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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_{Nmax}) was 13 μmol(CO_2) m^{-2} s^{-1}. Average stomatal conductance (g_s) and water-use efficiency (WUE) were greater at high irradiance, about 260 mmol(H_2O) m^{-2} s^{-1} and 2.15 g(C) kg^{-1}(H_2O), respectively. In the dark, g_s values were about 30 % of maximum g_s. Leaf nutrient contents on a leaf area basis were 131, 15, 36, 21, and 12 mmol m^{-2} for N, P, K, Ca, and Mg, respectively. *Ochroma* also accumulated a greater amount of soluble saccharides than starch, 128 *versus* 90 g kg^{-1}(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^{-3}), 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it may reach 11 m tall and 10 cm in diameter at breast height in about three years from planting (R.A. Marenco, unpublished), but its life cycle is short, 15 to 20 years (Francis 1991).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, photosynthate 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^{-1} (Raghothama 1999). In addition to

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Abbreviations: DM, dry matter; *E*, transpiration rate; g_s, stomatal conductance for water vapour; I_{comp}, compensation irradiance; PPFD, photosynthetic photon flux density; P_{Nmax}, photon-saturated photosynthetic capacity; P_N, net photosynthetic rate; R_D, 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_{Nmax} and leaf N content per unit area has frequently been observed (*e.g.*, Zotz and Winter 1994, Kitajima *et al.* 1997). Therefore, we hypothesised that P_{Nmax} 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, Zotz and Winter 1994, Carswell *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 μmol(photon) m^{-2} s^{-1}. During measurements, CO_2 concentration was maintained at 380 μmol(CO_2) mol^{-1}(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_{comp}) was estimated by the R_D/α ratio, where α 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_{Nmax} were 261 mmol(H_2O) m^{-2} s^{-1} and 13 μmol(CO_2) m^{-2} s^{-1}, respectively (Table 1). R_D was 1.25 μmol(CO_2) m^{-2} s^{-1}, and the I_{comp} was observed at 32 μmol(photon) m^{-2} s^{-1} (Fig. 1). PPFD saturation was reached at about 1 500 μmol(photon) m^{-2} 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_2O) at the strongest irradiance. This parameter increased with irradiance up to about 1 000 μmol(photon) m^{-2} 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_{Nmax} 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_{Nmax} and leaf nutrient content varied from 101 μmol(CO_2) mol^{-1}(nutrient) s^{-1} for N to 1 064 μmol(CO_2) mol^{-1}(nutrient) 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 μmol(CO_2) m^{-2} 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,

P_{Nmax} values found in this study for *Ochroma* are within the range observed for other pioneer tree species grown under natural environments (Zotz and Winter 1994, Ishida *et al.* 1999). *Ochroma* was photon-saturated at about 1 500 µmol(photon) m^{-2} s^{-1} (Fig. 1), which is consistent with the report of Oberbauer and Strain (1984), confirming that this species requires open or large gaps for its establishment, a characteristic of pioneer species. Mean I_{comp} value found in *Ochroma*, 32 µmol(photon) m^{-2} s^{-1}, was within the range previously reported for other tropical tree species (Marenco *et al.* 2001). Mean E increased consistently with irradiance suggesting that in open sites, growth rates of this species may be limited by soil water availability, particularly during the drought period. In darkness (PPFD = 0), the lowest g_s and E values were about 80.0 and 1.8 mmol(H_2O) m^{-2} s^{-1}, respectively (Fig. 2). These values represent about 30 % of maximum g_s [261 mmol(H_2O) m^{-2} s^{-1}] and 35 % of maximum E [4.95 mmol(H_2O) m^{-2} s^{-1}] (Table 1). These results are consistent with findings of Körner (1995) that in humid tropical forest g_s often remains above 25 % of maximum conductance. Because g_s responded linearly to irradiance, we conclude that stomata may perfectly track changes in irradiance during the day in this species. Also, these results suggest that *Ochroma* is rather inefficient in preventing water loss and may help to explain why this species is only found in humid regions with a short dry season. Maximum g_s values observed in this study are within the range reported for other rainforest tree species (*e.g.*, Sá *et al.* 1996). In all irradiances examined, g_s values showed a large standard deviation (Fig. 2), which confirms that g_s in *Ochroma* is highly sensitive to variations in air temperature, leaf to air vapour pressure differ-

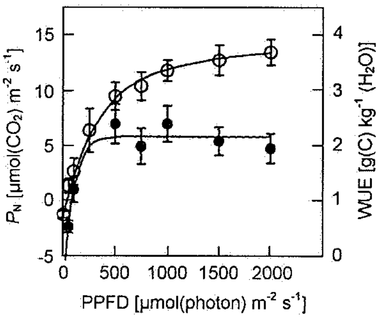

Fig. 1. Photosynthetic photon flux density (PPFD)-saturated photosynthetic rate, P_N (○), and water-use efficiency, WUE (●) in *Ochroma pyramidale* as a function of PPFD in central Amazonia. $P_N = \{[(\alpha\ PPFD + P'_{Nmax} + R_D) - ((\alpha\ PPFD + P'_{Nmax} + R_D)^2 - 4\ \alpha\ PPFD\ \Theta\ (P'_{Nmax} + R_D))^{0.5}]/2\ \Theta\} - R_D$, where α is apparent quantum yield, = 0.039; R_D is dark respiration rate, = 1.25; P'_{Nmax} or computed P_{Nmax}, = 15.05; Θ, curvature factor, = 0.51, r^2= 0.99. WUE = 3.08[0.70 − exp(−0.0112(PPFD + 6.24))], r^2 = 0.93. I_{comp} (R_D/α) = 32 µmol(photon) m^{-2} s^{-1}. Means of four plants and two leaves per plant (± SD).

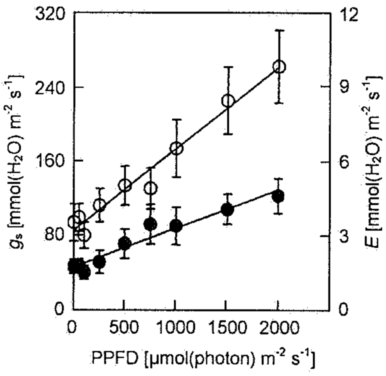

Fig. 2. Stomatal conductance, g_s, (○) and transpiration rate, E, (●) in *Ochroma pyramidale* as a function of the photosynthetic photon flux density (PPFD) in central Amazonia. g_s = 85.84 + 0.09 PPFD, r^2 = 0.97; E = 1.750 + 0.002 PPFD, r^2 = 0.94. Means of four plants and two leaves per plant (± SD).

Table 1. Gas exchange parameters, water-use efficiency (WUE), non-structural saccharides, and specific leaf area (SLA) in *Ochroma pyramidale*. Means of four plants (± S.E.).

Parameter	*Ochroma*
P_{Nmax} [µmol(CO_2) m^{-2} s^{-1}]	13.24 ± 0.94
g_s [mmol(H_2O) m^{-2} s^{-1}]	261.2 ± 79.1
WUE [g(C) kg^{-1}(H_2O)]	2.01 ± 0.13
Soluble saccharides [g kg^{-1}(DM)]	128.4 ± 18.4
Starch [g kg^{-1}(DM)]	90.3 ± 9.0
TNC [g kg^{-1}(DM)]	218.7 ± 18.9
Leaf size [cm^2]	465.2 ± 37.5
SLA [m^2 kg^{-1}(DM)]	9.72 ± 0.20

Table 2. Leaf nutrient contents and ratio of photosynthetic capacity, P_{Nmax} to nutrients in *Ochroma pyramidale*. Means of four plants (± S.E.).

Leaf nutrient	Content [g kg^{-1}(DM)]	 [mmol(nutrient) m^{-2}]	P_{Nmax} to nutrient ratio [µmol(CO_2) mol^{-1}(nutrient) s^{-1}]
Nitrogen	17.83 ± 0.04	131.00 ± 1.00	101.0
Phosphorus	4.62 ± 0.30	14.90 ± 1.86	890.9
Potassium	13.60 ± 0.81	35.80 ± 4.28	369.3
Calcium	7.99 ± 0.59	20.60 ± 3.04	644.3
Magnesium	2.72 ± 0.03	12.40 ± 0.67	1 064.3

ence, and water availability in the soil. The fact that stomata did not close completely at night, as it is generally expected for C_3 plants, suggests that when water is available in the soil, stomata remain partially open to maximise P_N.

Even though a rather low P_N was observed in *Ochroma*, this did not negatively affect biomass gain of this species because *Ochroma* may reach up to 11 m tall in about three years in this site (R.A. Marenco, unpublished). This indicates that photosynthates in *Ochroma* are mainly allocated to aboveground plant parts, wood production and leaves. Starch content was lower than soluble saccharide concentration suggesting that supply of photosynthates did not exceed demand of sink organs, mainly stems and new leaves. Leaf starch content tends to increase when sink demand is low (*e.g.*, Marenco *et al.* 1995) or under shortage of certain nutrients, particularly N, P, or S (*e.g.*, Ericsson *et al.* 1996). The sugar to starch ratio that was found in this study (*i.e.*, 1.4) was lower than previously reported for other C_3 species grown at near-optimal conditions (Grodzinski *et al.* 1998). Therefore, environmental factors might limit P_{Nmax} of *Ochroma* in this site. However, a low leaf starch content might also indicate a high export rate of photosynthates to sink organs (*e.g.*, growing tissue). Furthermore, the sugar to starch value was higher than those recently observed for either mid or late succession species grown in the same site (Marenco *et al.* 2001). Thus, this ratio might change along the succession gradient, with lower values for climax species and higher ones for pioneer species.

Leaf N content was lower than values previously reported for other pioneer trees, such as *Cecropia*, *Urera* (Kitajima *et al.* 1997), or *Ceiba* (Zotz and Winter 1994), whereas the leaf P content reported in this study was higher than those previously related for other pioneer trees (Raaimakers *et al.* 1995). However, our P values are within the range of leaf P content related by Tuohy *et al.* (1991). Because of the high Ca and P values we found low values for either P_{Nmax}/Ca or P_{Nmax}/P ratio, 0.64 and 0.89 mmol(CO_2) mol^{-1}(nutrient) s^{-1}, respectively. In contrast with P and Ca values, leaf Mg content was almost 50 % lower than that recently reported by Carswell *et al.* (2000) for *Cedrela*. However, our leaf K values matched closely those reported for other tropical tree species (Zotz and Winter 1994, Carswell *et al.* 2000). N and Mg are essential for photosynthesis. Ribulose-1,5-bisphosphate carboxylase/oxygenase contains about 20 % of leaf N content in C_3 plants and Mg plays a structural role in chlorophyll synthesis. Thus, considering that our N and Mg values were rather low, we suggest that N and Mg supplies limit P_{Nmax} of *Ochroma* in this site. Despite the probable effect of mineral nutrition on P_{Nmax}, the growth of *Ochroma* seems to be little affected by nutrient availability in this degraded landscape. Therefore, our results suggest that *Ochroma* could be useful in reforestation programs or to restore soil fertility in agriculturally unproductive fields. P_{Nmax} was likely limited by availability of N and Mg in the soil. Our results also suggest that stomata may efficiently track changes in irradiance during the day. *Ochroma* was rather inefficient in preventing water loss, which may help to explain why this species is only found in sites with a short dry season. Because starch content was lower than soluble saccharide content, the supply of photosynthates apparently did not exceed demand of sink organs. It remains to be elucidated whether assimilate partitioning between shoot and root or the efficiency for nutrient uptake, especially P and Ca, is the major factor responsible for the high growth rates commonly reported for *Ochroma*.

References

Carswell, F.E., Grace, J., Lucas, M.E., Jarvis, P.G.: Interaction of nutrient limitation and elevated CO_2 concentration on carbon assimilation of a tropical tree seedling (*Cedrela odorata*). – Tree Physiol. **20**: 977-986, 2000.

Ericsson, T., Kähr, M.: Growth and nutrition of birch seedlings in relation to potassium supply rate. – Trees **7**: 78-85, 1993.

Ericsson, T., Kähr, M.: Growth and nutrition of birch seedlings at varied relative addition rates of magnesium. – Tree Physiol. **15**: 85-93, 1995.

Ericsson, T., Rytter, L., Vapaavouri, E.: Physiology of carbon allocation in trees. – Biomass Bioenergy **11**: 115-127, 1996.

Francis, J.K.: *Ochroma pyramidale* Cav. Balsa – *Bombacaceae*. SO. – Institute of Tropical Forestry, USDA, SM-41. Río Piedras 1991.

Grodzinski, B., Jiao, J., Leonardos, E.D.: Estimating photosynthesis and concurrent export rates in C_3 and C_4 species at ambient and elevated CO_2. – Plant Physiol. **117**: 207-215, 1998.

Ishida, A., Toma, T., Marjenah: Limitation of leaf carbon gain by stomatal and photochemical processes in the top canopy of *Macaranga conifera*, a tropical pioneer tree. – Tree Physiol. **19**: 467-473, 1999.

Kitajima, K., Mulkey, S.S., Wright, S.J.: Seasonal leaf phenotypes in the canopy of a tropical dry forest: photosynthetic characteristics and associated traits. – Oecologia **109**: 490-498, 1997.

Koerselman, W., Meuleman, A.F.M.: The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. – J. appl. Ecol. **33**: 1441-1450, 1996.

Körner, C.: Leaf diffusive conductances in the major vegetation types of the globe. – In: Schulze, E.-D., Caldwell, M.M. (ed.): Ecophysiology of Photosynthesis. Pp. 463-490. Springer-Verlag, Berlin – Heidelberg – New York 1995.

Lorenzi, H.: Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. [Brazilian Trees: Handbook for Identifying and Cultivating Brazilian Trees.] – Plantarum, Nova Odessa 1992. [In Portug.]

Marenco, R.A., Gonçalves, J.F.C., Vieira, G.: Leaf gas exchange and carbohydrates in tropical trees differing in successional status in two light environments in central Amazonia. – Tree Physiol. **21**: 1311-1318, 2001.

Marenco, R.A., Lopes, N.F., Moreira, M.A.: Photosynthesis and leaf lipoxygenase activity in soybean genotypes lacking seed lipoxygenase isozymes. – Braz. J. Plant Physiol. **7**: 21-25, 1995.

Miyazawa, M., Pavan, M.A., Muraoka, T., Carmo, C.A.F.S., Mello, W.J.: [Chemical analysis of plant tissues.] – In: Silva, F.C. (ed.): Manual de Análises Químicas de Solos, Plantas e Fertilizantes. Pp. 172-223. Brazilian Agricultural Research Corporation (EMBRAPA), Brasilia 1999. [In Portug.]

Oberbauer, S.F., Strain, B.R.: Photosynthesis and successional status of Costa Rican rain forest trees. – Photosynth. Res. **5**: 227-232, 1984.

Passos, L.P.: Métodos Analíticos e Laboratoriais em Fisiologia Vegetal. [Laboratory and Analytical Methods in Plant Physiology.]. – Brazilian Agricultural Research Corporation (EMBRAPA). Coronel Pacheco 1996. [In Portug.]

Raaimakers, D., Boot, R.G.A., Dijkstra, P., Pot, S.: Photosynthetic rates in relation to leaf phosphorus content in pioneer versus climax tropical rainforest trees. – Oecologia **102**: 120-125, 1995.

Raghothama, K.G.: Phosphate acquisition. – Annu. Rev. Plant Physiol. Plant mol. Biol. **50**: 665-693, 1999.

Sá, T.D.A., Costa, J.P.R., Roberts, J.M.: Forest and pasture conductances in southern Pará, Amazonia. – In: Gash, J.H.C., Nobre, C.A., Roberts, J.M., Victoria, R.L. (ed.): Amazonian Deforestation and Climate. Pp. 241-263. John Wiley & Sons, Chichester 1996.

Thompson, W.A., Kriedemann, P.E., Craig, I.E.: Photosynthetic response to light and nutrients in sun-tolerant and shade-tolerant rainforest trees. I. Growth, leaf anatomy and nutrient content. – Aust. J. Plant Physiol. **19**: 1-18, 1992.

Tuohy, J.M., Prior, J.A.B., Stewart, G.R.: Photosynthesis in relation to leaf nitrogen and phosphorus content in Zimbabwean trees. – Oecologia **88**: 378-382, 1991.

Whitmore, T.C., Wooi-Khoon, G.: Growth analysis of the seedlings of balsa, *Ochroma lagopus*. – New Phytol. **95**: 305-311, 1983.

Zotz, G., Winter, K.: Photosynthesis of a tropical canopy tree, *Ceiba pentandra*, in a lowland forest in Panama. – Tree Physiol. **14**: 1291-1301, 1994.