ECOTROPICA

CONTRASTING RESPONSES OF TWO AMAZONIAN FLOODPLAIN TREES TO HYDROLOGICAL CHANGES

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Abstract. Two common evergreen tree species of Amazonian floodplains, *Laetia corymbulosa* (Flacourtiaceae) and *Pouteria glomerata* (Sapotaceae), were investigated. Their phenological and physiological reactions to the changing hydrological environment during the annual cycle was analyzed. Leaves were present during the whole year in both species, but a strong leaf loss and significant reduction of new leaf production was observed in *L. corymbulosa* in the non-flooded phase in a period of unusually strong drought, which was accompanied by a significant decrease in predawn leaf water potential, which fell from –0.03 MPa to below –2 MPa. New leaves were flushed with the onset of rain a few weeks later. *P. glomerata* showed a complete inhibition of new leaf production in the period of highest water levels. Predawn leaf water potential was more or less constant at –0.5 MPa throughout the year. Stress reactions to drought were not detectable in this species. Photosynthetic activity in *L. corymbulosa* was highest in the terrestrial phase (13 µmol CO_2 m^{-2} s^{-1}). In the first weeks after inundation, net CO_2 exchange rates were comparable with those of the terrestrial phase, but dropped drastically to 3 µmol CO_2 m^{-2} s^{-1} after approximately six months of waterlogging. In contrast, assimilation rates of *P. glomerata* were nearly constant during the whole annual cycle, ranging between 8 and 12 µmol CO_2 m^{-2} s^{-1}. The results show that *L. corymbulosa* reacts more sensitively than *P. glomerata* to environmental changes in the annual cycle, such as long-term waterlogging and drought. The two species show different morphological adaptations, such as aerenchymatous tissues and adventitious roots, while different leaf development (senescence), which is linked to the hydric conditions of the environment, is responsible for reductions and subsequent recovery (by new leaf flush) in photosynthetic rates. Thus, different phenological performances lead to different ecophysiological responses to the same environmental constraints to which the two species are subjected.

Resumo. Duas espécies de árvores sempreverdes das áreas inundáveis da Amazônia, *Laetia corymbulosa* (Flacourtiaceae) e *Pouteria glomerata* (Sapotaceae), foram investigadas com respeito a reações fenológicas e fisiológicas em função das condições hídricas ao longo do ano. As duas espécies apresentavam folhas durante o ano inteiro, entretanto *L. corymbulosa* mostrou forte queda de folhas e uma redução significativa da produção de folhas novas durante o período de seca que neste ano foi excepcionalmente pronunciado, e que levou a uma diminuição significativa do potencial hídrico das folhas (predawn leaf water potential) que caiu de –0.03 MPa para menos de –2 MPa. Novas folhas brotaram com o início das chuvas poucas semanas mais tarde. *P. glomerata* teve uma completa inibição da produção de folhas novas durante o período dos níveis dos rios altos. O potencial hídrico das folhas permaneceu mais ou menos constante em –0.5 MPa nesta espécie. Não foi possivel detectar reações de estresse a falta de água nesta espécie. A atividade fotossintética de *L. corymbulosa* foi maior na fase terrestre (13 µmol CO_2 m^{-2} s^{-1}). Nas primeiras semanas depois do começo da inundação as taxas líquidas de troca de CO_2 foram comparáveis áquelas da fase terrestre, mas cairam drasticamente para 3 µmol CO_2 m^{-2} s^{-1} aproximadamente após seis meses de inundação. Em contraste, as taxas de assimilação de *P. glomerata* permaneceram quase constantes ao longo do ciclo anual, variando entre 8 e 12 µmol CO_2 m^{-2} s^{-1}. Os resultados mostram que ao longo do ano *L. corymbulosa* reage de modo mais sensível ás modificações hidrológicas do que *P. glomerata*, ou seja á inundação e á Seca. As duas espécies produzem adaptações morfológicas diferentes, como por exemplo tecidos aerenquimatosos e raízes adventícias. As diferenças de estádio (folhas novas, maduras e senescentes), ligadas as condições hídricas do ambiente, são responsáveis pelas alterações nas atividades fotossintéticas, diminuição ou aumento, no caso da produção de folhas novas. Assim, diferenças fenológicas causam diferentes respostas ecofisiológicas sob as mesmas condições ambientais nas duas espécies analisadas. *Accepted 7 July 2004.*

Key words: *Amazonia, Brazil, chlorophyll content, floodplain forest*, Laetia corymbulosa, *leaf water potential, net photosynthesis, phenology*, Pouteria glomerata, *Várzea.*

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INTRODUCTION

Waterlogging is a stress factor which affects the physiological activity of plants (Coutts & Armstrong 1976, Jackson 1985). Diffusion of air in water is drastically reduced by flooding, and consequently oxygen is displaced by water resulting in hypoxic or even anoxic conditions in the rooting zone (Trought & Drew 1980, Brändle 1996). This inhibits mitochondrial respiration, the energy status cannot be maintained, water and ion uptake are inhibited, leading to reductions of stomatal aperture and photosynthetic activity (Kramer 1951, Gill 1970, Regehr *et al.* 1975, Pezeshki 1993). The type of reaction to waterlogging and its intensity depend on the degree of adaptation of the trees to the growth conditions, and on the time when anoxic conditions arise. In temperate and subtropical regions, flooding often occurs in winter, when trees reduce their physiological activity considerably and overcome unfavorable conditions in a state of rest (Moore 1978, Kozlowski 1984, Grosse & Schröder 1986, Janiesch 1991, Armstrong *et al.* 1994, Müller *et al.* 1994). Anoxic conditions in the rhizosphere do not have strong effects during dormancy (Broadfoot 1967), whereas in tropical regions – where the vegetation period extends over the whole year and growth is not limited by reductions of temperature or irradiance – the influence of anoxic conditions in the root zone can be considerable. Non-adapted species do not tolerate anaerobic conditions in the rhizosphere and die within few days or weeks (Gill 1970). Adapted species may survive several months of waterlogging or even complete submersion. In Amazonian floodplains, several hundred tree species with different sets of adaptations and strategies cope with the extreme flooding conditions in this environment (Junk 1989, Junk & Piedade 1997, Worbes 1997, Parolin 2003, Parolin *et al.* 2004). The formation of annual growth rings as a consequence of regular growth reductions indicates that flooding leads to reductions in growth and physiological activities in Amazonian floodplain trees (Worbes 1985, 1997). Nevertheless, several species maintain high photosynthetic levels throughout most of the flooded period (Schlüter & Furch 1992, Schlüter *et al.* 1993, Waldhoff & Furch 1998, Parolin 2000). This is made possible by the formation of adventitious roots, hypertrophic lenticels, aerenchymatous tissues in roots and parts of the stem, and fermentation processes or other physiological adaptations (Parolin *et al.* 2004). As indicated by some autecological studies, different tree species have different growth strategies and show different responses to this environmental stress, but these have been analyzed only in seedlings (Schlüter & Furch 1992, Schlüter *et al.* 1993, Waldhoff & Furch 1998, Parolin 2002, De Simone *et al.* 2001, 2003). These studies showed that there are clear seasonal variations in phenology and photosynthetic CO_2-assimilation. However, in spite of the extended flooding, CO_2-assimilation was high during the greatest part of the flooded period in the analyzed seedlings. Growth was not stopped for the entire flooding period. On the contrary, the level of CO_2-assimilation was comparable to that of the terrestrial phase in several months of the aquatic period.
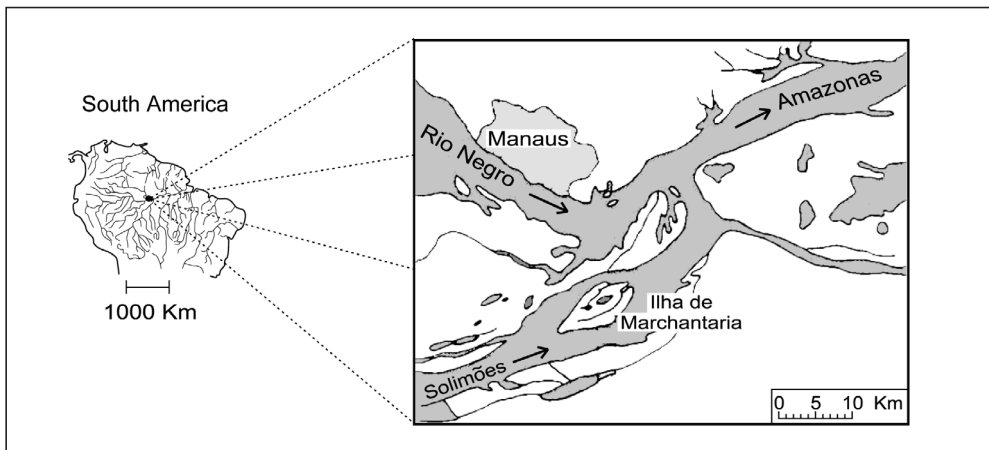

FIG. 1. Location of the Ilha de Marchantaria.

FIG. 2. Water level of the Rio Negro (m above sea level) in the study period (August 1997–June 1998). Mean monthly precipitation (mm) measured at the Ilha de Marchantaria (1991–1995). (0) = aquatic/dry phase (June to August), (1) = terrestrial/dry phase (September to November), (2) = terrestrial/wet phase (December to March), (3) = aquatic/wet phase (April to the beginning of June).
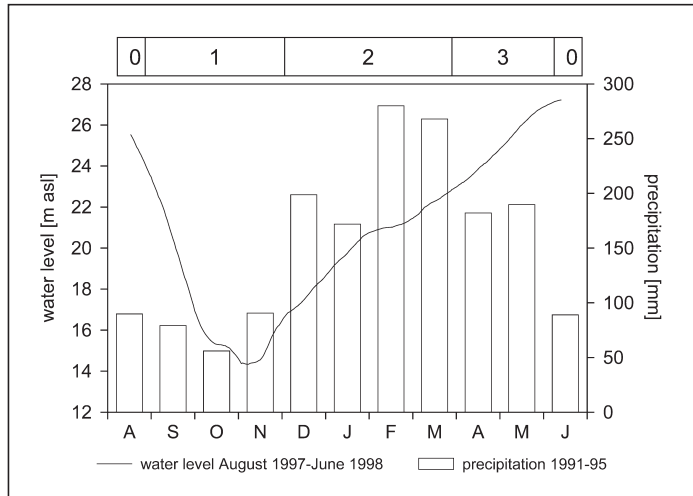
The intention of the present study was to investigate in detail the effect of hydric changes on gas exchange and water relations of two typical adult tree species of Amazonian floodplains. Both are evergreen species of similar height and of late successional stages belonging to the mid-level tree community, where inundation lasts on average 230 days per year. As the performance of leaves functions as an indicator for stress situations (Medina 1984, Lange *et al.* 1987), they were used to describe the physiological state of the adult trees in the field through the annual cycle.

METHODS

Study area. The study area was located on the Ilha de Marchantaria, a river island 15 km upstream from the confluence of the Amazon (Solimões) River with the Rio Negro, northeast of Manaus, Brazil (03°15′S, 59°58′W; Fig. 1). The climate is hot and humid. Mean monthly temperature is 26.6°C (Ribeiro & Adis 1984) and mean annual precipitation about 2105 mm, with 75 % falling in the rainy season from December to May (Fig. 2). The seasonality of precipitation in the catchment area of the Amazon (Solimões) River results in an annual cycle of river discharge; water levels near Manaus change with a mean amplitude of 9.90 m per year.

Tree species. Two common evergreen tree species of Amazonian floodplains were investigated: *Laetia corymbulosa* Spruce ex Benth. (Flacourtiaceae, local name sardinheira) and *Pouteria glomerata* (Miquel) Radl-kofer (Sapotaceae, local name abiurana). Both species belong to the 'mid-level tree communities' where inundation lasts on average 230 days per year (Junk 1989). At the study site, the position of the investigated individuals of *P. glomerata* was 22.91 m above sea level (asl) and 22.44 m asl in *L. corymbulosa*. The investigated trees were adults of 14 m height, with a dbh of 40 cm for *L. corymbulosa* and 54 for *P. glomerata*.

Since the canopy leaves could only be reached with a scaffolding up to 12 m above the ground (Fig. 3), only one individual per species was monitored for this study. All measurements were started at the end of the aquatic phase in August 1997 and were finished in the following aquatic phase in June 1998.

Phenology. Phenological behavior (production of new leaves, leaf senescence, development of buds, flowers, fruits and appearance of mature fruits) was monitored at weekly intervals. Leaf phenology was categorized as follows:
• juvenile: leaves not completely developed, light green color
• adult: leaves completely developed, green to dark green color
• senescent: symptoms of senescence (e.g., yellow and brown spots, etc.).

Leaf gas exchange. Measurements of net photosynthesis, transpiration, and stomatal conductance were carried out with a differential infrared gas analyzer (IRGA) (LI-COR, LI 6400 Portable Photosynthesis

FIG. 3. Scaffolding used for physiological measurements in the annual cycle.

System). To describe external variables, the instrument was equipped with a PAR sensor, located in the upper half of the leaf chamber, and an optional external quantum sensor. Over this leaf, air temperature and humidity were determined. These measurements were supplemented by micrometeorological data from a weather station.

Only adult leaves were taken for measurements, differentiating between leaves in positions exposed to the sun and leaves of the inner part of the canopy. Sun-exposed leaves were always taken from the top of a branch and shaded leaves from inner parts of the canopy, which are shaded almost the whole day. Two to five adult leaves of the inner and outer part of the canopy were measured between 08:00 and 12:00 h. Every two weeks, light dependency of net photosynthesis was investigated by measuring light saturation curves. The use of an artificial light source (LI-COR 6400-02 LED) provided light-saturated conditions for photosynthesis. Maximum net CO_2 exchange rate (A_{max}) was calculated using a tangenshyperbolicus function (modified after Jassby & Platt 1976):

$$A_I = (A_{max} - R) * \tanh\left(\frac{k*I}{A_{max} - R}\right) + R$$

A_I = light dependent net CO_2 exchange rate (µmol CO_2 m^{-2} s^{-1})

A_{max} = maximum net CO_2 exchange rate (µmol CO_2 m^{-2} s^{-1})

R = dark respiration and photorespiration (µmol CO_2 m^{-2} s^{-1})

K = initial slope (quantum yield) (µmol CO_2 µmol photons^{-1})

I = irradiance (µmol photons m^{-2} s^{-1})

Chlorophyll content. Mean leaf area of five leaves of the inner and outer part of the crown was determined monthly by means of a leaf area meter (ΔT Area Meter, Delta-T Devices). Leaves were collected in the field and directly transported to the laboratory in plastic bags on ice. Three to five discs of determined area (7.69 cm^2) were punched from each leaf for the determination of chlorophyll contents. The pieces were crushed in a mortar with quartz sand and $CaCO_3$ and subsequently extracted in ethanol. The extinction was measured by photometry (Kontron; Uvikon 930) at wavelengths of 650 and 665 nm. Chlorophyll contents were determined per leaf area (mg m^{-2}) according to Holden (1965):

$25.5 * E_{650} + 4 * E_{665} =$ Chl a+b in mg l^{-1}
$16.5 * E_{665} - 8.3 * E_{650} =$ Chl a in mg l^{-1}
Chl a+b − Chl a = Chl b
control: $33.8 * E_{650} - 12.5 * E_{665} =$ Chl b in mg l^{-1}

Leaf water potential. Leaf water potential was measured with a Scholander pressure bomb (PMS Instruments model 1000, Corvallis, OR, USA) according to the method described by Scholander & Perez (1968) and Cleary & Zaerr (1983). Leaves from shaded and exposed parts of the crown were taken for determining predawn leaf water potential between 06:00 and 07:00 h. Measurements were replicated at least three times for each position.

Statistical analysis. The annual cycle was divided into four phases related to the hydric status of soil and atmosphere (Fig. 2):

(0) = aquatic/dry phase (June to August)
(1) = terrestrial/dry phase (September to November). To allow unified leaf ages in each phase, *Laetia corymbulosa* measurements from the beginning of December were assigned to this group.
(2) = terrestrial/wet phase (December to March)
(3) = aquatic/wet phase (April to the beginning of June).

To compare the single phases, a descriptive analysis of data was carried out with an ANOVA using the statistical program SPSS (vers. 8.0), and 95 %-confidence intervals of the means of each phase were correlated to compare the phases (Sachs 1997).

RESULTS

Phenology. Laetia corymbulosa had all states of leaf development within the canopy at the end of the aquatic phase (Fig. 4). New leaf production occurred in exposed positions only and stopped there at the end of September. All leaves showed symptoms of senescence and leaf fall was pronounced until mid-November. After single rainfalls at the onset of the rainy season in November, flowering and new leaf flush began immediately and the crown was renewed entirely.

In the following months, continuous leaf production was observed at sun-exposed positions, but was reduced in February and stopped completely in the inner part of the crown, still in the terrestrial phase. Flowers faded within two weeks and mature fruits could be found in February, before waterlogging. Flowering and fruiting could occasionally be observed during the whole year but fruits dropped before being mature.

Pouteria glomerata was evergreen the whole year long (Fig. 4). In the terrestrial phase all states of development could be found. Leaf flush was pronounced at the end of September and in March. At the beginning of waterlogging, leaf production stopped completely, and symptoms of senescence became dominant. Flowering occurred with rising water table
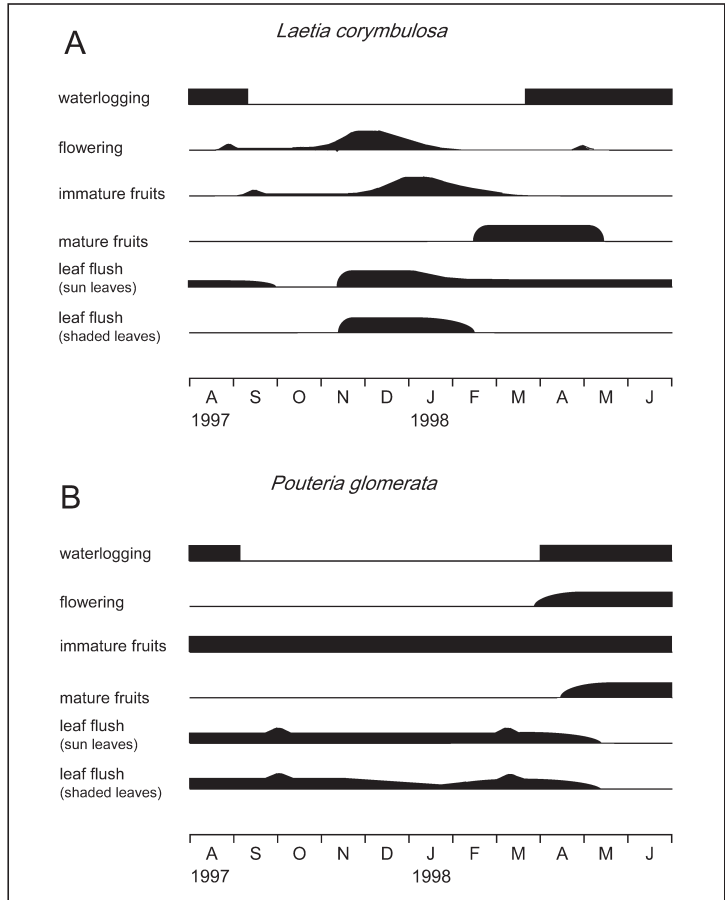

FIG. 4. Phenology of A *Laetia corymbulosa*, B *Pouteria glomerata* during the study period (August 1997 to June 1998).
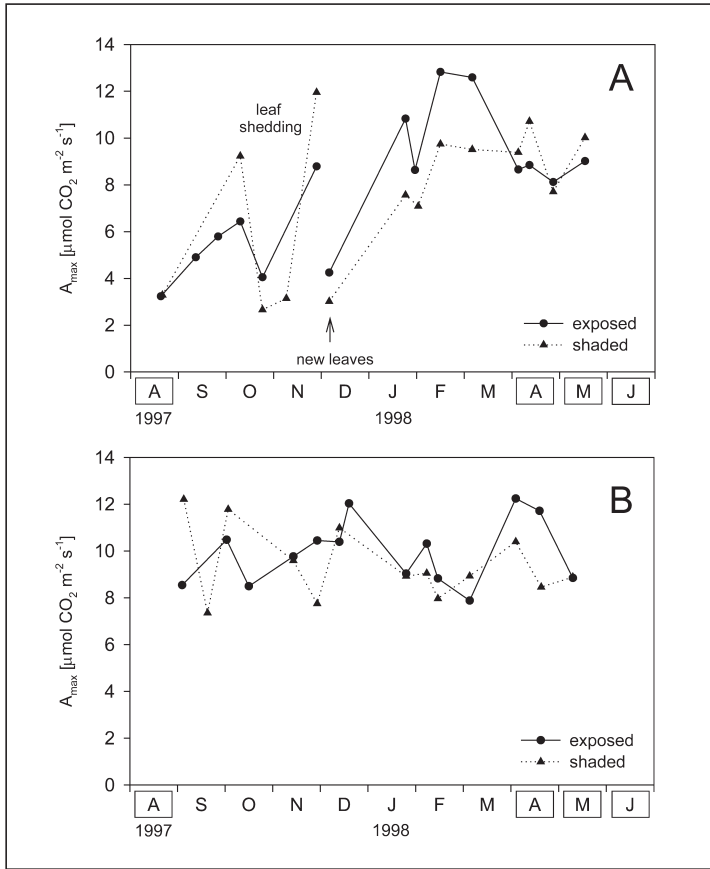
FIG. 5. Maximum net CO_2 exchange rates of exposed and shaded leaves of A *Laetia corymbulosa*, B *Pouteria glomerata*, from August 1997 to June 1998. Framed months = aquatic phase (tree waterlogged).

and continued during waterlogging. Fruits matured during the whole year, but mature fruits were released only at the beginning of the following aquatic phase. All fruits were able to float.

Gas exchange. L. corymbulosa showed extreme differences in photosynthetic activity over the year (Fig. 5a). At the end of the aquatic/dry phase about 3 μmol CO_2 m^{-2} s^{-1} were measured in sun and shade leaves. A_{max} values increased after waterlogging but decreased rapidly in October/November due to very dry conditions. New juvenile leaves exhibited the same low values in December as measured at the end of waterlogging. With aging, photosynthetic activity recovered and highest assimilation rates could be measured in leaves in exposed positions of the canopy in February (13 μmol CO_2 m^{-2} s^{-1}). During waterlogging, photosynthetic activity decreased and remained constant at

approximately 9 μmol CO_2 m^{-2} s^{-1}. Also shaded leaves showed increasing A_{max}-values when aging. Highest assimilation rates were measured in the inner crown at the begin of waterlogging (11 μmol CO_2 m^{-2} s^{-1}).

P. glomerata did not exhibit significant seasonal differences in photosynthetic activity (Fig. 5b). A_{max}-values of both sun and shade leaves ranged from 8 to 12 μmol CO_2 m^{-2} s^{-1}.

Chlorophyll content. Leaves of *L. corymbulosa* showed differences in chlorophyll content during the study period (Fig. 6a). Lowest values could be determined at the end of waterlogging and in the terrestrial/dry phase. After new leaf flush, the chlorophyll content rose continuously during waterlogging up to 639 mg m^{-2} for leaves in the outer, and 677 mg m^{-2} for leaves in the inner part of the canopy. The increase was statistically significant only for shaded leaves (Table 1).

By comparison, shaded leaves of *P. glomerata* had considerably higher contents of chlorophyll than exposed leaves (Fig. 6b). Values varied between 515 mg g^{-1} at the end of waterlogging and 673 mg m^{-2} at the end of the terrestrial phase. In the outer part, contents ranged from 438 to 604 mg m^{-2}; both values were determined in the terrestrial phase. Over the year no significant differences could be registered (Table 1).

Predawn leaf water potential. L. corymbulosa showed high predawn leaf water potentials at the end of the aquatic phase in August (–0.3 MPa, Fig. 7a). Simultaneously with the declining water table, the leaf water potential dropped below –2 MPa, which was significantly different from all other measurements during the year (Table 2). After the onset of rain, predawn leaf water potentials rose considerably and reached values of –0.18 MPa in the outer and –0.12 MPa

in the inner part of the canopy. Even during waterlogging water potential remained high.

In the terrestrial/dry phase *P. glomerata* did not show decreasing leaf water potentials despite a strong drought in that period (Fig. 7b). In exposed as well as in shaded parts of the canopy, values never dropped below –0.84 MPa. In the aquatic phase values were highest (–0.13 MPa) and significantly different from both terrestrial phases (Table 2b).

DISCUSSION

The investigated individuals of the two species exhibited different phenological and physiological patterns in the annual cycle as reactions to the changing hydric conditions.

Laetia corymbulosa, which is described as evergreen in the literature (Sleumer 1980), shed almost all leaves
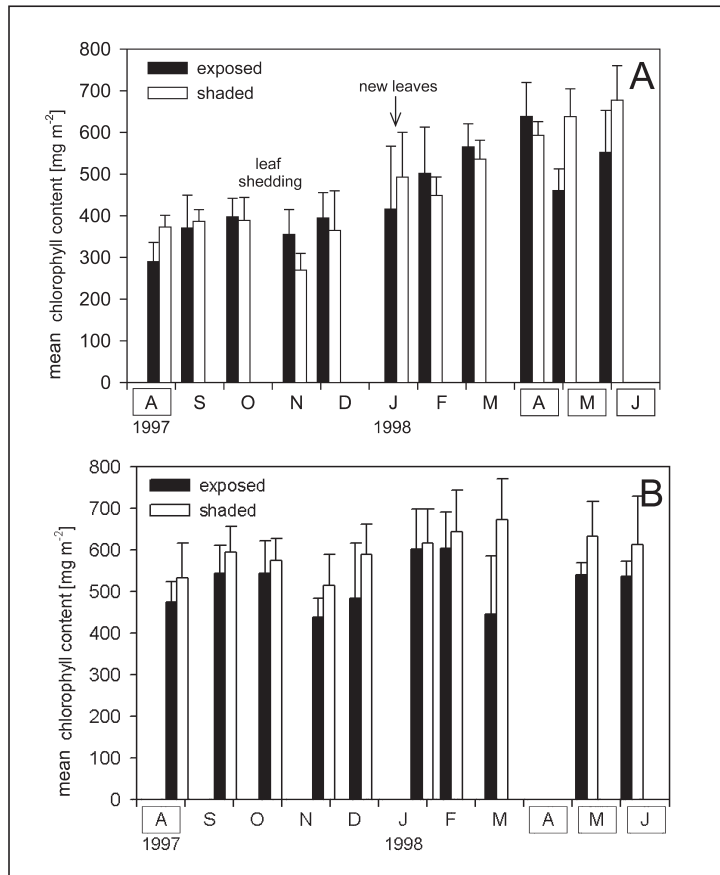

FIG. 6. Average chlorophyll content per leaf area of exposed and shaded leaves of A *Laetia corymbulosa*, B *Pouteria glomerata*, from August 1997 to June 1998. Framed months = tree waterlogged.

TABLE 1. Average chlorophyll content per leaf area (mg m^{-2}) of sun-exposed and shaded leaves of *Laetia corymbulosa* and *Pouteria glomerata* during each phase with standard deviation and sample size (n). Comparison of 95 %-confidence intervals of means of each phase. – = no intersection of the confidence intervals, significant difference between values of analyzed phases; + = intersection of the confidence intervals, no significant difference between values of the analyzed phases.

	n	chlorophyll content [mg m^{-2}] exposed	shaded		overlapping of confidence intervals exposed				shaded		
Laetia corymbulosa											
aquatic/dry (0)	5	290.2±45.7	372.7±28.0		(1)	(2)	(3)		(1)	(2)	(3)
terrestrial/dry (1)	18	378.0±59.0	351.3±71.1	(0)	–	–	–	(0)	+	–	–
terrestrial/wet (2)	15	494.6±122	492.3±76.0	(1)		–	–	(1)		–	–
aquatic/wet (3)	15	550.5±105	636.1±69.2	(2)			+	(2)			–
Pouteria glomerata											
aquatic/dry (0)	5	474.7±48.5	532.3±84.0		(1)	(2)	(3)		(1)	(2)	(3)
terrestrial/dry (1)	15	507.9±79.8	561.4±67.9	(0)	+	+	+	(0)	+	+	+
terrestrial/wet (2)	20	533.7±128	629.9±86.7	(1)		+	+	(1)		+	+
aquatic/wet (3)	10	537.7±31.9	622.2±96.5	(2)			+	(2)			+

as a reaction to very dry conditions during the terrestrial/dry phase. In the months September and October of 1997, the onset of rainfall began later than usual and precipitation was less than usual for these months (pers. comm. from local people of the Ilha de Marchantaria). Leaf shedding in *L. corymbulosa* thus may have been a reaction to strong drought: leaf area and consequently transpiration are in this way reduced, a so called "drought avoidance" strategy (Medina 1983, Ludlow 1989). Apparently this species is

TABLE 2. Average predawn leaf water potential [MPa] of sun-exposed and shade-leaves of *Laetia corymbulosa* and *Pouteria glomerata* during each phase with standard deviation and sample size (n). Comparison of 95 %-confidence intervals of means of each phase. For *Pouteria glomerata* no measurements were carried out in the aquatic/dry phase (0).

|	n	leaf water potential [MPa] exposed	shaded		overlapping of confidence intervals exposed				shaded		
Laetia corymbulosa											
aquatic/dry (0)	3	–0.33±0.13	–0.27±0.08		(1)	(2)	(3)		(1)	(2)	(3)
terrestrial/dry (1)	9	–1.24±0.74	–1.34±0.83	(0)	–	+	+	(0)	–	+	+
terrestrial/wet (2)	3	–0.18±0.06	–0.12±0.08	(1)		–	–	(1)		–	+
aquatic/wet (3)	6	–0.25±0.09	–0.41±0.31	(2)			+	(2)			+
Pouteria glomerata						exposed			shaded		
aquatic/dry (0)	–	–	–								
terrestrial/dry (1)	7	–0.66±0.26	–0.56±0.22	(1) + (2)		+			+		
terrestrial/wet (2)	6	–0.56±0.24	–0.42±0.15	(1) + (3)		–			–		
aquatic/wet (3)	6	–0.21±0.10	–0.17±0.06	(2) + (3)		–			–		
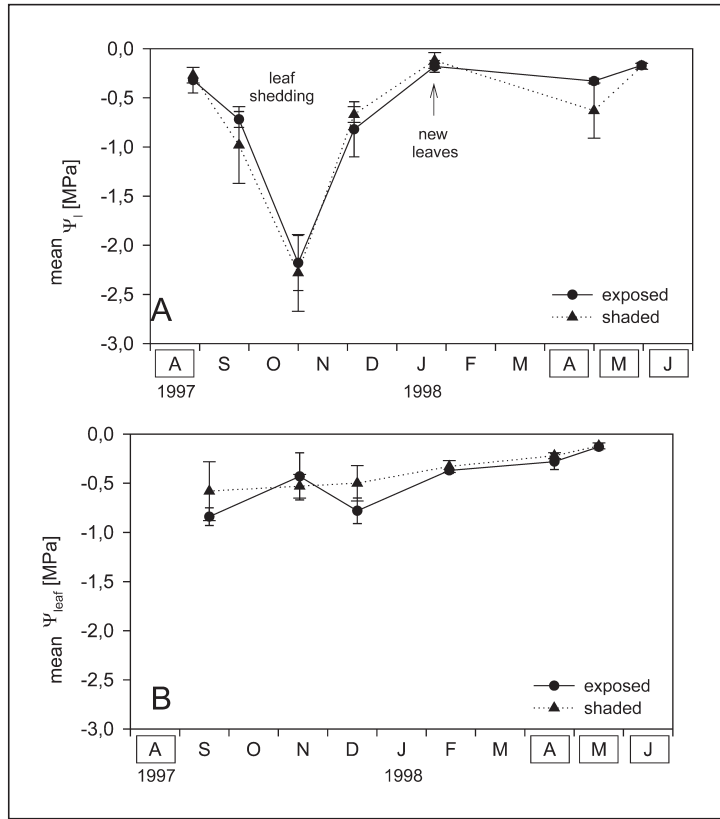
FIG. 7. Predawn leaf water potential of A *Laetia corymbulosa*, B *Pouteria glomerata*, from August 1997 to June 1998. Framed months = tree waterlogged.

extremely susceptible to drought: all other trees of this species on Marchantaria Island showed the same reaction. In this context it is valid to question whether *L. corymbulosa* is really evergreen or "brevi-deciduous". Long-term investigations of the phenology are necessary to answer this.

Pouteria glomerata did not show strong reactions to flooding nor to the drought period. It was evergreen throughout the whole study period, and only new leaf production was reduced in the waterlogged period. This seems to be a common feature among trees of Amazonian floodplains (Schlüter & Furch 1992, Schlüter *et al.* 1993, Waldhoff & Furch 1998, Parolin 2000), and it may be assumed that – resulting from the inhibition of root water and nutrient uptake by flooding – there is increased leaf senescence and, linked to this, decreased photosynthetic activity in the first weeks of flooding (Martin *et al.* 1994, Hikosaka 1996). These relations are purely specula-

tive as it is not possible – under the given conditions and field methods – to distinguish between direct effects of the environmental constraints (flooding, drought) and indirect effects of leaf age on photosynthetic performance.

Reactions to waterlogging: A comparison between the two tree species. In both species, as also observed in other trees of Amazonian floodplains, strong flushes of new leaves occurred at high water levels (Worbes 1997, Parolin *et al.* 2002, Schöngart *et al.* 2002). When the new leaves are fully expanded, photosynthetic assimilation may reach the highest values of the year, despite a water column of several meters on the tree stems (Parolin 2000), which was true also for the two species analyzed in this study. The two species seem to have different adaptation mechanisms which allow them to survive and to maintain high photosynthetic activity despite prolonged flooding and/or drought.

It is well known that stress reactions do not become apparent immediately in the form of a reduction in physiological activity. As stated in the stress concept of Selye (1936) and Larcher (1987), certain initial measures are taken to reestablish the normal level of resistance, i.e., development of morphological, anatomical, or biochemical adaptations like anaerobic metabolism, adventitious roots, or pressure ventilation.

Perhaps the considerable decrease in physiological activity in *L. corymbulosa* can be attributed to a lack of morphological adaptations. De Simone *et al.* (2003) could find neither the formation of adventitious roots nor of aerenchyma and intercellular spaces in the roots of seedlings of *L. corymbulosa* in response to low oxygen conditions. Within the roots no oxygen was detectable and thus no leakage of oxygen into the rhizosphere occurred (ROL). The observed suberization along walls of the hypodermal cell layers was not interpreted as an adaptation to flooding, but it is thought to function as a pathogen defense.

In comparison, *Pouteria glomerata* exhibits the formation of small intercellular spaces of schizogenous origin in the cortex, which supports the supply of the roots with oxygen (De Simone *et al.* 2001, 2003). Furthermore, a suberization of cells beginning immediately behind the root tip fulfil the function of a constitutive permeability barrier. Thus morphological adaptations in *Pouteria glomerata* may play a major role in overcoming anoxic soil conditions during the flooding period, whereas for *Laetia corymbulosa* the missing physiological and metabolic adaptations seem to cause leaf shedding in order to minimize the impact of flood stress.

Schlüter *et al.* (1993) observed in some species that energy reserves in the roots were not even exhausted after 300 days of submersion. Such energy mobilization seems to play a decisive role in the life cycle of *L. corymbulosa*. To provide enough energy, high fermentation rates in the roots are necessary. Probably the ability to produce leaves throughout the year, even in the aquatic period, seems to function as an additional supply of carbohydrates. Although physiological activities decreased after a few weeks of inundation, indicating a reduced energy mobilization, *L. corymbulosa* possessed sufficient reserves to survive prolonged periods with anoxic conditions.

In comparison, *P. glomerata* did not reveal any stress reactions during the aquatic phase, and thus adaptation mechanisms seem to work more efficiently in this species. Further investigations of metabolic processes are recommended in order to understand these mechanisms.

The differing sensitivity to changes in hydrological parameters in two tree species of similar size, successional stage, position in the flooding gradient, and physiognomy provides an example of the diversity of reactions to flooding and of life strategies in Amazonian floodplains.

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