Photoinhibition of photosynthesis in *Minquartia guianensis* and *Swietenia macrophylla* inferred by monitoring the initial fluorescence

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Abstract

We assessed the effect of the exposure to full sunlight (5, 35, and 120 min, *i.e.* T_5, T_{35}, and T_{120}) on fluorescence parameters of two young tropical trees, *Swietenia macrophylla*, a gap-demanding species, and *Minquartia guianensis*, a shade tolerant species. Fluorescence parameters (F_0, F_m, F_v/F_m) were recorded before treatments and after the transition to low irradiance (LI). Recovery from photoinhibition (measured as F_v/F_m) was monitored for 24 h at LI. In *Swietenia*, an almost complete restoration of the F_v/F_m values occurred in T_5 and T_{35} plants, when a rise in F_0 was observed after the transition to LI. This was inferred as indicative of dynamic photoinhibition. T_{120} led to a decline in F_0 in *Minquartia*, but not in *Swietenia*. The plants of both species were unable to recovery from photoinhibition after 24 h at LI, when F_0 declined or remained unchanged. This was interpreted as indicative of chronic photoinhibition. Compared with *Swietenia*, *Minquartia* was more susceptible to photoinhibition, as indicated by lower F_v/F_m values.

Additional key words: Amazonia; chlororespiration; chronic photoinhibition; dynamic photoinhibition; photodamage; photoprotection.

Introduction

Photon energy is essential for plant growth and development but an excessive irradiation may be harmful to plants and cause photoinhibition or the slowly reversible decline of photosynthesis (Long *et al.* 1994). In the forest floor tree species respond differently to photon availability. Shade tolerant species, like *Minquartia guianensis*, comprise more than 85 % of forest tree species and are able to grow at very low irradiance (LI), less than 2 % of full sunlight (Marenco and Vieira 2005), but they become photoinhibited when suddenly exposed to full sunlight. On the other hand gap-demanding species developed on sunny environments posses not only a higher photosynthetic capacity (Marenco *et al.* 2001), but also a higher capacity for a rapid increase of energy dissipation in the xanthophyll cycle (Demmig-Adams and Adams 1994), which leads to a lower net damage of photosystem 2 (PS2).

M. guianensis Aubl. (Olacaceae) is a canopy tree (grows up to about 30 m tall), has a dark grayish-brown, hard, heavy, and very durable wood. It grows well in lowland forests with an annual rainfall of 2–4 m, but its seedlings are unable to regenerate in open fields. *Minquartia* has a very irregular trunk, deeply fluted, and its timber is very resistant to decay, termite attack, and other injuries caused by wood-destroying organism. For this reason wood of this species has many uses in timber industry including railroad sleepers, fence posts, poles, flooring and planking on bridge construction (Hunter 1991). The high demand for timber of this species has contributed to its devastation in many places. Its seedlings are shade tolerant with a rather low respiration and photosynthetic rates (Marenco and Vieira 2005).

Swietenia macrophylla King (Meliaceae) is an intermediate species in the successional stage. Its wood is one of most valuable in the world. It occurs in low density in natural forests and requires large openings and usually grows well in open field (Marenco *et al.* 2001).

Irrespective of their succession status, shade leaves

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Abbreviations: F_m − maximal fluorescence; F_0 − initial fluorescence; F_v/F_m − potential maximum quantum yield of photosystem 2; HI − high irradiance; LHC − light-harvesting complex; LI − low irradiance; NPQ − non-photochemical quenching; OEC − oxygen evolving complex; P680 − reaction centre of PS2; PS2 − photosystem 2; Q_A − plastoquinone; q_E − energy-dependent quenching; q_I − photoinhibitory quenching; q_T − state-transition quenching.
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are more susceptible to photoinhibition than sun leaves (Aro *et al.* 1993a). However, the response to irradiance is affected by the succession traits to which a particular species belongs. Thus, in comparison with *Acer mono* (shade tolerant), *Betula platyphylla* (shade intolerant) was more photoinhibited when plants were grown at 5 % full sunlight than at higher irradiance (Kitao *et al.* 2000). The exposure of intact leaves to strong irradiance may lower the maximal fluorescence, F_m (Powles and Björkman 1982). Thus, a decline in the F_v/F_m ratio from its maximum, around 0.83 in dark-adapted and non-stressed leaves, may be taken as an indicator of photoinhibition.

Decline in F_v/F_m may be caused by either a rise in the initial fluorescence (F_0) or a decline in F_m. A rise in F_0 has been associated with a rapidly reversible damage to the D_1 protein of PS2 (Franklin *et al.* 1992), whereas a decline in F_m is often associated with the protective interconversion of violaxanthin to zeaxanthin, in two independent reactions (the xanthophyll cycle), which leads to non-radiative (non-photochemical quenching, NPQ) energy dissipation (Demmig-Adams and Adams 1992). According to the relaxation kinetics, NPQ can be divided into three components q_E, q_T, and q_I. The energy-dependent quenching (q_E) has a fast relaxation kinetic (few minutes), whereas q_I (photoinhibitory quenching) has the slowest relaxation time [h]. The second component of NPQ, q_T (state-transition quenching) relaxes in tens of minutes but does not appear to be important in higher plants (Müller *et al.* 2001).

The role of q_E, closely associated to the xanthophyll cycle, in energy dissipation is well-documented. Nevertheless, the actual biophysical mechanism of $^1Chl^*$ de-excitation remains to be elucidated. Xanthophylls may be involved directly (*i.e.* transfer of energy from $^1Chl^*$ to xanthophylls, which dissipates excitation energy as heat) or indirectly (*i.e.* xanthophyll acting as regulator of the light-harvesting complex, LHC, switching them from light-harvesting to energy dissipating complexes - Müller *et al.* 2001). Irrespective of the molecular mechanism, a decline in F_m is always observed when $^1Chl^*$ de-excitation involves non-photochemical quenching. Many mechanistic studies have shown that the exposure to an excessive irradiance leads to impairment of electron transport through PS2 with the involvement of the D_1 protein (the primary target for light stress) or other protein subunits (Aro *et al.* 1993b). The specific lesions caused to the PS2 reaction centre may be inferred by observing the fluorescence signal, particularly F_0, after irradiating the leaf and subsequent monitoring F_0 kinetic during recovery. Nevertheless, the mechanisms involved in the F_0 response to high irradiance (HI) are still to be elucidated.

Even though photoinhibition studies have intensified over the past decade, very little is known about the effect of photoinhibition on species native to the Amazon forest. In this work we use the fluorescence signal to assess how the tropical trees *S. macrophylla* (gap-dependent) and *M. guianensis* (shade tolerant) respond to the photoinhibitory irradiance for varying periods of time. An emphasis is given on the F_0 signal in order to infer about the occurrence of dynamic and chronic photoinhibition in irradiance-stressed plants.

Materials and methods

Study site and species: Seedlings of *Minquartia* (three-years-old), and *Swietenia* (one-year-old) were grown in plastic bags (3 000 cm^3) beneath a small natural forest located at Manaus, AM, Brazil. We used plants of different ages but similar sizes (approximately 0.3-m tall) at the beginning of the experiment. The substrate used for plant growth was soil from a natural forest collected from the first 0.2-m of soil surface. During the growing period, irradiance beneath the canopy of adult trees was about 10–20 μmol $m^{-2} s^{-1}$ for *Minquartia* and 80–100 μmol $m^{-2} s^{-1}$ for *Swietenia* (this species does not grow well at LI).

Irradiance and fluorescence parameters: Irradiance was recorded with a quantum sensor (*Li-191 SA*, *Li-Cor*, Lincoln, NE, USA) connected to a data-logger (*Li-1000*; *Li-Cor*). Photon exposure (fluence) was calculated as the product of irradiance by exposure time. Fluorescence parameters (F_0, F_m, F_v/F_m) were determined on intact leaves using a portable fluorometer (*PEA*, *MK2*, *9600*, *Hansatech*, Norfolk, UK). Fluorescence was induced given a saturation pulse (650 nm) of 3 000 μmol $m^{-2} s^{-1}$ on 4-mm diameter foliar discs.

To assess the photoinhibitory effect, we exposed the studied species on clear days to full sunlight (1 800–2 000 μmol $m^{-2} s^{-1}$) for 5, 35, and 120 min (hereafter referred to as treatments T_5, T_{35}, and T_{120}, respectively). Control plants were kept at LI during the experiment. After irradiance treatments, recovery from photoinhibition (measured as the F_v/F_m ratio) at LI (10–20 μmol $m^{-2} s^{-1}$) was monitored at 0.25, 0.50, 1, 2, 3, 5, and 24 h on 15-min dark-adapted leaves. Data were subjected to analysis of variance (ANOVA). A Tukey test ($p<0.05$) was used to compare means among treatments.

Results

Effect of irradiation on fluorescence parameters: F_0 rose in plants exposed to full sunlight for 5 min (T_5) or 35 min (T_{35}) up to about 15 % in *Swietenia* and 2 % in *Minquartia* (Fig. 1*A,B*). On the contrary, the exposure to full sunlight for 120 min (T_{120}) lowered F_0 in *Minquartia* but had little or no effect on *Swietenia* (Fig. 1*C*). In all treatments, irradiated seedlings showed a reduction in F_m closely correlated with the exposure time. In comparison with untreated plants, the reduction in F_m was greater in *Minquartia* than in *Swietenia*, 70 and 60 % at T_{120}, respectively (Fig. 1*F*). Compared with *Swietenia*, F_m and F_v/F_m decreased more drastically in *Minquartia*. In both species, only a slight reduction (5–8 %) of F_v/F_m values was observed when plants were exposed to T_5. However, T_{120} greatly reduced the F_v/F_m ratio, by 58 % in *Minquartia* and by 46 % in *Swietenia*.

Recovery from photoinhibition: In *Minquartia*, F_0 rose consistently during the first 2 h of the recovery period, then declined (in T_5) or levelled off (in T_{35}) (Fig. 1*A,B*). In *Swietenia*, however, a steep rise in F_0 was observed at the beginning of the recovery period in T_5 and T_{35} plants, whereas F_0 remained nearly constant (p>0.05) in T_{120}. In both species, F_m increased during recovery from photoinhibition, but in T_{35} and T_{120} plants F_m did not restore completely to the F_m values observed in control plants (Fig. 1*D-F*). The F_v/F_m ratio showed the same trend of maximal fluorescence. It declined in proportion with the exposure time to full sunlight. The effect of irradiation was more pronounced in *Minquartia*. The lack of recovery to pre-dawn F_v/F_m values of control plants clearly indicated the occurrence of chronic photoinhibition of PS2, particularly at T_{120}.

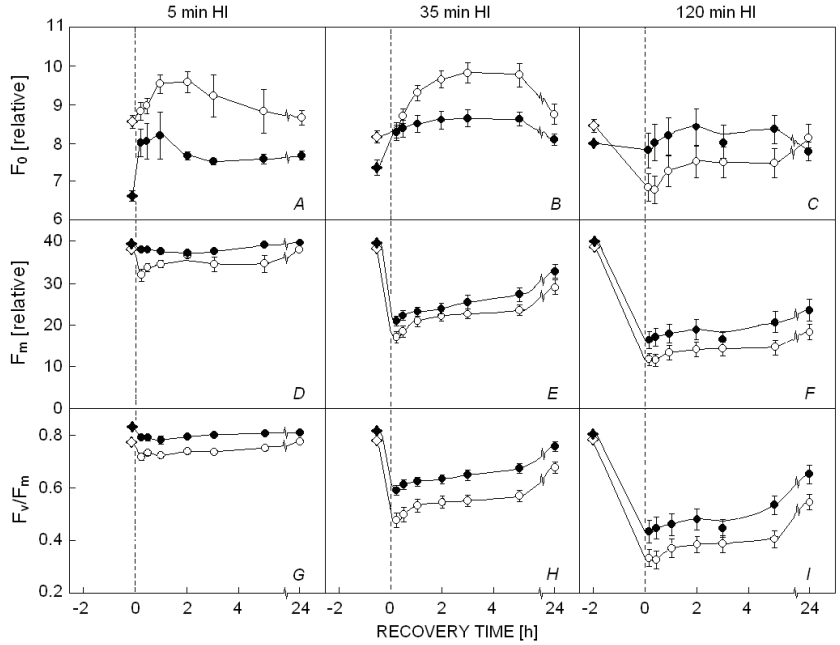

Fig. 1. Effect of time of exposure to full sunlight on fluorescence parameters in *Minquartia* (○) and *Swietenia* (●). Means of five plants and three leaves per plant. Standard error is shown when larger than the symbol. The diamonds (*left side of dashed-line*) indicate fluorescence values on dark-adapted leaves before sunlight (HI) exposure. The vertical dashed line indicates the beginning of recovery at low irradiance after the exposure to HI.

Effect of photon exposure on fluorescence parameters: In *Minquartia*, F_0 rose in plants exposed to fluences of 0–0.5 mol(photon) m^{-2} and in *Swietenia* F_o increased at fluences of 0–3 mol m^{-2}. After that, little reduction in F_0 was observed at higher photon exposure in *Swietenia*, whereas a consistent decline in F_0 was observed in *Minquartia* (Fig. 2). In both species, F_m values deeply decreased at fluences of 0–3 mol m^{-2}, then it decreased at a lower rate (Fig. 2). The F_v/F_m ratio declined as photon exposure increased. Lower F_v/F_m values were observed in *Minquartia* (0.4) than in *Swietenia* (0.5) at the highest irradiance stress (Fig. 2).

Discussion

Effect of irradiation on fluorescence parameters: The rise in F_0 observed after T_5 and T_{35} (Fig. 1*A-C*) is consistent with results obtained by Demmig-Adams *et al.* (1989) or Xu and Wu (1996). The irradiation of dark-adapted leaves may result in either a rise (at low photon exposure) of F_0 due to the inhibition of electron transfer from Q_A to Q_B or a decrease in F_0 after a high photon exposure (Demmig *et al.* 1987, Demmig-Adams *et al.* 1989). The D_1 protein of PS2 is the primary target of photoinhibition (Aro *et al.* 1993a) and thus a partial inactivation of the PS2 population may trigger a rise in F_0 (Demmig *et al.* 1987, Gilmore *et al.* 1996). With respect to leaf life span, we found that *Swietenia*, a species with shorter leaf lifetime than *Minquartia*, was less prone to photoinhibition as predicted by Osmond (1994). However, our results contradict those reported by Lovelock *et al.* (1998), who found that shade tolerant trees with longer leaf lifetimes dissipate more energy *via* photochemical mechanisms. This suggests that other factors in addition to leaf longevity may determine the susceptibility of a given species to photoinhibition, including leaf resistance to damage caused by ultraviolet radiation (Krause *et al.* 2003).

The decline in F_0 observed in plants exposed to full sunlight for 2 h (Fig. 1*C*) may be ascribed to damage to the D_1 protein followed by the activation of the xanthophyll cycle, which increased non-radiative energy dissipation (Demmig *et al.* 1987, Gilmore *et al.* 1996). Inactivation of PS2 associated to protein damage can be induced either at the acceptor side (*via* production of singlet oxygen) or the donor side (*via* generation of cation radicals, such as $P680^+$), both mechanisms leading to D_1 protein damage (Aro *et al.* 1993a), but the acceptor side mechanism seems to be more susceptible to photoinhibition than the donor side (Misra *et al.* 1997). Related to *Swietenia*, the effect of irradiance on F_0 was more pronounced in *Minquartia*. This indicates that with respect to fluorescence, the response of plants to irradiance may be species-dependent, which is consistent with the result obtained by others (Hong and Xu 1999, Krause *et al.* 2001). La Porta *et al.* (2004), for example, found that in *Cupressus sempervirens*, F_0 did not decline even after exposing the leaves to HI for one hour.

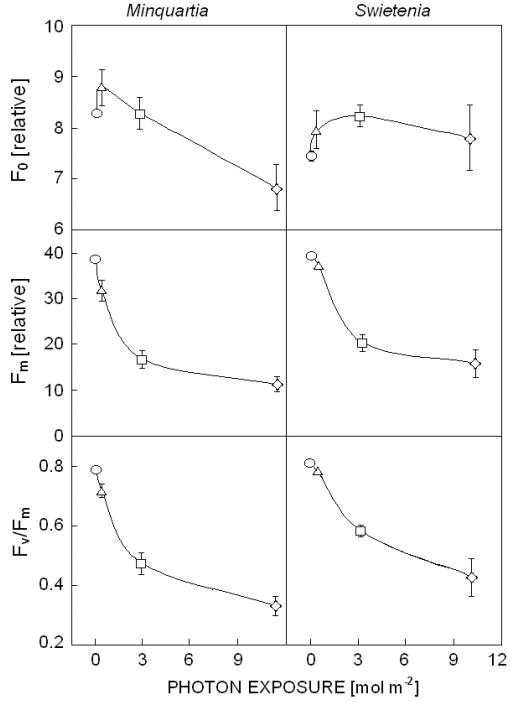

Fig. 2. Effect of photon exposure on fluorescence parameters in *Minquartia* and *Swietenia*. Means of five plants and three leaves per plant. Standard error is shown when larger than the symbol. The symbols denote the exposure time to 0 min or control (circle), 5 min (triangle), 35 min (square), and 120 min (diamond).

At the highest photon exposure (T_{120}), the effect of irradiation on F_0 was lower in *Swietenia* than in *Minquartia*, the shade-tolerant species. Decline in F_0 seems to be related to damage to subunits of the water splitting complex (Bertamini *et al.* 2004), apparently less susceptible to photoinhibition. Thus, we conclude that damage caused to the photosynthetic apparatus was more severe in *Minquartia* that in *Swietenia*. This is consistent with the results of Kitao *et al.* (2000) who observed differences on photoinhibition susceptibility between shade tolerant and shade intolerant species. Moreover, even species within the same succession trait (*e.g.* shade tolerant) may differ on the F_v/F_m response to HI (Castro *et al.* 1995). However, irrespective of the succession stage, shade leaves of tree seedlings acclimate to full-sunlight by similar physiological mechanisms (Krause *et al.* 2004).

A rise in F_0 is an indicative of damage to the D_1 protein of the PS2 reaction centre (Rintamäki *et al.* 1994). It precedes an increase in zeaxanthin content at low and moderate photon exposure (Demmig-Adams *et al.* 1989). On the other hand, a decline in F_0 may be indicative of irreversible damage to the 33-kDa protein of oxygen-evolving complex (OEC 33) in addition to an earlier damage to the D_1 protein (Barber and Andersson 1992). Furthermore, a decline in F_0 may coincide with an increase in zeaxanthin at HI (Demmig-Adams *et al.* 1989). An over-acidification of the lumen (pH < 5) may lead to destabilization of the OEC and consequently to photoinhibition (Kramer *et al.* 1999), which may also lead to a decline in F_0 (Demmig-Adams *et al.* 1989, Xu and Wu 1996).

In T_5, F_m remained nearly constant probably because at low photon exposure zeaxanthin is synthesized only little or not at all (Demmig-Adams *et al.* 1989), thereby leading to nil or very little non-radiative energy dissipation. It cannot be ruled out, however, that the fast relaxation of the energy dependent quenching (q_E) (Müller *et al.*

2001) may also explain why little change in F_m was observed in T_5. Decline in F_m at a high photon exposure (T_{35}, T_{120}) can initially be attributed to the photoprotective activation of q_E (related to the xanthophyll cycle) (Demmig *et al.* 1987) and then to the photoinhibitory quenching (q_I), which was probably also activated, as the exposure time to HI increased. The rise in F_0 at LI (Fig. 1*A,B*) and the strong decay of F_m at HI (Fig. 1*E,F*) led to a decrease in F_v/F_m in all treatments, particularly in T_{35} and T_{120} plants (Fig. 1*H,I*), consistently with the effect of irradiance on photo-protection and photo-damage, the inactivation of the photosynthetic apparatus.

Regarding NPQ components, q_E has been related to photoprotection *via* the xanthophyll cycle (Demmig-Adams *et al.* 1987) and is well-documented. However, it has been difficult to characterize q_I, since it may be associated to both photoprotection and photodamage (Müller *et al.* 2001), but it probably involves the D_1-protein turnover (Aro *et al.* 1993b). The rise in F_0 probably reflects dynamic photoinactivation of PS2, as the almost complete restoration of F_v/F_m required less than 5 min in both species (T_5) or about 24 h (T_{35} in *Swietenia*) at LI, which is consistent with the results of Hong and Xu (1999). Because a full restoration of F_v/F_m values took several hours we suggest that the D_1 protein repair cycle was involved in the recovery process (Aro *et al.* 1993b).

Recovery from photoinhibition: The increase of F_0 during the recovery phase at LI is contrary to expectations because at LI the amount of reduced plastoquinone (Q_A^-) should decrease (*i.e.* Q_A should become oxidized rather than reduced during incubation at LI). Increase in F_0 during recovery is consistent with non-photochemical (in the dark) reduction of Q_A (Groom *et al.* 1993). This chlororespiratory path probably involves the reduction of plastoquinone (PQ) by NAD(P)H (Peltier and Cournac 2002), which finally may lead to a rise in F_0.

During recovery, the rise in F_0 with time, as observed in T_5 and T_{35} (Fig. 1*A,B*), probably reflects the availability of NAD(P)H in the chloroplast, which may be derived from starch breakdown. Indeed, exogenous NADPH reduces PQ in the dark (Mills *et al.* 1979) leading to an increase in F_0 (Corneille *et al.* 1998). Moreover, if we assume that the rise in F_0 is a reliable indicator of photoinhibitory damage (Kitajima and Butler 1975, Demmig *et al.* 1987), then it seems reasonable to infer that F_0 decay during recovery (Fig. 1*A,B*) represents the reactivation of the population of PS2 reaction centre photo-damaged or inactivated by irradiation. This is consistent with the almost complete restoration of F_v/F_m by the time F_0 had relaxed (Fig. 1*A*, both species, and Fig. 1*B* for *Swietenia*).

Effect of photon exposure on fluorescence parameters: The effect of photon exposure on fluorescence parameters (Fig. 2) is consistent with the photon dosage response proposed by Anderson *et al.* (1997) and confirms that photo-inactivation of PS2 depends on the number of photons absorbed, as suggested by Anderson *et al.* (1998). The decline of F_v/F_m as a function of the photon exposure showed a biphasic trend (Fig. 2), with a fast initial fall, probably related to the photo-protective conversion of violaxanthin into zeaxanthin, followed by a second phase characterized by a slow decline in the F_v/F_m ratio. The second phase is apparently not associated with changes in the zeaxanthin pool (Lichtenthaler *et al.* 1992).

To conclude, in this study we show that by monitoring the minimal fluorescence F_0 following the light-to-dark transition it is possible to discriminate between dynamic and chronic photoinhibition. A rise in F_0 may indicate dynamic photoinhibition, whereas decay in F_0 may denote chronic photoinhibition probably *via* the activation of the photoinhibitory component of non-photochemical quenching (q_I). Chronic photoinhibition may also be observed when F_0 remains unchanged after plant transition to LI. More research is still required to clearly elucidate the mechanisms involved in F_0 signal at the molecular level.

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