



Struggle in the flood: tree responses to flooding stress in four tropical floodplain systems

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Abstract

Background and aims

In the context of the 200th anniversary of Charles Darwin's birth in 1809, this study discusses the variation in structure and adaptation associated with survival and reproductive success in the face of environmental stresses in the trees of tropical floodplains.

Scope

We provide a comparative review on the responses to flooding stress in the trees of freshwater wetlands in tropical environments. The four large wetlands we evaluate are: (i) Central Amazonian floodplains in South America, (ii) the Okavango Delta in Africa, (iii) the Mekong floodplains of Asia and (iv) the floodplains of Northern Australia. They each have a predictable 'flood pulse'. Although flooding height varies between the ecosystems, the annual pulse is a major driving force influencing all living organisms and a source of stress for which specialized adaptations for survival are required.

Main points

The need for trees to survive an annual flood pulse has given rise to a large variety of adaptations. However, phenological responses to the flood are similar in the four ecosystems. Deciduous and evergreen species respond with leaf shedding, although sap flow remains active for most of the year. Growth depends on adequate carbohydrate supply. Physiological adaptations (anaerobic metabolism, starch accumulation) are also required.

Conclusions

Data concerning the ecophysiology and adaptations of trees in floodplain forests worldwide are extremely scarce. For successful floodplain conservation, more information is needed, ideally through a globally co-ordinated study using reproducible comparative methods. In the light of climatic change, with increasing drought, decreased groundwater availability and flooding periodicities, this knowledge is needed ever more urgently to facilitate fast and appropriate management responses to large-scale environmental change.

Introduction

During the recent Darwin bicentennial year (2009) and throughout the 151 years since the publication of 'On the Origin of Species' (Darwin, 1859), discussion on the

'struggle for survival' has been topical and controversial. Darwin's theory of 'survival of the fittest' is a synonym for 'natural selection'. Darwin asked 'Can it be doubted, from the struggle each individual has to obtain subsistence, that any minute variation in structure,

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habits or instincts, adapting that individual better to new conditions, would tell upon its vigour and health?' (Darwin, 1842). Accordingly, the present study discusses the struggle for life in the forests of large flood-pulsed wetlands in relation to what is known of variations in structure, physiology and biochemistry that confer resilience. Contrary to the wisdom of Darwin, we cannot, unfortunately, deal with differences within populations because such data are very difficult to obtain for these huge ecosystems. Instead, our aim is to bring together data on responses of trees to flooding in the freshwater wetlands of tropical environments, emphasizing the varying responses to different wetland structures and flooding conditions extant in tropical freshwater floodplains of four continents. Although Gopal *et al.* (2000) have published a book on the biodiversity of wetlands and Junk (1997) produced a review of comparative biodiversity in floodplains around the world, there is no one publication which focuses on adaptation and survival of trees in tropical wetlands. The present article aims to fill this gap.

The four large wetlands chosen for our analysis are the Central Amazonian floodplains of South America, the Okavango Delta region of Botswana, Africa, the Mekong floodplains of South-east Asia and the tropical wetlands of Northern Australia (Fig. 1; Table 1). These ecosystems, each on a different continent, were chosen largely on the following pragmatic grounds. We looked for very large tropical freshwater floodplains with forest patches (i.e. trees occurring there naturally) where flooding occurs with regularity (the 'flood pulse' of Junk *et al.*, 1989), is characterized by high amplitudes and where it is long-lasting (weeks or months). We were careful not to include areas merely prone to flash floods following heavy rain. Our assessments are based on many diverse publications and disparate data concerning the effects of flooding on species richness, ecophysiology and distribution of tropical trees.

While selecting our four ecosystems, it soon became evident that data are extremely scarce, despite their importance for biodiversity and human resources (Wantzen and Junk, 2000). We were forced to exclude

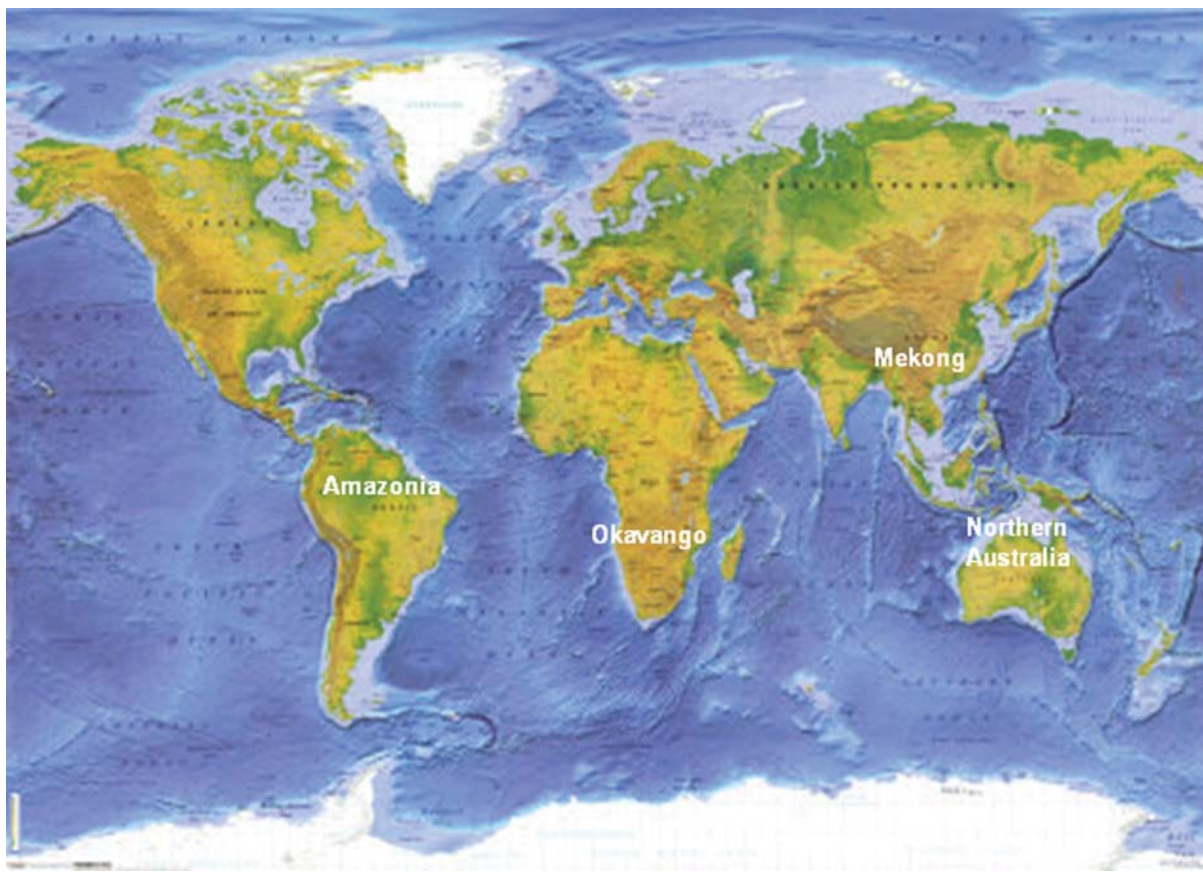


Fig. 1 Map indicating the approximate location of the four chosen floodplain forests.

Table 1 Characteristics of the four chosen floodplain ecosystems on four continents with a monomodal flood pulse

	Central Amazonia	Okavango Delta	Mekong Tonle Sap	Kakadu Region in Northern Australia
Continent	South America	Africa	Asia	Northern Australia
Geographical position	3°15'S, 59°58'W	18°30'–20°S, 22°–24°E	13°N, 104°E	13°2'S, 133°31'E
Latitude	0	19	13	12
Age of ecosystem (Irion <i>et al.</i> , 1997; Junk <i>et al.</i> , 2006)	2.4 million years	2.5 million years	7500 years	4000 years
Height asl (m)	0–50	1000	0–50	0–50
Connected rivers	Major river system	Major river system	Major river system	Smaller rivers
Floodplain area (km ²)	300 000	2500–8000; 28 000	15 000	99 000; 2900
Annual precipitation (mm)	2100	460–490	1600	1300–1450
Predictability of flooding	High	High	High	High
Flood amplitude	15 m	1.85 m	8.2 m	2–5 m
Mean/maximum flood height	8 m	Root level	<2 m	1 m
Flood duration where trees grow	7 months	Several weeks?	6–8 months	>6 months
Wetland main vegetation	Forest	Mainly grassland	Forest/grassland	Forest/grassland
Trophic status	Meso-eutrophic	Mesotrophic	Meso-eutrophic	Oligo-mesotrophic
Fire	No	Yes	No?	Yes
Salt	No	Yes!	No?	No?
Forest cover	Closed forest	Single trees	10 %, mosaic of stands of large trees and open areas	Open savanna to 70 % forest cover
Tree/canopy height	20–30 m	5–6 m	7–15 m	20 m
Woody species (Junk <i>et al.</i> , 2006)	>1000	180	70	21
Number of flood-tolerant tree species	>1000	10	15	5
Incidence of endemic tree species	High	Very low	Low	Low?
Tree species diversity	High	Very low	Few dominant species	Low?
Human pressure	Low	Low?	Very high (wars; fishing)	Minimal
Human impacts	Timber extraction; fishing; cattle ranching	Subsistence agriculture; fisheries	Timber; fishing; paddy rice	Cattle grazing; tourism; mining

Continued

Table 1 Continued

	Central Amazonia	Okavango Delta	Mekong Tonle Sap	Kakadu Region in Northern Australia
Changes	Increasing incidence and severity of drought	Soil salinization due to tree felling; expansion of agriculture; agrarian-degradation; predicted degeneration of major vegetation types from increased drying (Ringrose <i>et al.</i> , 2002)	Dramatic fluctuations in water level of Mekong River; frequent floods and lower water levels in dry season—an increasing problem for farming (IUCN, 1991).	Invasion by alien plants and animals; changed fire regime; water pollution from urban-tourism, mining and salinization; sea level rise (Junk <i>et al.</i> , 2006)

many of the largest wetlands, e.g. the Congo basin in Africa or the Orinoco floodplains in Venezuela, because only basic data on hydrology and climatology are available, with almost no information on plant distribution, tree adaptations and ecophysiology. It is important to bring attention to such poorly researched wetlands, which are often inaccessible for social and political reasons but are threatened by the ever-increasing human population and its need for water, waterways and hydroelectric power. The destruction is so fast that we may never learn of the adaptations underpinning the success of the tree species in these areas.

We are aware that differences between the four ecosystems are large, especially in respect of the influence of fire and salinity. Those which are dominated by grasslands (Okavango and Northern Australian floodplains) are subjected to regular fire (Heinl *et al.*, 2004, 2006, 2007), whereas in the forest-dominated floodplains of Amazonia and Mekong, fire plays no significant role. In the Okavango, the high evapotranspiration causes salinity problems, which are negligible in the remaining three ecosystems. Also, flooding amplitudes vary widely between the ecosystems, with about 2 m in the Okavango and Northern Australian, 8 m in the Mekong and 15 m in the Amazon floodplains (Table 1). This implies that complete submergence of saplings and trees occurs only in the Mekong and Amazon, posing different constraints for plant life than merely waterlogging of roots and stems (Parolin, 2009). However, our review is readily justified because the regular flood pulse is a major influence on all floodplain biology (Junk, 1989; Junk *et al.*, 1989) and a dominating stress which requires a suite of adaptations for its survival.

Throughout the world, wetland ecosystems are under increasing pressure from agriculture, urbanization of catchment areas, tourism and recreational activities, construction of impoundments and changes to

hydrology and climate. By comparing diversity and tree responses in four floodplain ecosystems on different continents, we attempt to improve our understanding of the factors influencing the spatial distribution of plants, diversity of species and adaptations, and thus contribute to our knowledge of tropical wetland ecology. In this way, we hope to assist in the successful restoration of degraded floodplains and promote the sustainable use and conservation of these highly valuable ecosystems.

Flooding as a stress factor

Flooding with freshwater, although less harmful than flooding with saltwater, poses a multitude of constraints on growth, survival and reproduction. Trees are basically terrestrial organisms and, in general, die more readily in response to flooding than to desiccation (Larcher, 1994). Flooding involves inundation of part or all of the aboveground structures, whereas waterlogging is restricted mainly to inundation of the soil and rhizosphere (Colmer and Pedersen, 2008). Totally submerged plants have no direct contact with atmospheric oxygen and sunlight is weak or extinguished. Inundated soils become hypoxic or anoxic within a few hours as the combined result of oxygen consumption by respiring roots plus micro-organisms and insufficiently fast diffusion of oxygen through water to replace the amounts consumed (Crawford, 1989, 1992; Armstrong *et al.*, 1994; Visser *et al.*, 2003). Oxygen depletion in soil is accompanied by increased levels of entrapped CO₂, anaerobic decomposition of organic matter, increased solubility of mineral substances, notably iron and manganese, and decreased redox potential (Joly and Crawford, 1982; Kozłowski, 1984). The resulting chemically reduced and potentially toxic compounds accumulate, their generation being the result of alterations in

the composition of the soil microflora as it responds to the changing conditions (Ponnamperuma, 1984). In some floodplains, e.g. those of the Amazon River, sedimentation rates can be extremely high and the deposition of sediment can decrease soil aeration and thus favour oxygen shortage in the rhizosphere (Wittmann *et al.*, 2004; Wittmann and Parolin, 2005). Elevated decomposition rates of highly productive floating and non-floating macrophytes in floodplains further decrease oxygen concentrations in the floodwater (Armstrong *et al.*, 1994).

In temperate zones, flooding frequently occurs during winter when plants are dormant and light intensities low. In contrast, the flooding period in tropical floodplains occurs when temperatures and light intensities are high and conditions overall are optimal for plant growth. Therefore, the trees are not dormant and must accommodate shortages of oxygen and, for submerged shoots, shortages of CO₂ too at a time when conditions favour fast respiration and depletion of reserves. This implies that extraordinarily efficient adaptations are

needed for survival. With all these constraints, imposed by flooding, this stress is clearly life-threatening for higher plants. The struggle for survival of flooding is therefore closely linked to the evolution of physiological, phenological, anatomical and morphological adaptations that confer tolerance and underpin successful and vigorous growth and fecundity despite the intense stress.

Floodplain ecosystems

Here we characterize four extensive floodplain ecosystems present on four continents (Table 1). They include the Central Amazon floodplains (where we have the broadest and deepest knowledge of tree ecophysiology), the Okavango Delta in Africa, the Mekong floodplains in South-east Asia (where relatively little is known about tree ecology) and the Northern Australian floodplains (where much is known about the herbaceous vegetation, but much less about tree responses to freshwater flooding; Table 2).

Table 2 Characteristics of the forest vegetation (distribution, phenology, physiological adaptations) in the four chosen floodplain ecosystems on four continents

	Central Amazonia	Okavango Delta	Mekong Tonle Sap	Kakadu Region in Northern Australia
Continent	South America	Africa	Asia	Northern Australia
Tree distribution				
Zonation of trees along the flooding gradient	Yes	Yes	Yes	Yes
Degree of endemism	Elevated	Low/absent	Low/absent	Low/absent
Leaf phenology				
Deciduous species: leaf shedding at high waters	Yes	No	Yes	?
Evergreen species	Yes	Yes	Yes	?
Reproductive phenology				
	Linked to high water + fish	?	Linked to high water + fish	?
Physiological adaptations				
Reduction of metabolism and growth during high waters	Yes	No	Yes?	?
Morpho-anatomical adaptations	Leaf xeromorphism; hypertrophic lenticels; adventitious roots; aerenchyma	?	?	?
Biochemical adaptations	Increased activity of fermentative enzymes; more VOC emission	?	?	?

South America: Central Amazonian floodplains

There are extensive floodplains along the Amazon River and its large tributaries throughout the Amazon basin. These contain large species-rich and highly adapted floodplain forests that cover more than 300 000 km² (Irion *et al.*, 1997). The mean annual temperature of 26.6 °C changes little, average rainfall is ~2100 mm year⁻¹ (Ribeiro and Adis, 1984) and noon light intensities can reach 3000 μmol m⁻² s⁻¹ at the water surface (Furch *et al.*, 1985). Seasonal variations in river levels subject trees to periods of up to 210 days of continuous flooding each year. The rate of change in the water level can be fast and reach 10 cm day⁻¹ (Junk, 1989), leading to a total rise of up to 16 m in western Amazonia, 10 m in Central Amazonia and 6 m in eastern Amazonia (Junk, 1989). The ‘flood pulse’ (Junk *et al.*, 1989) is monomodal and the timing is predictable, resulting in well-defined high-water (aquatic phase) and low-water (terrestrial phase) periods each year. The timing of the pulse is predictable, but irregularities occur in the maximum and minimum water levels. This can be of great relevance for seedling establishment (Scarano *et al.*, 1997). At high water levels, tree roots and stems are waterlogged, and small trees and seedlings may be completely submerged for several months by a water column of up to 8 m (Parolin *et al.*, 2004; Parolin, 2009). At low water levels, drought may be a stress factor for several weeks (Junk, 1997; Parolin *et al.*, 2010). Natural fires and salt are absent from this ecosystem. Although large terrestrial mammals play important roles for tree establishment and distribution in the grasslands of other floodplains, they play no significant role in the Amazonian floodplain (Junk and da Silva, 1997).

The differing origins of the various tributaries of the Amazonian River system can strongly influence water chemistry, e.g. sources in the western Amazon Andes or the Northern and Southern Amazonian Precambrian shields. The resulting seasonally flooded vegetation can roughly be differentiated into the nutrient-rich and highly productive white-water floodplains (várzea) and the nutrient-poor and less productive black-water or clear-water floodplains (igapó) (Fig. 2; Sioli, 1954; Prance, 1979). In Central Amazonia, both floodplain types undergo seasonal water-level changes of up to 10 m (Fig. 3). Trees establish at mean annual flood levels <7.5 m, corresponding to flooded and/or waterlogged periods of up to 300 days year⁻¹ (Wittmann *et al.*, 2004, 2006).

Human impact on Amazonian floodplains is increasing due to agriculture, cattle and buffalo farming, logging, civil construction projects, mining and reservoirs for hydro-electric power (Junk, 2000). Small-scale multiple uses and

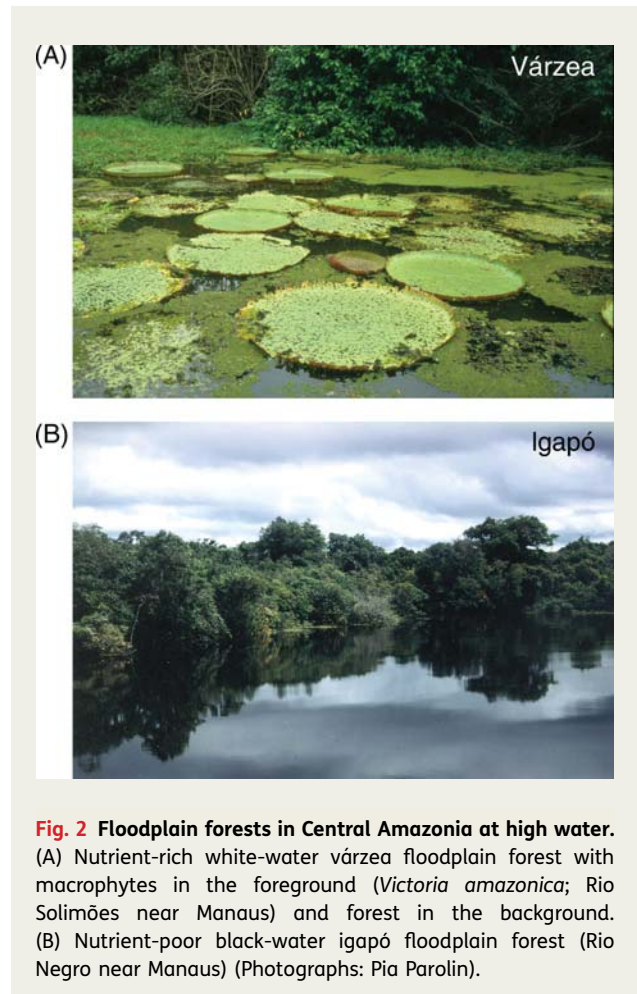


Fig. 2 Floodplain forests in Central Amazonia at high water. (A) Nutrient-rich white-water várzea floodplain forest with macrophytes in the foreground (*Victoria amazonica*; Rio Solimões near Manaus) and forest in the background. (B) Nutrient-poor black-water igapó floodplain forest (Rio Negro near Manaus) (Photographs: Pia Parolin).

ecotourism, however, provide sustainable management that partially limits the threats to this ecosystem.

Tree vegetation Amazonian freshwater floodplains harbour the most species-rich floodplain forests in the world (Wittmann *et al.*, 2006). In the nutrient-rich white-water várzea, there are more than 1000 flood-tolerant tree species (Fig. 3; Wittmann *et al.*, 2006). From igapó, the comparatively low number of inventories still does not allow reliable estimates of overall species richness. However, comparisons from both local and basin-wide scales indicate less species richness than in the várzea (Prance, 1979; Ferreira *et al.*, 2005; Wittmann *et al.*, 2010). Species-poor low-lying forests (low várzea) are remarkably similar throughout the Amazon basin even when separated by long distances. Species-rich high-várzea forests may be more floristically distinct, but share ~30 % of their tree species with the adjacent uplands (Wittmann *et al.*, 2006). Tree species richness and alpha-diversity of várzea forests are significantly correlated to flood



Fig. 3 Várzea floodplain forests in central Amazonia at low water (Photographs: Florian Wittmann, Max-Planck-Institute for Chemistry, Mainz, Germany).

height and length, and to the age of the forest stand (Wittmann *et al.*, 2006). Maximum species richness estimated from trees ≥ 10 cm in diameter at breast height (cm dbh) recorded in high-várzea forests of Amazonia amounts to 84 species ha^{-1} in the eastern parts of the basin, 142 species ha^{-1} in Central Amazonia and 157 species ha^{-1} in the southern part of western Amazonia (Wittmann *et al.*, 2010). Endemism is highest in highly flooded low-lying forests and was estimated to account for $\sim 39\%$ of the 186 most common Central Amazonian várzea tree species (Wittmann *et al.*, 2010). One hundred and twelve (60%) of the most frequent Central Amazonian várzea tree species are generalists and are also to be found in other neotropical ecosystems. Where flooding does not exceed 210 days year^{-1} (Junk, 1989), trees are the dominating life form, whereas in longer-flooded environments, grasses and macrophytes take over.

As a result of the different chemical compositions and nutrient inputs of the flooding water, depending on the

river catchment, the tree flora of the várzea and igapó differ substantially in species composition and diversity (Prance, 1979; Kubitzki, 1989). Comparisons at local and basin-wide scales suggest floristic similarities between both ecosystems to be $< 20\%$ (Wittmann *et al.*, 2010). The main reason for the diverging flora is the contrasting nutrient level. This seems to act as a distribution barrier for many white-water species migrating to the igapó and *vice versa*. In addition, alluvial dynamism varies, with the white-water floodplains being highly dynamic systems where constant processes of sedimentation and erosion create a large variety of micro-habitats, thereby increasing biodiversity (Salo *et al.*, 1986; Kalliola *et al.*, 1991; Wittmann *et al.*, 2004).

Flooding tolerance and tree distribution There is a clear zonation of plant communities in the Amazonian várzea along the flood-level gradient, which leads to characteristic species associations and forest types. Two main habitats are differentiated (Wittmann *et al.*, 2002): (i) low-várzea forests, influenced by mean inundations with heights between 3.0 and 7.5 m (corresponding to a mean inundation period of 50–230 days year^{-1}) and (ii) high-várzea forests, influenced by mean inundations with heights of < 3.0 m (< 50 days year^{-1}). However, the distribution of várzea tree families differs considerably between low- and high-várzea forests (Wittmann *et al.*, 2006): Fabaceae, Malvaceae, Salicaceae, Urticaceae and Brassicaceae are more important in low-várzea forests, whereas Euphorbiaceae, Moraceae, Palmae, Annonaceae, Meliaceae and Myristicaceae are more important in high-várzea forests.

The clear zonation of tree species along the flood gradient in both Amazonian igapó and várzea indicates the different levels of acclimation and adaptation that these species have evolved in order to cope with the seasonally hypoxic/anoxic sites. Trees may disperse to higher flooded sites than the parent trees and establish during the terrestrial phase, but they often prove to be intolerant of the peculiar site conditions or quickly lose out competitively to better-adapted species (Wittmann *et al.*, 2010). Many Amazonian floodplain tree species that tolerate high and prolonged inundation show adaptations against a wide range of potentially stressful conditions. For example, they tolerate high sedimentation rates when located near the river channels of white-water rivers and also tolerate poorly aerated soils when located in backwater swamps. Furthermore, they often tolerate full sunlight and drought during the terrestrial phases when low river water levels coincide with seasonally low precipitation. Trees that are successful at highly flooded sites are therefore light-demanding pioneer species which also have a high resprouting

capacity (Worbes *et al.*, 1992; Wittmann and Parolin, 2005). They also grow quickly and exhibit relatively short life cycles as, for example, in the white-water pioneers *Salix martiana* and *Cecropia latiloba* (Worbes *et al.*, 1992; Parolin *et al.*, 2002; Schöngart, 2003). These successful pioneer trees modify the local site conditions so much that new seedlings of the same species are no longer able to establish at the same site as the parent tree (Wittmann *et al.*, 2010).

Tree responses to flooding The terrestrial phase is the main growth period for trees in the Amazonian floodplains. In contrast, in the flooded period, growth decreases, metabolic activity slows and even complete dormancy is induced in many species. However, none of these responses lasts for the entire flooding period. Limited growth lasts for only a few weeks and is often followed by new leaf flush, flowering, fruiting and wood increment while the tree is still flooded (Worbes, 1997; Schöngart *et al.*, 2002). After fruit maturation, which usually occurs at high water levels (Kubitzki and Ziburski, 1994), seeds fall into the water and may float and/or are submerged for several weeks without losing their viability. Seed germination starts only when the flood recedes, although some may protrude a radicle (Scarano *et al.*, 2003) or even produce a complete seedling while floating (Oliveira-Wittmann *et al.*, 2007; Parolin, 2009). In most species, overall growth in height and new leaf production are not severely inhibited merely by waterlogging of the soil, and elongation may even be enhanced, as in *Senna reticulata*. Here, waterlogging is reported to accelerate seedling shoot growth considerably (Parolin, 2001).

Submergence of part of or the entire shoot is a more severe stress. Most tree species tolerate this in a state of rest and sprout new leaves soon after the water recedes. In species with leaves without a thick cuticle or thick outer epidermis walls, leaves rot fast when submerged and are shed after only a few days (Waldhoff and Furch, 2002). Other species may retain their leaves in a healthy state below water for several months. Leaf shedding during the aquatic phase has been documented not only in deciduous species but also in evergreen trees, which tend to produce new leaves only slowly at high water levels (Parolin *et al.*, 2002). Whether deciduous or evergreen, and regardless of whether leaves are kept or shed under water, the leaves of Amazonian floodplain trees exhibit traits that are generally considered as xeromorphic (Medina, 1983; Waldhoff, 2003).

Physiological responses to waterlogging of the soil include reductions of mean CO₂ uptake in aerial leaves ranging from 10 to 50 % slower than in the terrestrial phase (Parolin *et al.*, 2004). CO₂ uptake rises again

before the end of the flooded phase and remains high throughout the terrestrial phase (Parolin, 2000).

Morphological adaptations of the root system include hypertrophy of lenticels, formation of adventitious roots, development of aerenchyma, and the deposition of cell wall biopolymers such as suberin and lignin in peripheral cell layers (Schlüter and Furch, 1992; Schlüter *et al.*, 1993; De Simone *et al.*, 2002a, b). Different types of above-ground roots, e.g. plank-buttressing and adventitious roots, are closely related to flooding duration and habitat dynamics (Wittmann and Parolin, 2005). The development of adventitious roots in the oxygenated layer at the surface of the floodwater table and hypertrophy of lenticels on the surface of stems just above water level are thought to improve the internal oxygen status by facilitating the entry of oxygen into the root and the stem by the shortest possible pathway (Crawford, 1992). Pneumatophores are also familiar adaptations in mangroves but are absent in várzea trees (Junk, 1984) except in palms found in headwater regions and swamps (e.g. *Mauritia*, *Mauritiella*), where flood amplitudes are small. Stem nodulation and nodulated adventitious roots have been observed in various species, and are understood to be adaptations that allow legumes to fix nitrogen in a flooded environment (James *et al.*, 2001). The frequency of such nodulation among genera can be higher in flooded than in non-flooded sites in both várzea and igapó, indicating that nodulation may be favoured in flooded areas (Moreira *et al.*, 1992).

Increased activity of fermentative enzymes such as alcohol dehydrogenase (ADH), lactate dehydrogenase (LDH), glutamate–pyruvate transaminase (GPT) and malate dehydrogenase (MDH) has been observed under anaerobic soil conditions in the roots of several tree species (Schlüter and Furch, 1992; Schlüter *et al.*, 1993; De Simone *et al.*, 2002b). In addition, larger amounts of volatile organic compounds are emitted to the atmosphere by terrestrial vegetation when flooded (Kesselmeier and Staudt, 1999). Acetaldehyde and ethanol may be emitted in larger amounts by flooded trees and under other stress conditions such as sulphur dioxide and ozone exposure, water deficit, freezing and fast-changing light conditions (Kimmerer and Macdonald, 1987; Kesselmeier *et al.*, 1997). Acetaldehyde (and formaldehyde) is exchanged bi-directionally between the vegetation and the atmosphere, i.e. they are emitted or taken up, depending on environmental and atmospheric conditions (Kesselmeier *et al.*, 1997). Recent measurements in the *terra firme* Amazonian rain forest provide evidence that more short-chain aldehydes and the corresponding organic acids were taken up from the air than produced, although release was

observed when ambient concentrations were below a specific level (Rottenberger *et al.*, 2008).

Africa: Okavango Delta

The Okavango Delta (Fig. 4) is the world's largest inland delta. It is located in northwestern Botswana and fed by the Okavango River, which originates in Angola's western highlands. The floodwaters take ~9 months to flow from the source to the delta due to the extremely gentle gradient. The river discharges about 10 km³ of water onto the delta fan each year, augmented by about 6 km³ of rainfall, which sustains about 2500 km² of permanent wetland and up to 8000 km² of seasonal wetland. Interaction between this surface water and the groundwater strongly influences the structure and function of the wetland ecosystem. The climate is semi-arid, and only 2 % of the water leaves as surface flow and probably very little as groundwater flow. The bulk of the water is lost to the atmosphere. The Okavango River also delivers about 170 000 tonnes of bedload sediment and about 360 000 tonnes of solutes to the delta each year, most of which is deposited on the fan. Local rainfall is low, averaging 490 mm year⁻¹. This is greatly exceeded by the rate of evapotranspiration (1580 mm year⁻¹; Ellery *et al.*, 1993). Temperatures range from maxima of 33.7 °C in summer to 28.7 °C in winter, with a mean relative humidity of 60–78 % in summer and 43–63 % in winter (Bonyongo *et al.*, 2000). Precipitation data show <10 mm of rainfall per month from May through October, whereas between January and March, it lies between 120 and 320 mm. The Okavango Delta experiences seasonal flooding starting towards the north between October and April, and ending in May, June or July towards the southern part of the delta. Natural fluctuations in water level result from variations in annual rainfall in the catchment area and rainfall within the delta itself (Bonyongo, 1999). The delta is almost permanently flooded in the north, but only seasonally flooded in the south. The rain falls during the summer and first seeps into the parched ground before the rivers start flowing. As it is the dry season, the floodwaters gradually evaporate over the subsequent months, leaving their valuable salts and minerals in the ground.

Fire plays a role in this ecosystem (Heinl *et al.*, 2004, 2006, 2007). It is more frequent in the floodplains than on the drylands because of greater biomass and fuel load. The incidence of fire on the drylands correlates with annual rainfall events, while the frequency of fires on floodplains is determined mostly by flooding frequency. The greatest burn potential is found on floodplains that become flooded every second year. Temporal variations in flooding cause accumulation and sudden mobilization of nutrients which are readily utilized by well-

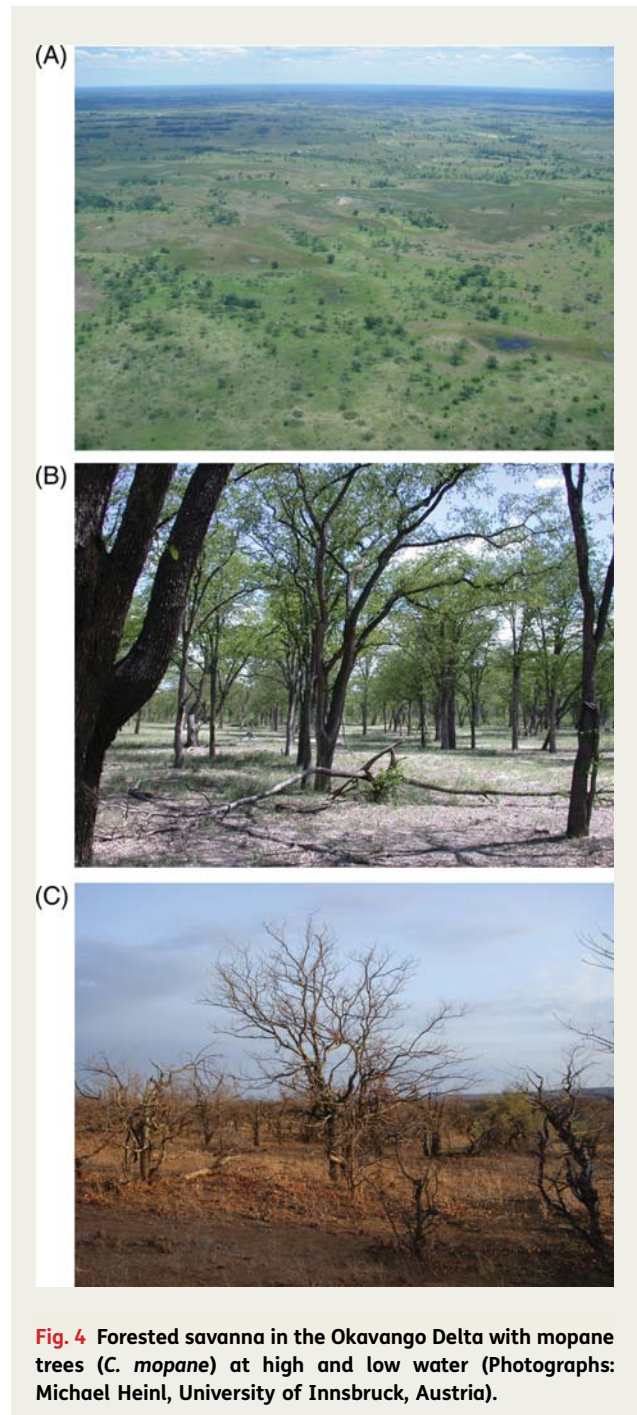


Fig. 4 Forested savanna in the Okavango Delta with mopane trees (*C. mopane*) at high and low water (Photographs: Michael Heinl, University of Innsbruck, Austria).

adapted plants. As a consequence, locally high biological productivity occurs, which, in turn, supports many grazing mammals (Heinl *et al.*, 2004, 2006, 2007; Tacheba *et al.*, 2009).

Changes in the types of vegetation cover, due to both human and natural causes, have taken place since the first vegetation map was produced in 1971 (Ringrose *et al.*, 2002). In the south-west, shifts to thorn trees

prevail, whereas in the eastern part of the country, widespread bush encroachment takes place. An increased human population density suggests that these are anthropogenic (agrarian-degradation) effects. Wherever broadleaved evergreen trees are cleared, widespread salinity occurs (Ellery *et al.*, 2000). In the sparsely settled central Kalahari region, changes from tree savanna to shrubs may indicate the influence of climate change with the associated effects of fires and local adaptations. Projection of future vegetation changes to about 2050 indicates degeneration of the major vegetation types due to expected drying of the local climate (Ringrose *et al.*, 2002).

Tree vegetation The floodplains consist mostly of grasslands with 1250 species (Ellery and Tacheba, 2003). Woody plants are found in the riverine forests (e.g. species of *Ficus*). On the higher, often salt-rich islands which are flooded less frequently, acacias, mopane (*Colophospermum mopane*; Fig. 4) and the woody shrub *Pechuel-loeschea leubnitziae* (a weed in many ecosystems) predominate. Ellery and Tacheba (2003) reported 43 woody species in total in the dryland riverine woodland. None of these is endemic since most of them also occur in South Africa and Namibia (M. Heinl, University of Innsbruck, Austria, pers. comm.). Despite an overall high plant species diversity in the delta, only 18 % of the vegetation is phanerophytes (trees), compared with 56 % hemicryptophytes and 8 % true aquatic species (Ellery and Tacheba, 2003).

Although seldom flooded, the riparian woodland trees have their roots in the water table in permanent and seasonal swamps (Ellery and Tacheba, 2003). Acacias and mopane are less flood tolerant with pechuel showing greater tolerance of flooding, and also of fire. Riparian woodlands are responsible for much of the water lost from the ecosystem and deplete groundwater by transpiration (Ringrose, 2003). This leads to the uptake of toxic solutes by the transpiring trees, which results in exceptionally good quality surface water. The trees therefore ensure that islands of vegetation function as ‘kidneys’ within the landscape—a reason why riparian woodlands are considered particularly important habitats in this ecosystem (Ellery and Tacheba, 2003).

Flooding tolerance and tree distribution Vegetation on islands in the perennial swamps of the Okavango Delta exhibits a marked zonation (Ellery *et al.*, 1993). This is related primarily to aspects of the hydrological regime such as depth, duration and timing of inundation, but mainly to soil and groundwater salinity (Ellery and Tacheba, 2003). Also, processes associated with

nutrient and sediment supply and sediment deposition, and with the nature of the substratum, play a role (Ellery and Tacheba, 2003). Trees, which are almost exclusively confined to islands, are particularly important as they lower the water table beneath islands relative to the surrounding wetlands and cause a net inward flow of groundwater (McCarthy, 2006). Island fringes are generally characterized by a broadleaf evergreen riparian community of *Syzigium cordatum*, *Ficus verruculosa*, *F. natalensis*, *F. sycamorus*, *Phoenix reclinata*, *Garcinia livingstonei* and *Diospyros mespiliformis*. This gives way to interiors dominated by *Acacia nigrescens*, *Croton megalobotrys* and *Hyphaene ventricosa*. The most central regions are characterized either by short, sparse grassland dominated by *Sporobolus spicatus* or are completely devoid of vegetation with sodium carbonate (trona)-encrusted soil surrounding a central pan of extremely high conductivity (Ellery *et al.*, 1993). Soil pH and mineral content (especially sodium) and groundwater chemistry (conductivity and pH) play a major role in the spatial distribution of plant communities. However, Bonyongo *et al.* (2000) state that the timing and duration of the seasonal flooding are the most important factors determining the species composition of the vegetation.

Tree responses to flooding The riparian trees remain green all year and partly sustain their growth as a result of groundwater uptake in the dry periods. Riverine forests in savanna areas depend on the river for their water supply (Hughes, 1988). Flooding and lateral groundwater flow stimulate growth (Ringrose, 2003). Renewal of leaf growth, however, is primarily related to rainfall, not to flood events in the distal delta (Ringrose, 2003). Regenerative phenology has not yet been described for the trees of the Okavango Delta. In general, however, riverine forests in African savannas show a high percentage of even-aged stands of trees, indicating that hydrological factors are important for tree regeneration because they provide spasmodically favourable circumstances for establishment (Hughes, 1988). Although there are some data on the phenology, growth rhythms, physiological responses and morphological adaptations to flooding in the non-woody vegetation (Ellery *et al.*, 1992; Mantlana, 2008), almost no published data were found for trees in the Okavango Delta. An exception is a recent study of leaf gas exchange of *C. mopane* in northwest Botswana (Veenendaal *et al.*, 2008). Here, differences in physiological and morphological traits between tall and short forms of mopane [*C. mopane* (Kirk ex Benth.) Kirk

ex J. Léonard] trees were compared. The tall form had a smaller leaf: fine-root biomass ratio, higher leaf nitrogen concentrations and less negative leaf water potentials. These differences appeared to be attributable to differences in root depth and density between the physiognomic types, and thus to different ways that the two growth forms exploit available soil water, the tall form having a consistently more conservative water-use strategy as the dry season progressed than the short form (Veenendaal *et al.*, 2008).

Asia: Mekong floodplains

The Mekong is the world's eighth-longest river (Sarkkula *et al.*, 2005). The lower Mekong basin in Cambodia and Vietnam includes floodplains (Fig. 5) which are among the few remaining global examples of relatively intact and functioning floodplains in a large river basin. This is the case despite its high-density human population of 54.8 million. It is widely accepted that this is one of the explanations for the highly productive fisheries of the Mekong and its very high biological diversity. The floodplains cover 795 000 km² (Sarkkula *et al.*, 2005). Since the only available data on tree ecophysiology come from Tonle Sap Lake, which is fed by the Mekong River, we concentrate on the 15 000 km² of floodplain forest of this lake.

At the peak of the wet season, the Tonle Sap can expand to 250 km long and up to 100 km wide in places. The lake is shallow, measuring only 1–2 m at its deepest in the dry season, rising to more than 10 m in the wet season. As a result, when it floods, the total inundated area increases 4-fold. Mean annual rainfall is 1600 mm. Much of this eco-region is flooded for at least 6 months—from August to January or February (Wikramanayake and Rundel, 2002).

Most of the delta's human inhabitants fish, farm and live at subsistence levels. Although the annual flood cycle of the Mekong provides resources for these people, it is a fragile balance. The floodplains of the Tonle Sap have been strongly affected by human activity and little of the original forest cover remains pristine. Throughout the dry season, burning is common, with fires used to clear land before ploughing or to facilitate access. Flooding has recently damaged the infrastructure and caused extensive loss of property and livelihood. At the same time, roads and their associated developments have had a considerable impact on flooding by fragmenting the wetlands and interrupting the natural flow of water, sediments, nutrients and aquatic life. These impacts negate the beneficial effects normally brought by the natural flood cycle. The most significant threat comes from infrastructure development, particularly 149 planned



Fig. 5 Asia: Mekong floodplains in Giang Province at high water (Photographs: Manfred Niekisch, Zoological Garden Frankfurt, Germany).

large hydroelectric dams (Wikramanayake and Rundel, 2002). An additional threat is the invasion of the giant mimosa (*Mimosa pigra*). This aggressive shrubby species becomes established in fallow fields and disturbed shrub land and swamp forest area after clearance or burning. Once established, giant mimosa forms dense, impenetrable thickets of spiny growth that choke out other native species and have little value as wildlife habitat.

Tree vegetation The swamp shrub lands and forest of the Tonle Sap Freshwater Swamp Forests eco-region include two forest associations that have been described for the extensive floodplain area of Tonle Sap. This is a short-tree shrub land covering much of the area and comprises a stunted swamp forest around the lake itself. Similar swamp forests are also present along the floodplains of the Mekong and other major rivers in Cambodia (Wikramanayake and Rundel, 2002). Swamp forest originally dominated the dry-season shoreline of Tonle Sap, covering about 10 % of the floodplain. It occurred in a mosaic of patch stands rather than as continuous forest stands (Wikramanayake and Rundel, 2002). Typically, these forests are flooded for 6–8 months each year and most species lose their leaves during this time. A continuous canopy 4 m high is formed by the dominant deciduous woody species. The most common species belong to the Euphorbiaceae, Fabaceae and Combretaceae together with *Barringtonia acutangula* and *Diospyros cambodiana*. *Terminalia cambodiana* is an important local endemic. The forest vegetation is

dominated by the flood-tolerant tree *Melaleuca cajuputi* ssp. *cumingiana* (Safford et al., 2009). The swamp forest is 7–15 m high. Although *M. cajuputi* may reach 40 m in Australasia, in the Mekong floodplain trees are no taller than 22 m even when 100 years old (Safford et al., 2009) and most commonly form bushes 3–6 m tall.

Flooding tolerance and tree distribution Little information is available on plant distribution and zonation along the Mekong River floodplains. In the Tonle Sap floodplain, the structure and composition of woody vegetation appear to be largely a function of the micro-heterogeneity of soil moisture and seasonal flood dynamics. Tree height is related to soil moisture conditions, with the tallest trees growing closer to the permanent lake basin and shorter ones at the periphery of the floodplain. Several species with shrubby growth forms in this peripheral community reach tree size in swamp forest habitats (Wikramanayake and Rundel, 2002).

Tree responses to flooding In the Mekong floodplains, the terrestrial phase is the main growth period for trees. Most woody species of the floodplain of Tonle Sap are deciduous, a probable adaptation to the periodic flood pulse (Safford et al., 2009). Rather than lose their leaves in the dry season, however, these species lose their leaves when submerged as the lake deepens and the plants become partially or totally submerged. However, there are several woody species that remain evergreen (Lamberts and Koponen, 2008), despite leaves being submerged for 6–8 months each year. With only a few exceptions, flowering and fruit production in the floodplain trees and shrubs are delayed for several months after the flush of new leaves. Fruits reach maturity at the time of submergence, suggesting that fish may be important dispersal agents (Safford et al., 2009). Unfortunately, no data on physiological responses to flooding and morphological adaptations of the Mekong floodplain tree species were found. There are some publications on the ecophysiology of non-flooded environments, mainly dealing with drought-prone deciduous and dry evergreen tropical forests (Tanaka et al., 2004; Ishida et al., 2006; Huete et al., 2008). Few, if any, studies describe the responses of trees typical of the Mekong floodplain.

Australia's tropical floodplain wetlands

Floodplain wetlands are uncommon in the mostly arid continent of Australia. However, an important partly forested wetland, the Kakadu National Park in Northern Australia, extends over 99 000 km² (Lowry and Finlayson,

2004). These floodplains are in an area broadly known as the 'wet-dry tropics'. These have been defined as areas with an annual rainfall of 600–1600 mm spread over 4–7 months. The size of forested wetlands comprises 2900 km². There is a wet season characterized by thunderstorms, tropical cyclones and rain depressions. These commence late in the year (November–December) and last for 3–4 months (Taylor and Tulloch, 1985). The hydrological cycle has been identified as being important in shaping the pattern of the vegetation in the freshwater wetlands (Finlayson et al., 1989). Water flows on a seasonal basis, starting early in the wet season and lasting until after the end of the rains. Flooding occurs once the catchment is saturated; heavy falls of rain later in the season generate more widespread flooding. Freshwater flow in the creeks and rivers ceases within a few months of the end of the rains, and the creeks and floodplains dry out except for a few permanent swamps and billabongs (Finlayson et al., 1990). Some creeks or river reaches are fed by springs or groundwater seeps. Analyses of the water quality within thick stands of submerged herbs and emergent grasses late in the wet season reveal that, in addition to variations in dissolved O₂ and CO₂ concentrations, the water becomes alkaline in the late afternoon when CO₂ concentrations are at their lowest.

Fire and invasive plants and animal species have a significant impact on the extent and distribution of plant species and of the land cover (Finlayson et al., 1990). Damage to the natural levees that separate freshwater and saline wetland communities caused by climate change and by feral animals (especially water buffalo) may also change the vegetation. Notable responses by floodplain vegetation have already occurred following the removal of feral buffalo (Skeat et al., 1996).

Tree vegetation Around 55 % of the terrestrial vegetation in the Kakadu Region is tropical tall grass savanna, composed of eucalypt-dominated open forest and woodland with a 1- to 2-m-tall grassy understorey (Finlayson, 2005). A further 30 % of the region is covered by heaths, and open woodlands with a sparse grass understorey. Closed-canopy monsoon rainforests are restricted to floodplains, besides lowland springs, rock outcrops and beach levees. The seasonally inundated floodplains include fringing woodland and forests, and billabongs (seasonally or permanently inundated lagoons associated with the floodplain or river channels) (Finlayson, 2005). The forests are inundated by up to 1 m of water during the wet season but are dry at other times.

Gallery and floodplain forests in monsoonal Northern Australia are mostly sclerophyllous and dominated by five closely related species of *Melaleuca* (Myrtaceae),

among which niche differentiation is unclear (Franklin *et al.*, 2007). The most important tree communities (Finlayson, 2005) include *Melaleuca* open forest and woodland with a tree canopy cover of 10–70 %. These are dominated by one or more *Melaleuca* species (*M. viridiflora* and *M. cajuputi* around the edges and at the northern end of the floodplain). The dominant species in the backswamps that are inundated for 6–8 months every year is *M. leucadendra*. There is also open woodland providing canopy cover of <10 % dominated by *M. leucadendra*. There are 12 terrestrial tree species, including *Eucalyptus* spp., *Pandanus spiralis*, *Lophostemon lactifluus* and *Syzygium suborbiculare*. Paperbark swamp forest is dominated by trees including *M. viridiflora*, *M. cajuputi* and *M. leucadendra*, and to a lesser extent *B. acutangula* and *Pandanus* spp.

The productivity of the floodplain vegetation changes with the annual cycle. This is indicated by periodic litterfall from *Melaleuca* trees. In an intensively sampled *Melaleuca* forest on the Magela floodplain, total litterfall was $\sim 0.7 \text{ kg m}^{-2} \text{ year}^{-1}$, whereas at a second site on the floodplain, less intensively investigated, a value of $\sim 1.5 \text{ kg m}^{-2} \text{ year}^{-1}$ was recorded (Finlayson, 1988). Comparative data for *Melaleuca* forests are limited to a small number of studies of different species found in the wetlands in southern Australia. These deposit an annual litterfall of $0.39\text{--}0.43 \text{ kg m}^{-2} \text{ year}^{-1}$ (Finlayson *et al.*, 1993). The distribution and density of trees on at least part of the floodplain were seen to change considerably between 1975 and 1990 (Finlayson, 2005), indicating the dynamic nature of the wetland environment.

Flooding tolerance and tree distribution The duration of flooding, depth of water and the velocity of water flow are major determinants of the vegetation composition of the floodplain (Finlayson *et al.*, 1989). The changing pattern is a function of both the flooding and drying phases of the hydrological cycle (Finlayson *et al.*, 1989, 1990). The vegetation of the floodplain billabongs is much influenced by adjacent plant communities on the seasonally inundated floodplain (e.g. grass mats extending across the floodplain and into the billabongs). Franklin *et al.* (2007) propose that *Melaleuca* forests occur where disturbance by fire and/or floodwater is too great for rain forest to persist, making them the wetland analogue of the eucalypt species that dominate the better-drained parts of north Australia.

Tree responses to flooding Little information is available on physiological responses and adaptations of trees in Australian floodplains. Cowie *et al.* (2000) have reviewed adaptations in wetlands by herbs and macrophytic vegetation, and summarized the nature of the floodplain

environment. They noted that variability due to changes in the hydrological cycle has resulted in many specific adaptations that enable the plants to establish and grow (Finlayson *et al.*, 1989). The few details given include that trees of the floodplains often have modified bark structures such as the corky bark of *Sesbania formosa* and *B. acutangula*, and the distinctive papery bark of some melaleucas which possesses internal, longitudinal, gas-filled passages. It is also said that the majority of seed-dispersal mechanisms involve water, even though many parts of the floodplains are drier for a longer period than they are wet. However, it is not clear if this also applies to trees. Nothing seems to be known of the physiological and morphological adaptations of trees of the Kakadu National Park. Responses to flooding by melaleucas of North Queensland have, however, been documented and these may be relevant to the Kakadu since this is an environment with a median duration of inundation of 75 days (McJannet, 2008). Using a heat-pulse method, McJannet found a strong relationship between tree size and tree water use, and showed that transpiration by *M. quinquenervia* was unaffected by inundation. This ability to transpire during flooding may be due to physiological adaptations of this species, and to dynamic root systems that can quickly respond to rising and falling water tables and dense networks of fine ageotropic roots, which grow on and within the papery bark. Waterlogged *M. quinquenervia* also develops negatively gravitropic roots (Sena Gomes and Kozłowski, 1980).

A study by O'Grady *et al.* (2006) of *Corymbia bella* and *M. argentea* in riparian zones of the Northern Territory, along the Daly River, showed that throughout the dry season predawn leaf water potentials were above -0.5 MPa , indicating that neither species suffered significant unrelieved water-deficit stress during the dry season. This was despite low soil matric potentials in the top 1 m of soil. There were also no seasonal differences in tree water use in either species. Xylem sap deuterium concentrations indicated that *M. argentea* trees along the riverbank relied principally on river water or shallow groundwater, whereas *C. bella* growing along the levee was reliant on deep soil water reserves (O'Grady *et al.*, 2006). This study demonstrates strong gradients of tree water use within tropical riparian communities in Northern Australia which probably can be extrapolated to the Kakadu Region.

Discussion

We have demonstrated that in all tropical continents, highly adapted tree species populate the floodplain.

There is little taxonomic overlap except for the Asian and Australian floodplain where the genus *Melaleuca* dominates, but *Barringtonia* also occurs in both ecosystems. Forest types range from highly diverse dense forests (Amazonia, Mekong) to gallery forests or small tree stands scattered in savanna-dominated environments (Okavango, Kakadu Region). In each floodplain, the aquatic phase occurs when temperature and light conditions are optimal for plant growth and development, implying the need for developmental and biochemical adaptations rather than relying on avoidance through dormancy (Parolin *et al.*, 2004). Flooding patterns vary, with durations ranging from more than half a year (Amazonia, Mekong, partly Kakadu) to only a few weeks (Okavango). The most important characteristic is the predictability of the time of the annual flood (the flood pulse concept of Junk *et al.*, 1989). This predictability has allowed the trees to form morphological and physiological adaptations against flooding. On the other hand, as a consequence of the differing flood intensities and different flooding tolerance of the plants along the flooding gradient, tree distribution presents clear zonation in all four ecosystems. However, our wish to compare the underlying physiological and morphological reasons for this zonation was frustrated by a lack of relevant published data. A small number of species from the Asian, African and Australian floodplains have been analysed to date, and the dearth in our knowledge is alarming in the face of the speed at which the floodplains are being damaged or destroyed and the pressing need for well-informed recovery programmes.

Clearly, it is difficult to be sure of the extent to which trees in the four ecosystems share similar underlying adaptations to flooding stress. Phenological data indicate that this may be the case. For example, many deciduous species respond to flooding with leaf shedding, presumably as a means of reducing transpiration and water loss at a time when hypoxic or anaerobic roots may offer large resistances to water uptake. However, evergreen species are common in each of the floodplains that we examined with the exception of the Australian wetlands. This indicates the possibility that other mechanisms exist to reduce transpirational losses, although here too a proportion of the leaves of evergreen trees is also lost during flooding.

Physiological adaptations similar to those well known in temperate and Amazonian species can also be expected in the tree species of the Mekong, Okavango and Kakadu floodplains. Among the most important will be root system adaptations to anoxia (Crawford, 2003; Gibbs and Greenway, 2003). These will include the accumulation of adequate carbohydrate reserves and the ability to switch to alcoholic fermentation as

an alternative, albeit inefficient, alternative source of energy to Krebs cycle-based aerobic respiration (Crawford, 2003). Induction of the activity of fermentative enzymes such as ADH, LDH, GPT and MDH has been observed under anaerobic growth conditions in Amazonian tree species (Schlüter and Furch, 1992; Schlüter *et al.*, 1993; De Simone *et al.*, 2002a; Ferreira, 2002), and this probably also applies to species of the Okavango, Mekong or Kakadu regions.

Underwater photosynthesis is common in temperate herbs (Mommer and Visser, 2005) and postulated for some tree species in Amazonian floodplains (Schlüter *et al.*, 1993; Waldhoff *et al.*, 2002; Parolin, 2009). It is possible that underwater photosynthesis, which both increases internal oxygen concentrations and raises energy supply, could partially alleviate the adverse effects of submersion. This may well be of adaptive significance in the trees of the Mekong floodplains where flood heights can exceed 2 m and might be associated with periods of complete submergence.

In the four floodplains that we examined, the terrestrial non-flooded phase is when tree growth is most vigorous. However, many tree species retain actively flowing phloem sap even during flooding (Waldhoff *et al.*, 2002; Visser *et al.*, 2003), indicating that active sources and sinks for respirable substrates operate under these conditions. A set of metabolic adaptations is inevitably required to achieve this. We suggest that in most tree species of the tropical floodplains, the primary morphological strategies in response to flooding are similar to those of temperate species (Jackson and Armstrong, 1999) or in the well-analysed tropical Amazonian floodplains (Parolin *et al.*, 2004, 2010). In particular, there must be a development of gas-filled spaces in the roots and stems to allow diffusion of oxygen from the aerial portions of the plant into the roots. Morphological adaptations that favour this are 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 and function by roots affected by lack of oxygen in the soil. Under experimental conditions with stable water levels, most species show the potential to produce adventitious roots. But, in the field, they are seldom found, probably because their formation is hampered by a rapidly changing water level. Leaves of tropical forests in general, and the Amazonian floodplain forests in particular, commonly have xeromorphic structures (Waldhoff, 2003). This attribute contributes to suppressing water loss at times of low water supply. This can apply to tree

crowns during the aquatic phase and to periods of drought in the terrestrial phase.

Strict comparability between the four ecosystems we studied is limited by region-specific constraints such as the influence of groundwater quality and the incidence of fire and/or salt. These constraints might also be responsible for the large differences in tree diversity encountered in the four ecosystems. It is also true that the two forested floodplains also exhibit striking differences in their diversity. Tree species richness in the Amazonian white-water floodplains (várzea) is ~10 times greater than that in the forests of Cambodia (Tonle Sap; [Campbell et al., 2006](#)) and about three times above that in the Brazilian Pantanal, another extensive wetland dominated by savannah ([Wittmann et al., 2006](#)). One reason for the comparatively high tree species richness in várzea forests of Amazonia is the coexistence of species well adapted to flooding and generalist species that also occur in the uplands ([Wittmann et al., 2006](#)). Very little is known about the number of generalists vs. specialists among floodplain trees. In Amazonia, only a few tree species occur along the whole flooding gradient, with most being restricted to very small topographic amplitudes ([Wittmann et al., 2002](#)). Only ~20% of all várzea tree species occur in both low- and high-land habitats, demonstrating the striking difference in ecophysiological constraints for tree survival and growth along the flooding gradient. In the other floodplains of the world, generalists may dominate, as in savanna ecosystems. However, we have too little information to speculate about the ecological amplitude of trees in floodplains.

The degree of flood tolerance depends, in large part, on the time taken to colonize the floodplains. Morphological adaptations may be remnants of pre-adaptations from non-flooded upland tree species ([Kubitzki, 1989](#)) which evolved further, leading over time to highly adapted species. Thus, the phylogenetic development of adaptations depends on the age of the ecosystem, and also on the dominating plant families that colonized these ecosystems originally. In each of the four ecosystems, there are large differences in developmental age (Table 1). This implies different stages of adaptations among the organisms living there. Amazonian and African floodplains are extremely old, dating at least to the Pleistocene (>12 million years old), or even earlier. Such ancient landscapes will have experienced several changes in climate and hydrology, i.e. during the glacial and interglacial periods. In contrast, the Mekong River basin and the Australian floodplains are much younger, and are thought to be no older than 7500 and 4000 years, respectively ([Junk et al., 2006](#)).

Conclusions and forward look

Our comparative review on the adaptive responses of trees to flooding in four tropical freshwater floodplains of different continents demonstrates that substantial data about the floodplain tree flora, its ecology and functioning are lacking. Despite many physiologically motivated studies on trees of the Central Amazonian floodplains, and a few studies on other tropical freshwater floodplains, we are still only at the start of our understanding of how terrestrial plants, especially trees, cope with extended periods of flooding. However, this knowledge is fundamental to understanding the evolution of flooded landscapes and their organisms, as well as their interaction with non-flooded ecosystems. The range of plant responses recorded in the different tropical floodplains leads us to the following conclusions:

- (i) Regular flooding is a severe stress to trees, resulting in reduced species richness compared with non-flooded uplands.
- (ii) The regular flood pulse has given rise to a large diversity of growth forms and adaptations by trees. These seem to increase in variety with the age of the respective floodplains and the climatic stability to which they were exposed.
- (iii) Most floodplain tree species are restricted to small topographic amplitudes along the flooding gradients, leading to a distinct zonation of tree species. This implies different mechanisms or combinations of mechanisms conferring zone-specific tolerance to flood stress. This zonation is not dependent on the height of the flooding amplitude. Most highly flooded (>2 m) tree species react to high-water periods with leaf shedding, which is associated with decreased metabolism and growth.
- (iv) The occurrence of evergreen tree species does not depend on the height and magnitude of flooding, since evergreen species are found in all three floodplains.
- (v) Although the responses of trees to flooding seem to be manifold, variability within an ecosystem is greater than that between ecosystems despite widely differing species/genera/families dominating the respective floodplains.
- (vi) Endemic tree species are rare, except in Amazonian floodplains. This may be the outcome of a markedly stable climate over geological time.
- (vii) Future research must address the current paucity of published data on the ecophysiology and adaptations and requirements of trees in the major floodplain forests.

(viii) Attention also needs to be given to small wetlands along small rivers or in remote places. These areas have been almost totally neglected.

Where possible, future studies should adopt methods which will allow comparisons to be made with confidence. Climatic change, increasing prevalence of droughts, alterations to groundwater availability and flooding periodicities make such work increasingly urgent since freshwater floodplain forests are a vital human resource that is under threat. They harbour many fish and mammal species, help moderate widespread flooding of inhabited areas, regulate river levels, improve water quality, act as substantial sinks for carbon and provide timber and non-timber forest products. Improving our understanding of their workings will underpin their preservation and effective future management.

Contributions by the authors

Both authors contributed to a similar extent in the preparation of this article.

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Conflict of interest statement

None declared.

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