

A chamber for measurement of net photosynthesis on a whole plant

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ABSTRACT. A limitation for quantifying photosynthesis with existing equipment is that they were designed to measure of plant parts, such as one leaf or group of few leaves, which has a great variability over the whole plant. As a consequence, it is difficult to integrate accurately the measurements taken on plant parts in order to assess the process over the entire plant. The objectives of this work were to show in detail a chamber built to measure whole plant photosynthesis and present measurements taken with this apparatus on coffee plants under field conditions. The chamber makes possible to obtain reliable measurements of CO₂ assimilation rates over canopies of different LAI and levels of light exposure. The plant with LAI equal to 1.84 had higher assimilation rates for the whole canopy, but autoshading decreased assimilation rates per leaf area unit, as compared with the plant with LAI of 0.86.

Key words: leaf area index, canopy photosynthesis, coffee plant.

RESUMO. Uma câmara para medir fotossíntese líquida em plantas inteiras. Os atuais aparelhos portáteis que medem fotossíntese no campo foram concebidos para proceder a leituras de uma folha, de parte de uma folha ou de um grupo de poucas folhas, que apresentam grande variabilidade em uma planta. A grande variabilidade entre as partes da planta dificulta a integração das medidas. Há, portanto, a necessidade de se desenvolver medidas do fluxo de CO₂ na planta como um todo, em seu ambiente natural, para então utilizar os valores medidos para avaliar a performance dos modelos em simular o processo envolvido. O objetivo deste trabalho foi mostrar os detalhes de construção de uma câmara para medir fotossíntese de plantas inteiras de cafeeiro, em condições de campo. Os resultados indicaram que a câmara construída tornou possível a medição da fotossíntese em plantas inteiras, em folhas expostas a diferentes intensidades de radiação solar. A planta com IAF 1,84 apresentou maior assimilação por planta e menor taxa fotossintética por unidade de área foliar do que aquela com IAF 0,86.

Palavras-chave: índice de área foliar, fotossíntese da copa, cafeeiro.

Introduction

Among the several processes simulated by most of the plant growth models reported in literature, photosynthesis is of major importance because it is responsible for carbohydrate surplus for plant growth. Assuming models as hypothesis of how plants behave under different environmental stimulus, there is a need to validate those models before applying them to simulate the system of interest.

In general, the equipments for measuring photosynthesis normally commercialized consist of three major components: a leaf chamber, an infrared gas analyzer and a console control. A limitation of quantifying photosynthesis with these equipments is that their chambers were designed for measurement of plant parts, such as one leaf or a group of few

leaves, which have a great variability over a whole plant, mostly due to differences in income radiation, water pressure deficit and physiological characteristics of each plant organ (Marur and Faria, 2006). As a consequence, it is difficult to integrate accurately the measurements taken on several leaves in order to assess the process over the entire plant. Therefore, there is a need to develop methods to measure CO₂ flux on a whole plant, in its natural environment, to test the performance of the models to simulate carbon fixation and even to compare different treatments in some studies.

The major benefit of the photosynthesis measurements on entire plants might be for crops with ununiform canopy, covering partially the soil, such as hedgerow crops. Among them, coffee has irregular horizontal foliage distribution, even for uniform row spacing, which leads to higher light

absorption by the clustered leaves and light penetration to the soil surface on the points where leaf cover is scarce. In addition, light interception by the canopy is affected significantly by solar elevation during the day and through the year, because of the variation on solar incidence angle. Therefore, the equipment to measure whole plant photosynthesis should integrate the effects of direct and diffuse absorbed radiation as a function of canopy height and width, leaf area index, leaf angle, row orientation, latitude, day of year and time of day.

Liu *et al.* (2000) presented an extensive review on chambers for measurements of processes on whole plants. The chambers range from the very simple, controlling a single environmental variable, to sophisticated conception, controlling multiple variables. Despite of a great interest in plant responses to controlled environments under natural light, the number of sunlit growth chambers is much less than those of indoor growth chambers. Furthermore, they generally must deal with problems of response time for an accurate control of temperature and humidity to compensate the interference of dramatic disturbances of solar irradiance.

The main objective of this work was to show in detail a chamber built to measure whole plant photosynthesis; the secondary objectives were to present measurements taken with this apparatus on coffee plants under field conditions and compare these measurements with the traditional method.

Material and methods

The following adaptations were performed on a portable photosynthesis system (PPS, Model 6200, Li-Cor, Inc., Lincoln, NE, USA), configured at absolute mode. The part of the PPS named “sensor head” was attached to a square wooden frame of 1m wide x 0.15 m high and 0.02 m thick (Figure 1A). In order to collect (and to devolve) the air sample around the plant, two plastic hoses of 1m each were connected into the inlet and outlet sensor head; the other end of each hose was connected to a T device, in whose extremities other 20 cm plastic hoses were installed. To provide for the system the average of temperatures from three different positions of the plant canopy, the original leaf thermocouple was replaced by another chromel-constantan wire (1.5 m long and 0.25 mm of diameter) from which three in-parallel junctions were turned (Figure 1A).

Eighteen fans powered by a 12 V battery were set at different heights and positions around the square wood frame described above to provide sufficient air mix for the system (Figure 1B). The part of the PPS

named “chamber” (0.25, 1 or 4 L volume) was replaced by a structure named “cover” with dimensions of 1 x 1 x 1 m and a pyramidal form at the top (1.19 m³ of total volume), enforced on the bounds by 0.015 m iron sheets and wrapped with an 88% light translucent plastic film.

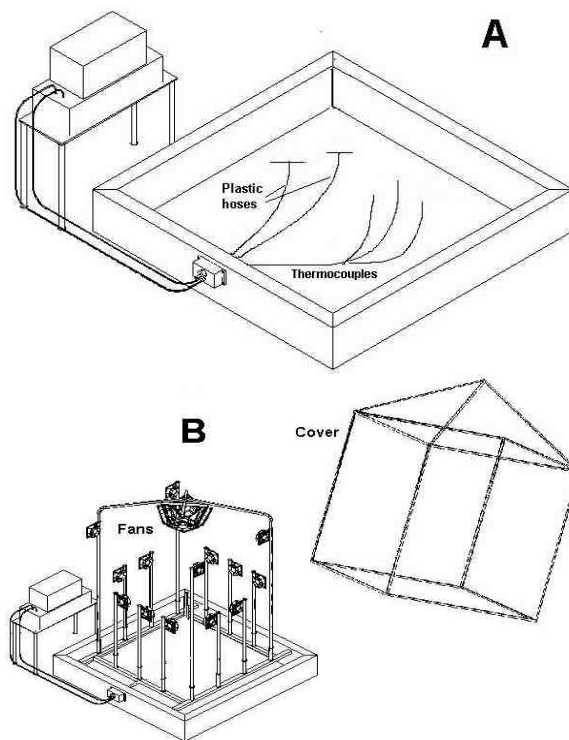


Figure 1. Details of the whole plant photosynthesis chamber. A: sensor head attached to the wooden frame, plastic hoses and thermocouples. B: cover and fans.

The adapted equipment was used to take measurements on coffee plants (*Coffea arabica* L.), grown under field conditions at the Experimental Station of the Instituto Agronômico do Paraná, in Londrina, State of Paraná, Brazil (latitude 23°18'S, longitude 51°09'W). Initially, soil surface was smoothed and covered with a plastic film to prevent soil gas entering in the system. Then, the wooden frame was closely settled on the ground to prevent air leaking from the closed system. During the measurements, the cover must be closely set on the wooden frame (Figure 2). In order to prevent gas leakage through some gaps between the cover and the wooden frame, a rubber tape was fixed on the superior side of the wooden frame (previous tests using injection of CO₂ gas showed no leakage from this apparatus).

Measurements of net photosynthetic rates of whole plants were made on May 7 and 8, 2003, from 8 to 18h, using two coffee plants with leaf area index

(LAI) of 0.86 and 1.84, respectively. The cultivar was Iapar 59, planted at spacing of 2.1 x 1.7 m, with sufficient soil water content to provide normal growth condition to the plants.



Figure 2. A view of the adapted equipment.

Each measurement was taken with air flow rate into chamber of about 1280 mol s^{-1} , according to the following sequence: a) turn on the fans after checking the joint thermocouples/leaves to ensure perfect connections; b) assure that CO_2 concentration around the plant is stabilized; c) place the plastic cover on the wooden frame; d) press “log key” at the consol control for initiating the measurement, which lasted 20 seconds; e) finishing the measurement, taking cover off and stopping fans. Net photosynthesis rates were automatically calculated from CO_2 changing rates, plant leaf area, chamber volume and inside air temperature and pressure. All this sequence was repeated in approximately 15 minutes intervals.

Net photosynthetic rates were also measured on individual leaves of those plants, with the one liter-chamber, from 7:30 to 10:00, on May 9. Measurements were taken on three leaves of each photosynthetically active radiation exposure (totally exposed, shaded and mid shaded). The meteorological conditions during the three days period were very similar, with clear sky.

Results and discussion

In general, since the moment the covering was placed on the wooden frame until the measurement was finished, it did not last more than sixty seconds. CO_2 concentration decreased at most 4 ppm (for example, from 360 to 356 ppm) and leaf temperature increased no more than 1.5°C from the beginning to the end of each measurement.

Daily course of CO_2 assimilation per leaf area

unit over the whole canopies, provided by the adaptation described, showed different rates for both plants during the morning period, when the plant with lower LAI presented higher assimilation rates (Figure 3). In both plants, the rates increased steadily since early morning to reach a plateau around 10:00, indicating that saturating irradiance had been reached. The peak rates were between 4 to $4.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the plant with LAI of 0.86 and about $3.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the plant with LAI of 1.84, corresponding to PAR around $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Figure 4). Maximum rates lasted until noon, and then decreased gradually during the afternoon. Photosynthesis rates in coffee plants may be maintained at high values even at temperatures above 30°C (DaMatta, 2004a). Thus, the lower rates observed at afternoon are probably due to the decreased stomatal conductance to water vapor in response to the air dryness.

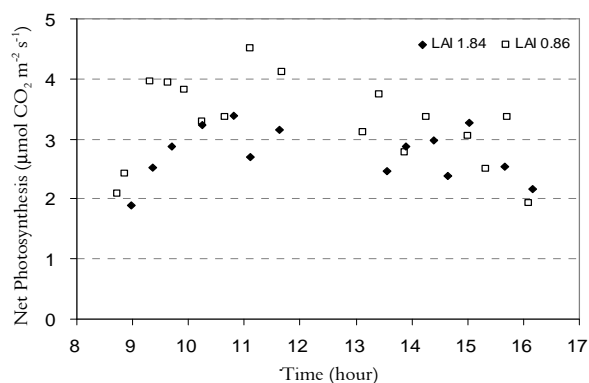


Figure 3. Daily course of photosynthetic rates per leaf area unit measured with the chamber on whole canopy of plants with different leaf area index (LAI), during May 7 and 8, 2003.

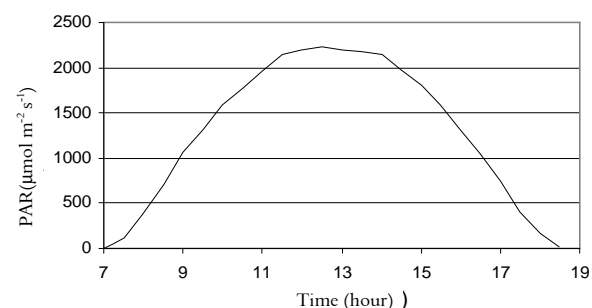


Figure 4. Daily course of photosynthetically active radiation (PAR) measured on the canopy of plants during May 7 and 8, 2003.

Even though the photosynthesis rates obtained on individual leaves (using the one-liter chamber) were different comparing in respect to light exposure at the same plant, they were statistically similar in both LAI, at each light exposure (Table 1). The rates were close to the measurements taken

from individual leaves of two-year-old greenhouse grown coffee plants by Nunes *et al.* (1993) and Fahl *et al.* (1994), from leaves of adult coffee trees planted on large spacing by Mazzafera *et al.* (1995) and Oliveira *et al.* (2001), and also from leaves of a coffee crop cultivated on high plant population by Marur *et al.* (2001). Photosynthesis rates were obtained even for low PAR ($80 \mu\text{mol m}^{-2} \text{s}^{-1}$), which indicates a lower light compensation point (LCP), such as also observed by Kumar and Tieszen (1976) and related by Rena *et al.* (1998), who found LCP for coffee leaves varying from 30 to $80 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Table 1. Photosynthesis rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) measured on individual leaves (using the one-liter chamber) from plants with different leaf area index (LAI), according to different light exposure during May 9, 2003.

Light Exposure	PAR $\mu\text{mol m}^{-2} \text{ s}^{-1}$	LAI	
		1.84	0.86
Exposed	1400	7.82 a A	8.27 a A
Shaded	90	1.64 b A	1.39 b A
Mid shaded	Intermediary	2.59 b A	2.65 b A

Data represent the mean value of four replicates. Means followed by the same letter are not significantly different (Tukey test, 5%). Capital letter refer to comparison among both LAI plants, in each light exposure.

Thus, since photosynthesis rate per leaf area unit of whole canopy (Figure 3) is resultant of the integration of all leaves, the differences between plants can be attributed to auto-shading, which is lower on the smaller plant.

The assimilated CO_2 for the whole plants, calculated by the product of leaf area and the values of photosynthesis rates shown in Figure 3, was higher for the plant with higher LAI (Figure 5). The peak rates were close to 1 gram $\text{CO}_2 \text{ plant}^{-1} \text{ h}^{-1}$ for the bigger plant and about 0.6 gram $\text{CO}_2 \text{ plant}^{-1} \text{ h}^{-1}$ for the smaller plant. Daily integrations of CO_2 assimilation per plant were equal to 6.8 and 3.8 g for the plants with higher and lower LAI, respectively.

All the above data make evident that caution should be taken when one calculates whole plant assimilation by multiplying LAI and mean rates of individual leaves. While assimilation rates of individual leaves in response to light exposure are measured satisfactorily using small chambers (a quarter-liter, one-liter or four liter chambers), the constraint to calculate the whole plant assimilation resides on the difficulty to estimate the mean rate, mostly because the canopy is exposed to different levels of incident PAR. The presented adaptations make possible to integrate assimilation rates of leaves under different levels of light exposure over the canopy, obtaining reliable measurements of photosynthesis for the entire plant. The calculated CO_2 assimilation rates, as shown in Figure 5,

include all the complexity involved on radiation interception on the canopy and physiological response of each leaf, which is practically impossible to consider using the traditional method.

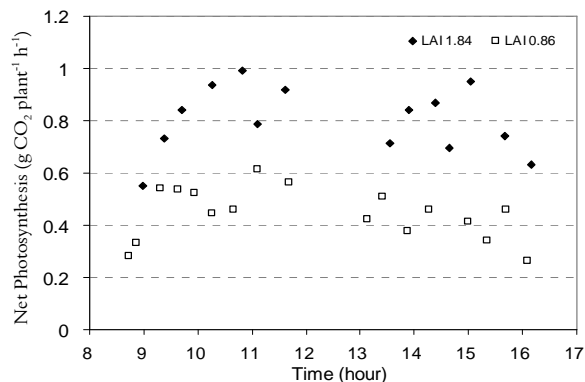


Figure 5. Calculated photosynthetic rates per plants with different leaf area index (LAI) during May 7 and 8, 2003.

Reinforcing our results, DaMatta (2004b) suggests that interpretation of short-term gas exchange measurements in individual leaves of stressed plants may be problematic if the total leaf area is not considered. Even if it is considered, short-term gas exchange measurements may not reveal differences in total carbon assimilation at the canopy level since the current gas exchange characteristics of a particular leaf may deviate considerably from those of the other levels.

The adaptations and the measurements shown in this paper can be useful for testing the existing photosynthesis models and eventually reformulating them. In addition, the chamber showed to be practical and easy to manage due to its low weight, requiring one person to do the work, in spite of its dimensions.

Conclusion

The chamber built to measure plant photosynthesis showed to be easy to manage and practical to measure photosynthesis rates of entire coffee plants;

- the apparatus makes possible to obtain reliable measurements of CO_2 assimilation rates over a canopy under different levels of light exposure and integrate measurements to obtain the whole plant photosynthesis of plants with different LAI;

- measurements using the chamber showed higher assimilation for the plant with higher LAI, but lower rates per unit leaf area because of auto-shading;

- the traditional method using the one-liter chamber gave good measurements of individual leaf

assimilation response to incident PAR, but it was considered to be inadequate to estimate whole plant photosynthesis because of the difficulty to integrate the dynamics of incident radiation in the canopy.

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