Plant physiology

Scientific and technologic research article

Gas exchange in young *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg. (Euphorbiaceae) plants in Antioquia (Colombia)

Intercambio gaseoso de plantas jóvenes de *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg. (Euphorbiaceae) en Antioquia (Colombia)

Intercâmbio gasoso de plantas jovens de Hevea brasiliensis (Willd. ex A. Juss.) Müll. Arg. (Euphorbiaceae) em Antioquia (Colômbia)

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Received: 11/11/2016
Accepted: 24/08/2017

Citation: Córdoba-Gaona, O., Monsalve-García, D. A., Hernández-Arredondo, J. D., Guerra-Hincapié, J. J., Gil-Restrepo, J. P., Martínez-Bustamante, E., Unigarro-Muñoz, C. A. (2018). Gas exchange in young *Hevea brasiliensis* (Willd. Ex A. Juss.) Müll. Arg. (Euphorbiaceae) plants in Antioquia (Colombia). *Corpoica Ciencia y Tecnología Agropecuaria*, *19*(1), 91-102.

DOI: https://doi.org/10.21930/rcta.vol19_num1_art:847

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Abstract

The aim of this study was to determine the behavior of the rubber plant *Hevea brasiliensis* regarding its photosynthetic performance in the rubber producer regions in Nordeste and Bajo Cauca, in the department of Antioquia, Colombia, as a baseline for future clonal performance studies among environments. Gas exchange was recorded using a portable infrared gas analyzer, and for the photosynthetic parameters for seven genotypes (clones) a medium value was calculated and was later used to estimate the area under the curve. The maximum photosynthetic value was reached at 8:00 hours in San Roque (10.97 µmol [CO_2] $m^{-2}s^{-1}$) and at 9:00 hours in Caucasia (7.84 µmol [CO_2] $m^{-2}s^{-1}$). Maximum transpiration was 3.55 mmol [H_2O] $m^{-2}s^{-1}$ in San Roque and 5.16 mmol [H_2O] $m^{-2}s^{-1}$ in Caucasia, while the maximum stomatal conductance was 0.18 mol [CO_2] $m^{-2}s^{-1}$ and 0.16 mol [CO_2] $m^{-2}s^{-1}$ in San Roque and Caucasia, respectively. The rubber plants in Caucasia had a higher accumulated net assimilation rate (271,934 µmol [CO_2] $m^{-2}day^{-1}$) than what was found in San Roque (226,287 µmol [CO_2] $m^{-2}day^{-1}$), showing a difference of 45.647,52 µmol [CO_2] $m^{-2}day^{-1}$. The highest carbon accumulation with the lowest light energy investment (697,638 µmol [CO_2] µmol $[photon]^{-1}day^{1}$) was found in San Roque. Therefore, regarding gas exchange and the use of light energy *Hevea brasiliensis* showed greater environmental adaptation in San Roque.

Keywords: Crop yield, environmental factors, gas exchange, *Hevea brasiliensis*

Resumen

El objetivo de este estudio consistió en conocer el comportamiento de *Hevea brasiliensis* en lo que se refiere al desempeño fotosintético, en las regiones caucheras del nordeste y el Bajo Cauca (Antioquia, Colombia), como base para futuros estudios de desempeño clonal entre ambientes. El intercambio de gases se cuantificó mediante un analizador infrarrojo de gases portátil, y en las variables fotosintéticas para los siete clones se calculó un valor medio, a partir del cual se estimó el área bajo la curva. El máximo valor de fotosíntesis se alcanzó a las 8:00 en San Roque (10,97 µmol [CO_2] $m^{-2}s^{-1),}$ y 9:00 en Caucasia (7,84 µmol [CO_2] $m^{-2}s^{-1).}$ La transpiración máxima fue de 3,55 mmol [H_2O] $m^{-2}s^{-1}$ en San Roque, y de 5,16 mmol [H_2O] $m^{-2}s^{-1}$ en Caucasia, mientras que la conductancia estomática máxima fue de 0,18 mol [CO_2] $m^{-2}s^{-1}$ y de 0,16 mol [CO_2] $m^{-2}s^{-1}$, respectivamente. Las plantas de caucho en Caucasia presentaron una mayor tasa de asimilación neta acumulada (271.934 µmol [CO_2] $m^{-2}día^{-1}$), superando los 226.287 µmol [CO_2] $m^{-2}día^{-1}$ de San Roque, lo que representa una diferencia de 45.647,52 µmol [CO_2] $m^{-2}día^{-1}$. La mayor acumulación de carbono con menor inversión de energía lumínica (697.638 µmol [CO_2] µmol $[fotón]^{-1}día^{-1}$) se obtuvo en San Roque. Por lo tanto, en lo que respecta al intercambio gaseoso y al uso de la energía lumínica, *Hevea brasiliensis* presentó una mayor adaptación ambiental en San Roque.

Palabras clave: *Hevea brasiliensis*, rendimiento de cultivos, factores ambientales, intercambio de gases

Resumo

O objetivo deste estudo consistiu em conhecer o comportamento de *Hevea brasiliensis* no que se refere ao desempenho fotossintético, nas regiões borracheiras do nordeste e do Baixo Cauca (Antioquia, Colômbia), como base para futuros estudos de desempenho clonal entre ambientes. O intercâmbio de gases foi quantificado mediante um analisador infravermelho de gases portátil, e nas variáveis fotossintéticas para os sete clones foi calculado um valor médio, a partir do qual foi estimada a área sob a curva. O máximo valor de fotossíntese foi alcançado às 8:00 em San Roque (10,97 µmol [CO_2] $m^{-2}s^{-1}$), e 9:00 em Caucasia (7,84 µmol [CO_2] $m^{-2}s^{-1}$). A transpiração máxima foi de 3,55 mmol [H_2O] $m^{-2}s^{-1}$ em San Roque, e de 5,16 mmol [H_2O] $m^{-2}s^{-1}$ em Caucasia, enquanto a condutância estomática máxima foi de 0,18 mol [CO_2] $m^{-2}s^{-1}$ e de 0,16 mol [CO_2] $m^{-2}s^{-1}$, respectivamente. As plantas de borracha em Caucasia apresentaram maior taxa de assimilação líquida acumulada (271.934 µmol [CO_2] $m^{-2}dia^{-1}$), superando os 226.287 µmol [CO_2] $m^{-2}dia^{-1}$ de San Roque, o que representa uma diferença de 45.647,52 µmol [CO_2] $m^{-2}dia^{-1}$. A maior acumulação de carbono com menor investimento de energia lumínica (697.638 µmol [CO_2] µmol $[fóton]^{-1}dia^{-1}$) obteve-se em San Roque. Portanto, no que se refere ao intercâmbio gasoso e ao uso da energia lumínica, *H. brasiliensis* apresentou maior adaptação ambiental em San Roque.

Palavras chave: fator ambiental, *Hevea brasiliensis*, rendimento de cultura, troca gasosa

Introduction

The rubber plant *Hevea brasiliensis* (Willd. Ex A. Juss.) Müll. Arg. is a deciduous perennial species of the Euphorbiaceae plant family. Its latex is used for the production of natural rubber. This species is widely distributed around the world and its center of origin and diversity is found in the Amazon basin in South America (Schultes, 1970; Silva, Gonçalves, Scarpare, & Costa, 2010).

According to the International Rubber Study Group (IRSG) in 2015 world production of natural rubber was 12.27 million tons, and consumption was 12.15 million tons (IRSG, 2016). These raw materials are mainly used in the automotive industry (ca. 70 %) (Clément-Demange, Priyadarshan, Hoa, & Venkatachalam, 2007; Priyadarshan, Gonçalves, & Omokhafe, 2009).

At the national level, the rubber census carried out in 2015 reported a cultivated area with rubber plants of 52,200 ha (Confederación Cauchera Colombiana [CCC] & Corporación Colombiana de Investigación Agropecuaria [Corpoica], 2015), with an average growth of ca. 3,000 ha per year, as Castellanos, Fonseca y Barón (2009) stated that 30,500 ha were reported in 2008 due to the progressive increase of new rubber plantations in Colombia(Sterling, Suárez, Rodríguez, Caicedo, Salas, & Virguez, 2015).

Therefore, it is necessary to have a greater knowledge of the behavior of *H. brasiliensis* in terms of the performance of important agronomical parameters such as yield and biomass production in the environmental conditions of the rubber plant cultivation regions of Colombia.

However, due to the fact that the rubber plant is a species that has a late use —when the plant has between five and seven years—, the yield record as a characteristic of agronomic and economic interest causes several processes to extend over a longer period of time, such as breeding programs (Rodrigo, 2007) and the explanation of the performance of *H. brasiliensis* in adverse or favorable environmental conditions (phenotypic stability and genotype by environment interactions).

Ecophysiological variables such as net photosynthesis (A), stomatic conductivity (g_s) and transpiration rate (E) have been widely studied, due to their applicability in explaining the natural rubber plant's adaptation phenomena to environmental conditions (Lambers, Pons, & Chapin, 2008; Nataraja & Jacob, 1999; Nugawela, Long, & Aluthhewage, 1995; Rodrigo, 2007); furthermore, other authors have mentioned positive associations between these variables and biomass production (Nataraja y Jacob, 1999; Samsuddin, 1986; Sobhana, Sethuraj, & Vijayakumar, 1995) and also dry rubber (Samsuddin, Tan, & Yoon, 1987).

Before knowing the performance of specific rubber plant genotypes in different environments, it is necessary to establish the way in which the species behaves in the rubber cultivating zones of Colombia. Therefore, the objective of this research was to know how this species behaves by studying several ecophysiological variables in the environmental conditions of the Nordeste and Bajo Cauca rubber regions in the department of Antioquia (Colombia); this will allow us to understand as a first step, the species' adaptation processes as a basis for future performance studies in terms of clonal material between environments.

Materials and methods

Location

This research was carried out in two small-scale clonal fields (SSCF) established in Antioquia as part of the project "Productivity improvement for competitiveness development and increase in the natural rubber chain through an applied research program and innovation in the department of Antioquia", financed with resources from *Sistema General de Regalías* (SGR) [General Royalties System] for the department of Antioquia.

The first SSCF of Bajo Cauca in Antioquia is located in the municipality of Caucasia, jurisdiction of Cacerí, Bella Palmira County, on the farm Las Golondrinas, at 07°60'00'' N and 75°15'00'' E, and at an altitude of 78.69 meters above sea level. It has an average temperature of 28 °C, an average annual rainfall of 2,575 mm, and a humid warm climate; it has typical Hapludult soils, clayey, with a pH of 4.4, and is classified as extremely acidic.

The second SSCF in the Nordeste region in Antioquia is located in the municipality of San Roque, jurisdiction of San José del Nus in the Research Center El Nus of Corpoica, at 06°26'17.2'' N, and 74°49'32.1'' E, at an altitude of 848 meters above sea level. It has an average temperature of 24 °C, an average annual rainfall of 2,500 mm, and a humid warm climate; it has Oxic Dystrudept soils, loamy-clay-sandy, with a pH of 4.5, and is classified as very strongly acidic (Córdoba, Monsalve, Vasco, Villa, Guerra, & Escobar, 2015).

Each SSCF included seven rubber plant clones (CDC 56, CDC 312, FDR 5788, FDR 4575, FX 4098, FX 3864 and GU 198). The clones of the CDC and FDR series are part of the CIRAD-Michelin Selection Collection (CMS); the FX clones (Ford Cross) belong to the hybridization program of the Ford Company; and the clones of the GU series are part of Guatemala's breeding program.

Each material was planted in plots with 20 individuals and with four replicates, at a planting distance of 7.0 x 2.8 m in a square. The plant material was acquired in the clonal garden of the Association of Rubber Reforesters and Cultivators of Caquetá (Asociación de Reforestadores y Cultivadores de Caucho del Caquetá [Asoheca]).

Gas exchange evaluation

In order to establish the photosynthetic behavior of the rubber clones, 45-days-old plants were evaluated after transplantation; diurnal gas exchange rates in the "daily curve" were recorded in each locality, with a frequency of one hour, from 6:00 hours to 18:00 hours; this was carried out with an infrared gas analyzer (IRGA) with a portable LCi photosynthesis system (ADC BioScientific).

Three to five measurements were taken on a mature, ontogenetic *D*, healthy, newly formed leaf; the following variables were determined: net assimilation rate (*A*), stomatal conductance (g_s), transpiration (*E*) and photosynthetically active radiation (*PAR*); from these values water use efficiency (*WUE*) was calculated as follows: *A/E*, and radiation use efficiency (*RUE*) was calculated the following way: *A/PAR*.

Statistical analysis

In each location and for each variable a mean value was calculated for the seven clones; these values were used to estimate the area under the curve (*AUC*) by fractionating the total area into smaller trapezoidal areas. The width of each area corresponds to the time between two measurements, while the height is the average value of two consecutive measurements. These individual areas were calculated using the trapezoid equation (Equation 1).

(Equation 1)

$$\text{Area} = 0.5 * (m_i + m_{i-1}) * (t_i - t_{i-1})$$

Where m_i corresponds to the i-th measurement, while t_i is the i-th time. Therefore, the AUC is the sum of all the individual areas estimated (Equation 2). This is a simple and efficient method when implementing flat geometry concepts.

(Equation 2)

$$\text{AUC} = \sum_{i=2}^{n} 0.5 * (m_i + m_{i-1}) * (t_i - t_{i-1})$$

The SAS® statistical environment macro that was developed in the current work is an adaptation of the routines detailed by Huang and Xiao (2010) and Shiang (2004), to calculate the areas above the horizontal axis (A > 0) such as photosynthesis (gross CO_2 assimilation), and below the horizontal axis (A < 0) such as dark respiration or photorespiration, as well as their difference, i.e. net CO_2 assimilation (carbon balance).

Programming in the SAS® macro to calculate the AUC uses DATA Steps language and SAS/BASE® product procedures, version 9.3 of the SAS system for Windows. With the PROC MEANS procedure, photosynthesis, respiration and carbon accumulation values by class were added, including the SUM option.

Results and discussion

Gas exchange

The rubber plant's diurnal photosynthetic behavior was established from the stomatal conductance behavior (figure 1); in the locality of San Roque it has an initial increase at 7:00 hours followed by a constant reduction until noon (12:00) when there is a partial closure of the stomata. From this point onwards, the stomata open again and remain this way until 16:00 hours, and then a new partial closure occurs.

In the locality of Caucasia the behavior is similar although the stomatic opening only occurs from 8:00 hours, the gradual reduction is seen as a minimum (0.06 mol [CO_2] $m^{-2}s^{-1}$) at 11:00 hours, with a subsequent and continuous increase; at 16:00 hours there is a new decrease and a further increase in the following hour, occurring a final partial stomatic closure at 18:00 hours.

The initial photosynthesis in both localities has a similar behavior (figure 2): a gradual increase from the beginning of the stomatic opening in leaves, until a maximum is reached at 8:00 in San Roque (10.97 µmol [CO_2] $m^{-2}s^{-1}$) and at 9:00 in Caucasia (7.84 µmol [CO_2] $m^{-2}s^{-1}$); this is followed by a progressive reduction until it reaches a minimum value at 12:00 in San Roque and at 11:00 in Caucasia. In this last locality, peaks that were even higher than the initial one were observed at 12:00 and at 13:00 hours; and in San Roque a peak with a lower intensity was seen at 14:00 hours; this is a type of

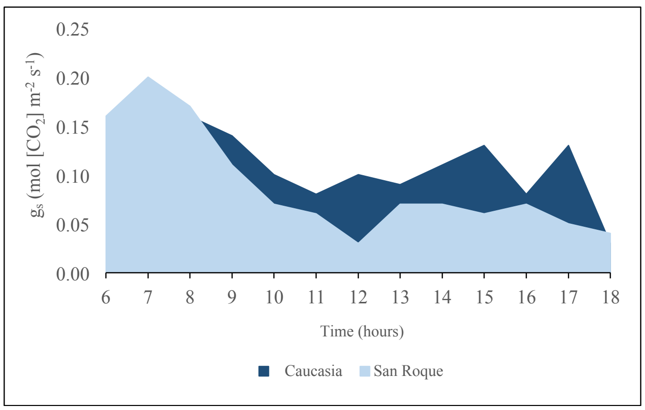

Figure 1. Stomatal conductance (g_s) of rubber plants in the municipalities of Caucasia and San Roque.
Source: Prepared by the authors

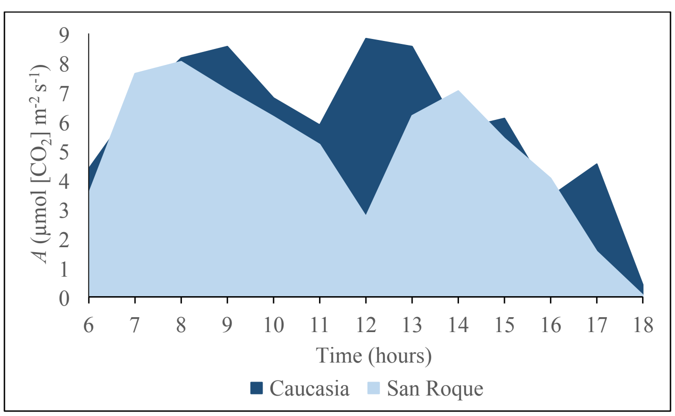

Figure 2. Net photosynthesis (A) of rubber plants in the municipalities of Caucasia and San Roque.
Source: Prepared by the authors

behavior that has also been found in transpiration values (figure 3). After the corresponding increases, a gradual decrease in photosynthesis occurs until it reaches a minimum at 18.00 hours.

When evaluating the photosynthetic activity during the leaf's ontogeny in three rubber plant clones, Miguel et al. (2007) pointed out that the clones PB 235, RRIM 600 and GT 1 had similar photosynthetic behaviors and reached their maximum net photosynthesis values, i.e. between 7 and 11 µmol [CO_2] $m^{-2}day^{-1}$, in the development *D* stage (fully expanded leaf). According to Bergonci (1981), cited by the above-mentioned authors, this indicates that the highest photosynthesis and highest stomatal conductance values are achieved in completely developed leaves.

On the other hand, Cavalcante and Conforto (2002) evaluated the gas exchange in five rubber plant clones in their establishment phase, and found no differences in the photosynthetic response of the different clones during the wet period of the western Paulista Planalto region; the mean values found were 9.45 µmol [CO_2] $m^{-2}s^{-1}$ with a transpiration value of 3.84 mmol [H_2O] $m^{-2}s^{-1}$ and a conductance value of 0.096 mol [H_2O] $m^{-2}s^{-1}$.

These transpiration values are similar to the ones obtained in this experiment, in which the maximum value (figure 3) was 5.16 mmol [H_2O] $m^{-2}s^{-1}$ in the municipality of Caucasia and 3.55 mmol [H_2O] $m^{-2}s^{-1}$ in San Roque. The maximum g_s was 0.16 mol [H_2O] $m^{-2}s^{-1}$ and 0.18 mol [H_2O] $m^{-2}s^{-1}$, respectively in each location.

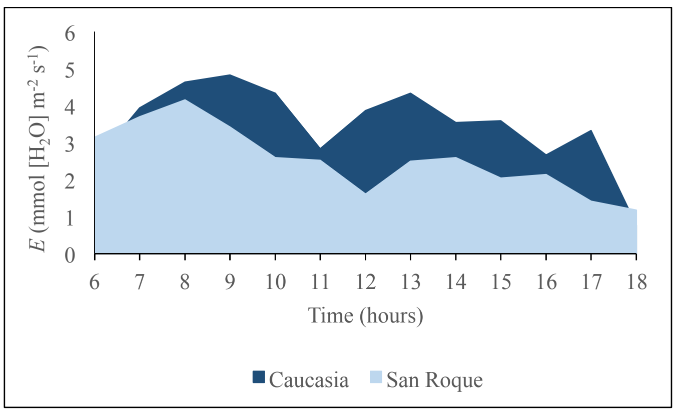

Figure 3. Transpiration (*E*) of rubber plants in the municipalities of Caucasia and San Roque.
Source: Prepared by the authors

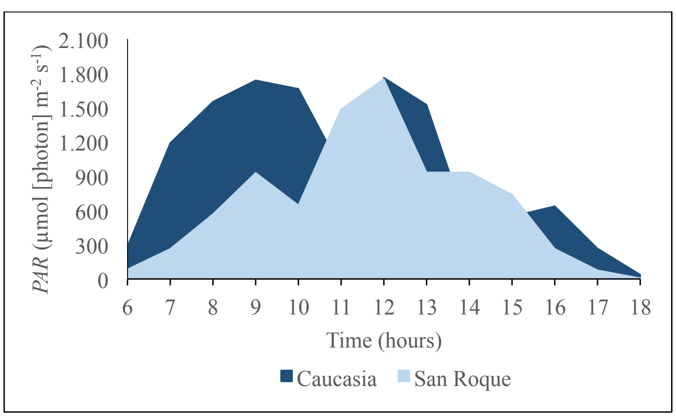

Figure 4. Photosynthetically active radiation (*PAR*) for rubber plants in the municipalities of Caucasia and San Roque.
Source: Prepared by the authors

Figure 4 shows the differential behavior of the photosynthetically active radiation (*PAR*): in the case of San Roque it begins with a gradual increase until it reaches a peak of 1,750 µmol [photon] $m^{-2}s^{-1}$ from which it decreases quickly until 18:00 hours. In Caucasia, the initial increase is much faster reaching values of ca. 1,500 µmol [photon] $m^{-2}s^{-1}$ at 8:00 hours, and then decreases to 1,000 µmol [photon] $m^{-2}s^{-1}$, increasing again until it reaches another peak between 12:00 and 13:00 hours, and then it decreases gradually until 18:00 hours.

In the locality of San Roque, the initial efficiency in the use of radiation (*RUE*) was higher; this was noticeably at 10:00 hours, moment in which the efficiency in Caucasia is 0 and 0.05 µmol [CO_2] µmol [photon]$^{-1}$ in San Roque. From 11:00 hours the values are similar, except at 11:00, 12:00 and 15:00 hours when rubber plants in Caucasia showed a slightly higher efficiency (figure 5).

The behavior of the water use efficiency (*WUE*) is substantially higher in the plants located in San Roque (figure 6), where they show a constant efficiency until 11:00 hours. It is important to note that the accumulated values between 11:00 and 13:00 hours are higher in Caucasia, which gives indications that there is a stomatal regulation in this region that allows avoiding large water losses. From that moment, an increase begins that reaches a maximum of 2.76 µmol [CO_2] mmol [H_2O]$^{-1}$ that stays constant until 15:00 hours.

In Caucasia, the evolution of the efficiency showed only a small increase between 11:00 and 13:00 hours until it reached a value of 2.29 µmol [CO_2] mmol

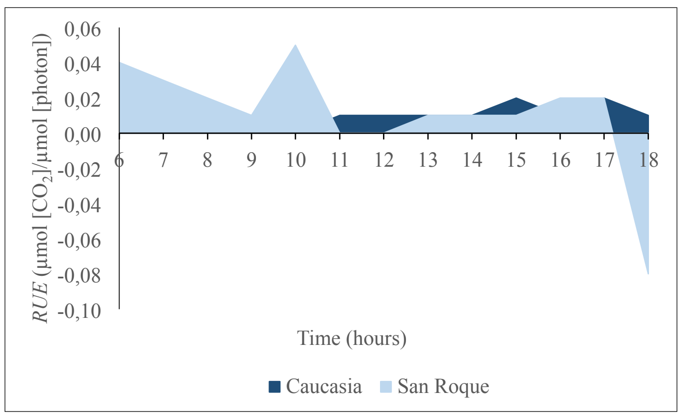

Figure 5. Radiation use efficiency (*RUE*) of rubber plants in the municipalities of Caucasia and San Roque.
Source: Prepared by the authors

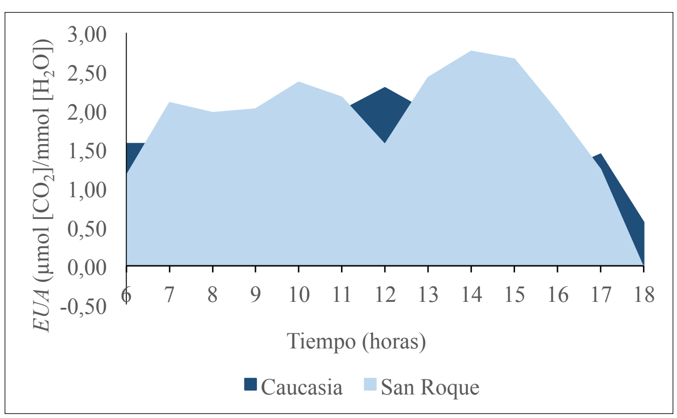

Figure 6. Water use efficiency (*WUE*) of rubber plants in the municipalities of Caucasia and San Roque.
Source: Prepared by the authors

$[H_2O]^{-1}$. During the whole period the variations remained close to 1.5 µmol $[CO_2]$ mmol $[H_2O]^{-1}$.

Area under the curve

According to the results for the estimation of the area under the curve for the two localities considered (table 1), rubber plants established in Caucasia had a higher accumulated net assimilation rate (*A*), i.e. 271,934.68 µmol $[CO_2]$ $m^{-2}day^{-1}$, which is higher than 226,287.16 µmol $[CO_2]$ $m^{-2}day^{-1}$ that was obtained in San Roque, showing a difference of 45,647.52 µmol $[CO_2]$ $m^{-2}day^{-1}$.

This can be explained by the fact that the photosynthetically active radiation (*RFA*) made a greater energy contribution in Caucasia, since in that locality a difference of 13,695,797 µmol [photon] $m^{-2}day^{-1}$ was recorded in comparison to San Roque.

After analyzing the relationship between net photosynthesis and *PAR*, which results in *RUE*, it was found that, contrary to what happened with the values of carbon assimilation and photosynthetic radiation recorded in Caucasia, the highest carbon accumulation with the lowest light energy investment (697,638 µmol $[CO_2]$ µmol $[photon]^{-1}$ day^{-1}) was obtained in San Roque (table 1).

This is an intrinsic adaptation feature to certain environmental conditions found in plants, such as light supply and ecophysiological characteristics, i.e. low compensation points and light saturation, that are found in rubber plants (Nataraja & Jacob, 1999); following these facts, De Costa (2000) stated that plants with a low light compensation point (*LCP*) have the facility to maintain a positive carbon balance and continue assimilating it, even with low absorbed radiation.

Regarding the transpiration rate (*E*) the rubber plants in Caucasia recorded the highest values, transferring to the atmosphere a total cumulative amount of 156,564.19 mmol $[H_2O]$ $m^{-2}day^{-1}$ compared to 110,946.11 mmol $[H_2O]$ $m^{-2}day^{-1}$ transferred in San Roque. This result is concomitant with the results found for the net photosynthesis variables and for the photosynthetically active radiation in the two localities studied.

Likewise, when analyzing the relationship between net photosynthesis and transpiration, commonly described as water use efficiency (*WUE*), it is observed that in San Roque (table 1) the plants managed to accumulate a greater amount of carbon in relation to water expenditure (85,770.72 µmol $[CO_2]$ mmol $[H_2O]^{-1}$ day^{-1}).

Table 1. Area under the curve for the gas exchange parameters and their efficiency in two localities

Parameter	Caucasia	San Roque
A (µmol $[CO_2]$ $m^{-2}day^{-1}$)	271,935	226,287
PAR (µmol [photon] $m^{-2}day^{-1}$)	44,723,101	31,027,304
g_s (mol $[CO_2]$ $m^{-2}day^{-1}$)	4,472	3,809
E (mmol $[H_2O]$ $m^{-2}day^{-1}$)	156,564	110,946
RUE (µmol $[CO_2]$ µmol $[photon]^{-1}$ $m^{-2}day^{-1}$)	417,568	697,638
WUE (µmol $[CO_2]$ mmol $[H_2O]^{-1}$ day^{-1})	69,656	85,771

A: net photosynthesis; *PAR*: photosynthetically active radiation; g_s: stomatal conductance; *E*: transpiration rate; *RUE*: radiation use efficiency; *WUE*: water use efficiency.
Source: Prepared by the authors

According to what was expressed by Phillips and Oren (2001), the plants can adapt to the microclimate or to the soil moisture of a given region, and even modify considerably the water expenditure, resulting in adequate plant transpiration maintenance. Therefore, it is probable that rubber plants will have a better adaptation to the water supply —both of the soil as well as of the environment— in San Roque.

The contribution of the PAR in Caucasia allowed obtaining the highest stomatal conductance rates (g_s), and it even led to a greater carbon assimilation compared to the one obtained in San Roque, as the carbon dioxide flow per unit area registered in Caucasia (4,471.75 mol [CO_2] $m^{-2}day^{-1}$) exceeded the value of 3,809.18 mol [CO_2] $m^{-2}day^{-1}$ achieved in San Roque (table 1).

The aforementioned suggests that in San Roque rubber plants have a higher stomatal control in relation to the entry and release of gases (flow); this allows the plants to be more efficient to capture carbon and in water consumption, since, as Mokhatar, Daud and Arbain (2011) have mentioned, in evaluations of rubber plants subjected to different irrigation levels, the reduction in stomatal conductance —caused by the closure of the guard cells— forces the stomata to decrease the transpiration rate, even though the photosynthetic rate is affected.

In general terms, although in the locality of Caucasia compared to what was observed in San Roque, rubber trees showed higher accumulated rates in the photosynthetic parameters, i.e. net photosynthesis (A), photosynthetically active radiation (*PAR*), transpiration (E) and stomatal conductance (g_s), the highest efficiencies in water and radiation uses were obtained in San Roque.

This can be explained by the fact that Caucasia has a humid warm climate that provides conditions for a better photosynthetic performance; however, the higher temperature and radiation makes water use efficiency (*WUE*) and radiation use efficiency (*RUE*) lower in relation to San Roque, where the average temperature (24 °C) and the PAR were lower.

Conclusions

The best photosynthetic performance of young rubber plants was found in the municipality of Caucasia, while the highest radiation and water use efficiencies was achieved in San Roque; these findings show that *H. brasiliensis* has a higher degree of adaptability to the climatic conditions in San Roque. However, it is probable that, if complementary water inputs are established to the current environmental supply of Caucasia, the ecophysiological behavior of the species can be improved in this region.

Acknowledgments

The authors want to thank the Government of Antioquia for financing of the special cooperation agreement 46000001081 of Sistema General de Regalías [General System of Royalties] of Antioquia in 2013, of which this research has been part of. Likewise, the authors express their gratitude to Universidad Eafit for administrating the Project; to Universidad Nacional de Colombia - Medellín Campus, Universidad de Antioquia, Servicio Nacional de Aprendizaje (SENA), the Colombian Corporation for Agricultural Research (Corporación Colombiana de Investigación Agropecuaria, Corpoica), Asociación Comité de Cultivadores de Caucho (Asculticaucho), Asociación de Productores de Caucho de Cargueros y Bijagual (Ascabia), as well as to the producers of the farm Las Golondrinas.

Disclaimer

This research is part of the special cooperation agreement 46000001081 of Sistema General de Regalías [General System of Royalties] of Antioquia in 2013 with the title "Productivity improvement for competitiveness development and increase in the natural rubber chain, through an applied research program and innovation in the department of Antioquia". The authors declare that the knowledge generated in this article is unpublished, it comes from original information and author rights of the researchers cited in this article have been met.

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