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Leaf gas exchange characteristics and chlorophyll fluorescence of three wetland plants in response to long-term soil flooding

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Abstract

The effects of soil flooding on gas exchange and photosystem 2 (PS2) activity were analyzed in leaves of *Phragmites australis*, *Carex cinerascens*, and *Hemarthria altissima*. Pronounced decrease in net photosynthetic rate and stomatal conductance with flooding was found only in *C. cinerascens.* No significant changes in PS2 activity were observed in all three species which suggests that the photosynthetic apparatus was not damaged. Among the three species, *H. altissima* is better adapted to flooding than *P. australis* and *C. cinerascens.*

Additional key words: *Carex cinerascens*; *Hemarthria altissima*; irradiance; net photosynthetic rate; photosystem 2; *Phragmites australis*; stomatal conductance; transpiration; water use efficiency.

Introduction

Seasonal fluctuations in water level are commonly found in natural wetlands and the tolerance of plants to this variation is the key factor for the composition of community and distribution of wetland species (Wassen *et al.* 2002). Soil flooding initiates a series of reactions leading to reduced soil oxidation-reduction potential (Eh) (DeLaune and Pezeshki 1991). In many species, reduced soil conditions may adversely affect plant physiological functioning such as plant nutrition, water relations, activity of photosynthetic enzymes, gas exchange, photosynthetic electron transport, and photosystem 2 (PS2) activity (Pezeshiki *et al.* 1996, Kozlowski 1997, Gravatt and Kirby 1998, Blanch *et al.* 1999, Pezeshki 2001, Yordanova and Popova 2001). Morphological processes in plants such as carbon assimilation and allocation, aerenchyma development, and enhanced porosity are also greatly influenced by soil flooding (Justin and Armstrong 1987, Rubio *et al.* 1995, Pezeshki 2001, Chen *et al.* 2002).

Swan islet wetland, the nature reserve dedicated to the protection of David's deer, is located in central China and is regularly flooded. Distinctive plant communities can often be found at predictable locations along specific gradients. The three wetland plant species studied here are commonly found in mixtures or forming mosaics of neighbouring patches: *Phragmites australis* (Cav.) Trin. *ex* Steudel, common reed, is a widespread species characteristic of the ecotone between terrestrial and aquatic environments. *Carex cinerascens* Kukenth is a rapidly growing grass. It is the most common wetland species in the marsh, establishing microsites on the periphery of saturated soil zones or slight drought sites. *Hemarthria altissima* (Poir.) Stapf *et* C.H. Hubb is a fast-growing weed, most commonly found in deep, fertile, and usually moist soil, but survives well in wetlands, on the periphery of saturated zones, or in seasonally flooded sites. They all exhibit a wide range of ecological amplitudes of adaptation to varying soil water availability during the flooding season and their distribution varies spatially in terms of water level within this marsh. The surface of the marsh can be divided into three classes: high lawns, low lawns, and hollows. Lawn level vegetation ranges from *P. australis* and *C. cinerascens* in drier areas to wet areas dominated by *H. altissima*. The three species are distributed regularly along the flood level according to the order of *P. australis*, *C. cinerascens*, and *H. altissima.* Hence, we assumed that the three species would show the similar sequence in their flood-tolerance. The extent to which the three grasses can resist and the mechanisms involved in long-term flooding response of these plants have been studied only rarely. Understanding how the plant species respond to flooding is important to help predict their productive potential under certain environmental conditions and the shift of vegetation pattern in wetland, and ultimately provides the information needed for successful wetland management.

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The objectives of this study were to investigate the effects of long-term soil flooding on the photosynthesis characteristics in *P. australis*, *C. cinerascens*, and *H. altissima* and to relate these responses to the species flood tolerance.

Materials and methods

Study area: Experiments were carried out in Swan islet wetland reserve (29°48′N, 112°33′E), from July to September in 2005. In the marsh, moderate slopes are found commonly due to frequent inundation. The experiment was performed in a sloping meadow (20×20 m, with a slope of 5° or so) where the soil composition was 33, 49, and 17 % of sand, silt, and clay, respectively, and the pH was 7.2. Two kinds of sample plot were selected: in the non-flooded treatment the water level was 20 cm below the soil surface and in the flooded treatment the water level was 20 cm above the soil surface. For each species, six randomly selected plants were measured in each treatment.

Photosynthesis and chlorophyll (Chl) fluorescence: Field measurement was carried out from July to September 2005. On days 0, 30, and 60 after initial flooding, the maximal net photosynthetic rate ($P_{\max}$) of the fourth expanded leaves was measured between 12:00 and 13:00 under natural solar irradiance (photosynthetic photon flux density, PPFD: 1 500–1 800 μmol m^{-2} s^{-1}), using a *Licor 6400* Portable Photosynthesis System (*Li-Cor*, Lincoln, NE, USA). Changes of intercellular CO_2 concentration (C_i) and transpiration rate (E) were recorded simultaneously. The diurnal courses of net photosynthetic rate (P_N) were examined from 06:00 to 18:00 at an interval of 2 h during a day using 8 replicates each time. Changes of PPFD, air temperature, leaf temperature, air humidity, and CO_2 concentration were recorded simultaneously. The response of P_N to step changes in PPFD was examined by an internal, red and blue radiation source under full irradiance (I). Ten PPFDs (0, 20, 50, 100, 200, 500, 1 000, 1 500, and 2 000 μmol m^{-2} s^{-1}) were set. The CO_2 concentration (C_a) of air entering into the chamber was regulated at 370 μmol mol^{-1} through a CO_2 mixer. The flux of air entering the cuvette was set at 400 mmol s^{-1}. Leaves were allowed to acclimate to each PPFD for at least 4 min before steady state gas exchange properties were observed and logged, and subsequently the PPFD in the cuvette was changed. P_N-PPFD curves were plotted using the mean values of P_N measured at each PPFD. Three replicates were made. Apparent quantum yields (α), dark respiration rates (R_D), and compensation irradiance (I_c) were estimated on the basis of the linear part (PPFD: 0–200 mmol m^{-2} s^{-1}) of the I-response curves using linear regression analysis. The saturation irradiance (I_s) was calculated according to Walker (1989).

Chl fluorescence was measured on fully-expanded leaves near those used for photosynthesis measurement using *LI-6400-40* fluorometer. F_0 (minimal fluorescence), F_m (maximal fluorescence), F_v (variable fluorescence), and F_v/F_m (maximal photochemical efficiency of PS2) were measured shortly after keeping the leaves in dark for 20 min. A red irradiance of 7 000 μmol m^{-2} s^{-1} was applied for measurements. Fluorescence parameters, electron transport rate (ETR), actual photon yield of PS2 (Φ_{PS2}), and photochemical (q_P) and non-photochemical quenching (q_N), were measured on light-adapted leaves using the equations of Genty *et al.* (1989).

Data analysis: Two-way ANOVA (*SPSS 11.5*) with two levels of flooding and three sampling dates was used to test the differences in means for photosynthetic responses including P_N, g_s, E, and water use efficiency (WUE). One-way analysis of variance (ANOVA) was used in the PS2 parameters. The Tukey procedure was used to examine all pair-wise group differences. Differences were considered significant at $p<0.05$.

Results

P_N in *P. australis, C. cinerascens*, and *H. altissima* was reduced in flooded conditions (Fig. 1, Table 2). On day 30, soil flooding reduced $P_{\max}$ by 15.5 and 11.3 % in flooded *C. cinerascens* and *H. altissima* (Fig. 1*B,C*) compared to the non-flooded plants, respectively. However, the $P_{\max}$ increased by 11.3 % in *P. australis* (Fig. 1*A*). At the end of the experiment, soil flooding reduced P_N by 4.0 % in *P. australis* and by 7.7 % in *C. cinerascens*, while P_N of *H. altissima* increased by 1.6 % (Fig. 1*C*). In *C. cinerascens,* there was a tendency for stronger reduction of photosynthesis between two conditions than in the other two species (Fig. 1, Table 2) while this reduction was not statistically significant after 60 d of flooding. No significant difference of photosynthesis between the two conditions was detected in *P. australis* and *H. altissima* (Table 2). After 60 d of flooding, $P_{\max}$ decreased in *P. australis* and *C. cinerascens* while a slight increase was observed in *H. altissima*, which was similar to the change of PS2 photochemical efficiency after 60 d of flooding (Fig. 4*E*).

Soil flooding caused a substantial decrease in E ($p<0.01$) and stomatal conductance, g_s ($p<0.05$) of *C. cinerascens* after 30 d of flooding, nevertheless, no significant difference was found in the other two species (Fig. 1). After 60 d of flooding, there were no significant differences found among the three flooded species

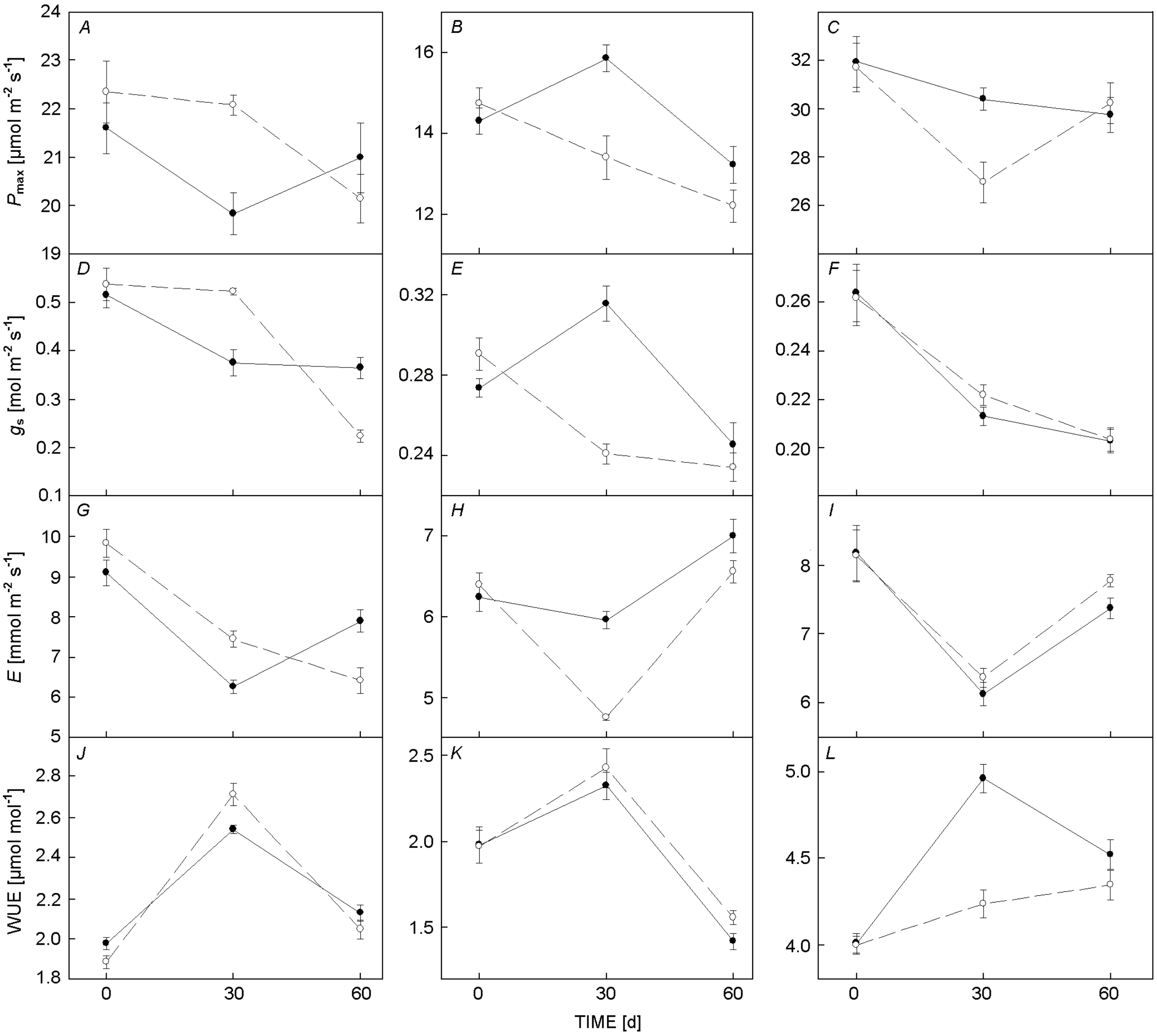

Fig. 1. Maximal net photosynthetic rate, P_{max} [μmol m^{-2} s^{-1}], stomatal conductance, g_s [mol m^{-2} s^{-1}], transpiration rate, E [mol m^{-2} s^{-1}], and water use efficiency, WUE [μmol $mmol^{-1}$] for flooded (*dashed line*) and non-flooded (*solid line*) conditions. Means ±SE ($n = 48$).

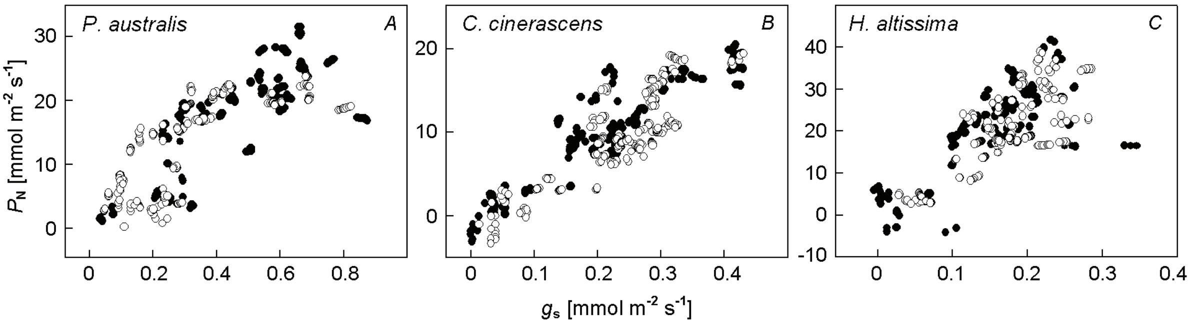

Fig. 2. Relationship between leaf conductance, g_s [mol m^{-2} s^{-1}] and net photosynthetic rate, P_N [μmol m^{-2} s^{-1}] for three wetland plants subjected to 60 d of flooding (○) or non-flooded (●).

as compared with the non-flooded plants. The reduction in P_N by flooding can be attributed to the closing of stomata and some non-stomatal factors (Pezeshki 2001). Stomatal limitation is probably the decisive factor causing the reduction of P_N (Kozlowski 1997). We found a close relationship between g_s and P_N in the three plant species (Fig. 2*A,B,C*) for *P. australis* and *C. cinerascens*. Particularly in *C. cinerascens*, the P_N obtained for non-flooded plants was higher than that for flooded plants. No apparent difference was found between P_N at the two hydro-conditions in *H. altissima*. This different response indicated that stomatal limitation may be the critical factor that affects photosynthesis of *C. cinerascens*. This was similar to the response of *Genipa americana* to soil flooding (Mielke *et al.* 2003).

For the calculated values of WUE, there were no significant effects of soil flooding found in *P. australis*, *C. cinerascens*, and *H. altissima* (Table 2). On the day 30, pronounced decrease ($p<0.05$, with a decline of 14.5 %) of flooded *H. altissima* was observed compared to the non-flooded plants (Fig. 1*L*). Among the three species, only the *H. altissima* showed a higher decrease of WUE with a 15.9 % decline between the two hydro-conditions according to the repeated ANOVA. For *P. australis* and *H. altissima*, similar response of P_N and E to soil flooding resulted in the relatively stable WUE.

As concerns diurnal course of activities of the three species, two-peaked curve was found in *P. australis* and *C. cinerascens*, while *H. altissima* showed a single-peaked curve. This may be partially correlated with the

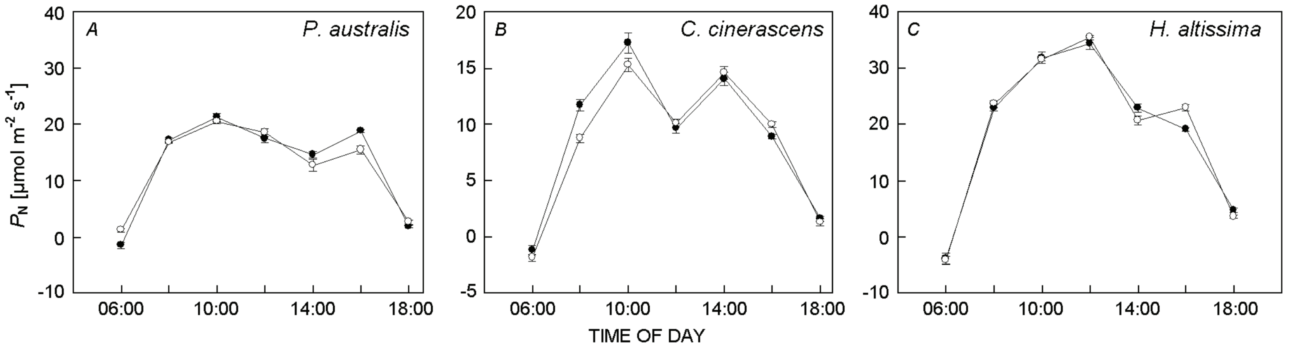

Fig. 3. Diurnal course of net photosynthetic rate, P_N [µmol m^{-2} s^{-1}] in *P. australis, C. cinerascens,* and *H. altissima* under non-flooded (●) and flooded (○) conditions for 60 d. Means ± SE.

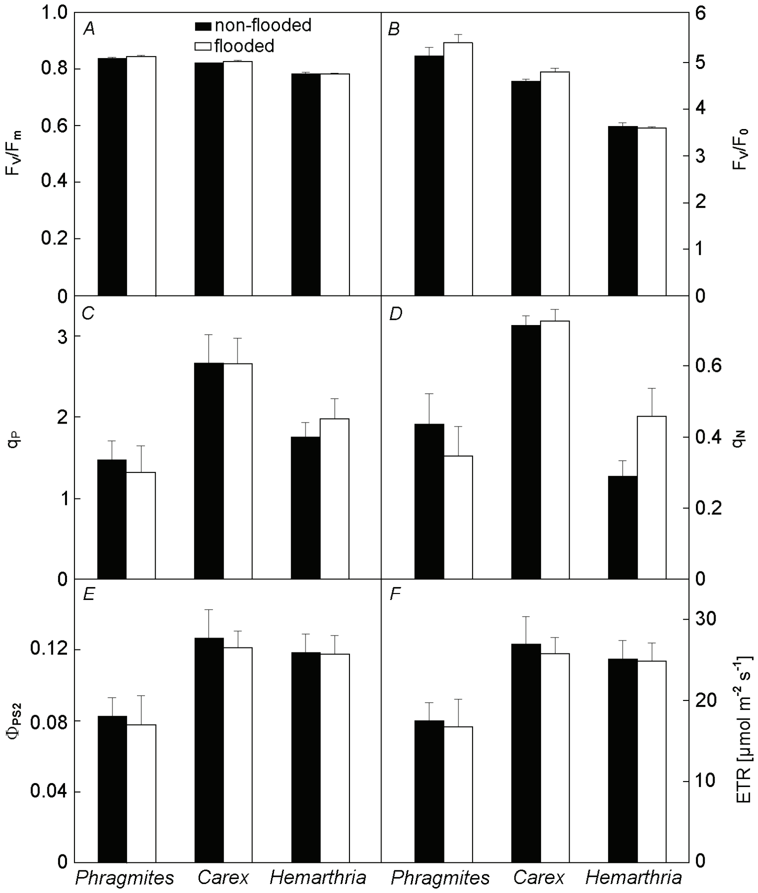

Fig. 4. Changes in the ratios of variable to initial fluorescence (F_v/F_0), variable to maximum fluorescence (F_v/F_m), the photochemical (q_P) and non-photochemical (q_N) efficiency, and electron transport rate (ETR) of tested three plant species grown under non-flooded and flooded conditions. The means represent 5 replications±SE.

Table 1. Photosynthetic parameters, *i.e.* dark respiration rate (R_D), apparent quantum yield (α), compensation irradiance (I_c), and saturation irradiance (I_s), estimated from the irradiance response curve. % represent the flooded *vs*. non-flooded. *Different letters* represent significant difference at the significant level of 0.05.

Parameter	Species	Condition non-flooded	flooded	%
R_D [µmol m^{-2} s^{-1}]	*P. australis*	$2.62±0.11^a$	$2.76±0.21^a$	105.3
	C. cinerascens	$1.58±0.09^a$	$3.07±0.18^b$	194.3
	H. altissima	$2.40±0.13^a$	$1.69±0.24^a$	70.4
α	*P. australis*	$0.0484±0.000^a$	$0.0421±0.002^a$	87.0
	C. cinerascens	$0.0376±0.001^a$	$0.0352±0.006^a$	93.6
	H. altissima	$0.0461±0.002^a$	$0.0493±0.009^a$	106.9
I_c [µmol m^{-2} s^{-1}]	*P. australis*	$48.50±1.93^a$	$60.06±3.46^b$	123.8
	C. cinerascens	$37.81±2.21^a$	$83.66±5.27^b$	221.3
	H. altissima	$49.77±1.42^a$	$41.27±3.52^a$	82.9
I_s [µmol m^{-2} s^{-1}]	*P. australis*	$885.74±22.04^a$	$857.71±26.11^a$	96.8
	C. cinerascens	$580.26±18.76^a$	$520.17±36.75^b$	89.6
	H. altissima	$877.10±11.65^a$	$838.42±32.54^a$	95.6

Table 2. Daily mean photosynthesis parameters and probability values of ANOVA to compare the effects of flooding on there species between 30 and 60 d of soil flooding. Net photosynthetic rate, P_N [µmol m^{-2} s^{-1}], stomatal conductance, g_s [mol m^{-2} s^{-1}], transpiration rate, E [mmol m^{-2} s^{-1}], and water use efficiency, WUE [µmol mol^{-1}]. % represents the flooded *vs*. non-flooded. $^*p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

Plant	Parameter	Non-flooded	Flooded	%	Condition	Duration	C×D
P. australis	P_N	16.76±0.45	15.16±0.49	90.45	0.670	0.365	0.081
	g_s	0.453±0.012	0.361±0.012	79.73	0.459	0.259	0.033^*
	E	7.18±0.18	6.29±0.20	87.56	0.550	0.468	0.048^*
	WUE	2.41±0.05	2.42±0.05	100.74	0.967	0.429	0.264
C. cinerascens	P_N	10.37±0.30	8.87±0.29	85.53	0.010^*	0.006^{**}	0.015^*
	g_s	0.248±0.007	0.242±0.004	97.58	0.593	0.001^{**}	$<0.001^{***}$
	E	4.66±0.12	4.51±0.11	96.78	0.705	$<0.001^{***}$	$<0.001^{***}$
	WUE	2.26±0.05	2.07±0.06	91.59	0.112	0.373	0.742
H. altissima	P_N	18.46±0.74	17.68±0.66	95.77	0.514	0.001^{**}	0.082
	g_s	0.159±0.006	0.157±0.003	98.74	0.801	0.097	0.413
	E	4.21±0.16	4.72±0.18	112.11	0.431	0.271	0.020^*
	WUE	5.15±0.27	4.53±0.16	87.96	0.295	0.190	0.136

photosynthetic pathway; *P. australis* and *C. cinerascens* have the C_3 photosynthetic pathway and *H. altissima* belongs to the C_4 type. Of the three species, *H. altissima* had the highest P_N (34.4 µmol m^{-2} s^{-1}) under high I and no midday depression was found. As shown by the P_N/I curve, soil flooding decreased P_N at both saturating and sub-saturating I, but no statistically significant difference was found between the two hydro-conditions in *P. australis*, *C. cinerascens*, and *H. altissima*. A reduction with flooding in the photosynthetic capacity found in many species that suffered a long-term flooding was not found in the three species which was evidenced by the steady apparent quantum yield. Pronounced increase of I_c was found in *P. australis* and *C. cinerascens*. Significant decrease of I_s ($p<0.05$) and increase of R_D ($p<0.01$) found in *C. cinerascens* would reduce the time of effective P_N and make plants consuming more CO_2 at night (Table 1).

Chl *a* fluorescence is a very sensitive tool to study the stress-induced damage to PS2. At the end of the experiment, no significant reductions in potential photochemical efficiency (F_v/F_m) were observed in the three species. F_v/F_m illustrated an overall similarity of the three species between the two hydro-conditions. In the same period, there were no statistically significant differences in F_v/F_0, Φ_{PS2}, ETR, and q_P; this suggested that there was no damage to photochemical reactions. In *H. altissima*, soil flooding caused a significant increment of q_N by 58.6 % ($p<0.01$) (Fig. 4*D*). q_N is the most common form of protection against excess photons and is associated with xanthophyll cycle activity (Maxwell and Johnson 2000).

Discussion

During the soil flooding period, all the three species did not show any apparent symptoms described for flood-intolerant species. Adventitious roots were found in *P. australis* and *H. altissima*. We found that the three species are resilient to long-term soil flooding, like many other wetland species (Ewing 1996, Kercher and Zedler 2004). Although there is some deficiency of P_N in response to soil flooding, they can grow well when subjected to permanent flooding.

As expected, the photosynthetic characteristics of *P. australis*, *C. cinerascens*, and *H. altissima* showed different response to long-term of soil flooding. P_N is drastically reduced in flood-sensitive plants (Pezeshki 2001). P_N of both flood-tolerant and flood-intolerant species were significantly reduced by flooding, however, this reduction was higher for flood intolerant species (Kozlowski 1997, Gealy 1998, Gravatt and Kirby 1998). On the other hand, flooding caused no significant P_N reduction in the flooding-tolerant tropical grasses *Echinochloa polystachya* and *B. mutica* (Baruch 1994). In our study, all the three species except *C. cinerascens* showed no significant reductions after long-term soil flooding (Table 2). Based on their overall response, none of the three species was highly sensitive to flooding, while *P. australis* and *H. altissima*, to some extent, were slightly more tolerant than *C. cinerascens*. The paradox of different flood-tolerance found between *P. australis* and *C. cinerascens* was out of our anticipation. This discordance may be partially explained by the wider ecological fitness of *P. australis* and the inter-specific competition between the two species.

The observed change in P_N after flooding might be attributed to the stomatal limitation and the effects on photosynthetic capacity (Kozlowski 1997). g_s in flooded plants usually follows the same pattern as the photosynthetic response (Olivella *et al.* 2000). In many studies, stomatal response was closely correlated to photosynthetic rate and flooding tolerance (Mielke *et al.* 2003). In our study, reduction of photosynthesis was accompanied with a pronounced reduction of g_s and E in flooded *C. cinerascens* compared to the non-flooded plants. A similar stomatal response among flood-tolerant and flood-intolerant plant species was also reported by Pezeshki *et al.* (1996). This suggests that stomatal limitation is the critical factor reducing photosynthesis of *C. cinerascens* under flooding.

Midday depression of P_N found in *P. australis* and *C. cinerascens* could be attributed to combination of stresses such as photoinhibttion, water stress, and heat stress (Flexas *et al.* 2004). The midday depression occurred in *P. australis* and *C. cinerascens* but not in *H. altissima* after 60 d of flooding (Fig. 3). This difference between species in the diurnal course of P_N was probably connected with the different response to water flooding. Among the three wetland species, *H. altissima* was relatively less sensitive in stomatal response to soil flooding (Fig. 2, Table 2), which suggested a relatively small soil to leaf hydraulic resistance in *H. altissima*. These traits may be one of the reasons for dominance of *H. altissima* in wetter sites than that of the other two species.

Chl *a* fluorescence is a very sensitive tool to study the stress-induced damage to PS2 (Ball *et al.* 1994, Maxwell and Johnson 2000). No significant difference was found in F_v/F_m, F_v/F_0, Φ_{PS2}, ETR, and q_P (Fig. 4). This suggests that soil flooding caused no damage to the photochemical reactions of the three species. Non-photochemical quenching is related to the thermal de-excitation of PS2. According to Demmig-Adams and Adams (1992), it is often related to light induced formation of the carotenoid zeaxanthin in the xanthophyll cycle (Maxwell and Johnson 2000). In our study, significant increase was found in *H. altissima* similarly to *Eschweilera tenuifolia* (Rengifo *et al.* 2005) and *Pouteria orinocoensis* (Fernández 2006). This photo-protection mechanism is enhanced under any stress due to an excess of reducing power ($NADPH+H^+$) brought by the decrease of CO_2 available at carboxylation sites or a sink limitation (Schreiber *et al.* 1986, Björkman and Demmig-Adams 1995).

In summary, our results demonstrated that all three plant species tested are flood-tolerant; they could survive 60 d of soil flooding. No damage to the photochemical apparatus of photosynthesis was observed under flooded conditions. Difference in gas exchange behaviour among the three species indicated the different flood tolerance of these species. Variations of P_N and g_s can be used as a bio-indicator to assess their ability to tolerate flooding. The depression will be found in the flood-intolerant species and no apparent effect in the more tolerant ones. Although no difference was found in the Chl fluorescence parameters, also this non-destructive measurement can be used as an early detection of relative flood tolerance in wetland species.

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