

Can the Chlorophyll-*a* Fluorescence be Useful in Identifying Acclimated Young Plants from Two Populations of *Cecropia Pachystachya* Trec. (Urticaceae), Under Elevated CO₂ Concentrations?

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Abstract The physiological behavior of PSII measured by chlorophyll *a* fluorescence explains stress responses; wonders if it can differentiate plants from different populations. For this purpose, acclimated young plants of two *C. pachystachya* populations were cultivated from seeds. Chlorophyll-*a* fluorescence was measured after fertilization and [CO₂]_e. In the first 48 h after fertilization there was a reduction in the maximum quantum yield of PSII, while the means obtained under [CO₂]_e were significantly higher than in other treatments (0.8 and 0.81). The variable PI best expressed the different conditions tested. Compared to their respective controls, the reduction of D_{Io}/C_S was 35.89 % in population (P) and 41.89 % in population (I), while the polyphasic fluorescence kinetics differed between treatments, but not necessarily between populations, except for post-fertilization at *I-P* steps. The analysis of kinetics between F_o and F_j (Wt) showed no *K* band during the *O-J* phase. The interferences found in PSII reinforces the idea of reversible damage to PSII. This effect is directly related to the reduced electron transport rate and increased non-photochemical dissipation and may be similar to those observed under field conditions after planting; adjustment time depends, among other factors, on the genetic potential of the species.

Keywords Electron transport · Native tree · Photosystem · Stress

Abbreviations

Chl- <i>a</i>	Chlorophyll a
[CO ₂] _a	Ambient atmospheric CO ₂ concentration
[CO ₂] _e	Elevated atmospheric CO ₂ concentration
ETR	Electron transport rate
PAR	Photosynthetically-active radiation
F _m	Maximal fluorescence of dark-adapted state
F _o	Minimal fluorescence of dark-adapted state
F _v	Variable fluorescence
F _v /F _m	Maximal quantum yield of PSII photochemistry
LHC II	Ligh-harvesting complex
OEC	Oxygen evolving complex
PAR	Photosynthetically-active radiation
PI	Performance index
PSII	Photosystem II
Q _A	Plastoquinones of PSII
Q _B	Secondary quinone acceptor of PSII

Introduction

The use of acclimated plants produced from seeds of regional populations can reduce post-planting mortality rates in heterogeneous planting [26], and therefore can decrease planting costs, data that address functional aspects of the photosynthetic machinery of plants from different populations are still scarce.

Energy dissipation in photosystems can be conveniently studied by the behavior of chlorophyll fluorescence. Especially Chl-*a* fluorescence constitutes a powerful tool to

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understand the responses of plants to several environmental stressors [12].

The kinetics of polyphasic fluorescence in Chl-*a* can be studied by the *OJIP* test [35], where *O* represents the minimum level of chlorophyll fluorescence in which the LHC-II molecules, the pheophytin (Phe_{D1}) and their acceptor primary quinone (Q_A), are in their oxidized state, or all reaction centers are opened. *P* is the maximum intensity of fluorescence emitted by the leaf, when the reaction centers and all Q_A molecules are in their reduced state. The *J-I* step is intermediate in such a way that the interval *O-J* represents the primary photochemical reactions of PSII, in which Q_A is reduced to Q_A⁻. *J-I* corresponds to the phase of electron transfer from Q_A to Q_B, controlled by the donor side of PSII during water photolysis in the OEC. *I-P* refers to the maximum fluorescence dissipation through the plastoquinone pool [24, 35].

Plastic plant responses, common in natural populations, suggest a complex adaptive trait that is not only structural but also physiological [20, 29]. Stress conditions, in general, tend to reduce the homeostatic capacity of a given system [34, 17]. Periods of stress are common after planting [33, 2], but planting check and mortality rates can be reduced by pre-acclimating seedlings [26]. During acclimation, the young plants are exposed to full sunlight, water and nutrient restriction, conditions to which the photosynthetic complex is able to adjust [39].

In addition to the stressors other factors can highlight the differences between populations of plants. The CO₂ enrichment, for example, can stimulate the rate of photosynthesis and promote changes in the PSII machinery (Satoh et al. [30], [1]), or reduce the PSII photochemical efficiency in certain cases [3]. Although the [CO₂]_e effects on plants growing in these conditions are widely studied, the short-term responses of acclimated plants returning to fertilized state, and submitted to CO₂ are not reported.

The plasticity of plant responses to different environmental conditions is considered important to guide the actions in reforestation, investigations concerning responses to stress factors at the population level from acclimated plants are still insufficient. We hypothesize that the acclimation period when immediately followed by fertilization is relevant to planting check responses. The mechanisms of adjustment are discussed, using variables of chlorophyll fluorescence in acclimated young plants of two *Cecropia pachystachya* Trec. (Urticaceae) populations in order to test the efficiency of this tool identify between–population variation and/or to better understand their establishment in field conditions.

Materials and Methods

Infructescences and fertile branches of *Cecropia pachystachya* Trec. (Urticaceae) were collected from 20

matrices selected in two different geographic micro-regions in the State of Mato Grosso do Sul - Brazil: the “Low Pantanal (MLP)” in the wetlands of the “Pantanal” biome, specifically in the “Paço-do-Iontra”, a sub-basin of the Miranda river, with geological substrate from the Cenozoic formation of the Pantanal (19°34′07.25″S and 57°02′17.02″ W), and “Paranaíba” (MPA) in forest fragments in the municipality of “Inocência” (19°38′13.14″S and 52°01′58.90″ W) with geological substrate from the Mesozoic formation Adamantina [9, 5]. To select the two plants populations was considered the geological substrate, distance between MLP and MPA, in addition to fact that are two distinct watersheds.

The mature infructescences were placed in plastic trays lined with filter paper for drying and subsequent manual processing of seeds. The seeds were separated from vegetable waste with the aid of sieves (Granutest, 1 and 0.5 mm), placed in labeled glass recipients and kept under refrigeration until sowing.

Seedlings were grown in shade-covered (50 %) nurseries and watered daily, from direct seeding in polyethylene tubes containing the agricultural substrate Plantimax[®]. After thinning, the seedling with the greatest apparent vigor from each cartridge was kept suspended in a tray [28], making batches of 36 individuals per replicate. Two replicates were set up per population for the populations of Pantanal (P) and Inocência (I). Seedlings were acclimated to nutritional stress by the absence of fertilization until the onset of symptoms of nutritional stress [17] manifested by chlorosis of mature leaves after approximately 3 months of development.

For the experiment we used a 5 mm glass chamber with external dimensions of 165×65×65 cm (L-H-W), 40 W fluorescent lighting, PAR between 36 and 40 μmol m⁻² s⁻¹ and a 14 h photoperiod-controlled timer. The reduction of indoor relative humidity was obtained by condensation provided by a thermostatically controlled refrigeration system with an oil compressor (60 Hz, 115–127 V). The air inside the chamber was circulated by two coolers powered by a 12 V 230 W source. The CO₂ was injected by a centralized system flow, and their concentrations were monitored with an IRGA PP System Ciras RC.

Three independent treatments were applied: (1) plants under nutritional stress (acclimated), field capacity, maintained in the greenhouse with PAR radiation between 386 and 450 μmol m⁻² s⁻¹ (control); (2) plants kept in the same environment but fertilized with Hoagland solution pH 6.7 [13] at a rate of 3 ml per tube (G1 and G2) and (3) fertilized plants kept in a chamber under different CO₂ concentrations (C1 and C2). These three treatments yielded five experimental conditions:

- (G)- Acclimated plants kept in greenhouse (control)
- (G1)- Plants kept in the greenhouse for 24 h after fertilization

- (G2)- Plants kept in the greenhouse for 48 h after fertilization
- (C1)- Plants kept in a chamber with [CO₂]_a for 48 h after fertilization
- (C2)- Plants kept in a chamber with elevated atmosphere [CO₂]_e, 663 ppm for 48 h after fertilization.

Chlorophyll-*a* fluorescence was measured in one leaf per individuals per replicate, for both populations on mature, fully expanded leaves of the 3rd node that were dark-adapted for 30 min. Readings were taken between 8 and 9 am with a 1 s 1500 μmol m⁻² s⁻¹ pulse using a Handy Pea Hansatech system. Instantaneous parameters (including PI) were obtained from phenomenological energy flow, as well as from data for evaluating the polyphasic fluorescence transient (*OJIP*), relative fluorescence kinetics ($V_t = (F_t - F_o)/(F_m - F_o)$) and analysis of the kinetics between F_o and F_j ($W_t = (F_t - F_o)/(F_j - F_o)$) [35].

Statistical analyses were performed with Bioestat 5.0 software, applying one-way ANOVA, and Tukey test for comparison of means. When variances were unequal, the non-parametric Kruskal-Wallis and Dunnett tests were used for the comparison of means ($p=0.05$).

Results

Fertilization as well as CO₂ concentrations significantly influenced the chlorophyll fluorescence parameters (F_o , F_m , F_v/F_m and PI) in young plants of both the Pantanal (P) and the Inocência (I) populations of *C. pachystachya*. Except for fluorescence area (Fig. 1d), populations did not differ from each other within the same treatment (Fig. 1 and Table 1). The means for (F_o) were highest in plants grown in the G2 (506 and 502), and lowest (357 and 359) in the C2 treatment (Table 1). In both populations (Fig. 1a), fertilization initially

Fig. 1 Comparison between acclimated young plants of *Cecropia pachystachya* (Urticaceae) populations from Pantanal (filled circles) and Inocencia (open circles): Abbreviations for treatments as in Table 1. ** $P<0.01$ and * $P<0.05$

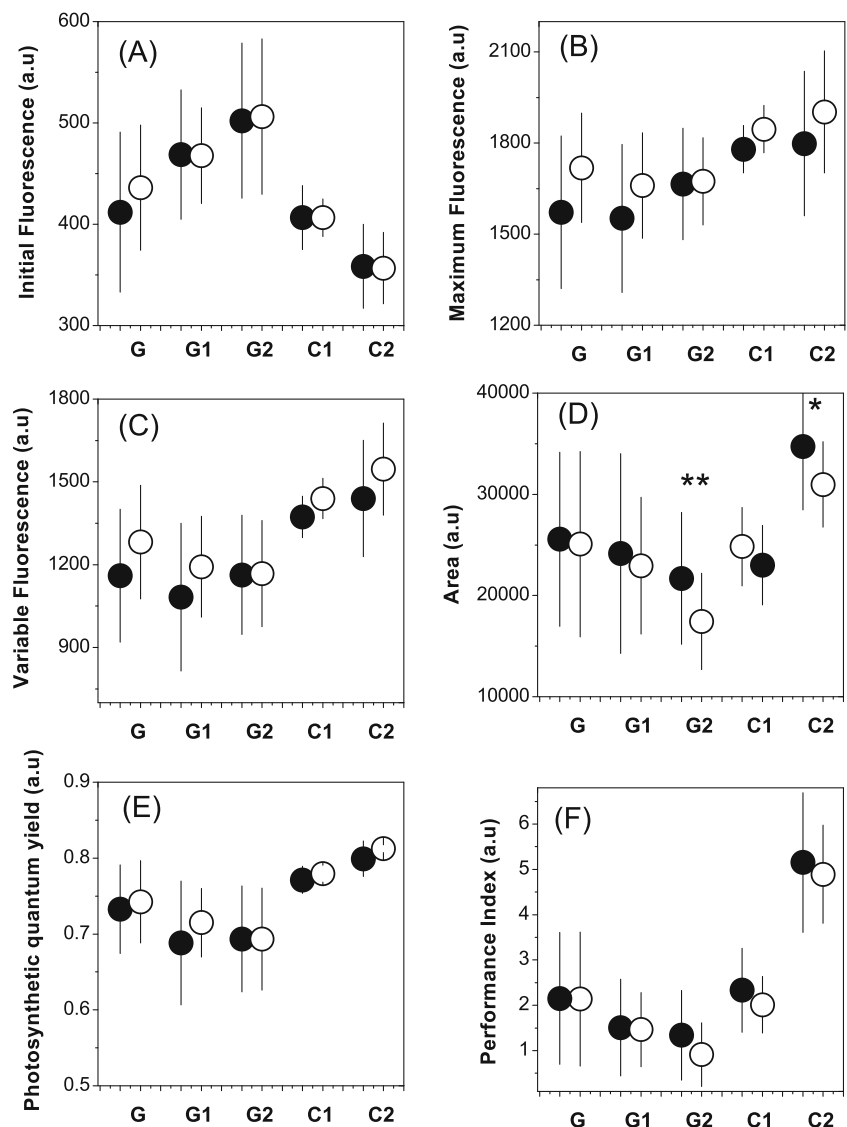


Table 1 Chlorophyll-*a* fluorescence of acclimated young plants of *Cecropia pachystachya* (Urticaceae), from Pantanal (P) and Inocencia (I) populations

Conditions	Fo	Fm	Fv	Fv/Fm	PI
PG(C)	412 b	1572 b	1160 cb	0.73 bc	2.15 b
PG1	469 a	1552 b	1083 c	0.69 c	1.51 b
PG2	503 a	1665 ab	1163 cb	0.69 c	1.34 b
PC1	407 b	1780 a	1373 ab	0.77 ac	2.33 b
PC2	359 b	1798 a	1440 a	0.80 a	5.15 a
IG(C)	436 ab	1718 ab	1282 bc	0.74 bc	2.14 b
IG1	468 a	1660 b	1193 c	0.71 c	1.46 bc
IG2	506 a	1674 b	1168 c	0.69 c	0.91 c
IC1	407 bc	1846 a	1440 ab	0.78 ab	2.01 b
IC2	357 c	1902 a	1546 a	0.81 a	4.89 a

Acclimated Control (C), plants kept in the greenhouse after fertilization for 24 h (G1) and 48 h (G2), plants kept in a chamber with atmospheric CO₂ concentration (C1) and under CO₂ enrichment (C2). Values in column followed by same letter, for each variable fluorescence, within each population, did not significantly differ from each other ($p>0.05$)

led to an increase in (Fo) while [CO₂]_e were responsible for a significant reduction in (Fo).

(Fm) varied significantly among treatments in both populations. Mean values were highest in treatments with [CO₂]_e (1798 and 1902) and lowest (1552 and 1660) in the G1 treatment (means for populations [P] and [I], respectively).

(Fm), (Fv) and (Fv/Fm) (Fig. 1b, c and e) did not differ between populations 48 h after fertilization, while fluorescence area was highest in both treatments with [CO₂]_e in the C2 treatment (Fig. 1d). (Fv) differed between treatments, with the smallest means measured in the G1 treatment for population (P), and in the G2 treatment for population (I) (Table 1).

For PSII photochemical quantum efficiency (Table 1 and Fig. 1d), means obtained under [CO₂]_e were significantly higher than in other treatments (0.8 and 0.81). Changes in fluorescence between populations (Fig. 1d) were very subtle; however, it was evident for both populations that [CO₂]_e was related to an increase in photochemical efficiency and lower deviation around the mean.

(PI) best expressed the differences in responses between treatments (Table 1), with means significantly higher (5.15 and 4.89) for doubled CO₂ concentrations (Fig. 1). Although averages varied significantly between treatments, the responses of both populations were similar (Fig. 1f). The distinct responses in G2 and C2 treatments reflected the new adjustment of plants to increasingly stressful conditions.

Means differed between all variables by specific flow except for ET_o/CS in population (P) and RC/CS_o in plants of both populations (Table 2). The two populations did not significantly differ within the same treatment, although there was a general reduction of intensity of DIO/CS between plants kept in the chamber and those kept in the greenhouse (Fig. 2).

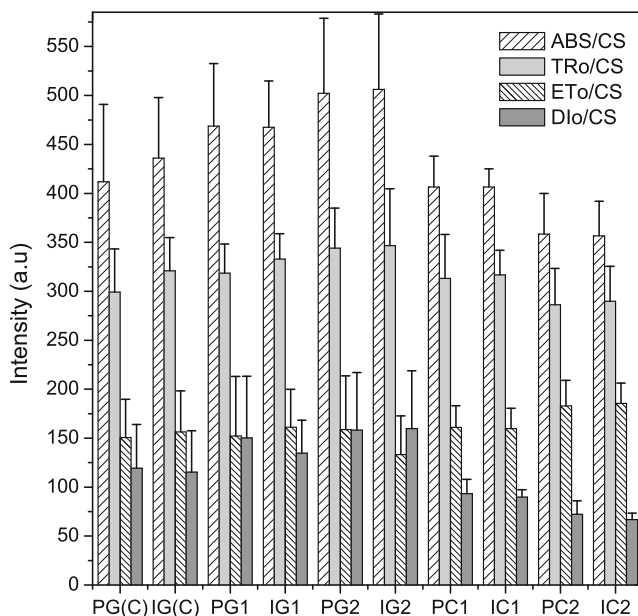
Table 2 Cross section parameters of chlorophyll-*a* fluorescence of acclimated young plants of *Cecropia pachystachya* (Urticaceae) from Pantanal (P) and Inocencia (I) populations

Conditions	TR _o /CS	ET _o /CS	DIO/CS	RC/CS _o	RC/CS _m
PG(C)	299 b	151 a	113 ac	217 a	865 bc
PG1	319 b	153 a	150 b	221 a	766 c
PG2	344 a	159 a	158 ab	225 a	774 bc
PC1	313 b	161 a	93 cd	234 a	1033 ab
PC2	286 b	183 a	72 d	245 a	1233 a
IG(C)	321 ab	156 ab	115 ab	233 a	950 ab
IG1	333 a	161 ab	135 a	229 a	828 b
IG2	346 a	133 b	160 a	221 a	755 b
IC1	317 ab	160 ab	90 bc	217 a	988 ab
IC2	290 b	185 a	67 c	224 a	1199 a

Abbreviations for treatments as in Table 1. Values in column followed by same letter, for each variable fluorescence, within each population, did not significantly differ from each other ($p>0.05$)

Compared to their respective controls, the reduction of DIO/CS was 35.89 % in population (P) and 41.89 % in population (I). In general, the highest means of ABS/CS, TR_o/CS and DIO/CS were measured in the G2 treatment, while C2 produced the lowest values for these variables and an elevation of RC/CS_m.

The chlorophyll-*a* fluorescence kinetics in acclimated plants of populations (P) and (I) (Figs. 3 and 4), did not differ between treatments within a population (Fig. 3a and b) or between populations in the same treatments (Fig. 3c and d).

**Fig. 2** Phenomenological variables of chlorophyll-*a* fluorescence in acclimated young plants of *Cecropia pachystachya* (Urticaceae) from Pantanal (P) and Inocencia (I) populations. Abbreviations for treatments as in Table 1

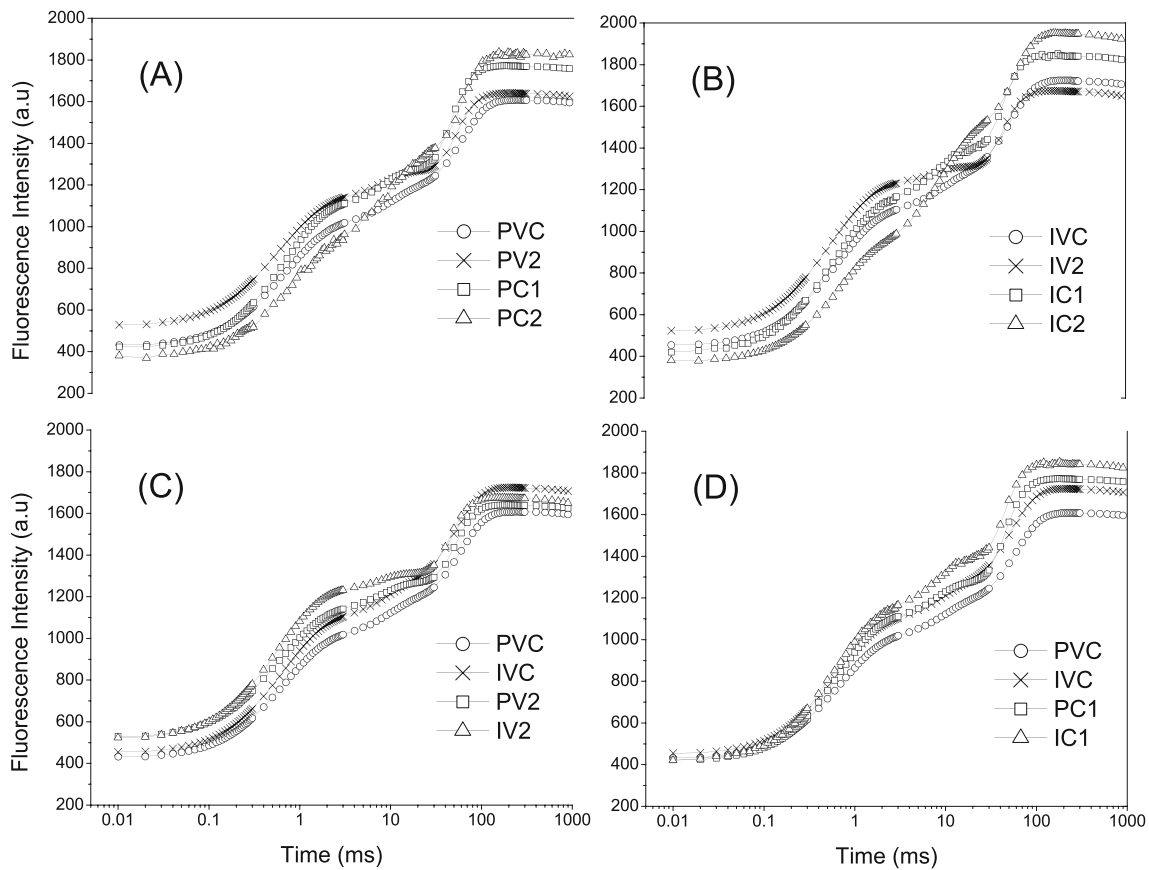


Fig. 3 Chlorophyll-*a* fluorescence kinetics in leaves from acclimated young plants of *Cecropia pachystachya* (Urticaceae) from Pantanal (P) and Inocencia (I) populations. Abbreviations for treatments as in Table 1

The sigmoidicity of the curves was not reduced in any of the treatments, but the curves of induction at 60 ms deviated from those of the control treatment (Fig. 3a and b). The reversal in fluorescence intensity was most evident 48 h after fertilization (PG2 and IG2) when plants were submitted to [CO₂]_e (PC2 and IC2), in this case after around 10 ms. Before this period (5 ms), the curves between populations in the same treatment were almost parallel (Fig. 4).

The *OJIP* analyses showed changes between *O*-*J*, *J*-*I* and *I*-*P* steps, which differed between treatments (Fig. 5a and b) and between populations in G2 treatments (Fig. 5c).

In the *O*-*J* interval, lower intensity of fluorescence was observed in IC2 and PC2. No inflection occurred between curves (Fig. 6a) During the *J*-*I* interval, the PGC curve showed the lowest intensity and differed from the other curves, except for those of IGC and PC1. Here, the intersections of PC2 and IC2 curves between 5 and 15 ms, stand out, with IC2 outperforming all other treatments (Fig. 5b).

In the *I*-*P* range the highest fluorescence intensities were measured for IC2, IC1 and PC2. The fluorescence curves also differed between populations in the same treatment, except for PG2 and IG2 (Fig. 5c).

Differences in relative fluorescence kinetics (*Vt*) were observed in the *J*-*I* phase between plants maintained in the

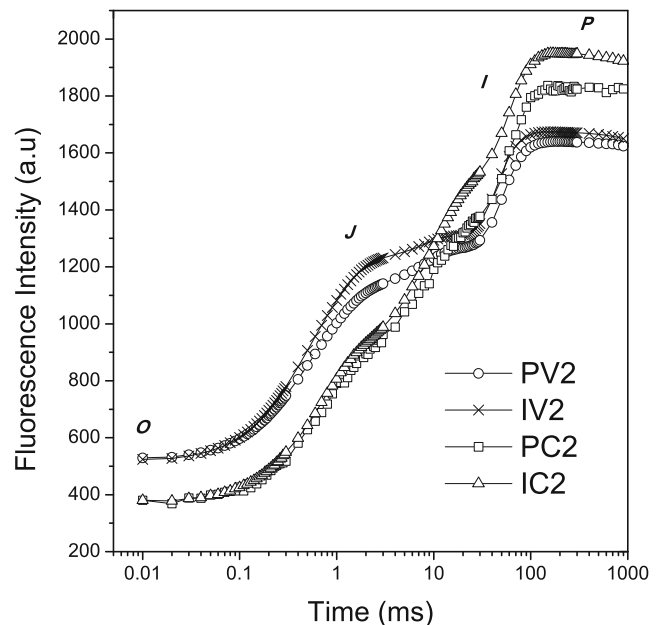
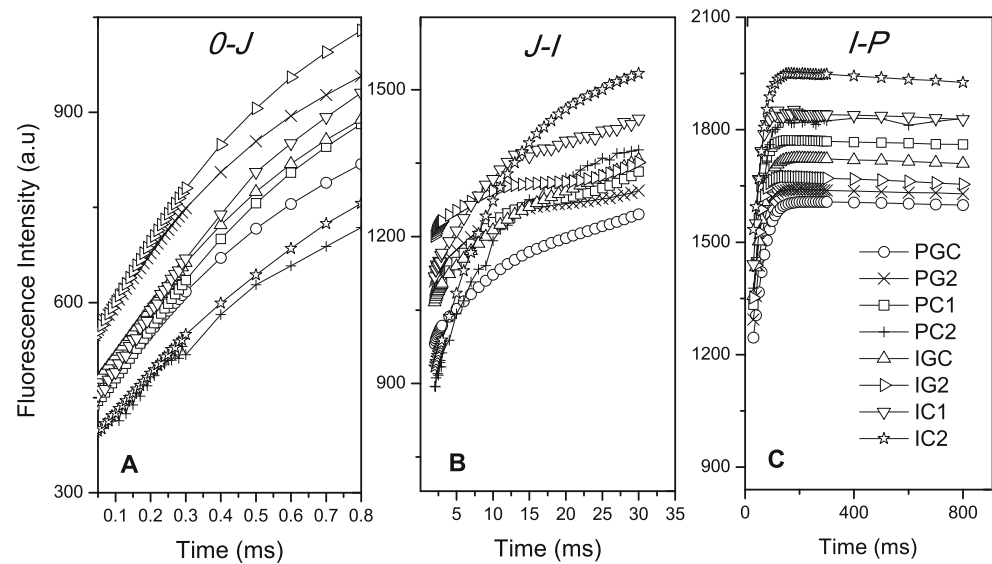


Fig. 4 Changes of the fluorescence kinetics, *O*-*J*-*I*-*P*, measured on *Cecropia pachystachya* leaves, averages of induction curves to compare plants 48 h after fertilization (PG2 and IG2) with plants submitted to CO₂ enrichment (PC2 and IC2)

Fig. 5 Linear chlorophyll-*a* fluorescence induction transients, *O*-*J*-*I*-*P* analyses of *O*-*J*, *J*-*I* and *I*-*P* steps in leaves from acclimated young plants of *Cecropia pachystachya* (Urticaceae) from Pantanal (P) and Inocencia (I) populations. Abbreviations for treatments as in Table 1



greenhouse for 24 h after fertilization (G2) and those kept in $[\text{CO}_2]_e$ (C2), both from population (I) (Fig. 6a). The analysis of kinetics between F_0 and F_j (W_t) showed no *K* band during the *O*-*J* phase (Fig. 6b).

Discussion

In general, the results obtained after fertilization reinstatement and $[\text{CO}_2]_e$ did not differ between populations of *C. pachystachya*, maybe related to the similarity of the location of naturally occurring plants. Although regarded as a widely distributed species [23], *C. pachystachya* mainly occurs in the lowlands and is associated to wetter soil, conditions

from which the seedlings used in this study originated. Local conditions influence the adaptive potential of populations [14, 32], such that functional responses of PSII in *C. pachystachya* can be expected to differ between populations from different environments. The morphological and physiological characteristics of tree species are strongly influenced by ecological factors and environmental development [31]. Lynn and Waldren [21] described different responses in photosynthetic rates between plants from terrestrial and wetland populations of *Ranunculus repens* (L.), when subjected to different water conditions. These authors linked physiological responses to morphological differences of leaves (mainly stomatal), associated with environmental differences [31]. Variations in stress response are common in natural populations, suggesting a complex adaptive trait that is not only structural but also physiological [29].

In another study, we find that there were no anatomical or morphological differences in the leaves of young plants from both populations, but seeds between 0 and 1 and 5 mm differed in size, proportion and germinability [18].

According to Lemos-Filho et al. [19], chlorophyll fluorescence can be specific to species, populations or progeny, although this does not apply to native tree species when grown in non-stressful conditions. In our study, plants were kept under nutritional stress and were acclimated, a condition dependent on the genetic capacity of the plant to resist stress [17]. However, acclimation had no effect in the populations studied, except on electron transfer in PSII.

Differences in Chl *a* fluorescence after resuming fertilization suggest a new destabilization of acclimated plants that may explain the increase in F_0 and reduction of F_v/F_m and PI. In contrast to our expectations, PSII function was not necessarily optimized immediately after resuming fertilization, resulting in a time lag that exceeded 48 h to elevate the metabolic activity in photosystems.

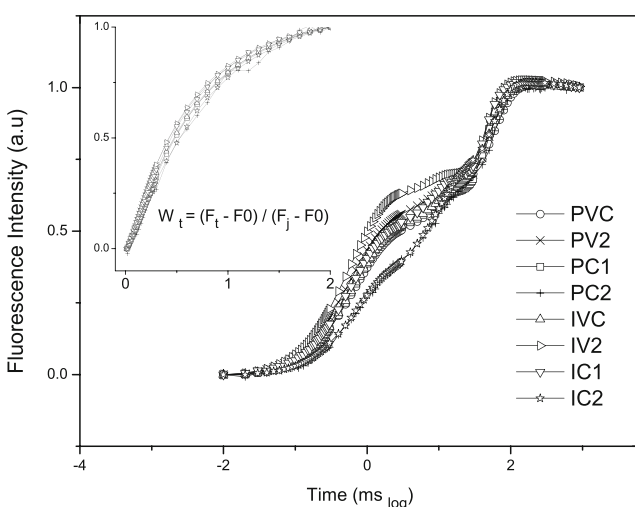


Fig. 6 Relative fluorescence kinetics (V_t) and kinetics between F_0 and F_j (W_t) in leaves from acclimated young plants of *Cecropia pachystachya* (Urticaceae) from Pantanal (P) and Inocencia (I) populations. Abbreviations for treatments as in Table 1

Although the role of nutrients in the photosynthetic process is well described, the mechanisms by which the resumption of fertilization negatively affects PSII quantum efficiency are unclear. Vincentz et al. [38] described the expression of nitrate and nitrite reductase in *Nicotiana plumbaginifolia* (Solanaceae) and found that the availability of metabolites N and C affects the expression of genes associated with the synthesis of these enzymes. According to Wykoff et al. [41], cultures of *Chlamydomonas reinhardtii* (Chlamydomonadaceae) transferred to phosphorus- or potassium-deficient media showed a rapid decline of photosynthetic rates. The phosphorus deficiency reduced O_2 rates to 76 % within 24 h and the photosynthetic rate to 96 % within 48 h without changes in cell viability. These data correspond to the findings of our study, which indicate that nutritional status can very quickly affect the functioning of PSII, suggesting interferences with the enzymatic activity of PSII components. These responses imply the possibility of acclimation to environmental constraints resulting from complex internal control mechanisms mediated by enzyme activity [41, 22].

The reduction in quantum efficiency after fertilization reinforces the idea of reversible damage to PSII. This effect is directly related to the reduced electron transport rate and increased non-photochemical dissipation ([41]; Moraes et al. [25]; [37]). Although F_o elevation and F_v reduction suggest inhibition on the PSII acceptor side [7], no changes to the K band were observed between 0 and 30 ms.

The results of our study support field observations of stress responses in plants, which imply that damage to PSII by reduction or stagnation of growth may be reversible. In general the resumption of plant growth is preceded by a period of stress after transplantation, which gradually decreases with the growth of new roots [33]. The concept of reversible and transient effects is supported by a reduction in F_v/F_m and PI, which can only be counteracted by $[CO_2]_e$. The PI reduction allows inferences about the decrease in photochemical efficiency and biomass accumulation in plants under stress [27].

The fast rise of F_v/F_m and PI values by the $[CO_2]_e$, also as a reversible response, shows the fine control on the PSII supra molecular complex. Changes in $[CO_2]_e$ depend on factors such as seasonality, and affect the PSII functionality [40, 4], in particular the quantum efficiency [6], and change the metabolic balance of leaves [1]. This directly affects the PSII kinases and oxide-reductions, implying important homeostatic changes in the chloroplasts [10] and results in the enhancement of carbon sequestration and biomass [36].

The disturbance caused by the resumption of fertilization (G2) in acclimated plants and the mechanisms by which $[CO_2]_e$ (C2) affect the PSII efficiency can be understood both by chl-*a* specific flux as well as by the Kautsky effect, as indicated by transient fluorescence curves (Figs. 2, 3, 4, 5 and 6). The plants released more energy in G2 (ABS/CS) and the

energy trapped by flux (TRo/CS) and non-photochemical dissipation (Dlo/CS) was also higher. An increase in CO_2 resulted in opposite responses (Fig. 2). Except for TRo/CS, similar results to G2 were described by Contreras-Porcía et al. [8] who studied the responses of desiccation tolerance in *Porphyra columbina* Montagne (Rhodophyta). The reduction of electron transfer rate (ETo/CS) in G2 and the average increase of this variable in the C2 treatment suggest disturbances in G2. The electron transfer in PSII is reduced under Mg^{2+} deficiency [43]. In contrast, $[CO_2]_e$ increases the rate of electron transfer through PSII [15] but also reverses the O_3 inhibitory effects on plant growth [42].

Greater absorption, trapping and non-photochemical energy dissipation, although not as a rule, resulted in a loss of PSII efficiency, whereas a decrease in these parameters was associated with an increase of efficiency with consequent photosynthetic gain. $[CO_2]_e$ increased photosynthetic rate and biomass in fully expanded soybean leaves, although alterations in amino acids and other nitrogen compounds were not detected [1].

It can be assumed that under field conditions, the same responses observed in G2 will be found after planting. The adjustment time may vary e.g. according to the genetic potential of the species, planting conditions and plant health. In heterogeneous plantations with native trees, certain periods of growth stagnation that vary among species will occur even under seemingly favorable conditions. This is known as planting check and may be associated with PAR radiation absorption, photochemical dissipations, and also with interferences detected in electron transport through PSII.

The polyphasic fluorescence kinetics of the three distinct steps *O-J*, *J-I* and *I-P* (Kautsky effect) differed between treatments, but not necessarily between the two populations, except for G2 in the range *I-P* (Figs. 3, 4 and 5). The fluorescence curves of both *C. pachystachya* populations almost overlapped at 5 ms of the *O-J* interval within the same condition. This supports the previous statement that differences between populations associated with gene expression would only become evident under effective stress. The *O-J* phase or thermal phase is significantly affected by stressors such as excessive light, heat, drought or photosynthetic inhibitors that are blocking the flow of electrons between Q_A and the secondary acceptor Q_B (Papageorgiou and [12, 37]; Jedmowski et al. [16]), such as DCMU. In *O-J* only a small fraction of Q_A and Q_B are reduced in PSII [11]. The changes observed during the *J-I* phase suggest interferences with electron transfer between Q_A and Q_B , optimized by CO_2 . This may be related to the induction of the bicarbonate ion in the protein D_1 and D_2 complex [11].

In our study, the behavior of F_o and F_m' (V_t) kinetics suggest a possible optimization of electron transfer on the acceptor side of PSII by CO_2 . These variables show the effects of resumed fertilization and of $[CO_2]_e$, as well as the absence

of changes in normalized curves between F_o and F_j (W_j), which showed no damage to the OEC (Fig. 6).

The effects of resumed fertilization as well as other factors that may influence the flow of electron transfer through the photosystems are important to understand plant responses to stress as well as plant restoration in the post-planting phase. The establishment of plants in reforestation depends on several aspects related to cultivation and planting of seedlings as well as the genetic potential of their progeny.

In conclusion, we suggest that the chlorophyll-*a* fluorescence is not a useful tool in identifying acclimated young plants considering that populations did not differ from each other within the same treatment.

Although changes in fluorescence between populations were very subtle; however, it was evident for both populations that $[CO_2]_e$ affect strongly the chlorophyll-*a* fluorescence parameters in special it was related to an increase in photochemical efficiency. Understanding the physiological responses associated with PSII provides useful information on the potential response of plants to environmental restrictions.

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