

LEAF MICRONUTRIENT CONCENTRATIONS AND POTENTIAL PHOTOSYNTHESIS IN *Ochroma pyramidale* ESTABLISHED IN A DEGRADED LAND

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ABSTRACT : In the Brazilian Amazon, large areas of abandoned lands may revert to secondary forest. In the process, pioneer tree species have an important role to restore productivity in old fields and improve environmental conditions. To determine potential photosynthesis (A_{pot}), stomatal conductance (g_s), transpiration (E), and leaf micronutrient concentrations in *Ochroma pyramidale* (Cav. ex Lam.) Urban a study was carried out in the Brazilian Amazon (01° 51' S; 60° 04' W). Photosynthetic parameters were measured at increasing $[CO_2]$, saturating light intensity (1 mmol (photons) $m^{-2} s^{-1}$), and ambient temperature. The rate of electron-transport (J), A_{pot} , and water-use efficiency (WUE) increased consistently at increasing internal CO_2 concentration (C_i). Conversely, increasing $[CO_2]$ decreased g_s , E , and photorespiration (P). At the CO_2 -saturated region of the CO_2 response curve (1.1 mmol (CO_2) mol^{-1} (air)), J was 120 $\mu mol (e) m^{-2} s^{-1}$ and A_{pot} reached up to 24 $\mu mol (CO_2) m^{-2} s^{-1}$. Likewise, at saturating C_i , g_s and E were 30 and 1.4 mmol (H_2O) $m^{-2} s^{-1}$, respectively, and P about 1.5 $\mu mol (CO_2) m^{-2} s^{-1}$. Foliar nutrients were 185, 134, 50, and 10 $\mu mol (element) m^{-2}$ (leaf area) for Fe, Mn, Zn, and Cu, respectively. It was concluded that $[CO_2]$ probably limits light saturated photosynthesis in this site. Furthermore, from a nutritional point of view, the low Fe to Cu ratio (15:1) may reflect nutritional imbalance in *O. pyramidale* at this site.

KEYWORDS: Balsa wood, electron-transport rate, reforestation, stomatal conductance, transpiration, water-use efficiency.

CONCENTRAÇÃO DE MICRONUTRIENTES NAS FOLHAS E FOTOSSÍNTESE POTENCIAL EM *Ochroma pyramidale* ESTABELECIDO NUMA ÁREA DEGRADADA

RESUMO : Extensas áreas abandonadas na Amazônia brasileira reverterem para floresta secundária. Neste processo, as espécies pioneiras desempenham um papel importante na recuperação da produtividade de campos abandonados e na melhoria das condições ambientais. Para determinar a fotossíntese potencial (A_{pot}), condutância estomática (g_s), transpiração (E), and a concentração de micronutrientes na folha em *Ochroma pyramidale* (Cav. ex Lam.) Urban um estudo foi realizado na Amazônia brasileira (01° 51' LS; 60° 04' LO). Os parâmetros

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fotossintéticos foram medidos a níveis crescentes de CO₂ sob luz saturante (1 mmol (fótons) m⁻² s⁻¹) e temperatura ambiente. A taxa de transporte de elétrons (J), A_{pot} e a eficiência no uso d'água (WUE) aumentaram consistentemente com aumentos na concentração interna de CO₂ (C_i). Ao contrário, aumentos na [CO₂] diminuiram g_s , E e a fotorrespiração (P_r). Na região da curva saturada pelo CO₂ (1.1 mmol (CO₂) mol⁻¹(ar)), J e A_{pot} foram 120 μmol (e m⁻²s⁻¹ e 24 μmol (CO₂) m⁻²s⁻¹, respectivamente. Paralelamente, sob C_i saturante, g_s and E foram 30 e 1.4 mmol (H₂O) m⁻²s⁻¹, respectivamente, enquanto que P_r foi em torno de 1.5 μmol (CO₂) m⁻²s⁻¹. Os teores de micronutrientes da folha foram 185, 134, 50 e 10 μmol (elemento) m⁻² (área foliar) para Fe, Mn, Zn e Cu, respectivamente. Foi concluído que a [CO₂] provavelmente limita a fotossíntese sob luz saturante neste sítio. Além disso, do ponto de vista nutricional, a baixa relação ferro:cobre, de 15 para 1, pode indicar um desbalço nutricional em *O. pyramidale* neste sítio.

PALAVRAS-CHAVE: condutância estomática, eficiência no uso d'água, pau-de-balsa, eflorestamento, taxa de transporte de elétrons, transpiração.

INTRODUCTION

Many factors, such as availability of water, carbon dioxide, light, and nutrients affect photosynthesis in several ways. Increases in CO₂ concentrations enhance photosynthetic rates in C₃ plant species. Whereas, compared with C₃ plants, C₄ plants, which are able to concentrate CO₂, show higher photosynthetic rates and are better adapted to tropical regions exposed to higher temperatures and soils with lower water availability. In Brazilian Amazonia, large areas of abandoned lands may revert to secondary forests (Houghton *et al.*, 2000). In this process pioneer tree species have an important role in restoring productivity in old fields and improve environmental conditions. Although pioneer tree species are greatly important to restore soil fertility of degraded lands, little is known about the physiology of pioneer trees in these degraded habitats.

In addition to CO₂, light and temperature, mineral nutrition affects

photosynthesis in several ways. Micronutrients such as iron, manganese, and copper are constituents of proteins involved in electron transfers. For example, Cu is a component of plastocyanin and Fe is a constituent of cytochromes and required for chlorophyll biosynthesis (Beale, 1999), whereas Mn plays a key role in photosynthetic O₂ evolution. Zn, on the other hand, is required as a structural component of several enzymes (*e.g.*, carbonic anhydrase, super oxide dismutase) and for ribosomes synthesis and activity (Marschner, 1995).

Ochroma pyramidale is a pioneer neotropical tree that grows under moist and warm conditions on disturbed lands or as a colonizer of large gaps in the secondary rain forest (Whitmore & Wooi-Khoon, 1983; Kammesheidt, 2000). Its high performance in large gaps has been attributed to a high investment in leaf biomass, which results in a high leaf area ratio (Dalling *et al.*, 1999). Its growth is faster in fertile soils when mean temperature ranges from 25 to 30 °C and

average annual rainfall is from 1500 to about 2000 mm (Francis, 1991; Butterfield, 1996). Besides its fast growth, direct solar radiation (full sun) apparently does not depress photochemical efficiency of *Ochroma* seedlings grown with adequate availability of water and nutrients (Castro *et al.*, 1995). Acclimation of *Ochroma* and other pioneer species to high-light stress under strong radiation has been attributed at least in part to their capability to increase the levels of photoprotective pigments (*e.g.*, *b*-carotene) and the chlorophyll *a/b* ratio (Krause *et al.*, 2001). *Ochroma* may exhibit high photosynthetic rates under ambient CO₂ concentrations (Oberbauer & Strain, 1984; Dalling *et al.*, 1999). However, in degraded landscapes, low availability of nitrogen and magnesium appears to be factors that limit carbon gain in this species (Marengo *et al.*, 2001a). The fast growth of *Ochroma* saplings makes this species potentially useful in reforestation projects on sites with proper management, but other species should be considered for reforestation over large regions on poor soils where plantation maintenance is scarce (Butterfield, 1996). When *Ochroma* is planted in mixtures with late successional, slower-growing species, it may provide shading for the seedlings of the slower-growing species and improve soil fertility by nutrient cycling.

In this study we hypothesized that potential photosynthesis (A_{pot}) (*i.e.*, the light-saturated photosynthesis at CO₂-saturated conditions) and other photosynthetic parameters, as well as the foliar micronutrient content of pioneer tree species are lower when grown in degraded lands than under controlled conditions or in mature forests. Therefore, we determined leaf gas exchange parameters and leaf micronutrient concentrations in *O. pyramidale* grown in a degraded landscape and

compared these values with published data (*e.g.*, Oberbauer & Strain, 1984; Neves *et al.*, 1999). We also compared A_{pot} with photosynthetic rates of C₄ plants, a group of plants with CO₂-concentrating mechanisms. In the absence of gas exchange data from C₄ tree grown in the open, we use C₄ data from herbaceous dicots reported elsewhere (Grodzinski *et al.*, 1998).

MATERIALS AND METHODS

Data were collected from *Ochroma pyramidale* (Cav. ex Lam.) Urban, Bombacaceae, (hereafter, *Ochroma*) grown on experimental plots located near Presidente Figueiredo (01° 51' S; 60° 04' W) in the Brazilian Amazon. *Ochroma* was chosen because it is one of the faster-growing species in the neotropical region under favorable conditions (Butterfield, 1996).

The region has a humid tropical climate and receives an annual precipitation of about 2200 mm, with a wet season from October through June. Mean temperature is around 27 °C. Net assimilation rate (A), stomatal conductance to water vapor (g_s), transpiration (E), and leaf dark respiration (R_d) were measured using an portable photosynthesis system with onboard LED light source and dioxide mixer to control CO₂ partial pressure (LI-6400, Li-Cor, Lincoln, Neb., USA). Data were collected from September 2000 to March 2001 on fully expanded leaves of similar age and appearance.

Four one-year-old plants were randomly selected for measurements from a population of around 100 saplings. Gas exchange parameters were measured on fully expanded leaves (two leaves per plant) between 0900 and 1500 h. Measurements were taken only in open sky days. Thus, when measurements were interrupted due to rainy conditions, a new set

of data was taken again another day, in the same plant.

Individual leaves were treated as sub samples. CO₂ response curves were determined for atmospheric CO₂ concentration (C_a) between 15 and 2000 μmol mol⁻¹. During measurements, light intensity was maintained at 1 mmol (photons) m⁻² s⁻¹ within the leaf chamber. Electron-transport rate (*J*) was determined according to Farquhard & Von Caemmerer (1982) as:

$$J = 4 (V_c + V_o),$$

where V_c and V_o are the rate of carboxylation and oxygenation, respectively. V_c is given by:

$$V_c = A + 0.5V_o + R_d.$$

The oxygenation rate (V_o) can be calculated as: V_o = (A + R_d) / (1/Φ - 0.5), being Φ described by the following equation as (Lambers et al. 1998):

$$\Phi = 2 (3.7 + 0.188 (T - 25) + 0.0036 (T-25)^2) / P_i,$$

where *T* is temperature (°C) and P_i is the CO₂ partial pressure (P_a). Because V_o is twice the rate of photorespiration, P_r was computed as: P_r = V_o/2. Net photosynthetic rate (*A*) data were fit using non-linear least squared regression, according to the model proposed by Herrick & Tomas (2001) as:

$$A = A'_{pot} [1 - (1 - y_o / A'_{pot})^{(1-C_i/T)}]$$

where y_o is the y-intercept, *T* is the CO₂-compensation point, and A'_{pot} is the computed A_{pot} (i.e., the actual light-saturated photosynthesis at saturating C_a).

Micronutrients (Fe, Zn, Mn, and Cu) were determined by atomic absorption spectrophotometry (Perkin Elmer 1100B, Überlingen, Germany) as described by Miyazawa *et al.* (1999). The ratio between A_{max} (i.e., net assimilation at saturating light

intensity and ambient CO₂) and micronutrient concentration was also calculated.

RESULTS

Gas exchange and electron-transport

At ambient C_a (C_i = 255 μmol(CO₂) mol⁻¹(air)), light-saturated photosynthesis (A_{max}) was 9.3 μmol (CO₂) m⁻²s⁻¹, whereas at saturating C_a (i.e., C_i = 1100 μmol (CO₂) mol⁻¹(air)), A_{pot} was 24 μmol(CO₂) m⁻²s⁻¹ (Figure 1). Electron-transport rates (*J*) increased from 81 to 120 μmol (e) m⁻² s⁻¹, at increasing [CO₂] above ambient C_a (Figure 1). The C_i/C_a ratios were 0.657 and 0.55 at ambient and saturating C_a, respectively.

E and g_s decreased at elevated C_i. *E* dropped from 2.7 to 1.49 mmol(H₂O) m⁻² s⁻¹ and g_s from 170 to 35 mmol (H₂O) m⁻² s⁻¹ at ambient and saturating CO₂ concentration, respectively (Figure 2). As a result of reduction in water loss and increases in *A* at increasing C_i, WUE was much lower at ambient C_a than at elevated CO₂ concentration (i.e., 5.43 versus 15.48 mmol(CO₂) mol⁻¹(H₂O)). The CO₂ compensation point (Γ) was estimated as 59.2 μmol(CO₂)mol⁻¹(air) (Figure 1).

Leaf micronutrients

Leaf micronutrient concentrations on a leaf area basis were 185, 134, 50, and 10 μmol (element) m⁻² for Fe, Mn, Zn, and Cu, respectively. The A_{max} to micronutrient ratio ranged from 50 to 883 mmol(CO₂) mol⁻¹(element) s⁻¹. Highest and lowest A_{max}:nutrient ratios involved Cu and Fe, respectively (Table 1). The Fe to Cu ratio was rather low (15:1), which may indicate nutritional imbalance in this species.

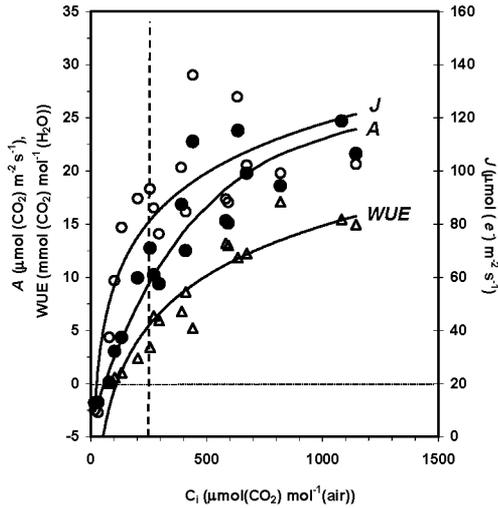


Figure 1. Electron-transport rates (J), net photosynthesis (A), and water-use efficiency (WUE) in *Ochroma pyramidale* grown in experimental plots near Presidente Figueiredo (AM) as a function of the internal CO_2 concentration (C_i). Vertical dashed line shows C_i at ambient CO_2 concentration (i.e., $C_i = 254 \mu\text{mol mol}^{-1}$; $C_i/C_a = 0.67$). Symbols: \circ , electron-transport rates; \bullet , net photosynthesis; Δ , water-use efficiency. $J(\circ) = -66.72 + 26.71 \ln C_i$, $R^2 = 0.79$; $A(\bullet) = 26[1 - (1+3.83/26)^{(1-C_i/59.2)}]$, $R^2 = 0.94$; $WUE(\Delta) = -32.02 + 6.78 \ln C_i$, $R^2=0.89$. The CO_2 compensation point (Γ) was $59.2 \mu\text{mol}(CO_2) \text{ mol}^{-1}$ (air); \ln , natural logarithm. Each point is the mean of four plants and two leaves per plant.

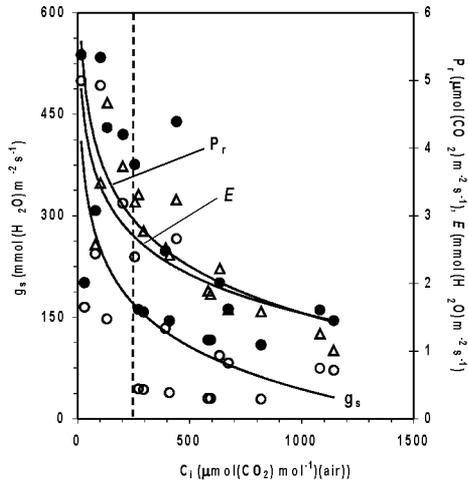


Figure 2. Stomatal conductance (g_s), transpiration (E), and photorespiration (P_r) in *Ochroma pyramidale* grown in experimental plots near Presidente Figueiredo (AM) as a function of the internal CO_2 concentration (C_i). Vertical dashed line shows C_i at ambient CO_2 concentration (i.e., $C_i = 254 \mu\text{mol}(CO_2) \text{ mol}^{-1}$ (air); $C_i/C_a = 0.67$). Symbols: \circ , stomatal conductance; \bullet , transpiration; Δ , photorespiration. $g_s(\circ) = 670.9 - 90.8 \ln C_i$, $R^2 = 0.49$; $E(\bullet) = 7.23 - 0.82 \ln C_i$, $R^2 = 0.41$; $P_r(\Delta) = 8.43 - 0.99 \ln C_i$, $R^2 = 0.64$; \ln , natural logarithm. Each point is the mean of four plants and two leaves per plant.

Table 1. Leaf micronutrient concentrations and A_{\max} to nutrient ratio in *Ochroma pyramidale* grown in experimental plots near Presidente Figueiredo, AM. Each value is the mean of four plants (\pm S.D).

Parameter	Mean \pm S.D (mg kg ⁻¹ DM)	Mean \pm S.D ($\mu\text{mol m}^{-2}$ leaf area)	Critical deficiency levels ¹ (mg kg ⁻¹ DM)	A_{\max} to nutrient ratio ² (mmol (CO ₂) mol ⁻¹ s ⁻¹)
Iron	100.5 \pm 19.1	185.1 \pm 3.53	50 to 150	50.2
Zinc	32.0 \pm 3.6	50.3 \pm 5.7	15 to 20	184.7
Manganese	71.5 \pm 5.5	133.9 \pm 10.3	10 to 20	69.5
Copper	6.5 \pm 1.0	10.5 \pm 1.6	1 to 5	883.6

¹Leaf critical deficiency content according to Marschner (1995)

²For an A_{\max} of 9.3 $\mu\text{mol}(\text{CO}_2) \text{ mol}^{-2}\text{s}^{-1}$

DISCUSSION

Gas exchange and electron-transport

Mean A_{\max} was much lower than previously reported for *Ochroma* (i.e., 9.3 versus 27 $\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$) (Figure 1, Oberbauer & Strain, 1984). This difference was attributed to the fact that Oberbauer & Strain collected their data from plants grown at near-optimal conditions. Thus, compared with *Ochroma* grown in controlled conditions, our results suggest that in this degraded landscape, environmental factors such as availability of nutrients in the soil may limit photosynthesis in this species. However, our A_{\max} values were comparable to values obtained for other pioneer tree species grown under natural environments (Zotz & Winter, 1994; Ishida *et al.*, 1999).

On the other hand, A_{pot} reported in this study is within the range observed for some C₄ dicot species such as *Amaranthus retroflexus* and *Gomphrena globosa* (Grodzinski *et al.*, 1998). One could suggest that expected increases in atmospheric [CO₂] could enhance photosynthetic rates of *Ochroma* in the future. However, we must

bear in mind that leaf response to short-term exposure to elevated [CO₂] should not be extrapolated to whole-plant response over the long-term because several factors may modulate plant response to permanent exposure to elevated atmospheric [CO₂]. Compared with ambient [CO₂], short-term exposure to elevated [CO₂] decreased P_r by 50%, from 2.9 to 1.46 $\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$ (Figure 1).

The CO₂ compensation point found in *O. pyramidale* (i.e., 59 $\mu\text{mol}(\text{CO}_2) \text{ mol}^{-1}$, Figure 1) was lower than previously reported for *Swietenia macrophylla*, another light-demanding species (Marenco *et al.*, 2001 b), due to the lower respiration rates of *Ochroma*. Our C_i/C_a values were lower than those previously reported for other rainforest species (Carswell *et al.*, 2000). Differences in the C_i/C_a ratio among plant species have been attributed at least in part to variation in stomatal conductance to CO₂ (Ehleringer & Cerling, 1995).

Transpiration rates and g_s decreased consistently at increasing [CO₂] confirming that at elevated CO₂ supply water loss may be reduced significantly. Thus, WUE was near three times higher at elevated [CO₂] than at

ambient CO₂ concentration (*i.e.*, 5.43 versus 15.48 mmol(CO₂) mol⁻¹(H₂O)). If this trend is maintained at the whole plant level, we may speculate that as atmospheric [CO₂] increases *Ochroma* could colonize areas with rainfall lower than 1500 mm year⁻¹ or areas with a longer drought period. Our maximum *J* values were similar to those previously observed in the upper canopy of *Inga* sp. in an undisturbed Amazonian forest (Carswell *et al.*, 2000), indicating that the photosynthetic system of *Ochroma* was apparently little or not affected by the harsh environmental conditions of this degraded landscape.

Leaf micronutrients

Little is known about the mineral composition of *Ochroma*. Therefore, in the absence of data from this species, we compared our results with those obtained from other tropical trees. Iron content of *Ochroma* was almost twice as high as those previously reported for other tropical trees (*e.g.*, *Ceiba pentandra*, *Virola surinamensis*), grown on low fertility soils (Neves *et al.*, 1999). However, these differences may not necessarily imply shortage of this element in the soil because variations in Fe content among species appear to be common for this element. In Burkina Faso, for example, leaf Fe content ranged from values as low as 14 mg kg⁻¹ up to 155 mg kg⁻¹ (Glew *et al.*, 1997).

Mn leaf content in *Ochroma* was within the range reported for *C. pentandra* and *V. surinamensis* by Neves *et al.* (1999). Zn leaf concentration, on the other hand, was higher in *Ochroma* than in those species studied by Neves *et al.* (1999). Compared with other tropical species, Mn, Zn, and Cu concentrations are within the range reported

by Glew *et al.* (1997). Taking into account the critical deficiency levels established for higher plants (Marschner, 1995), we may conclude that in terms of mineral nutrition, contents of Fe, Cu, and Zn were within the adequate range. On the other hand, Mn concentrations were slightly high, but lower than levels considered excessive for several plant species (*i.e.*, above 200 mg kg⁻¹) (Marschner 1995). Furthermore, from a nutritional point of view, the low Fe to Cu ratio (15:1) may reflect nutritional imbalance in *O. pyramidale* at this site. None of micronutrients examined was apparently insufficient or excessive for limiting the growth of *Ochroma* in this site, in which high growth rate has been observed (Barbosa *et al.*, 2000).

CONCLUSIONS

In this degraded landscape, a rather low A_{max} was found in *Ochroma* (9.3 μmol (CO₂) m⁻² s⁻¹). Mean A_{pot} reported in this study is within the range observed for some C₄ dicot species suggesting that under optimal environmental conditions photosynthetic rates of *Ochroma* may increase significantly. Transpiration rates and g_s lowered drastically at elevated [CO₂] confirming that at elevated CO₂ concentrations water loss may be significantly reduced, and as a result WUE may be increased. Considering the critical deficiency levels for most higher plants, we may conclude that the contents of Fe, Cu, and Zn were apparently adequate, whereas the content Mn was slightly high. Finally, none of the micronutrients examined was apparently insufficient or excessive for limiting the growth of *Ochroma* in this site, although the low Fe to Cu ratio (15:1) may reflect nutritional imbalance in this species.

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