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Vigorous tree growth in a flooded environment: flood adaptations and tree diversity in Amazonian floodplain forests

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Introduction

In Amazonian floodplain forests, more than one thousand tree species are adapted to the prolonged periods of flooding (Wittmann et al. 2006) and grow vigorously despite the constraints imposed by this stress factor. The main growing period for trees is the terrestrial low-water phase. During the aquatic phase, trees are subjected to periods of flooding with freshwater which last up to nine months every year.
Flooding causes drastic changes in gas exchange, bioavailability of nutrients, and concentrations of phytotoxins. Anoxic conditions prevail in the rhizosphere. The stress associated with flooding 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. Not so for the hundreds of tree species of Amazonian floodplains. A huge diversity of species has evolved (Wittmann et al. 2006) whose growth is not inhibited by flooding, due to a number of adaptations (Figure 1) and highly diverse survival strategies which enable them to colonize efficiently the floodplains despite the huge flooding amplitude and duration (Parolin et al. 2004).

Tree diversity

Tree species richness in Amazonian várzea is not as high as in the non-flooded uplands. However, Amazonian várzea forests are the most species-rich floodplain forests worldwide (Wittmann et al. 2006). Representatives of nearly all plant families characterizing the neotropical flora of woody plants can be found within the floodplain forests. Fabaceae are the most important várzea tree family, followed by Malvaceae, Euphorbiaceae, Moraceae, Palmae, and Salicaceae (Wittmann et al. 2006).
Species-poor low-lying forests (low várzea), highly resemble each other throughout the Amazon basin, even when separated by long geographic distances. Species-rich high-várzea forests may exhibit floristic distinctness, but share approximately 30% of all tree species with the adjacent uplands (Wittmann et al. 2006). In fact, tree species richness and alpha-diversity of várzea forests are significantly correlated to flood height and length, and to the forest stand age (Wittmann et al. in press). Maximum species richness ($\geq$ 10 cm dbh) recorded in high-várzea forests of Amazonia amount to 84 species ha^{-1} in the Eastern parts of the basin, to 142 species ha^{-1} in Central Amazonia, and to 157 species ha^{-1} in the southern part of western Amazonia (Wittmann et al. in press).
The worldwide unique high tree species diversity in Amazonian várzea has its reason in mainly two factors: a) relative stable environmental conditions within the Amazon basin over millions of years -even with expected tectonic and climatic changes during the tertiary and quaternary it is

likely that Amazonian white-water floodplains existed at least since the beginning of the Andean orogenesis, influenced of course by changing sizes of its area-, possibilizing species selection, adaption, radiation, and endemism over a geological time span; and b) a high diversity in habitats, which establish in dependence of the geo-hydrological set-up, triggering variations in species composition at local scale and continental-wide scale (Wittmann et al. in press). The coexistence of species well-adapted to flooding together with generalist species that also occur in the uplands strongly increase species diversity of these forests.

Zonation

There is a clear zonation of plant communities in the Amazonian várzea along the food-level gradient which leads to characteristic species associations and forest types. Two main habitats are differentiated (Wittmann et al. 2002): a) low-várzea forests, influenced by mean inundations with heights between 3.0 and 7.5 m (corresponding to an mean inundation period of 50 – 230 days $year^{-1}$), and b) high-várzea forests, influenced by mean inundations with heights of less than 3.0 m (< 50 days $year^{-1}$).

Only few tree species occur along the whole flooding gradient, whereas most of them are restricted to very small topographic amplitudes (Wittmann et al. 2002). Only approximately 20% of all várzea tree species occur in both low várzea and high várzea, demonstrating the striking difference of ecophysiological constraints for tree survival and growth in the two ecosystems. Most tree species (50%) occur only in the high várzea, 30% are restricted to the low várzea, indicating an inverse relationship between species richness and inundation height and length.

Diversity of adaptations to flooding

Flooding is the collective term for soil waterlogging and submergence. While adult trees are rarely submerged and have to cope with waterlogging of roots and stem, seedlings and saplings are subjected to several weeks to months of complete submergence in darkness, which is lethal to some species while others can survive (Wittmann et al. in press). The aquatic phase occurs in a period in which temperature and light conditions are optimal for plant growth and development. These extreme changes of hydric conditions in the annual cycle are tolerated by the trees because of a large variety of adaptations to flooding, starting at the seed stage with hydrochory and ichthyochory as main means of dispersal, followed by fast germination and high tolerance to complete submergence in seedlings, and ending in a not yet completely apprehended number of adaptations in adult trees, at phenological, physiological, morphological and anatomical levels. 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 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. Since trees which have an active sap flow have a need for adequate supplies of carbohydrate also in the flooded period, a set of metabolic adaptations are required for survival and growth despite flooding.

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). Morphological adaptations of the root system comprise hypertrophy of lenticels, formation of adventitious roots, plank-buttressing and stilt rooting, development of aerenchyma, and the deposition of cell wall biopolymers such as suberin and lignin in the root peripheral cell layers. The formation of aerial roots may compensate for losses of respiration. 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).

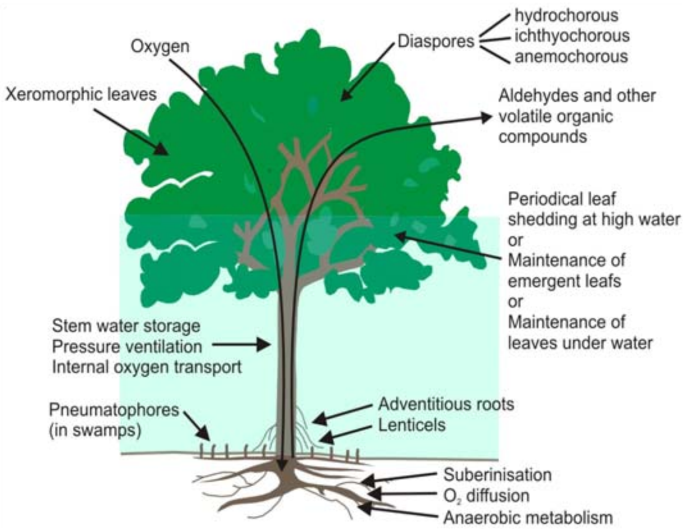

Figure 1: Potential adaptations against waterlogging found in Amazonian floodplain trees. Single species have a combination of different adaptations leading to their particular growth strategies and flooding tolerance.

The xeromorphic leaf structure described for trees of tropical forests is typical also for the floodplain species. 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. 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.

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. 2004). Deciduousness may then have assumed new functions in the floodplains, e.g. enhancing pollination by bats.

The main means of dispersal in Amazonian floodplain trees are hydro- and ichthyochory, which is emphasized by a close correlation between the timing of flooding and fruit maturation. The diaspores show morphological adaptations which enhance floatation, like spongy tissues or large air-filled spaces (Kubitzki & Ziburski 1994).

Population differentiation

Different adaptations and survival strategies related to morpho-anatomical, phenological and physiological responses to flooding were not only found between species along the flooding gradient, but also between different populations within a species. Intraspecific comparisons of populations growing in floodplains and in non-flooded Terra Firme forests showed clear differences, although it has yet to be analyzed whether these are of phenotypic or genotypic nature.

One typical species occurring both, in flooded várzea and non-flooded Terra Firme, is the Apocynaceae *Himatanthus sucuuba*. Clear differences were found in seedlings resulting from populations of the várzea and the Terra Firme concerning seed germination and seedling survival to submergence (Ferreira et al. 2007). Morphological and physiological differences were also found, e.g. in the amount and pathway of aerenchyma formation in the different populations. In waterlogged seedlings from várzea aerenchyma was formed by a schizogen pattern, in those from Terra Firme by a lysogen pattern.

Sustainable management

Understanding the adaptive strategies of the trees is the basis for understanding their distribution, their ecological needs for survival and regeneration, and together with models of growth parameters we have a basis for management options and the conservation of commercially exploited tree species.

Within the Amazon basin, 60-90% of wood extraction occurs in the floodplains which is favoured by the low costs for logging, skidding and transport (Parolin 2000). More than 50 tree species are used by locals, but only a few are commercially interesting. The easy accessibility and the high number of individuals of a species per area are advantageous. Natural resources like the production of oil, soap, resines, textile fibres, tannins, colours and medicines, aromas, latex, and fruits are of local and commercial importance. Timber is a very important good since 1900, where it was used for energy production in steamboats, and for civil and naval construction. Logging is done by hand or chainsaw, and the wood is transported by raft to Manaus where sawmills and timber industry are concentrated. Many commercially used tree species are threatened, especially in the vicinity of big cities. The high selective logging already caused a substitution of timber species, with high damages in the remaining stands, calling for rigorous management plans.

Conclusions and Outlook

Since also these forests, as most wetland ecosystems, are threatened by human overpopulation and overexploitation, the challenge to understand and thus maintain this ecosystem steadily increases. As the world largest and most diverse freshwater floodplain forests, várzea forests fulfil a variety of important economical and ecological functions, such as acting as food reservoir for many, partially endemic fish and mammal species, regulating the hydrological regime of the Amazonian Rivers, improving water quality, being a substantial sink of carbon, and providing important timber and non-timber forest products to the inhabitants.

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