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ORIGINAL ARTICLE

Physiological Response of Rice Seedlings (*Oryza sativa* L.) Subjected to Different Periods of Two Night Temperatures

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Night temperatures have shown an increase in rice-growing regions due to climate change in Colombia in recent years, causing a reduction in grain yield. The objective of this research was to study the effect of four different periods of exposure to two night temperatures (24°C vs. 30°C) on the physiological behavior of an Indica rice cultivar widely grown in Colombia. Fedearroz 60 ('F60') were grown under greenhouse conditions for forty-five days. After this period, 12 plants in each treatment was established in a growth chamber at 30°C from 18:00 to 24:00 to carry out the duration of the different periods of heat nighttime stress (4, 8, 12, and 16 days respectively). The control plants were kept in a greenhouse at 24°C. The results showed that leaf photosynthesis, carboxylation efficiency, and pigment content decreased in rice seedlings subjected to 30°C. Also, dark respiration and intercellular CO_2 concentration increased. These reductions in the variables as mentioned above were more severe during the first four days of exposure to 30°C than 24°C. In conclusion, these results suggest that these physiological variables may be useful to assess the tolerance of rice plants to high nighttime temperatures in plant breeding programs.

Key words: Chlorophyll fluorescence, Leaf photosynthesis, leaf respiration, Photosynthetic pigments

Rice is one of the most cultivated cereals in the world (FAO, 2002). In Colombia, this crop had a production of 1,925,687 tons on a total area of 455,000 ha during the year 2013 (FEDEARROZ 2015).

Climate change has generated adverse conditions such as extended periods of drought, floods and/or extreme temperatures in many regions of the world (Teixeira *et al*., 2013). In this sense, periods of high temperatures have been recorded in recent years in the rice producing areas in Colombia, and a negative impact on the performance of this crop has been observed (Castilla *et al*., 2010; Restrepo-Diaz and Garces-Varon, 2013; Sánchez-Reinoso *et al*., 2014).

Periods of heat stress, especially high night temperatures can adversely affect the physiology and consequently the yield of rice crops (Mohammed and Tarpley, 2014). On rice seedlings, high night temperatures (35-45°C) decreased the absorption of CO_2, the efficiency of the photosystem II and the ribulose-1,5-bisphosphate carboxylase/oxidase activity (RuBisCO) (Yin *et al*., 2010). Besides the effects on the properties of leaf gas exchange, a high night temperature reduces the chlorophyll content (Kumar *et al*., 2011; Dong *et al*., 2014), affecting the total chlorophyll and carotenoids ratio (Song *et al*., 2013; Dong *et al*., 2014). Another physiological response is the increased night respiration expressed as carbon loss (Lee and Akita, 2000; Mohammed and Tarpley, 2010). Mohammed and Tarpley (2010) mentioned that this carbon loss is one of the causes of yield reduction in rice crops. At a biochemical level, high temperatures (40/32°C day/night) also caused an increase in the antioxidant enzyme activity (superoxide dismutase, glutathione reductase) and the production of compatible osmolytes like proline (Kumar *et al*. 2011; Xue *et al*. 2012).

Both, the physiological and biochemical responses of plants to high night temperatures are determined by the duration of the stress period (Ashraf and Harris, 2013). In this regard, it has been reported that episodes of high night temperatures have increased in recent years in the rice producing areas in Colombia, and have adversely affected crop yields (Castilla *et al*., 2010). However, little is known about the physiological response of rice plants to the duration or periods of high night temperatures in tropical conditions. Therefore, the objective of this research was to evaluate the effect of different times of two night temperatures (24°C vs. 30°C) on the leaf gas exchange properties, dark leaf respiration, lipid peroxidation and production of proline in seedlings of a Colombian rice cultivar susceptible to daytime heat stress.

MATERIALS AND METHODS

Seeds from the cultivar Fedearroz 60 ('F60') were sown in 450 mL plastic pots containing soil. Pots were placed in a glass greenhouse located at Universidad Nacional de Colombia, Bogotá Campus. The average growing conditions in the greenhouse during the study were the following: 30°C day temperature, 24°C night temperature, 70% relative humidity and a natural photoperiod of 12 h. Twelve plants were sown per pot, and each pot was fertirrigated daily with 50 mL of a complete fertilizer solution (Wuxal®, Bayer CropScience, Bogotá D.C., Colombia) at a concentration of 2 mL. L^{-1} H_2O. The fertilizer composition was the following: Total nitrogen 160 g L, (ammonia-N 38 g L^{-1}, nitric N 12 g L^{-1}, urea N 110 g L^{-1}), assimilable phosphorus (P_2O_5) 160 g L^{-1}, Soluble Potassium (K_2O) 120 g L^{-1}, boron (B) 10 g L^{-1}, Copper (Cu)* 0.21 g L^{-1}, iron (Fe) 0.43 g L^{-1}, manganese (Mn) 0.36 g L^{-1}, molybdenum (Mo) 0.07 g L^{-1}, Zinc (Zn)*: 10 g L^{-1}. (*Chelated with EDTA - pH of 10% solution 6.5, density at 25 °C 1.40 g cm^{-3}).

At 45 days after emergence (DAE), 12 plants for each treatment (period of exposition to heat stress) were exposed to a night temperature of 30 °C from 18:00 to 24:00 h. Rice seedlings had four different periods of stress (4, 8, 12 and 16 days, respectively) through the experiment. The heat stress period started by transferring plants subjected to 30°C from the greenhouse to a growth chamber (MLR-351H, Sanyo, Bensenville, Illinois, USA) at 18:00 h. Then, plants were returned to the greenhouse at 06:00 h. The growing conditions in the chamber were: the first period of night temperature of 30°C between 18:00 and 24:00 h, and then, the temperature was adjusted to 24°C between 00:00 and 06:00 h. Finally, rice plants under high nighttime temperature were returned to the greenhouse. Control plants were always placed in the greenhouse

during the experiment (12 plants for each treatment) with an average night temperature of 24 ° C between 18:00 and 24:00 h. A night temperature of 30°C was selected because it is above the optimum temperatures reported for rice (between 23 and 25°C according to Krishnan *et al.* 2011 and Mohammed and Tarpley, 2014). Additionally, four different periods of heat stress were established following the frequency these environmental conditions have been reported in recent years in the rice producing areas in Colombia. Finally, the experiment lasted for 61 days.

Leaf gas exchange measurements were determined with a portable photosynthesis meter (LSPro-SD, ADC BioScientific Ltd.UK). The readings were performed in the middle of the penultimate leaf of the main stem of each seedling, between 10:00 and 13:00 h. The chamber conditions were: a constant photon flux of 1200 µmol $m^{-2}s^{-1}$, an average temperature of 30±2°C and a CO_2 concentration of 400±10 µmol mol^{-1} (environmental temperature and CO_2 concentration).

Water use efficiency and carboxylation efficiency were calculated by the equations described by Kumar *et al*., (2011) and Sikder *et al*., (2015)

$$Water\,Use\,Efficiency\left(WUE\right)=\frac{Pn}{E}$$

$$Carboxylation\,Efficiency\left(CE\right)=\frac{Pn}{C_i}$$

Where *Pn*, *E*, and *Ci* are the photosynthetic rate, transpiration, and substomatal carbon dioxide concentration, respectively.

Maximum PSII efficiency (F_v/F_m) was determined with a non-modulated fluorometer (Handy PEA, Hansatech Instruments, Kings Lynn, UK) in the same leaf where gas exchange measurements were performed. Leaves were dark-acclimated for 20 minutes and then a light pulse of 0.1 µmol $m^{-2}s^{-1}$ was applied to determine the minimum fluorescence (Fo). Subsequently, a saturation pulse of 3000 µmol $m^{-2}s^{-1}$ was applied, and the maximum fluorescence F_m was determined. With these data, it was determined that Fv/Fm = (Fm/(Fm-Fo)).

Leaf chlorophyll and carotenoid contents were estimated by macerating 50 mg of fresh leaves in a mortar with liquid nitrogen. Then, the sample was brought to a volume of 5mL using 80% acetone as a solvent and centrifuged at 10000rpm for 10 minutes. After that, absorbance readings were taken at wavelengths of 663nm, 647nm, and 470 with a spectrophotometer BioMate 3 UV-Vis (Wisconsin, USA). The chlorophyll *a* and *b* and carotenoid contents in leaves (mg L^{-1}) were determined by the formulas described by Lichtenthaler, (1987).

Dark Respiration was also determined using a portable photosynthesis equipment (LSPro-SD, ADC BioScientific Ltd. UK.) in the middle of the penultimate leaf of each seedling (same leaf used in photosynthesis) from 21:00 to 23:00 h as described by Mohammed and Tarpley, (2009a). In both treatments, the photon flux was adjusted to 0 µmol $m^{-2}s^{-1}$ and the chamber temperature to 30°C or 24°C depending on the treatment. The dark respiration was assumed as the CO_2 loss in the leaf.

The method described by Bates *et al*. (1973) was employed to determine the proline content in the leaf. 300 mg of fully developed leaves were homogenized with liquid nitrogen and mixed with 10 mL of sulfosalicylic acid 3% aqueous solution. Subsequently, the mix was centrifuged at 6000rpm for 30 minutes. 2 mL of the filtrate were extracted and reacted with 2 mL ninhydrin acid and 2 mL glacial acetic acid. The above mixture was placed in a water bath for one hour at 90°C, and the reaction was quenched with ice. Then, the reaction mixture was extracted with 4 mL toluene, stirring the test tubes vigorously with a vortex mixer. Absorbance was measured at 520 nm using a spectrophotometer (BioMate 3 UV-Vis, Thermo, USA). Proline content was determined using a standard curve and calculated on a fresh weight basis.

$$\frac{\mu mol\,Proline}{g\,fresh\,material}=\frac{\left[\frac{\left(\frac{\mu g\,Proline}{mL}\,x\,mL\,Toluene\right)}{\frac{115.5\,\mu g}{\mu mol}}\right]}{\left[\frac{g\,Sample}{5}\right]}$$

To determine the lipid peroxidation (represented as Malondialdehyde-MDA content) the thiobarbituric acid

method (TBA) described by Hodges et al. (1999). 300 mg of fully developed leaves were homogenized with liquid nitrogen. Subsequently, the homogenate was mixed with 3 mL of trichloroacetic acid 0.1%. The mixture was centrifuged at 3000 rpm for 10 min. Then, 2 mL of the supernatant were transferred to react in test tubes as follows: (a) with TBA (TBA +): 1 mL of supernatant with 4 mL of trichloroacetic acid 10% plus thiobarbituric acid 0.65%, and (b) Without TBA (-TBA): 1 mL of supernatant with 4 mL of trichloroacetic acid 10%. Subsequently, the test tubes were transferred to a water bath at 95°C for 25 min and the reaction was quenched with ice. Samples were centrifuged again at 3000 g for 10 min, and the absorbances were read at 440, 532 and 600 nm using a spectrophotometer (BioMate 3 UV - Vis, WI, USA). An extinction coefficient of 157 M mL^{-1} was used to obtain the MDA concentration. All physiological and biochemical variables were measured at 4, 8, 12 and 16 days after the onset of treatments in plants subjected to both, 30°C and 24°C.

Data were analyzed using a factorial design (night temperature (24 and 30°C)) vs. exposure time (4, 8, 12 and 16 days)) for a total of 8 treatments. Each treatment consisted of 12 plants as experimental units. The data obtained were tested with the Kolmogorov-Smirnov and Levene tests to check normality and homogeneity of variance, respectively. Then, an analysis of variance (ANOVA) was applied. Where a significant F-test was observed, means separation between treatments was obtained using Tukey's test, or by polynomial contrast for quantitative factors. Data were analyzed using the SPSS software (v20.0, IBM Company, USA) was performed.

RESULTS

Differences were not observed on the photosynthetic rate (P_n) along the experiment in control plants (24°C). However, a cubic response was observed throughout the experiment in plants subjected to high night temperatures (HNT), presenting a sharp drop in the carbon assimilation rate in rice plants under HNT for 16 days**.** In general, the P_n decreased about 12% in rice plants under night temperatures of 30°C compared to the control (24°C) (Fig. 1A). Likewise, similar trends were obtained in stomatal conductance (g_s) to those observed in the photosynthesis rate (Fig. 1B). Leaf transpiration (*E*) also showed a cubic behavior and no differences were seen in the experiment in both treatments. However, a drop in the transpiration rate was observed at 16 DAE in both night temperature conditions (Fig. 1C). On the other hand, internal CO_2 concentration (C_i) also presented a cubic response, and this was higher in plants subjected to 30°C compared to the control (24°C) at 4, 8 and 12 days after seed emergence (DAE). However, these differences did not continue at the end of the experiment (16DAE) (Fig. 1D).

Carboxylation efficiency understood as the P_n/C_i ratio was higher in control plants (24°C) throughout the experiment. However, differences were not observed at 16 DAE (Fig. 2A). Also, water use efficiency (WUE = P_n/E) showed similar trends to those found in P_n/ C_i (Fig. 2B). In general, the behavior of these two variables was 15% higher in control plants compared to HNT plants throughout the experiment.

Cubic responses were observed on dark leaf respiration (R_o) in both night temperatures. In this aspect, R_o showed an increase of ~70% during the first four days in plants subjected to a night temperature of 30°C. Then, it presented similar values to those obtained in control plants (24°C) between 8 and 12 DAE. At the end of the experiment (16 DAE), R_o was again higher in rice plants under a night temperature of 30°C in comparison to the control (Fig. 3). When the effect of two night temperatures was expressed as carbon balance (CO_2 fixated by photosynthesis minus the loss of this gas by dark respiration) analyzed, a lower CO_2 balance was observed in plants exposed to 30°C especially at 4 and 16 DAE, respectively (Fig. 4). In this sense, rice seedlings under HNT showed a drop of about 17% and 25% in the carbon accumulation during the periods of heat stress mentioned above.

PSII efficiency was also lower mainly in rice seedlings at 30°C between 4 and 8 DAE. At 16 DAE, control plants had the lowest values of Fv/Fm ratio, however; differences were not obtained between treatments (Fig. 4). Unlike the previous variable, the total chlorophyll and carotenoids content in rice leaves showed a negative linear response in relation to time in both conditions of temperature (Fig. 5). In this regard,

the content of photosynthetic pigments was always lower in plants under 30°C throughout the experiment.

Leaf lipid peroxidation (represented as MDA content) of rice plants under 24, and 30°C showed no significant difference throughout the test. However, a decrease in MDA content was observed at 16 DAE at both temperatures (Fig. 6A). On the other hand, the content of proline presented differences between night temperature treatments on days 12 and 16 (Fig 6B). The increase in this amino acid was higher in plants exposed to 30°C from 8 to 16 DAE compared to control plants that showed a reduction in the synthesis of this amino acid in the same period mentioned above.

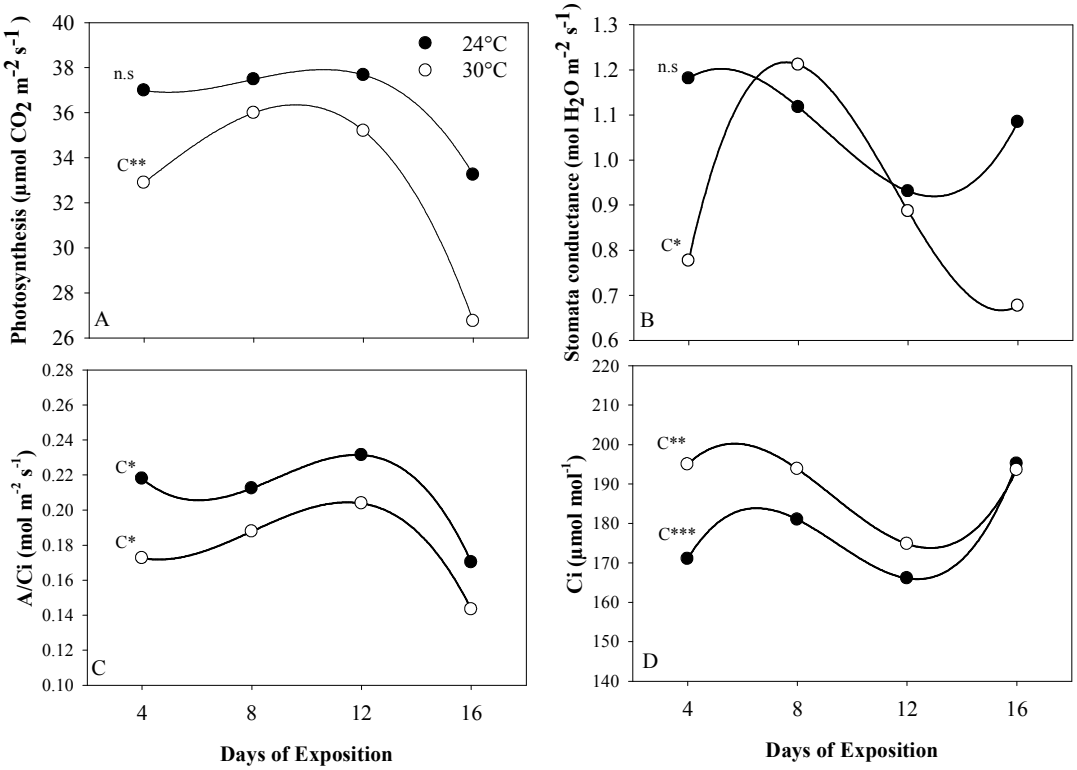

Figure 1. Effect of four different periods of exposition (4, 8, 12 and 16 days) to two night temperatures (24 vs. 30°C) on Photosynthesis (A), Stomatal Conductance (B), Transpiration (C) and Intercellular CO_2 Concentration D) in rice seedlings. Lines with letter C show a cubic behavior. NS,*, ** and *** represent non-significant and P≤ 0.05, 0.01 and 0.001 significance, respectively. Each point represents the average of 12 values

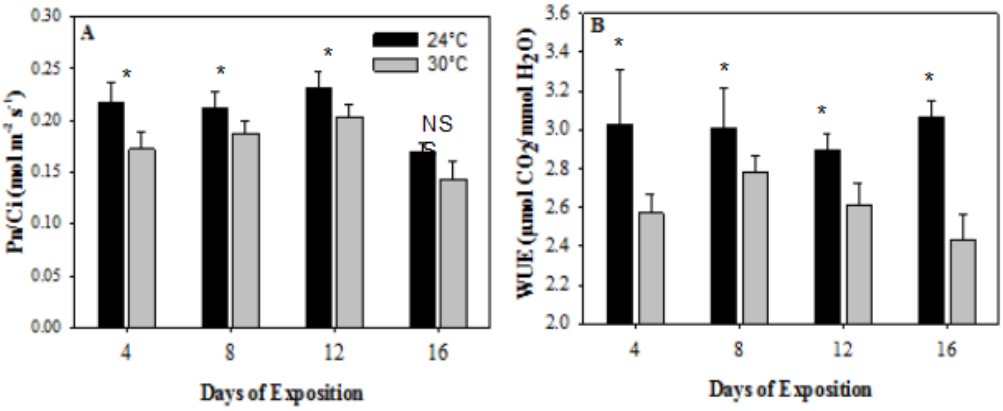

Figure 2. Effect of four different periods of exposition (4, 8, 12, 16 days) to two night temperatures (24 vs. 30°C) on Carboxylation efficiency (A) and water use efficiency (B) in rice seedlings. Each bar of the graph represents the means of twelve values. NS, and * represent non-significant and P≤ 0.05, significance, respectively. Vertical bars represent standard error.

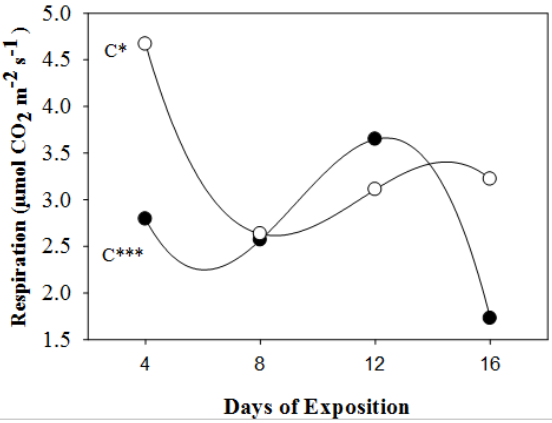

Figure 3. Effect of four different periods of exposition (4, 8, 12, 16 days) to two night temperatures (24 vs. 30°C) on Dark respiration in rice seedlings. Lines with letter C show a cubic behavior. NS,*, ** and *** represent non-significant and P≤0.05, 0.01 and 0.001 significance, respectively. Each point represents the average of 12 values.

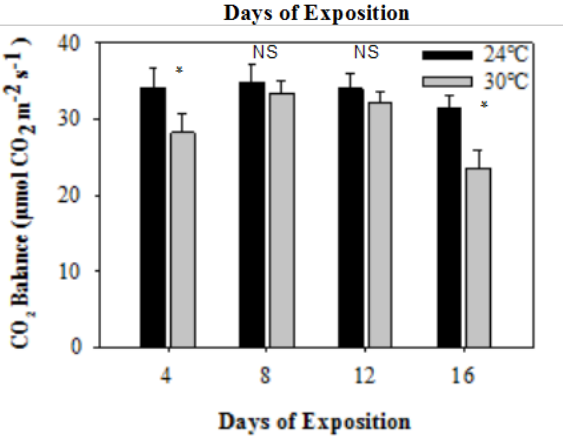

Figure 4. Effect of four different periods of exposition (4, 8, 12, 16 days) to two night temperatures (24 vs. 30°C) on CO_2 balance in rice seedlings. Each bar of the graph represents the means of twelve values. Vertical bars represent standard error. NS, and * represent non-significant and P≤ 0.05, significance, respectively.

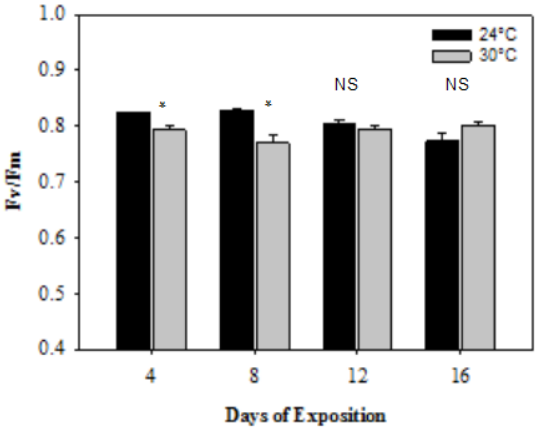

Figure 5. Effect of four different periods of exposition (4, 8, 12, 16 days) to two night temperatures (24 vs. 30°C) on Maximum PSII efficiency (Fv/Fm) in rice seedlings. Each bar of the graph represents the means of twelve values. Vertical bars represent standard error. NS, and * represent non-significant and P≤ 0.05, significance, respectively.

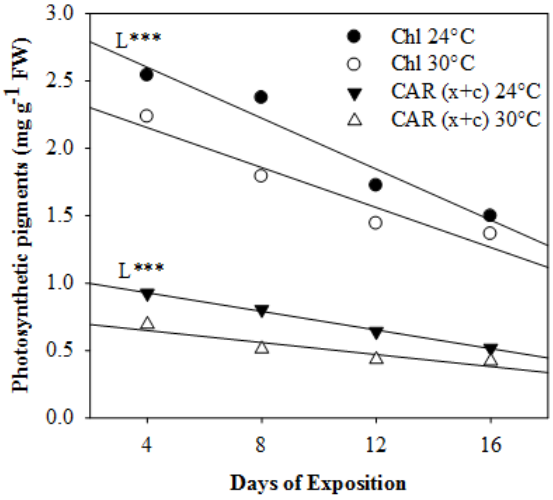

Figure 6. Effect of four different periods of exposition (4, 8, 12, 16 days) to two night temperatures (24 vs. 30°C) on Leaf Chlorophyll and Carotenoid contents in rice seedlings. Lines with letter L show a linear behavior (P≤0.001). Each point represents the average of 12 values.

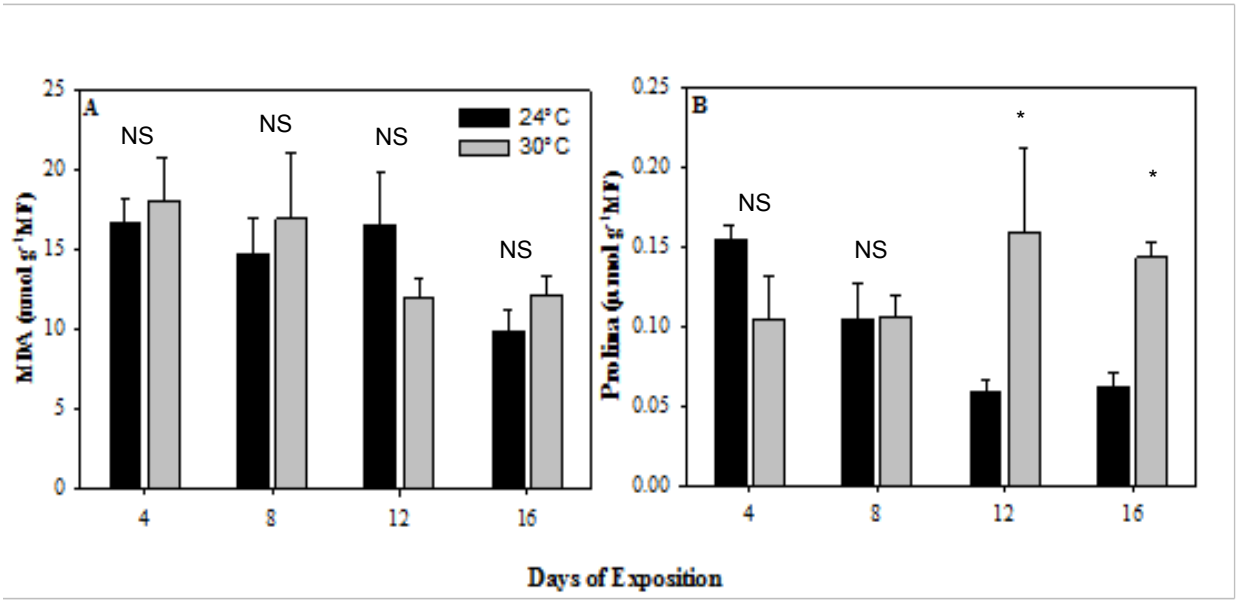

Figure 7. Effect of four different periods of exposition (4, 8, 12, 16 days) to two night temperatures (24 vs. 30°C) on leaf MDA (A) and Proline content (B) in rice seedlings. NS, and * represent non-significant and P≤ 0.05, significance, respectively. Each bar of the graph represents the means of twelve values. Vertical bars represent standard error.

DISCUSSION

Photosynthesis (Pn) is one of the most sensitive physiological processes to high temperatures during both, day and night (Ashraf and Harris, 2013). In the present study, the photosynthetic rate decreased around 15% due to a high night temperature (30°C) throughout the experiment (Fig. 1). Similar results were also obtained by Mohammed *et al*., (2013) where night temperatures of 30°C caused a Pn reduction of ~10% in rice. This Pn reduction may be due to the sum of the alterations of variables produced by HNT in both, the light phase and the carboxylation of the photosynthetic process stage. Regarding the light phase of Pn, it has been reported that prolonged periods of high night temperatures caused a reduction in the content of photosynthetic pigments and PSII efficiency in rice. In this sense, works carried out by Mohammed and Tarpley, (2009b) showed that long periods of HNT caused a reduction of photosynthetic pigments and Fv/Fm ratio, having an adverse impact on Pn in rice plants. Similar observations were also obtained in the present study where a reduction of the content of carotenoids and chlorophylls, and a lower Fv/Fm ratio were found in rice plants exposed to 30°C (Fig. 5). Also, a lower CO_2 assimilation may be because HNT cause limitations associated with the Calvin cycle (Song *et al.*, 2013; Mohammed and Tarpley, 2014). In this regard, a lower carboxylation efficiency and accumulation of intercellular CO_2 (Fig. 1 and 2) were observed. The low CE may mean less RuBisCO capacity to fix CO_2, causing a higher intracellular accumulation of CO_2 *(Kiran et al*., 2013). Concerning R_o, it showed an increase of about 50% in rice seedlings at 30°C compared to the control (24°C) at 4 and 16 DAE mainly (Fig.3). This carbon loss as respiration has also been reported by Mohammed and Tarpley, (2010) and Mohammed *et al*., (2013) who showed that night temperatures between 30 and 32°C caused an increase of R_o of about 50% in rice plants. A higher leaf respiration can be due to the following factors: a) to maintain electrons flow in the mitochondria; b) to avoid an oxidative stress (Plaxton and Podestá, 2006); c) to synthesize more ATP to produce NAD^+ (which is adversely affected by high temperature) (*Wahid et al*., 2007); and d) to increase protein synthesis and regeneration (Lambers *et al*., 2008). The processes described above are intended to reduce the adverse effects of HNT (Plaxton and Podestá, 2006).

Furthermore, MDA content showed no differences between the two night temperatures (Fig. 7A). However, these results contrast with other studies where the lipid peroxidation was higher when the night temperature

increased (Kumar *et al*., 2011; Xue *et al*., 2012). These results help to infer that a night temperature of 30°C does not cause further membrane damage at the cellular level in this Colombian rice cultivar despite the modifications in photosynthesis and respiration. Also, another biochemical response under conditions of thermal stress is the production of proline (Sánchez-Reinoso *et al*. 2014). In our study, proline production showed differences between night temperatures, with an increase of this osmolyte in rice seedlings at 30°C throughout the experiment (Fig. 7B).

The highest concentration of proline produced in plants under heat stress has been reported by other authors as (Kumar *et al*. 2011). They report that a temperature above 35/30°C (day/night) causes an increase in rice and corn seedlings. During a high temperature, proline accumulation increases the osmotic potential of cells, which helps to maintain the pressure potential, relative water content and cell homeostasis (Wahid and Close, 2007). Therefore, it can be inferred that proline accumulation in rice seedlings 'F60' is an acclimation to high night temperatures.

In conclusion, a high night temperature around 30°C causes a reduction in the photosynthetic rate and WUE mainly due to a lower rate of carboxylation. Likewise, plants increased respiratory rate and the concentration of proline as a possible mechanism of acclimatization to a high temperature, but there was no lipid peroxidation of membranes. All these changes are most noticeable during the first four days of exposure to 30°C. Finally, CO_2 assimilation, photosynthetic pigment content, and carboxylation efficiency are right indicates of susceptibility to heat stress because they showed changed due to treatments and can be used for the characterization of genotypes in plant breeding programs.

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