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Diurnal changes in leaf gas exchange and validation of a mathematical model for coffee (*Coffea arabica* L.) canopy photosynthesis

L.F. GÓMEZ[*,***], J.C. LÓPEZ[*], N.M. RIAÑO[*,***], Y. LÓPEZ[**], and E.C. MONTOYA[*]

Federación Nacional de Cafeteros de Colombia - Centro Nacional de Investigaciones de Café, CENICAFÉ, Chinchiná, Colombia[*]
Facultad de Ciencias Agropecuarias, Universidad Nacional de Colombia, Palmira, Colombia[**]

Abstract

Diurnal variations in net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), internal CO_2 concentration (C_i), and water use efficiency (WUE) were studied on individual leaves of coffee plants to determine the effect of climatic factors on photosynthetic capacity. P_N and E showed bimodal behaviour with the maximum values of P_N at mid-morning. At noon, under saturating photosynthetically active radiation (PAR) and high leaf temperature (T_l), P_N declined. In the afternoon (14:00), P_N slightly recovered in association with a decrease in T_l and in leaf-to-air vapour pressure deficit (VPD). Reductions in E during the morning were associated with decreases in g_s. Higher WUE in the morning was related to higher P_N and lower E. The reverse occurred in the afternoon. Goudriaan's simulation model, adapted for coffee canopy photosynthesis, was tested at the level of whole plant (P_{pl}). Three methods were used: (*a*) Whole plant net photosynthesis (P_{pl}) under semi-controlled conditions in a chamber. (*b*) P_{pl} estimation following Goudriaan's method (Gaussian integration) of instantaneous P_N in single leaves at three canopy depths and at three different hours assuming a photosynthesis unimodal behaviour. (*c*) P_{pl} using Goudriaan's method but at five different hours according to the bimodal behaviour reported above. Results of P_{pl} estimates using Goudriaan's model adapted for coffee canopy confirm the observed P_{pl} bimodal behaviour with high fitness degree of the measured whole plant photosynthesis. The high fitness found among observed and simulated data indicates that the modified model may be used as a subroutine for the general simulation model of coffee crop growth.

Additional key words: Goudriaan's model; leaf gas exchange; net photosynthetic rate; whole plant photosynthesis.

Introduction

Photosynthesis is the only natural conversion mechanism of photon energy into chemical energy and it is responsible for 90–95 % of the plant biomass accumulation. Crop photosynthetic rate can be calculated using single leaf net photosynthetic rate (P_N), responses to photosynthetically active radiation (PAR) and air temperature (T_a), leaf area index (LAI), radiation interception, and transmission and distribution through the canopy depending on crop architecture (de Wit 1965, Goudriaan 1986, Spitters 1986).

Photosynthesis is an essential process for developing the simulation models that enable estimates of plant growth and productivity (Ritchie 1995). Most research on photosynthetic activity in different species has used single leaf measurements, whereas photosynthesis by a whole plant or by a population of plants had been tested using mathematical and statistical methods (Goudriaan 1986, Amthor 1994). Other researchers have used biochemical,

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[***] Corresponding author; fax: +57-6-8506550, e-mail: nestorm.riano@cafedecolombia.com

Abbreviations: C_i – internal CO_2 concentration; CV – coefficient of variation; D – extraterrestrial day; E – transpiration rate; g_s – stomatal conductance; I_o – photosynthetically active radiation on the top of canopy; k – PAR extinction coefficient; LAI – leaf area index; n – day of the year; P_{max} – maximum photosynthetic rate; P_N – net photosynthetic rate; P_{pl} – whole plant net photosynthesis; PAR – photosynthetically active radiation; PPFD – photosynthetic photon flux density; RH – relative humidity; R_D – dark respiration rate; T_a – air temperature; T_l – leaf temperature; VPD – leaf-to-air vapour pressure deficit; WUE – water use efficiency; δ – sun declination angle; λ – local latitude; ε – photosynthetic efficiency.

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physiological, and physical variables to develop models that estimate P_N in single plants and plant communities (Acock 1991, Boote and Loomis 1991, Depury and Farquhar 1997). Nevertheless, most of the modelling developments have been carried out on annual species and only very few on perennials (kiwi *Actinidia deliciosa*: Buwalda and Meekings 1992; apple tree *Malus domestica* Borkh: Lakso 1992; some forest tropical species: Allen and Lemon 1976; coffee *Coffea arabica* L.: Quiroga *et al.* 1999).

Most research on external factors controlling the photosynthetic activity in coffee have been carried out on single leaves (Nutman 1941, Decker and Tio 1959, Tio 1962, Nunes *et al.* 1968, Kumar and Tieszen 1980, Hernandez *et al.* 1989, Meinzer *et al.* 1990, Riaño 1991). The first photosynthetic measurements in coffee plants were conducted by Nutman (1937) in Africa who found that CO_2 assimilation rate was greater under moderate irradiance than under full sunshine. Also subsequent researches studied the effects of PAR (Tio 1962, Ramalho *et al.* 1997), T_a (Nunes *et al.* 1968), relative humidity (RH) and leaf-to-air vapour pressure deficit (VPD) (Hernandez *et al.* 1989, Kanechi *et al.* 1995), and biochemical factors (López *et al.* 2000) on P_N, transpiration rate (E), stomatal conductance (g_s), and internal CO_2 concentration (C_i) under controlled conditions. Coffee leaves have the photosynthetic photon flux density (PPFD) optimum around 600 μmol(photon) m^{-2} s^{-1} and optimum temperatures range of 20–25 °C beyond which P_N decreases. Increases in air relative humidity and reductions in VPD (<1.5 kPa) have positive effects on net gas exchange since these variables affect stomatal behaviour (Hernandez *et al.* 1989).

The objective of this work was to study diurnal variations of photosynthesis in response to changes in the environmental conditions prevailing in the central coffee growing region of Colombia and to validate the photosynthetic simulation model for the whole coffee plant developed by Quiroga *et al.* (1999). Since there are very few studies on whole plant photosynthesis on coffee (Berry *et al.* 1989), in this work we used both single leaves and whole plant measurements.

Materials and methods

Localisation: The work was carried out at the Centro Nacional de Investigaciones de Café (CENICAFÉ) headquarters at Manizales (Colombia), 05º01’N, 75º36’W, at an altitude of 1 425 m, mean daily temperature of 21.3 °C, 2 473 mm of yearly rainfall, and 79.8 % relative humidity, with an annual average sunshine of 1 451.1 h (Cenicafé 1999).

First experiment: Diurnal changes of PAR, T_a, RH, leaf temperature (T_l), P_N, E, g_s, and C_i were measured on two expanded leaves per plant from the fourth apical node of five six-month-old coffee plants (*C. arabica* cv. Colombia). Plants were planted in pots containing soil and decomposed coffee pulp (3 : 1, v/v), (07:00 to 19:00 h, each hour). A portable CO_2/H_2O gas exchange system (*LCA-4, Analytical Development Co.*, UK) was used. VPD was calculated according to Caemmerer and Farquhar (1981), and water use efficiency (WUE) was determined on P_N/E basis.

Second experiment: Validation of the simulation model (Quiroga *et al.* 1999) was performed on *C. arabica* cv. Caturra plants grown under nursery conditions during 5 months, in polyethylene bags of 0.17 m diameter and 0.23 m high, on a soil–decomposed coffee pulp (3 : 1, v/v) substrate. Later they were transplanted into pots of 0.30 m diameter and 0.35 m high (22 kg of soil) with adequate water and nutrient supply. The measurements began three months after transplanting.

$\boldsymbol{P_N}$ is fundamental for application of Goudriaan's method. According to Goudriaan (1986), there are two ways to estimate P_{pl}. First, in the absence of data on arrangement of leaf insertion angles, coefficient of PAR extinction through the canopy (k), relation between PAR and P_N, and LAI changes through time, daily P_N measurements on individual leaves at different canopy depths as well as integrated P_{pl} calculations under the generated curves can be made. Second, if LAI values, radiation extinction coefficient through the canopy, extraterrestrial day hour (D), and PAR are known, Gauss integration method can be used.

Measurements on single leaves of coffee trees under controlled and natural conditions (Yamaguchi and Friend 1979, Kumar and Tieszen 1980, Riaño 1991, López *et al.* 1999) showed that the photon-saturating irradiance varied between 500–600 μmol(photon) m^{-2} s^{-1}. Calculated values for initial photosynthetic efficiency (ε) and compensating PPFD were 17.3 μg(CO_2) J^{-1} and 3.8 μmol(photon) m^{-2} s^{-1}, respectively. Up to date no data for whole plant photosynthetic efficiency (ε) and compensating PPFD for coffee exist in the literature.

The whole plant photosynthetic activity measurements were made using the following methods: (*a*) Foliar area and LAI of six plants were calculated according to Arcila (1987). Gas exchange on two plants chosen randomly was measured under transparent plexiglas chambers of 2.01 m^3, placed outdoors, and connected to a CO_2 and water vapour infrared analysis system (Gómez and Riaño 2001). Both chamber temperature and internal RH were stabilised using an electronically controlled conventional air conditioner (*Shimazu/Toshiba*, Japan). T_a, T_l, PAR, and RH inside and outside the chamber were measured using sensors connected to a data-logger (*Hydra Logger Fluke*, USA). Gas exchange was measured over 24 h d^{-1}, every two minutes, during cycles of 3, 4, 6, and

7 d for a total of 20 measurement days, during three months.

P_N was measured with a CO_2 and H_2O infrared gas exchange analyzer (IRGA) *ADC–LCA4* (*Analytical Development Co.*, UK), a data logger, and an *ADC–PLCA4* 6.25 cm^2 leaf chamber. The CO_2 IRGA was calibrated with synthetic air [503 $\mu mol(CO_2)\ mol^{-1}(air)$] and the H_2O IRGA with water vapour (1.15 kPa) generated with an *ADC-WG-601* device. Measurements were taken in the same way and in the same days as in the whole confined plants.

(*b*) Single leaf P_N was measured and integrated according to Goudriaan (1986), following Gauss integration method for three canopy depths and for 3 h d^{-1}, calculated according to:

$L_1 = (0.5 - \sqrt{0.15})$ LAI; $L_2 = 0.5$ LAI;
$L_3 = (0.5 + \sqrt{0.15})$ LAI

where L_1, L_2, and L_3 are lower, middle, and upper canopy plant depths, respectively.

$h_1 = 6 + (0.112709\ D)$; $h_2 = 6 + (0.5\ D)$;
$h_3 = 6 + (0.887298\ D)$;

where h_1, h_2, and h_3 are day hours when photosynthesis instantaneous rate is measured or calculated.

D = extraterrestrial day [h], calculated by:

$$D = \left(\frac{2}{15}\right) \arccos\left(-\tan\lambda\ \tan\delta\right)$$

where λ = local latitude (degrees) and δ = sun declination angle (degrees), calculated by

$$\delta = 23.45° \sin\left[\frac{360°\left(284 + n\right)}{365}\right]$$

where n = day of the year beginning on January 1st ($1 \leq n \leq 365$).

Using the single leaf measurements at different depths and on calculated day hours, the corresponding curves for both data groups were integrated. The first one was made using the measurements at the calculated hours according to Goudriaan (1986) (07:00–12:00 and 17:00 h) and the last one at 07:00–09:00–13:00–15:00 and 17:00 h using the results from the first experiment. The introduction of additional measurements increases agreement between measurements and the integrated values probably because single leaf photosynthesis follows a bimodal tendency (Nutman 1937, Riaño 1991).

(*c*) The photosynthetic simulation model adapted by Quiroga *et al.* (1999) for coffee tree was tested using local latitude, transplant date, genotype, crop density, calculated daily average temperature [°C], and daily sunshine [h] of the period between the date of transplant to the pots and the last measurement.

Data processing and statistical analysis: In the first experiment daily gas exchange curves were generated for every measurement day and areas under the curves were calculated using *AREA.XFM* subroutine of *SigmaPlot 5.0* (*SPSS*). In addition, a better model for the daily assimilation rate of CO_2 in the whole plant was obtained. Integration of results was carried out using the *SAS* program.

In the second experiment daily gas exchange curves were generated for every individual leaf and the area under the curve was obtained as previously described. To calculate the whole plant photosynthesis following Goudriaan's methodology (1986), maximum photosynthetic rate (P_{max}) values, dark respiration rate (R_D), and photosynthetic efficiency (ε) were estimated on incident PAR/net assimilation of CO_2 ratio basis for the whole plant canopy (P_{pl}), adjusted to an asymptotic exponential model (*SigmaPlot 5.0*, *SPSS*, USA)].

CO_2 net assimilation [$kg(CO_2)\ ha^{-1}(leaves)\ d^{-1}$] of confined whole plants (P_{pl}) and those calculated from other methods were compared using Tukey's test (0.05).

Results and discussion

Coffee leaf gas exchange: PAR and T_a showed similar diurnal trends with maximum values between 12:00 and 15:00 h [715.8 $\mu mol(photon)\ m^{-2}\ s^{-1}$ and 29.3 °C]. T_a, RH, and VPD were affected significantly mainly between 12:00 and 14:00 h by cloudiness variations (Fig. 1). High values of VPD (1.5 kPa) affect leaf gas exchange, in spite of moderate PAR values occurring during the experiments (Fig. 1*A*,*D*). Kanechi *et al.* (1995) reported similar results. For the Colombian coffee growing area, during dry periods with low cloudiness, PAR can reach values higher than 1 500 $\mu mol(photon)\ m^{-2}\ s^{-1}$, hence higher air temperature and VPD negatively affect CO_2 assimilation due to stomatal closure (Hernandez *et al.* 1989).

Between 09:00 and 16:00 h (Fig. 1*B*) T_l was higher than T_a, with differences up to 1.0 °C at noon. P_N increased from 07:00 to 08:00 h and then decreased to values similar to those reported by Kanechi *et al.* (1995) and Ramalho *et al.* (1997). The slight increase in P_N at 14:00 was probably due to increase in g_s. C_i also increased (Fig. 1*E*,*F*,*H*).

Variations in E (Fig. 1*G*) were closely associated with variations in g_s (Fig. 1*H*). During the day, g_s and E had a similar behaviour, but between 11:00 and 14:00 h, E increased significantly due to a rise in g_s. Stomata opening and closure in coffee leaves are very sensitive to changes in T_a and VPD (Hernandez *et al.* 1989, Kanechi *et al.* 1995). Nevertheless, increments in E cannot be explained only by increments in g_s, but also by increases in VPD (Fig. 1*D*).

C_i decreased from 07:00 to 10:00 (Fig. 1*F*) due to increases in P_N (Fig. 1*E*). C_i tended to increase after 10:00 as P_N decreased also indicating the coupling between P_N and C_i. This result may be used to estimate the leaf capacity to incorporate atmospheric CO_2.

Fig. 2 illustrates the relationships between C_i, PAR, and T_l. Above PAR of 600 µmol(photon) m^{-2} s^{-1} and T_l greater than 28 °C, C_i tended to increase. These trends can be partially explained by possible increase in photorespiration at both high PAR and T_l. These relationships are illustrated by the following mathematical models: $C_i = 425.1 - (0.64\ \text{PAR}) + (0.0005\ \text{PAR}^2)$ ($r^2 = 0.84$, $p<0.0001$) (Fig. 3*A*) and $C_i = 2\,507.8 - (141.9\ T_l) + (2.3\ T_l^2)$ ($r^2 = 0.62$, $p<0.0001$) (Fig. 2*B*).

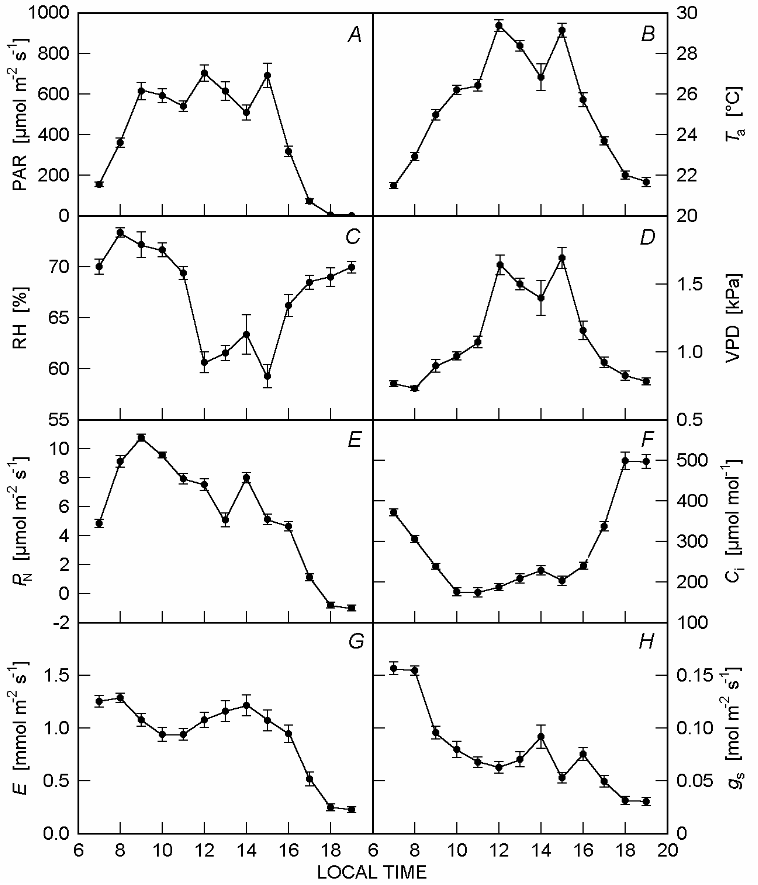

Fig. 1. Diurnal changes in photosynthetically active radiation, PAR (*A*), air (T_a) and leaf (T_l) temperature (*B*), relative humidity, RH (*C*), leaf air vapour pressure difference, VPD (*D*), net photosynthetic rate, P_N (*E*), internal CO_2 concentration, C_i (*F*), transpiration rate, *E* (*G*), and stomatal conductance, g_s (*H*) of coffee leaves during measurement days. *Vertical bars* indicate standard error of means.

P_N as a function of PAR (Fig. 2*C*) indicated that *PAR* saturation was reached at 400 µmol(photon) m^{-2} s^{-1}. However, above 1 000 µmol(photon) m^{-2} s^{-1}, photosynthesis was inhibited. Following the function $P_N = 5.9 - 7.4 \exp(-0.008\ \text{PAR})$ ($r^2 = 0.71$, $p<0.0001$), 71 % of photosynthetic variability is explained by PAR variations. This result agrees with values reported for coffee plants by Kumar and Tieszen (1976).

The effect of T_l on P_N is described by $P_N = -68.1 + (5.2\ T_l) - (0.09\ T_l^2)$ ($r^2 = 0.37$, $p<0.0003$) (Fig. 2*D*). Optimal P_N was reached when $T_l \sim 28$ °C, above which P_N tended to decrease, probably due to enhancement of photorespiration at high temperature (Boyer and Leegood 1997).

These results show that coffee leaves reach an optimum value of photosynthetic activity at PAR between 400–700 µmol(photon) m^{-2} s^{-1} and at air temperature between 26–29 °C. Diurnal behaviour of photosynthesis shows a smaller peak at 14:00 h suggesting a bimodal response (Fig. 1*E*). Other researchers reported similar results (Nutman 1937, Riaño 1991, López *et al.* 1999, Mosquera *et al.* 1999).

P_{pl} under semi-controlled conditions exhibited a bimodal response with a slight midday depression (Fig. 3*D*). P_{pl} was calculated from the data collected in 20 measurement days using the routine *AREA.XFM*, *SigmaPlot 5.0* (*SPSS*) for uneven time intervals. P_{pl} values were higher in days with moderate PAR and T_a, and high RH (Fig. 3*A*,*B*,*C*). The equation that describes the canopy assimilation rate (P_{pl}) during the day is:

$$y = a + bx + cx^2$$

where x = time fraction of hour, and $y = P_{pl}$ [kg(CO_2) ha^{-1}(leaves) d^{-1}]

Model parameters were highly significant ($p<0.0001$) for all studied days. Area under the curve was calculated following the method of Simpson. P_{pl} values obtained by this method (Table 2) were statistically similar to those calculated using the trapezoid method (*AREA.XFM*). The mean value for 20 measurement days was 183.9±27.7 kg(CO_2) ha^{-1}(leaves) d^{-1} [coefficient of variation (CV) = 15 %].

Daily P_{pl} calculated following the Goudriaan's method: The relation between photosynthesis and irradiance can be described by an asymptotic exponential function (Fig. 4), similar to the one found for single leaves, as follows:

$$Y = Y_0 + a\,[1 - e^{-bx}]$$

where Y_0 = -25.55 µg(CO_2) m^{-2} s^{-1} ($p<0.0001$) (dark respiration); a = 539.44 µg(CO_2) m^{-2} s^{-1} ($p<0.0001$) (maximum P_N); b = 0.0084 ($p<0.0001$); r^2 = 0.803, $Y = P_{pl}$ [µg(CO_2) m^{-2} s^{-1}], x = PAR [µmol(photon) m^{-2} s^{-1}].

Photosynthetic efficiency (ε) was calculated using the obtained parameters and equalling the calculated function to the function proposed by Goudriaan (1986):

$$Y_0 + a\left[1 - e^{-bx}\right] = (P_N + R_D)\left(1 - e^{\left(\frac{-I_0\varepsilon}{(P_N + R_D)}\right)}\right) - R_D$$

where Y = dark respiration (R_D), a = maximum photosynthesis (P_{max}), and x = PAR on the canopy (I_o). ε is 19.97 µg(CO_2) J^{-1}, and compensating PPFD (Γ_{light}) is 5.8 µmol(photon) m^{-2} s^{-1}.

To obtain P_{pl} using this method, LAI, extinction coefficient (k) for coffee (Castillo *et al.* 1997), *D*, and PAR incident on the canopy top variables (I_o) were used (Table 1).

P_{pl} estimated from P_N measurement on individual leaves: P_{pl} for three integration hours was lower than P_{pl}

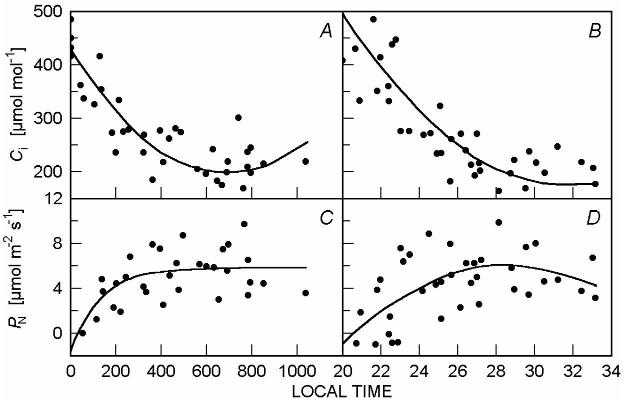

Fig. 2. Response of internal CO_2 concentration, C_i (*A*, *B*) and net photosynthetic rate, P_N (*C*, *D*) to photosynthetically active radiation, PAR (*A*, *C*) and leaf temperature, T_l (*B*, *D*) of coffee leaves.

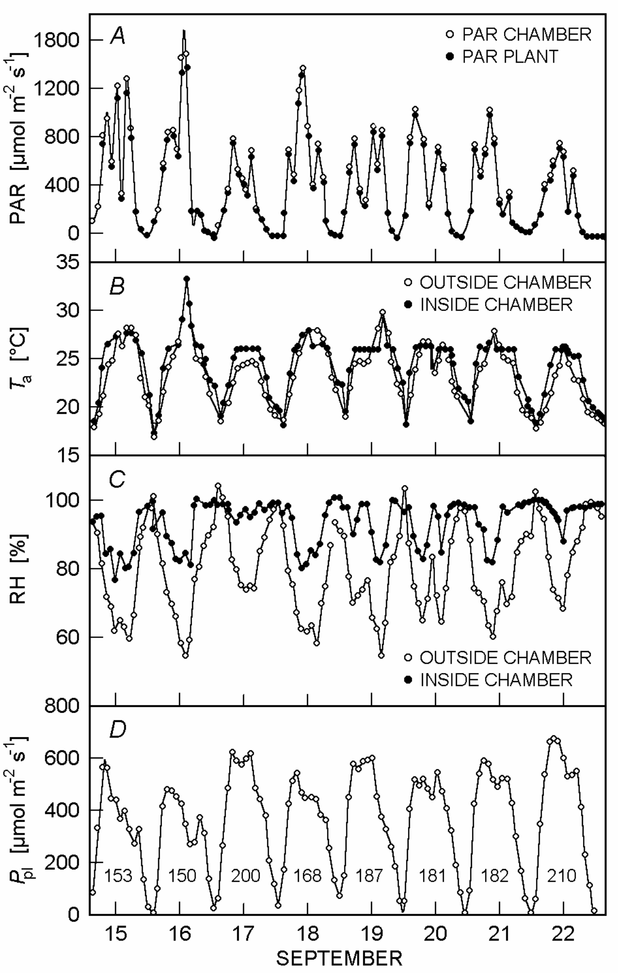

Fig. 3. Behaviour of photosynthetically active radiation, PAR (*A*), air temperature, T_a (*B*), relative humidity, RH (*C*), and CO_2 assimilation rate of the whole plant (P_{pl}) (*D*) under semi-controlled conditions during 8 d. *Values under the peaks* (*D*) correspond to integrated assimilation values [kg(CO_2) ha^{-1}(leaves) d^{-1}].

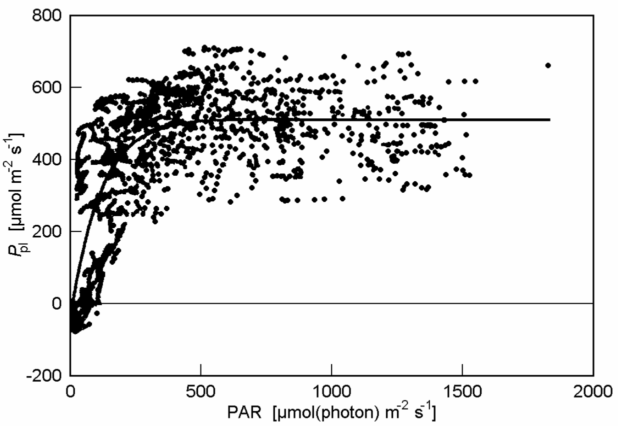

Fig. 4. Relation between photosynthetically active radiation (PAR) and whole plant photosynthesis (P_{pl}) under semi-controlled conditions during 8 d.

Table 1. Behaviour of P_{pl} as function of PAR calculated using Gauss integration method (Goudriaan 1986). Dimensions: I_o [W m^{-2}], D [h], P_{pl} [kg(CO$_2$) ha^{-1}(leaves) d^{-1}]. k was always 0.48, P_{max} was 539.4 μg(CO$_2$) m^{-2} s^{-1}, and $\in$ was 19.97 μg J^{-1}.

Cycle	Month	Day	LAI	I_o	D	P_{pl}
1	8	7	1.20	117	12.07	170.9
1	8	9	1.20	82	12.06	146.5
1	8	12	1.20	73	12.05	138.2
2	8	26	1.27	92	11.98	161.7
2	8	28	1.27	83	11.97	154.1
2	8	29	1.27	98	11.97	166.1
2	8	30	1.27	97	11.96	165.3
3	9	15	1.46	110	11.89	195.4
3	9	16	1.46	114	11.89	198.2
3	9	18	1.46	110	11.88	195.1
3	9	20	1.46	95	11.87	182.9
3	9	21	1.46	83	11.86	171.6
3	9	22	1.46	71	11.86	158.6
4	9	30	1.31	82	11.83	155.0
4	10	1	1.31	38	11.82	99.7
4	10	2	1.31	72	11.82	145.2
4	10	3	1.31	105	11.81	173.1
4	10	5	1.31	91	11.81	162.4
4	10	6	1.31	48	11.80	115.5
4	10	7	1.31	86	11.80	158.2
					Avg	160.7
					Std	24.6
					CV	15.3

measured for five integration hours (Table 2). High CV exhibited by the two methods was probably due to the difference in age and position of the leaves of every layer inside the canopy and the photosynthetic bimodal behaviour.

P_{pl} estimated from P_N measurement on individual leaves and calculated using the model for coffee tree was 175.1±28 kg(CO$_2$) ha^{-1}(leaves) d^{-1} with CV of 16 % (Table 2).

Comparison of P_{pl} measured and calculated for each integration method: Statistical differences ($p<0.01$) were found among methods. No statistical differences among cycles or interactions' method for cycle were found. According to Tukey test (0.05), P_{pl} that was obtained from single leaves' P_N and calculated for three hours (Goudriaan 1986) was the only value that differed from the other ones (Table 2).

P_{pl} values obtained from individual leaves' P_N (five points per day) by the Goudriaan's method and the Quiroga's modified method closely fit those obtained under semi-controlled conditions. Discrepancies were probably due to the observed bimodal response as compared with the parabolic response found by Goudriaan (1982) in various species growing in temperate zones. In self-shaded leaves of coffee plant the photosynthetic pattern was unimodal (Nutman 1937, Riaño 1991, López *et al.* 1999). However, at the growth stage of the plants

Table 2. Comparison between the values P_{pl} [kg(CO$_2$) ha^{-1}(leaves) d^{-1}] observed and estimated by the different methods. Averages with the same letter are statistically equal (Tukey 0.05).

Day	Semi-controlled		Goudriaan		Individual leaves	
	Quadratic	Trapezoidal	(all foliage)	adapted	3 h	5 h
1	147	147	100	119	32	90
2	150	148	116	119	48	95
3	153	154	138	123	60	106
4	155	154	145	123	70	120
5	157	157	146	182	71	138
6	160	159	154	182	83	138
7	168	169	155	183	93	145
8	178	178	158	183	103	159
9	181	181	159	185	108	160
10	181	182	162	188	109	167
11	182	183	162	189	110	169
12	184	184	165	189	113	180
13	189	188	166	190	115	181
14	192	192	171	190	134	192
15	193	193	172	191	149	208
16	207	206	173	192	179	214
17	209	208	183	192	192	233
18	219	220	195	193	192	236
19	220	223	195	194	204	256
20	253	252	198	194	241	297
Avg	183.9 a	183.9 a	160.6 a	175.1 a	120.3 b	174.2 a
Std	27.7	27.9	24.5	28.0	56.6	54.8
CV	15.0	15.2	15.3	16.0	47.0	31.5

utilized in this research, most of the leaves were directly irradiated and their P_{pl} exhibited bimodal behaviour.

Lower variations were observed in P_{pl} measured under semi-controlled conditions on 20 different days during a three-month period (CV = 15 %, Table 2). This was probably due to less variability in leaf age in young plants used in these experiments as compared to older ones (Riaño *et al.* 2000). Higher CV values found for P_N of individual leaves may be explained partly by differences in leaf age and position within the same canopy layers (Table 2). Thus, for P_{pl} estimated on the basis of single leaf P_N, it is advisable to use leaves of similar ages and positions within the layer correspondent to the accumulated LAI.

In conclusion, the Goudriaan photosynthetic model as modified by Quiroga *et al.* (1999) closely estimates true photosynthetic rates for whole coffee plant, when a P_N or P_{pl} bimodal behaviour is taken into account. Thus, the adapted model can be adopted as subroutine operation in a coffee plant growth model.

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