Photosynthesis and leaf nutrient contents in *Ochroma pyramidale* (Bombacaceae)

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Abstract

In *Ochroma pyramidale* (Cav. ex Lam.) Urb., photon-saturated photosynthetic capacity (*P*<sub>max</sub>) was 13 μmol(CO<sub>2</sub>) m<sup>−2</sup> s<sup>−1</sup>. Average stomatal conductance (*g<sub>s</sub>*) and water-use efficiency (WUE) were greater at high irradiance, about 260 mmol(H<sub>2</sub>O) m<sup>−2</sup> s<sup>−1</sup> and 2.15 g(C) kg<sup>−1</sup>(H<sub>2</sub>O), respectively. In the dark, *g<sub>s</sub>* values were about 30% of maximum *g<sub>s</sub>*. Leaf nutrient contents on a leaf area basis were 131, 15, 36, 21, and 12 mmol m<sup>−2</sup> for N, P, K, Ca, and Mg, respectively. *Ochroma* also accumulated a greater amount of soluble saccharides than starch, 128 versus 90 g kg<sup>−1</sup>(DM). The availability of N and Mg, but not P, Ca, or K, may limit photosynthetic rates of *Ochroma* in this site.

Additional key words: Amazonia; balsa wood; Ca; foliar nutrients; Mg; NPK; starch; stomatal conductance; transpiration; water-use efficiency.

Introduction

Balsa wood, *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Bombacaceae), is a pioneer neotropical tree species that grows under moist and warm conditions on disturbed lands or as a coloniser of large gaps in the secondary rain forest (Whitmore and Wooi-Khoon 1983). Its growth is faster when the mean temperature and annual rainfall range from 25 to 30 °C and 1 500 to about 2 000 mm annually. *Ochroma* may colonise a diversity of soils; however, it does not tolerate flooded soils (Francis 1991). Its heartwood is probably the lightest wood produced in commercial plantations. Because of the low density of its wood (0.17 g cm<sup>−3</sup>), this species has long been used for raft and boat building. At present, it is also used in making model aeroplanes and boats, toys, core stock, and insulation (Francis 1991, Lorenzi 1992). In central Amazonia it may reach 11 m tall and 10 cm in diameter at breast height in about three years from planting (R.A. Marencos, unpublished), but its life cycle is short, 15 to 20 years (Francis 1991). The fast growth of *Ochroma* saplings makes this species useful in reforestation projects because when planted in a mixture with late succession, slower-growing species, that pioneer may provide shading for the seedlings of the slower-growing species and improve soil fertility by preventing the loss of nutrients.

Plant productivity is determined by several factors, including the amount of foliage, the photosynthetic capacity of individual leaves, and the availability of nutrients in the soil as key factors in determining biomass gains. Mineral nutrition affects photosynthesis. Likewise, photosynthetic availability modulates uptake and metabolism of mineral nutrients. Thus, high biomass gains are obtained when environmental conditions are favourable for growth, e.g., under adequate irradiance and availability of water and nutrients in the soil. Shortage of nutrients such as N, P, or S tends to increase the starch content of leaves and enhances the root to shoot ratio (Thompson et al. 1992, Ericsson et al. 1996). In addition, a low availability of K or Mg decreases C fixation, and as a result the amount of carbon allocated to roots may be reduced (Ericsson and Kähr 1993, 1995). Mineral nutrients such as N and P usually control plant growth in natural ecosystems (Koerselman and Meuleman 1996). Under optimal growth condition, P content of biomass ranges from 2 to 5 g kg<sup>−1</sup> (Raghothama 1999). In addition to

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Abbreviations: DM, dry matter; E, transpiration rate; *g<sub>s</sub>* stomatal conductance for water vapour; *I*<sub>comp</sub>, compensation irradiance; PPFD, photosynthetic photon flux density; *P*<sub>max</sub>, photon-saturated photosynthetic capacity; *P*<sub>net</sub>, net photosynthetic rate; *R*<sub>0</sub>, dark respiration rate; SLA, specific leaf area; WUE, water-use efficiency; α, apparent quantum yield.

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nutrient availability, the adequate elemental ratio between essential nutrients is also important for reaching optimal plant growth. Thus, an N to P ratio in plant tissue lower than 14 may indicate that N is a limiting nutrient for biomass accumulation (Koerselman and Meuleman 1996). Consequently, a positive relationship between \( P_{\text{N, max}} \) and leaf N content per unit area has frequently been observed (e.g., Zott and Winter 1994, Kitajima et al. 1997). Therefore, we hypothesised that \( P_{\text{N, max}} \) and leaf nutrient content of pioneer tree species, such as *Ochroma*, is lower when grown in degraded lands than under controlled conditions or in mature forests. To test this hypothesis, we determined leaf gas exchange parameters and foliar nutrients in *Ochroma* grown in a degraded landscape and compared these values with those previously reported for *Ochroma* or other pioneer species (e.g., Oberbauer and Strain 1984, Zott and Winter 1994, Car- swell et al. 2000).

**Materials and methods**

The experimental site was located at Presidente Figueiredo (01°51'S; 60°04'W) in Brazilian central Amazonia. The region experiences a humid tropical climate and has an annual precipitation of about 2 200 mm and mean temperature of around 27 °C. Net photosynthetic rate (\( P_n \)), stomatal conductance (\( g_s \)), transpiration rate (\( E \)), and leaf dark respiration rate (\( R_d \)) were measured with a portable open gas exchange system with infrared gas analyser (*LI-6400, Li-Cor*, Lincoln, NE, USA). Values 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. In these plants, gas exchange parameters were measured in two leaves per plant between 09:00 and 15:00 h. Individual leaves were treated as subsamples. Photosynthetic irradiance-response curves were determined for photosynthetic photon flux densities (PPFD) between 0 and 2 000 \( \mu \text{mol(photon)} \text{ m}^{-2} \text{s}^{-1} \). During measurements, CO\(_2\) concentration was maintained at 380 \( \mu \text{mol(CO}_2\text{)} \text{ mol}^{-1}\text{(air)} \) within the leaf chamber, whereas temperature ranged from 28 to 34 °C. A non-rectangular hyperbola model was used for describing data obtained from irradiance-response curves. The compensation irradiance (\( I_{\text{comp}} \)) was estimated by the \( R_d/a \) ratio, where \( a \) is the apparent quantum yield. Gas exchange parameters were collected when \( P_n \), \( g_s \), and \( E \) attained stable values (i.e., coefficient of variation was lower than 1%), which was delayed about 15 min. Water-use efficiency (WUE) was computed as \( P_n/E \).

Total soluble saccharide and starch contents were determined in the same leaves used for gas exchange measurements (Passos 1996). Foliar nutrient contents were determined according to Miyazawa et al. (1999). N was determined by the Kjeldahl method. P was determined colorimetrically using the ammonium molybdate method. K, Ca, and Mg were determined by atomic absorption spectrophotometry (*Perkin Elmer 1100B*, Überlingen, Germany). Specific leaf area (SLA) was obtained as the leaf area to leaf mass ratio.

**Results**

Means of \( g_s \) and \( P_{\text{N, max}} \) were 261 \( \mu \text{mol(H}_2\text{O)} \text{ m}^{-2} \text{s}^{-1} \) and 13 \( \mu \text{mol(CO}_2\text{)} \text{ m}^{-2} \text{s}^{-1} \), respectively (Table 1). \( R_d \) was 1.25 \( \mu \text{mol(CO}_2\text{)} \text{ m}^{-2} \text{s}^{-1} \), and the \( I_{\text{comp}} \) was observed at 32 \( \mu \text{mol(photon)} \text{ m}^{-2} \text{s}^{-1} \) (Fig. 1). PPFD saturation was reached at about 1 500 \( \mu \text{mol(photon)} \text{ m}^{-2} \text{s}^{-1} \) (Fig. 1). Values of \( g_s \) and \( E \) increased linearly with increases in irradiance (Fig. 2). WUE was 2.15 g(C) kg\(^{-1}\)(H\(_2\)O) at the strongest irradiance. This parameter increased with irradiance up to about 1 000 \( \mu \text{mol(photon)} \text{ m}^{-2} \text{s}^{-1} \) and then showed a slight trend to decline at the higher irradiances (Fig. 1, \( F = 2.03, p = 0.18 \)). This is because \( P_{\text{N, max}} \) tended to remain stable at high irradiance, whereas \( E \) was consistently responsive to changes in irradiance. In Fig. 2 a high variation was observed in \( g_s \) at all irradiances. *Ochroma* accumulated a greater amount of soluble saccharides than starch, 128 and 90 g kg\(^{-1}\)(DM), respectively. Average SLA was 9.7 m\(^2\) kg\(^{-1}\)(DM) (Table 1). Leaf nutrient concentrations, on a leaf area basis, were 131, 15, 36, 20, and 12 mmol(nutrient) m\(^{-2}\)(leaf area) for N, P, K, Ca, and Mg, respectively. On average, the relationship be-tween \( P_{\text{N, max}} \) and leaf nutrient content varied from 101 \( \mu \text{mol(CO}_2\text{)} \text{ mol}^{-1}\text{(nutrient)} \text{ s}^{-1} \) for N to 1 064 \( \mu \text{mol(CO}_2\text{)} \text{ mol}^{-1}\text{(nutrient)} \text{ s}^{-1} \) for Mg (Table 2).

**Discussion**

\( P_n \) values observed in *Ochroma* were lower than previously reported by Oberbauer and Strain (1984), who found values as high as 27 \( \mu \text{mol(CO}_2\text{)} \text{ m}^{-2} \text{s}^{-1} \). This discrepancy was attributed to the fact that Oberbauer and Strain reported data from plants grown under near-optimal conditions in controlled environments. Nevertheless,