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Gas exchange of six tree species from Central Amazonian floodplains

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Abstract: In Central Amazonian floodplain forests, trees are subjected to periodical flooding. The gas exchange behaviour of six tree species with different growth strategies was compared between the non-flooded and flooded period. Photosynthetic assimilation and quantum yields were 20-50% lower in the flooded period in non-pioneers, and 10-20% lower in pioneers. The photosynthetic activities reported here appear to be related to successional status and growth strategy. Stomatal conductance, Ci and Ci/Ca increased in all species when flooded. Leaf age changed from mainly adult leaves at the beginning of flooding, to mainly senescent leaves in the middle of the flooded period and to young leaves towards the end of flooding. The main factor responsible for the reductions of physiological activities in the flooded period is concluded to be leaf age, which indirectly is determined by flooding.

Resumen: En los bosques de planicie de inundación en la Amazonía central, los árboles están sometidos a inundaciones periódicas. Se comparó el comportamiento de intercambio de gases de seis especies de árboles con diferentes estrategias de crecimiento entre el periodo inundado y el no inundado. La asimilación fotosintética y los rendimientos cuánticos fueron 20-50% más bajos en el periodo de inundación en las no pioneras, y 10-20% más bajo en las pioneras. Las actividades fotosintéticas reportadas aquí parecen estar relacionadas con la situación sucesional y la estrategia de crecimiento. La conductancia estomática, Ci y Ci/Ca se incrementaron en todas las especies durante la inundación. La edad de las hojas cambió de ser principalmente hojas adultas al principio del periodo de inundación, a ser hojas predominantemente senescentes a la mitad de este periodo, a hojas jóvenes hacia el final de la inundación. Se concluye que el principal factor responsable de las reducciones en las actividades fisiológicas en el periodo de inundación es la edad de la hoja, la cual está determinada indirectamente por la inundación.

Resumo: Nas florestas alagadas de várzea da Amazónia central, as árvores são sujeitas a alagamento periódico. O comportamento das trocas gasosas de seis espécies arbóreas, com estratégias de crescimento distintas, foi comparado entre os períodos não alagados e alagados. A assimilação fotossintética e os quantum rendimentos eram 20-25% mais baixos nos períodos alagados nas espécies não pioneiras, e 10-20% mais baixos nas pioneiras. As actividades fotossintéticas descritas neste trabalho parecem estar relacionadas com o status da sucessão e as estratégias de crescimento. A condutância estomática, Ci e Ci/Ca aumentou em todas as espécies quando inundadas. A idade das folhas mudou de folhas principalmente adultas no início da inundação para folhas principalmente senescentes a meio do período de inundação e, seguidamente, para folhas juvenis para o fim da inundação. Foi concluído que o fator principal responsável pelas reduções das actividades fisiológicas no período de inundação é a idade da folha, o que é, indiretamente, determinada pelo alagamento.

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Key words: Floodplain forest, flood stress, growth strategy, photosynthetic CO_2 assimilation, successional status, várzea.

Introduction

In Central Amazonian floodplain forests (*várzea*), the water level of the rivers rises up to 10 m every year and the trees are subjected to periodical flooding (Junk 1989). In the flooded period, water covers the roots and stems of the trees for up to 230 days a year causing a lack of oxygen in the rhizosphere which influences growth and gas exchange (Joly & Crawford 1982). Physiological activities and reactions to flooding are related to different ecological, morphological and phenological traits of the species (Bazzaz & Pickett 1980; Bazzaz 1991; Bazzaz & Miao 1993; Huc *et al.* 1994; Raaimakers *et al.* 1995; Reich *et al.* 1999). Although some studies of the metabolic activities of trees in Central Amazonian floodplain forests have been performed, most concern seedlings under controlled conditions (Meyer 1991; Parolin 1998; Schlüter 1989; Schlüter & Furch 1992; Schlüter *et al.* 1993; Waldhoff *et al.* 1998, Parolin in press). Little is known about photosynthetic CO_2 assimilation of adult trees in the field, and about the behaviour of species with different growth strategies (Parolin 1999; Parolin 2000; Piedade *et al.* 2000). In this study, we aimed to compare gas exchange behaviour of adult trees *in situ*, in the non-flooded and flooded period in Central Amazonian floodplains. Measurements were performed on six common tree species which cover a wide range of growth strategies. They represent different ecological traits related to successional status (pioneer/non-pioneer sensu Swaine & Whitmore 1988), leaf morphology (leaf form and size), and phenology (deciduous/ evergreen). The relationships between photosynthetic assimilation and stomatal conductance in relation to phenological and morphological traits, successional status and flooding seasonality were investigated.

Methods

The study sites lie on the Costa do Catalão and the Ilha da Marchantaria, a river island 15 km upstream from the confluence of Rio Amazonas and Rio Negro (3°15′ S, 59°58′ W), in nutrient rich white-water floodplains in the vicinity of Manaus/Brazil.

Seasonal rainfall occurs on a regular basis, with a marked dry season between June and September, and a rainy season from December to May. Mean annual rainfall ranges from 1700 to 2300 mm, and mean monthly temperature lies between 26.3°C and 27.2°C. Variation of the river water levels is markedly seasonal. The rising phase is between late December and early July, while the draining period lasts from the end of July to the end of November. During the high water period, most deciduous trees lose their leaves. Measurements for this study were made from April 1994 to June 1995.

The study species were *Cecropia latiloba* Miq. (Cecropiaceae, "Embaúba", evergreen pioneer), *Senna reticulata* Willd. (Irwin & Barn) (Caesalpiniaceae, "Matapasto", evergreen pioneer), *Nectandra amazonum* Nees (Lauraceae, "Louro", evergreen non-pioneer), *Crateva benthami* Eichl. in Mart. (Capparidaceae, "Catoré", deciduous non-pioneer), *Tabebuia barbata* E. Mey. (Bignoniaceae, "Capitarí", deciduous non-pioneer) and *Vitex cymosa* Benth. (Verbenaceae, "Taruma", deciduous non-pioneer) (Table 1). All chosen species are common in Central Amazonian whitewater floodplains and are typical representatives of different growth strategies (Prance 1979; Worbes *et al.* 1992).

The chosen trees were situated at a height of 18-21 m asl in the flooding gradient, which corresponds to flood durations of 4 (*Senna reticulata*) to 8 (*Cecropia latiloba*) months (Junk 1989). The chosen individuals were maximum 20 m from the river margin when it is at its lowest level. Only adult trees were chosen, with heights between 6 m (*Senna reticulata*) and 10-15 m. At high water, the stems were flooded up to 6 m high (except for *Senna reticulata*, which grows only on higher levels in the flooding gradient and was flooded up to 5 m). The tree crowns were not or only partially submerged.

Table 1. Species analysed in this study: characteristics of the leaves. Data are means of the whole study period (with standard deviation; for each species n=225).

Species	Successional stage	Phenology	Leaf form	Leaf area (cm^2)	Leaf dry mass (g)	Specific leaf area (cm^2g^{-1})
Cecropia latiloba	pioneer	evergreen	simple	1080.0±121	6.9 ± 1.5	144.6 ± 32
Senna reticulata	pioneer	evergreen	compound	659.9±314	3.5 ± 1.1	199 ± 37
Nectandra amazonum	non-pioneer	evergreen	simple	46.4± 6	0.6 ± 0.1	84.1 ± 12
Crateva benthami	non-pioneer	deciduous	compound	171.7±55	1.5 ± 0.9	101.9 ± 49
Tabebuia barbata	non-pioneer	deciduous	compound	309.3± 74	2.8 ± 1.1	111.1 ± 45
Vitex cymosa	non-pioneer	deciduous	compound	239.5± 64	2.6 ± 1.1	112.6 ± 23

For measurements of photosynthetic CO_2-uptake, fully exposed non-flooded sun leaves from each of five individuals per species were taken. Access to the leaves in the high water period was by boat, and during the low water period by wooden towers and ladders. Gas exchange was measured with an infra-red gas analyser (IRGA, ADC LCA-2, Analytical Development Co. Ltd., Hoddesdon, Herts, UK). Every month, 10-50 fully expanded, not flooded leaves of five marked adult individuals of each of the six species were chosen for measurements at high quantum flux density, with photon flux density (PPFD) reaching 2000 µmol $m^{-2}s^{-1}$. Light response curves were measured on 2-3 leaves every month. Irradiance incidence for light response measurements was controlled with neutral filters. CO_2 assimilation, stomatal conductance and internal CO_2 concentrations were calculated according to Coombs *et al.* (1985).

Table 2. Absolute maximum CO_2 assimilation (µmol CO_2 $m^{-2}s^{-1}$) measured under high light conditions (PPFD at 2000 µmol m^{-2} s^{-1}) in the non-flooded and flooded period in the six chosen species (EP evergreen pioneer, ENP evergreen non-pioneer, DNP deciduous non-pioneer).

Species	Success-ional stage	Maximum CO_2 assimilation: non-flooded	Maximum CO_2 assimilation: flooded
Cecropia latiloba	EP	21,0	17,9
Senna reticulata	EP	24,5	20,9
Nectandra amazonum	ENP	14,4	12,9
Crateva benthami	DNP	22,0	11,2
Tabebuia barbata	DNP	15,1	12,9
Vitex cymosa	DNP	19,6	16,3

Results

Photosynthetic assimilation - Photosynthetic CO_2 assimilation at high photon flux density, in the non-flooded terrestrial phase, ranged from a mean of 9.3 µmol m^{-2} s^{-1} for *Nectandra amazonum* (evergreen non-pioneer) to a mean of 20.0 µmol m^{-2} s^{-1} for *Senna reticulata* (evergreen pioneer). Absolute maxima for CO_2 assimilation measured under high light conditions were always higher in the non-flooded period than in the flooded period (Table 2).

In the flooded period, photosynthetic activities were lower in all species; in most cases the differences were highly statistically significant (Table 3). Mean photosynthetic activities of the four non-pioneers were reduced by 20-50% when flooded, compared to less than 10% in the two pioneer species. In the flooded period, photosynthetic assimilation was lower and covered a wider range, as shown by the photosynthetic light responses (Fig. 1a, b). Calculated quantum yields (Fig. 2a, b; Table 4) in the flooded period were 20-50% lower in the non-pioneers. The pioneers had 2-5% higher quantum yields when flooded.

Mean stomatal conductance (gs) increased between 5 and 35% in all species when flooded (Table 5). Mean ratio of intercellular CO_2 concentrations to CO_2 concentrations in the cuvette (Ci/Ca) also increased with flooding in all species (Table 5). Calculated mean intercellular CO_2 concentrations (Ci) increased with flooding in all species except *Cecropia latiloba* (evergreen pioneer) and *Crateva benthami* (deciduous non-pioneer) (Table 5).

Table 3. Photosynthetic assimilation under high light conditions (PPFD at 2000 µmol m^{-2} s^{-1}). Mean CO_2 assimilation (µmol m^{-2} s^{-1}) and standard deviation in the non-flooded and flooded period, differences in percent (non-flooded period = 100%), ANOVA F-ratio and probability p. Sample size = 80. EP evergreen pioneer, ENP evergreen non-pioneer, DNP deciduous non-pioneer.

Species	Successional stage	Mean CO_2 assimilation: non-flooded	Mean CO_2 assimilation: flooded	Difference (%)	F-ratio	p
Cecropia latiloba	EP	16.8 ± 1.5	15.0 ± 4.6	-10.5	2.21	n.s.
Senna reticulata	EP	20.0 ± 4.0	18.4 ± 4.3	-7.8	18.07	***
Nectandra amazonum	ENP	9.3 ± 2.4	7.6 ± 3.1	-18.7	6.36	*
Crateva benthami	DNP	10.7 ± 4.8	8.6 ± 1.0	-19.7	6.02	*
Tabebuia barbata	DNP	11.1 ± 2.3	8.6 ± 2.6	-21.9	13.38	**
Vitex cymosa	DNP	16.6 ± 1.5	8.4 ± 2.2	-49.2	161.05	***

Table 4. Quantum yield of the six species in the non-flooded and flooded period. Mean quantum yield (mol O_2 per mol quants) and difference between the non-flooded and flooded period in percent. EP evergreen pioneer, ENP evergreen non-pioneer, DNP deciduous non-pioneer.

Species	Successional stage	Mean quantum yield: non-flooded	Mean quantum yield: flooded	Difference [%]
Cecropia latiloba	EP	0.036	0.038	4.5
Senna reticulata	EP	0.029	0.030	2.2
Nectandra amazonum	ENP	0.018	0.014	-18.9
Crateva benthami	DNP	0.049	0.025	-49.3
Tabebuia barbata	DNP	0.029	0.018	-39.2
Vitex cymosa	DNP	0.018	0.011	-35.6

Table 5. Summary of gas exchange responses: stomatal conductance (gs), ratio of intercellular CO_2 concentrations to CO_2 concentrations in the cuvette (Ci/Ca), and calculated intercellular CO_2 concentrations. Means, standard deviation and difference between the non-flooded and flooded period in percent. n=80.

Species	gs (m mol $m^2 s^{-1}$)			Ci/Ca			Ci (µ mol mol^{-1})		
	Non-flooded	Flooded	Difference (%)	Non-flooded	Flooded	Difference (%)	Non-flooded	Flooded	Difference (%)
Cecropia latiloba	331 ± 65	382 ± 128	14.7	0.66 ± 0.02	0.69 ± 0.09	4.5	272 ± 27	262 ± 34	-3.7
Senna reticulata	402 ± 81	422 ± 137	5.0	0.61 ± 0.07	0.67 ± 0.07	9.8	231 ± 34	253 ± 29	9.5
Nectandra amazonum	209 ± 105	225 ± 114	7.3	0.71 ± 0.06	0.77 ± 0.07	8.5	281 ± 40	284 ± 24	1.1
Crateva benthami	232 ± 132	314 ± 105	35.2	0.67 ± 0.12	0.65 ± 0.18	-2.9	259 ± 42	240 ± 60	-7.3
Tabebuia barbata	186 ± 66	223 ± 104	19.8	0.62 ± 0.10	0.74 ± 0.05	19.4	240 ± 39	278 ± 21	15.8
Vitex cymosa	289 ± 56	289 ± 121	-0.1	0.60 ± 0.01	0.79 ± 0.07	31.7	230 ± 7	302 ± 26	31.3

Leaf area - Leaf area and specific leaf area of the total leaf and of the lamina were highest in the two pioneer species, and lowest in the evergreen non-pioneer *Nectandra amazonum* (Table 1).

Vegetative phenology - The two evergreen pioneer species produced new leaves continuously, but leaf production was decreased in the period of highest water levels. While in the non-flooded period senescent leaves represented only a very small percentage of total foliage, in the flooded period the proportion of old leaves was higher. After the reduction of leaf production, a strong flush was observed towards the end of flooding. This was similar in the four non-pioneers, including the evergreen *Nectandra amazonum*. The main period of leaf production was at the end of the flooded

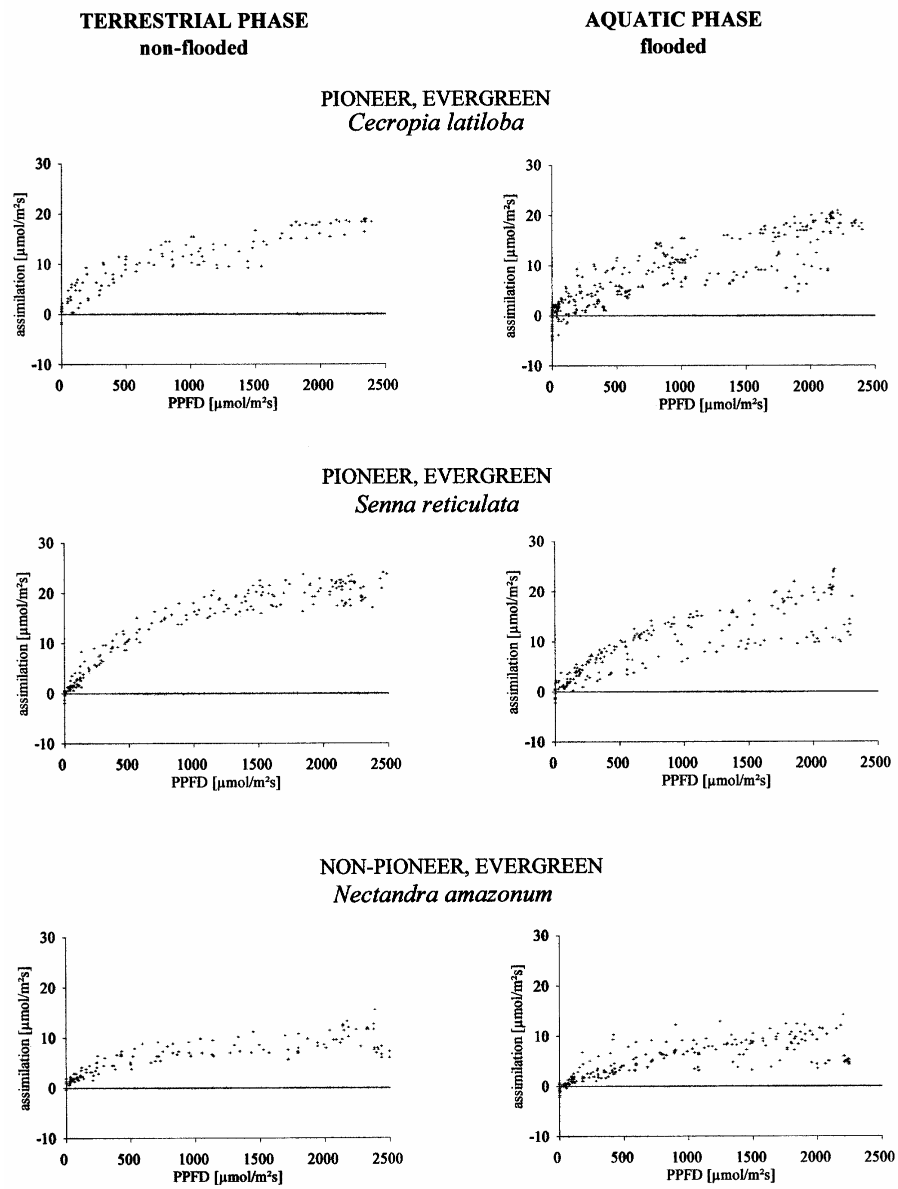

Fig. 1(a). Measured data points during 15 months of recording: Photosynthetic assimilation (A) as a function of photon flux density in the non-flooded terrestrial and flooded aquatic phase for the six analysed species. *Cecropia latiloba, Senna reticulata* and *Nectandra amazonum*.

phase. Leaf age changed from adult leaves at the beginning of flooding, to mainly senescent leaves in the middle of the flooded period and to young leaves towards the end of flooding. In the non-flooded period, adult leaves predominated.

Discussion

The photosynthetic patterns reported here appear to be related to successional status and growth strategy. Other studies report that early successional rain forest trees have mean photosynthetic assimilation of 8.8-27.7 µmol $m^{-2}s^{-1}$, compared

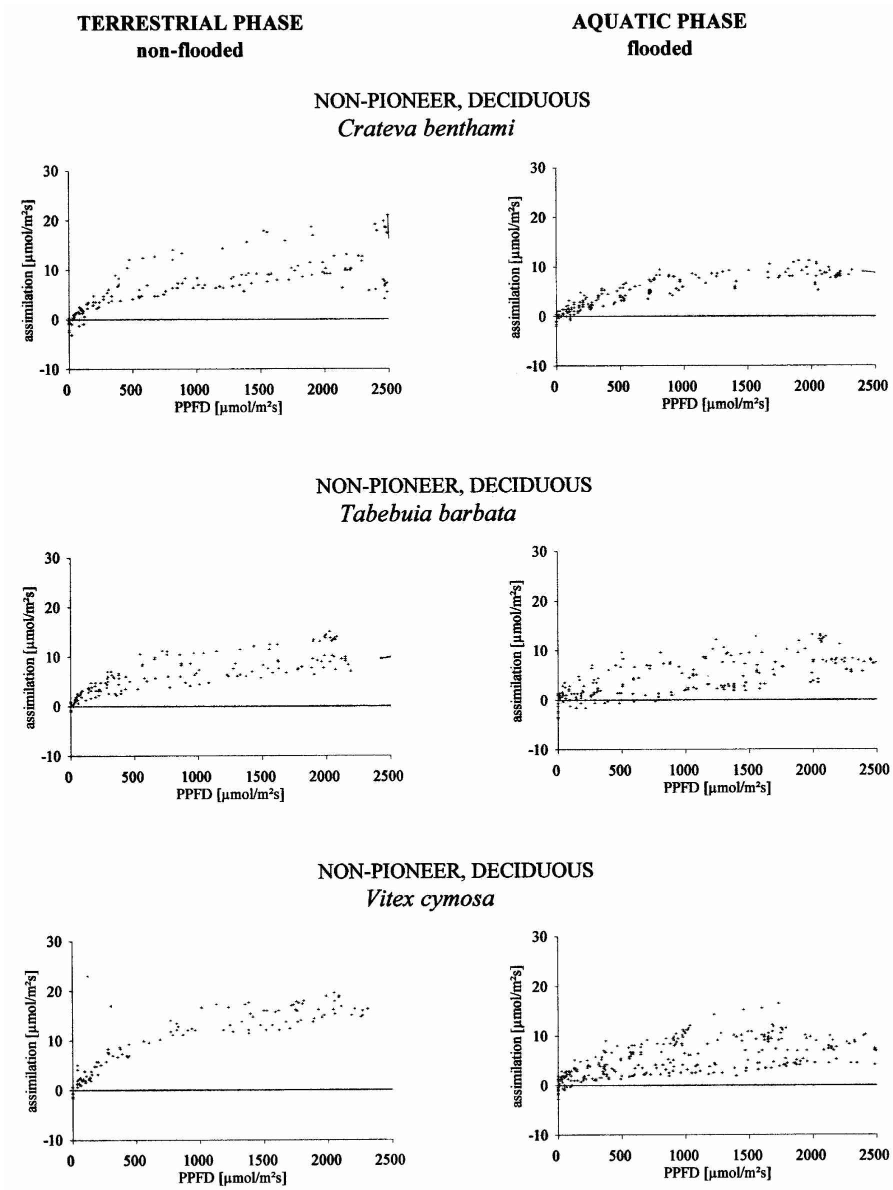

Fig. 1(b). Measured data points during 15 months of recording: Photosynthetic assimilation (A) as a function of photon flux density in the non-flooded terrestrial and flooded aquatic phase for the six analysed species. *Crateva benthami, Tabebuia barbata* and *Vitex cymosa*.

to 4.4-11.3 µmol m^{-2} s^{-1} in late successional canopy
trees (Bazzaz 1991; Bazzaz & Pickett 1980; Mooney *et al.* 1980; Oberbauer & Strain 1984). The data of this study fit this trend, the pioneer species having higher maximum photosynthetic rates than the non-pioneers. On the other hand, it is evident that a clear separation of two successional groups is difficult. In the non-flooded period, *Vitex cymosa* had similar mean photosynthetic assimilation (16.6 µmol m^{-2} s^{-1}) as the pioneer species, indicating a continuum between the two groups. This continuum is less visible in the flooded period, where differences between the assimilation of pioneers and non-pioneers are more distinct (pioneers 15.0-18.4 µmol m^{-2} s^{-1}, non-

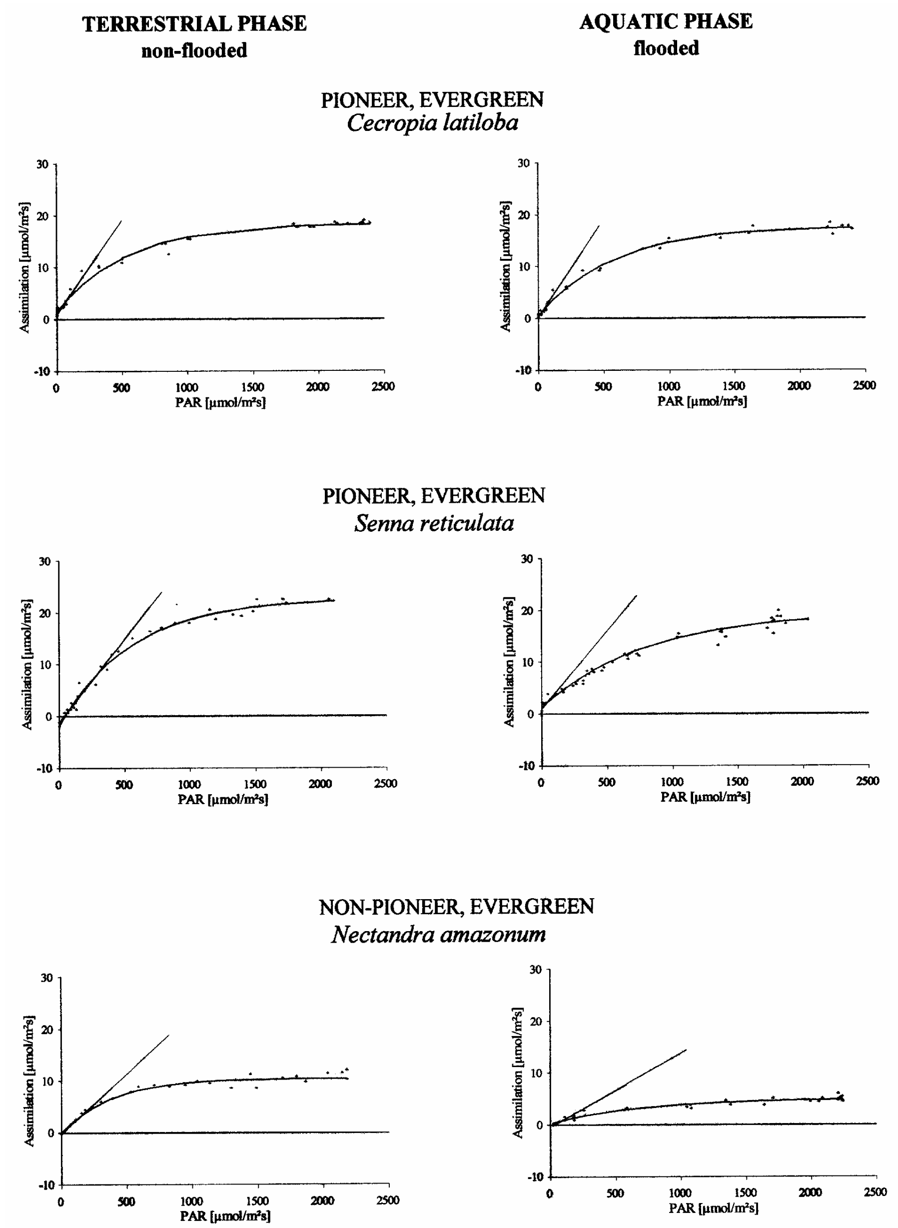

Fig. 2(a). Photosynthetic light response curves and quantum yield: selected curves of the non-flooded terrestrial and flooded aquatic phase for the six analysed species. The light response curves were measured 2-4 months after the onset of the draining or flooding period, i.e. at a minimum of 2 and a maximum of 4 months after the start of the terrestrial or aquatic phase, respectively. *Cecropia latiloba, Senna reticulata* and *Nectandra amazonum*.

pioneers 7.6-8.6 µmol m^{-2} s^{-1}). The same is true for quantum yield and stomatal conductance, where decreases in the flooded period were smaller in the pioneers than in the non-pioneers, emphasizing the gap between the two groups. No such pattern could be found for intercellular CO_2 concentrations and for the ratio of intercellular CO_2 concentrations to CO_2 concentrations in the cuvette (Ci/Ca).

All species showed reductions of photosynthetic assimilation in the flooded period. Two

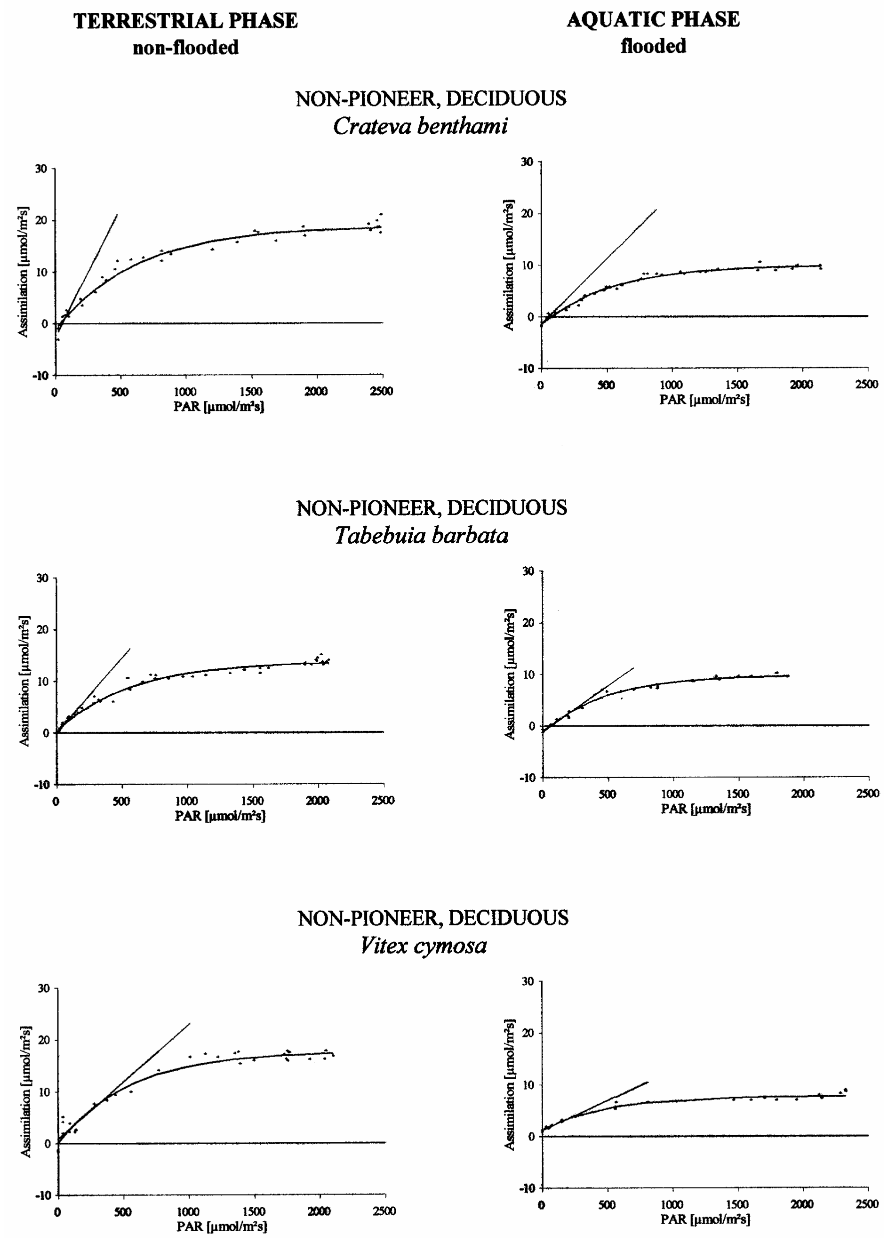

Fig. 2(b). Photosynthetic light response curves and quantum yield: selected curves of the non-flooded terrestrial and flooded aquatic phase for the six analysed species. The light response curves were measured 2-4 months after the onset of the draining or flooding period, i.e. at a minimum of 2 and a maximum of 4 months after the start of the terrestrial or aquatic phase, respectively. *Crateva benthami, Tabebuia barbata* and *Vitex cymosa.*

main factors can be responsible for this. Photosynthetic capacity itself can be affected, or stomatal effects can cause changes in CO_2-assimilation. Since in all six species stomatal conductances increased in the flooded period, this factor cannot be limiting for photosynthesis and does not seem to be responsible for the decrease of assimilation. This is reflected also by the generally higher intercellular CO_2 concentrations in the flooded period, which then cannot be limiting photosynthesis.

Maximum photosynthetic assimilation is also influenced by leaf age (Sestak 1985). Changes in leaf phenology were similar among the six deciduous and evergreen species, with a peak of leaf flush at the end of the flooded period. Although the duration and timing of the leafless period are not directly related to the time of highest water level (Wittmann & Parolin 1999), the production of new leaves occurred primarily in the high water period guaranteeing the presence of fully expanded, adult leaves throughout the non-flooded period. Young or adult leaves had higher photosynthetic activities than senescent leaves. In the months where there was a higher amount of senescent leaves on the trees, mean photosynthetic activity was reduced. Leaf age surely is an explanation for seasonal changes of photosynthesis in the six studied species.

Another factor closely related to photosynthetic assimilation is the degree of sclerophylly (Medina 1981; Medina & Francisco 1994). Leaf sclerophylly can be expressed by specific leaf area ($cm^2\ g^{-1}$, Medina 1981). Specific leaf area of the evergreen non-pioneer *Nectandra amazonum* was in the range of typical woody sclerophylls of Amazonian forests (47-76 $cm^2\ g^{-1}$, Medina 1981). Leaf area and leaf dry mass were low in *Nectandra amazonum*, emphasizing the sclerophyll character of this species. Maximum photosynthetic assimilation of 23 Venezuelan species with evergreen, sclerophyll leaves was 9.3 $\mu mol\ m^{-2}\ s^{-1}$ (Reich *et al.* 1991), which is identical to the values measured in *Nectandra amazonum* in the non-flooded period.

The two pioneer species, *Cecropia latiloba* and *Senna reticulata*, have opposite features from sclerophyll species, with high leaf area, leaf dry mass and specific leaf area (Table 1). Intermediate values were measured in the three deciduous non-pioneers. These leaf characteristics emphasize the role of leaf sclerophylly with relation to photosynthetic assimilation, which are highest in the non-sclerophyll pioneers, and lowest in the sclerophyll evergreen non-pioneer *Nectandra amazonum* (Table 1).

Conclusion

Photosynthetic assimilation of the six studied species showed specific patterns in relation to leaf morphology and successional stage. No patterns could be found in relation to phenological traits. Leafing patterns were similar in evergreen and deciduous species, with leaf loss and reduction of new leaf production concentrated in the flooded period. The main factor responsible for the reductions of physiological activities in the flooded period is concluded to be leaf age. Further studies of the effects of leaf age and other factors influencing photosynthetic assimilation, like water and nutrient supply, and water use efficiency, may contribute towards understanding variation in gas exchange responses of tropical floodplain forest trees subjected to periodical extended flooding.

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