



GAS EXCHANGE IN LEAVES OF *Coffea arabica* IRRIGATED

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ABSTRACT - We determined maximum net photosynthesis (P_{Nmax}) in *Coffea arabica* L. (cultivars Catuaí Vermelho, Obatã, and Ouro Verde) exposed to different thermal treatments during 14 h. The optimal temperature for (P_{Nmax}) in terms of photosynthetic photon flux density (PPFD) under 355 ppm of CO₂ was between 17-23°C. Under temperatures above 23°C there was a decrease in P_{Nmax} . Under saturating CO₂ rates (1,600 ppm) the optimum temperature range changed to 23-29°C for the Catuaí Vermelho cultivar. There was no increase in P_{Nmax} under CO₂ saturation for any of the cultivars. *C. arabica*'s photosynthetic process is strongly inhibited under 32 °C leaf temperature.

KEYWORDS: CO₂, net photosynthesis, plant thermal stress.

TROCAS GASOSAS EM FOLHAS DE *Coffea arábica* IRRIGADO

RESUMO - Foi determinadas a taxa máxima de fotossíntese líquida (P_{Nmax}) em *Coffea arabica* L. (cultivares Catuaí Vermelho, Obatã e Ouro Verde) submetidos a diferentes tratamentos térmicos durante 14 h. A região ótima de temperatura para P_{Nmax} em função do fluxo de fótons fotossinteticamente ativos (PPFD) sob 355 ppm de CO₂ foi entre 17-23 °C. Sob temperaturas acima de 23 °C ocorreu o declínio de P_{Nmax} . Sob CO₂ saturante (1600 ppm) houve deslocamento da faixa de temperatura ótima para 23-29 °C no cultivar Catuaí Vermelho. Não houve incremento de P_{Nmax} sob saturação de CO₂ em nenhum cultivar. O processo fotossintético do cafeeiro é extremamente inibido sob temperatura foliar de 32 °C.

PALAVRAS-CHAVE: CO₂, estresse térmico, fotossíntese líquida.

INTRODUCTION

Photosynthetic net carbon assimilation (P_N) is one of the growth components more sensible to temperature and is likely to be the first targeted by thermal stress (Larcher, 2000).

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Leaf temperature affects the photosynthetic performance by means of biochemical and biophysical changes (Pastenes & Horton, 1996). Therefore, plants exposed to moderate thermal stress would not have their photosynthetic apparatus damaged, but their carbon assimilation rates would be substantially reduced.

In Brazil, *Coffea arabica* L. crops are established mainly in areas where the average annual temperature varies between 18 °C and 22 °C (Barros *et al.*, 1997). The selection of cultivars has recently enabled the expansion of coffee crops to areas in which the average temperature varies between 24-25 °C with satisfactory productivity, such as the Northeast region of Brazil (DaMatta & Ramalho, 2006).

Under environmental CO₂ concentration, conditions (355 ppm) the photosynthetic carboxylation capacity in the mesophyll is not saturated (Tezara *et al.* 2002). The increase in CO₂ concentration may increase or maintain the net photosynthesis values in plants exposed to thermal stress and reduce the negative impact caused by temperature elevation to the carbon balance components.

The objective of this study was to determine the infra-optimal, optimal and supra-optimal temperatures for *C. arabica* biochemical and chemical processes. The positive and negative components of the carbon balance were related to analyze the balance of photosynthesis under irrigation and different thermal treatments. We also investigated if the increase in CO₂ concentration could reduce the impact caused by thermal stress on the carbon net assimilation.

MATERIAL AND METHODS

Plant material and growth conditions

Young four-month-old plants were grown in 20-L plastic bags containing Oxisol with animal organic matter (4:1). The soil was irrigated once a week until field capacity. The coffee seedlings were kept in a greenhouse. The average temperature in the greenhouse was 18.0±3.2°C during nighttime and 25.0±3.0°C during daytime. The soil in each bag was fertilized with 20 g of N (4.0 g), P (14.0 g), K (8.0 g), Zn (0.2 g), and B (0.1 g).

Thermal treatments within the incubator and thermal insulation of the root system

Responses for leaf net photosynthesis (P_N) in terms of photosynthetic photon flux density (PPFD) were obtained under different thermal treatments. The thermal treatments were applied using an incubator (1.25 x 0.52 x 0.17 m, model NT-708, Nova Técnica, Piracicaba, Brazil). The air temperature inside the incubator was kept steady at 17, 20, 23, 26,

29 or 32°C (± 0.1 °C). The relative humidity inside the incubator was kept constant at 70% ($\pm 10\%$). The treatments were concluded after the plants were kept for 14 hours inside the incubator.

Net photosynthesis (P_N) values with regard to photosynthetic photon flux density (PPFD)

P_N -PPFD curves were obtained at 8:00 a.m. We used an infrared gas analyzer (IRGA, model LCA-4, ADC, Hoddesdon, UK) to obtain leaf gas exchange values in P_N -PPFD curves. PPFD values between 2,000-800 $\mu\text{mol m}^{-2}\text{s}^{-1}$ were obtained applying variable voltage to the PLU-002 cannon.

The P_N -PPFD curve was adjusted using the empirical equation described by Prado & Moraes (1997),

$$P_N = P_{N_{\max}} (1 - e^{-k(\text{PPFD} - I_c)}) \quad (\text{I})$$

where P_N = net photosynthesis; $P_{N_{\max}}$ = maximum net photosynthesis; e = natural logarithm base; k = constant; PPFD = photosynthetic photon flux density; and I_c = PPFD compensation point.

Photorespiration, stomatal conductance and leaf transpiration determinations

Instantaneous determinations of stomatal conductance (g_s), transpiration (E), and of the ratio between internal and external CO_2 concentration (C_i/C_a) under PPFD values equal to or greater than 1,200 $\mu\text{mol.m}^{-2}\text{s}^{-1}$ in P_N -PPFD curves were used to calculate average g_s , E , and C_i/C_a values for each thermal treatment. We obtained between 33 and 42 g_s , E , and C_i/C_a values for each P_N -PPFD curve under saturating PPFD.

Net photosynthesis (P_N) with regard to external (C_a) and intercellular (C_i) CO_2 concentration

P_N - C_a and P_N - C_i curves were obtained under PPFD saturation (1.200 $\mu\text{mol.m}^{-2}\text{s}^{-1}$) using a GD gas diluter (ADC, Hoddesdon, UK) coupled to the LCA-4 IRGA (Monteiro & Prado 2006). We modified equation (I) replacing the PPFD component by CO_2 concentration and used the modified equation to adjust the P_N - C_a and P_N - C_i curves, thus obtaining the potential photosynthetic capacity, $P_{N_{\max}(\text{CO}_2)}$ ($\mu\text{mol.m}^{-2}\text{s}^{-1}$).

RESULTS

The highest $P_{N_{\max}}$ values under regular atmospheric concentration were observed at 17°C for the Ouro Verde (8.3 $\mu\text{mol m}^{-2}\text{s}^{-1}$) cultivar and under 20°C for the Obatã and Catuaí Vermelho cultivars, at 7.8 and 7.1 $\mu\text{mol m}^{-2}\text{s}^{-1}$ respectively (Table 1 and Figure 1). $P_{N_{\max}}$

decrease occurred beyond 20°C for all cultivars, and under 32°C the carbon assimilation was less than 1.4 $\mu\text{mol m}^{-2}\text{s}^{-1}$.

Stomatal conductance (g_s) and transpiration (E) under saturating PPFD decreased with leaf temperature elevation (Figure 2). The temperature elevation did not restrain the internal/external carbon concentration relationship values (C_i/C_a , Figure 2).

Under irradiance (PPFD) and CO₂ saturation conditions there was also a decrease in $P_{N\text{max}}$ with temperature elevation (Figure 3 and Table 1). The optimum temperature for carbon assimilation in the Catuaí Vermelho cultivar increased to 26°C under saturating CO₂ concentration. *C. arabica* showed no increase in $P_{N\text{max}}$ values in the P_N -CO₂ curves, since the maximum value obtained (8.5 $\mu\text{mol m}^{-2}\text{s}^{-1}$, Catuaí Vermelho under 26 °C) is close to the maximum value registered under regular atmospheric concentration (8.3 $\mu\text{mol m}^{-2}\text{s}^{-1}$, Ouro Verde under 17°C). Even under 1.600 ppm of CO₂, *C. arabica* photosynthesis is strongly inhibited at 32°C (Figure 3), especially in the Catuaí Vermelho and Obatã cultivars (1.6 and 1.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ respectively).

DISCUSSION

Contrasting with the scenario under less elevated temperatures, $P_{N\text{max}}$ inhibited under 32°C (Table 1 and Figure 1). This behavior showed by *C. arabica* confirms our expectation that besides producing a decrease in CO₂ photosynthetic fixation (He & Lee, 2001). Additionally, the significant reduction in $P_{N\text{max}}$ and $P_{N\text{max}}(\text{CO}_2)$ observed for the coffee plant under 32°C confirms the RuBisCO activation state is intensely affected by elevated temperatures.

The absence of a displacement in $P_{N\text{max}}$ optimum temperature for the Obatã and Ouro Verde cultivars indicates possible mesophyll limitation to net photosynthesis. On the other hand, photosynthetic models assume that a constant C_i/C_a ratio under temperature (Figure 2) and CO₂ atmospheric concentration elevation indicates a parallel adjustment of the stomatal apparatus and of the photosynthetic activity in the mesophyll (Morison & Lawlor, 1999). Reduced CO₂ mesophyll conductance due to abiotic stress may produce large differences between C_i and effective carbon concentration in the chloroplast (Bota *et al.*, 2004).

The displacement in optimum temperature for net assimilation only for the Catuaí Vermelho cultivar cannot be explained exclusively based on the results obtained here. Interspecific differences in answers to temperature and CO₂ concentration interactions are

expected among genotypes and cultivars due to the different development forms and expansion of meristems and organs, and to the assimilates' allocation pattern in these organs (Morison & Lawlor, 1999).

Carboxylation efficiency is generally correlated to RuBisCO activity (von Caemmerer, 2000). Its activity decreases when g_s becomes lower than $0.10 \text{ mol m}^{-2}\text{s}^{-1}$ (Tezara *et al.* 2002, Bota *et al.* 2004). The results obtained here show the stomatal conductance was always below this value at temperatures above 17°C (Figure 2). Stomatal diffusion limitation would already be reaching its potential at cool temperatures, therefore it suffered less variation under thermal stress.

Elevated CO_2 concentrations do not enhance coffee's net photosynthesis (Figure 3). In this sense, some other previous reports are also divergent. *Triticum aestivum* showed only 10% increase in $P_{N\text{max}}$ under doubled regular C_a , and an increase of only 4°C in environmental temperature decreased its photosynthetic capacity and carboxylation efficiency (Delgado *et al.* 1994).

CONCLUSIONS

C. arabica cultivars show greater carbon fixation between $17\text{-}23^\circ\text{C}$. Coffee plants show no increase in carbon gain under saturating CO_2 conditions, but the Catuaí Vermelho cultivar shows optimum temperature range displacement for higher temperature values ($23\text{-}29^\circ\text{C}$). Coffee plants' photosynthetic process is strongly inhibited under a 32°C leaf temperature, both under regular atmospheric conditions and under saturating CO_2 conditions.

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Table 1. Potential photosynthetic capacity with regard to internal CO₂ concentration ($P_{Nmax} (CO_2)$, $\mu\text{mol m}^{-2}\text{s}^{-1}$) in *Coffea arabica* Catuaí Vermelho, Ouro Verde and Obatã cultivars kept under thermal treatment for 14 hours at 17, 20, 23, 26, 29 and 32 °C.

cv.	17 °C	20 °C	23 °C	26 °C	29 °C	32 °C
Catuaí	6.8	7.6	7.2	8.4	3.8	1.6
$P_{Nmax} (CO_2)$ Obatã	4.8	5.6	5.3	4.4	3.3	1.4
Ouro Verde	7.3	6.1	6.3	4.9	3.8	3.0

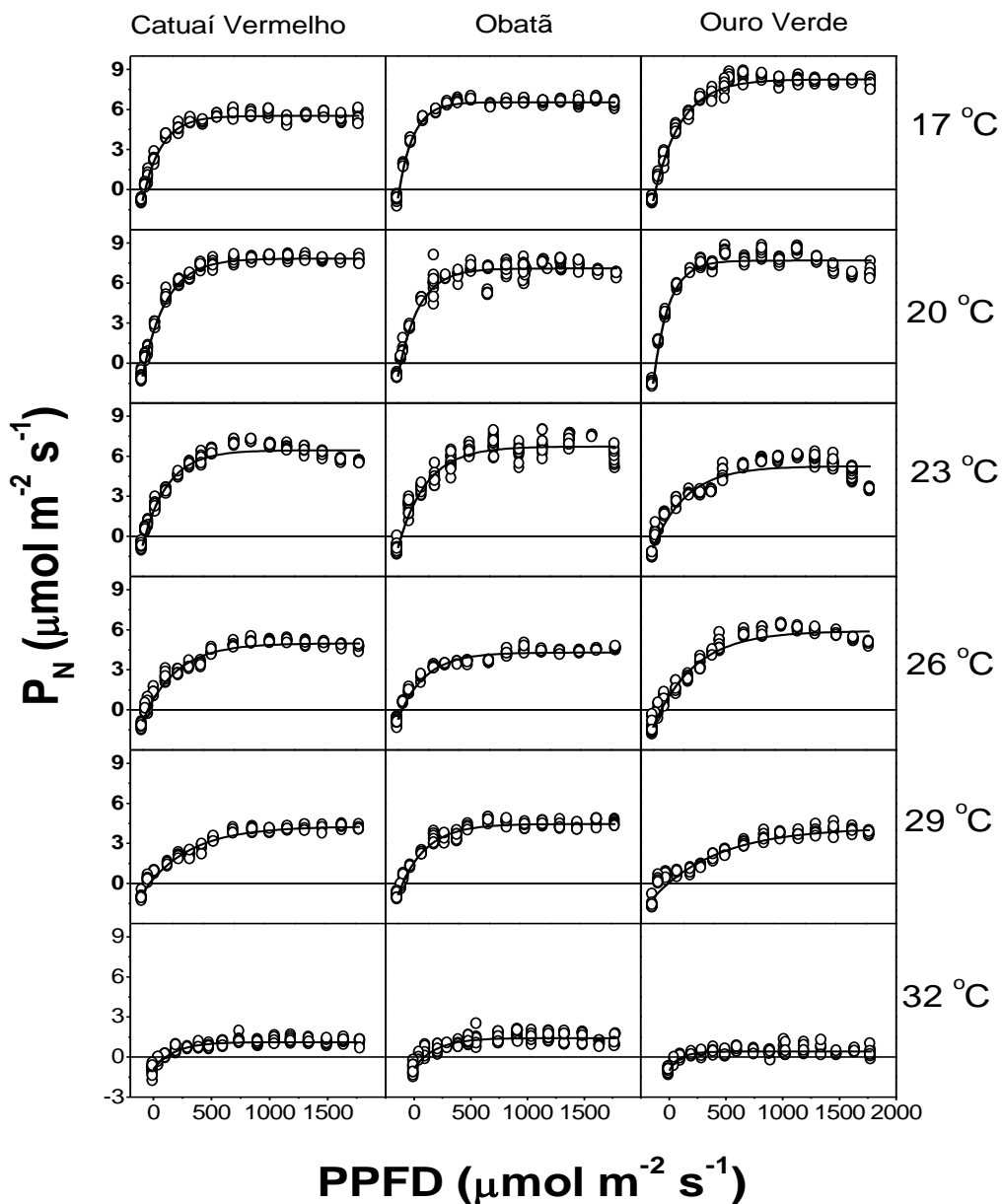


Figure 1. Net photosynthesis (P_N , open circles) with regard to photosynthetically active photon flux (PPFD) under regular CO₂ atmospheric concentration (355 ppm) in *Coffea arabica* cultivars Catuaí Vermelho, Obatã and Ouro Verde after 14 hours in an incubator under 17 °C (upper panels), 20 °C, 23 °C, 26 °C, 29 °C and 32 °C (lower panels).

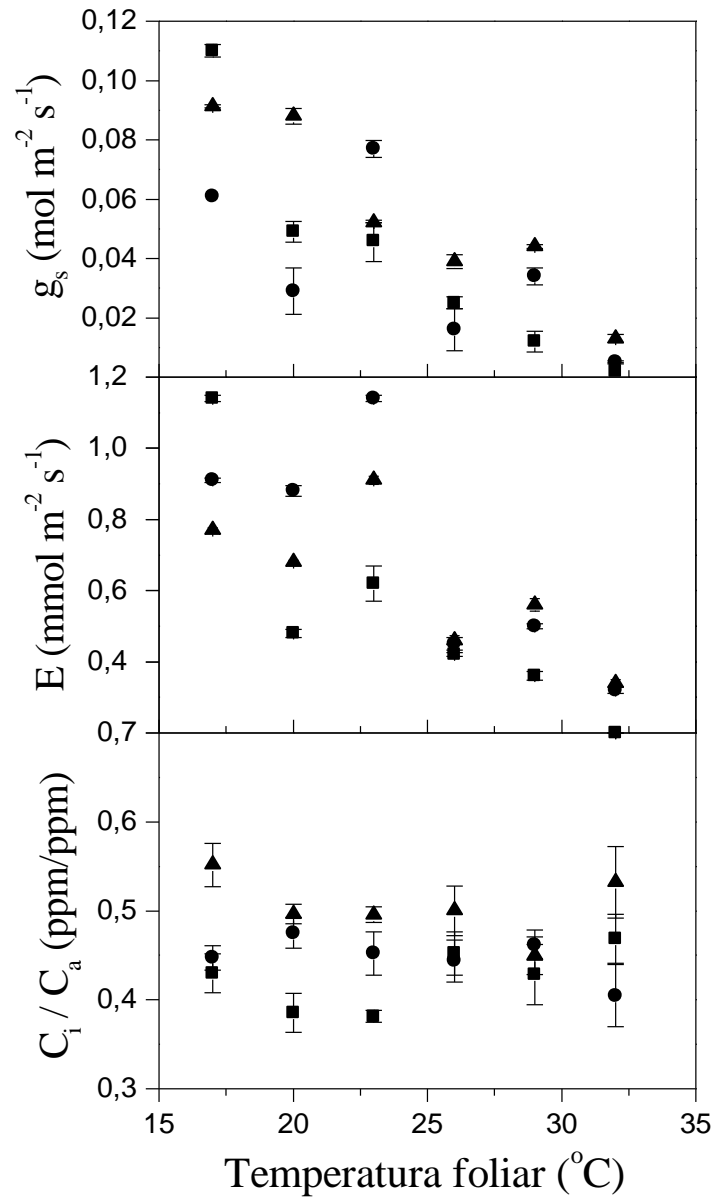


Figure 2. Stomatal conductance (g_s), transpiration (E) and internal/external concentration ratio (C_i/C_a) under photosynthetically active photon flux (PPFD) $\geq 1.200 \mu\text{mol m}^{-2} \text{s}^{-1}$ after 14 hours under different temperatures in *Coffea arabica* cultivars: Catuaí (■), Obatã (●) and Ouro Verde (▲). Each symbol represents the average value ($42 \geq n \geq 33$) and the bars represent standard error.

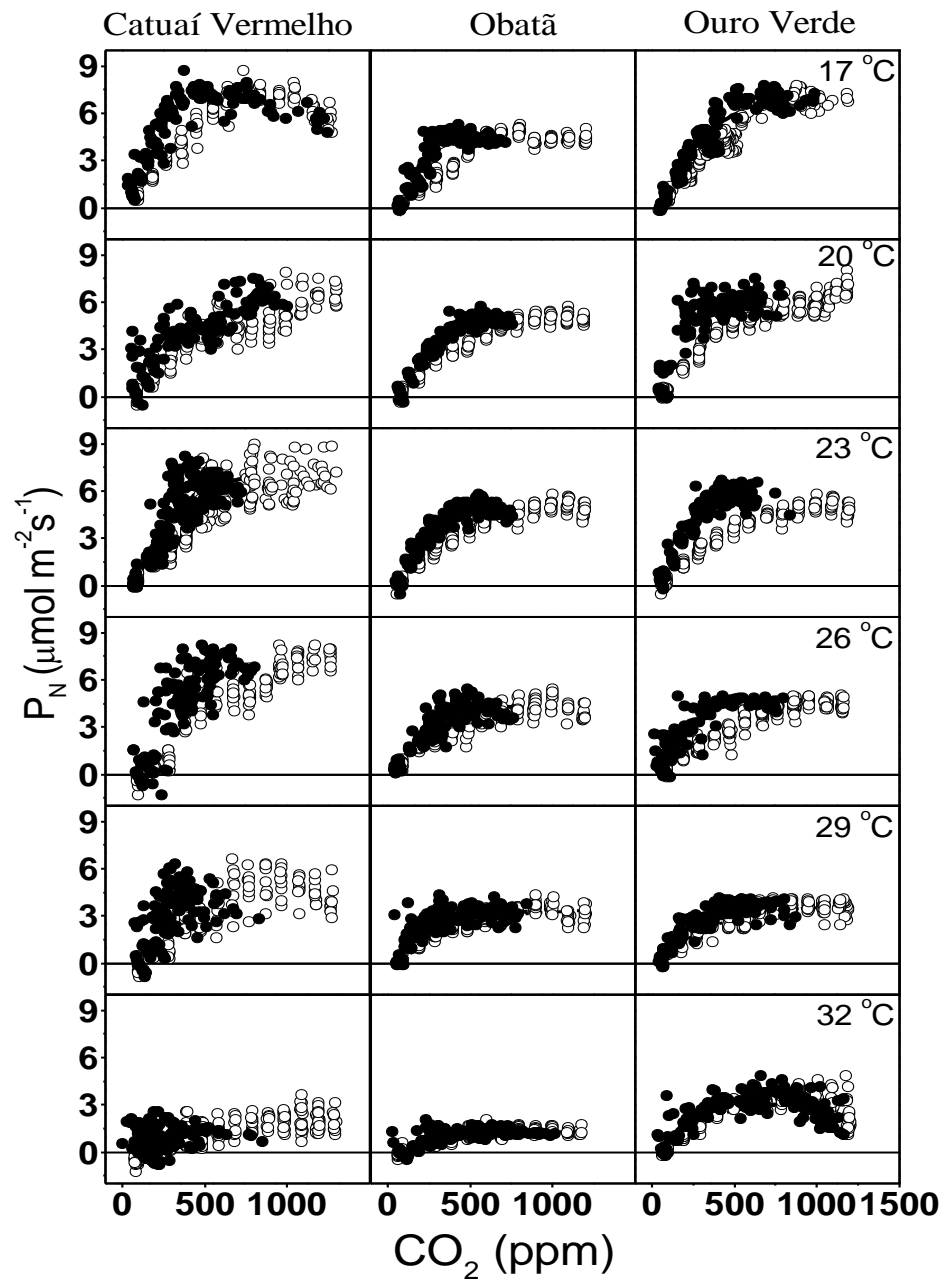


Figure 3. Net photosynthesis (P_N) under saturating ($1.200 \mu\text{mol m}^{-2}\text{s}^{-1}$) photosynthetically active photon flux (PPFD) with regard to external (C_a , open circles) and intercellular (C_i , solid circles) CO_2 concentrations in *Coffea arabica* Catuaí Vermelho, Obatã and Ouro Verde cultivars after 14 hours in an incubator under 17, 20, 23, 26, 29 and 32 °C.