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Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees

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Abstract Plants in central Amazonian floodplains are subjected to waterlogging or complete submersion for 50–270 days every year. Most trees have growth reductions, photosynthetic activity can be reduced for some weeks to months, and leaf fall increases during the high-water period, but leaf flush, flowering and fruiting also occur in waterlogged plants. Whether flooding can trigger the changes in phenology, growth and metabolism of the plants has not yet been established. The aim of this study was to analyse the extent to which waterlogging was directly responsible for morphological, phenological and physiological changes in floodplain seedlings. In two flooding experiments performed at different times of the year, the effects of waterlogging, submersion and drought were tested in seedlings of six species with different growth strategies. One experiment was performed in the period of highest precipitation and rising river levels, and a second experiment in the period of highest river levels and the onset of the period of lowest precipitation. All results were comparable in the two experiments, and the morphological, phenological and physiological responses were linked to the treatments. Height growth and new leaf production were not severely affected in the waterlogged seedlings. All waterlogged plants produced adventitious roots, lenticels and stem hypertrophy. Submersion and drought caused a state of rest, but soon after the water had receded, leaves resprouted. Five to 12 weeks after the end of submersion, the seedlings reached the height of the control plants, showing a high ability to compensate the period of rest induced by submergence. Only the three deciduous species subjected to waterlogging showed a different phenological behaviour in the two experiments, perhaps related to genetically fixed phenological rhythms which are synchronous to those of adult trees in the field.

Keywords Drought · Floodplain forest · Growth strategies · Submersion · Várzea · Waterlogging

Introduction

Plants in central Amazonian whitewater floodplains (seasonal várzea; Prance 1979) are subjected to regular periods of waterlogging or complete submersion which can last between 50 and 270 days every year (Junk 1989). The water column can reach 10 m (Junk et al. 1989). However, in the dry months of the terrestrial phase, when river levels and precipitation are low (between September and November; Fig. 1), drought may be a relevant factor limiting plant growth.

Hundreds of tree species with different phenological and ecological traits grow in várzeas (Klinge et al. 1990; Worbes et al. 1992). Whether evergreen or deciduous, fast-growing light-demanding pioneer or slow-growing shade-tolerant non-pioneers (sensu Swaine and Whitmore

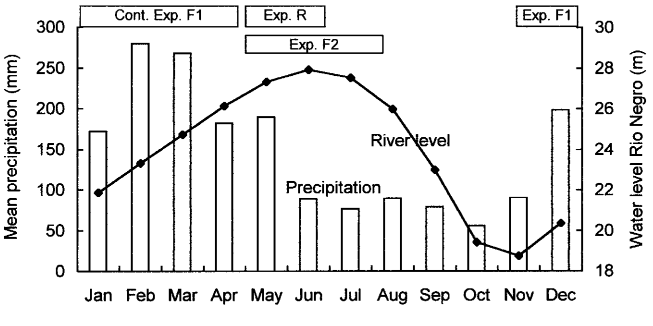

Fig. 1 Average water level of the Rio Negro measured at the port of Manaus (1987–1998), and average precipitation measured on the Ilha da Marchantaria near Manaus, with timing of the flooding experiments (*Exp. F1* and *Exp. F2*) and the recovery experiment (*Exp. R*)

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1988), the periodical lack of oxygen in the rhizosphere and, in the case of seedlings and small plants, complete submergence only affect growth and metabolism of the trees to a certain extent (Waldhoff et al. 1998; Parolin 2000). Most tree species show increased leaf fall, but also leaf flush, flowering and fruiting during the high-water period (Adis et al. 1979; Kubitzki and Ziburski 1994; Worbes 1997; Wittmann and Parolin 1999). Annual growth rings are formed in the wood of most tree species in central Amazonian floodplains as a consequence of regular growth reductions (Worbes 1989). Changes in root formation and function, leaf respiration, leaf chlorophyll contents, water potential and photosynthetic assimilation have been observed in the flooded period in seedlings of the várzea (Scholander and Perez 1968; Furch 1984; Schlüter and Furch 1992; Schlüter et al. 1993). Adult trees reduced photosynthetic CO_2 production and transpiration in some months of the flooded period (Waldhoff et al. 1998; Parolin 2000). An experiment in a growth chamber showed that waterlogging can induce the production of typical adaptations against flood stress, e.g. adventitious roots and stem hypertrophy (Waldhoff et al. 1998).

These studies suggest that the changes between flooding, waterlogging, and the drained period are responsible for differences in growth and metabolism in the floodplain trees and seedlings in the annual cycle. However, whether these changes are directly linked to flooding, or if other factors are responsible, such as irradiation, air humidity and/or intrinsic, genetic factors is not yet clear. The aim of the present study was to analyse the extent to which waterlogging is directly responsible for morphological, phenological and physiological changes in seedlings of the várzea. For this purpose, two flooding experiments were performed under semi-controlled conditions in situ at different times of the year. The effects of submersion and drought, which regularly occur in the várzea, were also tested in seedlings of six species with different growth strategies.

Materials and methods

Study species

The study species were *Cecropia latiloba* (Cecropiaceae, “Embaúba”, evergreen pioneer), *Senna reticulata* (Caesalpiniaceae, “Matapasto”, evergreen pioneer), *Nectandra amazonum* (Lauraceae, “Louro”, evergreen non-pioneer), *Crateva benthami* (Capparidaceae, “Catoré”, deciduous non-pioneer), *Tabebuia barbata* (Bignoniaceae, “Capitarí”, deciduous non-pioneer) and *Vitex cymosa* (Verbenaceae, “Tarumã”, deciduous non-pioneer). The species will henceforth be referred to by genus only.

Species were defined as deciduous if the adult trees lose at least 70% of their foliage in a defined period of the year (Piedade et al., in press). All chosen species are common in central Amazonian whitewater floodplains and are typical representatives of different growth strategies (Prance 1979; Worbes et al. 1992).

Flooding, drought and recovery experiments

Seeds of the six study species were collected in the field and placed in plastic bags containing 2 l of várzea soil for germination and seedling production. Two flooding experiments (Exp. F1 and F2) were performed in the Amazon Research Institute (INPA) in Manaus, Brazil (Fig. 1).

Table 1 Water temperature, pH, O_2 concentration, and conductivity in each of four tanks of Exp. F2 with waterlogging and flooding of seedlings. Average and SD of measurements performed at 1000 hours at weekly intervals for 12 weeks

	Waterlogging	Flooding
Water temperature (°C)	25.7±0.8	26.7±1.3
pH	7.02	7.15
O_2 concentration (% saturation)	49.5±24	60.2±18
O_2 concentration (mg/l)	4.18±2	4.69±1
Conductivity (µS/cm)	130.7±55	118.3±35

Exp. F1 was performed from December 1994 to April 1995 (Fig. 1), corresponding to the period of highest precipitation (average rainfall in December to April was 235.7 mm) and rising river water levels. Exp. F2, performed between May 1995 and August 1995, corresponded to the period of highest river water levels and the beginning of the period with low precipitation (average rainfall was 78.5 mm). Recovery from flooding was measured in seedlings from Exp. F1 after the end of this experiment, from May to June 1995 (Exp. R, 8 weeks, simultaneously with Exp. F2).

The environmental conditions at the study site, in an open area of 15×15 m, surrounded by tall natural vegetation, were designed to reproduce the natural light and temperature conditions. In twelve tanks of 1.5×2.5 m, 24 seedlings were placed randomly for 12 weeks. Sample size per species and hydric condition was n=16. At approximately 12 weeks of age, seedlings were subjected to four hydric conditions: control (well-watered), waterlogged (roots and parts of the stems flooded, water height 30 cm), submerged (whole plant flooded, water height 80 cm) and drought (watered only once every 2 days, only in Exp. F2). Ground water from the INPA was used in the tanks and was changed at weekly intervals. Water temperature, pH, O_2 concentration and conductivity are described in Table 1. Light penetration into the water was higher (>80 cm) than under natural conditions in the whitewater of the várzea where Secchi depths are between 25 and 40 cm (Junk 1970).

Measurements

Morphological adaptations (formation of adventitious roots, lenticels and stem hypertrophy), leaf phenology, survival and height increment, photosynthetic CO_2 assimilation, and chlorophyll fluorescence were analysed at weekly intervals. Seedling biomass (total dry weight), specific leaf weight, leaf water content and leaf chlorophyll content were measured with destructive methods at the end of Exp. F2 at 12 weeks. Seedling biomass (dry weight of leaves, stem, and roots) was measured after 24 h of oven drying at 105°C. Specific leaf weight was determined by dividing leaf dry weight (g) by leaf area (m^2) (Medina 1983). Leaf area was measured with a leaf area meter (ΔT Area Meter; Delta-T Devices). Leaf water content (g) was calculated from the difference between leaf fresh and dry weight. Leaf chlorophyll content per leaf dry weight was determined from five round leaf samples cut with a borer (diameter 1.4 cm, area of total leaf sample 1.54 cm^2×5= 7.69 cm^2). The leaf samples were ground with quartz sand and $CaCO_3$, the chlorophyll was extracted with ethanol and its concentration was determined with a spectrophotometer (Uvikon 930; Kontron) at 650 nm and 665 nm. Chlorophyll concentrations were calculated according to Holden (1965).

Gas exchange was measured with an infra-red gas analyser (IRGA, ADC LCA-2; Analytical Development Co., Hoddesdon, UK). Photosynthetic measurements were performed at photon flux densities (PFDs) between 1,500 and 2,300 µmol m^{-2} s^{-1}, after saturation in the six species had been measured at 1,000 µmol m^{-2} s^{-1}

PFD. Ambient CO_2 levels in the cuvette were 369–386 µmol, with a relative humidity of 33–51% and temperatures between 36 and 38°C.

Since underwater measurement devices were not available, CO_2 assimilation of the formerly submerged plants of *Nectandra*, the only species which did not shed leaves underwater, was measured after taking the plants out of the water and letting them dry in air for 5 min. CO_2 assimilation rate (A) and transpiration were calculated according to Coombs et al. (1985). Chlorophyll fluorescence was measured with the Plant Efficiency Analyser (PEA; Hansatech, King's Lynn, UK).

Results

Morphological adaptations to flooding

After 2–8 weeks, the waterlogged seedlings formed adventitious roots, lenticels and/or stem hypertrophy (Table 2), but did not do so in the control, or with submersion or drought. Only one submerged individual of *Nectandra* produced adventitious roots, which grew to a length of 10.5 cm (compared to 37 cm in waterlogged individuals), demonstrating the capacity of this species to produce adventitious roots when totally submerged. The longest adventitious roots were formed by waterlogged *Senna*, with a length of 150 cm after 4 weeks, compared to less than 40 cm in the other species.

Leaf phenology

All species subjected to flooding and drought shed leaves. When subjected to waterlogging, the three evergreen species shed 0–30% and the three deciduous species 20–50% of the leaves present at the start of the experiment. All seedlings submitted to submersion shed 100% of their leaves (except *Nectandra*: 60%), and those subjected to drought shed 40–100%.

New leaves were produced continuously in the waterlogged seedlings, but not in seedlings under submersion and drought (Table 3). An exception was found in submerged seedlings of *Cecropia* and *Nectandra* which sprouted new leaf buds underwater and expanded the leaves as soon as the plants emerged, after the end of the experiment.

In both experiments, the evergreen seedlings subjected to waterlogging showed small changes in leaf number (Fig. 2A), whereas the deciduous species had clear increases (*Crateva*, *Vitex* in Exp. F2; Fig. 2B) or decreases (Exp. F1; Fig. 2B).

Survival, height increment and recovery after flooding

All seedlings survived all experimental treatments, except *Senna* which had no survival after 3 weeks of submersion and only 50% survival after 4 weeks of drought.

In Exp. F1, height extension was lower in waterlogged and submerged seedlings than in the control (Fig. 3). With submersion, height growth stopped after 1–3 weeks in all species. One to 5 weeks after the end of waterlogging or submersion (Exp. R), all species initiated new height increment and after 5–12 weeks they reached the height of the control plants.

Table 2 Formation of adventitious roots (*AdvR*), lenticels (*Lent*) and stem hypertrophy (*SHyp*) in seedlings of six study species in Exp. F1 and F2 (– no production, + low, ++ medium, +++ strong) (ecological species group (sensu Swaine and Whitmore 1988): *P* pioneer, *NP* non-pioneer, *EV* evergreen, *DE* deciduous)

Species	Ecological group	Control AdvR, Lent, SHyp	Waterlogging			Submersion AdvR, Lent, SHyp	Drought AdvR, Lent, SHyp
			AdvR	Lent	SHyp		
Cecropia latiloba	P EV	–	++	+++	+	–	–
Senna reticulata	P EV	–	+++	+++	–	–	–
Nectandra amazonum	NP EV	–	++	–	–	(+)	–
Crateva benthami	NP DE	–	++	+++	+	–	–
Tabebuia barbata	NP DE	–	+	++	–	–	–
Vitex cymosa	NP DE	–	++	–	–	–	–

Table 3 Leaf loss and production of new leaves in seedlings of six study species in Exp. F2 (– no production/loss, + 30%, ++ 60%, +++ 100%; (+) production of leaf buds, see text) (ecological species group: *P* pioneer, *NP* non-pioneer, *EV* evergreen, *DE* deciduous)

Species	Ecological group	Leaf loss				Production of new leaves			
		Control	Waterlogged	Submerged	Drought	Control	Waterlogged	Submerged	Drought
Cecropia latiloba	P EV	–	–	+++	++	+	+	(+)	–
Senna reticulata	P EV	–	–	+++	+++	+	+	–	–
Nectandra amazonum	NP EV	–	–	+	++	+	+	(+)	–
Crateva benthami	NP DE	–	+	+++	++	+	++	–	–
Tabebuia barbata	NP DE	–	+	+++	+	++	+	–	++
Vitex cymosa	NP DE	–	+	+++	+	++	+	–	++

Table 4 Height increment (in %) in seedlings subjected to waterlogging for 12 weeks, compared to the control (=100%), in the six study species under experimental conditions after 12 weeks (Exp. F2). *F*-ratio and statistical probability (**$P \leq 0.01$, ***$P \leq 0.001$, *n.s.* not significant). *n* per species=12

Species	Control (%)	Waterlogging	Submergence	Drought	*F*-ratio	*P*
Cecropia latiloba	46.7	13	4.4	14.3	2.84	n.s.
Senna reticulata	21.6	0.9	–	–20.1	1.36	n.s.
Nectandra amazonum	12.4	13.3	–12.2	–11.3	2.89	n.s.
Crateva benthami	5	10.1	–0.6	5.2	2.00	n.s.
Tabebuia barbata	47.2	2.2	6.4	28.3	11.68	**
Vitex cymosa	105	51.2	–1.2	21.8	20.34	***

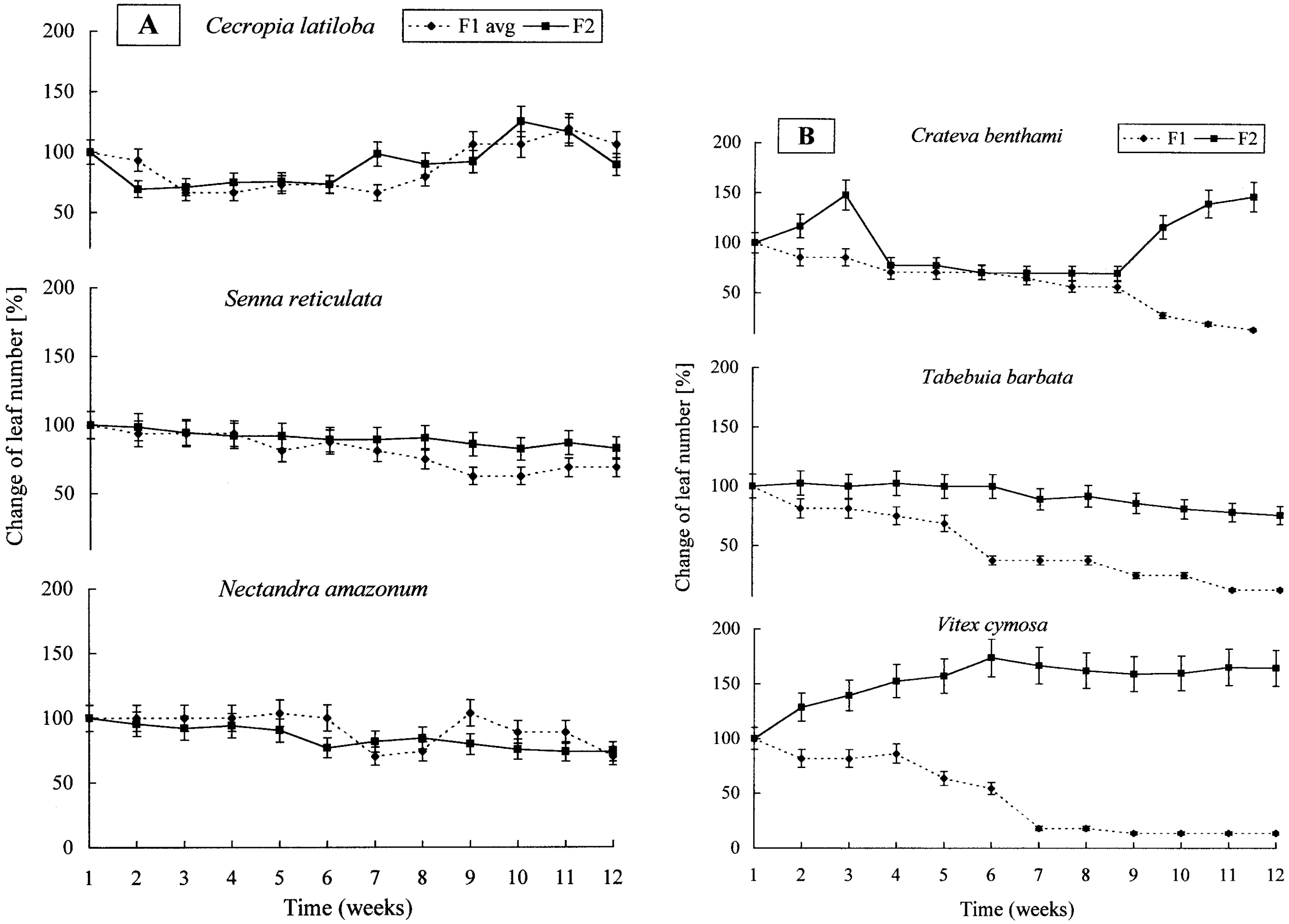

Fig. 2A,B Change in leaf number (in %) in waterlogged seedlings at 12 weeks. Mean leaf loss and production of new leaves in Exp. F1 and F2, with SD. **A** Evergreen species. **B** Deciduous species

In Exp. F2, mean seedling height increment was lower with waterlogging, submersion and drought than in the control; reductions were stronger in seedlings subjected to drought than in those subjected to waterlogging, except for *Tabebuia* (Table 4). Negative growth increments in *Senna* and *Nectandra* were caused by the drying of the stem apical meristem. After 12 weeks, the differences in height increment compared with the control were statistically significantly lower in the waterlogged seedlings of *Tabebuia* and *Vitex* (Table 4).

Seedling biomass and root:shoot ratio

The differences in biomass induced by waterlogging, compared to the control seedlings, ranged between an increment of 186% (*Crateva*) and a decrease of 45% (*Cecropia*). In all species, the changes, whether biomass increase or decrease, were highly significant after 12 weeks of experimental treatment (Table 5).

Total biomass was highest in the control, or in the waterlogged individuals (Exp. F2; Table 5). In waterlogged *Senna*, which had the highest biomass of all species and treatments, the production of adventitious roots was mainly responsible for the high biomass as shown by the high root:shoot ratio of the waterlogged *Senna* individu-

Table 5 Biomass (dry weight) of seedlings subjected to waterlogging for 12 weeks, compared to the control (=100%), in the six study species under experimental conditions after 12 weeks (Exp. F2). *F*-ratio and statistical probability (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$). *n* per species=12

Species	Control (g)	Waterlogging	Submergence	Drought	*F*-ratio	*P*
Cecropia latiloba	3.4	1.9	1.2	3.2	17.97	***
Senna reticulata	13.9	21.7	–	2.7	8.71	**
Nectandra amazonum	7.9	6.3	4.4	7.2	6.08	*
Crateva benthami	3.2	6.2	1.8	4.5	12.64	***
Tabebuia barbata	8.9	1.5	1.3	2.4	24.97	***
Vitex cymosa	5.9	4.6	0.6	3.2	35.39	***

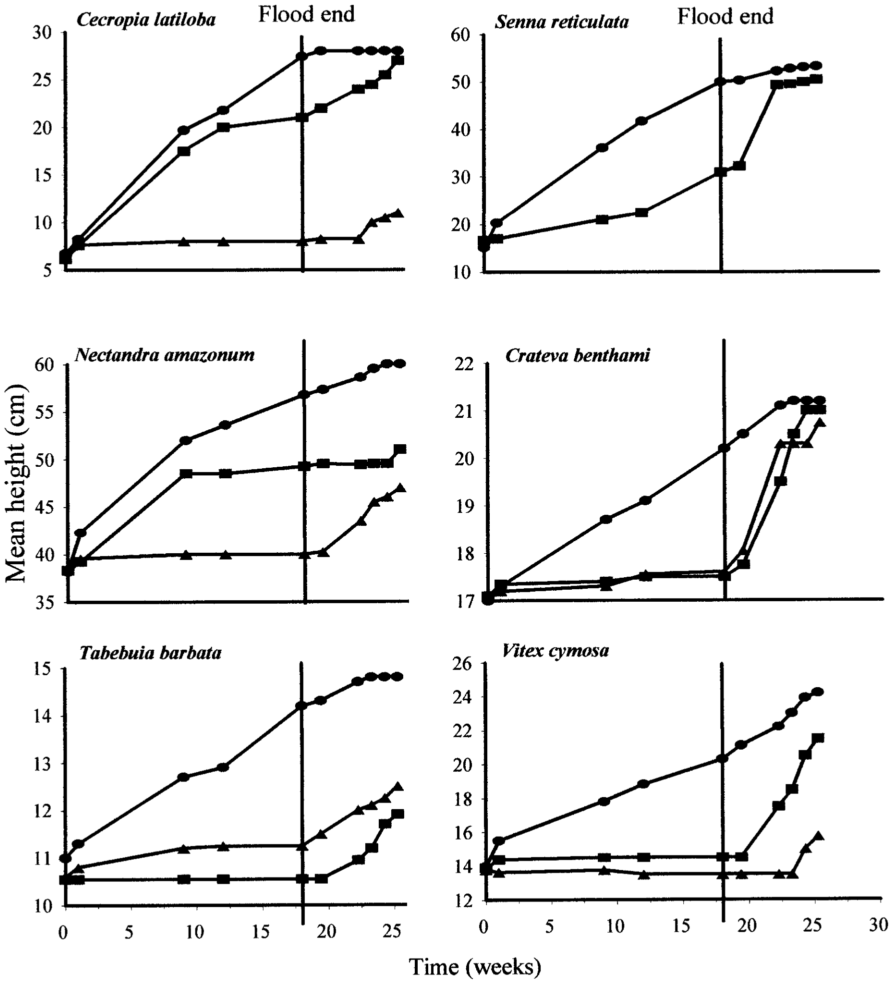

Fig. 3 Height growth (Exp. F1) in seedlings exposed to control conditions (*circles*), waterlogging (*squares*) and submersion (*triangles*) for 18 weeks, and recovery (Exp. R) after flood end: *Cecropia latiloba* (pioneer, evergreen), *Senna reticulata* (pioneer, evergreen; does not tolerate submersion), *Nectandra amazonum* (non-pioneer, evergreen), *Crateva benthami* (non-pioneer, deciduous), *Tabebuia barbata* (non-pioneer, deciduous), *Vitex cymosa* (non-pioneer, deciduous)

als (Exp. F2; Fig. 4). In the waterlogged individuals of *Cecropia*, *Nectandra* and *Vitex*, there were no differences compared to the control. In *Crateva* and *Tabebuia*, the waterlogged individuals had less roots than in the other conditions.

Leaf chlorophyll content, leaf water content and specific leaf weight

Chlorophyll contents varied between pioneer and non-pioneer species. Mean chlorophyll content per leaf dry weight was higher in the waterlogged pioneers than in

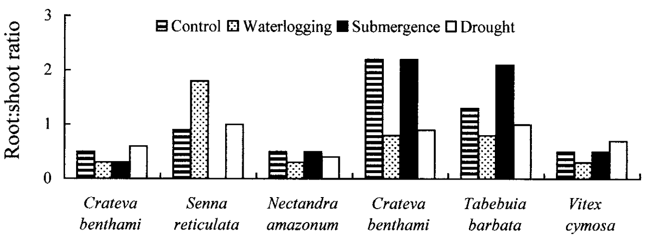

Fig. 4 Root to shoot ratio after 12 weeks in seedlings of six study species under experimental conditions (Exp. F2)

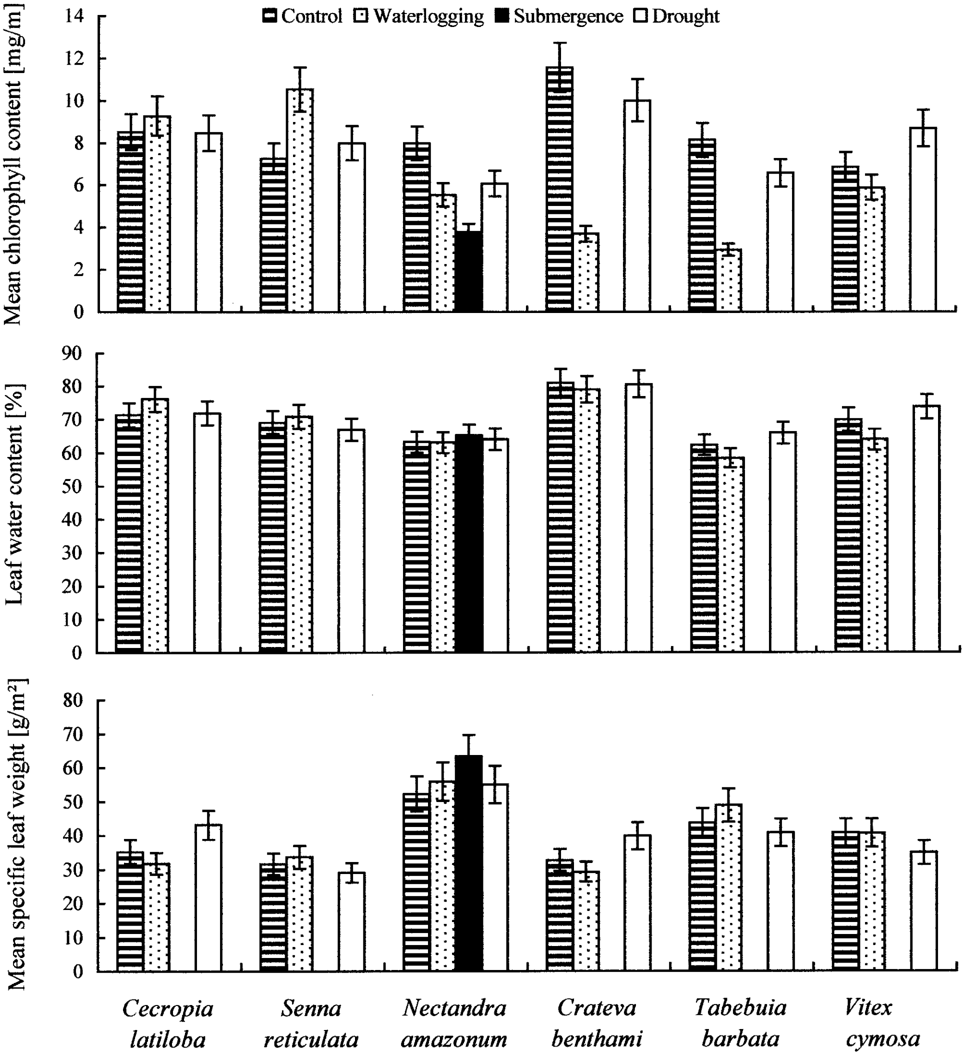

Fig. 5 Mean chlorophyll content per leaf dry weight, mean leaf water content and mean specific leaf weight with SDs after 12 weeks in seedlings of six study species under experimental conditions (Exp. F2). No data are presented for the submerged individuals because they shed all their leaves underwater, with the exception of *Nectandra amazonum*

Table 6 Changes in CO_2 assimilation and transpiration at maximum photon flux density (in %) with waterlogging, compared to the control (=100%), in seedlings of six study species under experimental conditions after 12 weeks (Exp. F2). *F*-ratio and statistical probability (**$P \leq 0.01$, ***$P \leq 0.001$, *n.s.* not significant). *n* per species=30

Species	CO_2 assimilation			Transpiration		
	Changes with waterlogging (%)	*F*-ratio	*P*	Changes with waterlogging (%)	*F*-ratio	*P*
Cecropia latiloba	–24.8	5.03	*	4.1	0.03	n.s.
Senna reticulata	15.3	2.04	n.s.	0.9	0.01	n.s.
Nectandra amazonum	21.7	6.83	**	26.7	13.58	***
Crateva benthami	–93.7	128.69	***	–80.5	90.67	***
Tabebuia barbata	–103.3	290.28	***	–104.9	240.88	***
Vitex cymosa	–53.0	70.02	***	–34.9	11.86	**

the controls, and lower in the waterlogged non-pioneers than in the controls (Exp. F2; Fig. 5). Leaf water content was similar between different treatments in the six species (Fig. 5). Specific leaf weight of the six species was not considerably different between treatments, except for *Cecropia* which had higher specific leaf weights with drought, and *Nectandra* with submergence (Fig. 5).

Photosynthetic CO_2 assimilation and transpiration

Mean CO_2 assimilation at maximum PFD (A_{max}) was equal or lower in all treatments compared to the control (Exp. F2; Fig. 6), with the exception of *Senna* (*F*-ratio 2.04, n.s.; Table 6) and *Nectandra* (*F*-ratio 6.83, $P \leq 0.01$) which had increased CO_2 assimilation with water-

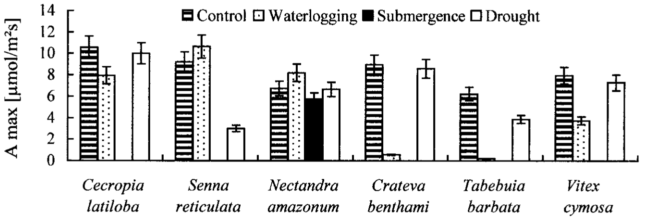

Fig. 6 Mean CO_2 assimilation at maximum photon flux density (A_{max}) with SDs after 12 weeks in seedlings of the six study species under experimental conditions (Exp. F2). No data are presented for the submerged individuals because they shed all their leaves underwater, with the exception of *Nectandra amazonum*. Measurements on submerged *N. amazonum* were performed 5 min after emergence and air drying

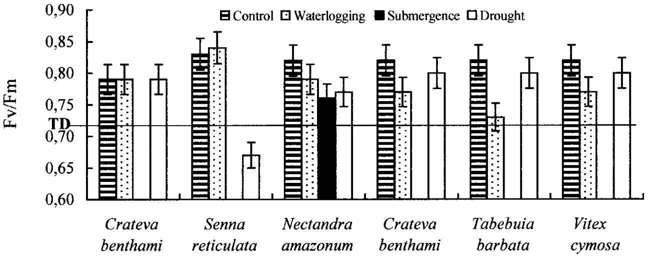

Fig. 7 Photochemical yield (Fv/Fm) with SDs after 12 weeks in seedlings of six study species under experimental conditions (Exp. F2)[*TD* threshold of disturbance (Störungsschwellenwert; Bolhàr-Nordenkampf and Götzl 1992)]. No data are presented for the submerged individuals because they shed all their leaves underwater, with the exception of *Nectandra amazonum*. Measurements on submerged *N. amazonum* were performed 5 min after emergence and air drying

logging. Five minutes after emersion, the submerged *Nectandra* had almost the same CO_2 assimilation as the control plants. Transpiration of the two pioneer species, *Cecropia* and *Senna*, did not change significantly with waterlogging (Exp. F2; Table 6). In *Nectandra*, transpiration increased by 27% in waterlogged seedlings (**$P \leq 0.001$), and in the deciduous species transpiration decreased by 35–105% (**$P \leq 0.01$) compared to the control (Exp. F2; Table 6).

Photochemical yield (chlorophyll fluorescence)

The photochemical yield Fv/Fm, after 12 weeks, was equal to the control in the waterlogged pioneers (*Cecropia*, *Senna*) (Exp. F2; Fig. 7). The waterlogged non-pioneers had 4–11% lower Fv/Fm than the control (Table 7). In all species and all conditions, Fv/Fm was higher than 0.72, a value which according to Bolhàr-Nordenkampf and Götzl (1992) indicates the lower limit of natural variation called 'Störungsschwellenwert' (threshold of disturbance; H.R. Bolhàr-Nordenkampf, personal communication). Only in *Senna* subjected to drought was Fv/Fm lower and entered the range of reversible damage (>0.6; Bolhàr-Nordenkampf and Götzl 1992). The submerged seedlings of *Nectandra*, 5 min after emersion had an Fv/Fm value similar to the control ($P > 0.05$).

Table 7 Changes in photochemical yield Fv/Fm (in %) with waterlogging, compared to the control (=100%), in seedlings of six study species under experimental conditions after 12 weeks (Exp. F2). *F*-ratio and statistical probability(*$P \leq 0.05$, **$P \leq 0.01$). *n* per species=30

Species	Changes with waterlogging (%)	*F*-ratio	*P*
Cecropia latiloba	0	0.09	n.s.
Senna reticulata	1.2	12.23	**
Nectandra amazonum	–3.7	3.39	n.s.
Crateva benthami	–6.1	2.31	n.s.
Tabebuia barbata	–11	16.32	**
Vitex cymosa	–6.1	7.06	*

Discussion

Morphological adaptations, growth and photosynthetic activity with waterlogging

The capacity to produce adventitious roots, lenticels and stem hypertrophy was found in all six species when they were waterlogged. The additional root aeration provided by these formations diminishes the oxygen deficiency in the rhizosphere and permits continuous growth and photosynthetic activity (Crawford 1989, 1992; Waldhoff et al. 1998). Therefore, height growth and new leaf production were not severely affected in the waterlogged seedlings, and could even increase. The capacity of *Senna*, in particular, to increase photosynthetic activity with waterlogging was probably linked to its high capacity to produce adventitious roots.

Under natural conditions in the floodplains, adventitious roots, lenticels or stem hypertrophy were observed only in a few juvenile and adult individuals of the study species. This might be related to the constant change in water level, with seedlings being waterlogged only for a few days to weeks and are soon totally submerged. This experiment shows the potential capacity to produce morphological adaptations which might have a function in lakes and ponds formed after the rivers recede at the beginning of the terrestrial phase. Another possibility is that the morphological adaptations result from the origin of most of the species from terra firme, and differences depend on the time taken to colonize the floodplains (Kubitzki 1989). Further experiments are needed to test the role of adventitious roots, e.g. by comparison with seedlings whose adventitious roots are artificially removed, or with seedlings of the same species established in the non-flooded terra firme. The root biomass formed under the different hydric conditions need not necessarily be related to flooding: plants in flooded soil allocated less biomass to roots. On the other hand, in *Mentha* *aquatica*, rhizome formation depended on plant size and was not affected by water level, which was explained by different abilities to oxygenate their belowground roots (Lenssen et al. 2000).

Effects of complete submersion

Complete submersion is a relevant factor for seedling establishment in central Amazonian floodplains. With the high oscillations in river levels, newly established plants cannot avoid a more or less prolonged period of total submersion. Without the capacity to withstand this, plant establishment is not possible on the lower levels in the flooding gradient. The seeds do not germinate while they are submerged. In some of the study species, mainly *Crateva* and *Nectandra*, seed opening and radicle extension were observed in submerged seeds, but none grew to a seedling (Parolin, in press). The species chosen for this study survived the experimental phase without losses, except for *Senna* which does not tolerate complete submersion. Its distribution in the flooding gradient is restricted to the uppermost levels, and new seedling establishment occurs only in years when the high water level is particularly low (Parolin 1998). The other five species, which survive submersion, occur along the entire flooding gradient. Their height growth stopped and leaves were shed as a consequence of submersion, leaving them in a state of rest. Soon after the water had receded, rapid resprouting of the leaves and high growth activities were observed, which are essential in the floodplains: the emersion phase can be very short at low levels in the flooding gradient, plants must maximize use of this short growth period. The fact that 5–12 weeks after the end of submersion, the seedlings reached the height of the control plants (Fig. 3) shows that they have a high ability to compensate the period of rest induced by submergence and return to their allometric proportions within the terrestrial period. The high root:shoot ratio measured in submerged *Crateva* and *Tabebuia* may be an important trait for growth and rapid recovery after the end of flooding in these species. *Nectandra* did not shed leaves underwater; their sclerophyllous character might be an adaptation to withstand total submergence. The comparably high photosynthetic activity which was measured in *Nectandra* 5 min after emersion shows that the physiological function of the leaves is preserved underwater. Whether this species is able to photosynthesize underwater is not known. Other species, e.g. the legume tree *Macrolobium acaciaefolium*, is presumably able to perform photosynthetic activity in submerged leaves (Schlüter and Furch 1992).

Effects of drought

In the seedlings subjected to drought, the patterns of leaf loss and leaf production were similar to those of the submerged seedlings. The strong leaf loss in both deciduous and evergreen species, and the low production of new leaves, show that drought can affect seedling establishment in the dry months of the non-flooded period with little precipitation. *Tabebuia* and *Vitex* produced new leaves with drought and showed little reduction of height increment compared to the other species. *Tabebuia* originates from tropical savannas (Kubitzki 1989) which might explain pre-adaptations to dry environments.

Senna had high growth reductions when subjected to drought, as shown by reduced biomass, $A_{\max}$ and Fv/Fm. This species is highly adapted to waterlogging and performed very high photosynthetic rates even when 80% of the tree was submerged in the field (Parolin 1998, 2000), but it appears to be highly susceptible to complete submersion and drought.

The two temporally separated flooding experiments

The two flooding experiments (Exp. F1 and F2) were performed in the same conditions, but at different times in the annual cycle (Fig. 1). Since the results were comparable in the two experiments, the morphological, phenological and physiological responses were directly linked to the treatments, i.e. to waterlogging and submergence in the experimental tanks, and not to other environmental conditions, such as precipitation and light incidence.

The only differences between the results of the two experiments were found in the deciduous species subjected to waterlogging: in Exp. F1, leaf number decreased continuously, but not so in Exp. F2 (Fig. 2B). In Exp. F1, leaf loss was higher (*Crateva*, *Tabebuia* and *Vitex*), and the production of new leaves was lower (*Crateva*) in the period corresponding to high precipitation and rising river levels. With respect to precipitation and related air humidity and irradiance, the rainy season (December to May) is presumably more favourable for plant growth, and the need to reduce ethe transpirational surface is small (Reich and Borchert 1982). Thus, a lower leaf number should have been expected in Exp. F2 which corresponds to the dry season, but it was lower in Exp. F1. This might be related to intrinsic factors, i.e. genetically fixed phenological rhythms, or to the production of seasonal leaf phenotypes with different photosynthetic characteristics, as was found for trees in tropical dry forests: the leaves produced at the end of the wet season had higher photosynthetic capacities than leaves produced during the early rainy season (Kitajima et al. 1997). Further studies of photosynthetic activity in relation to vegetative phenology and leaf age are needed here.

In the field, adult trees of the chosen deciduous species reduce leaf number towards the beginning of waterlogging (Parolin 2000). With the rise in river levels, the negative influence of the lack of oxygen in the rhizosphere on plant growth is compensated by a reduction in transpirational surface, specifically leaf number (Borchert 1983). This pattern seems to be reflected in the phenological behaviour of the seedlings in the experiments, which is synchronous to that of adult trees in the field.

A reduction in the transpirational surface by a decrease in leaf area is achieved in *Senna* which produces new leaves almost constantly and is thus able to react to environmental conditions very quickly (P. Parolin, unpublished data).

Role of different growth strategies

Every species exhibited its individual pattern of responses to flooding or drought rather than fitting into a pattern linked to the growth strategy (evergreen/deciduous, pioneer/non-pioneer). The growth strategies of the study species did not seem to be relevant to the efficiency of growth and survival. Although deciduousness is often seen as an adaptation against flood or drought stress ("drought avoidance strategy"; Borchert 1983; Medina 1983; Wright and Cornejo 1990), in the study species, a deciduous habit was as effective as an evergreen one for growth and survival.

Conclusions

This study suggests that the different hydric conditions (waterlogging, submergence and drought) are directly responsible for the changes in growth and metabolism in the seedlings of the study species under the given experimental conditions. To a certain extent, other factors influence the reactions to flooding: in the chosen deciduous species, the differences between the two temporally separated experiments indicated that genetic factors may play a role. But in these species also, waterlogging, submergence and drought were directly responsible for morphological, phenological and physiological changes which occurred in both experiments, at different times of the year.

A further conclusion which can be drawn from these results is that species that grow and photosynthesize well when waterlogged do not necessarily do well when submerged. These two types of flooding events require different adaptations for growth and survival.

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