SEASONAL CHANGES OF PHENOLOGY AND PHOTOSYNTHETIC CO_2-ASSIMILATION OF TREES IN CENTRAL AMAZONIAN FLOODPLAINS

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Abstract

In Central Amazonian floodplains (várzea), trees are subjected to periodic flooding. The present study describes seasonal variation of phenology and photosynthetic CO_2-assimilation in relation to flooding in six tree species with different growth strategies. Under flooding, leaf senescence increased and photosynthetic assimilation declined. Before the end of flooding, new leaves were flushed and CO_2-assimilation rose to values which are comparable to the dry phase over a considerable part of the aquatic phase. No trends were observed relating to different growth strategies in response to periodic flooding.

Key words: *Amazon, flooding stress, floodplains, growth strategy, phenology, photosynthesis, waterlogging*

Resumo

Nas áreas inundáveis de várzea da Amazônia Central as árvores estão sujeitas a inundação periódica. O presente estudo descreve a variação da fenologia e assimilação fotossintética com respeito a inundação em seis espécies de árvores com diferentes estratégias de crescimento. Sob inundação, a senescência das folhas aumentou e a taxa de assimilação fotossintética diminuiu. Antes do fim da inundação, brotaram folhas novas e a taxa de assimilação subiu atingindo valores comparáveis ao período não inundado. O pa-

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pel das diferentes estratégias de crescimento parece ter pouca importância nas respostas à inundação periódica

Introduction

In seasonal várzea forests, the nutrient rich white water floodplains of the Amazon and its tributaries, trees are subjected to periods of flooding of up to seven months a year (Junk 1989). Water levels can reach 8 m on the tree (Figure 1), submerging seedlings and small trees. Tall, adult trees, or trees standing on higher levels in the flooding gradient, suffer inundation of the roots and parts of the stems which causes a lack of oxygen in the rhizosphere which affects tree growth (Figure 2). Gessner (1968) compared the growth conditions in the aquatic phase with temperate winters and introduced the term "physiological winter", indicating that the active period is the dry phase only. Leaf fall and reductions of growth and metabolic activity which he observed in the aquatic phase led him to the assumption that trees in floodplains reduce their activity like trees of temperate forests in the period of unfavourable conditions. In fact, most tree species in Central Amazonian floodplains form annual growth rings as a consequence of regular growth reductions (Worbes 1989). Physiological, anatomical and morphological alterations, e.g. root formation and function, leaf respiration, leaf metabolite and chlorophyll content, water potential and photosynthetic O_2-production are induced by flooding in várzea species (Meyer 1991, Parolin 1997, Schlüter 1989, Schlüter & Furch 1992, Schlüter *et al.* 1993, Scholander & Perez 1968). There is a seasonal variation of the metabolic activity in adult trees which seems to be linked to the periodicity of leaf fall and the production of new leaves (Parolin 2000, Piedade *et al.* in press). Trees shed their leaves and reduce the production of new leaves in the period of unfavourable hydric conditions (Wittmann & Parolin 1999). Leaves are shed to reduce the transpirational surface, an adaptation which regulates tree water status and reduces both drought and flood stress (Borchert 1994, Medina 1983). Tree growth is then reduced leading to the formation of growth rings (Worbes 1989). When tree water status has recovered, new leaves can be flushed and tree growth restarts (Borchert 1994). Photosynthetic CO_2-assimilation is a direct expression of the metabolic activity of a tree. Reductions are caused by leaf senescence, nutrient supply and environmental factors, as e.g. flooding (Pezeshki 1993, Pezeshki *et al.* 1996, Sesták 1985).

The aim of the present study was to describe the patterns of vegetative phenology and photosynthetic CO_2-assimilation. The main question was: does the aquatic phase represent an unfavourable period which is comparable to the temperate winter as postulated by Gessner? The present study tried also to consider the role of different growth strategies by comparing species which are typical pioneers and non-pioneers (*sensu* Swaine & Whitmore 1988), and which are evergreen and deciduous. It was aimed to answer the question whether species with different growth strategies reacted to the flooded period with similar changes of photosynthetic activity.

Methods

The study was carried out in the whitewater floodplains in the vicinity of Manaus, Brazil. The floodplain forests of these sites are situated between 21 and 27 m above sea level and are subjected to a maximum high water level of 8 m, corresponding to a mean period of inundation of up to seven months per year (Junk 1989). Seasonal rainfall from December to May is followed by a dry season from June to November (Figure 4). Three to four months after the onset of the rains, the water level of the rivers rises and reaches the highest peak in June at 28 ± m above sea level. The lowest level is reached in November at 18 ± m above sea level. The water level oscillation of approximately 10 m is very regular and predictable. The study period from April 1994 to June 1995 included one terrestrial and two aquatic phases. Six common tree species of the whitewater floodplains, with different growth strategies, were chosen for this study (Table 1). Vegetative phenology, i.e. the timing of leaf fall and of the production of new leaves, was monitored qualitatively every month in five chosen individuals per species all occurring on the same elevation in the flood gradient and of similar diameter at breast height (dbh), located randomly in the four study areas. A tree was called deciduous if it lost almost all the leaves and the remaining leaves were senescent. Evergreen trees were those which changed leaves continuously. Once a month, photosynthetic CO_2-uptake was measured between 9.00 and 12.00 a.m. with an infra-red gas analyser (IRGA, ADC LCA-2, Analytical Development Co. Ltd., Hoddesdon, Herts, UK) on five adult individuals of the six chosen tree species in the field. Ten fully expanded, non-flooded leaves of the marked individuals of each species were chosen for measurements at high quantum flux density, with photosynthetically active radiation (PFD) over 2000 µmol m^{-2} s^{-1} producing maximal rates of photosynthesis (A_{max}).

Results

Phenology

Leaf shedding and replacement occurred continuously in the evergreen species (*Cecropia latiloba*, *Senna reticulata* and *Nectandra amazonum*). In the deciduous species (*Crateva benthami*, *Tabebuia barbata* and *Vitex cymosa*), a short leafless period (4 weeks) followed pronounced leaf fall which lasted for two to three months in the period of highest water levels. The flush of new leaves started or occurred completely before the end of flooding in all species. The pioneer species (*Cecropia latiloba*, *Senna reticulata*) produced new leaves during the whole year, but leaf production was reduced for two to four months in the period of the highest water peak.

Photosynthetic CO_2-uptake

CO_2-uptake as an average was lower during the aquatic phase than in the non-flooded terrestrial phase in all species (Table 1, Figure 5). CO_2-uptake in the aquatic phase was around 10 % lower than in the terrestrial phase in the pioneer species, and between 20 and 50 % in the non-pioneer species. Only in *Cecropia latiloba* were the differences not statistically significant.

In all species mean CO_2-uptake remained high in the first one to four months of flooding, ranging from an average of 9.3 $\mu mol\ m^{-2}\ s^{-1}$ (*Nectandra amazonum*) to 20.0 $\mu mol\ m^{-2}\ s^{-1}$ (*Senna reticulata*). Maximum measured CO_2-uptake was 24.5 $\mu mol\ m^{-2}\ s^{-1}$ in *Senna reticulata*, minimum 3.2 $\mu mol\ m^{-2}\ s^{-1}$ in *Tabebuia barbata* and *Nectandra amazonum*. In the flooded period, mean CO_2-uptake declined by 8 % (*Senna reticulata*) to 49 % (*Vitex cymosa*) for some weeks to months, reaching mean values between of 7.6 $\mu mol\ m^{-2}\ s^{-1}$ (*Nectandra amazonum*) and 18.4 $\mu mol\ m^{-2}\ s^{-1}$ (*Senna reticulata*). In this period, deciduous trees shed their leaves. Mean CO_2-uptake rose again before the end of the aquatic phase reaching values which remained high through the terrestrial phase. With the onset of flooding, mean CO_2-uptake was reduced again after one to two months.

Discussion

The six chosen species showed characteristic seasonal variations of the vegetative phenology and photosynthetic CO_2-uptake which are summarized in Figure 6. The scheme represents the plasticity of photosynthetic activity of the six species during the annual cycle. In the aquatic phase, CO_2-uptake is high (a) in the first months of flooding, and is reduced after some months (b). In the second part of the aquatic phase, CO_2-uptake rises again (c) to levels which are comparable to those of the terrestrial phase, or even more elevated (d). This takes place before the end of flooding in all species. During the terrestrial phase, the range of photosynthetic assimilation is smaller again (e), and reductions (f) can occur which are probably related to water shortage in the driest months.

The seasonal changes of photosynthetic assimilation of the chosen species was closely related to leaf age and indirectly determined by flooding. With flooding of the roots, tree water status probably decreased, leaves were shed to reduce transpirational surface and water loss, and photosynthetic assimilation decreased as a consequence of lower photosynthetic capacity of senescent leaves (Sesták 1985). When new leaves were flushed, photosynthetic CO_2-uptake rose again although the roots were still flooded, and reached a maximum when the young leaves were fully expanded.

The aquatic phase represented an unfavourable period for the six tree species, as shown by the shedding of leaves, by the reduced production of new leaves, and by the reduction of photosynthetic assimilation during inundation. The terrestrial phase was the main vegetation period for the six species. Still, the aquatic phase cannot be considered as a "physiological winter" as postulated by Gessner (1968) since this implies a reduction of growth and metabolic activity which lasts for the whole unfavourable period. This is clearly not the case in the six species analysed in this study. The trees performed high photosynthetical assimilation in a considerable part of the aquatic phase, where values were reached that were comparable or even higher than those of the terrestrial phase. Furthermore, in the months where photosynthetic assimilation was reduced, most species produced flowers or fruits (Gottsberger 1978, Kubitzki & Ziburski 1994). The photosynthetic activity of the trees was high the whole year round, not only during the terrestrial phase. There was no period of rest or a reduced metabolic activity lasting for the whole aquatic period in the six chosen species.

The role of different growth strategies did not seem to be important concerning the reactions to flooding. Although pioneer species had less reductions of photosynthetic assimilation than non-pioneers when flooded, most seasonal changes did not show a pattern linked to the growth strategies. Most species of the várzea have morphological adaptations like advetitious roots, lenticels, or pressure ventilation (Graffmann 2000, Parolin 1998, Waldhoff *et al.* 1998), which allow them to maintain growth and photosynthetic activity at high levels also with waterlogging. The analyzed species of the floodplains do not show prolonged periods of rest. Even leaf-shedding species produced flowers and fruits in the 2-8 weeks in which they did not have leaves, so that in spite of flooding, physiological activity was high during the whole year. These species are not specialized on one hydric condition, but are adapted to the change between extreme hydric conditions. With this, they reflect the optimal compromise (sensu Stearns 1992) for a life in the periodical change between drought and prolonged flooding.

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Table 1: Species chosen for this study, with successional stage (*sensu* Swaine and Whitmore 1988) and phenological traits, and difference between the CO_2-uptake at maximal quantum flux density (A_{max}) in the terrestrial and the aquatic phase in percent, with F-ratio of the ANOVA and statistical probability p.

Species	**Successional stage**	**Phenology**	**Difference A_{max} [%]**	**F-ratio**	**p**
Cecropia latiloba (Cecropiaceae)	pioneer	evergreen	-10.5	2.21	n.s.
Senna reticulata (Caesalpiniaceae)	pioneer	evergreen	-7.8	18.07	***
Nectandra amazonum (Lauraceae)	non-pioneer	evergreen	-18.7	6.36	*
Crateva benthami (Capparidaceae)	non-pioneer	deciduous	-19.7	6.02	*
Tabebuia barbata (Bignoniaceae)	non-pioneer	deciduous	-21.9	13.38	**
Vitex cymosa (Verbenaceae)	non-pioneer	deciduous	-49.2	161.05	***

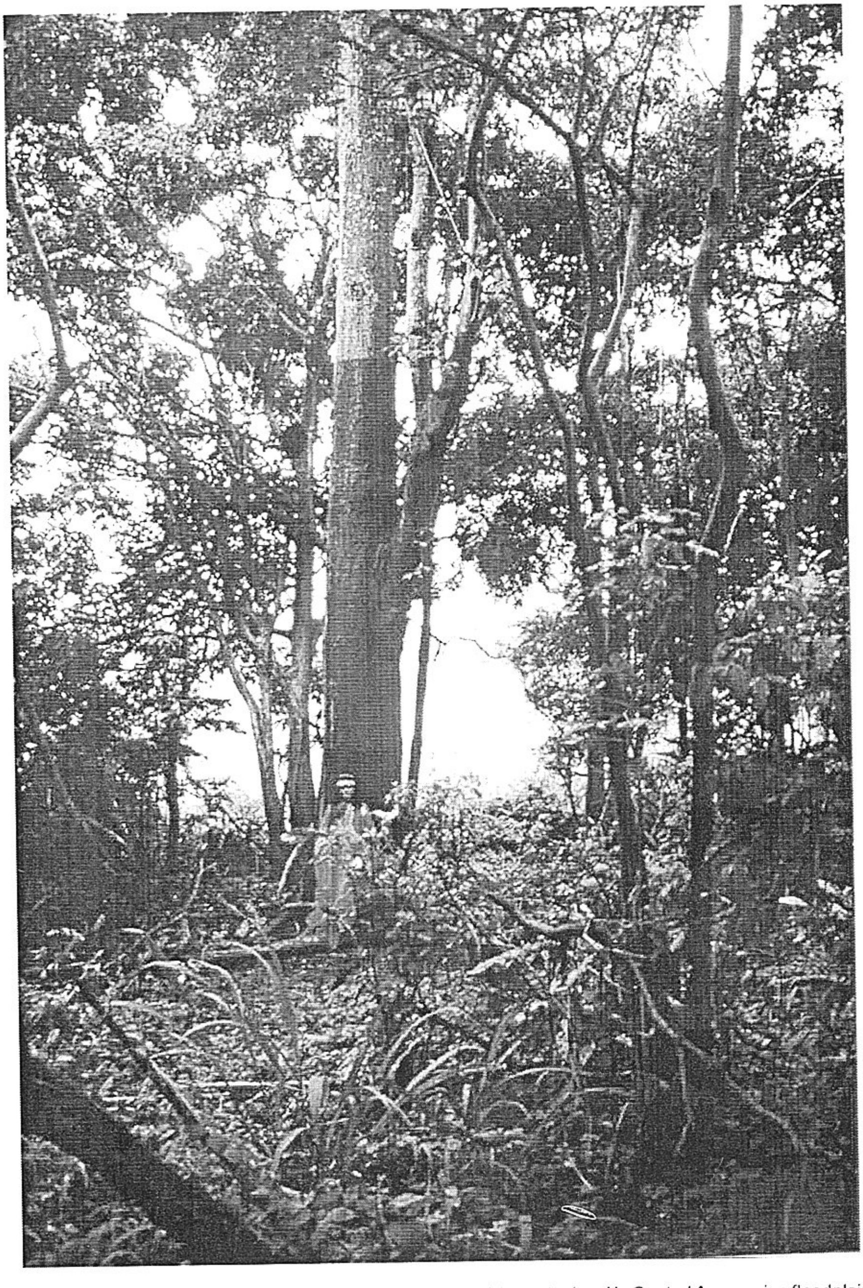

Figure 1: Photograph taken at low water illustrating the change of the water level in Central Amazonian floodplains: on the tree stem, the mark of the former year's high water level is visible. Behind, a small sidearm of the Amazon River.

Figure 2: Várzea forest in the flooded period (Ilha da Marchantaria).

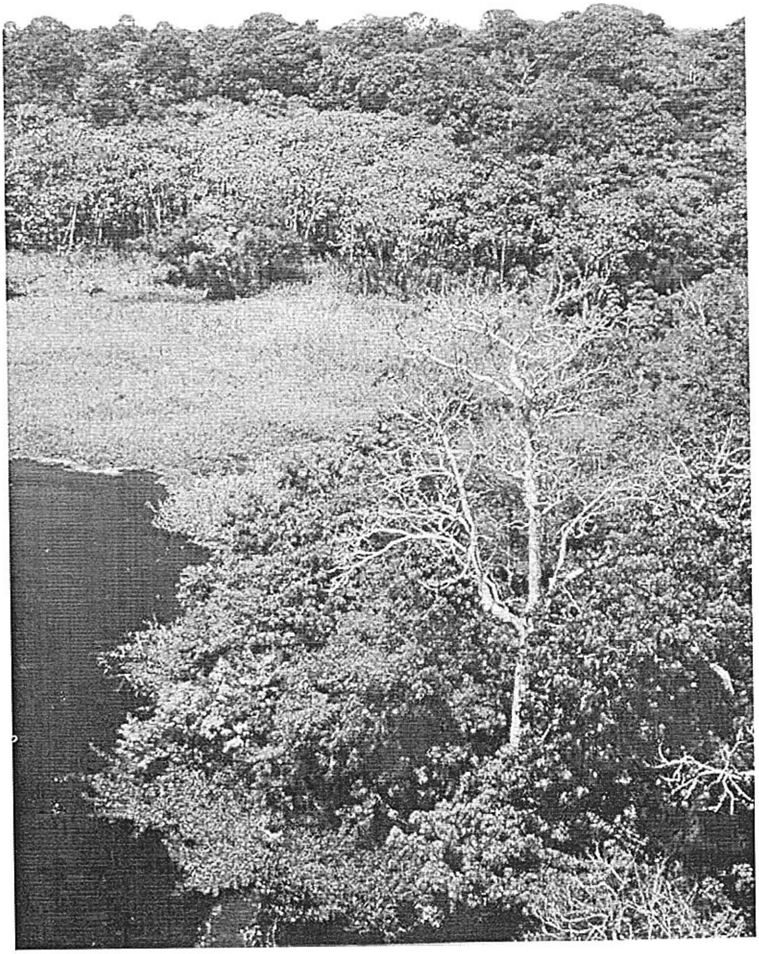

Figure 3: Várzea forest with the chosen species of different successional stages. On the forest border there is a monospecific stand of *Cecropia latiloba*, behind which grows a diverse forest with species of higher successional stages.

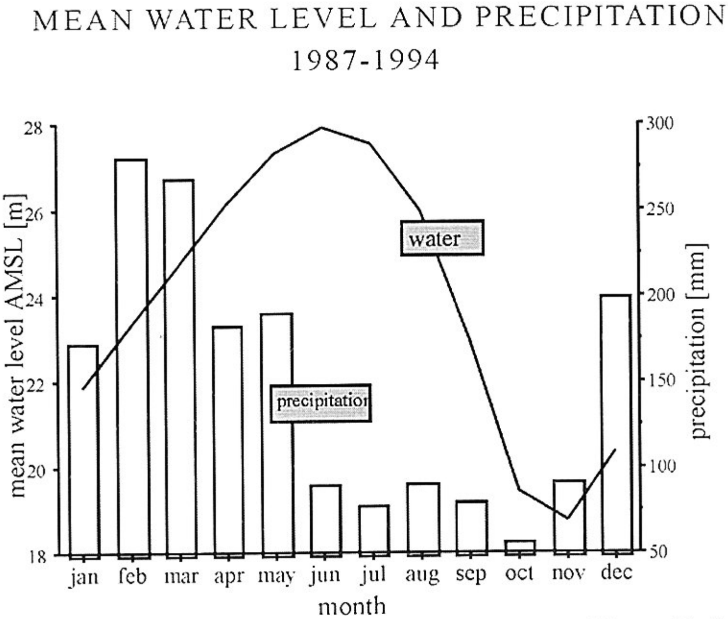

Figure 4: Mean monthly precipitation and mean river level measured at the harbour of Manaus (Rio Negro); average from 1987 to 1995.

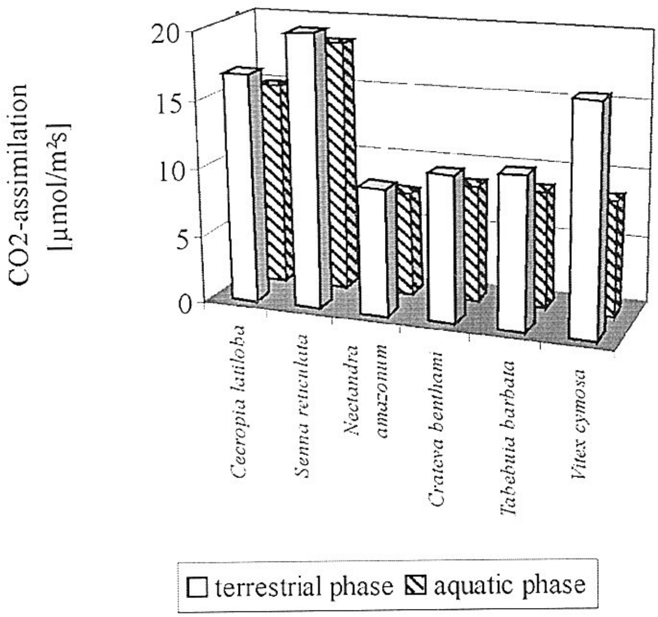

Figure 5: Mean CO2-uptake at maximum quantum flux density (Amax) in the six species during the terrestrial and the aquatic phase.

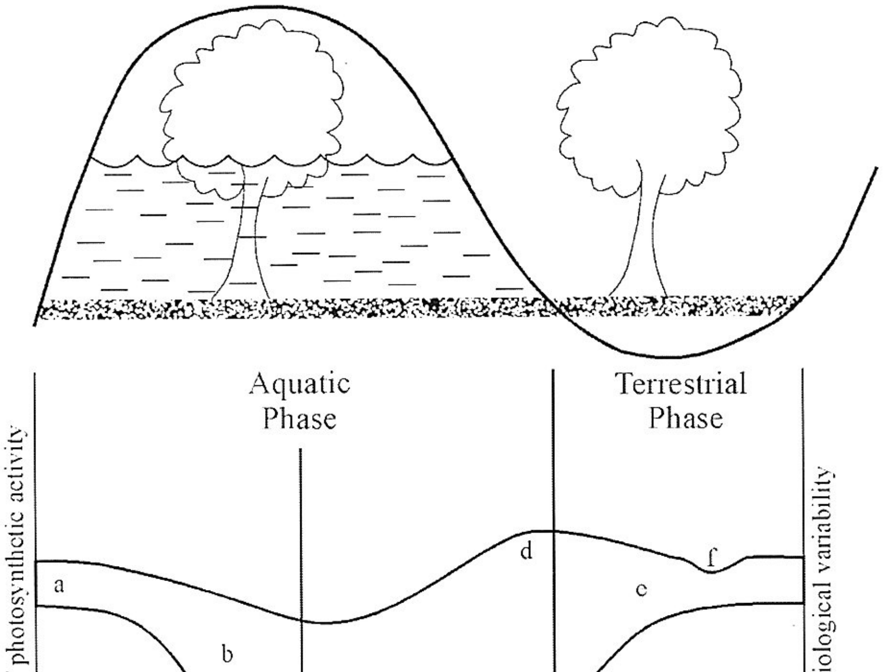

Figure 6: Schematic presentation of changes of photosynthetic CO2-uptake during the annual cycle in the six species (explanations see text).