INTRODUCTION

Sudden exposure to high light intensity, as it might occur in gaps of tropical forests, may lead to photoinhibition of photosynthesis of saplings and seedlings (Krause & Winter, 1996). Shade tolerant species are more susceptible to photoinhibition than full sunlight-adapted species (Demmig-Adams & Adams, 1992; Kitao et al., 2000a). The term photoinhibition describes the slowly reversible and light-dependent re-
duction of the photochemical efficiency when plants are exposed to light intensities above values that can be used for photochemical reactions (Long et al., 1994). Manwood (Minquartia guianensis Aubl.) and other shade tolerant species have a low capacity for photosynthesis at a saturating light intensity (Marenco & Vieira, 2005) and a low capacity for D1 protein degradation, and can accumulate a high population of non-functional photosystems II (Anderson et al., 1997; Krause et al., 1999). Under sunny conditions, sunlit leaves experience light saturation and the energy of additional photons not used in carbon assimilation may lead to photoinhibition (Choudhury & Behera, 2001; Demmig-Adams & Adams, 2006).

Cloudiness may influence photosynthesis by affecting photon fluence (Graham et al., 2003; Costa & Marenco, 2007). Clouds reduce both the intensity of ultraviolet (UV) irradiance reaching the Earth surface (Madronich et al., 1998) and the vapour pressure deficit, VPD (Gu et al., 1999; Roderick et al., 2001). Photosynthesis tends to be higher at low VPD (Marenco et al., 2006), whereas the efficiency of the PSII may decrease by UV irradiance, particularly in shade-adapted plants (Krause et al., 1999; 2003). Thus, the aim of this study was to determine the effect of cloud cover on photoinduction and fluorescence characteristics of manwood saplings, and the recovery from photoinduction at low light intensity.

**MATERIAL AND METHODS**

Three-year-old and 0.3-m tall saplings of manwood (Minquartia guianensis Aubl., Olacaceae), were grown in plastic bags (3 L) beneath a small natural forest located in Manaus, AM, Brazil (03°05' S, 59°59' W). The substrate consisted of soil from a natural forest collected from the first 20-cm layer (pH 5.5 and clayey texture). During the growing period, plants were watered daily. The maximum irradiance beneath the canopy of adult trees was about 20 μmol m⁻² s⁻¹ at midday.

The initial (the signal emitted when the PSII reaction centers are open, F₀) and maximum fluorescence (the signal emitted when all the PSII reaction centers are closed, Fₘ) were determined from 12 h dark-adapted leaves of non-stressed plants. Plants were exposed to full irradiance on clear days or under overcast conditions. On clear days, they were exposed to 10 min (T₁₀), 45 min (T₄₅), and 90 min (T₉₀), whereas on cloudy days for 120 min (T₁₂₀), 300 min (T₃₀₀), and 420 min (T₄₂₀). Control plants were kept at low irradiance (10 to 20 μmol m⁻² s⁻¹ or in the dark at night). Following irradiance treatments, recovery from photoinhibition (measured as the Fₐ/Fₘ ratio) at low light (10 - 20 μmol m⁻² s⁻¹ or in the dark, at night) was monitored at 0.25, 0.50, 1, 2, 3, 5, and 48 h on 15-min dark-adapted leaves.

Photosynthetic photon flux density (PFD) was measured with a quantum sensor (LI-191 SA, Li-Cor, Lincoln, NE, USA) connected to datalogger (LI-1000; Li-Cor). Fluence (mol m⁻²) was calculated as the product of irradiance and time of illumination. Data were analysed using the standard error of means.

**RESULTS AND DISCUSSION**

In comparison with control plants kept at low light, F₀ increased (28%) with photon fluence in saplings subjected to irradiance treatments on cloudy days (Figure 1A). On clear days, however, F₀ was unaffected by irradiance, except for a sharp rise (21%) during the first 10 min of exposure (0.8 mol (photon) m⁻²) to full sunlight (Figure 1A). The rise in F₀ could be a result of any of the following reasons: (1) a functional dissociation of the antenna complex from the PSII reaction center, such as that occurring during heat damage (Armond et al., 1978; Kitao et al., 2000b); (2) Damage to the D1 protein of the PSII reaction center, as impairment of electron transport from QA to QB may result in a rise in F₀ (Gilmore et al., 1996), and (3) Chlororespiration, a nonphotochemical reduction of QA by reducing equivalents supplied in the dark from a stromal pool of NAD(P)H (Peltier & Cournac, 2002).

The first hypothesis does not appear to be plausible to explain the observed rise in F₀ on cloudy days because leaf temperature is often low under cloud cover. The impairment of electron transport from QA to QB due to D1 protein damage is a reasonable explanation for the increase in F₀, because damage to the D1 protein may occur at any light intensity (Tyystjärvi & Aro, 1996). Finally, the effect of chlororespiration cannot be ruled out, as the addition of exogenous NAD(P)H to chloroplasts induces an increase in F₀ as a result of electron donation to QA (Mills et al., 1979; Cornelle et al., 1998). This is an attractive hypothesis as plastoquinones may remain reduced in the dark for...
several hours following a period of illumination (Groom et al., 1993). Changes in $F_o$ in plants subjected to high irradiance are similar to those observed by Dias & Marenco (2006; 2007). They explained the constancy or decrease in $F_o$ under full sunlight on the ground of a severe damage to the photochemical apparatus, for example damage to the water splitting complex of the PSII reaction center at high light intensities. Increasing photon fluence exacerbates photoinhibition due to damage to proteins of the PSII reaction center, particularly the D1 protein and under prolonged light exposure subunits of the oxygen evolving complex are also affected (Bertamini et al., 2004). Plants transferred from deep shade to full sunlight had lower growth rates than those switched from full shade to partially shade conditions because of PSII damage in the open (Oberbauer & Strain, 1985). These authors suggest that in the event of a large treefall gap in a dense forest, understory plants may require a substantial period of acclimation before they respond to an increase in irradiance.

Compared with control plants, $F_m$ always declined after the exposure to irradiance in both light environments (Figure 1B), but the reduction in $F_m$ was greater on sunny days than under cloudy conditions. The decrease in $F_m$ can mainly be attributed to damage to the D1 protein because the pool of xanthophyll pigments, involved in the xanthophyll cycle is rather low in shade-adapted plants (Demmig-Adams & Adams, 1992; 1996). Although there is a positive correlation between the extent of photoinhibition and the amount of zeaxanthin formed during plant exposure to high irradiance (Thiele et al., 1998), D1 protein inactivation is probably the prevailing mechanism leading to photoinhibition in understory shade-acclimated leaves abruptly exposed to full sunlight when new gaps open up (Mulkey & Pearcy, 1992). Cloudiness in this study reduced the effect of full sunlight on $F_m$ at high fluences (Figure 1B), perhaps by reducing the amount of UV radiation reaching the plant (Madronich et al., 1998), as UV radiation exacerbates the photoinhibitory effect of solar radiation (Krause et al., 1999; 2003).

The $F_v/F_m$ ratio declined with fluence of photons in all treatments, with lower values being observed in plants exposed to light on clear days (Figure 1C). The fall in $F_v/F_m$ occurred irrespective of the trend followed by $F_o$, indicating that the $F_v/F_m$ ratio was determined primarily by $F_m$ values. Thus, the longer the ex-
posure time to full sunlight the greater the decrease in the potential photochemical efficiency. The $F_v/F_m$ ratio fell 54% in saplings submitted to $T_m$ on sunny days; that is, in plants exposed to a fluence of 9.7 mol m$^{-2}$ (Figure 1C). However, a lower decrease in $F_v/F_m$ (46%) was observed in plants subjected to a similar fluence (9 mol m$^{-2}$, $T_{420}$) on cloudy days. Reduction of the $F_v/F_m$ ratio, as observed in this study after plant exposure to high light intensity, is a well-documented phenomenon and is a measure of the decline of the potential maximum quantum yield of PSII (Björkman & Demmig, 1987; Genty et al., 1989). Indeed, a decline in $F_v/F_m$ suggests that the integrity of the PSII was altered, and indicates photoinhibition of photosynthesis (Long et al., 1994).

For a given intensity of irradiance reaching the leaf surface, $F_v/F_m$ values were lower on clear days than under overcast conditions (Figure 1C). This suggests that in addition to its effect on light attenuation, changes in light quality due to cloudiness may also have a mitigating effect of photoinhibition. The attenuating effect of cloudiness on photoinhibition could be associated with a reduced proportion of UV radiation in the solar spectrum on cloudy days (Madronich et al., 1998; Calbó et al., 2005). Krause et al. (1999) reported that photoinhibition is less severe in UV-decreased sunlight, particularly in shade-adapted plants (Krause et al., 2003). As the extent of photoinhibition depends on the synergistic effects of leaf temperature and irradiance, periods of cloudiness may reduce photoinhibition of plants growing in gaps (Mulkey & Pearcy, 1992). Not surprisingly, it has been reported that on cloudy days, $F_v/F_m$ values may remain unchanged or even increase (Flexas et al., 2000).

Decline in $F_m$ and $F_v/F_m$ with photon fluence can be separated in two phases. The first phase is represented by a sharp drop, particularly in $F_m$, between 0 and 5 mol m$^{-2}$ (Figure 1B-C). At higher fluences, a gradual decline in $F_m$ and $F_v/F_m$ was observed (second phase). In this phase $F_m$ tended to level off. Decline in $F_m$ and $F_v/F_m$ with photon fluence confirms the hypothesis of Anderson et al. (1997), who demonstrated that a reduction of photochemical efficiency depends on the amount of absorbed photons. Thus, photoinactivation of PSII is a light dosage effect with an increase in the amount of light energy absorbed leading to a decline in $F_m$, irrespective of exposure time or light intensity. The precipitously fall (first phase) in $F_m$ from 0 to 3 mol m$^{-2}$ (Figure 1B) may be related to photoprotection processes. This phase probably involves the activation of the xanthophyll cycle whereby the excess of energy is dissipated as heat (Demmig-Adams & Adams, 1992). The second phase (gradual decline in $F_m$ and $F_v/F_m$, Figure 1B-C) is not clearly understood and does not appear to be associated with changes in the zeaxanthin pool (Lichtenthaler et al., 1992).

The content of functional PSII ($y$) was calculated as: $y$ (% of control plants) = 968.20(1/$F_o$ - 1/$F_o^{*}$) (Figure 1D). In this figure, a sharp decline of functional PSII complexes may be observed at low fluences in plants subjected to full irradiance on clear days, but at higher fluences, cloud cover had no clear effects on PSII photoinactivation, perhaps because at higher fluences photoinhibited PSII reaction centers may confer, as they accumulated, additional protection of the remaining but still functional PSII complexes, as suggested by Öquist et al. (1992).

Compared with control plants, $F_o$ increased during the first six hours while recovering from photoinhibition at low light, particularly at low to moderate photon fluence on cloudy days (Figure 2A-B). An increase in $F_o$ indicates a less severe damage to the PSII, and suggests little or no damage to the water splitting complex (Bertamini et al., 2004). Thus, recovery from photoinhibition (restoration of the $F_v/F_m$ values) took less time in irradiance treatments that reached higher $F_o$ values following the light treatments. Recovery from photoinhibition involves the reactivation of the PSII reaction centers involving D$_1$ protein turnover (Aro et al., 1993; Xu & Wu, 1996). Depending on the amount of time required to restore $F_v/F_m$ ratios at low light, photoinhibition can be dynamic or chronic (Osmond, 1994). Dynamic photoinhibition, as observed for $T_m$, has been associated with down-regulation of PSI activity (Osmond, 1994). Chronic photoinhibition, such as observed in this study at high fluences (e.g. $T_{300}$, $T_{420}$), is slowly reversible is characterized by a slow recovery of the maximum potential quantum yield of PSII at low light (Figure 2H-I).

$F_m$ did not restore to values observed in control plants within 48 h at low light (Figure 2D-F). This is not surprising, as recovery from photoinhibition may often take a few days in severely photoinhibited plants (Mulkey & Pearcy, 1992; Dias & Marenco, 2006; 2007). Finally, although photon fluence is the most important factor determining the extent of photoinhibition, cloudiness may alleviate the photoinhibitory effect of irradiance, perhaps because clouds generally reduce surface ultraviolet irradiance, thereby relieving the effect of irradiance on photoinhibition of shade-adapted plants. These results may be important taking into account that the increased rate of deforestation of the Amazonian forest may reduce cloudiness in some parts of the Amazon region (Fearnside, 1995), which could affect photosynthesis and growth of understory shade-acclimated plants suddenly exposed to full sunlight.
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**REFERENCES**


