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Stomatal resistance and transpiration rates of shaded and unshaded cacao trees

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Abstract

Measured leaf stomatal resistances (Rs) were used to estimate transpiration rates (TR) on different canopy layers of shaded and unshaded cacao trees. Data taken on a sunny and an overcast day were used to compare the stomatal and transpirational behavior of the canopies. Stomatal resistances on the overcast day for the unshaded tree increased gradually from the upper to the lower canopy layer, with a consequent decrease in TR. The Rs for the leaves of the shaded tree were lower for the bottom than for the upper canopy layer leaves. This was presumably due to the higher irradiance received by the lower canopy layers. Greater irradiance in the bottom layers of the shaded tree was caused by the shade of an *Erythrina fusca* that impeded light penetration to the upper layers even at lower solar angles. Stomatal resistances and TR, on the sunny day for the unshaded tree and between two areas of the upper canopy on the shaded tree, were closely correlated to irradiance. Estimated daily TR, for the shaded tree, were of the same order of magnitude of TR computed by other authors by different methods.

Key words: Theobroma cacao, stomatal resistance, transpiration, micrometeorology

Resistência estomática e taxas de transpiração de cacaueiros sombreados e não sombreados

Resumo

Medidas de resistência estomática (Rs) foram usadas para estimar a taxa de transpiração (TR) em diferentes camadas da copa de cacaueiros sombreado e sem sombreamento, em dias ensolarado e nublado. Na árvore sem sombreamento, durante o dia nublado, os valores da resistência estomática apresentaram um aumento gradativo da camada superior para a inferior, com conseqüente decréscimo da TR. Na árvore sombreada, os valores da Rs foram menores nas folhas da camada inferior do que nas da parte superior da copa. Isto foi causado, provavelmente, pela maior irradiação recebida pelas camadas inferiores da copa, devido à sombra de *Erythrina fusca*, a qual impediu a penetração de luz nas camadas superiores, mesmo em ângulos solares menores. Resistência estomática e TR, no dia ensolarado, no cacaueiro não sombreado e em dois pontos amostrados da camada superior, no cacaueiro sombreado, mostraram estreita correlação com a irradiação. As transpirações estimadas diariamente, para o cacaueiro sombreado, foram da mesma ordem de magnitude que aquelas computadas por outros autores por diferentes métodos.

Palavras-chave: Theobroma cacao, resistência estomática, transpiração, micrometeorologia

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Introduction

Transpiration rate (TR) of trees can be difficult to determine because of the large canopy size. Due to the high cost of equipment for measuring TR, attempts have been made to calculate TRs of trees by more inexpensive and simpler means. Alvim (1959) calculated TR of cacao leaves by weighing detached leaves after different periods of time. He assumed that a mature cacao tree have approximately 5000 leaves, and therefore estimated that it may transpire about 40 liters of water per day, depending upon region and climatic changes. This estimation also assumes that all leaves transpire at the same rate. Cadima and Alvim (1982) estimated (TR) of cacao trees measuring, gravimetrically, changes in volumetric soil water content. They calculated that under well-watered conditions an adult cacao tree could transpire 45 liters per day. In their study, corrections for vertical water movement were not done. Also, it was assumed that losses due to evaporation were minimal, since the soil was covered with plastic sheets. Therefore, all the soil water lost was presumably due to cacao transpiration.

In this report the diffusion through the stomatal opening due to difference in vapor pressure gradient between leaf and air was calculated from direct measurements of stomatal resistance and leaf and air temperatures. This approach was used to estimate the dynamics of water lost by the canopy and canopy layers of shaded and unshaded adult cacao trees, and to compare the estimated TR to values computed by other methods.

Materials and Methods

This study was conducted in September 1985, at the experimental farm of the Cacao Research Center (CEPEC), situated 22 km west of the port of Ilhéus in the state of Bahia, Brazil (lat. 14° 47' S. long. 39° 16' W, 86 m above sea level). Leaf stomatal resistances (Rs) were determined in shaded and unshaded cacao trees in a 7-year old plantation of the cultivar 'Catongo', planted at 3 x 3 m. The shaded cacao plant was growing at a distance of about 2.0 m from an *Erythrina fusca* shade tree. The unshaded tree was located about 15 m from the shaded tree in such a way that it received direct solar radiation from about 0800 h local time to approximately 1700 h. The cacao trees were chosen for canopy similarity and uniformity. Stomatal resistance was measured in the final three leaves of a flush of similar age (about 90 days after flushing), at different canopy layers in both trees as shown in Table 1. The soil at the research site, classified as Typic Tropudalf serie Sede, was more than 1.5 m deep, well-drained, and at soil-water field capacity on the measuring days.

Stomatal resistances were determined with a diffusion porometer (Delta MK II, Delta Devices, England), photosynthetic photon flux density (PPFD) with a quantum sensor (LI-190, LICOR Inc., USA), and dry and wet bulb temperature with a psychrometer (Assmann, Casella, England) located at 2.0 m above ground. Transpiration rates (TR) in mmoles H_2O m^{-2} s^{-1} were calculated utilizing the following equation: TR = Mw/RT (e^* - ed)/Rs; where Mw is the molecular weight of water (18), R is the gas constant (8.3143 x 10^{-3} m^{-3} Pa $mmol^{-1}$), T is the air temperature (degrees Kelvin), e^* is the saturation vapor pressure (Pa) at the leaf temperature as measured by the thermistor of the porometer and assuming that the intercellular leaf spaces were at saturation, and ed is the vapor pressure (Pa) for the air mass calculated from the wet bulb temperature of the Assmann psychrometer.

An overcast (Sept. 13) and a sunny (Sept. 19) day, from several days of measurements, were chosen in order to compare the stomatal and transpirational behavior within and between canopies. On Sept. 13, pooled averages were computed from about 0900 h to approximately 1500 h because environmental conditions were relatively uniform during that period. Comparisons between means were done by Students 't' tests using pooled variance estimates (Steel and Torrie, 1960). The analyses were executed utilizing the Statistical Analysis Systems package (SAS Institute, 1982).

Leaf area indices (LAI) for the shaded and unshaded trees were calculated from leaf area densities (m^2 m^{-3}). Leaf area densities were measured in successive layers of 0.3 m in trees located in the

Table 1 – Description and irradiance characteristics of canopy locations in which leaf temperature and stomatal resistance were measured on shaded (S) and unshaded (U) 'Catongo' cacao trees.

Point	Direction	Description
		September 13, 1985
1U	NW	Lower canopy. Maximum PPFD 45 μE m^{-2} s^{-1}
2U	NE	Middle canopy. Maximum PPFD 150 μE m^{-2} s^{-1}
3U	N	Upper canopy. Maximum PPFD 1700 μE m^{-2} s^{-1}
1S	N	Lower canopy. Maximum PPFD 200 μE m^{-2} s^{-1}
2S	W	Middle canopy. Maximum PPFD 150 μE m^{-2} s^{-1}
3S	NW	Upper canopy. Maximum PPFD 80 μE m^{-2} s^{-1}
		September 19, 1985
1U	NW	Lower canopy. Maximum PPFD 1150 μE m^{-2} s^{-1}
2U	NE	Middle canopy. Maximum PPFD 1350 μE m^{-2} s^{-1}
3U	N	Upper canopy. Maximum PPFD 2100 μE m^{-2} s^{-1}
1S	W	Upper canopy. Maximum PPFD 50 μE m^{-2} s^{-1}
2S	N	Upper canopy. Maximum PPFD 340 μE m^{-2} s^{-1}

same experimental area (Miyaji, Silva and Alvim, s. d.). These data were also used to calculate LAI distribution of shaded and unshaded trees.

Daily transpiration per tree, for a photoperiod of 10 hours (L $tree^{-1}$), was calculated by multiplying instantaneous TR by the percentage of leaf area at a specific canopy layer. The resulting value was multiplied by 9 m^2, based on a 3 x 3 m spacing. Total daily transpiration for the tree was, therefore, the summation of the transpiration rates at each canopy layer.

Results

Stomatal resistance. Diurnal courses of mean leaf Rs for the shaded and unshaded trees, at different canopy layers, on an overcast day (Sept. 13, 1985) are plotted in Figs. 1A and 2A, respectively. The unshaded tree showed a distinct difference between Rs measured at the top and that measured at lower canopy layers. Stomatal resistance increased gradually from top to bottom of the canopy. Pooled mean Rs ($\pm$ standard error) for upper canopy layer leaves was 200 $\pm$ 24 s m^{-1} until about 1500 h from which Rs began to increase. The maximum measured mean Rs value for upper canopy leaves was 640 $\pm$ 46 s m^{-1} at about 1700 h when incident PPFD was 55 $\mu E\ m^{-2}\ s^{-1}$ (Fig. 2C). Pooled Rs average for lower layer leaves was 570 $\pm$ 31 s m^{-1} until 1500 h from which it increased to 1350 $\pm$ 150 s m^{-1} at approximately 1700 h. Irradiance at 1700 h for the lower layer leaves was 4 $\mu E\ m^{-2}\ s^{-1}$ (Fig. 2C). The pooled Rs averages from lower and upper layer leaves were significantly different from each other ($P < 0.05$). Middle canopy had a pooled mean value of 363 $\pm$ 22 s m^{-1} until about 1500 h increasing thereafter. Stomatal resistance for the leaves in the middle canopy layer were significantly different ($P < 0.05$) from lower and upper layer leaves.

The Rs pattern in the shaded tree was different than that of the unshaded tree. Upper canopy leaves had higher resistances than middle layer leaves. The pooled Rs average measured for the upper canopy layer was 750 $\pm$ 36 s m^{-1} until about 1500 h. Pooled Rs averages for the middle and lower canopy layers were 460 $\pm$ 25 and 345 $\pm$ 22 s m^{-1}, respectively. These values were significantly different ($P < 0.05$) from each other and from Rs of upper canopy leaves.

Stomatal resistances measured on both shaded and unshaded trees on the sunny day (Sept. 19) are plotted in Figs. 3A and 4A, respectively. The relative Rs differences among leaves of the upper, middle, and lower canopy on the unshaded cacao tree were maintained. That is, leaves of the upper layer had lower Rs than those of the middle and bottom layers. For the shaded tree, depending upon radiation interception, the leaves that received greater irradiance levels had lower Rs. Stomatal resistances, for this day, were more variable among canopy layers in each tree and between trees than for the overcast day. This may be explained by brief periods of light penetration (sunflecks), which impinged upon the leaves affecting the dynamic behavior of stomata. Also, Rs began to increase about two hours earlier than

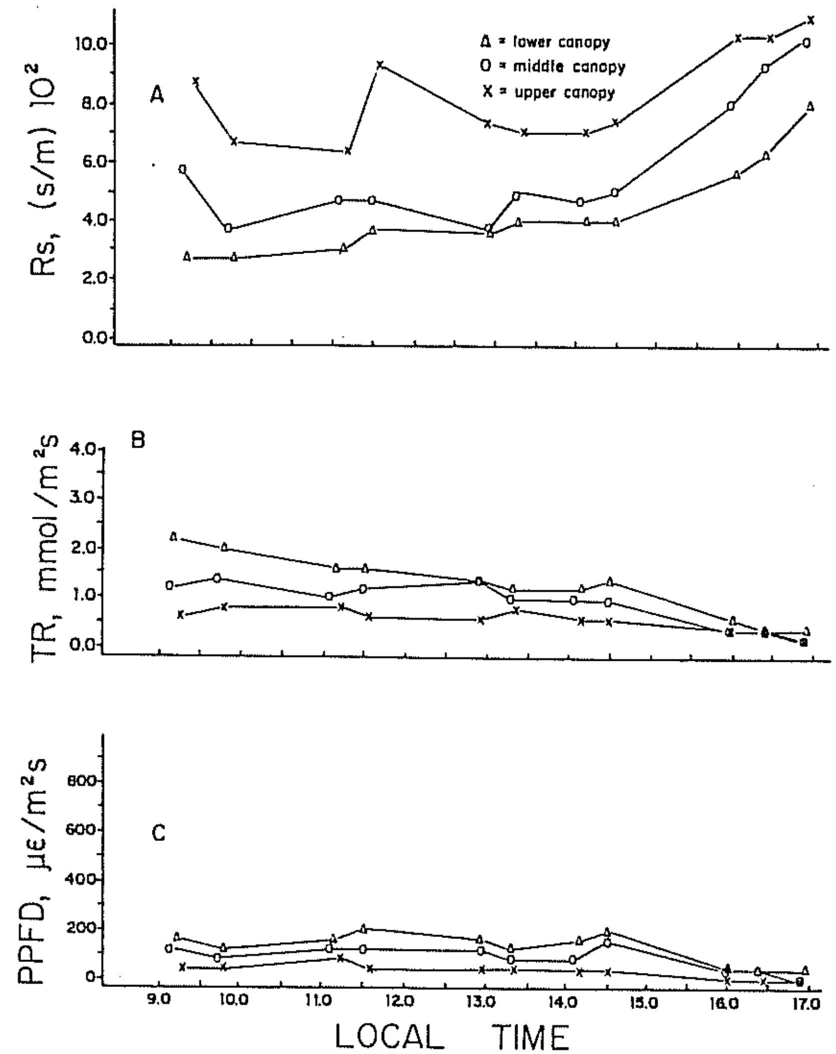

Figura 1 – Stomatal resistance (Rs), transpiration rates (TR) and photosynthetic photon flux density (PPFD) measured at different leaf layers on a shaded cacao tree on Sept. 13, 1985, an overcast day.

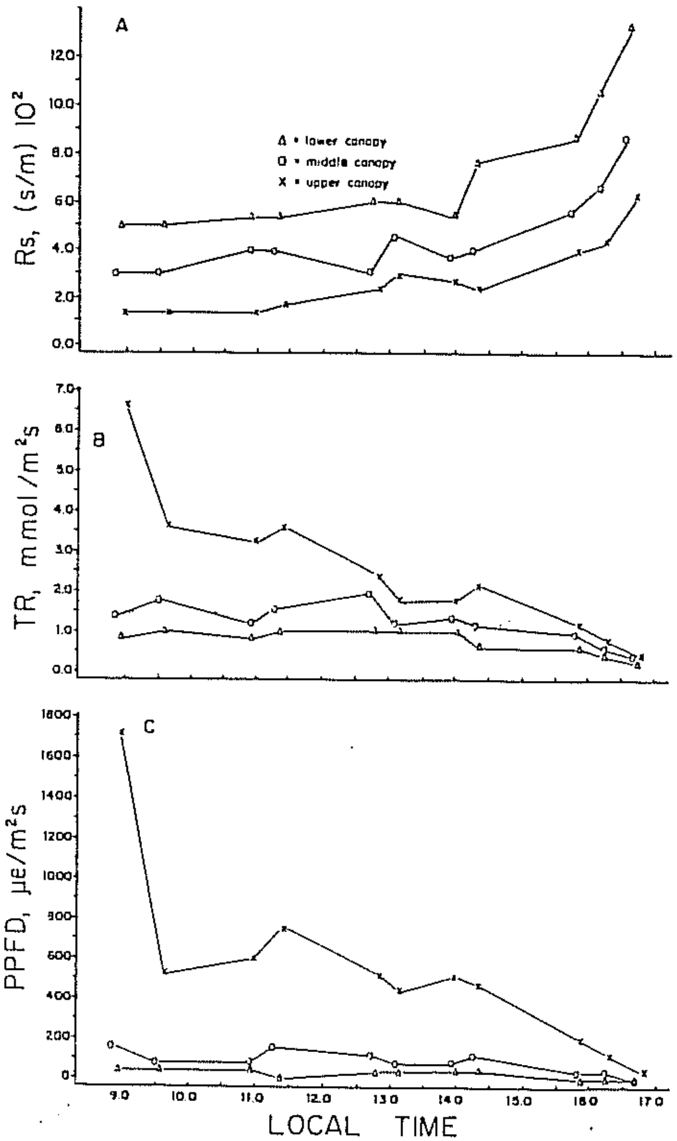

Figura 2 – Stomatal resistance (Rs), transpiration rates (TR) and photosynthetic photon flux density (PPFD) measured at different leaf layers on an unshaded cacao tree on Sept. 13, 1985, an overcast day.

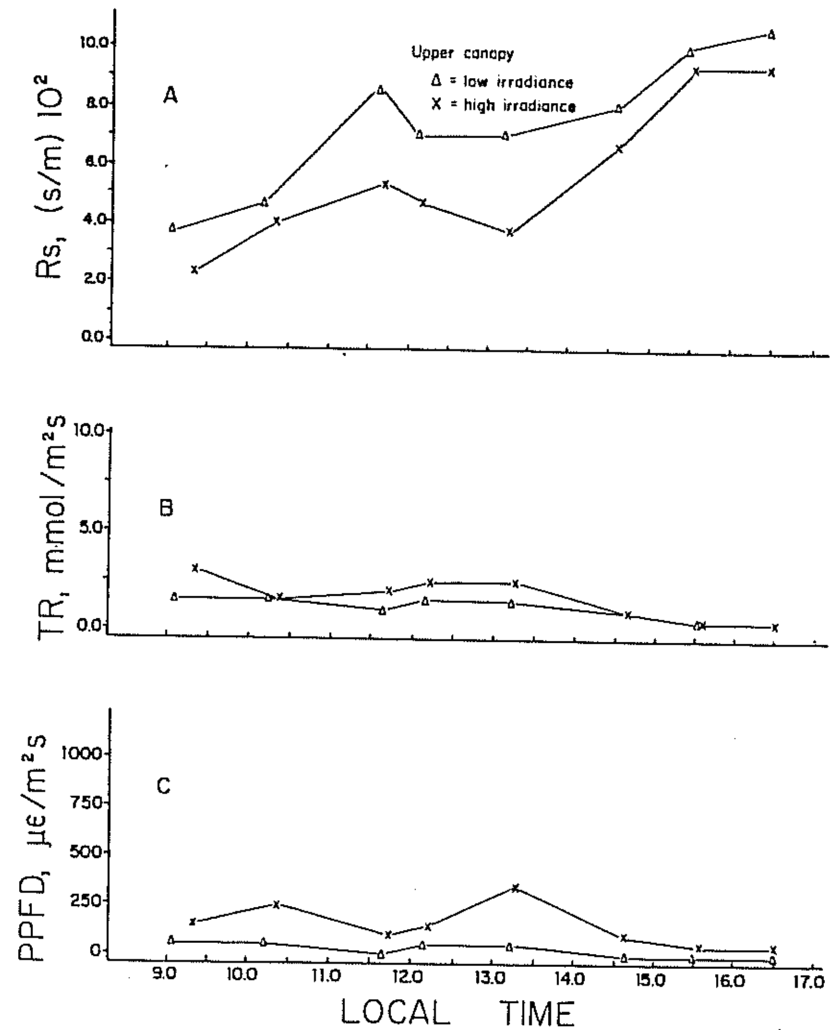

Figura 3 – Stomatal resistance (Rs), transpiration rates (TR) and photosynthetic photon flux density (PPFD) measured at different leaf layers on a shaded cacao tree on Sept. 19, 1985, a sunny day.

during the overcast day in which radiation, measured at the top of the canopy, was about 75% lower.

Transpiration rates. Daily time courses of estimated mean TR for both trees under the conditions studied are presented in Figs. 1B and 2B for Sept. 13. Transpiration rates of leaves of the upper canopy on the unshaded tree were higher than rates for the leaves of the middle and lower canopy. Also, TR for the upper canopy leaves gradually decreased as the day progressed. Lower and middle canopy leaves showed a relatively constant TR for most of the day, although decreasing after 1500 h. A pooled TR average of 1.48 ± 0.29 mmol H_2O m^{-2} s^{-1} for middle canopy layer leaves was significantly higher than that for lower layer leaves, maintaining a pooled mean TR difference of 0.71 ± 0.16 mmol H_2O m^{-2} s^{-1} higher than lower leaves until 1500 h, decreasing thereafter. Transpiration rates, on Sept. 13, for the shaded tree were lower than those for the unshaded tree. Also, a different TR pattern was observed. Pooled TR averages for upper, middle, and lower layer leaves were 0.70 ± 0.03, 1.17 ± 0.05, and 1.60 ± 0.12 mmol H_2O m^{-2} s^{-1}, respectively, until about 1500 h. These values were significantly different from each other ($P < 0.05$).

Transpiration rates on Sept. 19 were higher and more variable on both cacao trees than TR measured on Sept. 13. Peak midday average TR for the upper canopy layer leaves of the unshaded tree was 7.1 ± 19 mmol H_2O m^{-2} s^{-1}, wheareas middle and lower canopy leaves had midday peaks of 2.9 ± 0.25 and 2.6 ± 0.8 mmol H_2O m^{-2} s^{-1}, respectively (Fig. 4B). Midday TR averages for the shaded tree were 2.44 ± 0.19 and 1.65 ± 0.11 mmol H_2O m^{-2} s^{-1} for the two upper canopy layers measured (Fig. 3B). Leaf temperatures, T_L, leaf-to-air temperature difference, DT, and leaf-to-air vapor pressure gradient, VPG, for the cloudy day, Sept. 13, were similar on both shaded and unshaded cacao tree (Table 2). Values for T_L, DT and VPG were, approximately, 27.0 °C, 3.0 °C, and 0.54 kPa, respectively. However, on the sunny day, Sept. 19, T_L were about 7 °C higher than T_L recorded on the cloudy day. Also, DT and VPG were twice as much those measured for the cloudy day.

Leaf temperatures measured on the sunny day for leaves of the upper canopy of the unshaded tree, were almost 2 °C higher than T_L of the lower and middle canopy. Also the upper leaf canopy had higher DT and VPG than the lower layers (Table 2).

For the shaded tree, on the sunny day, the point of the upper canopy layer in which the irradiance was higher, T_L and DT were about 1 °C lower than T_L and DT of the point of lower PPFD incidence. Also, VPG was about 0.2 kPa lower.

Discussion

For the unshaded tree, on both the overcast (Sept. 13) and sunny days (Sept. 19), estimated TR for the upper canopy was higher than TR for the middle and lower canopies. This pattern was expected, because Rs decreased gradually from top to bottom of the canopy, and also because of the inverse relationship betwen TR and Rs. For the shaded tree,

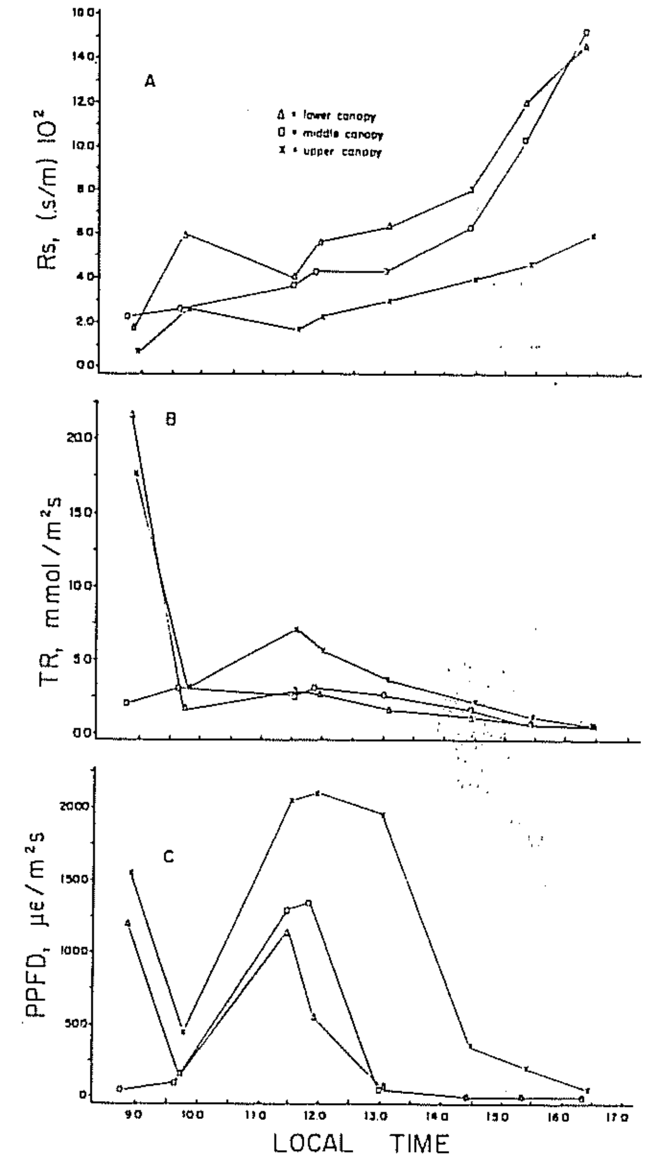

Figura 4 – Stomatal resistance (Rs), transpiration rates (TR) and photosynthetic photon flux density (PPFD) measured at different leaf layers on a unshaded cacao tree on Sept. 19, 1985, a sunny day.

Table 2 – Canopy locations, number of measurements taken (n), average (± standard error) of photosynthetic photon flux density (PPFD), leaf transpiration rate (TR), leaf stomatal resistance (Rs), leaf temperature (TL), leaf-to-air temperature difference (DT), and leaf-to-air vapor pressure gradient (VPG) for unshaded (U) and shaded (S) 'Catongo' cacao trees[1].

Point	n	PPFD $E\ m^{-2}\ s^{-1}$	TR mmol $m^{-2}\ s^{-1}$	Rs $s\ m^{-1}$	TL °C	DT °C	VPG kPa
September 13, 1985							
1U	10	28± 5	0.9±0.1	600±40	26.7±0.3	2.9±0.2	0.55±0.05
2U	18	107± 8	1.4±0.1	385±20	27.8±0.2	3.0±0.2	0.57±0.03
3U	18	550±25	2.5±0.2	220±20	26.8±0.2	2.9±0.1	0.56±0.03
1S	15	156± 6	1.4±0.1	370±20	26.7±0.1	2.8±0.1	0.54±0.02
2S	18	106±15	1.2±0.1	460±20	26.7±0.1	2.8±0.1	0.54±0.02
3S	13	41± 8	0.7±0.1	730±65	26.3±0.1	2.4±0.1	0.46±0.02
September 19, 1985							
1U	12	445±208	2.0±0.3	610±70	33.3±0.5	4.3±0.4	1.13±0.12
2U	12	675±271	2.3±0.2	470±40	33.1±0.5	4.1±0.3	1.08±0.12
3U	9	2030± 29	5.5±0.7	230±20	34.9±0.3	5.6±0.4	1.53±0.11
1S	9	25± 3	1.4±0.1	750±50	33.6±0.3	4.3±0.3	1.14±0.08
2S	8	208±57	2.2±0.2	440±40	32.8±0.3	3.5±0.3	0.91±0.08

[1] Averages were computed from 1030 to 1430 local hour.

on a cloudless day (Sept. 19), TR were higher for leaves of the lower and middle canopy layer than on the upper layer.

The difference in TR between an overcast and a sunny day may be explained by the different canopy layers exposure to irradiance and because of the particular location of the tree at the research site. Photosinthetic photon flux density was high (1700 $\mu E\ m^{-2}\ s^{-1}$) at 0900 h, from which a cover of cumulustratus sharply decreased PPFD for the rest of the day (Fig. 2C). Although, this particular day was characterized by low irradiance, the upper leaves of the unshaded tree received more radiation than leaves at the other locations on both trees.

This was not the case for the upper leaves of the shaded tree in which the shadowcast from the *Erythrina fusca* impeded radiation penetration even at lower solar angles. Therefore, the shadowcast from the *Erythrina* on the

upper canopy of the shaded tree was greater than that on its outer lower layers in which irradiance was high (Fig. 1C). Although these results may seem inconsistent they demonstrate real situations of shaded cacao plantation and are in agreement with those of Lachenaud (1983), who concluded that results about the influence of shade in physiological aspects of cacao seems to contradict each other.

On Sept. 19, measurements of Rs were done at two upper canopy locations on the shaded tree. Diffusive resistances were higher on the leaves that received less radiation. Even though, there was a difference in radiation distribution for both trees, Rs was a direct function of the irradiance received in each layer.

Stomatal resistances were lower and TR, T_L, DT, and VPG higher on Sept. 19 than the same parameters measured on Sept. 13. This was most certainly the result of the higher radiation on Sept. 19, although, occasional clouds covered the experimental area (Fig 4C). Average TR, on Sept. 19, for the upper canopy layer leaves of the shaded tree were not statistically different due to high variability. However, it is clear that one of the upper leaf layer transpired more than the other as a direct result of lower Rs and higher PPFD. This also explains the lower T_L and DT (Table 2).

Transpiration rates and LAI per canopy layer for the shaded and unshaded trees are presented in Table 3. The LAI estimations showed that 18.6 and 46.9% of the total LAI was located at the upper 0.9 m on the shaded and unshaded tree, respectively. Leaf area index was also used to estimate TR in each layer for the whole photoperiod (10 h) (Table 3).

The modeled TR data show that on an overcast day an unshaded cacao tree could transpire about 45 L $tree^{-1}$ (1.2 L $m^{-2}\ d^{-1}$), assuming that all leaves are transpiring at the same rates as the layer from which TR was estimated. The shaded tree, on the other hand, could transpire about 26 L $tree^{-1}$ (0.8 L $m^{-2}\ d^{-1}$) (Table 3).

On the sunny day, however, both trees showed a substantial difference in TR as compared to the overcast day. Estimated daily TR for the unshaded tree was 90 L $tree^{-1}$ (2.4 L $m^{-2}\ d^{-1}$). The two measured points of the upper canopy layer leaves on the shaded tree averaged near 40 L $tree^{-1}$ (1.2 L $m^{-2}\ d^{-1}$) when 100% of their LAI were exposed to the incoming irradiance.

Estimations of daily TR, for the overcast day on both trees and on the shaded canopy layers for the sunny day, are of the same order of magnitude of TR calculated by Alvim (1959) and Cadima and Alvim (1982). However, the unshaded cacao tree on the sunny day showed an average TR more than twice the TR estimated by those authors .

The results presented in this report are lower than those values found for *Eucalyptus* and *Helianthus* which transpire 7.5 and 4.4 L $m^{-2}\ d^{-1}$ (day of 10 h), respectively and in agreement with transpiration rates found for typical mesophytes which transpire about 2.5 L $m^{-2}\ d^{-1}$ over brief periods in sunny warm conditions (Wilson, 1924; Martin and Clements, 1983, cited by Milburn, 1979; Rogers, Allen and Calvert, 1983).

Table 3 – Canopy locations, daily transpiration rates (TR), leaf area index (LAI), percentage LAI per location, and daily transpiration for each layer of unshaded (U) and shaded (S) 'Catongo' cacao trees.

Point	TR[1] 9 m^{-2} d^{-1}	LAI[2]	LAI[3] %	FRACTION TR[4] L $layer^{-1}$ d^{-1}
		September 13, 1985		
1U	583.2	4.1	10.1	2.2
2U	907.2	4.1	43.0	14.4
3U	1620.0	4.1	46.9	28.0
				44.6
1S	907.2	3.8	31.4	9.7
2S	777.6	3.8	50.1	13.3
3S	453.6	3.8	18.6	2.9
				25.9
		September 19, 1985		
1U	1296.0	4.1	10.1	4.8
2U	1490.4	4.1	43.0	23.6
3U	3564.0	4.1	46.9	61.7
				90.1
1S	907.2	3.8	8.6	5.8
2S	1425.6	3.8	18.6	9.1

[1] Transpiration rates assuming a 10 hour photoperiod.

[2] Leaf area index (LAI) for a whole tree estimated from data of Miyaji, Silva and Alvim (1986).

[3] Percentage LAI for the canopy locations. From data of Miyaji, Silva and Alvim (1986) assuming three upper, three middle and three and four lower canopy layers for unshaded and shaded cacao tree, respectively. Each layer had 0.30 m depth.

[4] Transpiration rates in each location estimated using LAI of column 3, fraction LAI per location (column 4), ground area of 9 m^2, and assuming that all leaves in each location were transpiring at the same rate.

On the other hand, given the LAI distribution estimated from data of Miyaji, Silva and Álvim (1986) and the radiation penetration found for the trees under study, more than 60% of the water could be transpired by upper canopy layers of unshaded trees whereas on shaded trees than 5% of the water absorved might be transpired by its top layers. However, even in shaded trees some top layer leaves may be under direct radiation and therefore transpiring and photosynthesizing at different rates than leaves at the same layer but under lower irradiance regimes (Fig 3C and Table 3 for 1 S and 2S. Sept. 19).

In cacao, as well as other trees, leaves shade each other from radiation. Their orientation, if not random, is extremely varied and this determines their degree of exposure to radiation (Butler, 1976). Therefore, the TR values presented in this report, in which it is assumed similar leaf TR for all the leaves in the layer in which the measurements were done, should be seen as estimations of a phenomenon that depends on many factors affecting the behavior of individual leaves as shown in Table 3 for 1 S and 2S on Sept. 19.

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