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Water relations, chlorophyll *a* fluorescence, and contents of saccharides in tree species of a tropical forest in response to flood

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Abstract

We studied the seasonal changes in water relations, chlorophyll *a* fluorescence, and leaf saccharide contents of the tropical flood-tolerant trees *Acosmium nitens*, *Campsiandra laurifolia*, *Eschweilera tenuifolia*, *Symmeria paniculata*, and *Psidium ovatifolium*. Xylem water potential increased with flooding to a larger extent than leaf sap osmotic potential in all the species, and soluble sugars contributed up to 66 % of osmotic potential at maximum flooding. Starch was accumulated in leaves. Maximum quantum yield of photosystem 2 decreased in emerged leaves, values being always higher than 0.76. Daily maximum net photosynthetic rate and leaf conductance decreased in all the species. This reduction was associated in all the species but *S. paniculata* with the absence of a compensatory increase in non-photochemical quenching.

Additional key words: *Acosmium nitens*; *Campsiandra laurifolia*; *Eschweilera tenuifolia;* net photosynthetic rate; *Psidium ovatifolium*; soluble sugars; starch; stomatal conductance; *Symmeria paniculata.*

Introduction

Flood tolerance varies greatly with, among other factors, plant species and age, and time and duration of flooding (Kozlowski 1997). Physiological changes associated with flooding include a reduction in leaf conductance (g_s) and photosynthetic rate, P_N (Pezeshki 1993, Batzli and Dawson 1997, Fernández *et al.* 1999), the development of water deficit in the leaves (Crawford 1982, Ruiz-Sánchez *et al.* 1996), different response to following drought (Elcan and Pezeshki 2002), and a decreased xylem water potential (ψ) and leaf sap osmotic potential (ψ_s).

Photoinhibition, the decline in quantum yield of net CO_2 fixation and net O_2 evolution associated with loss of photosystem 2 (PS2) activity, can be caused by excess photons (Long *et al.* 1994). After prolonged excess irradiation, a slowly reversible decrease in maximum quantum yield of PS2 (F_v/F_m) and light-saturated P_N may take place (Long *et al.* 1994, Osmond and Grace 1995). Environmental conditions that strongly limit photosynthetic C metabolism intensify photoinhibition. During the dry season in tropical environments the high irradiance, high temperature, and water deficit can cause chronic photoinhibition. The reported decrease in P_N and g_s by flooding in tropical forests (Fernández *et al.* 1999) may be partly due to photoinhibition.

Although the literature on plant responses to flooding is abundant on temperate species, there are far fewer reports on the effect of flooding on chlorophyll (Chl) *a* fluorescence and photoinhibition in tropical wild species (Parolin 2001, Waldhoff *et al.* 2002). The study of the possible occurrence of photoinhibition under flood acquires relevance in tropical species given that, in the absence of marked seasonal changes in temperature and irradiance, water stress by deficit during the dry season, and by excess during flood becomes the most important environmental factor affecting plant performance.

The evaluation of photosynthetic capacity through measurements of Chl *a* fluorescence may help elucidate whether previously observed decreases due to flooding in P_N of tropical seasonally flooded trees (Fernández *et al.* 1999) are due solely to stomatal closure caused by

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Abbreviations: Chl – chlorophyll; g_s – stomatal conductance to water vapour; NPQ – non-photochemical quenching coefficient; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PS – photosystem; RH – relative humidity; ψ – xylem water potential; ψ_s – leaf sap osmotic potential; Φ_{PS2} – quantum yield of photosystem 2.

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flooding or else, limitation by non-stomatal factors may have increased (Lawlor 2002). Decreases in F_v/F_m as well as Φ_{PS2} may imply photodamage and therefore decreased photosynthetic capacity, although they may also evidence increased photoprotection (Adams *et al.* 1994). Thus, measuring non-photochemical quenching may provide insight on the mechanisms, or deficient function thereof, of photoprotection in emerged leaves of flooded trees.

The accumulation of starch in the root system during the period previous to the flood is a mechanism that can take place to compensate for the lack of oxygen by supplying substrates for anaerobic respiration, thus contributing to the survival of plants under anoxia or hypoxia (Laan and Blom 1990, Crawford 1996). In seedlings of *Nissa sylvatica* an increase in the root starch content was found during flooding (Angelov *et al.* 1996); in *Betula pubescens* starch that accumulated in roots during drainage is hydrolysed during flooding at such a rate as to drive a sugar-rich sap flow and decrease xylem sap osmotic potential (Crawford 1996). Starch accumulation in leaves was reported for flooded plants (Islam and Macdonald 2004) but the role of this accumulation is not clear. A reduction in transport of photosynthates to sink organs may cause starch accumulation in leaves of flooded plants.

We followed the seasonal changes in physiological parameters of five tree species that grow in the seasonally flooded forest of the Mapire river. Precipitation in the Mapire forest is markedly seasonal, the rainy season extending from May to December; the height of the water column increases from May until August. The species of this study are all important evergreen components of this forest. In a previous study of these species, ψ increased with height of the water column, suggesting that flooding does not cause water stress in these trees (Fernández *et al.* 1999).

The aim of the present work was to evaluate the seasonal changes in plant water status, parameters derived from measurements of Chl *a* fluorescence, and leaf saccharide contents in emerged leaves of adult trees of *Acosmium nitens* (Vog.) Benth. (Papilionaceae), *Campsiandra laurifolia* Benth. (Mimosaceae), *Symmeria paniculata* Benth. (Polygonaceae), and *Psidium ovatifolium* Berg. (Myrtaceae). Measurements of P_N and g_s were also made as a reference for photosynthetic capacity. We put the emphasis on the seasonal changes in: (*1*) ψ_s that may help evidence increases in turgor; (*2*) Chl fluorescence parameters that may suggest the occurrence of photoinhibition, and (*3*) the contribution of leaf sugars to leaf ψ_s and the accumulation of starch in leaves.

Materials and methods

Study site and plant material: Measurements were made on trees growing along a 100-m-long transect near the mouth of the Mapire river at 7º42'N, 64º46'W. Trees of the evergreen species studied, *A. nitens*, *C. laurifolia*, *E. tenuifolia*, *S. paniculata*, and *P. ovatifolium*, were chosen because of their importance and location along the gradient towards the river bed, in this order. The length of time and depth of flooding for these trees increases in the same order (for details of the field site see Fernández *et al.* 1999). Sampling was done by walking during the dry season and by canoe during flooding. Measurements were taken on the youngest fully expanded emerged leaves; leaves with obvious signs of senescence were not sampled. Rainfall data were obtained and changes in the water column height of the river Mapire calculated from the values for the river Orinoco measured at the nearby Musinacio hydro-meteorological station. Measurements were made between February 1998 and January 2000.

Measurements: Photosynthetic photon flux density (PPFD) was measured under full exposure with an *LI-185* quantum meter (*LI-COR*, Lincoln, NE, USA), air temperature with thermistors (*Yellow Springs Instruments*, Yellow Springs, OH, USA), and relative humidity (RH) with a hygrometer (*Abbeon*, Santa Barbara, CA, USA). Air temperature and RH were measured 1.5 m above ground in the shade. Xylem water potential was measured at 06:00 h in leaf-bearing branches ($n = 6$) using a pressure chamber (*PMS*, Corvallis, OR, USA); leaf sap osmotic potential (ψ_s) of these samples was measured in disks frozen and maintained in liquid nitrogen, defrosted and placed in C-52 chambers connected to an HR-33T micro-voltmeter (*Wescor Inc.*, Logan, UT, USA) operated in the psychrometric mode. Leaf gas exchange was measured ($n = 6$) with a double (CO_2 and H_2O) *CIRAS 1* infrared gas analyser connected to a *PLC(B)* assimilation chamber (*PP Systems*, Hitchin, UK). Measurements were made under full sun exposure, avoiding clouds or rain, between 09:00 and 14:00 h, when the highest daily values of P_N had been previously recorded (Fernández *et al.* 1999), and at an incident PPFD $\geq$ 1 200 µmol m^{-2} s^{-1}. Conditions during measurement were a leaf temperature of 34 ± 2 °C and a leaf-air water vapour pressure deficit of 3.1 ± 0.1 kPa. RH of the air stream entering the chamber was fixed; daytime leaf-air water vapour pressure deficit in the field ranged between 1.3 and 7.2 kPa during the dry season and between 0.53 and 4.00 kPa during flooding. Chl *a* fluorescence was measured with a pulse-amplitude modulated photosynthesis yield analyser (*Mini-PAM, Walz*, Effeltrich, Germany). The maximum quantum yield of PS2, $F_v/F_m = (F_m - F_0)/F_m$ (Genty *et al.* 1989), was measured in leaves ($n = 6$) collected in the morning and dark-adapted for a minimum of 4 h. Previous determinations indicated that values thus determined were higher than those measured *in situ* at the minimum dawn PPFD that allowed us to find our way in the forest. PPFD dependency curves of relative quantum yield of PS2

(Φ_{PS2}) were done ($n = 3$) automatically using the program in the fluorometer on leaves dark-adapted for at least 2 h by raising the "actinic light" in eight consecutive steps at 2-min intervals. The relative quantum yield of PS2 was calculated as $\Phi_{PS2} = (F'_m - F_s)/F'_m$ (Genty *et al.* 1989), where F_s is the steady-state fluorescence in the light and F'_m is the maximal fluorescence in the light. The Stern-Volmer coefficient of non-photochemical quenching (NPQ) was calculated as $(F_m - F'_m)/F'_m$ (Adams *et al.* 1994). Chl content was determined in acetone extracts of leaves discs ($n = 6$) after Bruinsma (1963) using a spectrophotometer (*Spectronic 401, Milton Roy*, Rochester, NY, USA). Leaf soluble sugar and starch contents were determined in samples ($n = 6$) collected at 08:00 and 16:00 h, respectively, digested in ethanol (sugars) and perchloric acid (starch), and glucose equivalents were determined spectrophotometrically in the coloured products of the reaction with the anthrone reagent (McCready *et al.* 1950).

Statistics: On a given date, a different individual was sampled each time; each data point is a different tree. Significance was assessed by one-way (season) ANOVA at $p \leq 0.05$. Values of F_v/F_m, Φ_{PS2}, and NPQ were arcsine-transformed before performing the ANOVA.

Results

Daily changes in microclimatic variables during the period of study varied less than 15 % throughout the seasons. Instantaneous maximum PPFD was 1 600 µmol m^{-2} s^{-1}, and maximum/minimum air temperature and RH were 33/27 °C and 80/58 %, respectively. Mean integrated PPFD was 36 mol m^{-2} d^{-1} with a minimum of 17 mol m^{-2} d^{-1} in June and a maximum of 50 mol m^{-2} d^{-1} in November.

Values of ψ (Fig. 1) increased with flooding in all the species, whereas changes in ψ_s were less marked. The ψ and ψ_s of *A. nitens* during the dry season were the lowest measured among all the species. ψ_s was as low as ψ during the dry season, increasing with flood water to values lower than ψ which in turn increased five times with flooding. In *E. tenuifolia*, an increase of three times in ψ took place between the dry season and the flood, while ψ_s increased at rising waters only by 25 % relative to the dry season. In *C. laurifolia* ψ increased five times with flooding, whereas ψ_s was as low or even lower than during the dry season. In *S. paniculata* ψ increased six times with flooding, ψ_s increasing only by 27 % and remaining unchanged until falling waters. In *P. ovatifolium* ψ and ψ_s increased with rising waters three and two times, respectively, remaining high until falling waters. An increase with flooding in pressure potential was evidenced in all the species.

Fig. 2 shows the seasonal changes in F_v/F_m and Chl content. Values of F_v/F_m in *A. nitens* were lowest under drought and under flooding, when Chl content was also lowest. In *E. tenuifolia*, a significant decrease in F_v/F_m was found at rising waters, values remaining constant until falling waters; Chl content showed an increase of 21 % at falling waters. A significant reduction in F_v/F_m occurred in *C. laurifolia* at rising waters and Chl content decreased by 42 % with flooding, remaining constant until falling waters. No significant changes were found in *S. paniculata* in F_v/F_m, whereas Chl content decreased by 45 % with rising waters and, although it increased again under flooding, it was lower than during the dry season. In *P. ovatifolium* F_v/F_m decreased at rising waters, increasing again under flooding; Chl content remained unvaried throughout the seasons. For all the species, the mean value of F_v/F_m never decreased below 0.76.

The P_N and g_s (Fig. 3) increased nearly twice in *A. nitens* from the dry season to rising waters-flooding, with a further increase of 1.6 times in P_N at falling waters. In *E. tenuifolia*, P_N and g_s were nearly halved at rising waters relative to the dry season, recovering at falling waters to the highest values. In *C. laurifolia* the highest P_N was measured during the dry season as well as under flood, while g_s was highest under flooding; at rising waters P_N and g_s became nearly zero. The P_N and g_s of *S. paniculata* were highest during the dry season, diminishing strongly at rising waters; P_N increased three times and g_s seven times under flooding and at falling waters relative to rising waters. In *P. ovatifolium* the highest values of P_N and g_s were obtained during the dry season and at falling waters, decreasing to less than half at rising waters-flooding.

Variations in leaf sugar and starch contents are shown in Fig. 4. In *A. nitens* leaf sugar content was highest during the dry season and at falling waters, whereas starch content increased with rising waters-flooding. In *E. tenuifolia* both sugar and starch contents were highest at rising waters-flooding and lowest during drought and at falling waters. Sugar content did not vary significantly with season in *C. laurifolia* except for a decrease of 34 % at rising waters, whereas starch content was highest by nearly five times at rising waters than during the dry season. In *S. paniculata* sugar and starch contents increased with rising waters-flooding 3.5 and 5 times, respectively, starch content decreasing again at falling waters. Sugar content of *P. ovatifolium* decreased on average by 33 % at rising waters and under flooding, whereas starch content increased nearly three times; at falling waters sugar content increased twice and starch content was halved. Starch content increased with flooding in all the species, while the seasonal changes in sugar content did not follow a clear trend among species.

The contribution to ψ_s of the osmotic potential calculated for the soluble sugars present in the leaf sap (Table 1) increased markedly with flooding in all the

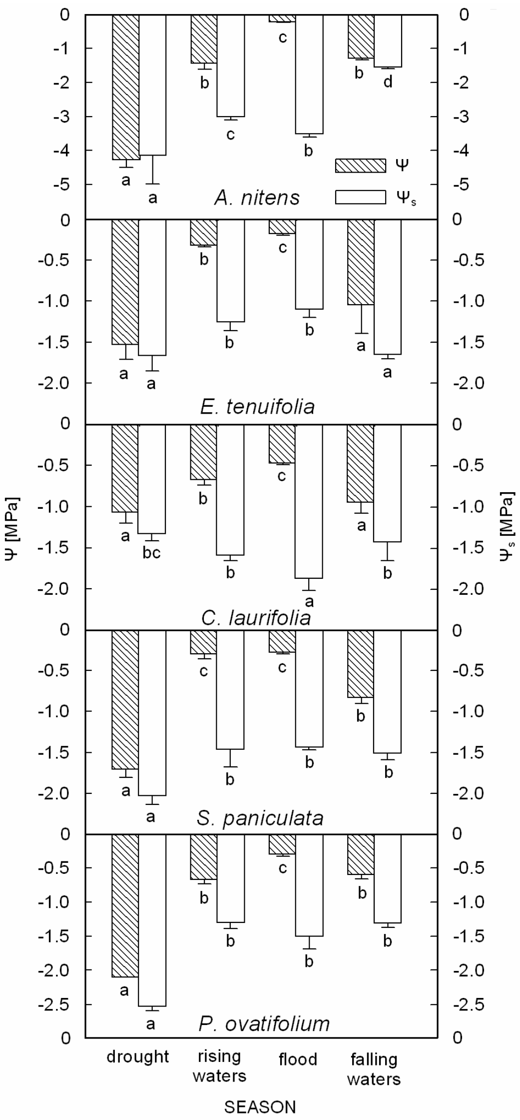

Fig. 1. Seasonal changes in xylem water potential (ψ) and leaf sap osmotic potential (ψ_s) of trees of the species indicated. Means ± one SE ($n = 6$). *Different letters bellow bars* indicate significant differences ($p<0.05$).

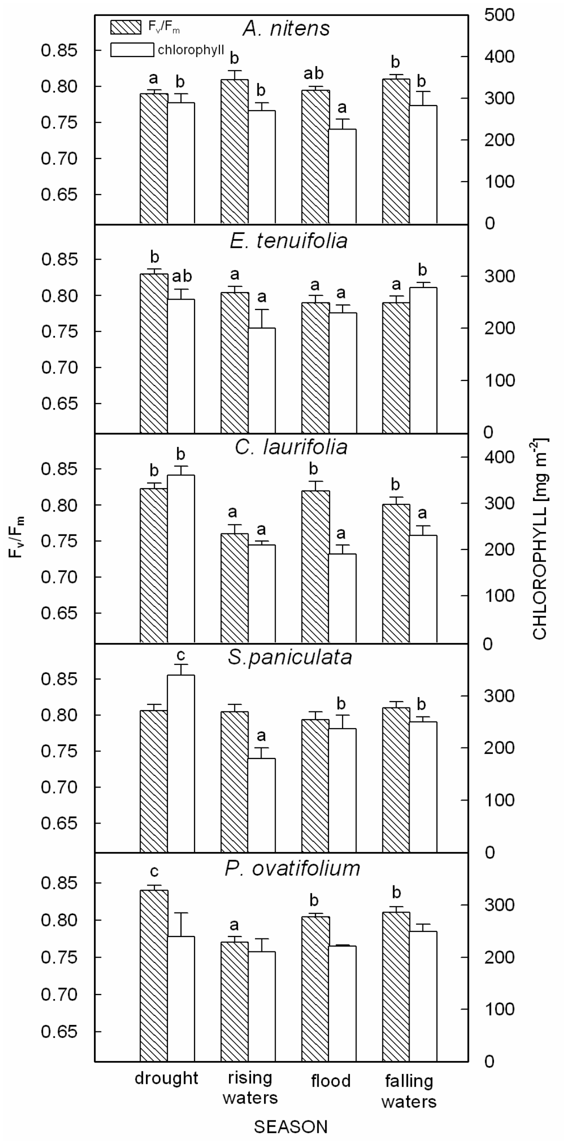

Fig. 2. Seasonal changes in maximum quantum yield of photosystem 2 (F_v/F_m) and chlorophyll content of trees of the species indicated. Means ± one SE ($n = 6$). *Different letters above bars* indicate significant differences ($p<0.05$).

species, except for *A. nitens*, to a maximum of 66 % in *S. paniculata*, decreasing again at falling waters, except for *P. ovatifolium*, in which it remained constantly high.

In order to determine whether reductions in P_N were related to decreases in fluorescence parameters and given that decreases in F_v/F_m were small and values were near the accepted maximum of 0.83 in unstressed plants, we analysed the PPFD curves of plants of each species done on the same dates when the lowest and the highest P_N were found for each species (Fig. 5). In *A. nitens*, a decrease in Φ_{PS2} at the lowest P_N was not compensated by a relative increase in NPQ compared to values for the highest P_N. In *E. tenuifolia* and *C. laurifolia*, no difference in the PPFD curve of Φ_{PS2} was found but NPQ was relatively higher for the highest P_N. In *S. paniculata* the PPFD curves for the lowest and the highest P_N were similar, coinciding with the absence of significant changes in F_v/F_m. In *P. ovatifolium*, a decrease in Φ_{PS2} for the lowest P_N was not compensated by an increase in NPQ.

We observed that hypertrophied lenticels and adventitious roots appeared in all trees 1–2 months after rising waters; the species which produces the least adventitious roots is *A. nitens*.

Discussion

Values of ψ, P_N, and g_s found in the present study closely resemble those reported by Fernández *et al.* (1999), indicating that the response pattern of these five tree species to flooding is highly repeatable. In the present study, marked increases in ψ of all the species with height of the water column were found, whereas the increase in $ψ_s$ was in some cases smaller or nil. The observed decrease in $ψ_s$ relative to ψ led to increases in pressure potential during flooding. Assuming that plants at rising waters and under flood have higher relative water content than during drought, lower values of $ψ_s$ on these dates suggest an active accumulation of osmotically active solutes. In trees of *Acer negundo* maintained at a high soil water potential in the field, a seasonal decline in $ψ_s$ without changes in ψ was detected (Foster 1992). In four of the species studied here soluble sugars significantly contributed to this decrease in $ψ_s$. In *A. nitens*, the contribution was low; nitrogenous compounds supplied by nitrogen fixation in this legume may make a significant contribution.

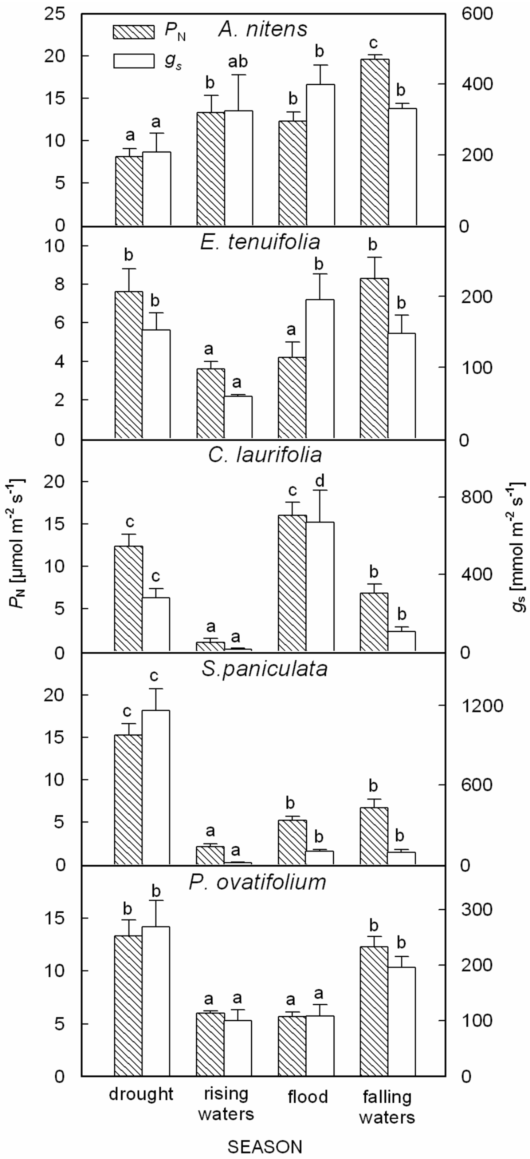

Fig. 3. Seasonal changes in net photosynthetic rate (P_N) and stomatal conductance (g_s) of trees of the species indicated. Means ± one SE ($n = 6$). *Different letters above bars* indicate significant differences ($p<0.05$).

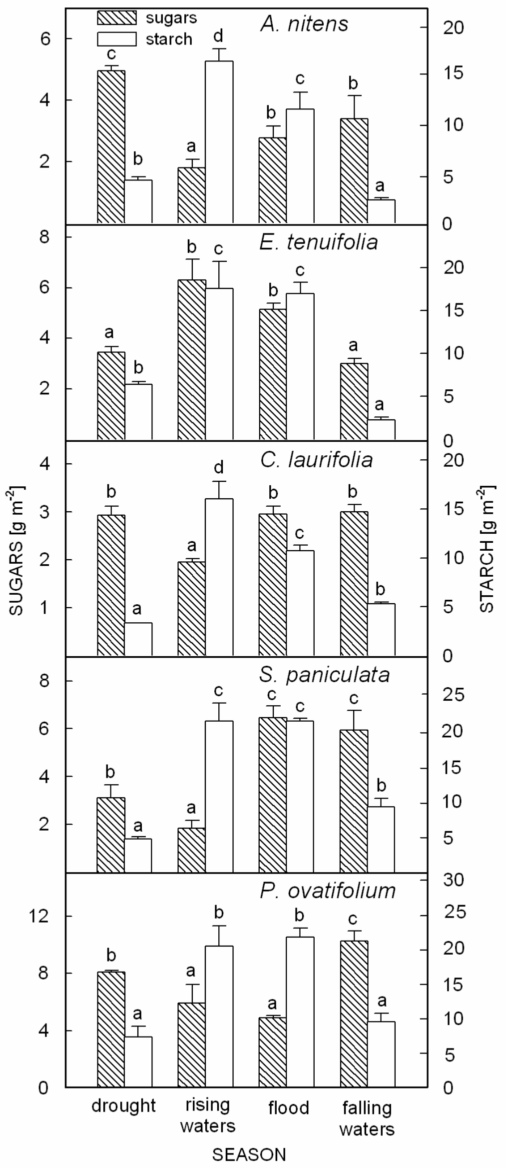

Fig. 4. Seasonal changes in soluble sugar and starch content of leaves of the species indicated. Means ± one SE ($n = 6$). *Different letters above bars* indicate significant differences ($p<0.05$).

Decreases in F_v/F_m occurred during both drought and flooding for a maximum of 6 %, values being within the range previously proposed to characterise plants not chronically photoinhibited (0.71–0.83 according to

Table 1. Seasonal changes in the relative contribution of soluble sugars to the leaf sap osmotic potential (ψ_s) in the species indicated. Values were calculated with the means of the leaf osmotic potential of the xylem sap and the soluble sugar content.

	Relative contribution [% of ψ_s]				
	A. nitens	*E. tenuifolia*	*C. laurifolia*	*S. paniculata*	*P. ovatifolium*
Drought	7.4	13.7	26.2	12.8	21.6
Rising waters	8.2	63.0	24.1	14.4	48.3
Flood	5.6	62.6	35.5	66.0	47.2
Falling waters	19.8	10.6	22.5	34.7	46.6

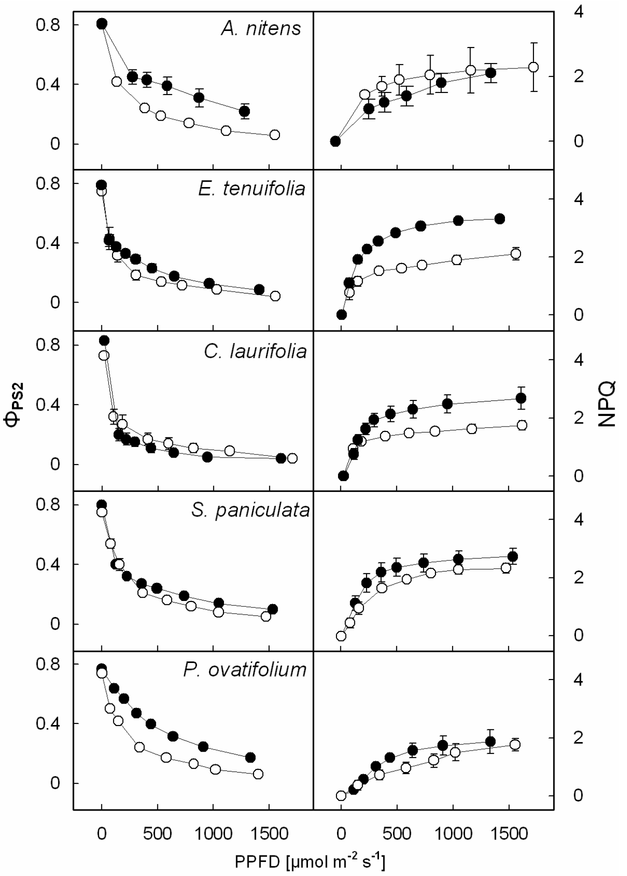

Fig. 5. Response curves of relative quantum yield of photosystem 2 (Φ_{PS2}) and the non-photochemical quenching coefficient (NPQ) to photosynthetic photon flux density (PPFD) in the species indicated. Curves were done during the season when the lowest (○) and the highest (●) net photosynthetic rates were measured. Means ± one SE (*n* = 3).

Bolhàr-Nordenkampf and Öquist 1983, and 0.78 according to Adams *et al.* 1990); a value as low as 0.76 was measured only in *C. laurifolia* at rising waters. A clear pattern of changes in F_v/F_m in relation to flooding was not found but decreases were related to decreases in P_N, suggesting that the latter were partly due to decreases in F_v/F_m. No changes in F_v/F_m were found during flooding in seedlings of *Glycine max* and *Helianthus annuus* (Guidi and Soldatini 1997), several tropical species (Parolin 2001), and *Boltonia decurrens* (Smith and Moss 1998). In contrast, a severe decline in F_v/F_m down to 0.6 under flooding was found in *Quercus rubra* (Wagner and Dreyer 1997) and in the tropical species, *Senna reticulata* (Parolin 2001). The diversity in reported results indicates that photoinhibition does not generally occur in flooded plants.

A sustained decrease in F_v/F_m and Φ_{PS2} associated to increase in NPQ may reflect increased photoprotection through the xanthophyll cycle rather than photodamage (Adams *et al.* 1994); decreases in F_v/F_m accompanied by increases in NPQ are evidence of overnight retention of one of the components of the xanthophyll cycle, zeaxanthin (Adams *et al.* 1995). The threshold of F_v/F_m indicative of chronic photoinhibition is aided by the comparison of changes in Φ_{PS2} and NPQ. In this study, decreases in Φ_{PS2} not compensated by an increase in NPQ were associated in all cases but *S. paniculata* with decreases in P_N, supporting the hypothesis of the occurrence of photoinhibition.

Values of F_v/F_m between 0.45 and 0.10 were measured by Waldhoff *et al.* (2002) in plants of *S. paniculata* growing in an Amazonian igapó that had been submerged for up to 180 d, suggesting that a longer and deeper submergence does indeed cause chronic photoinhibition in this and, presumably, all the species in the flooded forest. It can be confidently predicted that leaves of *S. paniculata*, as well as of the other species studied by us in the Mapire river forest, may experience such a severe photoinhibition after many months of submergence.

Changes in F_v/F_m did not obey changes in Chl content, which decreased with rising waters-flood in all the species but *P. ovatifolium*. In leaves of *S. paniculata* measured in Central Amazonia, changes in Chl content were associated with leaf age, rather than with depth and length of flooding (Waldhoff *et al.* 2002).

Gas exchange rates decreased with rising waters in all the species but *A. nitens*, which is the sole species to suffer water deficit and the last one in the gradient to become flooded. Afterward, resumption of high rates at flooding and falling waters was found in all the trees examined, suggesting that an acclimation process took place. The parallel changes with flooding in P_N and g_s found in our study suggest that the diminution in P_N was due to stomatal closure. Decreases in P_N and g_s were reported in the flood-tolerant species, *Prioria copaifera* (Lopez and Kursar 1999) and *Alnus rubra* (Batzli and

Dawson 1997). We do not rule out an increase in non-stomatal limitation of photosynthesis and are currently assessing this possibility through P_N/intercellular [CO_2] curves.

The recovery of P_N and g_s after rising waters may be explained by the appearance of hypertrophied lenticels and adventitious roots that help alleviate hypoxia. In plants of *Larix laricina*, a flood-tolerant species, values of g_s were higher than in the flood-intolerant *Picea mariana* apparently due to the appearance of adventitious roots and an increase in root hydraulic conductivity (Islam and Macdonald 2004).

All the studied trees accumulated starch in their leaves under flooding, this accumulation not always being related to a higher P_N. Similarly, flooded seedlings of the tolerant species *L. laricina* showed a marked increase in shoot starch after 27 d of flooding, as opposed to seedlings of the intolerant species *P. mariana* (Islam and Macdonald 2004), which suggests that starch accumulation in leaves is a tolerance mechanism. In our investigation, starch accumulation occurred at rising waters, when P_N of all the species was very low or at least lower than the maximum. This suggests that photosynthates could not be translocated to other sinks and that the mechanisms responsible for alleviating hypoxia had not begun operating. In all the species starch content began to decrease during maximum flooding or at falling waters, coinciding with the resumption of high P_N. Enhanced starch and sugar accumulation was observed in woody species under flooding, suggesting that this is a consequence of reduced phloem translocation from shoot to root (Kreuzwieser *et al.* 2004).

We conclude that the accumulation in leaves of osmotically active metabolites, mostly sugars, may be a mechanism whereby these trees tolerate flooding by increasing pressure potential, which allows the resumption of high g_s and P_N. Also, that flooding does not reduce F_v/F_m below the threshold value assumed for healthy plants. The reduction in P_N was associated in all the species but *S. paniculata* to the decrease in Φ_{PS2} not compensated by an increase in non-photochemical quenching. Changes in Chl *a* fluorescence, leaf gas exchange, and saccharide contents obey in a complex manner to intensity of flooding, duration and height of water column, with species-specific effects that depend on the location of the tree along the flood gradient.

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