FLOOD-TOLERANT TREES OF AMAZONIAN FLOODPLAINS ALSO TOLERATE DROUGHT

Pia Parolin[1]

Resumo
Na planície amazônica, as árvores estão regularmente sujeitas a períodos de inundação que variam do encharcamento da rizosfera até a submersão da planta toda. Entretanto, a falta de água durante alguns períodos do ano também pode afetar intensamente o crescimento das árvores. A seca é especialmente crítica para o estabelecimento de plântulas, pois as condições mais secas prevalecem quando as águas baixam e o estabelecimento ocorre. Diante as mudanças climáticas, aumentos na frequência e intensidade de períodos secos justificam uma análise das respostas das árvores a estes drásticos eventos. A presente resenha visa reunir os dados que nos permitam entender as diferentes respostas à seca de árvores primariamente resistentes a inundações.
Palavras chave: tolerância a inundação, submersão, respostas à seca, florestas tropicais, estabelecimento de plântulas.

Abstract
In the Amazonian floodplains, trees are subjected to regular periods of flooding which ranges from waterlogging of the rhizosphere to submergence of the whole plant. However, the lack of water during certain periods of the year can strongly affect tree growth as well. Drought is especially critical for seedling establishment, because the driest conditions prevail in the same time as flood waters recede and establishment takes place. In the light of climatic changes, increases in frequency and intensity of dry periods justify an analysis of tree responses to these drastic events. The present review aims at bringing data together which enables us to understand the different responses of primarily flood-resistant trees to drought.
Key words: flooding tolerance, submergence, drought responses, tropical lowland forests, seedling establishment

Introduction

Wetland forest ecosystems are maintained primarily by the nature of their hydrological regime, including both periods of wetting and drying. While the flood regime is recognized as a key driver of forest community dynamics and adaptive life history traits, dry periods can also play important roles in forested wetlands. In comparison to the abundant research on tree responses to flooding in wetland forest systems (*e.g.,* Kozlowski, 1984; Vartapetian and Jackson, 1997; Visser *et al*., 2003), the eco-physiological responses of floodplain species to drought has received less attention (but see Casanova and Brock, 2000; Elcan and Pezeshki, 2002; Lopez and Kursar, 2007). Additionally, the influence of drought in moist tropical forests has been a less obvious direction of research

[1]University of Hamburg, Germany e-mail:pparolin@botanik.uni-hamburg.de

until recent attention to increasing drought frequency and severity associated with climate change patterns (Malhi and Wright, 2004; Marengo *et al*., 2008). Emerging research suggests that the effects of drought may be severely underestimated for tropical forests worldwide (ter Steege 1994b; Engelbrecht *et al*., 2007; Baltzer *et al.,* 2008; Poorter and Markesteijn, 2008) as well as for tropical forested wetlands (Casanova and Brock, 2000; Lopez and Kursar, 2007a). Comparative research from the tropics is needed to broaden the understanding of plant responses to overlapping stresses and how diverse tropical forest communities might reflect those species-specific responses (Engelbrecht *et al.,* 2007).

An extensive literature is available on the physiological plant responses to drought (Kozlowski and Pallardy, 2002; McDowell *et al*., 2008), flooding (Kozlowski, 1984; Crawford, 1996; Visser *et al.,* 2003; Jackson and Colmer, 2005; Jackson *et al.,* 2009), and anaerobic stress (Vartapetian and Jackson, 1997). There is a substantial growth of interest in species-based research on the physiological traits and genetic makeup that permit drought tolerance, as well as the ecological aspects of drought in plant community dynamics and species distributions. However, drought and flooding are rarely considered simultaneously, despite the occurrence of drought in wetland ecosystems (Streng *et al.,* 1989; Hall and Harcombe, 1998; Elcan and Pezeshki, 2002; Capon, 2007). A recent meta-analysis of Northern Hemisphere woody plant species addresses this gap, reporting simultaneous drought and waterlogging tolerance for only 2.6% of 806 northern hemisphere temperate shrub and tree species (Niinemets and Valladares, 2006). Such comparative studies support the broad hypothesis that woody plants have evolved tolerance for overlapping stresses, including flooding and drought, but that trade-offs exist (due to the physiological limitations that vary among species) that limit plant population growth and species diversity. To complement our understanding of plant responses to the overlapping physiological stresses of drought and flooding, further meta-analyses are needed for tropical forest species.

Amazonian floodplain forests (Figure 1) hold over one thousand species that have evolved a variety of adaptive responses to annual cycles of flooding and drying (Junk *et al.*, 1989; Parolin *et al.*, 2004; Wittman *et al.,* 2006). Seasonally flooded forests experience intra-annual fluctuations in wet and dry seasons, with water levels up to 12 m (Goulding *et al.*, 2003) and supra-annual droughts associated to El Niño climatic events (Walsh and Newberry, 1999; Schöngart and Junk, 2007; Marengo *et al.*, 2008). While the dry season provides a window of opportunity for plant colonization and growth on otherwise anaerobic floodplain soils, drought induces variable eco-physiological responses to water stress, resulting in differential mortality among species. Drought-induced responses among tropical woody species include desiccation avoidance strategies such as leaf shedding, reduction of leaf size, rapid closure of stomata, waxy leaf cuticles, and high allocation to root biomass relative to stems (Kozlowski and Pallardy, 2002). Floodplain trees may be unlikely to experience water stress in dry periods due to a shallow water table, yet high foliar evaporation rates may exceed root respiration rates for species without

tap roots. However, seedlings with shallow root systems may be particularly susceptible to drought on floodplain soils (Casanova and Brock 2000; Middleton 2000). As such, drought resistance may be as important as flooding tolerance for floodplain forest species composition. The present paper focuses specifically on floodplain tree response to the dry phase of the annual flooding cycle, thus complementing previous reviews addressing adaptive responses to flooding (Parolin *et al*., 2004, 2010).

The role of drought in Central Amazonian floodplains has not been sufficiently explored, despite two decades of research on floodplain tree species responses to waterlogging and submergence (*e.g.,* Worbes, 1985; Meyer, 1991; Schlüter and Furch, 1992; Schlüter *et al.,* 1993; Waldhoff and Furch, 1998; De Simone *et al.,* 2002*a*, *b;* Gribel and Gibbs, 2002; Waldhoff *et al.,* 2002; Waldhoff and Furch, 2002; Parolin *et al.,* 2004; Ferreira *et al.,* 2005, 2007, 2009; Maia *et al.,* 2005; Oliveira-Wittmann, 2006; Parolin *et al.,* 2006; Piedade *et al.,* 2006; Wittmann *et al.,* 2006; Parolin *et al.,* in press *a, b, c*; Horna *et al.,* in press; Parolin, 2009). Within these studies, plant responses to drought do appear as single observations or as comparative treatments to flooding in field measurements and experiments. In the present review, we summarize these isolated results and observations to consolidate existing knowledge on adult and seedling ecophysiological responses to drought among woody Amazonian floodplain species, and their implications for species distribution. The focus lies on the nutrient-rich white-water floodplains, so-called *várzea*, and nutrient-poor blackwater floodplains, so-called *igapó*.

To address the role of drought in the ecophysiology of Amazonian floodplain tree species, we analyse the phenological, anatomical, and physiological responses to drought observed among trees and how drought influences the physiological performance, mortality and species distributions of trees and seedlings. Using available data from a range of publications, these questions are addressed to understand the role of drought for tree ecophysiology in comparison with flooding stress. The present paper first briefly introduces the hydrologic and edaphic parameters typical of Central Amazonian floodplains, followed by a descriptive section on the phenological, anatomical and physiological traits of floodplain species that may serve for drought alleviation as well as germination, mortality and survival strategies for desiccation avoidance. Finally, we discuss drought tolerance and avoidance strategies, and the potential effects of climatic change on species composition in Central Amazonian floodplain forests.

Precipitation, flooding regime, and soils of Central Amazon floodplains

Rainfall patterns. The broad-scale patterns of the East-West rainfall and dry season duration gradient in the Amazon Basin (Sombroeck, 2001) may differ dramatically between upland and floodplain regions. In Central Amazonian floodplains, rainfall can be up to 45% less than in the surrounding uplands (Irion *et al.*, 1997), due to the effect of local river-breeze circulation away from water bodies and early-daytime ascending cloud-formation over forested uplands (Molion and Dallarosa, 1990; Sombroek, 2001). Remotely sensed data on

relatively low cloud cover over Amazon-Solimões River floodplains concur with previous observations, particularly during the dry season (Sioli, 1984). Decreased rainfall is not observed in all Amazon floodplains; in contrast, Lower Amazon floodplains at the Amazon-Tapajós River Confluence experience higher rainfall due to compensation for lower daytime rainfall by heavy nocturnal rainfall in floodplains (Fitzjarrald, 2008). This local-scale variation in precipitation regimes between floodplains and uplands may be crucial for understanding when trees may be subjected to drought conditions.

Rainfall recordings in the region of Manaus are among those best documented in the Amazon, with records dating back to 1902. The climate in Manaus is hot and humid, with a weak thermal periodicity (mean annual temperature 26.6℃) and high relative humidity (75. 6% in September, 86.7% in April) (Salati and Marques, 1984; Ribeiro and Adis, 1984; Weischet, 1996). The warmest months are August to November (27.2-27.6℃) , the coldest January through April (25.9-26.1℃). Precipitation is clear ly periodic, with a rainy season from December to April and a dry season from June to October. Total rainfall in Manaus averages 2100 mm yr^{-1}, and in the dry months evaporation can exceed precipitation thus leading to drought events (Irion *et al.*, 1997). From precipitation records of 1966-1993, mean precipitation during the dry season (August-November) in Manaus is estimated at 357± 85 mm, of which more than 60% falls as heavy rain over less than 3 days (Junk and Krambeck, 2000). Mean monthly evaporation rates range from 40 mm during the rainy season to up to 90 mm during the dry season (Junk and Krambeck, 2000). Since all available physiological data on adult trees and seedlings were recorded in the vicinity of Manaus, the following climate, river level and soil data are presented from the Manaus region.

River water levels. The water-level gauge near the confluence of the Solimões and Negro Rivers represents the runoff correlated to the mean precipitation in a catchment area of approximately 3.0 million km^2, encompassing the Andean and western Amazon watershed (Richey *et al.*, 1989; Schöngart and Junk, 2007). The mean amplitude between annual flood minima and maxima of the Amazon River averaged 10.28 m in the period 1903-2006. The flood pulse is somewhat predictable: the maximum flood level occurs in 55% of years in late June (Irion *et al.*, 1997). Precipitation and water discharge of the major Amazonian rivers seem to be directly related to the El Niño Southern Oscillation (ENSO) (Adis and Latif, 1996; Marengo and Nobre, 2001). El Niño causes lower maximum flood-levels and prolonged dry periods, whereas La Niña events cause high flood-levels and longer flood periods (Ronchail *et al.*, 2005; Schöngart and Junk, 2007). The lowest maximum water-level in central Amazonia occurred during the strong El Niño event of 1926 at 21.76 m asl, almost 6 m lower than the average maximum water-level (27.72 m asl) (Schöngart and Junk, 2007). The last two decades have been marked by unusually strong El Niño events in 1982/83, 1997/98, prolonged dry periods from 1990-1995 and a recent severe drought in 2005 unrelated to El Niño (Marengo *et al*., 2008). The increasing frequency and severity of droughts

(Table 1) has raised the question whether the human induced greenhouse effect strengthens the behaviour of the ENSO (Timmermann *et al.*, 1999; Houghton *et al.*, 2001; Trenberth, 2001). However, drought events are rarely a subject in literature. Droughts of varying intensity have occurred in the Amazon basin and in the floodplains in the past century, and are clearly natural events in floodplains, as indicated by reports of severe droughts in 1860 and in 1774 that had pronounced effects on the forest biome (Sombroek, 2001).

Soils and water availability. Amazonian floodplain soils are alluvial-hydromorphic, often lacking stable and defined horizons (Oliveira *et al.*, 2000). Where a marked dry season occurs, pockets of vertisols may also develop within the regularly inundated *várzea* (Roosevelt, 1980). Depending on water chemistry of the flooding rivers, soil types differ considerably in texture, porosity, nutrients, and moisture holding capacity. While nutrient-rich white-waters generally enrich alluvial soils or maintain comparatively high nutrient-levels, soils of nutrient-poor black-waters are leached with each flooding event. In white-water floodplain (*várzea*) forests, soil porosity averages 46%. Soils are silty, but sand and clay grain sizes may be prevalent, depending on the hydro-geomorphology, *e.g.,* distance of the site to the main river channel, and topographical position (Wittmann *et al.*, 2004). At the beginning of the dry season, plant growth can continue because of sufficient water availability in the soils. Root biomass and root production in *igapó* and várzea forest are mainly restricted to the upper 30 cm of the soil (Meyer, 1991; Worbes, 1997). Dry bulk density ranges between 1.3 and 1.6 g cm^{-3} on the Islands Marchantaria and Careiro in Central Amazonian floodplains near Manaus (3°15´S, 59°58´W, Oliveira *et al.*, 2000).

Soil water content in forested levees varied with depth and time, mainly influenced by rainfall and the flood pulse. During flood drawdown, in October, the mean water content of the soil profile varied between 23 and 33%, as compared to a mean water content of 33-42% (equivalent to 66-84% water filled pore space) after the onset of rain (Kreibich, 2002). Soils are driest in November/December (Worbes, 1986). Differences between soil layers are prominent, with the driest soils at 20-60 cm depth and the wettest layers below the water table at 300-450 cm depth (Worbes, 1986; Kreibich, 2002).

Tree responses to flooding

In response to waterlogging, trees form adventitious roots, lenticels, and stem hypertrophy (Parolin *et al.*, 2004). In stems and roots, aerenchyma is formed, and cell wall biopolymers such as suberin and lignin are deposited in the root peripheral cell layers (De Simone *et al.*, 2002a). Physiological adaptations include the induction of activity of fermentative enzymes such as alcoholdehydrogenase (ADH), lactate dehydrogenase (LDH), glutamate-pyruvate transaminoferase (GPT), and malate dehydrogenase (MDH) under anaerobic growth conditions (Schlüter and Furch, 1992; Schlüter *et al.*, 1993; De Simone *et al.*, 2002b). Other plant responses linked closely to submergence tolerance include a reduction of growth and metabolism, as well as leaf

shedding (Worbes, 1997; Schöngart *et al.*, 2002). Many species maintain their leaves without apparent damage for months or years despite prolonged submergence; some species may sprout new leaf buds and photosynthesize underwater (Parolin, 2009). Another response to submergence is the shift to anaerobic pathways in the leaves (Schlüter, 1989) and the formation of antioxidant compounds and vitamins in plant leaves that may minimize plant damage by alleviating oxidative challenge and organ damage under submersion (Oliveira-Wittmann, 2006).

Vegetative phenology and biomass allocation as responses to drought stress

Stress caused by drought occurs when water availability is deficient for plant metabolism (Lichtenthaler, 1998). In Amazonian floodplains, drought stress is mainly caused by low soil moisture availability and high evaporation rates during dry periods. In contrast to many other stress factors, drought stress does not start abruptly but increases over time (Larcher, 2001), emphasizing the importance of drought duration for plant survival.

Leaf shedding, wilting and flushing. In Central Amazonian floodplains trees often shed their leaves during the high water period (Parolin *et al.*, 2002a; Schöngart *et al.*, 2002). Paradoxically, plants under both drought and flooding conditions may experience water stress, and as such similar physiological responses in leaf phenology may be triggered by both flooded and desiccated plants. Whereas drought-induced water stress is a result of low soil water availability, water stress in the flood season is caused by anoxia-induced reductions in water permeability in root tissue (Kozlowski, 1984). Water uptake during anoxia is mediated by water channel proteins in the plasma membrane known as aquaporins, which are blocked or 'gated' by cytosol acidosis, an effect of oxygen deficiency in cell tissues (Tournaire-Roux *et al.,* 2003). As such, leaf senescence during flooding may be an adaptation to the reduced water status of trees as a consequence of disturbed root function and decreased water uptake during flooding (Gill, 1970; Kozlowski, 1984; Meyer, 1991; Blom and Voesenek, 1996). During drought, leaf shedding may be an adaptation to avoid drought stress by decreasing transpiration, or by the production of smaller leaf surfaces, as observed for *Senna reticulata* (Parolin *et al.*, 2005).

Wilting has been observed during drought periods for *Astrocaryum jauari* and *Macrolobium acaciifolium*, which colonize the highest flood-levels in both, white-water and black-water floodplain forests (Schlüter, 1989). Complete leaf senescence may last for a few months as observed for *Pseudobombax munguba*, *Ceiba pentandra* and other water-storing (stem succulent) Bombacaceae (Gribel *et al.*, 1999; Schöngart *et al.*, 2002), or it may be as brief as four weeks (*e.g., Tabebuia barbata*) (Parolin, 1997). New leaf flush occurs in two distinct peaks, one during flood drawdown (Aug-Sept) and the second peak at the onset of the rainy season (Nov-Dec) (Worbes, 1997). The peaks of leaf fall and new flushes may be a response to rapidly drying soils during the brief dry season between the termination of flooding and the onset of the rainy

season (Worbes, 1986). During this period, the soils are partially dried out to the wilting point for a few weeks, supporting the hypothesis that vegetative phenology is responding to drought.

Under experimental conditions, seedlings' leaves of the evergreen floodplain species *Nectandra amazonum* did not senesce when subjected to drought, whereas waterlogged and flooded plants shed most leaves (Waldhoff *et al.*, 2000). In contrast, leaves of the evergreen *Laetia corymbulosa* and *Pouteria glomerata* senesced under dry experimental conditions with a relative humidity of 45% (under ambient conditions, humidity is never below 80%) (Oliveira-Wittmann, 2006).

Changes in seedling growth and biomass allocation. Seedling establishment and early growth occur during the non-flooded phase and may be subjected to drought stress for a brief period of approximately four weeks before the onset of the rainy season. Seedling size prior to environmental stress by flooding or drought is important for seedling survival across annual cycles of drying and submergence (Engelbrecht *et al.*, 2006; Markesteijn and Poorter, 2008). An advantage of large seedling size is the enhanced total carbohydrate pool in stem and root tissue (Myers and Kitajima, 2007; Ferreira et al., 2009), which has important implications for drought tolerance. The stored resources either allow evergreen species to maintain basic metabolic functioning during stressful dry periods, or they permit deciduous species to flush new leaves at the onset of the wet season (Newell *et al.*, 2002).

Drought can cause pronounced negative impacts on seedling growth, as shown by a series of greenhouse experiments (Figure 2, 3; Parolin, 2001a; Waldhoff *et al.*, 1998; Waldhoff *et al.*, 2000). In comparing the responses of potted seedlings of six tree species to flooding and drought treatments, one study found that patterns of leaf senescence and leaf production were similar in seedlings under submerged and drought conditions, while waterlogged and control seedlings performed better in terms of growth and survival (Parolin, 2001a). After 12 weeks of drought, the average total leaf number among seedlings was significantly reduced in comparison to control seedlings. Pronounced leaf loss and delayed flushing of new leaves in response to drought conditions were also observed among deciduous and evergreen species, indicating that moderate water deficiency in soils may inhibit leaf growth (Brunold *et al.*, 1996). Reductions in seedling biomass accumulation and photosynthetic activity in response to drought were also observed among *Senna reticulata,* a submergence-intolerant shrub. This species is highly adapted to waterlogging with very high photosynthetic rates (maxima of up to 30 µmol CO_2 $m^{-2}s^{-1}$) even when 80% of the tree is waterlogged (Parolin, 2001b), but it is highly susceptible to drought.

Not surprisingly, substantial reductions in height growth, leaf number and stem diameter were reported for three out of six woody species (*Pseudobombax munguba, Cecropia latiloba* ; Figure 2, and *Tabernaemontana juruana*) when subjected to experimental drought conditions, in comparison to well-watered controls and waterlogging treatments (Waldhoff *et al.*, 1998). In

comparison to controls, height growth was 31% lower among evergreen *Tabernaemontana juruana* seedlings; 78% lower among the deciduous *Pseudobombax munguba;* and 89% lower among the light-demanding pioneer *Cecropia latiloba*. *Tabebuia barbata* seedlings produced new leaves during drought and showed only slight reductions in height increment. This apparent drought tolerance may be explained by the fact that the genus *Tabebuia* originates from tropical savannas (Kubitzki, 1989) and presumably has pre-adaptations to dry environments. Such responses are similar to those found in upland forest seedlings that suffer reduction in height increments during drought (Delissio and Primack, 2003).

Drought stress is alleviated by a high relative biomass investment to the root system among seedlings. Seedlings of dry forest species enhance water foraging capacity in deep soil layers by an increased biomass allocation to the roots, thus minimizing the risk of cavitation and increasing the ratio of root biomass to transpirational leaf surface (Markesteijn and Poorter, 2008). In an experiment with seedlings of six tree species with different growth strategies (evergreen – deciduous, pioneer – non-pioneer), changes in the root:shoot ratio had no clear trends (Table 2). In *Cecropia latiloba, Senna reticulata* and *Vitex cymosa* root:shoot ratio increased after 12 weeks of drought as compared to the control treatment, whereas in *Crataeva benthamii, Nectandra amazonum* and *Tabebuia barbata* root:shoot decreased (Waldhoff *et al.*, 1998). While high biomass investment to the root system may be a strategy for drought tolerance for some species, it may not be apparent for others that nonetheless grow well in dry conditions.

Changes in adult tree growth. The growth period of Amazonian floodplain trees is concentrated in the non-flooded phase, which lasts approximately 150-250 days per year, depending on the location of trees along the flooding gradient (Worbes, 1997). Annual inundation by floodwaters causes reduction in the cambial activity of many species (Worbes, 1997). As such, radial increment and shoot extension are a function of the length of the non-flooded phase. This pattern in wood growth is unlike non-flooded upland forests, where annual reductions in cambial activity coincide with the months with lowest precipitation (Worbes, 1986). The effects of extreme drought on floodplain tree woody growth is largely unknown, although tropical upland tree species can display drought-induced intra-annual growth rings with variation among species related to leaf phenology (Borchert, 2002). Regionally, biomass accumulation by floodplain trees peak at intermediate rainfall levels, whereby drought stress is low, but solar irradiance and soil aeration are sufficient for photosynthetic activity and growth. As such, tree growth may benefit from short dry spells, due to lower interception of sunlight in continuously clear skies and potentially reduced attacks from hydrophilic fungal pathogens and diseases. The relationship between drought severity, pathogen attacks, and biomass accumulation and woody growth of Amazonian floodplain trees is largely unknown and requires further study.

Anatomical traits linked to drought adaptations

Adaptations to flooding can also alleviate drought stress (Parolin et al., 2010), such as adventitious roots, aerenchyma, or leathery xeromorphic leaves (Parolin *et al.*, 2004). In leaves, morphological adaptations against drought include small, thick leaves with sclerophyllous structures and increased epicuticular waxes to reduce transpiration (Medina, 1983; Waldhoff *et al.*, 1998). Such structures are found in the leaves of most Amazonian floodplain tree species (Schlüter, 1989; Waldhoff and Furch, 2002; Waldhoff, 2003). Xeromorphic traits are found on leaves of tree species across many tropical forest types as protection against excess evaporation, heat and light (Roth, 1984). Epidermal leaf structures such as waxes or hairs can reflect light to protect leaves from high solar irradiance. Some leaves (*Licania apetala, Senna reticulata, Cassia leiandra,* and *Quiinia rhytidopus*) are covered with papillae that may also protect leaves from reflected irradiance or waxes which prevent water influx (Schlüter, 1989; Fernandes-Côrrea and Furch, 1992; Schlüter and Furch, 1992; Waldhoff and Furch, 2002; Waldhoff, 2003). However, these also enhance drought tolerance by decreasing cuticular water loss and preventing photodamage.

Roots. Enhanced allocation to roots is a common adaptive response to drought, as increased root biomass provides greater access to limited soil water and a greater root:shoot ratio (Brunold *et al.*, 1996). Root production increases continuously through the dry season (Oct-Feb) in several species of Amazonian floodplain trees (Meyer, 1991). In floodplain forests, fine root production is mainly restricted to 0-20 cm deep (Meyer, 1991; Worbes, 1997). During an extremely dry month root production was considerably lower than during the other non-flooded months (Meyer, 1991), indicating that – as frequently found in trees – root growth may be inhibited by water shortage (Brunold *et al.*, 1996). Several Amazonian floodplain species display suberization of roots, preventing water loss and leaching of stored solutes into the rhizosphere during drought periods (Zimmermann *et al.*, 2000). Additionally, lignin and suberin deposits in *Tabernaemontana juruana* roots may be advantageous for preventing desiccation during the dry season (De Simone *et al.*, 2002b).

Physiological responses to drought

Most typical physiological reactions to drought, such as accumulation of prolin and betain, osmotic regulation, or stomatal density and control, have rarely been studied among the one thousand plus tree species of Amazonian floodplains. The available data are summarized in the following section.

Leaf water potential and xylem sap flow. Water balance, osmotic relations and turgor are poorly understood aspects of Amazonian floodplain tree physiology, especially in relation to drought as most measurements are often recorded during the flooded period. A few studies have analysed leaf water potential and stem sap flow across the entire annual cycle (*e.g.,* Müller, 2002; Parolin *et al.*, 2005; Horna *et al.*, in press). Leaf water potential, an indicator of

plant water balance (Fernandes-Correa and Furch, 1992), ranges between an average of -7.6 bar and -15 bar among Amazonian floodplain trees (Parolin, unpubl. data). The least negative potentials were measured in *Senna reticulata*, and the most negative ones in *Nectandra amazonum*. Inter-annual differences in mean monthly leaf water potentials may be substantial, as shown by the values for of five species in June over two consecutive years. However, leaf water potentials in the driest months tend to be continuously low across years, similar to that of some deciduous species (*e.g., Crataeva benthamii*, *Tabebuia barbata*) at the onset of waterlogging in April. *Laetia corymbulosa*, a tree species not particularly drought tolerant, has the lowest negative values during the dry months of the terrestrial period (-1.24 to -2.7 MPa in October/November, as compared to -0.18 to -0.33 MPa for the remainder of the year) (Armbrüster *et al.*, 2004). Leaf shedding has rarely been observed to follow decreasing xylem water fluxes but sap fluxes decreased simultaneously with prolonged leaf shedding in five analysed species (Parolin *et al.*, 2005). Water limitation did not lead directly to drought damage on leaves but may indirectly trigger leaf-shedding through hormone signals. Stem water storage can buffer water shortage during the daytime (Parolin *et al.*, 2005). Seasonal changes in xylem flux density in twelve common tree species of the Central Amazonian floodplain forests showed that xylem flux density in deciduous trees was strongly influenced by tree phenology (Horna *et al.*, in press).

Leaf chlorophyll and nitrogen contents. Under experimental drought conditions (Table 2), *Tabernaemontana juruana* had 12% higher total leaf chlorophyll content than in the control, whereas it was considerably reduced under waterlogged conditions (Waldhoff *et al.*, 1998). Similarly, *Cecropia latiloba* seedlings in drought conditions had 40% less chlorophyll content than that of the control. Chlorophyll concentrations also decreased in *Astrocaryum jauari* and *Macrolobium acaciifolium* as reaction to drought stress (Schlüter 1989). In contrast, some species display increased chlorophyll contents during drought than in the control (Parolin et al., 2010). The ratio of chlorophyll a:b also differed between species subjected to drought conditions, increasing from 2.4 (control) to 2.8 (drought) in *Tabernaemontana juruana* but decreasing from 3.5 (control) to 3 (drought) in *Pseudobombax munguba*. The ecological implications of these parameters with respect to drought tolerance are unclear, and may be a mere consequence of leaf senescence as is the case of changes in leaf nitrogen content, or of sun and shade leaves. Leaf nitrogen content peaked with highest annual nitrogen contents during the months with less water supply (October, November) among six adult tree species (Parolin *et al.*, 2002b). The observed peak in nitrogen is simultaneous with full expansion of new leaves, which have higher nitrogen contents than senescing leaves, after flushing at the end of the aquatic period.

Photosynthesis. Reductions in CO_2 assimilation are caused by leaf senescence, changes in nutrient supply and environmental stresses, such as flooding or drought (Pezeshki, 1993; Pezeshki *et al.*, 1996; Sesták, 1985).

Drought often leads to a gradual reduction of photosynthesis and stomatal conductance over time (Slot and Poorter, 2007). As a general trend, Amazonian floodplain forests species are highly susceptible to drought and respond to water shortage by decreasing photosynthetic CO_2 assimilation, such as is observed in juvenile *Astrocaryum jauari* and *Macrolobium acaciifolium*, and adult *Senna reticulata* and *Laetia corymbulosa* (Schlüter, 1989; Parolin, 2000; Armbrüster *et al.*, 2004). Species that maintain constant photosynthetic activity under mild drought conditions include *Eschweilera tenuifolia*, *Hevea spruceana*, *Nectandra amazonum* and *Pouteria glomerata* (Parolin, 2000; Maia and Piedade, 2002; Armbrüster *et al.*, 2004). In *Pouteria glomerata*, shaded leaves had the highest annual photosynthetic activity during the drought period, probably due to a very deep root system that supplies water to the trees (Armbrüster *et al.*, 2004).

In an experimental study, seedlings of *Nectandra amazonum* had the same photosystem II (Fv/Fm) response to drought as to other hydric conditions (control, waterlogged and almost submerged) with Fv/Fm = 0.78 (Waldhoff *et al.*, 2000). These authors suggest that solar irradiance may pose a greater stress than water shortage for the leaves of *Nectandra amazonum*. *Tabernaemontana juruana* had similar responses to control and drought treatments after 3 months, with light response curves reaching 20 µmol CO_2 $m^{-2}s^{-1}$, as compared to the waterlogged plants which averaged 5 µmol CO_2 $m^{-2}s^{-1}$. In *Pseudobombax munguba*, light response curves showed a decrease in assimilation from 14 to 6 µmol CO_2 $m^{-2}s^{-1}$ during a one-month drought period, dropping to 4 µmol CO_2 $m^{-2}s^{-1}$ after four months of drought (Waldhoff *et al.*, 1998).

Data from a detailed field study of six common species which were monitored for 15 months give insight into the details of photosynthetic performance across the annual cycle of flooding and drying (Parolin, 2000). Photosynthetic activity in adult trees in the field was lower in the months with less water availability in comparison to those with flooding or sufficient precipitation. There is no typical response in photosynthetic activity to drought in adult trees in Amazonian floodplains. Species present a broad variety of responses, depending on their successional stage or phenological strategy (*e.g.,* deciduous, evergreen). While four species had 20% lower mean photosynthetic activities in the flood season (and -50 % in the deciduous *Vitex cymosa*), the evergreen *Nectandra amazonum* and *Senna reticulata* had higher mean photosynthetic CO_2 assimilation in the 1-2 months during the waterlogged period than in the dry season (Parolin, 2000).

In the drier months (Sept - Nov), the evergreen *Cecropia latiloba* and the deciduous *Tabebuia barbata* and *Vitex cymosa* showed abrupt increases of photosynthetic CO_2 assimilation, most likely a result of recent new leaf expansion. With subsequent flooding of the roots, tree water status decreased, leaves were shed to reduce transpirational surface and water loss, and photosynthetic assimilation decreased as a consequence of lower photosynthetic capacity of senescent leaves (Reich *et al.*, 1999; Sesták, 1985). When new leaves were flushed – which occurs during the flood season –

photosynthetic CO_2-uptake increased again and peaked when the young leaves were fully expanded. Thus, *Nectandra amazonum*, *Senna reticulata* and *Crataeva benthamii* showed very high – if not the highest – mean monthly CO_2 assimilation during low rainfall. This trend may be an artefact of belowground access to water by deep roots or increased light availability, such that drought stress may not have been experienced by the trees during measurement.

Transpiration and stomatal conductance. Reductions in transpiration and prevention of xylem cavitation are important for tree survival and growth during drought (Poorter and Markesteijn, 2008). However, due to inhibition of aerobic root respiration during the flood season, greater reductions in transpiration are observed in the flooded period than in the dry period for many floodplain tree species, except *Tabebuia barbata* (Parolin, 2000). Transpiration reaches the lowest rates at peak flooding (Jun-Aug). For example, transpiration rates for *Cecropia latiloba* range between 6000 and 9000 µmol $m^{-2}s^{-1}$, but drop in July and August to below 2000 µmol $m^{-2}s^{-1}$ ($p = 0.0001$, Parolin, 2000). Similarly, another pioneer species, *Senna reticulata*, has transpiration rates of 7000-9000 µmol $m^{-2}s^{-1}$ during the dry season, which drop to 1000 µmol $m^{-2}s^{-1}$ at peak flood in June (Parolin et al., 2010).

Stomatal conductance for CO_2 or water vapour is an index of stomatal aperture (Buschmann and Grumbach, 1985). In six tree species (Parolin, 2000), stomatal conductance ranged between 200 and 400 mmol $m^{-2}s^{-1}$, decreasing 5-35% in the flood season. Stomatal conductance peaked at the end of the waterlogging, when trees kept their oldest leaves and displayed the lowest CO_2-assimilation. Only in *Crataeva benthamii* there was a decrease in stomatal conductance in the dry period (Sept) of less than 100 mmol $m^{-2}s^{-1}$. The present data on patterns of stomatal conductance suggest that the measured trees did not experience water stress during average dry periods.

Root respiration. Exceptional droughts can decrease root respiration, particularly among juvenile trees. In a study of two juvenile species – the palm *Astrocaryum jauari* and the legume tree *Macrolobium acaciifolium* – root respiration was measured in the field (Schlüter, 1989). Contrary to adults, juvenile *Astrocaryum jauari* have a shallow rooting system, reaching only 50 cm depth until the age of 6 yrs, making them vulnerable to low soil moisture availability. In contrast, *Macrolobium acaciifolium* forms a deep taproot. For both species a marked decrease in root respiration was observed during an exceptionally dry period of low rainfall (Oct-Nov, 1986 and 1987). While oxygen turnover increased continuously after the end of the flood season, root respiration dropped from 110 µl O_2 $g^{-\text{fresh weight}}$ to 50-60 µl O_2 $g^{-\text{fresh weight}}$ in *A. jauari*, and from 170-180 µl O_2 $g^{-\text{fresh weight}}$ to 40-90 µl O_2 $g^{-\text{fresh weight}}$ in *M. acaciifolium* (Schlüter, 1989). This drop in oxygen consumption by roots may be a direct response to low water availability in soils, or indirectly due to reduced ion transport in the rhizosphere.

Carbon balance. The combined effects of drought on plant photosynthesis, transpiration and respiration have broad implications for ecosystem carbon budgets. Based on measurements from five adult floodplain tree species, severe drought conditions correlated with low total ecosystem respiration REd, whereas photosynthetic activity was moderately reduced and no change in canopy structure was observed (Horna, 2002). Thus, trees displayed a relative increase in carbon uptake (64.6 gC m−2), due to the combined effect of low CO2 loss by roots and moderate C gain by aboveground live biomass. Short-term increases in carbon uptake during the dry season by aboveground live biomass are also demonstrated in upland forests (Baker *et al*., 2008; Bonal *et al*., 2008). However, the latent effects of drought on tree mortality and fire susceptibility ultimately result in net carbon losses in forest ecosystems over the long term (Mier *et al*., 2008; Brando *et al*., 2008). Total carbon output of aboveground woody tree biomass of a Central Amazon floodplain forest during the dry period (Nov-Jan) averaged an annual low of 360 gC cm^{-2}, peaked at 550 gC cm^{-2} during rising water (Feb-Apr), then gradually drops to 480 gC cm^{-2} at high water levels (May-July) and 420 gC cm^{-2} with receding water levels (Aug-Oct) (Horna, 2002). Carbon output rates from tree branch surfaces varied with species and time of day, but were generally low in the dry season and with no diurnal variation in *Crataeva benthamii, Tabebuia barbata, Albizia multiflora*, *Vitex cymosa* and *Pouteria glomerata*. Branch carbon release rates were minimal during the dry season, with exception of *Vitex cymosa* which had fully developed new leaves in October, coinciding with high carbon output.

Mortality, germination and survivorship with drought

Drought is an important agent of seedling mortality in dry and moist tropical forests (Engelbrecht *et al.*, 2006; Slot and Poorter, 2007). However, the dry period exposes moist oxygenated soils that provide a unique opportunity for tree seed germination and seedling establishment. For the Central Amazonian floodplains, no data are available on the mortality of adult trees due to drought. Exceptional droughts in upland Amazon forests increase both tree mortality and forest flammability (Williamson *et al.*, 2000; Nepstad *et al.*, 2004). The flooded forests on higher levels along the Negro River undergo cyclic fires during the dry season, particularly those on podzolic white-sand soils, suggesting that flooded forest susceptibility to dry season fires may vary along the flood gradient.

Seeds of Amazonian floodplain trees are especially vulnerable to drought. Seed viability when exposed to air post-dispersal may be brief, drying out or rotting within a few days (*e.g., Tabebuia barbata* and *Nectandra amazonum*) or weeks (*e.g., Senna reticulata* and *Aldina latifolia*; Parolin *et al.*, in press a), whereas many species can tolerate weeks to months of submergence (Parolin, 2009). Floodplain trees fruit during the flood season, releasing seeds during flooding, and germination generally is initiated by flood recedence (Parolin *et al*., 2004). Seeds are thus exposed to aerobic conditions, and readily germinate on moist or wet sediment and soils. In exceptionally dry

years with rapidly declining water availability in upper soil layers, seedling establishment may be severely limited (Worbes, 1986).

Seedlings are particularly vulnerable to drought, due to shallow root systems and limited water storage. Seedling mortality can be a result of cavitation, negative carbon balance, and interactions with biotic agents that exacerbate drought stress (McDowell *et al*., 2008). Tropical forest seedlings vary in drought tolerance or sensitivity, ultimately affecting plant species richness, composition, and of adult communities (Engelbrecht *et al.*, 2005; Baraloto *et al.*, 2007; Baltzer *et al.*, 2008; Poorter and Markesteijn, 2008). In a field study, tree seedling mortality was higher during the dry season than during flooding (Ziburski, 1990). Seedling mortality in the dry season, particularly during low rainfall, was 100% among *Vitex cymosa*, 97% among *Crataeva benthamii*, 70% among *Senna reticulata* and *Psidium acutangulum*. With the exception of *Senna reticulata*, mortality was consistently higher during the dry season than during submergence, suggesting that seedlings have a higher tolerance of submergence than drought. In another field study in stands of *Macrolobium acaciifolium*, 50% of seedlings survived the submerged period while a high percentage (value not specified by the author) died during the subsequent period of drought (Schlüter, 1989). Tree seedlings of seasonally flooded forests vary between species in sensitivity to flood and drought stress (ter Steege, 1994a). While many studies focus on flood tolerance as a key mediator for seedling population and community dynamics, the few studies that measure the effect of drought on seedling mortality suggest that drought can play an important role on seedling survival and species composition (Parolin, 2001; Elcan and Pezeshki, 2002; Stroh *et al*., 2008).

Flood and drought. Flood and drought may have interactive effects on seedling survival. Extended periods of flooding may “predispose” seedlings to drought stress by reducing root biomass and root depth; however research on temperate seedlings fail to show interactive effects (Smith and Huslig, 1990; Elcan and Pezeshki, 2002). To test the effects of flooding and drought on floodplain tree seedlings, a common garden experiment was established in the floodplain forests of the Dry Belt Corridor of the Lower Amazon Basin (Lucas, pers. comm.). Tree seedlings raised from collected seeds were transplanted into 22 plots of 5x5 m (N=5 per species per plot) along a flood gradient in three floodplain forests in the region of Santarém (State of Pará, Brazil, 02˚25’S, 54˚42’W). The low mortality for four tree species – two evergreen species (*Garcinia brasiliensis* and *Nectandra amazonum)* and two deciduous species (*Vitex cymosa* and *Pseudobombax munguba*) suggest that deciduous species have a higher tolerance of drought during early seedling establishment.

Survival strategies

Drought responses include stress-induced chemical and hormonal signals in plants that may result in reduced growth or induced reproduction. Some species have responses similar to dry forest species: water foraging capacity is enhanced by an increased biomass allocation to the roots in deeper

soil layers (Markesteijn and Poorter, 2008). Strategies for drought stress may be divided into two categories: a) those **tolerant** of drought, e.g., plants with plasmatic tolerance to low water potentials or low osmotic potentials in their sap, or b) those **avoiding** drought, e.g., plants with morphological or physiological traits to overcome water stress without greatly reducing water potential (Medina 1983; Waldhoff *et al.*, 1998). Such avoidance may be more accurately referred to as a delay of drought stress, as prolonged drought will eventually lead to mortality for many tropical species (Markesteijn and Poorter, 2008).

Similar to upland species, seedlings of Amazonian floodplains represent varying life history strategies that result in different strategies for drought alleviation. Evergreen species may delay drought stress by increasing biomass investment in long-lived organs, avoiding cavitation and minimizing transpiration. Drought avoidance is achieved by maintaining baseline metabolic functioning with low water availability, especially in newly resprouting deciduous species. The probability of xylem cavitation is reduced, while plants maintain gas exchange, hydraulic conductance and cell survival at low water potentials (Tyree *et al.*, 2003; Engelbrecht and Kursar, 2003). Alternatively, deciduous species can maximize resource capture during their restricted growth season when there is no flooding and no drought. At the community level, drought intolerant species are filtered out of dry habitats (Markesteijn and Poorter, 2008) and are perhaps confined to wetter habitats along the flooding gradient.

Evergreen vs. deciduous species. Deciduousness is a major determinant of seedling desiccation survival (Poorter and Markesteijn, 2008), but at the expense of a shorter growing season. Leaves of deciduous species require a lower biomass investment but higher investment of nutrient allocation to new foliar tissue. Deciduous species are often highly efficient in reabsorbing nutrients before shedding their leaves (Paz, pers. comm.). Evergreen species can delay drought stress by maximizing water access**,** while minimizing transpirational water loss via the high root:shoot ratios, high specific root lengths, small leaf area, and high stomatal control (cf. Paz, 2003; Slot and Poorter, 2007; Poorter and Markesteijn, 2008).

Although deciduousness is considered a possible adaptation against drought stress (Borchert, 1983; Medina, 1983; Wright and Cornejo, 1990), studies show no differential survival or growth between deciduous and evergreen species in Central Amazon floodplains (Parolin, 2001a). Alternatively, leaf shedding may be a phylogenetically retained trait adapted to environments in which the species evolved. For example, many genera of the Bombacaceae originated in semi-arid environments and are thus adapted to tolerate periodical drought, using strategies such as leaf shedding to decrease transpirational water loss. Species such as *Pseudobombax munguba* migrated into the floodplains (Kubitzki, 1989) and retained genetically fixed phenological traits. Deciduousness may have assumed supplementary ecological functions in the floodplains, such as enhancement of showy flowers for bat pollination.

Drought and species distribution

Several studies show that dry spells and drought frequency and severity, such as those associated to El Niño events, can shape species distribution in tropical wet and dry forests (Borchert, 1994; ter Steege, 1994; Engelbrecht and Kursar, 2003; Lopez and Kursar, 2003; Bunker and Carson 2005; Engelbrecht *et al.*, 2005; Poorter and Markesteijn, 2008). As such, supra-anual extreme environmental conditions may play a key role in plant species distribution (ter Steege, 1994), and overlooking the impact of severe events may result in failure to identify critical mechanism structuring ecological communities (Bunker and Carson, 2005). Tree species distribution, composition, and richness in Amazonian floodplain forests are understood to be largely mediated by the flooding gradient (Junk, 1989; Ayres, 1993; Ferreira, 2000; Wittmann *et al.*, 2002; 2004). Tree species are zoned along the flooding gradient, most of them restricted to limited topographic ranges. In Central Amazonian floodplain forests, less than 10% of 222 recorded tree species occurred along the entire flood gradient (Wittmann *et al.*, 2004). At a basin-wide scale, species similarity between low-*várzea* forests (mean flood height > 3 m, flooded period > 50 d year^{-1}) and high-*várzea* forest (< 3m, < 50 d year^{-1}) amounted to approximately 30 % (Wittmann *et al.*, in press).

While flooding is understood to be a crucial factor influencing tree species distribution, there is also a well-defined gradient in the light requirement of *várzea* tree species (Wittmann and Junk, 2003). At the community scale, high-*várzea* species are more shade-tolerant than those of the low-*várzea*, the latter habitat of which includes the light-demanding pioneer species. However, few studies in the region have focused on the impact of drought as a determinant of species distribution. Droughts are likely influence tree establishment in floodplains and thus affect community composition. Both flooding and drought can be interpreted as stress factors that correlate with a reduction in plant diversity (Worbes, 1997). It is hypothesized that drought has differential impact on tree assemblages along the flooding gradient. The most affected species should be highly-flood adapted and endemic to the low-*várzea*, including evergreen pioneer species with small seeds and low water-storage capacity (Borchert, 1994). The alluvial soils at these elevations next to river banks are predominately sandy (Wittmann *et al.*, 2004) and thus plants are subject to rapid desiccation. Dissociating the relative effects of drought, flooding, and light that limit establishment of floodplain species is complex, as pioneer species are light-demanding and as such generally more adapted to drought than late-successional species. In addition, pioneers often make use of mass-dispersing seedlings generally with high mortality rates (Wittmann and Junk, 2003; Oliveira Wittmann *et al.*, 2007).

In more diverse floodplain forests at higher elevations, drought may be a less limiting factor, as water loss from intermediate clayey soils below a dense-canopy forest is reduced. In fact, the regeneration of several late-successional species coincides with dry periods with low-water levels and increased establishment rates during dryer years (*e.g., Hura crepitans*, *Sterculia apetala*, *Guarea guidonia*, *Ocotea cymbarum*; Marinho, 2008). Similarly,

individuals of the same species have the highest radial increments in years with exceptionally low flood levels (Rosa, 2008). These floodplain species which are restricted to higher elevations may have greater sensitivity to flooding than species at lower elevations (Wittmann *et al.*, 2006). Further research is needed to understand how these high elevation late-successional species react to drought events in the floodplain.

The origin of drought tolerance in Amazonian floodplain trees

Many Amazonian floodplain species are widely distributed across tropical ecosystems, including regions with climatically or edaphically induced aridity (Prance, 1979; Kubitzki, 1989; Worbes, 1997). For example, the overwhelming majority of *várzea* tree species (62%) has widespread occurrence among non-flooded neotropical ecosystems, such as Western Amazonian upland forests (Wittmann, pers. comm.). Arid ecosystems share 5.6 % (Brazilian *cerrado*), 14% (Caribean Islands), 17% (Paraguay-Paraná River Basin including the hyper-seasonal savannas of the *Pantanal* and *Chaco*), and 24% (Colombian savannas) of all *várzea* tree species. In addition, 16% of all *várzea* tree species occur at altitudes > 1.800 m asl, some are even frost-tolerant, involving physiological mechanisms for tolerance against periodical water deficits (Wittmann, pers. comm.).

Evidence of tropical rainforest ecosystems in South America dates from at least the early Paleocene (Burnham and Graham, 1999; Rull, 1999; Johnson and Ellis, 2002; Burnham and Johnson, 2004). Theoretically, the tropical climate in equatorial Amazonia together with the continuous uplift of the Andes would have created the physical conditions for the development of floodplain forests beginning in at least the early Paleocene (Wittmann *et al.*, in press). Considering the series of drought and flood periods over a geological time scale, many floodplain species may have evolved and drought-resistance or avoidance strategies that have been retained in present-day floodplain species.

Flooded forests are proposed as a potential refuge for upland species during previous eras of frequent and prolonged drought (Baraloto *et al.*, 2007) – and many of these migrant upland species may have pre-adaptations to cope with flooding and drought especially when they originate from neotropical savannahs.

Climatic changes during the tertiary and quaternary affected global sea levels and thus resulted in periodic reductions (e.g., during the LGM) and expansions (during the interglacials, formation of the Lago Amazonas) of floodplain forest area (Vuilleumier, 1971; Van der Hammen, 1974; Frailey *et al.*, 1988; Tuomisto *et al.*, 1992; Irion *et al.*, 1997; Oliveira and Mori, 1999). The postulated species shift from dry to moist climatic conditions combined with a spatial reduction of flooded areas, however, may have affected floodplain species to a lesser extent than upland species, because the flooded ecosystems persisted as small refugia during glacial maxima. Riparian connectivity among floodplain forest patches and adapted dispersal mechanisms of floodplain trees may have reduced species losses at regional scales (Wittmann, 2001), with the floodplains acting as linear refuges for

sensitive upland species during periods with dryer climatic conditions (Pires, 1984).

Climatic changes: effects of more severe and more frequent droughts?

To predict responses among species to changes in water availability, we need to understand how species are adapted to drought (Markesteijn and Poorter, 2008). For Central Amazonia, there are two scenarios that predict opposing trends in flooding patterns of major Amazonian rivers. In the first scenario, the loss of floodplain forests results in increases in runoff and river discharge (Foley *et al.*, 2005). In the second scenario, increasing temperatures and CO_2-concentrations result in a decrease in flood level (Foley *et al.*, 2005). To what extent altered precipitation patterns will affect the flood pulse of the Amazonian rivers remains unclear. While the Western Amazonian headwater region is expected to increase in precipitation amount (IPCC, 2007), the East Amazon tributaries would experience tailback of riverwaters as a result of predicted sea-level rise. Overall, the region most likely to experience increasing drought from both deforestation and climate change is the Eastern Amazon, including its floodplains (Fisher *et al.*, 2007; IPCC, 2007; Mahli *et al.*, 2008).

Increasing drought stress may ultimately cause a change in mortality, establishment, and species population densities in tropical rainforests (Williamson *et al.*, 2000; Delissio and Primack, 2003). For Central Amazonian upland forests, drought effects are most evident in decreased plant-available water, leaf water potential, and, to a lesser extent, in the canopy leaf-area index (Asner *et al.*, 2004). In these forests, tree mortality increased 50% following a period of drought during the1997/98 El Niño event (Williamson *et al.*, 2000). More intense droughts in both frequency and strength are probable to affect Amazonian floodplain forests at both the species and community levels, especially near the flood-induced tree lines. In Amazonian black-waters, forest flammability may increase during extended droughts, leading to possible species losses at local and regional scales. Ecological niche models (Peterson and Vieglais, 2001) of abundant pioneer tree species in Central Amazonian white-water forests predicted that lower flood levels will increase competition with newly colonizing less flood-tolerant species at high elevations on the floodplain (Wittmann, pers. comm.). Pioneer species like *Clitoria amazonum*, *Cassia leiandra,* and *Simaba multiflora* are endemic to the high-*várzea* and lose their competitive advantage when establishing outside highly flooded habitats (Wittmann *et al*., 2006). In addition, their populations are restricted to small geographic regions along the East-West gradient. Once displaced downwards on the flooding gradient, the species may either become extinct due to habitat reductions on steeper river banks or may have the plasticity to survive and adapt to altered environmental conditions.

Discussion

Several hundred tree species with differing life history traits survive the extreme hydric conditions of Amazonian floodplains. Among these coexisting species, a diversity of strategies evolved, alleviating both drought and flooding stress. The diversity of species subject to this cyclical recurrence of both

drought and flooding stress, particularly at the more vulnerable seedling phase, demonstrate that many species may evolve to tolerate overlapping extreme stresses.

Convergent adaptations to drought and flooding. The available data suggest that individuals experiencing drought stress are more likely to be at the seedling phase. There is sparse evidence for adult floodplain tree species suffering mortality or reduced growth during dry periods or severe drought, and drought-related tissue damage or loss may be avoided by investment in root biomass and changes in vegetative phenology and xeromorphic leaf traits. Furthermore, flood and drought stress may result in both advantages and disadvantages for floodplain species growth and survival – for example, exposure to drought at seedling stages may enhance drought tolerance at later stages by early investment in belowground biomass (Kozlowski and Pallardy, 2002).

Foliar morphological and physiological traits such as epicuticular waxes, stomatal control, and deciduousness prevent excessive water loss via evapotranspiration through foliar tissue during both drought and flooding. As a result, whole plant metabolism – root respiration, evapotranspiration, and photosynthesis – is regulated to maintain water status and a positive carbon balance during both flooding and drought. The data suggest that photosynthesis and evapotranspiration rates drop more sharply during flooding than during the dry season, implying that changes in plant metabolism are more severe in the flood season than average dry seasons.

Shifts in tree and seedling biomass allocation concur with patterns observed in other forest ecosystems, where drought triggers a relative increase in allocation to root biomass. However, in contrast to their upland counterparts, floodplain tree growth is restricted to the non-flooded season, coinciding with the dry season. While tap roots may provide adequate water access during drought years, fine surface roots in the upper aerobic soil layer are responsible for supplying nutrients for growth and cell metabolism. Tree growth and production of defensive secondary compounds could be compromised. Broad root systems are also advantageous in a flooded environment for providing stability against soil and sediment erosion and wind storms. Amazonian floodplains are characterized by frequent erosion and deposition of fluvial sediments, and the edge/area ratio of forest stands on narrow floodplain levees make trees highly susceptible to windfall during the dry season. Although there is little research on root architecture in Amazonian floodplain trees, studies of upland species of the same genera (*e.g., Hura crepitans, Tabebuia, Cedrela*) suggest that pioneer species invest more in root branching and length for soil exploration, while non-pioneers invest heavily in thicker roots for storage or defence (Coll *et al*., 2008). As such, floodplain species of different functional types may experience variable response to drought depending upon allocation patterns within the root system. Allocation to superficial roots permits accessibility to nutrients in aerobic topsoils for fast growth early during flood drawdown when flood-intolerant mycorrhizae are inactive. However, allocation

to tap roots may be an advantage for longer-lived late successional species that are subjected to drought.

Flooding vs. drought. Drought can play as important a role as flooding in floodplain forests, in terms of species trait evolution, ecophysiological adaptation and species composition and diversity (Lopez and Kursar, 2007a). Many species have adaptations that allow them to cope with both flooding and drought stress, with some adaptations having the same effect for both extreme hydric conditions. Drought stress is an induced stress to which mechanisms for tolerance or avoidance are congruent for both drought and flooding, *e.g.* outtake of free radicals (to prevent oxidative damage) in the cell with special enzymes (Lösch, 1996). In seedlings, patterns of leaf loss and leaf production are similar under drought and flooded conditions: strong leaf loss in both deciduous and evergreen species, low production of new leaves, both resulting in a decrease of transpiring surface area.

A straightforward niche-based model for tropical forest biodiversity has been challenged by recent studies comparing relative drought and flood tolerance of floodplain and upland tree species. Many *terra firme* tree species display flood tolerance, despite their absence in seasonally inundated habitats (Engelbrecht *et al*., 2005; Baraloto *et al*., 2007; Poorter and Markesteijn, 2008). Conversely, floodplain tree species also display drought tolerance (Parolin, 2001; Elcan and Pezeshki, 2002). Seasonally flooded plant communities are adapted to amphibious environments (*i.e.,* the Aquatic-Terrestrial Transition Zone, ATTZ, *sensu* Junk, 1989), whereby plant community assemblage is dependent upon alternate dry and inundated periods (Crawford, 1996). Given the natural oscillation in wet and dry periods on an annual and supra-annual time scale, as well as the recent geological history of Amazon climate change and savanna-forest expansion/retraction (Anhuf *et al.*, 2006; Mayle and Power, 2008), it is expected that many tropical floodplain forest species display adaptations for variable flood and drought tolerance or avoidance strategies to survive in this dynamic ecosystem (Lopez and Kursar, 2007). Periodical drought events in large-scale tropical river ecosystems are as predictable as flooding in normal, non-drought years, thus facilitating plant adaptations against drought, waterlogging (summarized in Parolin *et al.*, 2004) and submergence (summarized in Parolin, 2009). However, exceptionally severe or extended droughts in anomalous years present physiological constraints for flood-adapted tropical tree species, and these are supposed to play an important role for survival.

Conclusions

There are many factors associated with drought besides water stress, for example increased fire frequency and intensity, high temperature stress, and pathogen attacks associated with water stress. In addition to species tolerance to water stress, these secondary effects may also be important mediators of tropical forest wetland ecology and deserve further investigation.

Exposure to drought, particularly at early growth stages, could have potentially beneficial effects on later plant growth, survival, or reproduction (*sensu* Kozlowski and Pallardy, 2002). Drought may induce higher biomass allocation to underground roots and stems, thus providing increased carbon resources to tolerate physical damage and other disturbances.

Although over 1000 species occur in the Amazon floodplain forests, their distribution and diversity vary widely from monospecific stands, palm-dominated forests, to highly diverse forests. While flood tolerance explains species distributions across a flood gradient (Wittmann *et al*., 2006), drought may be significant in explaining variation in species composition and diversity within given flood levels (Lopez and Kursar, 2007b). Most significant effects of drought could be at the seedling stage, ultimately affecting species distribution and diversity of floodplain forests.

Drought may be a more pronounced stress for floodplain species at the seedling stage. While adult trees can tap the relatively shallow water table in floodplains, seedlings may be more subject to water stress due to their shallow root systems.

Acknowledgments

We thank the technicians and boat crews of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus) for helping with the field measurements. The studies were financed by the INPA/Max-Planck project. We thank the “Working Forests in the Tropics” Program and the IAF Grassroots Development Fellowship for financing research in Santarém, and IPAM and UFPA-Santarém for logistical support.

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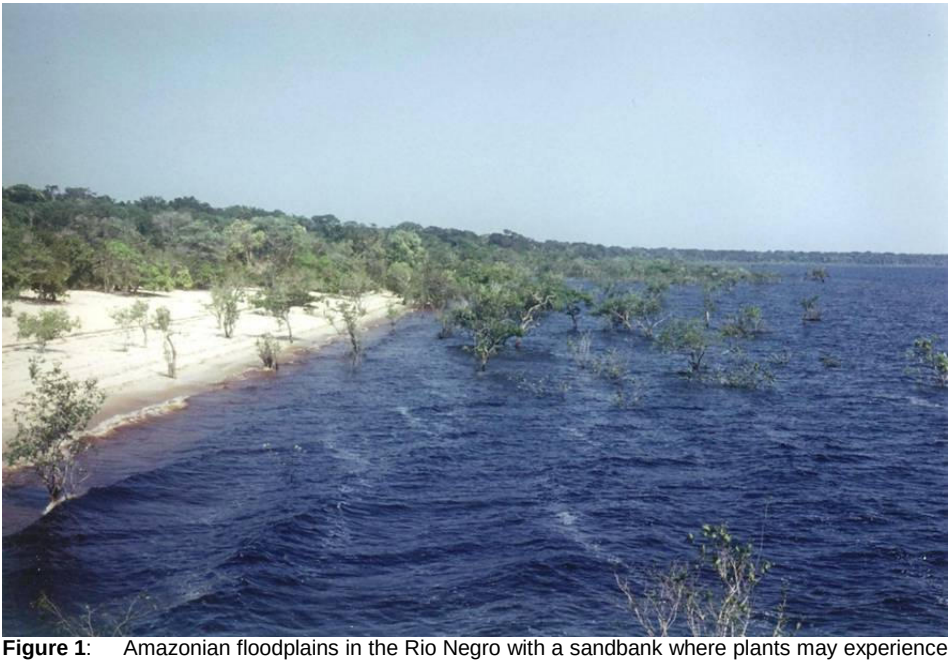

Figure 1: Amazonian floodplains in the Rio Negro with a sandbank where plants may experience drought.

Figure 2: Seedling of *Cecropia latiloba* after five days of drought under experimental conditions.

Figure 3: Seedlings of *Crateva benthami* and *Vitex cymosa*, two tree species of Amazonian floodplains, subjected to twelve weeks of drought, well watering, waterlogging and submergence (from left to right) under experimental conditions.

Table 1: Number of years without any or with permanent floods, depending on the height in the flooding gradient (changed, after Junk & Krambeck 2000)

Altitude in masl	Mean length of terrestrial phase (days) n = 95y	Years with permanent flood	Years without flood (dry)
30	never flooded	0	95
29	3816	0	87
28	712	0	52
27	375	0	21
26	264	0	4
25	225	0	2
24	195	0	1
23	162	0	1
22	122	0	1
21	100	6	0
20	79	14	0
19	63	25	0
18	44	42	0
17	34	66	0
16	32	84	0

Table 2: Root:shoot ratio and chlorophyll contents per leaf dry weight in six tree species with different growth strategies (EV evergreen, D deciduous, P pioneer, NP non-pioneer)

		Root:shoot ratio		Leaf chlorophyll content	
Species	**Growth strategy**	**Control**	**Drought**	**Control**	**Drought**
Cecropia latiloba	D NP	0,5	0,6	8,52	8,47
Crataeva benthamii	D NP	2,2	0,9	11,59	10,02
Nectandra amazonum	EV NP	0,5	0,4	7,99	6,08
Senna reticulata	EV P	0,9	1	7,27	8,00
Tabebuia barbata	D NP	1,3	1	8,15	6,59
Vitex cymosa	D NP	0,5	0,7	6,89	8,71