DIVERSITY OF ADAPTATIONS TO FLOODING IN TREES OF AMAZONIAN FLOODPLAINS

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Abstract

One of the biggest flood pulsed environments worldwide occurs in the floodplain forests of the Amazon basin. Biodiversity in terms of species richness is high in these forests. More than 1000 flooding tolerant trees grow there, many of them are endemic. Also functional diversity in terms of life cycle strategies and ecophysiological responses to the periodical flooding is remarkable in this ecosystem. Tree species show a large variety of responses to the extreme changes of hydric conditions in the annual cycle. Difficult conditions for tree growth are caused by 3-7 months uninterrupted periods of waterlogging or even submergence with high amplitudes, rapid changes of water levels, anoxic conditions in the rhizosphere, and high sedimentation. High diversity may result from the fact that this extreme site has only a reduced number of abiotic factors representing stress for the trees, and the regular disturbances may even represent a driving force for resistance and adaptive evolution. The high complexity of the system and the short but regular occurrence of factors enhancing tree growth in the low-water period allowed the formation of highly diverse survival strategies. Most tree species have wide ranges of ecological tolerance. However, these ranges are still narrow enough to allow a spatial succession along the flood gradient supporting the theory of continuous adaptation to different habitats as driving force for diversification. In fact, functional diversity has clear consequences for plant distribution along gradients of flooding intensity, which are reflected in a clear vegetation zonation in Amazonian floodplain forests.

Keywords: flooding tolerance, submergence, seedling establishment, Amazonian floodplain forests

Amazonian floodplain forests

One of the biggest flood pulsed environments worldwide occurs in the floodplain forests of the Amazon basin (Figure 1). In these periodically flooded forests which cover a total area of 300.000 km^2 (Junk, 1997), biodiversity is very high, not only in in terms of species richness but also in terms of life cycle strategies and ecophysiological responses to the periodical flooding. Trees display a huge variety of adaptations and a high functional diversity (Parolin et al. 2004). The aim of this paper is to outline the diverse adaptations encountered in a dozen tree species analysed so far, and in pointing out the lacks of knowledge we still face knowing that we understand very little of the more than 1000 flooding tolerant trees of Amazonian floodplains, many of which are endemic (Wittmann et al., 2006; Wittmann et al., 2010).

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Flooding stress

Floodplains are harsh environments physiologically. Stress on plants imposed by flooding of the soil and deeper submergence constitutes one of the major abiotic constraints on growth, species distribution and agricultural productivity (Jackson & Colmer, 2005). When an organic soil is flooded, the oxygen available is quickly depleted through metabolism by organisms that use oxygen. Because oxygen diffuses much more slowly through water than through air, atmospheric oxygen does not reach the roots.

In any discussion of the physiology of oxygen deprivation in perennial plants it is important to distinguish between short-term and long-term tolerance. Species that are only tolerant of short periods of anoxia frequently accelerate glycolysis and thus overcome temporary energy shortages (Crawford et al., 2003). By contrast, species that are able to endure long-term anoxia of oxygen deprivation have been shown to down-regulate their metabolism. In Amazonian floodplains, this distinction is reflected in a clear vegetation zonation along the flooding gradient, with little flooding tolerant trees on the higher levels and highly flood tolerant trees on the low levels of the inundation gradient (Junk, 1989; Ferreira, 2000; Wittmann & Junk, 2003; Parolin et al., 2004). This zonation is similar to temperate forests where the hydrological conditions determine to a large extent zonation patterns (Blom, 1999): for softwood species, such as Salicaceae, the interaction between water levels and timing of seed dispersal is the dominating process determining their establishment success on river banks. Their strategy is well adapted to irregular, high and prolonged floods. Hardwood species are more flood-sensitive and inhabit the more stable sites which often are high in the flooding gradient. On the other hand, one of the most flooding tolerant species in igapó is the hardwood tree *Eschweilera tenuifolia* which tolerates waterlogging for up to four consecutive years (Figure 2).

Flooding stress has resulted in a wide range of biochemical, molecular and morphological adaptations that sanction growth and reproductive success under episodic or permanently flooded conditions that are highly damaging to the majority of plant species (Jackson & Colmer, 2005). Not so for the hundreds of tree species of Amazonian floodplains. All trees inhabiting Amazonian floodplains are plants whose growth is not inhibited by flooding (Gill, 1970). They have a number of adaptations and highly diverse survival strategies which enable them to colonize efficiently the floodplains despite the huge flooding amplitude and duration (Parolin et al., 2004).

A new development in flooding ecology is the unravelling of the molecular regulation of hormonally controlled processes. The expression of an ethylene receptor gene in *Rumex palustris* was highlighted by Blom (1999) and it may be expected that Amazonian floodplain trees exhibit similar genes but nothing is known here to date.

Adaptations to flooding in plants are usually considered as either tolerance adaptations or else avoidance mechanisms (Crawford et al., 2003). In the former, metabolic adaptations have been found which allow some plants to endure anaerobic conditions for a length of time sufficient to overcome the period of oxygen deprivation caused by flooding. In the latter, aerenchyma and other structures facilitate aeration of the inundated root. Both these aspects of flooding have been extensively discussed (Armstrong et al., 1994) and are by no means mutually exclusive as there are examples of flood-tolerant species which employ both types of adaptation categories (Crawford et al., 2003), and several more can be found in Amazonian floodplains.

Flooding is the collective term for soil waterlogging and submergence (Jackson & Colmer, 2005). It causes substantial stress for terrestrial plants, particularly if the floodwater completely submerges the shoot as was found in various temperate herbs (Visser et al., 2003; Mommer & Visser, 2005). Especially when trying to understand the distributional patterns of species it is important to differentiate between their being subjected to waterlogging or complete submergence.

Waterlogging means that there is a substantial change in the rhizosphere: a flood sensitive plant when inundated rapidly loses its oxygen supply to the roots. This shuts down aerobic metabolism thus reducing nearly all metabolic activities such as cell division and nutrient absorption. Anaerobic glycolysis works for some needs inititally, but it is inefficient, and toxic endproducts accumulate. These two problems will cause death fairly rapidly in trees which are not adapted to waterlogging conditions.

The formation of aerenchymatous roots and the capacity to elongate shoot parts upon submergence are among the main responses of surviving plants (Blom, 1999). When the flood covers only the roots and parts of the stem, the protrusion of leaves above the water surface may enable the plants to restore a free diffusion pathway between the air and the root system which is of vital importance for some species (Laan and Blom, 1990). Contrary to this, with complete submergence no such oxygen supply is possible. The main problems during submergence are shortage of oxygen due to the slow diffusion rates of gases in water, and depletion of carbohydrates, which is the substrate for respiration (Mommer & Visser, 2005). These two factors together lead to loss of biomass and eventually death of non-adapted submerged plants.

As said previously, trees in Amazonian floodplain forests are subjected to flooding and/or waterlogging depending on their position in the flooding gradient. Small trees and seedlings on every position are likely to be completely submerged. Thus, different combinations of adaptations and strategies have evolved to cope with flooding stress (Figure 3). The species which do not tolerate submergence have an ‘escape’ strategy and need adaptations which are not necessarily required by the species growing on low levels in the flooding gradient that tolerate prolonged submergence which they cannot escape from (Parolin, 2002a). Species with the ‘escape-strategy’ tend to grow fast on the higher levels in the flooding gradient, in order to maintain at least part of the plant above the water surface. Rapid juvenile growth enables the plants to extend their foliage as high as possible before the normal flood level returns (Parolin, 2002a). On low levels in the flooding gradient, with water columns exceeding 10 metres, the probability of a seedling to be able to grow over the water level is low and only highly flood tolerant species can survive there. They need other strategies than fast growth to tolerate several weeks to months of submergence, e.g. physiological and morphological adaptations (Siebel et al., 1998). Obviously these two contrasting patterns of plant adaptation to flooding, submergence tolerance versus escape from submergence, are not necessarily mutually exclusive, and highly tolerant, fast-growing species may be expected as well as not tolerant, slow growing species.

Physiological adaptations

The aquatic phase occurs in a period in which temperature and light conditions are optimal for plant growth and development, implying the need for adaptations (Parolin et al. 2004). Trees do not only persist in a dormant state, but grow vigorously during most of the year, including the aquatic period. The flooding period of Amazonian floodplains does not correlate with a temperate winter (‚physiological winter' *sensu* Gessner, 1968) implying reductions of growth and metabolic activity to complete dormancy as observed for trees of temperate forests in the period of unfavorable growth conditions. Although in Amazonian floodplains the terrestrial phase is the main growth period for tree species, at high water the periods of limited growth last only few weeks, and new leaf flush, flowering, fruiting and wood increment occur in most trees while flooded (Worbes, 1986, 1989, 1997; Parolin et al., 2002; Schöngart et al., 2002). Since trees which have an active sap flow have a need for adequate supplies of carbohydrate also in the flooded period (Crawford et al., 2003; Ferreira et al, 2009), a set of metabolic adaptations are required for survival and growth despite flooding.

Anaerobic metabolism

Anoxia can be one consequence of waterlogging and submergence of plants. Anoxia in plant tissues reduces the rate of energy production by 65-97% compared with the rate in air. Thus, adaptation to anoxia always includes coping with an energy crisis (Gibbs & Greenway, 2003). In all the flood-tolerant forests so far examined it would appear that possession of adequate carbohydrate reserves is a prerequisite for flooding tolerance (Crawford et al., 2003). In fact, carbohydrate levels at the end of the dry season in most Amazonian floodplain species are high, with the exception of palms and the most aquatic of other woody species, for which the dry season is the stress period and the wet season the period when they accumulate carbohydrate reserves (Scarano et al., 1994).

Species with an insufficient oxygen supply need to switch over to fermentation, resulting in subsequent transport of ethanol to the leaves and emission of ethanol and its oxidation products. Species with improved oxygen supply of the roots, like *Salix martiana*, will produce no or rather low amounts of ethanol (Haase et al., 2003).

The induction of activity of fermentative enzymes such as alcoholdehydrogenase (ADH), lactate dehydrogenase (LDH), glutamate-pyruvate transaminoferase (GPT), and malate dehydrogenase (MDH) has been observed under anaerobic growth conditions in greenhouse experiments on young seedlings and trees (Schlüter & Furch, 1992; Schlüter et al., 1993; De

Simone et al., 2002a). In waterlogged seedlings of *Himatanthus sucuuba*, ADH concentrations rose 15 days after the onset of hypoxic conditions and remained high throughout the 120 days of the experimental period (Ferreira, 2002). In seeds of the same species collected in non-flooded terra firme, ADH concentrations decreased after 30 days and seedling mortality was 100 % at the end of the experiment (Ferreira et al, 2009).

Kreuzwieser et al. (1999, 2000) showed that roots of vascular plants affected by anoxia produce high amounts of ethanol which is transported into the leaves where it can be re-metabolized by oxidation, thereby generating acetaldehyde and acetic acid as an intermediate; however, a fraction of these compounds may be lost to the atmosphere.

The emission of ethanol and acetaldehyde in Amazonian flood plain tree species is inducible in response to flooding in many species (Rottenberger, 2003). A pronounced diurnal pattern in acetaldehyde and ethanol emissions was observed with zero exchange at night, a strong emission burst in the morning, followed by a decrease in the afternoon, resulting from an ethanol accumulation in the roots at night when stomata are closed and transport is restricted by a lack of transpiration, followed by transport to the leaves driven by the light-induced transpiration stream as soon as stomata open.

There are large inter-specific differences not only in the ethanol production in the roots but also in the subsequent metabolic conversion inside the leaves. While *Tabernaemontana juruana* emits predominately ethanol, suggesting a limitation of leaf ADH, *Laetia corymbulosa* is a strong acetaldehyde emitter, indicative of a high ADH activity. Hence, the differences in emission rates can be related to species-specific metabolic adaptations, reflected by increased ADH activity and/or morphological adaptations of the plant to improve the oxygen availability in the roots, like formation of adventitious roots and development of aerenchyma.

Underwater photosynthesis

Light increases the survival of terrestrial plants under water, indicating that photosynthesis commonly occurs under these submerged conditions – at least in temperate herbs as described by Mommer & Visser (2005). Such underwater photosynthesis increases both internal oxygen concentrations and carbohydrate contents, compared with plants submerged in the dark, and thereby alleviates the adverse effects of flooding. Although conditions under water are unfavourable with respect to light and carbon dioxide supply, photosynthesis may provide both oxygen and carbohydrates, resulting in continuation of aerobic respiration (Mommer & Visser 2005). Additionally, several terrestrial species show high plasticity with respect to their leaf development (Waldhoff & Furch, 2002; Waldhoff, 2003; Mommer & Visser, 2005; Waldhoff & Parolin, 2010). In a number of species, leaf morphology changes in response to submergence, probably to facilitate underwater gas exchange. Such increased gas exchange may result in higher assimilation rates, and lower carbon dioxide compensation points under water, which is particularly important at the low carbon dioxide concentrations observed in the field. As a result of higher internal carbon dioxide concentrations in submergence-acclimated plants, underwater photorespiration rates are expected to be lower than in non-acclimated plants (Mommer & Visser, 2005). Furthermore, the regulatory mechanisms that induce the switch from terrestrial to submergence-acclimated leaves may be controlled by the same pathways as described for heterophyllous aquatic plants.

In several Amazonian floodplain species, submerged leaves maintained their vitality despite almost complete darkness below water (Parolin et al., 2009): even at water depths of 1-7 m, with a quantum flux of 1-10 µmol $m^{-2}s^{-1}$ (PAR), Fv/Fm values lay below this threshold, showing a negative correlation with the duration of submergence (Waldhoff et al., 2002). When lighted, these submerged leaves began electron transport, which, however, appeared to be inhibited shortly after the start. The question about the mechanisms that maintain the photosynthetic apparatus almost undamaged during the submersion is still open. Leaves of adult trees that were submerged in darkness (> 1m depth) recovered the Fv/Fm-yield while still under water, during falling water levels, independently of how long the leaves were submerged prior to the measurements. There is a correlation between light intensity and the maintenance/recovery of the photosynthetic apparatus (PSII). In a greenhouse experiment, the light harvesting complex of submerged seedlings of *Tabernaemontana juruana, Pouteria glomerata, Laetia corymbulosa, Gustavia augusta*, and *Nectandra amazonum* did not deteriorate, Rubisco was decomposed only to a low extent, and new proteins with unknown function were synthesized and accumulated during submergence (Krack, 2000). The same seedlings survived submergence only if they were well supplied with nutrients before flooding and if they were at least five months old (Krack, 2000), indicating that these processes imply high energy costs. Nevertheless, the energy balance in submerged seedlings is highly effective: in the palm *Astrocaryum jauari*, the energy reserves in the roots were not exhausted after 300 days of submersion (Schlüter et al., 1993).

Structural adaptations

Aerenchyma

The primary morphological plant strategy in response to flooding is the development of air spaces in the roots and stems which allow diffusion of oxygen from the aerial portions of the plant into the roots (Jackson & Armstrong, 1999). Thus the roots do not have to depend on getting oxygen from the soil. "Regular" plants may have a porosity (% air space in roots and stems) of 2-7% of their volume, while a wetland plant may be up to 60% pore space by volume (http://kingfish.coastal.edu/biology/sgilman/778Plants.htm). Schizogeny and lysigeny, are the common patterns of root cortex lacunar formation in most wetland higher plants (Evans, 2004; Seago et al., 2005). Aerenchyma can substantially reduce internal impedance to transport of oxygen, nitrogen and various metabolically generated gases such as carbon dioxide and ethylene, especially between roots and shoots (Jackson & Armstrong, 1999). Such transport lessens the risk of asphyxiation under soil flooding or more complete plant submergence, and promotes radial oxygen loss from roots leading to oxidative detoxification of the rhizosphere.

The promotion of longitudinal oxygen transport by aerenchyma appears to be essential for improving the root's energy status for water and nutrient uptake (Jackson & Armstrong, 1999).

Micro-electrode investigations on 2-3 months-old cuttings from *Salix martiana* showed that their well oxygenated aerenchymatous adventitious roots were able to build up a several millimeters thick oxygenated layer around the whole roots, suggesting a mechanism of detoxifying reduced phytotoxins by radial oxygen loss (ROL) (De Simone et al., 2002a, Haase et al., 2003). In older roots from adult trees which are submerged by a several meter high water table, the formation of aerenchyma may be less important for longitudinal oxygen transport, because the lacunae are destroyed by secondary root thickening and the long gas diffusion distances (Parolin et al. 2004). In this case an improvement of the root's energy status is achieved by reducing the number of oxygen-consuming cells in the root cortex (De Simone et al., 2002b).

Root suberization

The formation of suberized and lignified barriers in the exodermis is part of a suite of adaptations to flooded or waterlogged conditions, adjusting transport of solutes and gases in and out of roots (De Simone et al., 2003). The deposition of suberin in radial (Casparian bands) and tangential cell walls of the exodermis equips the root with a hydrophobic barrier that contributes to the plant's overall resistance (De Simone et al., 2002a). It is supposed that a heavily suberized exodermis limits radial oxygen loss (ROL) from the root to the rhizosphere, conserving oxygen for root growth in oxygen-depleted soils (Colmer et al., 1998). Determination of oxygen distribution in the roots and rhizosphere of four analysed tree species revealed that radial loss of oxygen could be effectively restricted by the formation of suberized barriers but not by lignification of exodermal cell walls (De Simone et al. 2003).

Suberin also acts as a component of the wound- and pathogen-induced plant defense response, preventing infection by microbial pathogens (Mohan et al., 1993a, b; De Simone et al., 2003).

Suberization appears to prevent loss of water and stored solutes into the rhizosphere during drought periods, which may represent an important protective feature during the terrestrial phase (Zimmermann et al., 2000; Parolin et al., 2010a).

Adventitious roots and hypertrophy

Soil inundation usually inhibits root formation and branching, and growth of existing roots and mycorrhizae (Kozlowski, 1997). This is not the case in Amazonian floodplains, where tree roots grow below water and mycorrhizae are not affected (Meyer, 1991).

The development of adventitious roots – i.e. roots above the ground or above the anoxic zone or above the level of the water – is important in flooded environments. These roots grow in the oxygenated layer at the surface of the flood-water table, and together with hypertrophied lenticels at the stem above the water table, improve the internal oxygen status by facilitating the entry of oxygen into the root and the stem by the shortest possible pathway. Several tree species, e.g. *Salix martiana* and *Tabernaemontana juruana*, under experimental conditions respond to low oxygen concentrations by forming adventitious roots capable of longitudinal oxygen transport (Haase et al., 2003). Thus, the formation of aerial roots may compensate for losses of respiration (Kozlowski, 1984; Schlüter & Furch, 1992).

While under experimental conditions with stable water levels most species show the potential to produce adventitious roots, in the field they are seldom found, probably because their adaptive value with rapidly changing water levels is to question (Parolin et al., 2004).

Pneumatophores, knees and pneumatodes

Pneumatophores which e.g. in mangroves stick out of the mud from the main roots and are exposed during low tides, and “knees” as typical adaptations to enhance root aeration (Granville, 1974) are absent in várzea trees (Junk, 1984). They were described only for *Pithecellobium latifolium* occurring in “tidal várzea” near the mouth of the Amazon (Scarano et al., 1994), where tidal floodings with low water columns are common. According to Kubitzki (1989), their formation is impeded in Central Amazonia because of the high amplitudes of water-level fluctuations. On the other hand, aeration through respiratory apparatus like pneumatodes is potentially possible: under experimental conditions several species produced these negatively geotropic aerial roots in a similar way as described for the mangrove species *Laguncularia racemosa* (Geissler et al., 2002) or the palms *Mauritia flexuosa* and *Euterpe oleracea* (Granville, 1974).

Plank-buttresses and stilt roots

Richards (1952) mentioned the high abundance of buttresses and stilt roots in tropical freshwater swamp forests, as compared to non-flooded habitats. Segal *et al.* (1987) stated that buttressing served as reliable indicator for inundation in a study where wetland boundaries were delimited by abrupt and obvious changes in ecosystem structure. Ayres (1993) described that in várzea forests near Tefé, Amazonia, frequency of tree species forming buttresses is linked to the flood-level gradient. He stated that many species in low várzea develop buttresses to increase plant support as an adaptation to water velocity, high sedimentation rates or erosion. Buttressing or butt swell may be an example of hypertrophy, an increase in the diameter at the base of the stem. The role of this is supposed to be the increase of air space which allows for increased movement of gases. Besides that, the wide base provides extra support for shallow rooted structures on a soggy substrate.

According to Navez (1930), buttress formation is the direct response of the tree to the mechanical stimulation of strains set up by gravity and wind. In fact, buttressed roots are effective as structural members, supporting large trees on substrates that offer poor anchorage, since they reduce danger of tree failure (Henwood, 1973). Plank buttressing in tropical trees may also be related to a competitive mechanism, since the physical presence of buttresses presumably hinders the neighbor establishment of other large trees and of soil-rooted woody vines (Black & Harper, 1979).

Different types of aboveground roots are closely related to flooding duration and habitat dynamics (Figure 4, 5; Wittmann & Parolin, 2005). Plank buttressing is more common on sites subjected to lower sediment rates. Where sedimentation rates are high, e.g. on natural stands of *Salix martiana*, adventitious roots can replace the function of the ordinary root system, which often dies under several decimetres of sediment. In fact, the primary belowground root of *Salix martiana* reaches depths of up to six meters, but the main root function is shifted to several well-defined layers of fine secondary roots stacked up along the main root with a space of 30-40 cm. The same was found in *Alchornea castaneifolia*, which also produced stilt roots up to 40 cm above the ground surface (Wittmann & Parolin, 2005).

Pressurized gas transport

Pressurized gas transport is considered by some authors as a specific adaptation to flooding enhancing the improvement of oxygen transport to the roots of wetland trees (Grosse et al., 1991; Graffmann et al., 2008). In some Amazonian floodplain species, convective gas transport by pressurized ventilation is thought to improve the oxygen supply of the roots as shown for floating plants, grasses and temperate trees like alder (*Alnus glutinosa*) (Grosse, 1997). This mechanism is described as such: the heat energy of sun irradiation drives a gas flow from the stem base to the roots. Gas transport between the loading area (stem base) and the sink area (roots) depends on the permeability of gases in the plant tissue. Tracer gas measurements give information about this gas permeability (Grosse et al., 1996; Grosse, 1997). Furthermore the influence of induction of pressurized ventilation to the tracer gas transport rate gives information about the importance of convective gas flow by pressurized gas transport to root aeration (Grosse, 1997). Polarographical measurements showed that pressurized gas transport seems to be not a species specific adaptation-mechanism, but typical for plants of temporarily flooded habitats (Grosse, 1997). The central hypothesis is that pressurized gas transport significantly contributes to internal aeration of roots in Amazonian floodplain saplings growing on the higher levels in the flooding gradient, with low water columns, and is an important adaptation for establishment in these temporarily inundated habitats in the weeks of rising and lowering water levels. Gas transport measurements carried out under experimental conditions with saplings of five Amazonian tree species showed that internal aeration of the roots was improved under conditions of pressurized gas transport (Graffmann et al., 2008).

On the other hand, in a recent publication, Armstrong & Armstrong (2005) stated that pressurized gas flow to submerged roots does not occur to any significant degree in alder, but stem photosynthesis, using internally sourced CO_2 from respiration and the transpiration stream, may play an important role in root aeration in young trees and measurably affect the overall carbon balance of this and other species. This statement was based on the observation that the claims for pressurized gas flow generated in the stem by a light-induced thermo-osmosis have seemed inconsistent with root anatomy. In their measurements, Armstrong & Armstrong (2005) found that internal pressures rose by several kPa when shoots were exposed to high light flux and radial O_2 loss (ROL) increased substantially, but both were due to O_2 accumulation from stem photosynthesis using internally sourced CO_2. Increased stem pressures had little effect on O_2 transport, which remained largely diffusive. Oxygen flux from stems in high light periods indicated a net C gain by stem photosynthesis (Armstrong & Armstrong, 2005). Further measurements and research is needed to understand this mechanism and its adaptive advantages.

Nitrogen fixation

Stem-nodulation and nodulated adventitious roots were observed in various species and are understood as adaptations that allow legumes to fix N_2 in a flooded environment (James et al., 2001). In fact, the frequency of nodulation among genera was found to be higher in flooded than in non-flooded sites in both várzea and igapó, indicating that nodulation may even be favored in flooded areas (Moreira et al., 1992).

Leaf structure

The xeromorphic leaf structure described for trees of tropical forests (Roth, 1984) is typical also for the floodplain species (Waldhoff & Furch, 2002; Waldhoff, 2003). It helps to cope with insufficient water supply to the tree crowns during the aquatic phase, and with periods of drought occurring occasionally in the terrestrial phase (Parolin et al., 2010a). Apparently, the leaves which are not shed and maintain their functions despite prolonged submergence do not require different or additional morphological and/or anatomical traits.

Resprouting

A high reiteration capacity and vigorous resprouting after damage through rotting or mechanical injury may be considered as a further adaptation to effective establishment (Parolin et al., 2004). It is not only found in early successional species like *Senna reticulata* or *Cecropia latiloba*, but also in species of later successional stages as for example *Platymiscium ulei*, *Piranhea trifoliata* and *Tabebuia barbata* (Worbes, 1997; Parolin, 2001a). *Salix martiana* shows intensive vegetative propagation through parts of broken stems, and the lower branches of *Eugenia inundata* become rooted (Worbes, 1997), thus contributing to fast and effective establishment in the short terrestrial period.

Phenological adaptations

Leaf shedding

The vegetative phenology may regulate water loss and gas exchange. Leaf shedding during the aquatic phase has been documented to occur not only in deciduous species but also in evergreen trees, which tend to reduce new leaf production at high water levels (Parolin et al., 2010b; Parolin et al., 2002).

Deciduousness may be advantageous at times of low tree water status: water loss of the trees is reduced by the reduction of the transpiring area through the shedding of leaves (Borchert, 1991). If leaf shedding cannot be afforded, for instance because of low nutrient availability, other protections against water loss can be found, such as sclerophyllous leaves which are typical for evergreen species (Medina, 1983) and are found especially in igapó trees (Prance, 1979).

In seasonally dry regions like savannas, where many species from the floodplains originate (Kubitzki, 1989), trees shed their leaves and reduce the production of new leaves in a period of dry conditions (Reich & Borchert, 1982; Wright & Cornejo, 1990; Gribel *et al.,* 1999). This pattern is described as a strategy of 'drought-avoidance' (Medina, 1983). In floodplains, where flooding disturbs the root function and thus water uptake, the water status of a tree is reduced (Gill, 1970; Kozlowski, 1984; Meyer, 1991; Blom & Voesenek, 1996).

A reduction in the transpirational surface by decreasing leaf area is achieved in *Senna reticulata*, which produces new leaves almost constantly and thus is able to react to environmental conditions very quickly (Parolin, 2001b). Complete deciduousness may last for some months as observed for *Pseudobombax munguba*, *Ceiba pentandra* and other Bombacaceae (Gribel et al., 1999), but it may be as short as four weeks (e.g. *Tabebuia barbata*) despite waterlogging durations of seven months (Parolin, 1997).

On the other hand, leaf shedding may not be a strategy but rather an endogeneously triggered rudiment related to the species' origin. Trees of the Bombacaceae family for example originate in semi-arid environments and are adapted to tolerating periodical drought – drought avoidance being enhanced by leaf shedding. When the species migrated into the floodplains (Kubitzki, 1989), not all of them lost their genetically fixed phenological patterns. Deciduousness may then have assumed new functions in the floodplains, e.g. enhancing pollination by bats.

Fruit maturation and seed release

The main means of dispersal in Amazonian floodplain trees are hydro- and ichthyochory (Gottsberger, 1978; Goulding, 1980; Moegenburg, 2002; Mannheimer et al., 2003), which is emphasized by a close correlation between the timing of flooding and fruit maturation (Ziburski, 1991; Parolin et al., 2002).

In fact, the most homogeneous phenological trait among the floodplain trees is the period of fruit maturation during high water or at the end of the flooded period, as was first documented by Ziburski (1991) for 33 tree species from várzea and igapó.

The diaspores show morphological adaptations which enhance floatation, like spongy tissues or large air-filled spaces (Kubitzki & Ziburski, 1994; Williamson et al., 1999; Williamson & Costa, 2000).

Reproductive adaptations

Submergence tolerance and dormancy of seeds

The seeds of Amazonian floodplain trees are extremely submergence tolerant. They even need water to maintain their viability: as long as the seeds of 12 analysed species were in the water, they remained viable (Parolin & Junk, 2002). Seeds which were kept in the air dried or decomposed within a few days (e.g. *Tabebuia barbata*, *Nectandra amazonum*) or weeks (e.g. *Senna reticulata, Aldina latifolia*), whereas submerged seeds of ten of the 12 species remained viable for at least 60 days if the water was changed frequently (Parolin, 2001a). This stands in contrast to the majority of land plants, whose seeds lose their viability if submerged for prolonged periods (Hook, 1984). Seeds that opened under water had a higher viability than seeds that remained closed: a higher percentage germinated, and they germinated faster after water receded, compared with the non-swollen seeds of all species (Parolin et al., 2009).

Most seeds have the ability to survive long periods of flooded conditions while floating – often in a dormant state (Ziburski, 1990). Many species which are not dormant, germinate faster when subjected to flooding than without a previous contact with water (Ziburski, 1991). Many seeds are dormant for several months, as long as they are covered by water (Ziburski, 1991), but many seeds lack dormancy, and a precise timing of diaspore release during inundation is important for the dispersal and germination immediately after the water retreats. The period between the floods sometimes lasts only a few weeks, and some seedlings which do not tolerate complete flooding (e.g. *Senna reticulata* in várzea, Parolin, 1998, and *Mora paraensis, Swartzia polyphylla* in igapó, Ziburski, 1991), apparently depend on an efficiently timed release for establishment and survival. Fruiting in várzea occurs later than in igapó, perhaps as an adaptation to the strong sediment deposition in várzea (Ziburski, 1991): this permits the colonization of freshly deposited sediments without the danger of burial, as shown for *Vitex cymosa* and *Cecropia latiloba* (Kubitzki & Ziburski, 1994).

Germination

Germination starts immediately after the retreat of the flood, but it is not clear if submergence is directly responsible for the inhibition of seed germination (Parolin et al., 2004).

In nutrient-poor igapó, average seed masses are higher (7.1 g) than in nutrient-rich várzea (1.2 g) (Parolin, 2000). At high elevations in the flooding gradient the larger seeds enable rapid height growth which allows an escape from submergence. Because of the short duration of the non-flooded period and strong competition with highly productive macrophytes and grasses, fast germination and growth may be crucial for survival of tree species. Especially species which do not tolerate submersion have to grow tall quickly in order to maintain some leaves above the water surface when the flood comes. In the case of *Senna reticulata*, which succumbs to submersion, seedlings grow to a height of four meters in the first terrestrial period of less than eight months (Parolin, 2001b). Several species grow up to one meter in the same period, for example the early successional species *Cecropia latiloba* and *Salix martiana*, or two meters in species with large seeds like *Aldina latifolia*, *Mora paraensis* und *Vatairea guianensis* (Parolin, 2002a, b).

Seeds of some várzea tree species are able to germinate and to emit radicles when still buoyant and/or submerged (Ferreira, 2002; Parolin & Junk, 2002; Scarano et al., 2003), but the emission of the epicotyl in these species was inhibited. Contact with the river water did not disturb but on the contrary enhanced germination (Oliveira-Wittmann et al., 2007).

Seeds of *Carapa guianensis* germinate while floating (Scarano et al., 2003). In an experiment with twelve tree species (Parolin & Junk 2002) to test whether seed germination occurs only in non-flooded seeds, four species (*Crateva benthami, Mora paraensis, Nectandra amazonum*, and *Vatairea guianensis*) showed radicle growth while submerged, but none of the species under investigation was able to produce a shoot as long as it was submerged (Oliveira, 1998; Oliveira & Piedade, 2002; Parolin & Junk, 2002).

Oliveira-Wittmann et al. (2007) showed that in *Salix martiana*, *Laetia corymbulosa* and *Vitex cymosa*, there was a higher percentage of germination in the flooded seeds than in the non-waterlogged seeds, while fruit-fibre involved seeds of *P. munguba* showed an opposite trend. From buoyant seeds of *P. munguba* and *S. martiana*, seedlings with entirely formed cotyledons were developed while still in water. The ability of seeds to germinate while inundated has both advantages and disadvantages, depending on the conditions of the inundation. Species whose seeds can germinate and grow under flooded conditions may have an advantage to use the short non-flooded period. However, among the species germinating in water no establishment was observed once the germinated seedlings fell on the soil (Ziburski, 1990; Oliveira & Piedade, 2002). They could not protrude the root into the soil (i.e. establish) when placed in the substrate.

Phylogenetic development of adaptations

Flooding stress is a strong driver of adaptive evolution (Jackson & Colmer, 2005). The regularity of the recurrence of flooding, i.e. the predictability of the flood pulse (*sensu* Junk et al., 1989), enhances the evolution of specific adaptive traits and may have led to the large variety of species which are able to succesfully colonize, establish and dominate the floodplains (Parolin et al., 2004). Morphological adaptations may be remnants of pre-adaptations from the non-flooded terra firme species where floodplain trees originate from (Kubitzki, 1989). The degree of flood tolerance may also depend on the time taken to colonize the floodplains. Some species have the potential for the development of adaptive traits – as revealed in waterlogging experiments – but do not show them in the field in average years (Parolin et al., 2004). For example, under natural conditions in the floodplains, adventitious roots, lenticels, or stem hypertrophy were observed only in few individuals probably due to the constant change in water level (Parolin, 2001b). Although not frequently encountered in the field, their function may be important in years with flooding anomalities (Parolin et al., 2004).

Diversity of adaptations

The present paper gave an overview of the physiological and morphological mechanisms which we understand so far and which lead to high flooding tolerance in some tree species. However, even in the analysed species the mechanisms which lead to certain responses are not understood. We expect that especially physiological and chemical pathways which are new to science will come to light as soon as we analyse in detail the function of, for example, submerged leaves.

The overview of adaptations to flooding found in only few dozens of tree species shows that there is a considerable diversity of possible responses to waterlogging and/or submergence. The more trees we analyze, the more combinations of adaptations we will probably find. However, the immense lack of knowledge about the ecophysiology of the trees of this remarkable ecosystem is striking. Many of the 1000 flooding tolerant trees of Amazonian floodplains are almost unknown: we know the botanical name and a morphological description of the tree physiognomy. Characteristics which are important for forest management and reafforestation, such as understanding requirements for seed germination, early establishment and flooding tolerance are not known for most species. Since also Amazonian floodplain forests – as most tropical forests worldwide – are threatened by human activities, knowledge about the flooding tolerance and growth requirements of these species is urgently needed.

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Figure 1: Amazonian floodplains: várzea forest at high water in the vicinity of Manaus, Brazil (Pia Parolin).

Figure 2: *Eschweilera tenuifolia* on lowest sites flooded up to four consecutive years in igapó (October 1994, Rio Jaú; Pia Parolin).

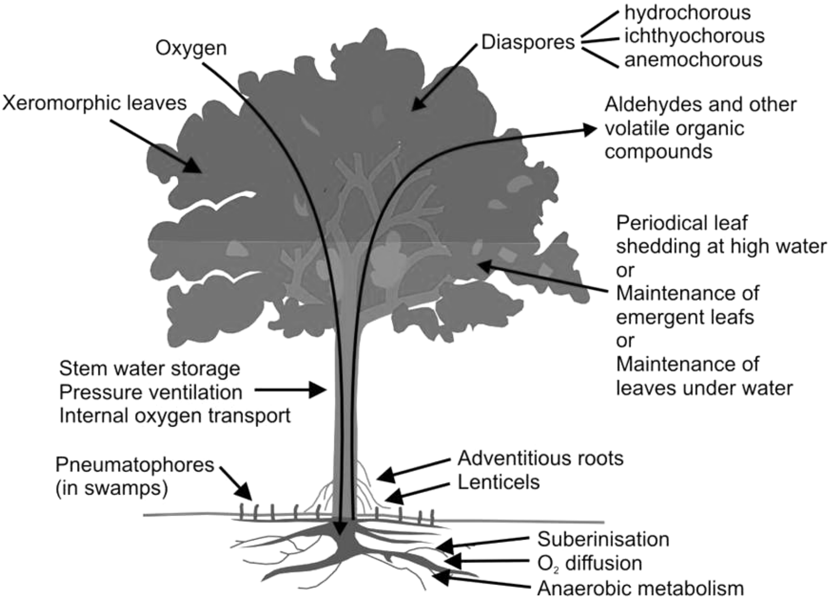

Figure 3: Scheme of possible adaptations found in Amazonian floodplain trees. Single species have a combination of different adaptations leading to their particular growth strategy. See text for explanations of single adaptations.

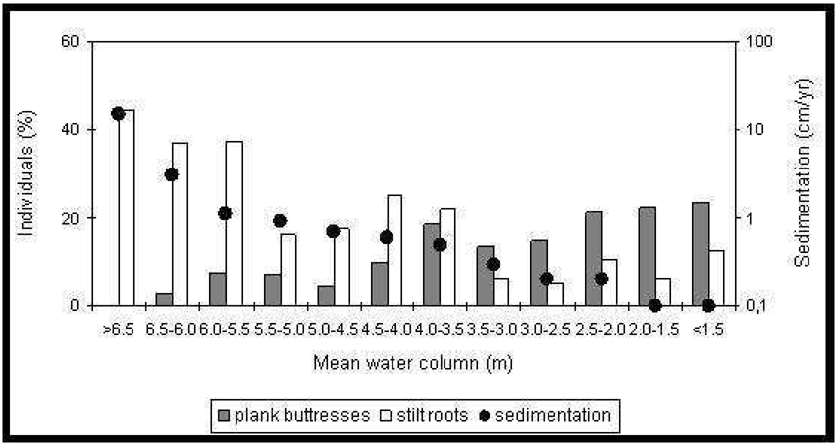

Figure 4: Different types of aboveground roots are closely related to flooding duration and habitat dynamics: Relative frequency of buttressing and stilt rooting trees (n = 755, 3.1 ha) along a flood and sedimentation gradient (from Wittmann & Parolin 2005).

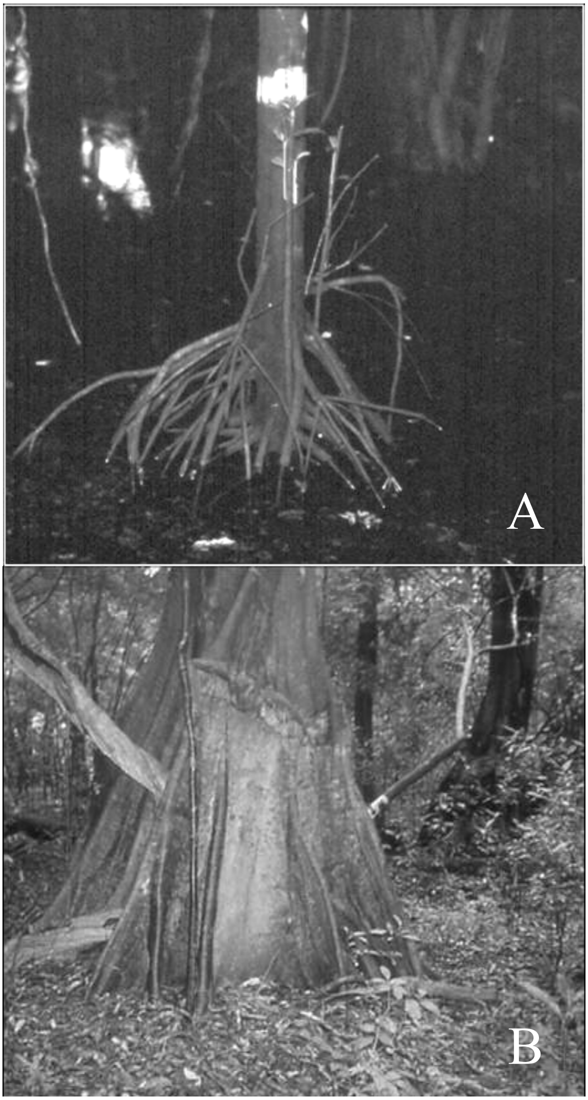

Figure 5: Stilt roots in *Buchenavia sp*. (A) and buttresses in *Aspidosperma riedelii* (B) (Florian Wittmann).