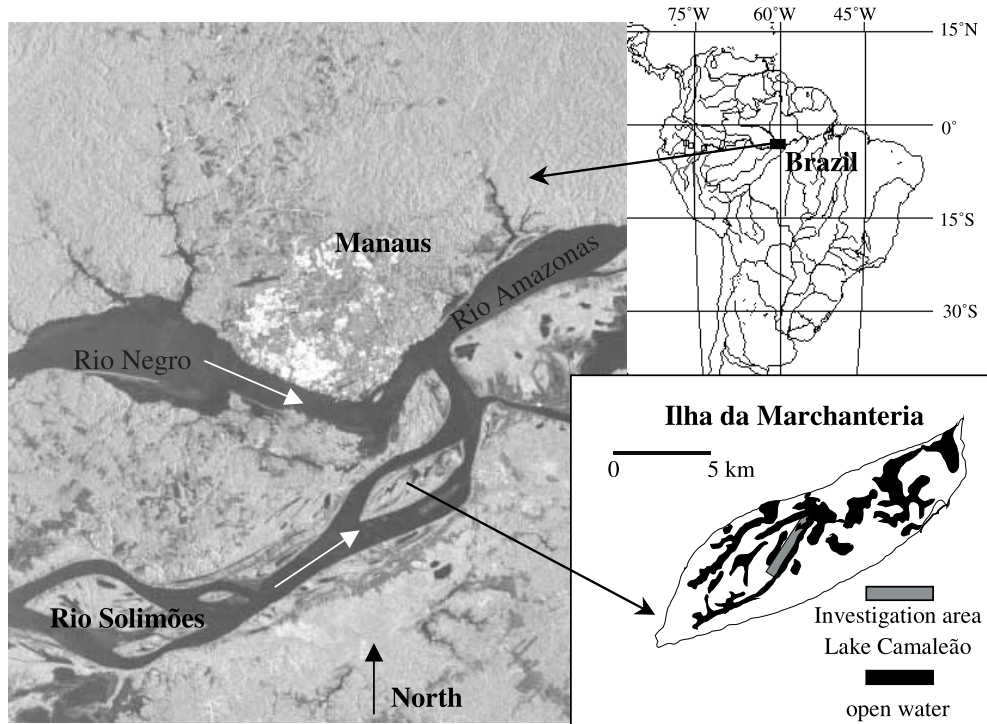
Figure 1. Study site, Ilha da Marchanteria.

are listed together with the number of observed trees, those monitored by dendrometer bands and the importance-value index from a vegetation analysis of Klinge *et al.* (1996) of the same study area.

Records

The growth rhythm of the stem was observed for 15 tree species using permanently installed dendrometer bands at stem heights between 5 and 7 m. This height was necessary to enable observations during the flooding. For a period of 26 mo starting in June 1998 measurements of changes in diameter increment were carried out monthly. The increment rates were calculated for every tree by the difference of two consecutive measurements and for each tree species by the average of monthly increments for all individuals. The phenology of these trees, including leaf shedding, leaf flushing, flowering and fruiting was observed monthly through binoculars. The phenology from eight additional species was recorded from April 1999 for a period of 17 mo.

At the study site the water depth was measured several times and the values compared with the data of the water-level at the nearby Rio Negro Station in Manaus, to calculate the length of the submerged period in the study area. Additionally the water-level was calculated as the mean of a given month at
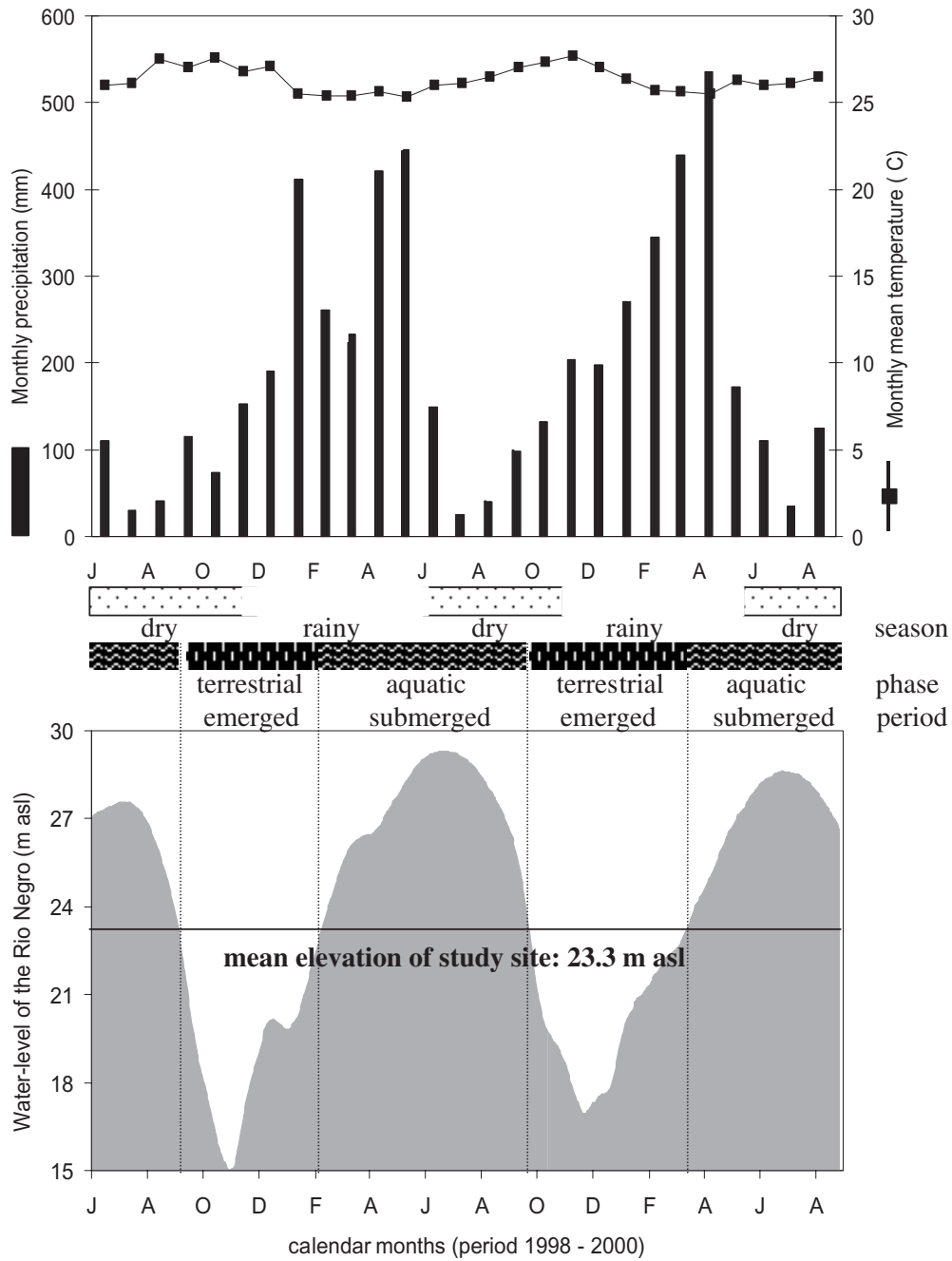
Figure 2. Above, monthly precipitation and temperature (data from the National Institute for Meteorology) and below, water-level fluctuations of the Rio Negro (data from the archive of J. A. Nunes de Mello, INPA-CPGC) from June 1998 to August 2000. The comparison between the seasonal variations of precipitation and the water level shows a displacement in the recurrent periodicity of about 2–3 mo.

the study site. Data for the monthly precipitation were obtained from the climate station in Manaus about 12 km from the investigated stand. Multiple regression analysis was conducted between the monthly increment rate of a tree species as dependent variable, and the mean water-level at the study site in the corresponding month and the total monthly precipitation as independent variables. For a further comparison with non-flooded forest sites growth and precipitation data were adopted from a study on a Venezuelan research forest (Worbes 1994, 1999).

RESULTS

Leaf phenology

In all ecotypes the peak of leaf shedding occurs during the first half of the aquatic phase, the maximum of leaf flushing in the late flooded period

Table 1. Investigated tree species classified into different ecotypes listed by scientific names, family, number of individuals and Importance-Value Indices (IVI) after Klinge *et al.* (1996) for a stand in the same study area. Species with dendrometer bands (d) were studied for a period of 26 mo between June 1998 and August 2000, those without for 17 mo from April 1999 until August 2000.

Scientific name	Family	Number of trees	IVI
Evergreen			
Calophyllum brasiliense Cambess.	Clusiaceae	1 (d)	0.4
Cecropia latiloba Miq.	Cecropiaceae	3	15.9
Eschweilera ovalifolia (DC.) Nied.	Lecythidaceae	2	–
Gustavia augusta L.	Lecythidaceae	3 (d)	1.4
Laetia corymbulosa Spruce ex Benth.	Flacourtiaceae	3 (d)	38.5
Nectandra amazonum Nees	Lauraceae	3 (d)	15.5
Pouteria glomerata (Pohl ex Miq.) Radlk.	Sapotaceae	4 (d)	0.7
Garcinia brasiliensis Mart.	Clusiaceae	1 (d)	–
Zygia inaequalis (Humb. & Bonpl. ex Willd.) Pittier	Leguminosae–Mimosoideae	3	–
Brevi-deciduous			
Alchornea castaneifolia (Baill.) Müll. Arg.	Euphorbiaceae	3	0.5
Annona sp.	Annonaceae	3	2.3
Luehea cymulosa Spruce ex. Benth.	Tiliaceae	3 (d)	19.5
Macrolobium acaciifolium (Benth.) Benth.	Leguminosae–Caesalpinioideae	3 (d)	14.3
Piranhea trifoliata Baill.	Euphorbiaceae	4 (d)	1.7
Triplaris surinamensis Cham.	Polygonaceae	3 (d)	5.3
Deciduous			
Albizia multiflora (Kunth) Barneby & J. W. Grimes	Leguminosae–Mimosoideae	3 (d)	2.8
Cordia sp.	Boraginaceae	3 (d)	8.4
Crataeva benthamii Eichler	Capparaceae	3	54.4
Psidium acutangulum DC.	Myrtaceae	3	0.4
Pterocarpus amazonum (Mart. ex Beth.) Amshoff	Leguminosae–Papilionoideae	3	12.8
Tabebuia barbata (E. Mey.) Sandwith	Bignoniaceae	3 (d)	1.2
Vitex cymosa Bertero ex Spreng.	Verbenaceae	3 (d)	24.9
Stem-succulent			
Pseudobombax munguba (Mart. & Zucc.) Dugand	Bombacaceae	3 (d)	32.6
Total		66 trees	253.5 (84.5%)

(Figure 3). Evergreen species exchange their leaves throughout the entire aquatic phase. Senescent leaves are shed constantly while new leaves flush synchronously or shortly before the end of leaf fall. Many evergreen species show a second slight leaf exchange in the dry season. Brevi-deciduous tree species also drop leaves during the aquatic period but in a relatively shorter period. The trees remain bare for a few weeks during the submersion phase. Deciduous tree species shed senescent leaves from the beginning of the flooding and appear bare around the maximum water-level. The peaks between leaf fall and leaf flush are distinctly separated. Generally deciduous species flush new leaves towards the end of the submerged period with an extension into the dry season. In contrast to all other species, the stem-succulent tree *Pseudobombax munguba* flushes new leaves later after the end of the flooded period. This species also appears bare in the submerged period. An increasing time lag between maximum leaf fall and leaf flush was observed in the order evergreen, brevi-deciduous, deciduous and stem-succulent.

Flowering and fruiting

The peak of flowering and fruiting occurs during the aquatic phase (Figure 4). No significant preferences within the different ecotypes in the time of flowering and fruiting could be detected. Some species flower at the end of the submerged period (*Luehea cymulosa*, *Pterocarpus amazonum*, *Piranhea trifoliata*, *Macrolobium acaciifolium*, *Crataeva benthamii*), occasionally with a long extension into the rainy season (*Nectandra amazonum*). The fruits mature in the following flooded period. Other species start flowering in the terrestrial phase (*Albizia multiflora*, *Psidium acutangulum*, *Cordia* sp., *Annona* sp., *Calophyllum brasiliense* and occasionally *Laetia corymbulosa*) and fruits mature during the aquatic phase. *Triplaris surinamensis*, a wind-dispersed species (Worbes 1986), is unique in maturing fruits only in the terrestrial phase. The majority of the tree species studied complete the whole reproductive phase of flowering and fruiting within one aquatic phase (*Cecropia latiloba*, *Tabebuia barbata*, *Eschweilera ovalifolia*, *Gustavia augusta*, *Zygia inaequalis*, *Garcinia brasiliensis*, *Pouteria glomerata*, *Alchornea castaneifolia*, *Pseudobombax munguba* and *Vitex cymosa*). Most fruits mature during the aquatic phase or towards the end of submersion phase with extension into the terrestrial phase. *Laetia corymbulosa* and *Cordia* sp. do not show a regular periodicity in flowering and fruiting.

Stem diameter variations

All tree species studied show a distinct annual seasonality in diameter growth. All trees have high monthly increment rates during the terrestrial phase (Figure 5). During the first half of the aquatic phase, diameter change decreases to zero indicating a cambial dormancy for at least 2 mo in the period between April and August. Diameter growth starts again immediately after flushing new leaves. A strong decrease of diameter growth in most species occurs in December at the end of the dry season.
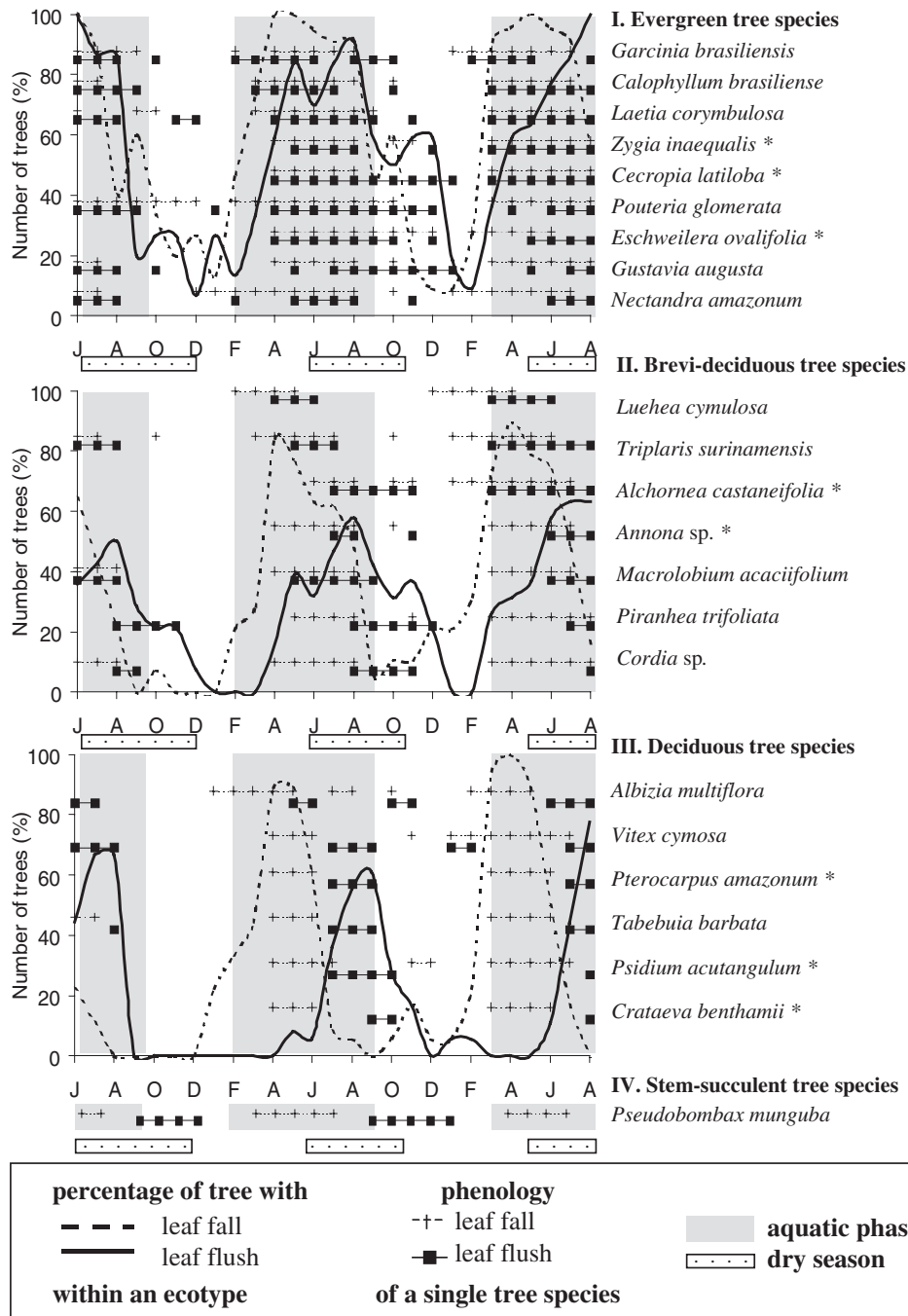
Figure 3.   Leaf phenology of tree species in a tropical whitewater floodplain forest classified into different ecotypes: I. Evergreen tree species; II. Brevi-deciduous tree species; III. Deciduous tree species; IV. Stem-succulent tree species. The leaf fall and leaf flush is shown as a percentage of all individuals within an ecotype and for each separate tree species. The species within an ecotype are listed in a chronology regarding the appearance of new leaves. The phenological observations are related to the aquatic phase (grey area) and the dry season (horizontal dotted bars). Phenological recordings were carried out between June 1998 and August 2000. Tree species marked with * were observed from April 1999 until August 2000.
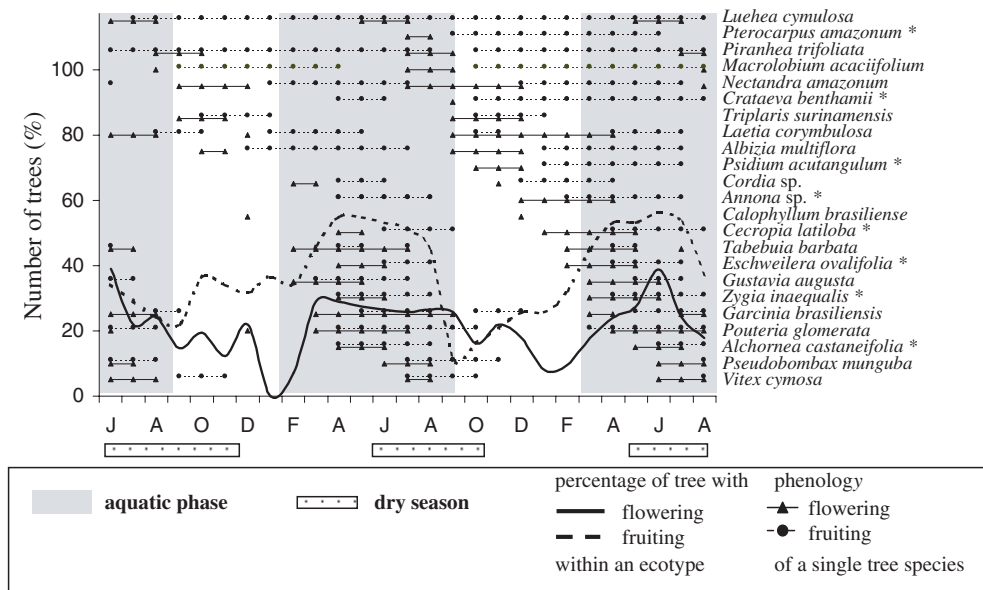
Figure 4.   Flowering and fruiting of tree species in a tropical whitewater floodplain forest shown in percentage of all observed individuals and for each separate tree species. The species are listed in a chronology regarding the appearance of flowers. The phenological observations are related to the aquatic phase (grey area) and the dry season (horizontal dotted bars). Phenological recordings were carried out between June 1998 and August 2000, species marked with * were observed from April 1999 until August 2000.

There is little difference in time and duration of the cambial dormancy among ecotypes. The stem-succulent *Pseudobombax munguba* (Figure 5i) has a growth period 2 mo displaced from the other species, between October and June, with a maximum of monthly diameter change at the beginning of the aquatic phase. In brevi-deciduous tree species the cambial dormancy of *Luehea cymulosa* (Figure 5c) occurs 2 mo before that of *Piranhea trifoliata* (Figure 5e). *Albizia multiflora* (Figure 5f) stops growing 1 mo earlier than the other deciduous tree species.

There is a strong negative correlation between the monthly increment rates and the mean water-level of the same month for deciduous and brevi-deciduous species (Table 2) indicating a strong impact of the flood-pulse on tree development with low diameter increment at high water-level. Only a few species have a strong positive correlation between the increment rates and the monthly precipitation. An increasing correlation between monthly diameter increment and monthly precipitation can be observed in the order deciduous, brevi-deciduous, evergreen and stem-succulent species. Diameter increment of *Pseudobombax munguba* has the highest correlation coefficient with monthly precipitation, but no significant correlation with water-level fluctuations.

DISCUSSION

The causes and triggering factors of phenological behaviour in tropical trees have been disputed for almost 100 y. Endogenous rhythms (Klebs 1915) or
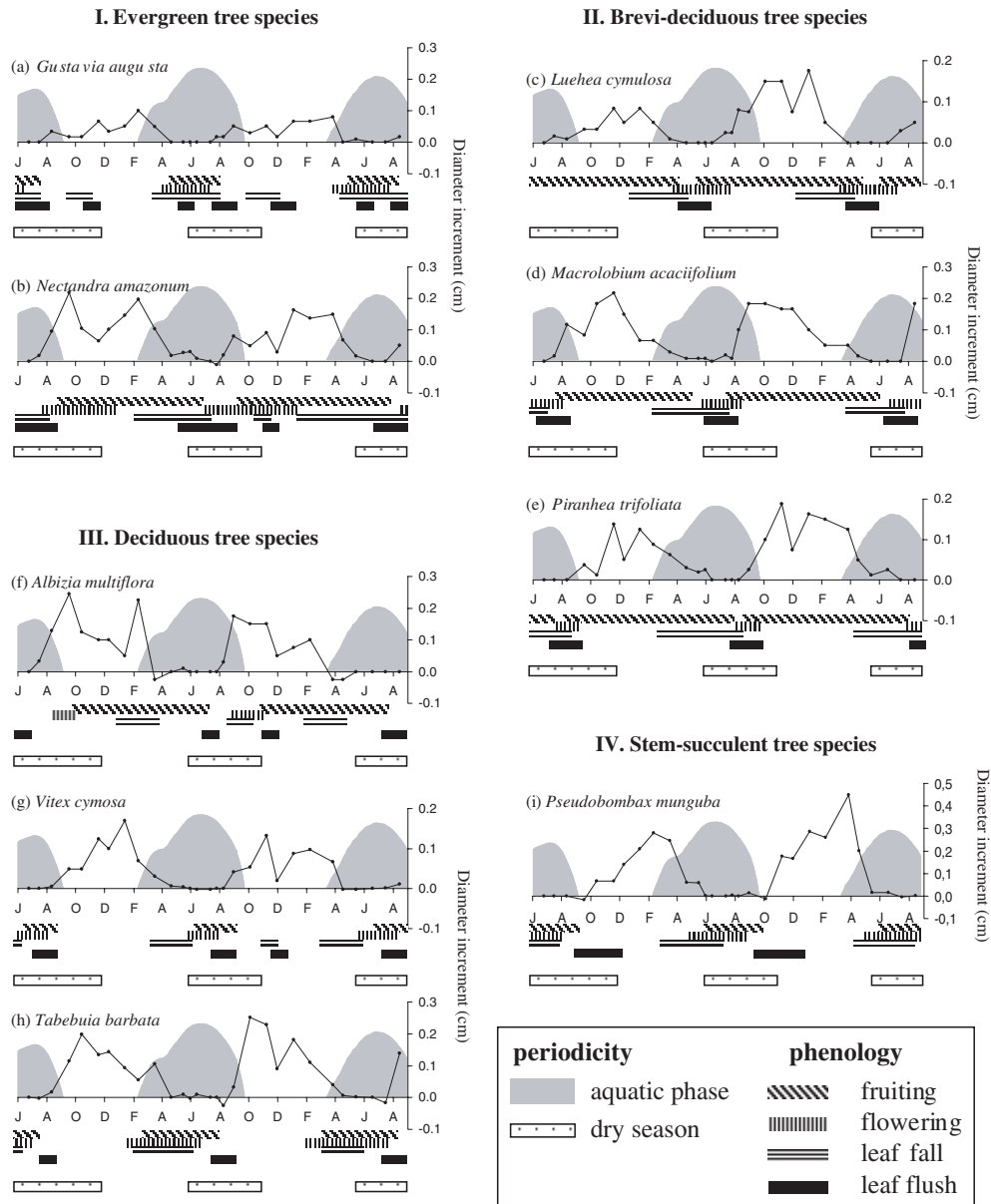
Figure 5. Phenology and variations in stem diameter increment derived from dendrometer measurements in a tropical whitewater floodplain forest for different ecotypes: I. Evergreen tree species: (a) *Gustavia augusta*; (b) *Nectandra amazonum*. II. Brevi-deciduous tree species: (c) *Luehea cymulosa*; (d) *Macrolobium acaciifolium*; (e) *Piranhea trifoliata*. III. Deciduous tree species: (f) *Albizia multiflora*; (g) *Vitex cymosa*; (h) *Tabebuia barbata*. IV. Stem-succulent tree species: (i) *Pseudobombax munguba*. The results are related to the flooded period (grey area) and the dry season (horizontal dotted bars) for the study period between June 1998 and August 2000.

Table 2. Statistical analysis between monthly increment rates and climate factors for tree species classified into ecotypes from tropical floodplain forests (present study) and from a tropical semi-deciduous forest (underlined species) of the Caparo Forest Reserve in Venezuela (data obtained from Worbes 1994, 1999). The asterisks indicate significant correlation at the 95% confidence level.

Tree species	Mean water level	Precipitation	Precipitation
	Multiple regression (Floodplain forest)		Linear regression (Semi-deciduous forest)
	t-statistics	t-statistics	R^2
Evergreen tree species			
Nectandra amazonum	−1.82	2.24*	
Gustavia augusta	−2.26*	2.48*	
Evergreen species	−2.27*	2.52*	
<u>*Cordia apurensis*</u> Agostini			0.91*
Brevi-deciduous tree species			
Macrolobium acaciifolium	−4.92*	−2.75*	
Luehea cymulosa	−3.12*	−0.87	
Piranhea trifoliata	−4.07*	2.10*	
Brevi-deciduous species	−5.69*	−1.18	
<u>*Terminalia guianensis*</u> Augl.			0.32
Deciduous tree species			
Tabebuia barbata	−4.87*	−1.22	
Vitex cymosa	−4.99*	0.91	
Albizia multiflora	−2.62*	−1.22	
Deciduous species	−5.21*	−1.15	
<u>*Cedrela odorata*</u> L.			0.14
Stem-succulent tree species			
Pseudobombax munguba	−1.32	6.27*	
<u>*Bombacopsis quinata*</u> (Jacq.) Dugand			0.81*
Mean (all species)	−5.65*	1.08	

other, still unknown, factors (Wright & Cornejo 1990) have been used to explain the great diversity of phenological patterns. Others have shown the concurrence between seasonally varying precipitation and leaf exchange (Coster 1923) and traced back many differences in specific behaviour to the existence of different functional ecotypes at one site under identical climatic conditions (Borchert 1994, Reich & Borchert 1984). Some major problems and misunderstandings obstruct the view of the principal causes of phenological patterns in the tropics:

(1) In many early studies and reviews (Studhalter 1955) there is either no clear definition of climate conditions of the study site (Koriba 1958) or the findings from different climate types are compared inappropriately with each other (Wright & Cornejo 1990).

(2) Many researchers exclusively report flowering and fruiting phenology without reference to leafing.

(3) The diversity of specific patterns at one site is often interpreted as independence from environmental factors and not as differing adaptations or tolerances to these factors.

To avoid these misunderstandings we attempt to consider both reproductive and vegetative phenology using the model of functional ecotypes of Borchert (1994) to explain different patterns among species.

In the tropics, there is often a distinct seasonality of precipitation frequently with one pronounced dry season per year of one or more mo of less than 50 mm rainfall (Worbes 1995). Even under ever-humid conditions, short and mostly unpredictable dry seasons occur in different months of the year (Medway 1972). In the floodplains of the great tropical rivers like the Amazon, Mekong or Congo, a monomodal and predictable flood-pulse (Junk *et al.* 1989) is the dominating triggering factor, responsible for changing growth conditions in the annual cycle.

Our results show strong relations of leaf expansion, leaf fall, cambial activity, flowering and fruit ripening to the flood-pulse. In all species there is very little or no positive change in stem diameter indicating cambial dormancy during the high-water phase. During this time species either shed their leaves and remain bare or gradually replace them. With few exceptions, trees flower during the high-water period. Similar relations among flowering, leaf phenology and cambial activity, as a response to the dry season, are documented for non-flooded sites in West Africa (Mariaux 1969), Brazil (Alvim & Alvim 1978), Costa Rica (Reich & Borchert 1984) and Venezuela (Worbes 1999).

To explain the phenomenon of different specific responses to one climate factor at one site we follow the classification into functional ecotypes evergreen, brevi-deciduous, deciduous and stem-succulent. In the Amazonian floodplain forests we found distinct differences in the length of leaf abscission in agreement with the findings of Borchert (1994). We classified tree species according to their leaf-fall behaviour. Evergreen, brevi-deciduous and deciduous species differ in stem water potential and their ability to rehydrate the stem during the dry season. High stem water potential enables trees to flush leaves and to flower during the time of high water stress. The water stress may be induced either by water deficit in the soil during the dry seasons on the terra firme or, as we showed in this study, by inundation of the floodplains. The same situation is given because flooding causes anaerobic conditions in the roots leading to a reduction of root activity, a reduced water conductance and consequently a water deficit in the crown (Worbes 1986, 1997). Thus we can explain the differences of phenological patterns for floodplain trees in the same way as for trees of the dry forests. The fact that few species such as *Ceiba pentandra* (L.) Gaertn. (Bombacaceae), *Cedrela odorata* (Meliaceae), *Hura crepitans* (Euphorbiaceae) and some others occur in both habitats may support this hypothesis (Worbes *et al.* 1992).

In the floodplain forests the inundation phase is followed by a short dry season, when the rainfalls start late. When water retreats from the forest stands, the soil water content decreases for some weeks, sometimes reaching the permanent wilting point (Worbes 1986). Then diameter growth decreases

and a second slight peak of leaf fall and flush may occur. Evergreen species seem to be more sensitive than other ecotypes to this phenomenon, whereas the stem-succulent species *Pseudobombax munguba* does not respond. This species flushes and starts diameter growth much later than the other species observed, in this way partially avoiding the drought stress in October.

These functional and water-budget-related explanations of leaf fall behaviour contrast with the thesis of an influence of photoperiod on tree phenology in the tropics (Borchert & Rivera 2001, Daubenmire 1972, Frankie *et al.* 1974, Tomlinson & Longman 1981). This latter hypothesis is supported by observations from perhumid forests such as La Selva in Costa Rica, where tree species always have one leaf exchange in February and March (Breitsprecher & Bethel 1990, Hazlett 1987). The rainfall in February and March is more than 100 mm mo^{-1} and thus drought stress is not likely. However, in these months precipitation is definitely lower than in the rest of the year, and there is a distinct rainfall seasonality.

Another strong hint comes from greenhouse experiments, when flushing is induced by varying the length of the photoperiod. For example Borchert & Rivera (2001) describe stem-succulent species such as *Bombacopsis quinata* (Jacq.) Dugand (Bombacaceae) and *Plumeria rubra* L. (Apocynaceae) that react to the change in daylength, although they never respond to rainfall or irrigation in the dry season. Borchert & Rivera (2001) relate flushing of stem-succulents to increasing day length after the equinox. We do not understand the biological significance of the equinox in this context, since days become constantly longer after the winter solstice.

Our results contribute an additional facet in this discussion if we compare the times when trees of the different phenological ecotypes shed and flush leaves in the floodplain forest and in the non-flooded forest (terra firme). We showed that in both habitats the reactions of trees to growth stress are similar independent of the nature of the stress factor. There are surely several specific adaptations such as a deep root system with access to the ground water table in some species of the dry forest (Borchert 1994) or the switch to anaerobic metabolism during inundation in trees of the floodplains (Schlüter & Furch 1992). Both factors cause drought stress in the crown during the unfavourable conditions. What differs is the beginning and the end of the stress periods in non-flooded and flooded sites in the Amazon region. Due to the enormous catchment area there is a time lag between the beginning of the rainy season and the beginning of the flood period of about 2 mo. The same is true for the end of the respective stress periods, as described above. Thus we can consider these conditions as a natural experiment to test the hypothesis of a climatic growth trigger against the hypothesis of a photoperiodic trigger.

Unfortunately we do not have available consistent published data on phenology from the Amazonian terra firme. We use therefore our data from a forest

Evergreen tree species

Brevi-deciduous tree species

Deciduous tree species

Stem-succulent tree species

Figure 6. Comparison between stem diameter increment and leaf phenology of tree species belonging to different ecotypes from a whitewater floodplain forest of the southern hemisphere (present study) and from a semi-deciduous forest of the northern hemisphere (Caparo Forest Reserve) for the corresponding months. The comparison comprises for each ecotype one tree species of the Amazonian floodplains and one from the Caparo Forest Reserve. Data for diameter increment are obtained from Worbes (1999) carried out between October 1979 and April 1982, phenological recordings are obtained from Franco (1978) for a period of 16 mo between June 1976 and September 1977. Statistical analysis between monthly increment rates and monthly precipitation are shown in Table 2.

in the northern hemisphere from the Reserva Florestal de Caparo (7°20′–7°40′ North, 70°30′–71° West) in West-Llanos, Venezuela (Worbes 1999). The climate in this region is characterized by a mean temperature of 24.6 °C and an annual precipitation of about 1750 mm (Franco 1978). A seasonal drought occurs from December until April (< 50 mm precipitation mo^{-1} from January to March). A cambial dormancy of 3–4 mo during the dry season has been shown from dendrometer bands (Worbes 1999). Tree species shed and flush their leaves according to their affiliation with the different phenological ecotypes. A linear regression analysis between monthly increment and monthly precipitation shows congruence with the behaviour of floodplain tree species within one ecotype (Table 2). Strong correlation between precipitation pattern and diameter growth can be observed for evergreen and stem-succulent species, while for brevi-deciduous and deciduous tree species this relation is weak or absent, the same as for species from the Amazon floodplains.

For an easier comparison of the results with the floodplain data we have shifted the calendar dates between northern and southern hemisphere by 6 mo in Figure 6. If the photoperiod was the dominant growth factor, the phenological stages would coincide at equivalent positions of the sun. However, there is a shift of about 3 mo in leaf fall, leaf flush and cambial dormancy for evergreen, brevi-deciduous and deciduous species in congruence with the flood-pulse or with the dry season (Figure 6). This indicates that the climatic stress factors are more important than variations in day length.

The stem-succulent tree species shows a different behaviour. *Pseudobombax munguba* remains without leaves until the end of the submersion phase, starting to flush in September/October until the beginning of the rainy season. Thus its dormancy period is almost synchronous with that of *Bombacopsis quinata* in the Caparo semi-deciduous forest with only a slight shift of 1 mo. Borchert & Rivera (2001) relate the phenology of the stem-succulents to an endo-dormancy of vegetative buds controlled by the photoperiod. In our Amazonian study area the difference between the longest and the shortest day amounts to about 20 min. That means a change of the day-length between consecutive days is about 6 s, however, there are indications of a higher sensitivity of stem-succulents to moderate drought stress in comparison with the other phenological ecotypes (Worbes 1999). This may explain why *Pseudobombax munguba* abridges the period where the leaves are exposed to water stress in the dry season.

Overall, our results show that the overwhelming majority of tree species of Amazonian floodplains respond to the flood-pulse more than to seasonal variation in precipitation. We find that Borchert's concept of functional ecotypes convincingly explains the different phenological behaviour of tropical tree species as a reaction to periodical stress factors rather than to photoperiod. However, our results are based strictly on observations and experimental verification is needed.

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