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ORIGINAL ARTICLE

Characterization of photosynthesis and transpiration in two rubber tree clones exposed to thermal stress

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Abstract

Temperature is one of the most important factors influencing physiological responses of rubber trees, so much so that it is a limiting factor in the expansion of rubber tree plantations in Brazil. The aim of this research was to investigate the influence of thermal stress, characterized by different thermal amplitudes, on photosynthesis, stomatal conductance, transpiration and leaf temperature. Seedlings of two rubber tree clones, RRIM 600 and CDC 312, were exposed to three different environments which were characterized by the following daily temperature ranges: 25–30 °C (*E*1); 25–42 °C (*E*2) and 10–42 °C (*E*3). Gas exchange and leaf temperature measurements were performed during the experimental period. The results show that gas exchange was affected by higher thermal amplitudes (*E*2 and *E*3). Photosynthesis, stomatal conductance and transpiration were lower in *E*2 and *E*3 environments, being more pronounced in *E*3. It was also observed that, due to the higher thermal amplitude in *E*2 and *E*3, there was an increase in intercellular CO_2 concentration. Reduction in transpiration rates culminated in an increase in leaf temperature in *E*2 and *E*3, being more pronounced in the CDC 312 clone than in RRIM 600.

Keywords Ecophysiology · *Hevea brasiliensis* · Leaf temperature · Photosynthetic apparatus · Thermal amplitude

1 Introduction

Hevea brasiliensis Müll. Arg. is the most appropriate species for exploitation of natural rubber due its productivity and the quality of the latex produced (Hayashi 2009). Commonly known as the rubber tree, the species is responsible for about 40% of natural and synthetic rubber available for consumption in the world (Vinod et al. 2010; Berthelot et al. 2016). The demand for natural rubber grows at a rate of more than 3.5% per year, driven mainly by the development of tire industry; it is estimated that there is a need to plant 4.3–8.5 million hectares of new rubber tree plantations in order to meet global demand in 2024 (Warren-Thomas et al. 2015). However, the expansion of these cultivated areas, especially into non-traditional growing regions, involves plants being subjected to challenging meteorological conditions (Kositsup et al. 2009; Khazaai et al. 2017) which can cause problems associated with plantation sustainability and production (Ahrends et al. 2015).

The optimum growth rate in the rubber tree occurs when the air temperature is around 28 °C (Kositsup et al. 2009).

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In the areas where the expansion of the rubber tree crop takes place in Brazil, the optimum temperature and water availability occur during the late spring and early summer (Alvares et al. 2013), this being the period when planting of new crops takes place. However, in some years, due to climatic variability, long dry periods have occurred after planting the new crops (Servain et al. 1999). Under these conditions, there is an expressive increase in the air thermal amplitude, which becomes more intense closer to ground where the seedlings are located. The temperature close to the ground during the day reaches more than 40 °C, while at night, due to low concentration of water vapor in the atmosphere, the radiation balance becomes more negative, and consequently, the temperature can reach close to 10 °C (Alvares et al. 2013; García-Plazaola et al. 2015). Thus, the seedlings are exposed to extreme temperature conditions, causing great problems for Brazilian heveiculture. Moreover, with climate change, an increase in temperature and evaporative demand and higher frequencies of extreme events, such as drought in the rainy season, are expected in both traditional and non-traditional areas (Masaki et al. 2011; Sopharat et al. 2015). These changes may further harm Brazilian heveiculture.

Problems related to extreme temperatures involve various physiological processes of plants. Low temperatures are responsible for reducing photochemical efficiency which, in turn, limits the CO_2 assimilation rate. It can also lead to photoinhibition and injury of the cell membranes (Ray et al. 2004), affecting the quantum yield of Photosystem II (PSII) (Alam et al. 2005) by causing damage to the photosynthetic machinery of the plant (Rodrigo 2007). High temperatures inhibit photosynthesis (Mathur et al. 2014) and increase respiration (Pinheiro and Chaves 2011), leaving plants prone to thermal stress (Shaheen et al. 2016). These situations can lead to a rapid depletion of the carbon stored by the plant (McDowell 2011) with consequent losses in productivity.

Research on the variation of air temperatures and the thermal stress suffered by rubber plants is of great importance for the management and development of better adapted genetic material (Cheng et al. 2015; Rivano et al. 2016). This type of research has great potential to assist in the development of rubber tree plantations, providing increased productivity, more efficient use of natural resources, cost reduction, as well as enabling the expansion of cultivation to new areas and making the activity more profitable and environmentally sustainable.

In view of the problems caused by thermal stress during the planting period of new rubber tree areas in Brazil, a study to identify the effects of thermal stress suffered by each specific genetic material is needed. As a result, the present study aims to investigate the influence of thermal stress, characterized by different thermal amplitudes, on gas exchange and on leaf temperature in two rubber tree clones, RRIM 600 and CDC 312.

2 Materials and methods

Study site – The study was conducted in greenhouses with controlled temperature and relative humidity at the Laboratory of Meteorology and Forest Ecophysiology at the Federal University of Espírito Santo, in the municipality of Jerônimo Monteiro, Espírito Santo State, Brazil (latitude 20°47′2″S, longitude 41°23′48″W, 120 m altitude).

Each greenhouse was lined with 4-mm-thick honeycomb polycarbonate plates and consisted of an aluminum structure and galvanized steel. The cooling system consisted of an air conditioner and a pad cooling system installed inside the greenhouse.

Plant material – Clones of RRIM 600 and CDC 312 were produced by grafting scions (type: chip budding) onto rootstocks IAN 893, produced by seed and with 1 year old. These clones were chosen due to their resistance to the fungus *Microcyclus ulei* (P. Hem.) v. Arx. and because they are widely recommended for non-traditional areas of rubber tree cultivation in Brazil. Furthermore, the RRIM 600 clone is tolerant to tapping panel dryness and CDC 312 presents adaptability to various growing conditions (Marques et al. 2009).

Growing conditions – At 30 days after grafting, the seedlings were transplanted into 21-L pots, followed by an acclimatization period of 107 days in a greenhouse with temperatures varying between 25 and 30 °C. The reason for subjecting plants to stress after 107 days of acclimatization is that approximately 100 days after planting is when seedlings undergo the highest temperatures and thermal amplitude in Brazil. The substrate used was composed of biostabilized pine bark, vermiculite, charcoal mill and phenolic foam. Fertilization was carried out according to fertilization recommendations for rubber trees in Espírito Santo State (Prezotti et al. 2007).

Soil water content was monitored using a Hydrosense II CS 658 sensor (Campbell Scientific, Inc., Logan, UT, USA) for irrigation management, calibrated according to Nóia-Júnior et al. (2017), which allowed water level in the substrate to be kept at field capacity. Every day at 7 am, the soil moisture was measured with the sensor and water was replenished in the amount required to return the soil to field capacity.

After acclimatization, the irrigation was maintained and clones of rubber tree were subjected to three different thermal amplitude conditions (treatments). Treatments applied after the acclimatization periods were characterized as follows (Fig. 1):

- *Environmental conditions E*1 Standard conditions, characterized by the continuation of thermal conditions used during the acclimatization phase, i.e., with temperatures varying between 25 and 30 °C. Thermal amplitude was the lowest among the treatments (± 5 °C).
- *Environmental conditions E*2 Temperatures varying between 25 and 42 °C, with intermediate thermal amplitude (± 17 °C).
- *Environmental conditions E*3 Temperatures varying between 10 and 42 °C, with the highest thermal amplitude (± 30 °C).

The mean value for photosynthetic photon flux density in the period studied was 248 µmol m^{-2} s^{-1}. The relative humidity was controlled and remained constant throughout the experiment with a value of 70% in all environments. Seedlings were kept under treatment conditions for a period of 7 days which covered the time required for the seedlings subjected to high thermal amplitudes to reach zero photosynthesis (0 µmol CO_2 m^{-2} s^{-1}). After this period, the plants were very weakened, with marked abscission of leaves, which prevented the continuation of the study for a longer duration.

In all environments, lower temperatures were attained during nighttime periods. An automatic meteorological station was installed for microclimatic characterization of the environments within each greenhouse. Each station was composed of temperature and relative humidity sensors using a CS500 model (Campbell Scientific, Inc., Logan, UT, USA), a Sun Calibration Line Quantum with 10 sensors (model SQ-311; Apogee Instruments, Logan, UT, USA) and an infrared radiometer (model SI-111; Campbell Scientific, Inc., Logan, UT, USA). The data were stored in a data logger (model CR 1000; Campbell Scientific, Inc., Logan, UT, USA) with scanning every 10 s and storing of average values every minute.

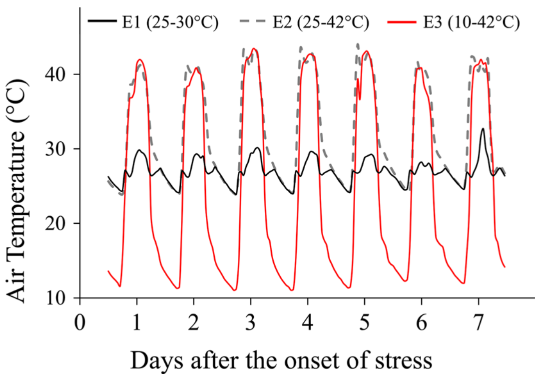

Fig. 1 Daily variation in air temperature during the 7-day experimental period, simulating environments with different thermal amplitudes

Gas exchange measurement – Gas exchange evaluations were carried out using the two clones during the 1st, 3rd, 5th and 7th days from the beginning of the experimental period. Measurements included net photosynthetic rate (A, µmol CO_2 m^{-2} s^{-1}), transpiration rate (E, mmol H_2O m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}) and intercellular CO_2 concentration (C_i, µmol CO_2 mol^{-1}). The measurements were conducted using a portable infrared gas analyzer (IRGA) (model Li-COR 6400; LI-COR Inc, Lincoln, NE, USA) with a 6-cm^2 chamber and a red blue light-emitting diode light source. At each replication, photosynthesis measurements were logged after 3–4 min stabilization using a light intensity of 1000 µmol m^{-2} s^{-1}, as recommended by Wang (2014), flow rate of 200 µmol s^{-1} and ambient CO_2 mol fraction of 400 µmol mol^{-1}. Evaluations were conducted every 2 h, between 8 am and 4 pm, in fully expanded leaves in the upper third of the plant, using five replications per treatment for each clone. Instantaneous carboxylation efficiency (EiC) was established through the relationship between net photosynthetic rate and intercellular CO_2 concentration (A/C_i).

Leaf temperature measurement – Leaf temperature measurements were taken on the 1st, 3rd, 5th and 7th days from the beginning of the experimental period, every 3 h between 8 am and 6 pm, using an infrared radiometer (model SI-111; Campbell Scientific, Inc., Logan, UT, USA). The radiometer was directed at the central part of a leaf, located in the middle third of the plant, where 11 measurements were recorded.

Statistical analysis – The statistical analyses were carried out using the software R (R Core Team 2017). To analyze the response of each variable to the environments studied, the data were submitted to an analysis of variance (ANOVA) and, when significant (F-test $P < 0.05$), the mean values were compared using the Tukey test ($P < 0.05$). Subsequently, to identify differences in slopes of the regressions line, the data were submitted to an analysis of covariance (ANCOVA). In order to obtain an integrated assessment of the temperature effects on the studied clones, the data were subjected to a principal component analysis (PCA).

3 Results and discussion

On all evaluation days and with both clones, values for A, g_s and E were higher and C_i lower in environment $E1$ (Figs. 2, 3). It is also noted that A reduced throughout the

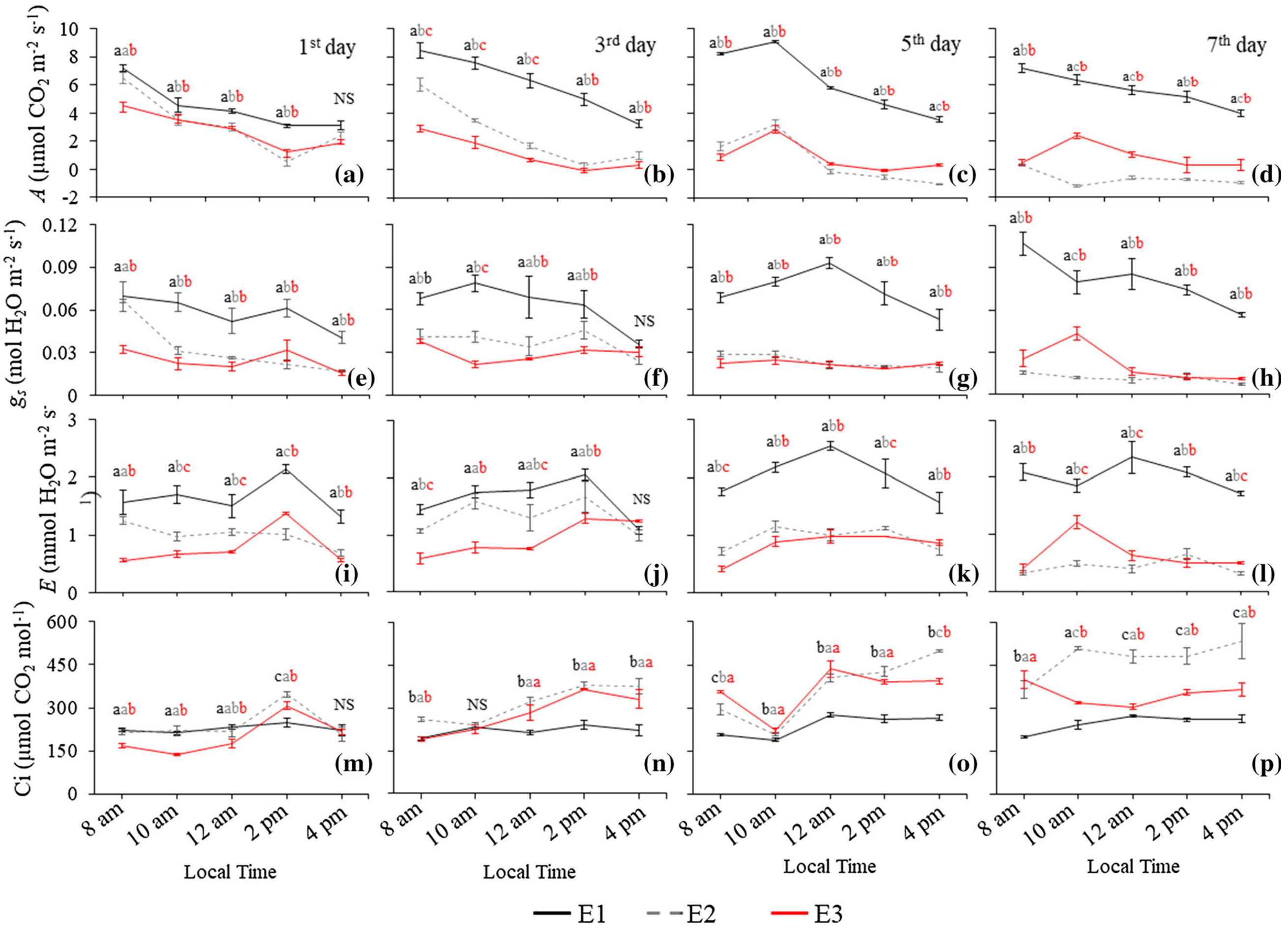

Fig. 2 Diurnal variation in net photosynthesis (A), stomatal conductance (g_s), transpiration rates (E) and intercellular CO_2 concentration (C_i) in RRIM 600 under three environmental conditions, on the 1st, 3rd, 5th and 7th days of experimentation. Data are mean values ± standard error of five replicates. *NS* not significant. Different letters for the same time-point represent a statistically significant difference (Tukey, $P < 0.05$). The color of each letter represents the respective treatment. (Color figure online)

day. In environments $E2$ and $E3$, this reduction also occurred each day, increasing the difference between these and $E1$. On the seventh day, the difference was maximized since the values of A in these environments were close to 0 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$.

The reduction of A capacity throughout the day, which occurred in all environments studied, is a common phenomenon across species (Kosugi et al. 2009; Kamakura et al. 2012). Photosynthetic capacity usually starts to decrease as early as sunrise which, in natural environments, is compensated for by an increase of solar radiation flux in the early morning (Koyama and Takemoto 2015). However, the reduction of A in $E2$ and $E3$ was more intense, indicating the sensitivity of clones to environments with higher thermal amplitude. The mechanisms that govern the photosynthetic rates under these environments are not yet fully understood. The main hypotheses relate to the sensitivity of the enzyme Rubisco activase to thermal denaturation (Crafts-Brandner and Salvucci 2004; Sharkey 2005; Makino and Sage 2007) and inhibition of the electron transport chain, caused mainly by problems related to PSII (Song et al. 2010). However, the thermosensitivity of ATP synthase is also indicated as a major cause of inhibition of the electron transport chain (Szymańska et al. 2017).

Although the clones of RRIM 600 and CDC 312 responded similarly to the different environments, there were important differences between them. In $E2$, at 10 am on the seventh evaluation day, RRIM 600 presented positive values for A (2.37 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$), while CDC 312 presented negative values (− 0.44 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) (Figs. 2, 3). The difference between the responses of the clones was even clearer when analyzing C_i. In $E2$, clone RRIM 600 showed a reduction of C_i within the seventh day. Although small differences between the clones were demonstrated, they were not sufficient to indicate which clone was more resistant to the study conditions.

The difference between $E2$ and $E3$ in relation to $E1$ can be easily seen. However, when evaluating the morning period of the first and third day, the difference between $E2$ and $E3$ is also prevalent. On the first day at 8 am, lower

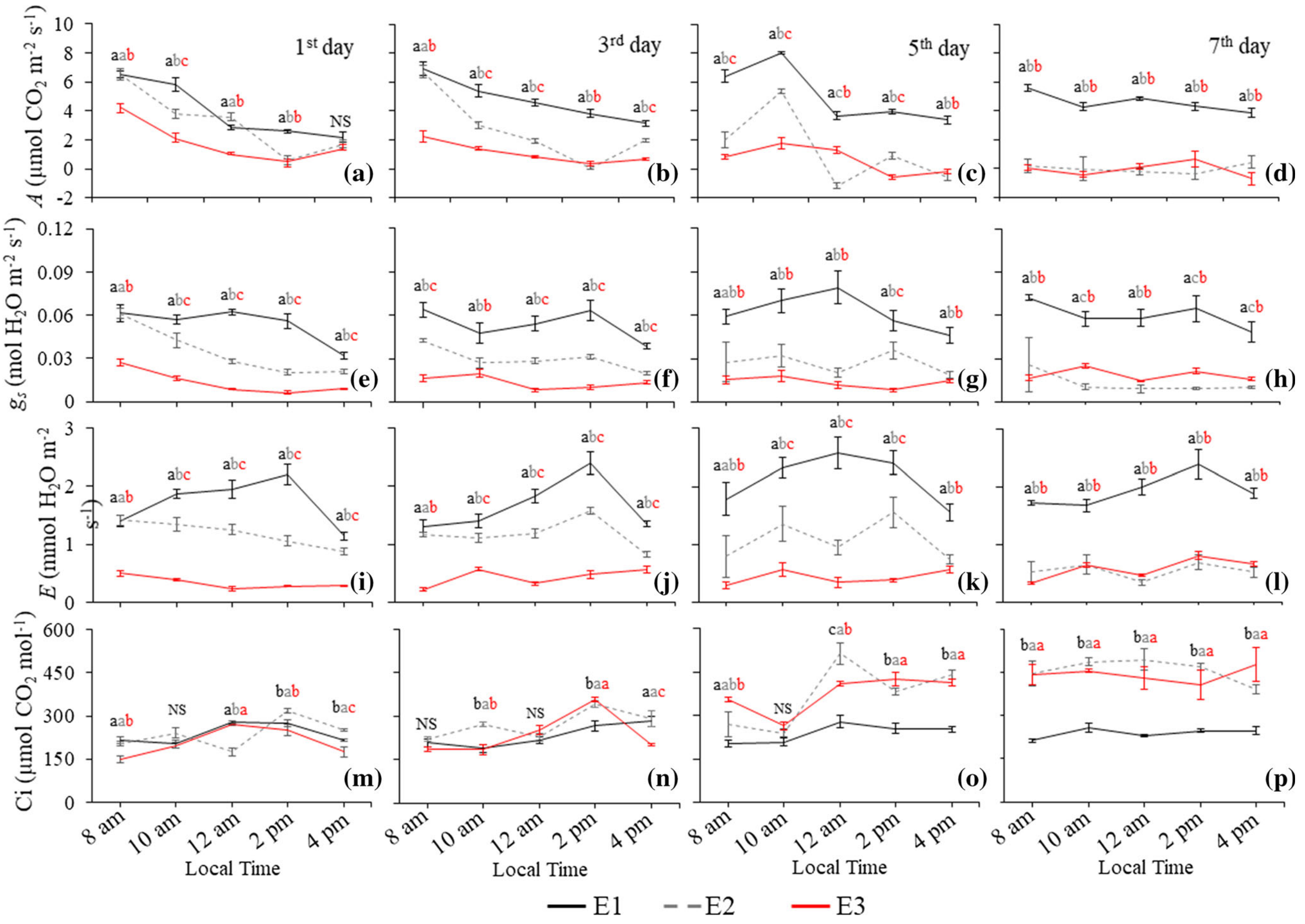

Fig. 3 Diurnal variation in net photosynthesis (A), stomatal conductance (g_s), transpiration rates (E) and intercellular CO$_2$ concentration (C_i) for CDC 312 under three environmental conditions, on the 1st, 3rd, 5th and 7th days of experimentation. Data are mean values ± standard error of five replicates. *NS* not significant. Different letters for the same time-point represent a statistically significant difference (Tukey, $P < 0.05$). The color of each letter represents the respective treatment. (Color figure online)

values of A, g_s, E and C_i in $E3$ were observed with both clones. In order to make the difference between the environments more explicit, the relationship between $E2/E1$ and $E3/E1$ was investigated. This relationship was tested for each of the variables, A, g_s, E and C_i, at 8 am, a time at which the temperature difference between the environments was most marked. The relationship is presented in Fig. 4.

The clones submitted to $E2$ showed a more gradual reduction of A, while in $E3$ this decrease was more rapid (Fig. 4). These results indicate the higher sensitivity of the clones to the highest thermal amplitude. On the other hand, there was a gradual increase in C_i for $E2$ and $E3$ when compared to $E1$. However, values for C_i in $E3$ in the first days of the experiment were less than or equal to those in $E1$. This result indicates that, although photosynthetic rates at 8 am on the first day were already lower in $E3$ than in $E1$, plants were still using the available carbon efficiently within the sub-stomatic chamber. To illustrate this efficiency more clearly, Fig. 5 was constructed.

The ratio A/C_i (Fig. 5), referred to as instantaneous carboxylation efficiency (EiC), for RRIM 600 and CDC 312, at 8 am (time of lowest temperature) and at 2 pm (time of highest temperature). Figure 5 shows that the clones had their highest EiC rate at 8 am. However, there was a reduction of EiC with treatments $E2$ and $E3$ over time. It was also noted that RRIM 600 had already presented a reduction of EiC in $E2$ compared to $E1$, whereas CDC 312 showed no reduction of EiC in the same environment.

It was also noticed that EiC was the same in all environments on the first day at 8 am. It should be remembered that, at this same time in $E3$, the variables A, g_s and E were already lower with both clones (Figs. 2, 3). This result indicates that low temperatures (characterized by $E3$ at 8 am) had not yet affected the process of carboxylation performed by the plants and that the reduction in photosynthesis was exclusively due to stomatal closure (g_s), which made the entry of CO$_2$ difficult, making it less available for photosynthesis (lower C_i; Figs. 2, 3).

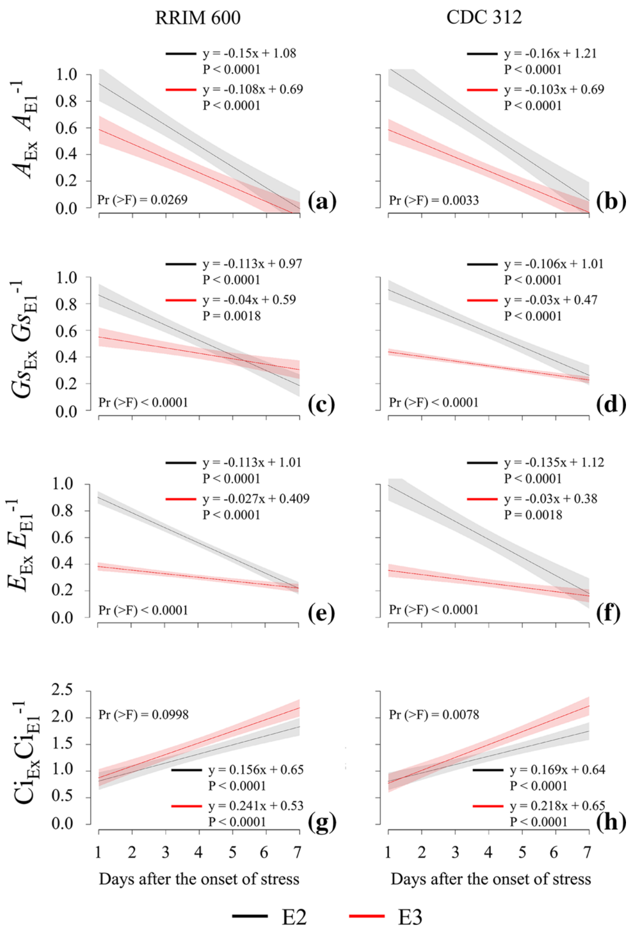

Fig. 4 Relationship of *E*2 and *E*3 on *E*1 environments, showing the photosynthetic rate (*A*), transpiration rate (*E*), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) during the 7-day period at 8 am on each day for rubber tree clones RRIM 600 and CDC 312. The polygons correspond to an area of the confidence interval (95%). The *P* value, from variance analysis (ANOVA, $P < 0.05$) of the regressions, is represented by *P*. The *P* value, from covariance analysis (ANCOVA, $P < 0.05$), is represented by Pr(> *F*). On the *y*-axis, the variables for *E*2 or *E*3 (*Ex*) are presented in relation to *E*1 (e.g., $A_{Ex\ (x\ =\ 1\ \text{or}\ 2)}\ A_{E1}$)

The low temperature of *E*3 may have reduced membrane fluidity, affecting the transport of solutes between cells and decreasing their concentration, especially potassium, in guard cells. The reduction in the solute concentration in guard cells can generate a loss of osmotic pressure and turgidity, and consequently, resulting in stomatal closure (Wang et al. 2012; Szymańska et al. 2017).

Stomatal closure, which culminated in reduction in values of *A*, may also have resulted from a possible increase in the concentration of abscisic acid (ABA) in leaves. Several authors who have investigated the effect of low temperatures on plants suggest that increase in ABA concentration is a chemical signal in plant defense and an inducer of cold resistance (Smith and Dale 1988; Sales et al. 2012; Guo et al. 2014).

At the time of higher temperature time (2 pm), the clones had lower values of *A* which explains why the clones become less efficient in assimilating CO_2 (Figs. 2, 3). According to Zhao et al. (2013), high temperatures cause increased respiration which modifies the CO_2/O_2 ratio inside the leaf, reducing the carboxylation work of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBP) (Yamori et al. 2014) and resulting in a reduction of EiC.

Reduction of EiC with over time may have also been caused by damage to PSII (Song et al. 2010). The lower rates of EiC can be explained by a decrease in activity of Rubisco activase at high temperatures, since this protein is highly sensitive to thermal denaturation (Crafts-Brandner and Salvucci 2004; Yamori et al. 2012). Moreover, this result may also be related to mesophyll conductance response to temperature which, in turn, relates to variation in both the activation energy for membrane permeability to CO_2 and the effective path length for liquid phase diffusion (von Caemmerer and Evans 2015). Results suggest that the photosynthetic machinery was impaired by thermal amplitudes caused by *E*2 and *E*3. Thermal stress suffered by plants also culminated in the increase in leaf temperature of clones.

The diurnal variation in the difference between leaf temperature and air temperature (Δ*t*) for RIMM 600 and CDC 312 in the three environments studied is presented in Fig. 6. It can be seen from this variable that the clones behaved differently in different environments.

Plants in *E*3 presented greater differences between leaf and air temperature in the first hours of the first day, which can be explained by stomatal closure that occurred at these times (Figs. 2, 3).

Leaf temperatures of RRIM 600 differed from air temperature by 5.49 °C in *E*2 and by 6.37 °C in *E*3. In addition, CDC 312 presented Δ*t* maximum of 6.49 °C in *E*2 and of 6.85 °C in *E*3, while Δ*t* of the same clones in *E*1 did not exceed 2.17 °C throughout the experiment.

At high temperatures, both clones reduced water loss by closing their stomata. Thus, there was also a reduction in transpiration rates, limiting leaf cooling capacity by latent heat flux (Mathur et al. 2014), which is one of the most important processes for regulating leaf temperature (Garruña-Hernández et al. 2014). This explains why high leaf temperatures can impair plant growth and productivity (Vijayakumar et al. 1998).

The PCA approach allowed an integrated assessment of the effects of the environments studied on RRIM 600 and CDC 312 clones (Fig. 7). At 8 am, the first two principal components (PC) explained 94.8% of the data variance, while at 2 pm, the first two PCs explained 93.5% of the variance. At both times, the variables *A*, g_s, EiC and LT presented more importance in the PC1, while C_i and *E* were, respectively, the most relevant in the PC2.

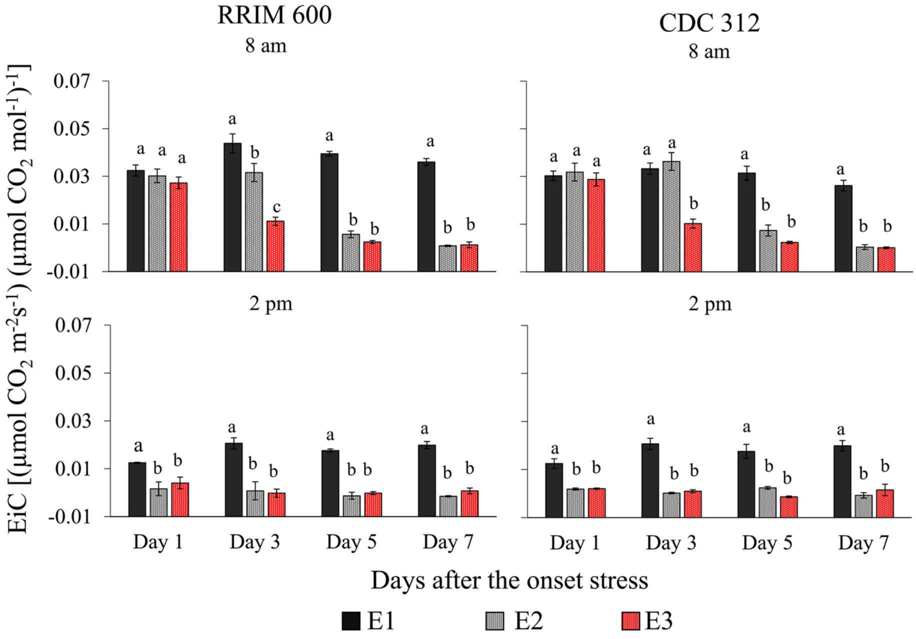

Fig. 5 Instantaneous carboxylation efficiency (EiC) for RRIM 600 and CDC 312 under three environmental conditions on the 1st, 3rd, 5th and 7th days of experimentation. Data are mean values ± standard error of five replicates. *NS* not significant. Different letters for the same day represent a statistically significant difference (Tukey, $P < 0.05$)

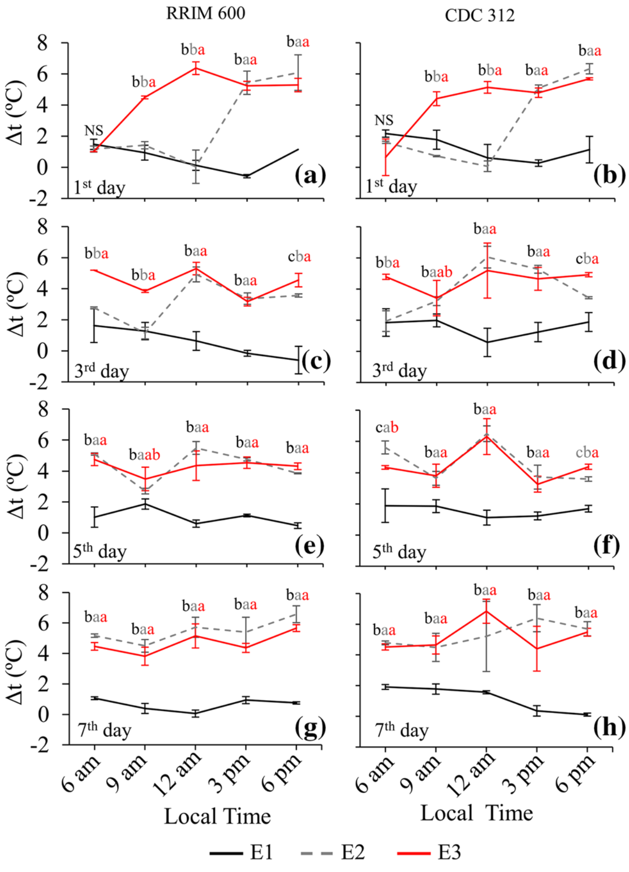

Fig. 6 Diurnal variation in the difference between leaf temperature and air temperature (Δt) for RRIM 600 and CDC 312 under three environmental conditions on the 1st, 3rd, 5th and 7th days of experimentation. Data are mean values ± standard error of 10 replicates. *NS* not significant. Different letters for the same time-point represent a statistically significant difference (Tukey, $P < 0.05$). The color of each letter represents the respective treatment. (Color figure online)

At 8 am, the data from the *E*2 environment showed a highest dispersion and are presented in the four quadrants, while at 2 pm, the data were concentrated in the right-hand quadrants. This indicates that the afternoon period of stress was very intense in this environment. In *E*3, all points are located in the right-hand quadrants at both times, showing that stress was always intense. It is important to highlight the high positive correlations between the variables E/g_s and A/EiC and the negative ones presented between $E{:}g_s$/LT and A:EiC/C_i.

Using the PCA approach, it is possible to observe that the clones respond in a very similar way to the environments studied. Differences between clones occurred at specific times during the experiment (e.g., at 2 pm on day 1), but were insufficient to indicate differences in terms of resistance or susceptibility patterns between them.

The present study indicated that the rubber tree clones investigated are sensitive to thermal amplitudes characterized by temperatures higher than 40 °C and/or near to 10 °C. These findings are consistent with results of other studies with the same species (Kositsup et al. 2009; Tian et al. 2016), although none of these studies demonstrated the effect of thermal stress characterized by high thermal amplitudes shown here. Other studies report that, when exposed to high and low temperatures, several plant species reduce their net photosynthesis (Zhou et al. 2007; Varhammar et al. 2015), instantaneous carboxylation efficiency (Sage and Kubien 2007), stomatal conductance and transpiration (Zhang et al. 2015), which is similar to the results found in this study. It should be emphasized, however, that patterns of resistance and susceptibility vary

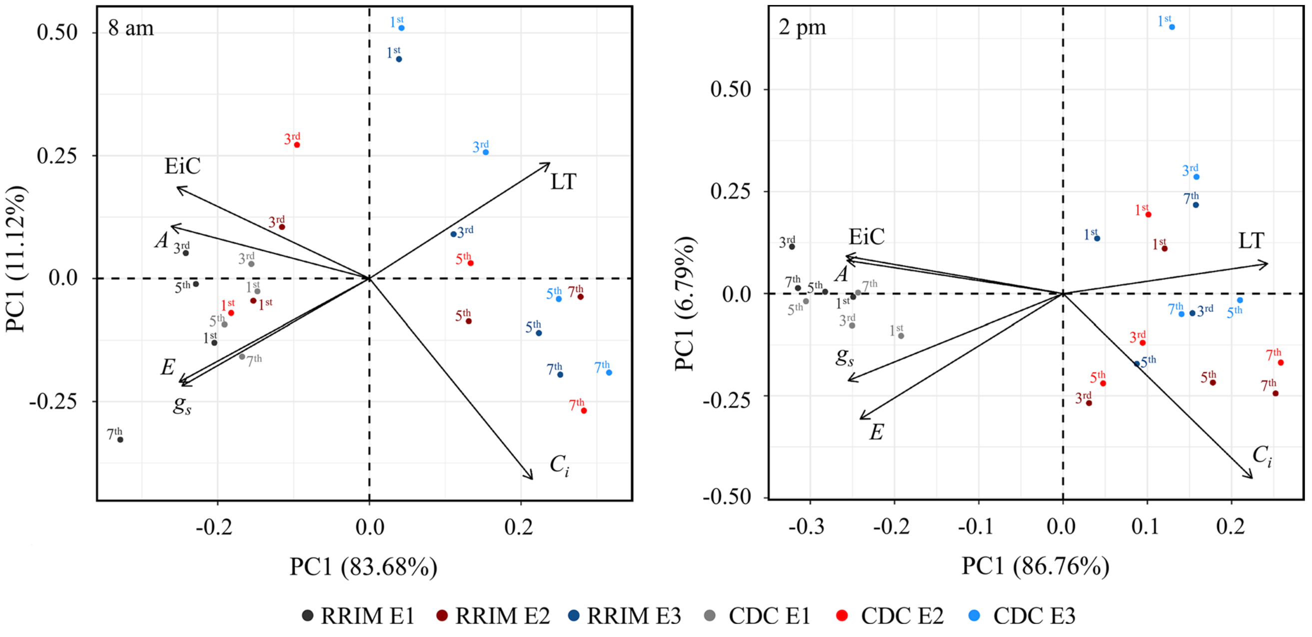

Fig. 7 Biplot of the loadings of the original variables in the first two canonical variables. The percentage of total variance explained by each canonical variable is indicated in parentheses

within a variety or cultivar (clone) of a species, which makes studies like these extremely important.

In the clones studied here, leaves reduced the stomatal conductance under conditions of high air thermal amplitude, which lead to reductions in net photosynthesis and transpiration. Thermal stress generated an increase in intercellular CO_2 concentration, which may indicate damage caused to the photosynthetic machinery of the plants. The high thermal amplitude also increased the leaf temperatures of the clones.

Results of this research demonstrate that there may be limitations to the environmental conditions which are suitable for these two clones. These results provide an important basis for further research aimed at developing rubber trees clones with an increased physiological capacity to grow in environments with greater diurnal changes in night and day temperatures.

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