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PHENOLOGY OF SIX TREE SPECIES FROM CENTRAL AMAZONIAN VÁRZEA

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Resumo. Em áreas inundáveis por rios de água branca da região amazônica, os períodos de inundação podem durar até 230 dias por ano. O objetivo deste trabalho foi analisar a influência da inundação na fenofase vegetativa (mudança foliar) de seis espécies de árvores para determinar se a fase aquática representa um período comparável ao 'inverno fisiológico'. Para isso, foi determinada a quantidade das folhas nas árvores por medidas de radiação usando um fotômetro de integração quântica. Os resultados mostram que a fase aquática significa um período de atividade fisiológica reduzida, acompanhado do pico de queda de folhas. Entretanto, o período de queda e produção foliar, assim como o tempo em que as árvores ficaram caducas, não está diretamente relacionado à inundação. Todas as espécies produziram folhas novas semanas antes do final da inundação. A troca de folhas foi atenuada na fase aquática, enquanto uma alta atividade fisiológica ocorreu na maior parte do tempo em que ficaram inundadas. Para as espécies analisadas, a inundação não representa um fator de estresse, que limite o período reprodutivo ou as estratégias de crescimento.

Abstract. Amazonian várzea forests are seasonally flooded by whitewater rivers. Flood periods last up to 230 days every year. The aim of the present study was to analyze the vegetative phenology of six tree species and the extent to which the aquatic phase may represent an unfavorable period ('physiological winter') for the trees. Leaf amount on the trees was determined by measurements of light incidence using an integrating quantum photometer. The results show that there is a period of increased leaf loss during the aquatic phase, but timing of leaf shedding and of leaf flush, and the duration of the leafless period were not directly related to the time of highest water level. All species started to produce new leaves while they were still flooded. Leaf flush occurred several weeks to months before the end of the aquatic phase. For the species analyzed, there was no period of rest and stagnation of phenological and growth activities during the whole aquatic phase, indicating that flooding did not represent a high stress factor. *Accepted 06 May 1999.*

Key words: *evergreen, deciduous, leaf shedding, leaf flush, flowering, fruiting, light measurements, floodplain forest, várzea, Amazonia, Brazil.*

INTRODUCTION

Amazonian várzea forests are seasonally flooded by whitewater rivers (Prance 1979) which occur along the Amazon River and its main tributaries. They are characterized by regular extended flood periods which reach a mean height of 10 m near Manaus and last up to 230 days (Junk 1989).

The impact of the prolonged flooding on the trees growing in the floodplain forests is shown by phenological changes and the reduction of wood increment during the aquatic phase (Worbes 1986). Physiological, morphological and anatomical changes have been found in várzea trees during flooding (Worbes 1985, Fernandes-Corrêa & Furch 1992, Schlüter & Furch 1992, Schlüter *et al.* 1993). From early observations Gessner (1968) concluded that the flooding represents an extremely unfavorable period for the physiology of the trees, leading him to introduce the term 'physiological winter'. On the other hand, some studies have shown that flooding does not impede high photosynthetic rates, which are reduced only for a short part of the flooded phase, and are often linked to leaf senescence (Maia 1997, Parolin 1997). If flooding has an influence which is comparable to the temperate winter, we would expect leaves to be shed at the beginning of the aquatic phase and not produced again until the end of flooding.

Qualitative descriptions of the phenology of várzea species exist but are focused mainly on reproductive phenology (Ziburski 1991) or on vegetation analyses (Revilla 1990, Ferreira 1991). Quantitative measurements of vegetative phenology, i.e., leaf loss and flush, have not yet been performed. The aim of the present study therefore was to analyze and attempt to quantify the changes in the vegetative, and to a lesser extent reproductive, phenology of tree species during the highest water level until the end of flooding. The question whether the aquatic phase represents an unfavorable period like a temperate winter is discussed.

METHODS

Study area. The study was performed on the southwest portion of Ilha de Marchantaria, an island of approximately 45 km^2 in the lower Rio Solimões (3°15'S, 59°58'W) in Central Amazonia, Brazil (see Wittmann 1997). With a mean amplitude of 10 m between low and high water levels most of the island, whose mean height a.a.s.l. (above average sea-level) is between 20 and 29 m, is flooded annually between February and September (Fig. 1). The 1 ha study area lay between 22.2 and 24.3 m a.a.s.l. The flood height on the stems was 4.5 m (on the edge of the plot) to 6.5 m (in the middle of the plot). According to Junk (1989) the vegetation plots belong to the mid-level tree community, subject to a mean flood duration of 230 days per year.

Species. Species chosen for phenological recordings included three evergreen trees, *Cecropia latiloba*, *Laetia corymbulosa*, and *Nectandra amazonum*, as well as three deciduous species, *Pseudobombax munguba*, *Psidium acutangulum*, and *Vitex cymosa*. The six included both canopy and understory species, as well as pioneers and non-pioneers (Berg 1978, Pires & Prance 1985, Worbes *et al.* 1992). An inventory of the study area showed that these species represent 84.9% of all trees with height > 150 cm (Wittmann 1997). Two individuals of each species representative of average height, crown expansion and stem diameter were marked for continuous phenological recordings. They grew in similar positions with respect to flood duration and exposure to the sun.

Phenological recordings. Leaf shedding and flushing, flowering and fruiting were recorded between June 13, 1996 and September 10, 1996. To increase the objectivity of phenological binocular observations, the light transmitted through the crowns was measured twice weekly between 11:00 and 13:00, i.e., at the time of the highest sun position, with an integrating quantum photometer (Li-cor, Li 188b) at fixed horizontal positions on the tree stems below the canopy (90° to incident light). Control measurements of the absolute sun irradiation were performed on a fixed point outside the tree canopy. Calculations of the % transmittance were made using the formula:

$$\text{leaf amount on tree } xL = x_{present} - x_{min} / x_{max} - x_{min} * 100$$

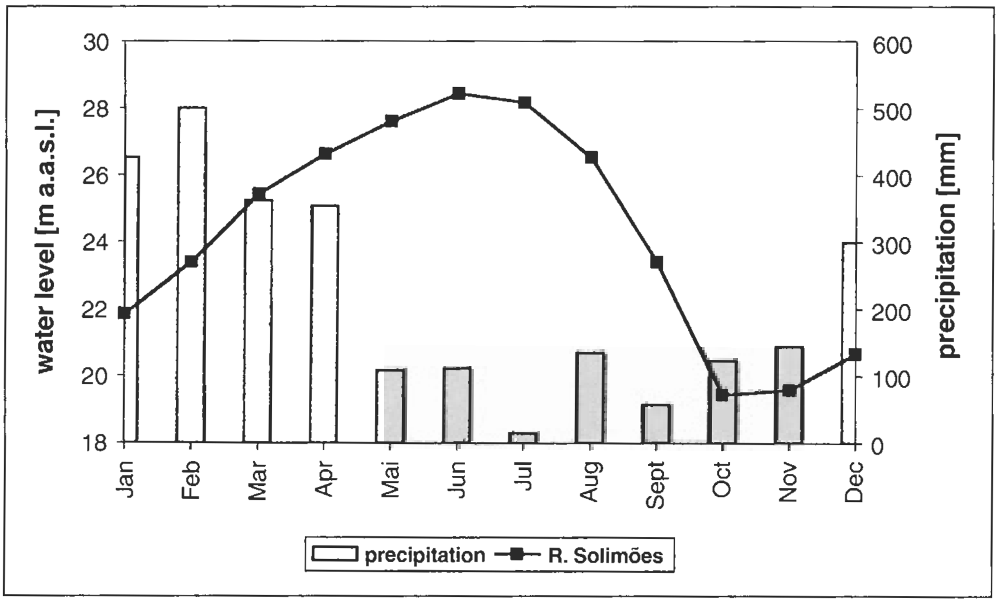

FIG. 1. Mean monthly precipitation and mean water level of the Amazon (Solimões) River in 1996, measured at Iranduba (20 km southwest of the study area). Sources: Embrapa, Manaus and Engenharia dos Portos, Manaus.

where $x_{present}$ is the irradiation measured currently, x_{min} is the lowest (0–20%), and x_{max} is the highest (80–100%) irradiation measured in the study period (Wittmann 1997).

Additionally, leaf amount was estimated twice weekly from May 1996 with the aid of binoculars (Fournier 1974, Augspurger 1983). Quantitative measurements of leaf fall and fruit production were performed with leaf traps.

Five leaf traps of 1 m^2 were placed below one individual per species and emptied twice weekly. Mean area of the leaves in the traps was determined with a leaf area meter (ΔT Area Meter, Delta-T Devices) every month. The fruits were counted.

RESULTS

Leaf phenology. Cecropia latiloba and *Laetia corymbulosa* lost up to 40% of their leaves, *Nectandra amazonum, Psidium acutangulum*, and *Vitex cymosa* lost up to 90%, and *Pseudobombax munguba* lost 100% of its leaves during the aquatic phase (Fig. 2).

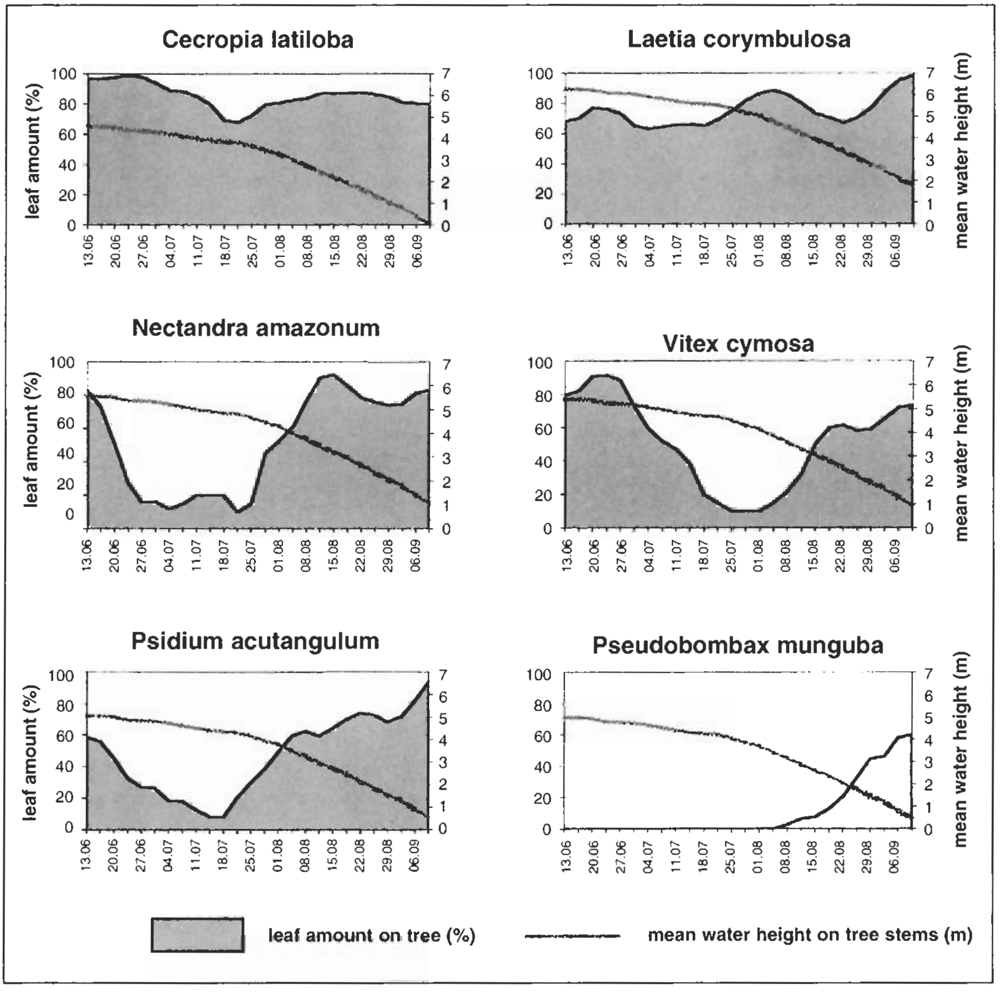

FIG. 2. Leaf amount on the trees, estimated in the study period, with mean water height measured on the tree stems.

Although in all species leaves were shed in the period of highest or decreasing water levels (Fig. 3), the timing and duration of the periods of lowest leaf amount were not always congruent with the aquatic phase. Leaf shedding started between 4 and 16 weeks after the start of flooding (Fig. 4). New leaves were flushed 4 to 14 weeks before the end of flooding.

Flowering phenology. Cecropia latiloba, Laetia corymbulosa, Nectandra amazonum, and *Pseudobombax munguba* flowered in the terrestrial phase, or at the beginning of the aquatic phase, long before the highest water levels (Fig. 4). *Psidium acutangulum* and *Vitex cymosa* flowered in the aquatic phase, during or after the highest water levels.

Fruiting phenology. All species started to produce fruits in the aquatic phase (Fig. 4). In *Laetia corymbulosa* and *Psidium acutangulum*, fruit maturation ended long before the period of highest water levels.

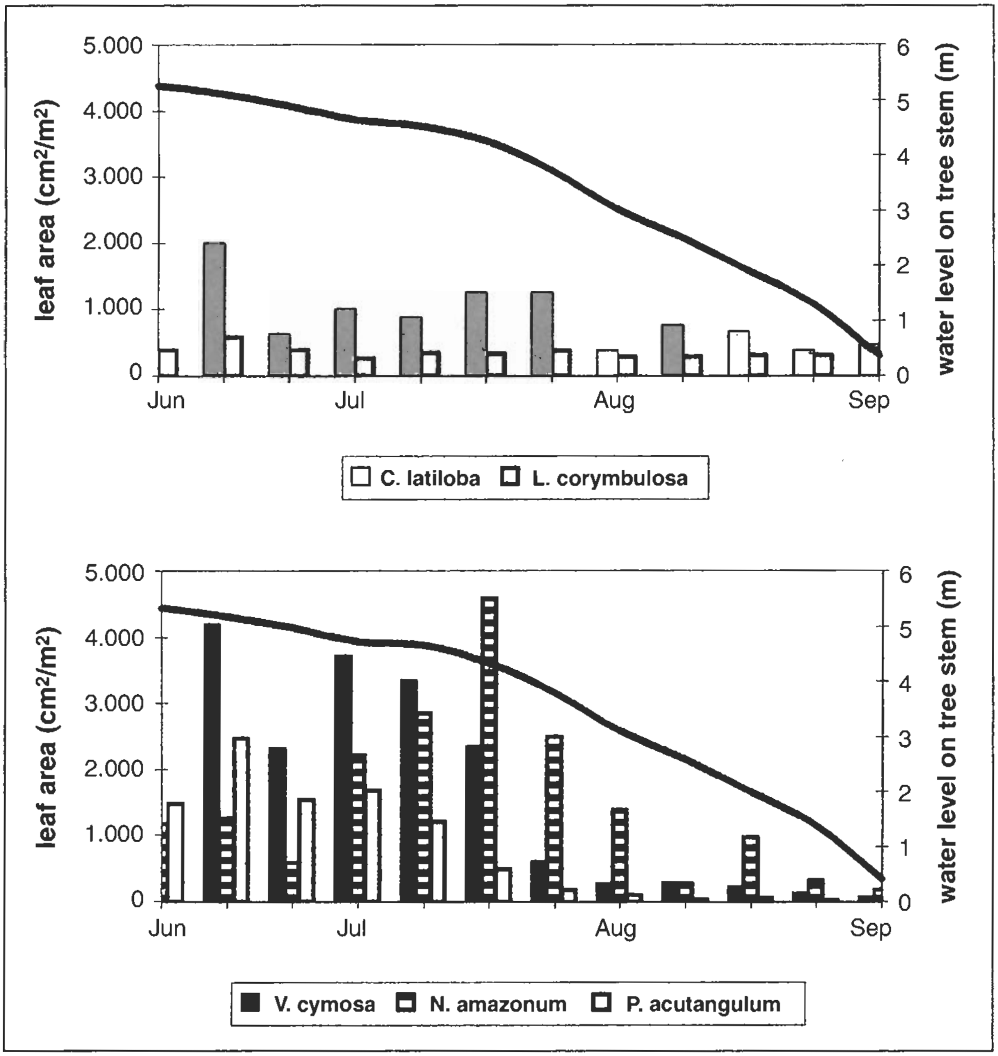

FIG. 3. Leaf area (cm^2 m^{-2}) of leaves collected in five leaf traps of 1 m^2 each in the study period. Data for *Pseudobombax munguba* are missing because it had no leaves.

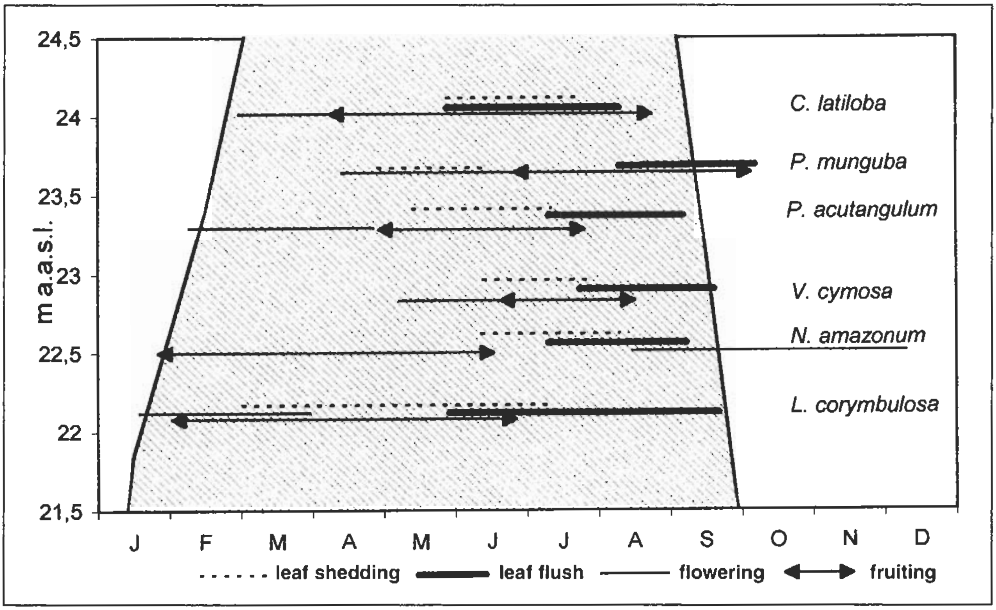

FIG. 4. Phenological behavior of the investigated tree species, with position of the trees in the flood gradient (m above sea-level) and resulting duration of the flooded period. Flowering data of *Pseudobombax munguba* from Worbes 1997, *Vitex cymosa* and *Nectandra amazonum* from Parolin 1997. Fruiting data of *Cecropia latiloba* and *Vitex cymosa* from Parolin 1997.

In the other species, fruit maturation, as monitored with the 1 m^2 traps, also occurred during the aquatic phase or (in *Vitex cymosa*) towards the beginning of the terrestrial phase (Fig. 5).

DISCUSSION

This study shows that there is a period of decreased physiological activity as expressed by leaf loss during the aquatic phase. This might lead to the well documented formation of annual increment rings in the wood (Worbes 1989). On the other hand, timing of leaf shedding and of leaf flush, and duration of the leafless period, were not directly related to the time of the highest water level. Most species kept their leaves for several months, the water column on the stems reaching up to a height of 6 m without visible phenological changes. Leaf flush, flowering and fruiting occurred even several weeks to months before the end of the aquatic phase.

The analyses of phenological events along a transect with different flooding duration showed that the flooding water was not necessarily the trigger (Ferreira 1991). The present data set is not sufficient to supply evidence for the relationship between flooding and phenology. Possible triggers and endogenic rhythms could be analyzed by experiments, e.g., transplantation of plants to other positions in the flooding gradient or to non-flooded terra firme. Also, different years with differing precipitation and river level regimes should be compared. The existing database, also in the literature, for such analyses is still very small for any várzea species.

The results of this study sugget that flooding did not represent a stress factor leading to complete stagnation of all activities as postulated by Gessner's 'physiological winter'. The interruption of the vegetation period was limited to a small part of the aquatic phase, and there was high activity in the other months. All species had their strongest leaf flush, flowering and fruiting in this period. The typical endogenic rhythms of phenological sequences in tropical trees of non-flooded forests, *leaf fall ⇒ flowering ⇒ flushing* (Borchert 1991), were not altered by flood stress in the species analyzed. Among tho-

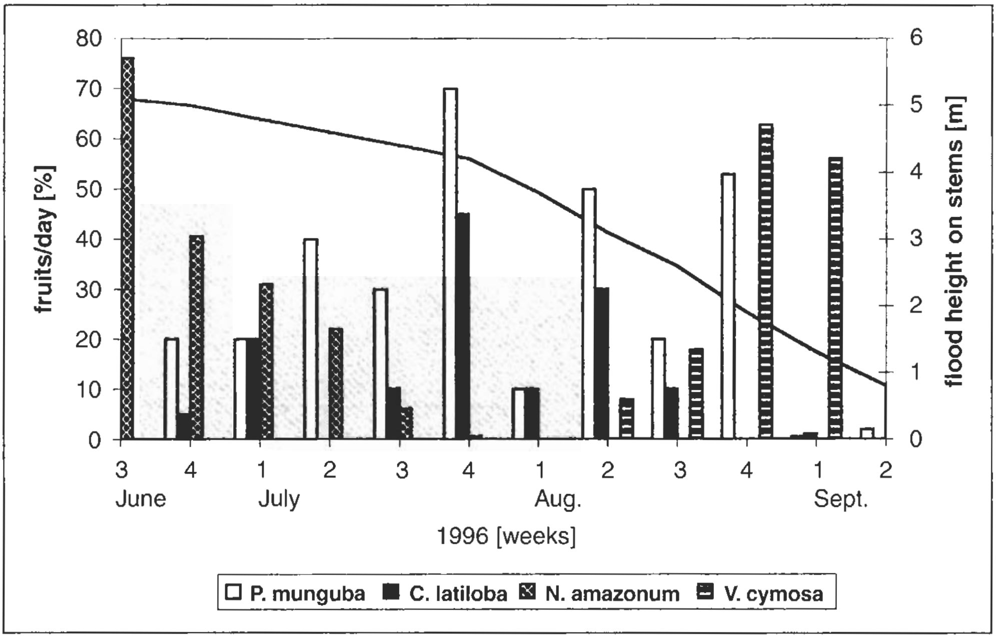

FIG. 5. Number of fruits in the traps (1 m^2) in the study period, with mean water height measured on the tree stems.

se species, there is the 'steady-state' strategy (*Psidium acutangulum*), where few flowers are produced for a long period of time, as well as the 'mass flowering' strategy (*Vitex cymosa*), where flowering occurs only for a short duration but with high numbers of flowers (Frankie *et al.* 1974, Newstrom *et al.* 1994). The dominance of one or other of these strategies has been related to the occurrence and competition of potential pollinators (Ziburski 1991) and is not primarily dependent on the annual flooding. With regard to dispersal, there are strong links between flooding and phenological events of tree species in várzea. Most species of the floodplains are hydrochoric and/or ichthyochoric. Dispersal strategies may have selected for the correlation between fruit maturation and highest water levels (Ziburski 1991). In fact, most diaspores have special adaptations which enhance buoyancy for hydrochoric dispersal (Kubitzki & Ziburski 1994), or are important in the diets of fish (Goulding 1980, Waldhoff *et al.* 1996). The long periods of regular, predictable flooding ('flood pulse concept', Junk *et al.* 1989) appear to have resulted in a variety of growth strategies in Central Amazonian várzea forests.

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