

REVIEW

Drought responses of flood-tolerant trees in Amazonian floodplains

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- **Background** Flood-tolerant tree species of the Amazonian floodplain forests are subjected to an annual dry period of variable severity imposed when low river-water levels coincide with minimal precipitation. Although the responses of these species to flooding have been examined extensively, their responses to drought, in terms of phenology, growth and physiology, have been neglected hitherto, although some information is found in publications that focus on flooding.
- **Scope** The present review examines the dry phase of the annual flooding cycle. It consolidates existing knowledge regarding responses to drought among adult trees and seedlings of many Amazonian floodplain species.
- **Main Findings** Flood-tolerant species display variable physiological responses to dry periods and drought that indicate desiccation avoidance, such as reduced photosynthetic activity and reduced root respiration. However, tolerance and avoidance strategies for drought vary markedly among species. Drought can substantially decrease growth, biomass and photosynthetic activity among seedlings in field and laboratory studies. When compared with the responses to flooding, drought can impose higher seedling mortality and slower growth rates, especially among evergreen species. Results indicate that tolerance and avoidance strategies for drought vary markedly between species. Both seedling recruitment and photosynthetic activity are affected by drought.
- **Conclusions** For many species, the effects of drought can be as important as flooding for survival and growth, particularly at the seedling phase of establishment, ultimately influencing species composition. In the context of climate change and predicted decreases in precipitation in the Amazon Basin, the effects of drought on plant physiology and species distribution in tropical floodplain forest ecosystems should not be overlooked.

Key words: Drought responses, Amazonia, floodplain forests, tree ecology, várzea.

INTRODUCTION

Amazonian floodplain forest ecosystems are maintained primarily by the nature of their hydrological regime, including periods of wetting and drying (Fig. 1). In these forests, the flood regime is recognized as a key driver of forest community structure and adaptive physiological responses. Recent reviews summarize tree responses to annual waterlogging and submergence in detail (Parolin, 2009). However, the role of the dry periods has been mostly ignored for Amazonian floodplains, despite growing evidence of the importance of drought for species distribution patterns in other tropical floodplains (Lopez and Kursar, 2007) and tropical rain forests (Engelbrecht *et al.*, 2007). Among the first to raise the relevance of the dry phase in Amazonian floodplains were Keel and Prance (1979) who stated that drought may represent more limitations for survival than flooding for the local vegetation. However, little further study or analysis has since been published. Therefore, the goal of the present review is rectify this shortcoming by assembling and assessing evidence that periods of drought occurring during the dry phase alter Amazonian floodplain forests as a result of differential species responses, especially among seedlings and juvenile trees.

Drought is defined by insufficient water availability for plants, a consequence of soil moisture depletion by low precipitation and high evapotranspiration rates. Although

operational definitions propose climatic indices for drought by precipitation and evapotranspiration below ecosystem-specific minima (Quiring, 2009), drought is generally defined with reference to plant responses (Gutschick and BassiriRad, 2003; Neumann, 2008). Plants may experience drought as drought stress, which is tolerated or avoided by morphological, physiological and phenological mechanisms. Like other environmental stresses, drought events have duration, frequency and severity, as measured by a combination of climate and impact data on plant productivity. For the purposes of understanding the occurrence of drought in Amazonian floodplains and species-specific responses, we consider drought stress as insufficient water availability to sustain normal plant metabolism (Lichtenthaler, 1998).

In Amazonian floodplains, drought stress is mainly caused by low soil moisture availability in silty soils coupled with high evaporation rates during dry periods. The duration of the dry season in floodplain forests varies considerably along the rainfall gradient across the Amazon Basin (Sombroek, 2001). Floodplains are subjected to 1–5 consecutive months of precipitation below 100 mm month⁻¹ from the western Amazon to the Dry Belt Region in the eastern Amazon (Sombroek, 2001). The dry season coincides with the termination of flooding and the end of the rainy season (Worbes, 1986), when the top horizons of soils lose sufficient moisture to reduce soil water availability to wilting point (Fig. 2). In addition, El Niño supra-annual climatic events cause regular

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FIG. 1 Seasonal extremes in the Amazonian floodplains: (left) high-water period with waterlogged trees, and (right) development of drought.

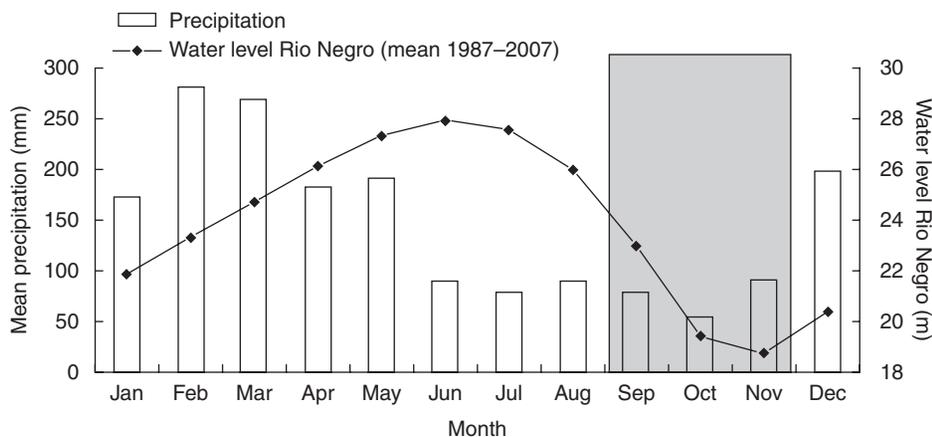


FIG. 2 Mean precipitation and water level in central Amazonia, with timing of flooding and drought in normal years. The driest months are highlighted by shading.

drought in floodplains, reducing rainfall and increasing moisture loss by wind transport and raising average temperatures (Walsh and Newberry, 1999; Schöngart and Junk, 2007; Marengo *et al.*, 2008). In contrast to many other stress factors, drought stress does not start abruptly but increases gradually over time (Larcher, 2001), emphasizing the importance of drought duration for plant survival.

Trees of Amazonian floodplains have evolved a suite of traits to cope with flooding and drought (Chaves *et al.*, 2003). The efficacy of these adaptations for drought tolerance or avoidance can be studied by measuring physiological responses, growth and survival. Trees have age-specific responses and different susceptibilities to environmental stresses (Kozłowski and Pallardy, 2002), and, as such, the physiological responses for seedlings, juveniles and adult trees belonging to different species are addressed here. While many studies focus on flood tolerance as a key mediator for seedling population and community dynamics, the few available studies suggest that drought can also play an important role on seedling survival, which in turn triggers changes in tree species composition and distribution (Parolin, 2001; Elcan and Pezeshki, 2002; Stroh *et al.*, 2008).

In the present paper, the potential occurrence and effect of drought (water deficiency) on floodplain woody plants during the dry season is discussed. Two main questions are addressed: (1) which phenological, anatomical and physiological responses can be observed at different drought intensities? (2) how do these responses influence mortality and species distributions of Amazonian floodplain trees?

THE AMAZONIAN FLOODPLAIN ECOSYSTEM

Amazonian floodplains extend over 300 000 km² and hold >1000 tree species (Wittmann *et al.*, 2006) that have evolved a suite of adaptive traits to cope with annual cycles of flooding and drying (Junk *et al.*, 1989; Parolin *et al.*, 2004). They experience intra-annual fluctuations with changes in river-water levels of up to 12 m, known as the 'flood pulse', which last >7 months a year (Junk *et al.*, 1989). Annual precipitation in equatorial Amazonia generally amounts to >2000 mm, with a distinct increase from east to west (Sombroek, 2001). Precipitation is clearly periodic, with a rainy season from December/January to April/May and a dry season from June/July to October/November

(Fig. 2). There is a lag time of 3–4 months between the rainy season and the flood season, whereby floods rise after the onset of the rainy season and fall after the rainy season has ended (Fig. 2). As such, floodplain vegetation is subjected to a limited ‘dry period’ of low flood levels and low rainfall, where monthly evaporation can exceed precipitation (Irion *et al.*, 1997; Junk and Krambeck, 2000). To differentiate between the short dry period and the extended non-flooded period, we refer to the ‘dry season’ or ‘dry phase’ as the period of time during which vegetation is not flooded.

Droughts of varying intensities have occurred in the Amazon Basin in the past centuries (Fig. 3), as indicated by severe droughts in 1925–26, 1860, and 1774 that had pronounced effects on both upland and floodplain forests, i.e. by increased forest flammability and widespread fires (Sternberg, 1987; Sombroek, 2001, Williams *et al.*, 2005; Marengo *et al.*, 2008). Most drought events are related to El Niño Southern Oscillations (ENSO), which cause lower flood-levels and prolonged dry periods in Amazonian floodplains (Adis and Latif, 1996; Marengo and Nobre, 2001). During the 20th century, extended dry periods and associated droughts occurred on average every 4.35 years [see Quinn and Neal (1992) for the period 1925–1982, and Schöngart *et al.* (2004) for the period 1800–2000]. Mean precipitation during such dry periods is significantly lowered by approx. 36%, with maximum reductions of up to 50% (Marengo *et al.*, 2008), and the start of the rainy season is delayed by up to 2 months (January to March) (Schöngart *et al.*, 2004). The last three decades have been marked by unusually strong El Niño events in 1982/83, 1997/98, prolonged dry periods from 1990 to 1995 and a recent severe drought in 2005 unrelated to El Niño (Marengo *et al.*, 2008).

The soils of Amazonian floodplains are alluvial-hydromorphic (Oliveira *et al.*, 2000). Where a marked dry season occurs, pockets of vertisols may also develop within the periodically inundated white-water floodplains (várzea; Roosevelt, 1980). In várzea forests, soil porosity averages 46%. Soils are silty, but sand and clay grain sizes may be prevalent depending on the distance and elevation of sites relative to the river level (Wittmann *et al.*, 2004). Root biomass and root production in black-water floodplains (igapó) and várzea 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 in central Amazonian floodplains near Manaus (3°15'S, 59°58'W; Oliveira *et al.*, 2000), in Santarém further east dry bulk density varies from 0.9 to 1.6 (C. Lucas, unpubl. res.).

Soil water content in forested levees varies with depth and time, mainly influenced by rainfall and the flood pulse. During flood drawdown, mean water content of the soil profile varies between 23 and 33%, as compared with a mean water content of 33–42% (equivalent to 66–84% water-filled pore space) after the onset of rain (Kreibich, 2002). 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).

ADAPTIVE TRAITS FOR DROUGHT TOLERANCE/DESSICATION RESISTANCE

Many of the same anatomical characteristics that help a plant survive flooding can also alleviate drought stress. Adventitious roots, aerenchyma, leathery xeromorphic leaves, etc., encountered in Amazonian floodplain tree species commonly recognized as adaptations to flooding stress (Parolin *et al.*, 2004; Wittmann and Parolin, 2005) may alleviate stress associated with drying as well. Floodplain tree adaptations to drought may have evolved on the floodplain during dryer glacial epochs (e.g. Late Pleistocene) or may be traits retained from upland species or genera that migrated into the floodplains. Given that some floodplain tree species may have originated in adjacent savannas and uplands where drought events are frequent and common (Prance, 1979; Kubitzki, 1989; Wittmann *et al.*, 2009), adaptive traits that tolerate or avoid water stress may be prevalent.

Leaves

Morphological adaptations against drought stress 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 as protection against excess evaporation, heat and light (Roth, 1984; Schlüter, 1989; Waldhoff and Furch, 2002; Waldhoff, 2003). Epidermal leaf structures such as waxes or hairs can reflect light to protect leaves from high solar irradiance. The common floodplain pioneer *Cecropia latiloba* has a white abaxial leaf surface that may reflect light reflected off the water surface at high water, while also reflecting high irradiance during dry periods with low cloud cover. Glandular and non-glandular hairs were found on leaves from several woody floodplain species, including *Cassia leiandra*, *Nectandra amazonum* and *Pouteria glomerata* (Waldhoff and Furch, 2002; Waldhoff,

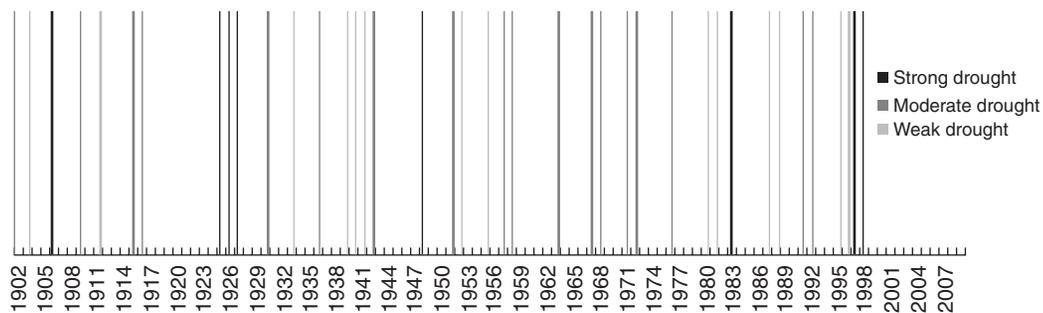


FIG. 3 Exceptional droughts in the past century (data from Sombroek, 2001) with strong, moderate or weak droughts (no definitions available for specification of precipitation amount and soil water availability).

2003). The abaxial leaf surface of *Licania apetala*, *Senna reticulata*, *Cassia leiandra* and *Quinia rhytidopus* is covered with papillae that may also protect leaves from reflected irradiance. Additionally, stomata are abaxial and sunken in many species. In the palm *Astrocaryum jauari*, a waxy structure is located above the stomata to further inhibit evaporation (Schlüter, 1989). Epicuticular waxes are also found on leaf blades of many floodplain tree species (Waldhoff and Furch, 2002; Waldhoff, 2003). Although these waxes may function primarily to prevent water influx in inundated leaves (Fernandes-Côrrea and Furch, 1992; Schlüter and Furch, 1992), they also enhance drought resistance by decreasing cuticular water loss and preventing photodamage.

Vegetative phenology

The peaks of leaf fall are during flood drawdown (August to September) and at the onset of the rainy season (November to December) in central Amazon floodplains (Worbes, 1997). Thus, during dry periods, leaf shedding may be an adaptation to avoid drought stress by decreasing the transpiring surface area (Borchert, 1983; Medina, 1983; Wright and Cornejo, 1990), or by the production of smaller leaf surfaces or fewer leaves (Fig. 4; Parolin *et al.*, 2005). However, there is little evidence for an adaptive advantage of deciduous over evergreen species in Amazonian floodplains (Parolin, 2001). The variation in timing of leaf senescence may also 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 (Kubitzki, 1989).

RESPONSES OF AMAZONIAN FLOODPLAIN TREE SPECIES TO DRY PERIODS AND DROUGHT

Whether Amazonian floodplain tree species experience drought conditions is questionable, given shallow water-tables

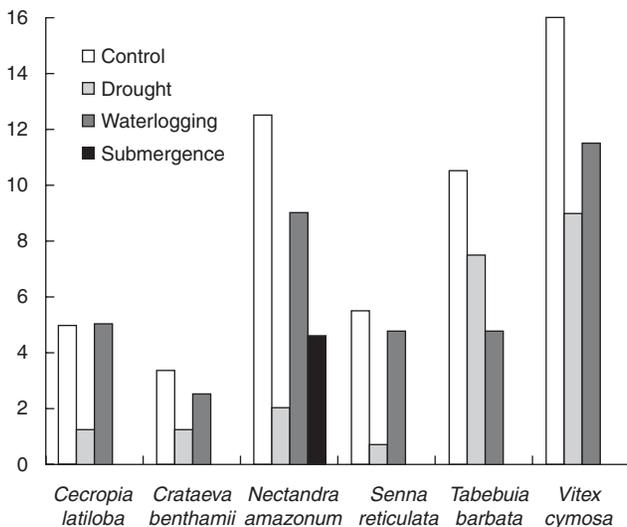


FIG. 4 Leaf number after 12 weeks of experimental conditions (control, drought, waterlogging and submergence) in seedlings.

and deep tap-root access to water levels among some species during dry periods. However, there are measurable physiological changes in plants that can indicate whether plants are susceptible to drought and respond to water stress (Table 1). They may portray strategies to prevent excessive water loss and desiccation (Kozłowski and Pallardy, 2002), ultimately avoiding desiccation or drought stress. Here evidence for physiological changes in floodplain trees is discussed that suggest internal regulation of water balance in dry periods and exceptionally dry years. This is followed by a discussion on seedling responses to experimental drought.

Physiological responses and water status regulation

Photosynthetic CO₂ uptake. Some Amazonian floodplain trees respond to water shortage by decreasing photosynthetic CO₂ assimilation (Schlüter, 1989; Parolin, 2000; Armbrüster *et al.*, 2004). For example, light response curves of *Pseudobombax munguba* showed a decrease in assimilation from 14 to 6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ during a 1-month dry period, dropping to 4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ after a 4-month dry period (Waldhoff *et al.*, 1998). In contrast, during the driest months (September to November), the evergreen *Cecropia latiloba* and the deciduous *Tabebuia barbata* and *Vitex cymosa* showed abrupt increases in photosynthetic CO₂ assimilation, most likely a result of recent new leaf expansion (Fig. 5). With subsequent flooding of 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 (Sesták, 1985; Reich *et al.*, 1999). 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), probably due to deep root systems that supply water to the trees (Armbrüster *et al.*, 2004).

Transpiration and stomatal conductance. In dry conditions, transpirational losses are high, and soil water availability in the upper profile is too low to compensate for the increased water demands, thus causing negative water balances in plants with shallow root systems. Therefore, 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 (Parolin, 2000).

Stomatal conductance for CO₂ or water vapour is an index of stomatal aperture (Buschmann and Grumbach, 1985). In six tree species [0]from Amazonian várzea (Parolin, 2000), stomatal conductance ranged between 200 and 400 $\text{mmol m}^{-2} \text{ s}^{-1}$, decreasing 5–35% in the flood season. Stomatal conductance peaked at the end of the waterlogged period, when trees bore their oldest leaves and displayed the lowest CO₂ assimilation. Only in *Crataeva benthamii* was there a decrease in stomatal conductance in the dry period (September) of $<100 \text{ mmol m}^{-2} \text{ s}^{-1}$. With the present data, patterns in stomatal conductance suggest that the measured

TABLE 1. Summary of published results on the physiological responses among floodplain forest tree species that could indicate regulation of water status for the avoidance of drought during dry periods

Physiological trait	Response	Value	Species	Citation
Leaf phenology	Senescence	–	None	Parolin <i>et al.</i> (2005)
Leaf water potential	Decrease	–1.24 to –2.7 MPa	<i>Laetia corymbulosa</i>	Armbrüster <i>et al.</i> (2004)
Photosynthetic CO ₂ uptake	Decrease	4–14 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	<i>Pseudobombax munguba</i>	Waldhoff <i>et al.</i> (1998)
Stomatal conductance	Decrease	<100 $\text{mmol m}^{-2} \text{ s}^{-1}$	None, except <i>Crataeva benthamii</i>	Parolin (2000)
Root respiration	Decrease	50–60 $\mu\text{L O}_2 \text{ g f. wt}$ and 40–90 $\mu\text{L O}_2 \text{ g f. wt}$	<i>Astrocaryum jauari</i> and <i>Macrolobium acaciifolium</i> (juvenile)	Schlüter (1989)
Vitamin E	Increase	α -Tocopherol 6 $\mu\text{g m}^{-2}$ and δ -tocotrienol 9 $\mu\text{g m}^{-2}$	<i>Garcinia brasiliensis</i> (seedling)	Oliveira-Wittmann (2006)

All traits were measured on plants in the field in the Manaus region except Vitamin E concentrations, which were measured on seedlings subjected to experimental drought.

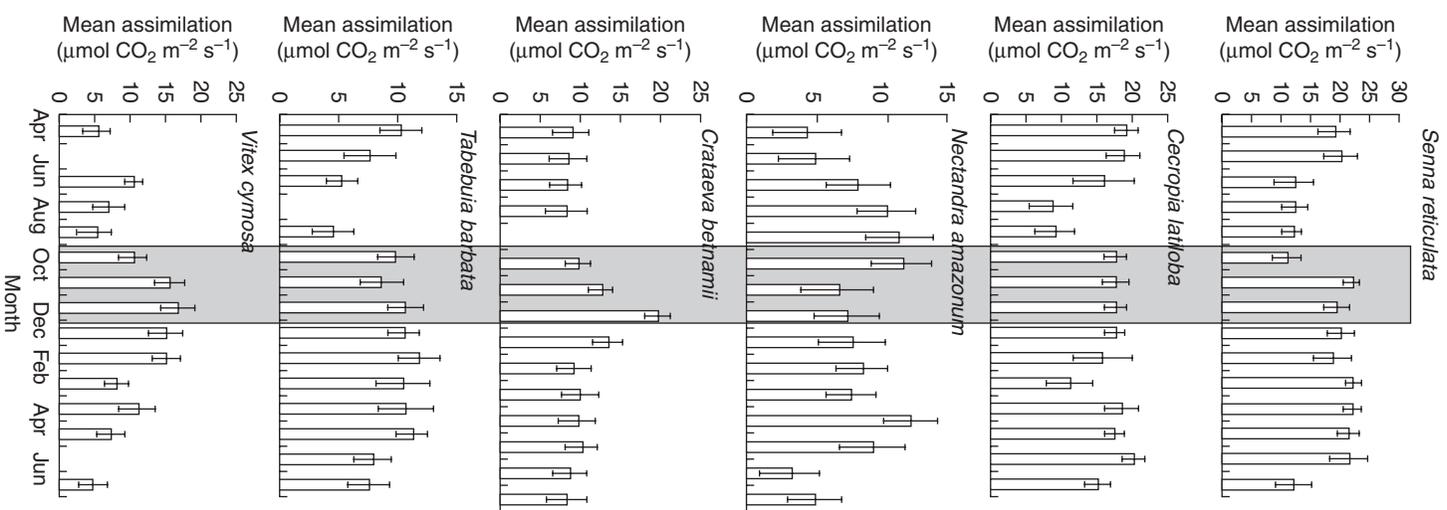


FIG. 5 Mean monthly photosynthetic CO₂ assimilation at maximum quantum flux (A_{max}) of six species measured between April 1994 and June 1995. The number per species and month = 10. The driest months are highlighted by shading.

trees did not experience water stress during average dry periods.

Leaf water potential. Leaf water potential, an indicator of plant water balance (Fernandes-Corrêa and Furch, 1992), ranges

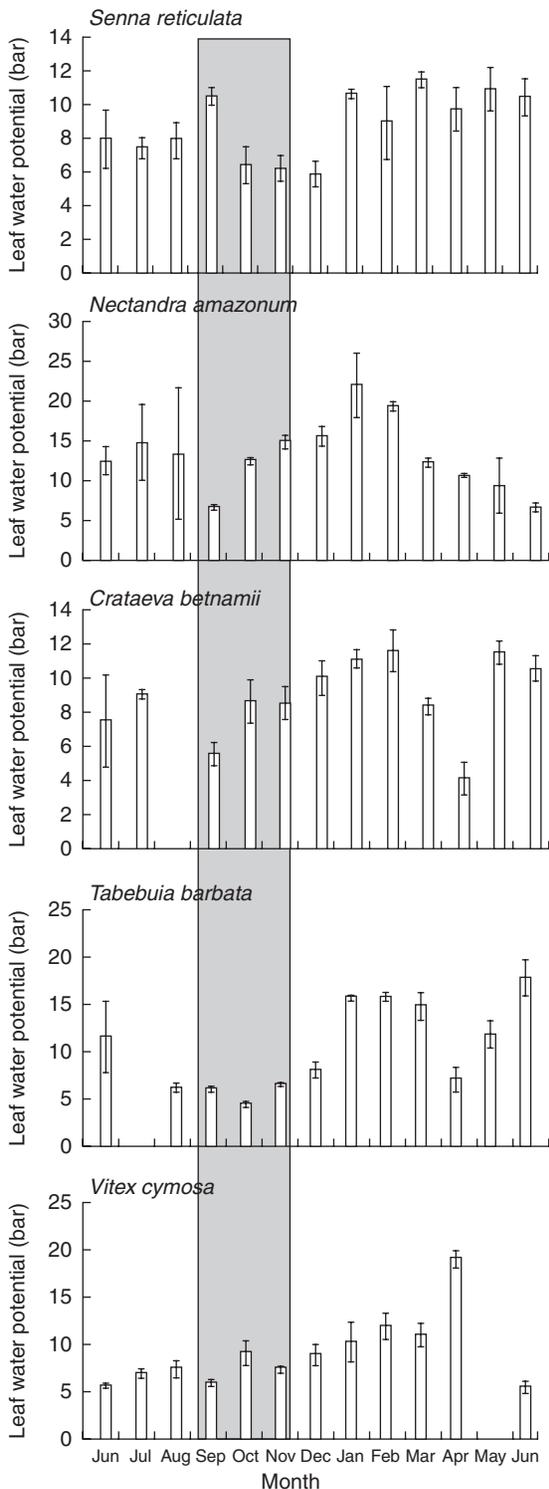


FIG. 6 Mean leaf water potential (bar) of five species measured between June 1994 and June 1995. Number of leaves measured per species and month = 5. The driest months are highlighted by shading.

between an average of -0.76 and -1.5 MPa among Amazonian floodplain trees (P. Parolin, unpubl. res.). Mean monthly leaf water potentials vary between species, and intra- and inter-annual differences are substantial but with no

apparent link to the hydric status (Fig. 6). However, leaf water potentials in the driest months tend to be continuously low across years. For example, *Laetia corymbulosa*, a tree species not particularly resistant to desiccation, has the lowest negative values during the dry months of the terrestrial period (-1.24 to -2.7 MPa in October/November, as compared with -0.18 to -0.33 MPa for the remainder of the year; Armbrüster *et al.*, 2004).

Xylem flux. Xylem flux density in deciduous trees is strongly influenced by tree phenology (Horna *et al.*, 2009). Decreasing soil moisture availability does not lead directly to leaf damage but might indirectly trigger leaf-shedding by hormone signals to prevent plant water loss. Sap fluxes decrease simultaneously with prolonged leaf shedding in five tree species (Parolin *et al.*, 2005). Stem water storage can buffer water shortage during the daytime (Müller, 2002; Parolin *et al.*, 2005). Overall, water balance, osmotic relations and turgor are poorly understood aspects of Amazonian floodplain tree physiology, especially in relation to drought as measurements are often recorded during the flooded period.

Root respiration. While tree metabolism may be unaffected in average dry years, exceptional droughts may decrease root respiration, particularly among juvenile trees. In a study of 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 years, 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 (October to November in 1986 and 1987). While oxygen turnover increased continuously after the end of the flood season, root respiration dropped from $110 \mu\text{L O}_2 \text{ g f. wt}$ to $50\text{--}60 \mu\text{L O}_2 \text{ g f. wt}$ in *A. jauari*, and from $170\text{--}180 \mu\text{L O}_2 \text{ g f. wt}$ to $40\text{--}90 \mu\text{L O}_2 \text{ g f. wt}$ 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.

Proteins and vitamins. The production of vitamin E (α -tocopherol, an antioxidant) in foliar tissue is known to reduce drought-induced stress. To date, only laboratory-based data exist regarding this parameter. In drought treatments, the highest concentrations of α -tocopherol and δ -tocotrienol were found in the leaves of *Garcinia brasiliensis* (Oliveira-Wittmann, 2006). Within 90 d of the start of drying, the levels of α -tocopherol rose from 2 to $6 \mu\text{g m}^{-2}$, while concentrations of δ -tocotrienol reached $9 \mu\text{g m}^{-2}$. In correlation with increased vitamin E, seedlings displayed slower growth rates and lower photosynthetic activity under drought. Under normal metabolic conditions, the formation of oxygen radicals and the peroxidation of lipidic membranes are in a dynamic equilibrium with the activity of the antioxidant systems (Blokhina, 2000). With the stresses associated with drought, this equilibrium may be disturbed and lead to oxidative stress, as observed in *Garcinia brasiliensis* (Oliveira-Wittmann, 2006).

Seedling responses to drought

Seed germination. Seeds of Amazonian floodplain trees are especially vulnerable to drought. Seed viability when exposed to air after dispersal is 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.*, 2009). Many floodplain trees fruit during the flood season, releasing seeds during flooding, and germination generally is initiated when floods recede (Parolin *et al.*, 2004). Seeds are thus exposed to aerobic conditions, and readily germinate on moist or wet sediment and soils. If, thereafter, water availability rapidly declines in upper soil layers, seedling establishment may be severely limited (Worbes, 1986).

Seedling growth and biomass allocation. Seedling establishment and early growth occur during the dry phase. They are subjected to water shortage for approx. 4 weeks before the onset of the rainy season (Fig. 2) which causes substantial reductions in height growth, leaf number and stem diameter (Parolin, 2001; Waldhoff *et al.*, 1998, 2000).

High biomass investment to the root system was documented for seedlings of *Cecropia latiloba*, *Senna reticulata* and *Vitex cymosa* where the root:shoot ratio increased significantly after 12 weeks of drought as compared with the control treatment (Waldhoff *et al.*, 1998) indicating a strategy for desiccation resistance. However, in other species (e.g. *Crataeva benthamii*, *Nectandra amazonum* and *Tabebuia barbata*) although the root:shoot ratio decreased under drought stress, they grew well in dry conditions.

Seedling survival. In a field study, tree seedling mortality was higher during the dry season than during flooding (Ziburski, 1990; Oliveira-Wittmann *et al.*, 2009). 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*, and 33% in *Eschweilera ovalifolia* (Oliveira-Wittmann *et al.*, 2009). Mortality was consistently higher during the dry season than during submergence, suggesting that Amazonian floodplain tree seedlings have a higher resistance to submergence than drought. The mortality of tree species in a common or garden experiment suggests that deciduous species have a higher resistance of drought during early seedling establishment than evergreen species (Fig. 7; C. Lucas, unpubl. res.).

Ecosystem responses to drought

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 R_{Ed} , 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 g C m^{-2}), due to the combined effect of low CO_2 loss by roots and moderate C gain by above-ground live biomass. Total carbon output of above-ground woody tree biomass of a central Amazon floodplain forest during the dry period (November to January)

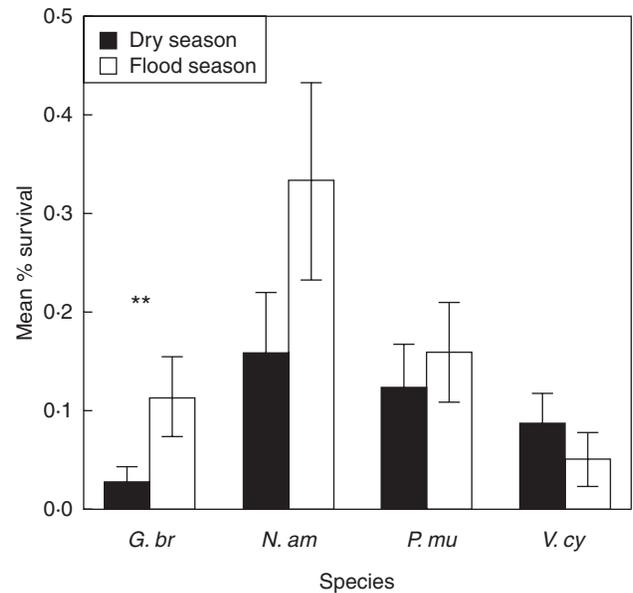


FIG. 7 Average seedling mortality with standard error bars, of two evergreen várzea tree species, *Garcinia brasiliensis* (*G. br*) and *Nectandra amazonica* (*N. am*) and two deciduous species, *Pseudobombax munguba* (*P. mu*) and *Vitex cymosa* (*V. cy*) in the dry versus flooded season, as indicated. Data are averaged across 21 plots in three forest stands in the dry versus flooded season in a common or garden experiment in the Lower Amazon region of Santarém-PA. Two-way *t*-tests comparing within species means are significant (*) for *G. br* ($t = -2.04$, $df = 27$, $P = 0.05$); but non-significant for *N. am* ($t = -1.94$, $df = 29$, $P = 0.062$); *P. mu* ($t = -0.51$, $df = 40$, $P = 0.61$); or *V. cy* [$t = 1.00$, $df = 42$, $P = 0.32$ (R version 2.9.0, www.r-project.org/)] (C. Lucas, unpubl. res.).

averaged an annual low of 360 g C cm^{-2} , peaked at 550 g C cm^{-2} during rising water (February to April), then gradually dropped to 480 g C cm^{-2} at high water levels (May to July) and 420 g C cm^{-2} with receding water levels (August to October) (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.

DISCUSSION

This review provides evidence for species responses to water stress during dry periods of the annual flooding cycle in Amazonian floodplain forests, particularly among seedlings and juveniles. Differential species responses to dry periods suggest that some tree species regulate internal water balance during dry periods, which may avoid drought stress. Seedlings were the only phase in floodplain-tree life history to provide evidence for differential growth and survival among species that could eventually alter species composition. Although drought occurs in Amazonian floodplains (Marengo *et al.*, 2008), there remains a missing link as to whether or not adult and juvenile trees experience drought stress sufficient to induce mortality, alter fertility and affect species distribution.

Adult trees have both morphological traits and physiological strategies that may reduce excessive water loss during the dry season. Tropical floodplain tree species reduce evapotranspiration with similar traits employed by upland and savannah

species, including epicuticular waxes, trichomes, reflective surfaces and papillae. Given that trees potentially can experience physiological water stress during dry periods and flood periods (Tournaire-Roux *et al.*, 2003), trees may employ similar strategies for avoiding water loss during dry and wet seasons. It was found that some species reduce leaf water potential, foliar surface area and xylem flux thereby reducing transpirational water loss during the dry period. Furthermore, some species reduce photosynthetic rates and root respiration to slow metabolic pathways that require more water. Despite these apparent mechanisms to maintain water potential within trees, there is sparse evidence for adult floodplain tree species suffering mortality or reduced growth during dry periods. Rather, drought-related tissue damage or loss may be avoided by investment in root biomass and changes in vegetative phenology and xeromorphic leaf traits.

In the field and the laboratory, seedlings show species-specific responses to low soil water availability in dry periods. The available data suggest that individuals experiencing drought stress are likely to be at the seedling phase. In contrast to adult and juvenile species, seedlings have shallow root depths and limited rooting systems, making them susceptible to drought stress.

It is found that seedlings exposed to experimental drought are susceptible to high mortality rates during seed germination and seedling establishment phases. Seedling mortality increased during the dry season, particularly among evergreen species (C. Lucas, unpubl. res.). However the dry season coincides with the first 2–3 months of seedling establishment and growth, when seedlings naturally have a higher probability of death (Alvarez-Clare and Kitajima, 2009).

Results of different studies suggest that floodplain species have variable resistance and avoidance strategies for preventing water stress. For some species, drought may impair survival at the seedling phase, potentially influencing future composition and succession of floodplain forests. Seedling recruitment and photosynthetic activity are affected by drought events and may thus lower net productivity and shift species composition.

Several hundred tree species with differing life-history traits survive the extreme hydric conditions of Amazonian floodplains with the aid of diverse strategies which have evolved to alleviate both drought and flooding stress. The diversity of species subject to this cyclical recurrence of hydric stresses, particularly at the more vulnerable seedling phase, demonstrates that many species may evolve to tolerate overlapping extreme stresses. Flood and drought stress may result in both advantages and disadvantages for floodplain species growth and survival; e.g. exposure to drought at seedling stages may enhance drought resistance at later stages by early investment in below-ground biomass (Kozłowski and Pallardy, 2002). However, in contrast to their upland counterparts, growth by floodplain trees is restricted to the non-flooded season, coinciding with the dry season.

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; Engelbrecht and Kursar, 2003; Lopez and Kursar, 2003; Engelbrecht *et al.*, 2005; Poorter and Markesteijn, 2008). As such, supra-annual extreme environmental conditions may play

a key role in plant-species distribution (ter Steege, 1994). Overlooking the impact of severe events may result in failure to identify critical mechanisms 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). Tree species are zoned along the flooding gradient, most of them restricted to limited topographic ranges (Wittmann *et al.*, 2004). However, few studies in the region have focused on the impact of drought as a determinant of species distribution. 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. Disentangling 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 with generally 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. The regeneration of several late-successional species appear to be timed to dry periods with low-water levels with increased establishment rates during dryer years (e.g. *Hura crepitans*, *Sterculia apetala*, *Guarea guidonia* and *Ocotea cymbarum*; Marinho, 2008). Further research is needed to understand how these high elevation late-successional species react to drought events in the floodplain.

Origin of drought resistance in Amazonian floodplain trees

Floristic evidence suggests that many Amazonian floodplain species are widely distributed across the Neotropics, including regions with climatically or edaphically induced aridity (Prance, 1979; Kubitzki, 1989; Worbes, 1997). Considering the series of drought and flood periods over a geological time scale, many floodplain species may have evolved 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 and expansions 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), where the floodplains acted as linear refuges for sensitive upland species during periods with dryer climatic conditions (Pires, 1984).

Drought in light of climatic changes

Climate change models predict a decrease in annual rainfall, an increase in dry season length and greater inter-annual

rainfall variability for the tropics (Bawa and Markham, 1995; Hulme and Viner, 1998; IPCC, 2007). Given this expected increased frequency and severity of drought in the Amazon basin, the effects of drought on floodplain forest ecosystems should not be underestimated. Annual precipitation has declined over much of the humid tropics during the 20th century. Bunker and Carson (2005) suggest that this trend may reduce tropical forest diversity by weakening density-dependent mechanisms that maintain diversity. In addition, plots dominated by dry-forest species experienced higher growth in response to irrigation and also far lower dry-season mortality relative to plots dominated by wet-forest species. Their results suggest that dry-forest species may benefit from any increase in dry season length or severity. To which extent this has to be expected in Amazonian floodplain forests is still not clear. More intense droughts in both frequency and strength are likely 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. Research which has been conducted during ‘normal’ conditions may overlook the impact of severe events and thus fail to identify critical mechanisms structuring ecological communities (Bunker and Carson, 2005).

Recommendations for future research

The present review highlights the lack of information available to evaluate if Amazonian floodplains experience drought and how species respond to drought stress. With predicted increased drought frequency and severity in the Amazon Basin, it will be important to understand the effects of drought stress on floodplain forests. As such, this review is concluded with proposals for future research:

- (a) Investigate whether or not seedlings experience drought stress in the field.
- (b) Investigate interactive effects of increased fire frequency and intensity, high temperature stress, and pathogen attacks associated with water stress on floodplain-species distribution.
- (c) Explore relationships between drought severity, pathogen attacks, biomass accumulation and woody growth. In the light of habitat destruction and logging, knowledge of basic information to guarantee sustainable forest regeneration and management is still scarce, and further studies are urgently required here.

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