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Two Amazonian floodplain trees react differently to periodical flooding

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Abstract: We tested if two Amazonian floodplain tree species, *Laetia corymbulosa* (Flacourtiaceae) and *Pouteria glomerata* (Sapotaceae), react in a similar way to the extreme changes of hydrologic conditions. They have several features in common and both belong to the "alternative energy metabolism" strategy. A strong leaf loss and significant reduction of new leaf production was observed in *L. corymbulosa* in a period of unusually strong drought, accompanied by a significant decrease in predawn leaf water potential. *P. glomerata* was not affected by drought, but showed a complete inhibition of new leaf production in the period of highest water levels. Photosynthetic activity in *L. corymbulosa* was highest in the terrestrial phase (13 µmol CO_2 m^{-2} s^{-1}). In the first week after inundation net CO_2-exchange rates were comparable to those of the terrestrial phase, but dropped drastically to 3 µmol CO_2 m^{-2} s^{-1} after approx. 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 to both drought and long-term waterlogging than *P. glomerata*. Both species belong to the same strategy group as defined by root metabolism and show predictable reactions to the changing hydrological conditions, and the reactions are linked to the hydric environment. On the other hand, they show very different phenological and physiological patterns and thus stand for the high diversity of species and of strategies of trees of Várzea floodplains.

Resumen: Probamos si dos especies arbóreas de la planicie inundable amazónica, *Laetia corymbulosa* (Flacourtiaceae) y *Pouteria glomerata* (Sapotaceae), reaccionan de forma similar a cambios extremos en las condiciones hidrológicas. Estas especies comparten varios rasgos y ambas pertenecen a la estrategia de "metabolismo energético alternativo". En *L. corymbulosa* se observó una fuerte pérdida foliar y una reducción significativa en la producción de nuevas hojas durante un periodo de sequía inusualmente fuerte, acompañado por un decremento significativo en el potencial hídrico de la hoja antes del amanecer. *P. glomerata* no fue afectada por la sequía, pero mostró una inhibición completa de nueva producción foliar en el periodo de niveles más altos de agua. La actividad fotosintética en *L. corymbulosa* fue más alta en la fase terrestre (13 µmol CO_2 m^{-2} s^{-1}). En la primera semana después de la inundación las tasas netas de intercambio de CO_2 fueron semejantes a las de la fase terrestre, pero cayeron drásticamente a 3 µmol CO_2 m^{-2} s^{-1} después de aprox. seis meses de anegación. En contraste, las tasas de asimilación de *P. glomerata* fueron casi constantes durante todo el ciclo annual, variando entre 8 y 12 µmol CO_2 m^{-2} s^{-1}. Los resultados muestran que *L. corymbulosa* reacciona con mayor sensibilidad tanto a la sequía como a la anegación de largo plazo que *P. glomerata*. Ambas especies pertenecen al mismo grupo estratégico definido por el metabolismo radicular y muestran reacciones predecibles a las condiciones hidrológicas cambiantes, y las reacciones están ligadas al ambiente hídrico. Por otro lado, muestran patrones fenológicos y fisiológicos

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muy diferentes y por lo tanto representan la alta diversidad de especies y de estrategias de los árboles en la planicie inundable de la várzea.

Resumo: Testamos se as espécies arbóreas de duas planícies alagadas amazónicas, *Laetia corymbulosa* (Flacourtiaceae) e *Pouteria glomerata* (Sapotaceae), reagiam da mesma maneira às condições das mudanças hidrológicas extremas. Elas apresentam várias características comuns e ambas pertencem ao grupo das que usam estratégias ditas de "energia de metabolismo alternativo". Na *L. corymbulosa* observou-se uma forte perda de folhas e uma significativa redução de produção de novas folhas num período de seca acentuada e não usual, acompanhada por uma descida significativa no potencial hídrico foliar no inicio da madrugada. Já para a *P. glomerata* ela não foi afectada pela seca, mas mostrou uma inibição total para a produção de novas folhas no período dos níveis de água mais elevados. A actividade fotossintética na *L. corymbulosa* foi a mais elevada na fase terrestre (13 µmol CO_2 m^{-2} s^{-1}). Na primeira semana depois da inundação, as taxas de troca do CO_2 eram comparáveis às da fase terrestre, mas baixaram drasticamente a 3 µmol CO_2 m^{-2} s^{-1} depois de aproximadamente seis meses de encharcamento. Em contraste, as taxas de assimilação da *P. glomerata* foram praticamente constantes durante todo o ciclo anual situando-se entre os 8 e os 12 µmol CO_2 m^{-2} s^{-1}. Os resultados mostram que a *L. corymbulosa* reage de forma mais sensível que à secura e alagamento por períodos longos do que a *P. glomerata*. As duas espécies pertencem ao mesmo grupo de estratégia definida pelo metabolismo da raiz e mostram reacções previsíveis às mudanças de condições hidrológicas, reacções estas que estão ligadas ao ambiente hídrico. Por outro lado, elas mostram padrões fenológicos e fisiológicos bastante diferentes e assim respondem pela elevada diversidade de espécies e das estratégias das árvores nas várzeas alagadas.

Key words: Biocoenotic extreme-site rule, flood gradient, flood pulse concept, life strategies, whitewater floodplain forest, zonation.

Introduction

Amazonian Várzea forests cover approximately 200.000 km^2 along the main Amazonian rivers (Junk 1993, 1997). This seasonal floodplain is characterized by a monomodal predictable flood-pulse causing inundations of upto 210 days per year with water columns of 10-15 m (Junk *et al.* 1989). The hydrologic periodicity of the flood pulse results in the regular and predictable change between a terrestrial and an aquatic phase. The high sediment load of the nutrient-rich whitewater rivers results in high dynamics of the rivers and the adjacent floodplains and in a high nutrient input which enhances plant productivity but hinders root aeration and leaf photosynthesis in submerged leaves or in leaves which are covered by mud after emergence. The hypoxic and often anoxic soil conditions cause the need for adaptations, such as e.g. adventitious roots. In the terrestrial period, when river waters have receded and precipitation is low, periods of drought may occur which cause the need for a completely different set of adaptations to cope with the lack of water. Nevertheless, about 1000 tree species grow in the Várzea, many with high commercial value, and all of them being extremely flooding tolerant (Parolin *et al.* 2004).

Different levels of adaptations result in tree zonations along the gradient of flooding and sedimentation (Wittmann *et al.* 2002). There are, however, some features that are similar among the trees. Phenological cycles are linked to the hydrologic periodicity (Parolin *et al.* 2002; Schöngart *et al.* 2002): fruit and seed maturation are concentrated in the period of high water levels, and thus diaspore dispersal occurs mainly by hydrochory and/or ichthyochory (Goulding 1980; Kubitzki & Ziburski 1994). This is in congruence with the Flood Pulse Concept (Junk *et al.* 1989) which states that the predictable flood pulse changes the environmental conditions in a predictable way, and that the organisms of Amazonian floodplains show predictable reactions to these.

Previous studies have shown that although there is a clear relation between the flood pulse and ecophysiological reactions of the trees (e.g. Armbrüster *et al.* 2004; Parolin *et al.* 2004; Scarano & Crawford 1992; Schlüter *et al.* 1993; Waldhoff *et al.* 1998; Worbes 1985) there is no clear pattern of reactions and most trees react in rather specific ways. De Simone *et al.* (2003) classified this diversity basing on the root physiology and root anatomy of six analysed species. They found three main metabolic strategies (for details see De Simone *et al.* 2003):

1. Dormancy: Prevention of loss of energy reserves by down-regulated metabolism
2. Alternative energy metabolism and pathogen defense: Energy gain through fermentation processes (ADH, GPT); suberization of root zones as barrier for pathogens and phytotoxins
3. Internal aeration and radial oxygen loss: Improved root energy status provided by high root porosity; detoxification of phytotoxins by radial oxygen loss.

In the present study, we wanted to test two trees which at a first glance appear to be quite similar and which both belong to the "Alternative energy metabolism" strategy (see Appendix for explanations). We tested the ecophysiological reactions in the annual cycle of two tree species, *Laetia corymbulosa* Spruce ex Benth. (Flacourtiaceae, local name sardinheira) and *Pouteria glomerata* (Miquel) Radlkofer (Sapotaceae, local name abiurana). The two species have several features in common: typical common trees of Amazonian floodplains; belong to the late successional stage; grow in the same position in flooding gradient and belong to the mid-level tree community, and thus are subjected to the same flood durations; similar height and dbh classes; similar leaf shape and size; evergreen; leaves are submerged for several months without apparent damage (Waldhoff & Furch 2002); light harvesting complex functions in submerged seedlings, with only little Rubisco decomposition (Krack 2000); chloroplast shape and starch content change with long-term submergence (Waldhoff *et al.* 2002); energy is gained through fermentation processes (De Simone *et al.* 2003); there is a high suberization of the roots which functions as barrier for pathogens and phytotoxins.

Since these two species have so many features in common it might be expected that ecophysiological reactions to the hydrologic periodicity are similar. In order to test this, we monitored phenology, leaf photosynthesis and leaf water potential in the annual cycle in two adult trees of the same size which grew in a few meters distance in the Várzea near Manaus.

Materials and methods

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). 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. 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.

At the study site, the position of the investigated individuals of *P. glomerata* was at 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 cm for *P. glomerata*.

Since the canopy leaves could only be reached with a scaffolding up to 12 m above the ground, 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 consecutive aquatic phase in June 1998.

Phenological behaviour was monitored at weekly intervals in terms of production of new leaves, leaf senescence, development of buds, flowers, fruits and appearance of mature fruits. Measurements of net photosynthesis were carried out with a differential infrared gas analyser (IRGA) (LI-COR, LI 6400 Portable Photosynthesis System). Only adult leaves were taken for measurements, differentiating between leaves of 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. 2-5 adult leaves of the inner and outer part of the canopy were measured between 8 and 12 a.m. 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.

Leaf water potential was measured with a Scholander pressure bomb (PMS Instruments model 1000, Corvallis, OR, USA) according to the method described by Scholander *et al.* (1965) and Cleary & Zaerr (1983). Leaves from shaded and exposed parts of the crown were taken for determining predawn leaf water potential between 6 and 7 a.m.

Results

Senescence and leaf-fall was pronounced until mid November in *L. corymbulosa* whereas, *P. glomerata* was evergreen the whole year long (Table 1). New leaf production of *L. corymbulosa* occurred in sun exposed positions only and stopped there at the end of September; in *P. glomerata* leaf flush was pronounced in the end of September and in March. In November, flowering and new leaf flush began immediately after the onset of rainfall in *L. corymbulosa*. Continuous leaf production was observed at sun exposed positions. Flowering and fruiting could be observed during the whole year in *L. corymbulosa*. In *P. glomerata*, flowering occurred with raising water table and continued during water logging. Fruits matured during the whole year, but mature fruits were released only at the beginning of the following aquatic phase in *P. glomerata*.

Leaf photosynthesis of *L. corymbulosa* showed a high seasonal variation in leaf photosynthetic performance in sun-exposed and in shaded leaves, related to leaf shedding and flushing, with clear drought effects in October and November. *P. glomerata* showed only low seasonal variation in leaf photosynthetic performance and no drought effects. Both species showed only little differences between sun-exposed and shaded leaves in the annual cycle. Mean photosynthetic values were clearly lower in the waterlogged months than in the terrestrial period in *L. corymbulosa*, but not so in *P. glomerata* (Fig. 1).

Leaf water potential was less negative in the waterlogged months in both species (Fig. 2). *L. corymbulosa* showed a high seasonal variation in leaf water potential in both sun-exposed and shaded leaves and again high drought effects in October and November, whereas in *P. glomerata* there was only a low seasonal variation in leaf water potential, little differences between sun-exposed and shaded leaves and no drought effects.

Discussion

The results indicate that despite the similarity of the two species, with respect to their occurrence in the microhabitats of the Várzea, and to similarities in their physiognomy and some physiological features, the phenological and photosynthetic performance was clearly distinct between the two. The changes in the annual cycle were higher in *L. corymbulosa*, and differences were strongly linked to the drought period and less to the flooding impact. This species reacted more sensitively to drought and to long-term waterlogging than *P. glomerata*. These differences

Table 1. Phenology of *L. corymbulosa* and *P. glomerata* (1997-1998).

		Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Waterlogging												
Flowering	*L. corymbulosa*	x			x	x	x				x	
	P. glomerata									x	x	x
Fruit maturation	*L. corymbulosa*								x	x	x	
	P. glomerata									x	x	x
Leaf flush	*L. corymbulosa*				x	x	x					
	P. glomerata	x	x	x	x	x	x	x	x	x		

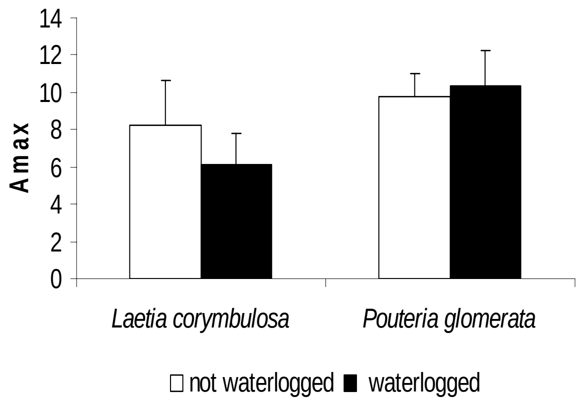

Fig. 1. Leaf photosynthesis of *L. corymbulosa* and *P. glomerata* in the waterlogged and non-waterlogged months.

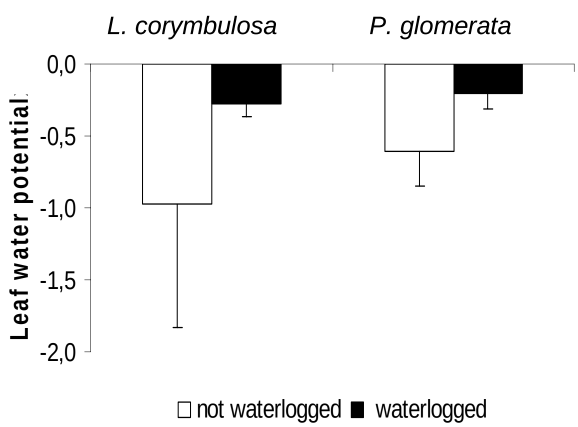

Fig. 2. Leaf water potential of *L. corymbulosa* and *P. glomerata* in the waterlogged and non-waterlogged months.

may be related to different morphological adaptations: *L. corymbulosa* does not form aerenchymatous tissues and adventitious roots, as opposed to *P. glomerata* (Armbrüster *et al.* 2004). Also, *L. corymbulosa* is a strong acetaldehyde emitter (Parolin *et al.* 2004) which is indicative of high ADH activity. A decline in the emission rates is associated with progressive and pronounced reductions in leaf physiological activities, indicating that the tree shows a poor acclimation to unfavorable conditions. Although the physiological processes did not stop completely also under stress in both species, there were clearly different reactions of the two species despite their similar metabolic pathways found in the roots (De Simone *et al.* 2003).

The finding that similar life-forms and similar physiognomies subjected to extreme conditions show clearly distinct reactions stand in contrast to the “Biocoenotic extreme-site rule” (BESR) formulated by Thienemann in 1918. The BESR states that organisms living in extreme sites show a high uniformity and a low ecological amplitude of the species. This rule was formulated for temperate regions. In fact, looking at temperate floodplain forests like the bald cypress stands in Louisiana / USA or European floodplains (e.g. of the Elbe River near Hamburg), the trees exhibit this high uniformity, with very few species occurring and a high uniformity of life strategies among them. Within the genus *Salix*, Ellenberg (1996) shows the rectification of adaptations with respect to leaf forms: the species growing in floodplains always have lanceolate leaves as an adaptation to low resistance to the flowing water they often are submerged in periodically. In other ecosystems, *Salix* spp. have other leaf forms.

It is obvious that concepts which were developed for temperate ecosystems do not necessarily apply to tropical forests, and the two tree species analysed in this paper show this very clearly. *L. corymbulosa* and *P. glomerata* showed predictable reactions to the changing hydrological conditions, and the reactions are linked to the hydric environment in both species – although *L. corymbulosa* appeared to react stronger to drought than to flooding, whereas, *P. glomerata* did not show reactions to any of these changes. Although they belong to the same strategy group as defined by root metabolism, they perform very different phenological and physiological patterns and thus stand for the high diversity of species and of strategies to be expected among the trees of Várzea floodplains. We believe that the more species are analysed on an annual basis, the more combinations of adaptations and survival strategies we will find. With an increasing need for conservation of the remaining Várzea forests, and the necessity for reafforestation of deforested areas, the knowledge of ecophysiological traits and life history strategies of the common tree species is of fundamental importance. Knowing that there are little rules and every tree is different, this creates a challenge for investigation of this unique ecosystem.

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Appendix

"Alternative energy metabolism strategy" (De Simone *et al*. 2003). Another adaptive strategy is represented by the group of late-successional evergreen species, which either show continuously production of new leaves (e.g., *L. corymbulosa)* or do not shed their leaves during the aquatic phase (e.g., *Tabernaemontana juruana, P. glomerata).* In tissues suffering from oxygen starvation, breakdown of aerobic respiration is followed by a decline in the energy status and synthesis of anaerobic stress proteins. In *T. juruana* and *L. corymbulosa,* a decline of the energy status and increased activities of alcohol dehydrogenase and glutamate pyruvate transaminoferase were observed in greenhouse experiments. The induction of fermentative enzymes under low oxygen has also been recorded in other Várzea tree species, and includes lactate dehydrogenase and malate dehydrogenase. Since induction of fermentative enzymes alone is not sufficient to sustain alternative energy metabolism during the aquatic phase, it can be assumed that the plants exhibit increased expression of genes encoding sucrose mobilizing enzyme such as sucrose synthase. Low-oxygen-induced sucrose synthase catalyzes the first essential step in carbon use by sucrose-importing cells, converting sucrose and UDP to UDP-glucose and fructose. Besides increased rates of fermentation and glycolysis, the availability of carbohydrates has to be assured, because the low energy yield through fermentation requires a high carbon flow to meet the plant requirements. Investigations on the carbohydrate content of roots from several Várzea tree species indicate that this demand is met by translocating and storing carbohydrates in the roots during the terrestrial phase, which can be utilized during the flooding period. Utilization of photosynthates by root respiration can threefold increase in stressed plants. Maintenance of photosynthesis during the aquatic phase is assumed to play an important role in supporting carbohydrate supply of the roots. Photosynthetic activity under water-logged conditions could reach the same or even higher values than during the terrestrial phase. Although ethanolic and lactic fermentation results in direct energy gain, their end products are supposed to have toxic effects on root metabolism, either by causing cell injury after reoxidation of ethanol to acetaldehyde, or by cytoplasmic acidification, a common phenomenon in flooding-intolerant plants. Várzea tree species have been shown to maintain fermentation for several months, indicating the presence of intemal mechanisms that help avoid accumulation of acetaldehyde in the cytosol. Ethanol is soluble in the lipid bilayer and can readily diffuse out of the root to the surrounding solution where it is diluted or metabolized by microorganisms. Ethanol from the external medium can be transported from the poorly aerated roots to the well-aerated leaves where it is emitted to the atmosphere as a volatile organic compound. It is another mechanism to get rid off the end products of fermentation. Investigations on the leaf emissions from *T. juruana, L. corymbulosa,* and *P. glomerata* under simulated flooding conditions revealed that high amounts of ethanol are transported with the transpiration stream in xylem to the leaves and emitted either as ethanol as such or, after reoxidation, as acetaldehyde (J. Kesselmeier *et al.,* personal communication). This strategy is of crucial importance, since suberin deposited in the root exodermis is assumed to restrict diffusion of ethanol into the rhizosphere. Evergreen species from the Várzea and Igapó floodplains develop scleromorphic leaves with massive layers of epicuticular waxes, similar to species from dry habitats. The scleromorphic leaf structure aids in regulating the water status by reducing water loss during both the terrestrial and the aquatic phase. Epicuticular waxes belong to the group of tissue-sealing biopolymers which play an important role as a barrier for water and solutes, gases and pathogens. The principle of sealing tissues is not only restricted to leaves but occurs also in roots of evergreen tree species. Young root zones of *T. juruana* and *P. glomerata* are characterized by massive suberin deposits in radial and tangential cell walls of the hypodermis. Since both species possess only low root porosities, the suberin layer functions as a barrier against oxygen loss from the roots to the rhizosphere. Although no data on the oxygen concentration in root cortex of *P. glomerata* are available, its root anatomy suggests that hypoxic conditions can prevail in roots exposed to the upper layer of the water-table. This means that both species are capable of maintaining hypoxic conditions and preventing the roots from becoming anoxic by oxygen leakage to the rhizosphere. This is achieved by a heavily suberized hypodermis, developed immediately behind the root tip, thus being a suitable barrier to oxygen leakage. However, because of the strong internal sink and the inefficient longitudinal transport of oxygen from the nonsubmerged stem, in deeply submerged roots the barrier function of suberin against oxygen loss to the rhizosphere appears to be less important. Based on microelectrode oxygen measurements, the suggestion was put forward that apoplasmic deposition of suberin generally functions as a barrier to gaseous compounds. This is of particular importance for tolerance to the penetration of hydrogen sulfide (H_2S) and methane (CH_4), which has been shown to accumulate both in soils and in the deep water layers in the värzea during flooding. The restriction of gaseous diffusion leads to the assumption that suberin plays an important role in preventing the entry of nongaseous substances. However, a putative role of these barriers to avoid a cytosolic accumulation of toxic iron ions could not be confirmed. A clearer picture has emerged concerning the role of suberin in pathogen defense. In the highly suberized species *T. juruana* and *P. glomerata,* the entry of pathogens along the whole root system is mechanically prevented by suberin. In young roots of *L. corymbulosa,* a large amount of para-hydroxybenzoic acid in rhizodermal cell walls suggests that the mechanical barrier function is supported by the release of toxic phenolics during microbial attack."