# Leaf water potential, gas exchange and chlorophyll *a* fluorescence in acariquara seedlings (*Minquartia guianensis* Aubl.) under water stress and recovery

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The physiological performance of acariquara (*Minquartia guianensis*) seedlings submitted to water deficit and the recovery of physiological parameters during rehydration were investigated in a greenhouse experiment. The analyzed parameters were: leaf water potential, gas exchange and chlorophyll *a* fluorescence. After thirty-five days, non-irrigated plants exhibited a leaf water potential 70 % lower compared to control plants (irrigated daily) and the stomatal conductance reached values close to zero, inducing a severe decrease in gas exchange (photosynthesis and transpiration). Six days after the beginning of the rehydration of drought-stressed plants, the results demonstrated that water stress did not irreversibly affect gas exchange and quantum efficiency of photosystem II (PSII) in *M. guianensis* seedlings, since four to six days after rehydration the plants exhibited total recovery of the photosynthetic apparatus. We conclude that *M. guianensis* presented good tolerance to water stress and good capacity to recover the physiological performance related to leaf water status, photosynthesis and photochemical efficiency of PS II under hydric stress, suggesting substantial physiological plasticity during the juvenile phase for this tree species.

**Key words**: chlorophyll *a* fluorescence, photochemical efficiency of PSII, stress physiology, tree species, water deficit.

**Potencial hídrico foliar, trocas gasosas e fluorescência da clorofila *a* em plantas jovens de acariquara (*Minquartia guianensis* Aubl.) sob estresse hídrico e reidratação:** Investigou-se, em regime de casa de vegetação, o desempenho fisiológico de plantas jovens de acariquara (*Minquartia guianensis*) submetidas à deficiência hídrica e sua recuperação durante o processo de reidratação. Os parâmetros analisados foram: potencial da água nas folhas, trocas gasosas e fluorescência da clorofila *a*. Após trinta e cinco dias, o potencial da água nas folhas das plantas sem irrigação foi 70 % menor do que nas plantas do controle (irrigadas diariamente) e a condutância estomática alcançou valores próximos de zero, induzindo diminuição severa nas trocas gasosas (fotossíntese e transpiração). Seis dias após o início da reidratação prevista para as plantas submetidas ao tratamento sem irrigação, os resultados demonstraram que o estresse hídrico não afetou de forma irreversível as trocas gasosas e a eficiência quântica do fotossistema II (PSII) em plantas jovens de *M. guianensis*, uma vez que após o período de quatro a seis dias de reidratação, as plantas exibiram recuperação total do aparato fotossintético. Nós concluímos que *M. guianensis* apresentou boa tolerância ao estresse hídrico e boa capacidade de recuperação do desempenho fisiológico relativo ao potencial hídrico foliar, fotossíntese e eficiência fotoquímica do PSII sob condições de estresse hídrico, sugerindo substancial plasticidade fisiológica durante a fase juvenil dessa espécie arbórea.

**Palavras-chave:** déficit hídrico, eficiência fotoquímica do PSII, espécie arbórea, fisiologia do estresse, fluorescência da clorofila *a*.

## INTRODUCTION

*Minquartia guianensis* Aubl. (acariquara) is a tropical tree species of the Olacaceae family. The wood of adult trees is typically used for furniture, structural timber, and other kinds of wood applications (Lorenzi, 1998). Extractive and selective exploration and the advance of agricultural frontiers (both common practices in the Brazilian Amazon region) are reducing its natural vegetative habitat and making the process of regeneration difficult (Marenco and Vieira, 2005). Informations about the strategies used by plants in response to the availability of primary resources (temperature, carbon dioxide, nutrients, light and water) are indispensable in order to improve the management and sustainable use of different species with elevated economic potential. In addition, these resources directly interfere in the photosynthetic process, which greatly contributes for the successful establishment of a plant species in a determined environment (Gonçalves et al., 2003; Gonçalves et al., 2005).

Furthermore, the intensification of climate change in the Amazon has promoted great alterations in climatic factors, as confirmed by the low precipitation in the year 2005 (Marengo and Nobre, 2005). The climate of Central Amazonia has a mean temperature of 26.2–26.6ºC and annual precipitation of 2100–2500 mm, characterized by a distinct dry season between June and November (Irion et al., 1997) and, exceptionally low precipitation during the rainy season in the Amazon Basin is generally correlated with the El Niño phenomenon (Marengo and Nobre, 2001). The El Niño phenomenon, originating from the tropical Pacific Ocean, is the strongest natural interannual climate fluctuation affecting societies and economies of many countries through flooding and severe droughts (Allan et al., 1996).

In the context of reduced precipitation, the response of photosynthesis to drought merits special attention, especially because water is an electron donor that allows for the maintenance of this process. In addition, water deficiency affects physiological and metabolic processes in plants, including cellular growth, protein synthesis, stomatal opening, photosynthates and nutrient transport (Angelopoulos et al., 1996; Nepomuceno et al., 1998).

Under conditions of low water availability, reductions in stomatal conductance constitute one of the first strategies used by plants to diminish transpiration rate and maintain turgescence (Eckstein and Robison, 1996). While the loss of water vapor becomes slow due the process of stomatal closure, it also reduces the absorption of carbon dioxide ($CO_2$), and consequently, photosynthesis (Souza et al., 2001). Accordingly, the stomatal behavior in response to situations of hydric stress may be indicative of water use efficiency for the production of photosynthates (Plaut, 1994).

The exposure to stress may induce alterations in plant photobiological processes resulting in stomatal restrictions on the supply of carbon dioxide, loss of water vapor, as well as limitations on non-stomatal components, with damage to the reaction centres of photosystems I and II (PSI and PSII), thereby compromising photosynthesis efficiency (Angelopoulos et al., 1996). According to Bolhàr-Nordenkampf et al. (1989), Bolhàr-Nordenkampf and Öquist (1993) and Baker (1993), changes in the photochemical efficiency of plants under drought conditions may be assessed by the analysis of chlorophyll *a* fluorescence efficiency associated with PSII.

The objective of this work was to investigate the leaf water potential, gas exchange and chlorophyll *a* fluorescence parameters in *M. guianensis* seedlings when submitted to hydric deficiency as well as during the rehydration process.

## MATERIAL AND METHODS

*Study area and experiment installation*: The study was conducted in the greenhouse of the Coordenação de Pesquisas em Silvicultura Tropical (CPST) at *campus* III (V8), of the Instituto Nacional de Pesquisas da Amazônia (MCT-INPA), Manaus, AM, Brazil (3º8'S, 59º52'W). *M. guianensis* seedlings, approximately 12 months old, were selected according to their uniformity in size (40 cm height) and health state. The plants were grown in plastic pots (30 x 25 cm), containing a mixture of earth, sand and organic matter (3:1:1, v/v/v) and submitted to a period of 60 days of adaptation to light and temperature under greenhouse conditions. During this period, all the pots were irrigated daily to maintain field capacity (field capacity was considered reached when water percolated through the pot to the container under it and soil was saturated). Each plastic pot contained one plant.

After the adaptation period, plants were separated randomly in two groups of twelve plants. One group continued to receive daily irrigation (control treatment) and the other was induced to drought stress (non-irrigated treatment). For both treatments leaf water potential, gas exchange and chlorophyll *a* fluorescence parameters were determined throughout the experiment. Non-irrigated plants began to receive daily irrigation when their rates of net photosynthesis reached values close to zero. Leaf water potential, gas exchange and chlorophyll *a* fluorescence continued to be measured for six days in order to monitor the recovery process.

*Leaf water potential*: The water potential in leaves ($\Psi$w) was determined according to Scholander et al. (1964) using a pressure chamber (PMS Instrument CO, Corvalis, Oregon, USA). The readings were taken between 9:00 and 10:00 am using healthy leaves situated in the middle-third of the plants, fully expanded and uniform in terms of age. The increment of pressure applied was 0.2 MPa and the waiting time for sieve extrusion was five minutes.

*Gas exchange measurements*: For the gas exchange measurements a portable open system infrared gas analyzer (LI-6400, LI-COR, Lincoln, Nebraska, USA) was used, in accordance with the methodology described by Marenco et al. (2001). The measurements were made in for one leaf per plant, between 9:00 and 11:00 a.m. using completely expanded healthy leaves, located in the middle-third of the plants and uniform in terms of age. The leaf chamber was adjusted to a photosynthetic photon flux density (PPFD) of 1000 $\mu mol.m^{-2}.s^{-1}$, with a concentration of carbon dioxide ($CO_2$), temperature and water vapor of approximately 400 $\mu mol.mol^{-1}$, 31±1°C (standard deviation) and 21±1 $mmol.mol^{-1}$, respectively. Measured variables include net photosynthesis (*A*), stomatal conductance ($g_s$) and transpiration (*E*). Water use efficiency (*WUE*) was determined by the ratio of net photosynthesis to transpiration (*A/E*).

*Chlorophyll a fluorescence*: For the determination of chlorophyll *a* fluorescence yield, readings were taken with a pulse fluorometer of modulated amplitude (OS5 - FL Modulated Chlorophyll Fluorometer, OPTI-SCIENCES), using leaves submitted to ambient light (when the photosynthetic apparatus is at full capacity) and leaves submitted to darkness (when the photosynthetic apparatus is fully recovered) according to Schreiber et al. (1994). The optic fiber was maintained at a constant distance of 2 cm at an angle of approximately 60° in relation to the adaxial surface of the leaf. The light pulses had a duration of 0.8 s and an intensity of 1000 $\mu mol.m^{-2}.s^{-1}$. In leaves submitted to darkness, readings were always taken between 4:00 and 5:00 a.m., and in leaves submitted to ambient light readings were taken between 9:00 and 11:00 a.m. (with the same leaves used for fluorescence emission at dawn). The following chlorophyll *a* fluorescence parameters were calculated: maximum quantum efficiency of PSII primary photochemistry ($F_v/F_m$), according to van Kooten and Snel (1990); effective quantum yield of PSII [$\Phi_{PSII} = (F'_m - F_S)/F'_m$], according to Genty et al. (1989); apparent rate of photochemical transport of electrons through PSII (ETR = $\Phi_{PSII} \times PAR \times 0.5 \times 0.84$), according to Schultz (1996). The coefficient of photochemical quenching [$q_L = [(F'_m - F_S)/F'_m] - F'_o \times F'_o/F_S$] was determined according to Kramer et al. (2004) and the coefficient of non-photochemical quenching of excitation energy [$NPQ = (F_m - F'_m)/F'_m$] according to Schreiber et al. (1994). Where: $F_o$ = initial fluorescence in leaves submitted to a period to darkness; $F_m$ = maximum fluorescence in leaves acclimated to darkness; $F_v$ = variable fluorescence in leaves acclimated to darkness ($F_v = F_m - F_o$); $F'_o$ = initial fluorescence in leaves submitted to ambient light; $F'_m$ = maximum fluorescence in leaves acclimated to ambient light; $F_S$ = stable fluorescence in leaves acclimated to ambient light; PAR = incident photosynthetically active radiation in the leaf; 0.5 corresponds to the proportion of absorbed *quanta* that are used by the PSII reaction centers; and 0.84 represents the proportion of incident irradiance that is absorbed by the leaf.

*Experimental design and statistical analysis*: The experimental design was completely randomized with two treatments and twelve replicates, considering each plant as a repetition. The statistical analyses were carried out using the program MINITAB – *Statistical software*. The results obtained were submitted to an analysis of variance and the means compared by the Tukey test (P<0.05).

## RESULTS AND DISCUSSION

### Stress imposition

*Leaf water potential and gas exchange*: The leaf water potential (Ψw) in *M. guianensis* seedlings on the twentieth day after the imposition of drought showed significant differences between treatments (figure 1).

For *Copaifera langsdorffii* (Prado et al., 1994), *Stryphnodendron adstringens* (Rocha and Moraes, 1997) and *Malpighia emarginata* (Nogueira et al., 2001) submitted to water deficiency, reduction of net photosynthesis (*A*) to values close to zero occurred when leaf water potential reached values of approximately -3.5 MPa, -2.7 MPa and between -4.5 and -5.7 MPa, respectively. In this experiment, seedlings of *M. guianensis* submitted to irrigation presented, at 35 days after the initial suspension of irrigation, average values of Ψw of approximately -3.18 MPa, and these were associated with stomatal closure and a net photosynthetic rate close to zero (figure 1 and 2A).

Because stomata exert an important influence on photosynthesis through regulation of both the loss of water vapor (transpiration) and the absorption of carbon dioxide (carbon assimilation), plants usually show a parallel decrease between stomatal conductance ($g_s$) and net photosynthesis (*A*) with increased drought (Ni and Pallardy, 1992). In *M. guianensis* seedlings submitted to water deficiency, net photosynthesis and stomatal conductance rates were reduced to about 50 % of those for irrigated plants (control) after 25 days of drought imposition. After thirty-five days of drought the closing of stomatal pores was observed in the non-irrigated treatment, and consequently net photosynthesis and stomatal conductance reached values close to zero (figures 2A and 2B).

Transpiration (*E*) values ranging between 1.12 and 1.29 $mmol.m^{-2}.s^{-1}$ were observed for *M. guianensis* seedlings irrigated (control) during the whole experimental period. In the plants submitted to water deficiency, however, at twenty days after suspension of irrigation, stomatal conductance was about 25 % less than in control plants, and the loss of water vapor reduced to about 50 % in non-irrigated plants (figure 2C).

The stomatal control of transpiration is a mechanism used by different species to restrict loss of water and to overcome periods of drought, as verified by Naves-Barbiero et al. (2000) in the woody species *Rapanea guianensis* and *Roupala montana* of Brazilian grasslands, by Silva et al. (2003) in *Tabebuia aurea* plants, and by Souza et al. (2001) in vine seedlings.

In *M. guianensis* seedlings submitted to water deficiency a continuous decrease in stomatal conductance was observed as the stress progressed (figure 2B), while water use efficiency (*WUE*) was gradually elevated (figure 2D). As evidenced by the readings taken on the 20th day after the imposition of stress, values of leaf water potential, net photosynthesis and stomatal conductance of non-irrigated plants were reduced close to 25 % and transpiration decreased approximately 50 %, while the water use efficiency increased to 60 % in relation to the values shown by control plants (figures 1 and 2A-D).

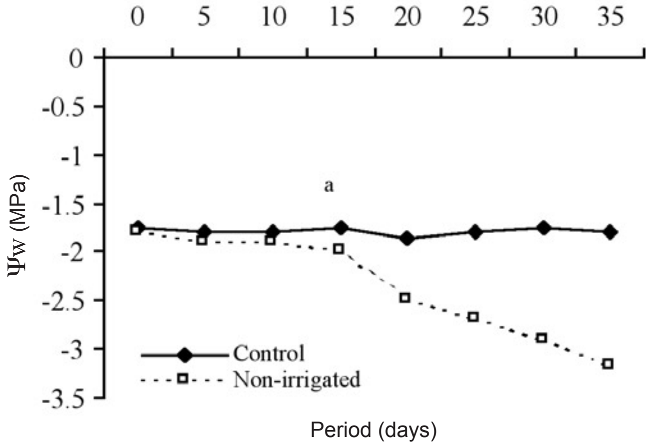

**Figure 1.** Leaf water potential (Ψw) in *Minquartia guianensis* seedlings under different treatments regarding water availability. Mean values followed by the same letters for treatments are not different at $P \leq 0.05$ using the Tukey test. n = 12.

The results show that reduced $g_s$ under drought conditions increased *WUE* and led to a greater decline in *E* than in *A*, consistent with the results for *Copaifera langsdorffii* (Prado et al., 1994) and *Stryphnodendron adstringens* (Rocha and Moraes, 1997).

*Chlorophyll a fluorescence*: Twenty-five days after the installation of the experiment, reductions of approximately 10 % were observed in the maximum quantum efficiency of PSII primary photochemistry ($F_v/F_m$), 20 % in the effective quantum yield of PSII ($\Phi_{PSII}$), 12 % in the photochemical quenching of excitation energy ($q_L$), and 23 % in the apparent photochemical transport of electrons (ETR) in *M. guianensis* seedlings submitted to the non-irrigated treatment, in relation to the control plants. At thirty-five days, when net photosynthesis was close to zero, these reductions were 15 % for $F_v/F_m$, 25 % for $\Phi_{PSII}$, 24 % for $q_L$ and 40 % for ETR (figures 3A to 3D).

Under stress, a decrease in the ratio of $F_v/F_m$ has been attributed to the inactivity of the PSII reaction centers due to the degradation of the D1 and D2 proteins responsible for the transfer of water electrons to chlorophyll *a* associated with the PSII reaction center (Hao et al., 1999; Lazár, 1999). Thus, in *M. guianensis* seedlings maintained under drought, the decline in the $F_v/F_m$ ratio could be related to damage to the protein structures of the photochemical complexes of the thylakoid membranes. Therefore, the capacity of the plastoquinone complexes, responsible for the photochemical transport of electrons between photosystems I and II, to carry out oxireduction reactions may have been affected, as reflected in the progressive reduction of $\Phi_{PSII}$ and ETR after twenty-five days without irrigation (figures 3B and 3D).

The photochemical quenching of excitation energy ($q_L$) is related to both the proportion of electrons transported from PSII and stomatal opening for absorption of $CO_2$. The decline in values of these variables is, as a rule, indicative of an increase in quinone A ($Q_A$) in the reduced state due to the increase in the proportion of inactive PSII reaction centres (Quick and Horton, 1984; Dietz et al., 1985; Genty et al., 1989). Therefore, it is likely that the behavior of the stomatal complex and electron transport observed in *M. guianensis* seedlings in the treatment without irrigation contributed to the decline in the rate of photochemical quenching of excitation energy (figure 3C).

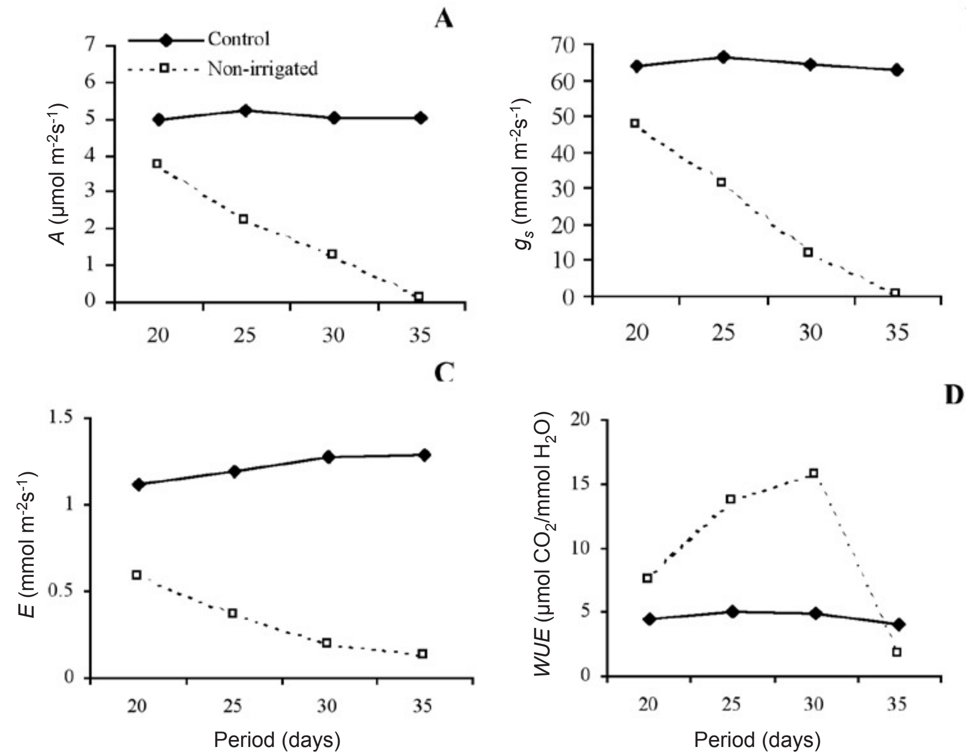

**Figure 2.** Net photosynthesis - $A$ (**A**), stomatal conductance - $g_s$ (**B**), transpiration - $E$ (**C**) and water use efficiency - *WUE* (**D**) in *Minquartia guianensis* seedlings under different treatments regarding water availability. Mean values followed by the same letters for treatments are not different at $P \le 0.05$ using the Tukey test. n = 12.

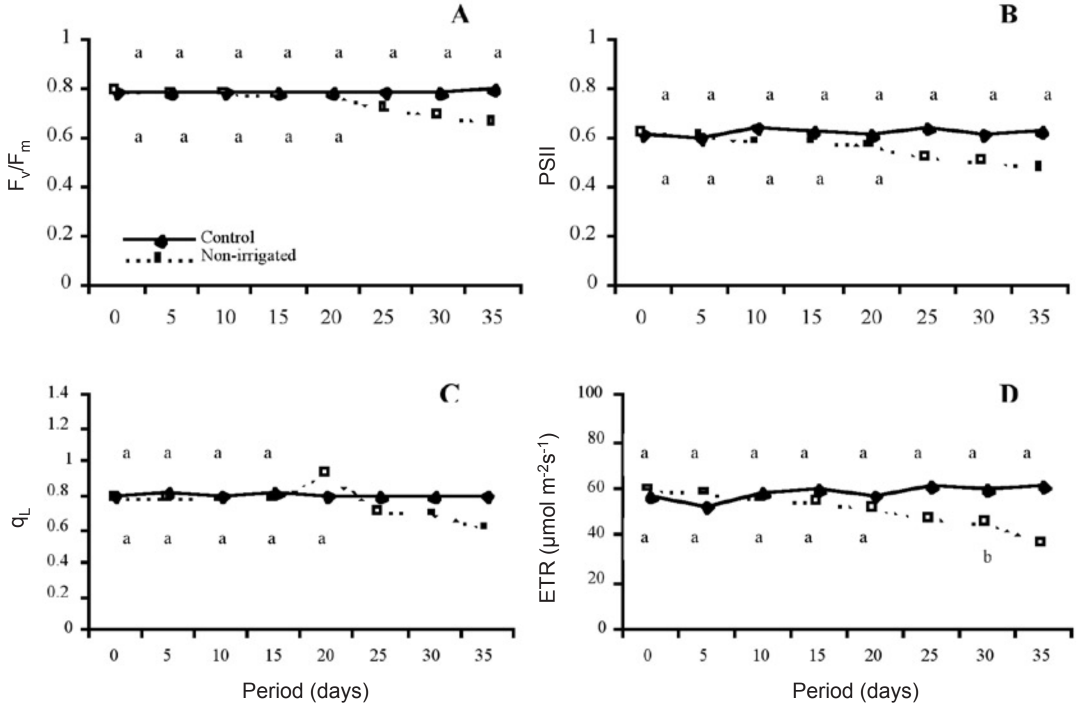

**Figure 3.** Maximum quantum efficiency of PSII primary photochemistry - $F_v/F_m$ (**A**), effective quantum yield of PSII – $\Phi_{PSII}$ (**B**), photochemical quenching of the excitation energy - $q_L$ (**C**) and apparent photochemical electron transport ratio - ETR (**D**) in *Minquartia guianensis* seedlings under different treatments regarding water availability. Mean values followed by the same letters for treatments are not different at $P \le 0.05$ using the Tukey test. n = 12.

Nevertheless, under conditions of stress, plants can activate the protective mechanisms of PSII that dissipate the excess excitation energy through non-photochemical processes (Casper et al., 1993). Although the two processes of quenching of excitation energy (photochemical and non-photochemical) are competitive, that is, the increase in one process causes the decrease in the other (Krause and Weis, 1991), such a response did not occur in *M. guianensis* seedlings submitted to drought. In these plants, non-photochemical quenching of energy excitation (NPQ) remained similar to the values observed in control plants during the entire experimental period (figure 4). Such behavior is consistent with the light protection activity of the nicotinamide adenine dinucleotide (phosphate) - dehydrogenase (*Ndh*), a component of the respiratory electron transport chain within the chloroplast thylakoid membrane (chlororespiration) (Bennoun, 1982; 2002). In the light, the *Ndh* complex is able to oxidize stromal reductant and thus act as an emergency electron sink for photosynthetic electron transport, in order to avoid the generation of reactive oxygen species in the stroma (Nixon, 2000).

**Stress recovery**

*Water potential and gas exchange*: The increase of leaf water potential values (Ψw) in non-irrigated *M. guianensis* seedlings was verified 24 h after initiation of the rehydration process, but this increase was only 5 % in relation to the value considered critical for photosynthesis. However, Ψw of rehydrated plants only reached values statistically equal to those observed in control plants four days after rehydration (figure 5A).

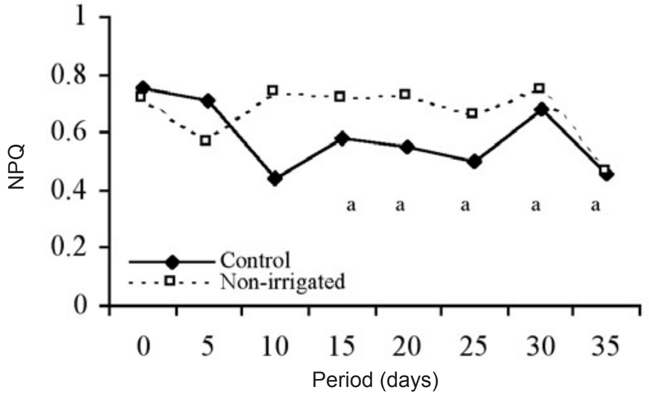

**Figure 4.** Non-photochemical quenching of the excitation energy (NPQ) in *Minquartia guianensis* seedlings under different treatments regarding water availability. Mean values followed by the same letters for treatments are not different at $P \leq 0.05$ using the Tukey test. n = 12.

The increase of leaf water potential values in stressed plants to the same level shown by control plants indicated that the mesophyll of stressed plants was not irreversibly affected by drought. This premise is corroborated by the behavior of net photosynthesis, stomatal conductance and transpiration, which presented a gradual process of recovery after the resumption of irrigation (figures 5B to D).

The time for recovery of gas exchange variables ($A$, $g_s$ and $E$), analyzed in *M. guianensis* seedlings after the period of hydric stress was compatible with the average period of recuperation shown by other tree seedlings submitted to drought. Calbo and Moraes (1997) observed that young *Mauritia vinifera* plants, maintained without irrigation for forty-one days, showed total recovery of photosynthetic rates five days after rehydration. In *Bactris gasipaes* seedlings under water deficiency for thirteen days, there was total recovery of leaf water potential, photosynthesis and transpiration three days after replacement of water in the soil (Oliveira et al., 2002). In *Stryphnodendron adstringens* seedlings without irrigation for thirty days, total recuperation of water potential and gas exchange variables ($A$, $g_s$ and $E$) occurred in 48 h (Rocha and Moraes, 1997), whereas in *Euterpe oleracea* plants without irrigation for sixty-one days, the time for recuperation of gas exchange parameters was fourteen days after irrigation (Calbo and Moraes, 2000).

*Chlorophyll a fluorescence*: Four days after resumption of irrigation the maximum quantum efficiency of PSII primary photochemistry ($F_v/F_m$) was reestablished (figure 6A). However, the effective quantum yield of PSII ($\Phi_{PSII}$) only reached values similar to those of plants under treatment with irrigation on the sixth day after rehydration (figure 6B).

On the other hand, the apparent rate of photochemical transport of electrons (ETR), in non-irrigated plants, reached values statistically equal to those of control plants on the second day after the resumption of irrigation (figure 6D). It is possible that processes such as the Mehler reaction and photorespiration also contributed to the reestablishment of the flux of electrons, since from only the fourth day after resuming irrigation, photochemical quenching of excitation energy ($q_L$) showed total recuperation, reaching values equal to those previously observed during the period of water deprivation (figure 6C).

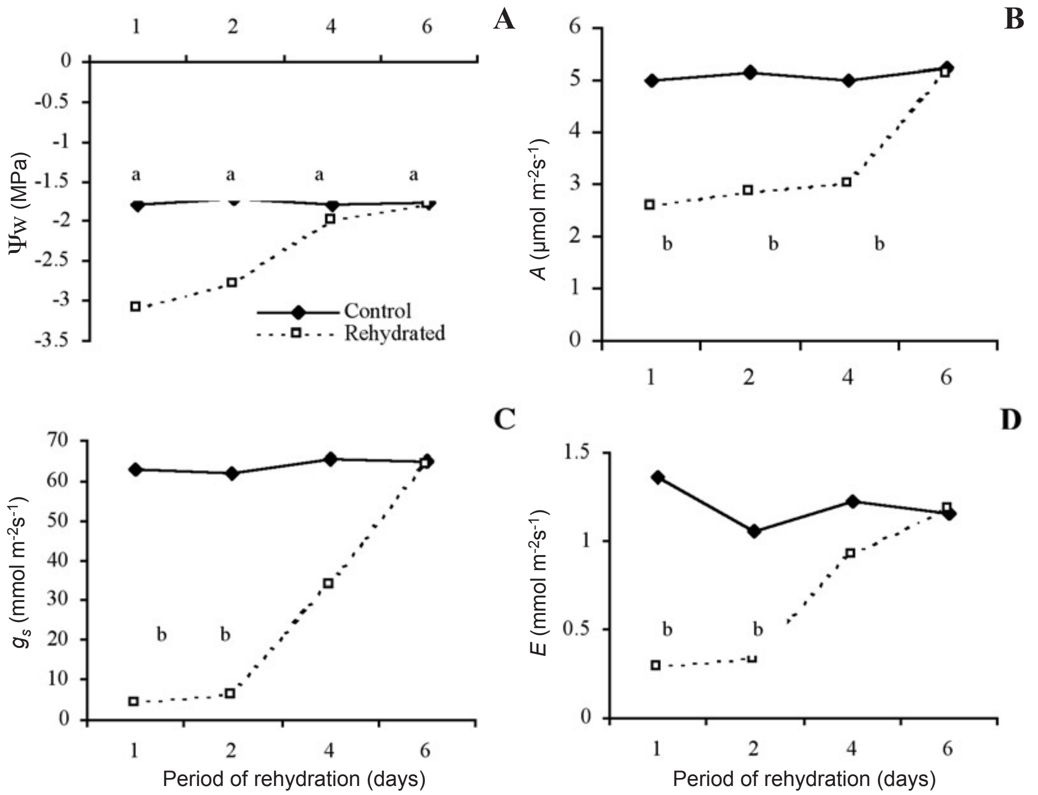

**Figure 5.** Effect of rehydration on leaf water potential - Ψw (**A**), net photosynthesis - *A* (**B**), stomatal conductance - $g_s$ (**C**) and transpiration - *E* (**D**) in *Minquartia guianensis* seedlings. Mean values followed by the same letters for treatments are not different at $P \leq 0.05$ using the Tukey test. n = 12.

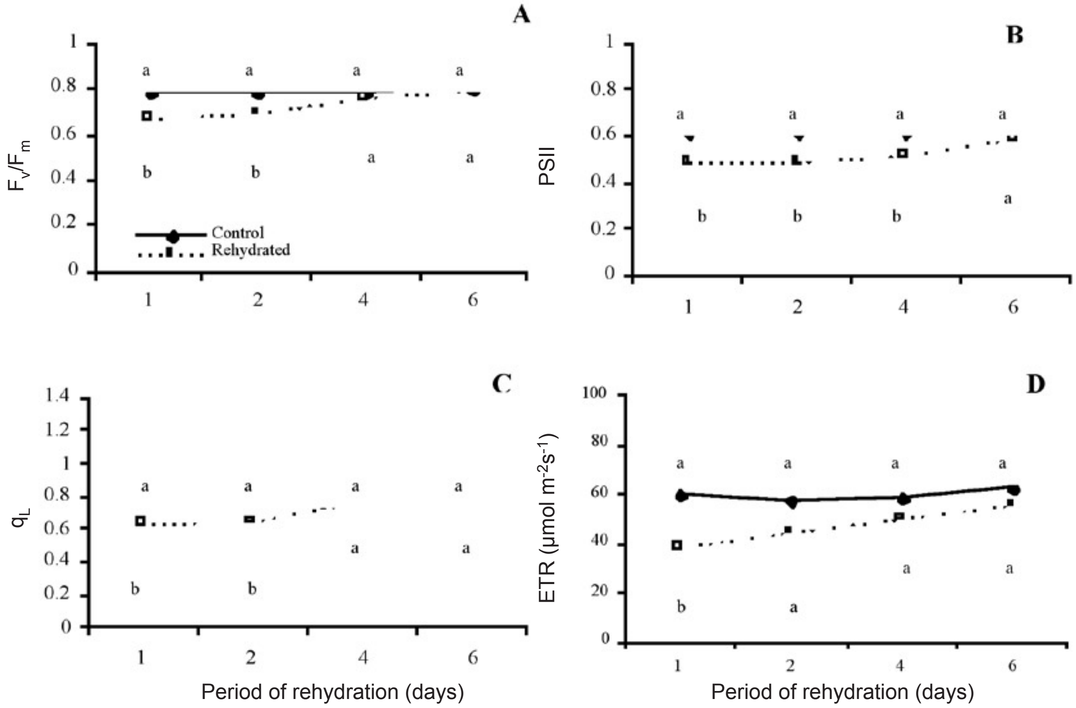

**Figure 6.** Effect of rehydration in maximum quantum efficiency of PSII primary photochemistry - $F_v/F_m$ (**A**), effective quantum yield of PSII - $\Phi_{PSII}$ (**B**), photochemical quenching of the excitation energy - $q_L$ (**C**) and apparent photochemical electron transport ratio - ETR (**D**) in *Minquartia guianensis* seedlings. Mean values followed by the same letters for treatments are not different at $P \leq 0.05$ using the Tukey test. n = 12.

## CONCLUSION

The suspension of irrigation for thirty-five days influenced the regulation of the hydric relationships of *M. guianensis* seedlings, reducing leaf water potential, stomatal conductance and transpiration and, increasing water use efficiency in order to guarantee the functioning of biochemical and metabolic processes, including $CO_2$ assimilation and production of photosynthates.

Seedlings of *M. guianensis* relied on the regulation of stomatal conductance as a strategy to tolerate periods of drought, as shown by their capacity for maintaining positive values of photosynthesis with reduced stomatal pore opening associated with leaf water potential values almost two times lower than under conditions of ample water supply. The decline in the quantum efficiency of PSII of *M. guianensis* seedlings during drought may be attributed to the activation of protective mechanisms, as rehydrated plants totally recovered their photosynthetic activity. Therefore, *M. guianensis* was tolerant to drought and capable of recovering physiological performance with respect to leaf water status, photosynthesis and photochemical efficiency of PSII under hydric stress, characterizing significant physiological plasticity, during the juvenile phase, for this tree species.

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