

Original Research Article
**GAS EXCHANGE OF OITICICA SEEDLINGS IN
RESPONSE TO POTASSIUM FERTILIZATION
AND WATER TURNING**

ABSTRACT

Aims: This objective of this work was to evaluate the effects of water deficiency on physiological aspects of oiticica plants, as well as the capacity of potassium fertilization to attenuate such effects.

Study design: The treatments were distributed in an entirely randomized design (*DIC*), consisting of a 4x4 factorial, with four levels of potassium (K) and four water turning, with five repetitions.

Place and Duration of Study: The experiment was conducted in a shaded environment, with 50% light interception, in the Forest Nursery of UAEP/UFCG, between January 2020 and July 2020.

Methodology: The relative water content (*RWC*), transpiration (*E*) and photosynthesis (*A*) rates, stomatal conductance (*gs*), and internal CO₂ concentration (*Ci*) were evaluated, and from the values of *A* and *E*, the intrinsic water use efficiency (*EUAi*) was calculated and, with the data of *A* and *Ci*, the carboxylation efficiency (*A/Ci*).

Results: There was significant interaction of treatments in the parameters *RWC*, *E*, *gs*, *A* and *EUAi* and isolated effect of water turning on *Ci* and *A/Ci*. Irrigation daily or every five days provided the maintenance of higher water status and better stomatal behavior, and the plants were sensitive to water stress provided by longer water turnings (every 10 and 15 days). The fertilization with 100 and 150 mg dm⁻³ of K kept the values of *E* and *A* high, even under low water availability.

Conclusion: Potassium fertilization proved to be effective in attenuating the negative effects caused by water deficiency on gas exchange and *WUEi* of the seedlings, with highlights for 100 and 150 mg dm⁻³ of K levels.

Keywords: Caatinga. Forest essence. Seedlings production. Water stress.

1. INTRODUCTION

In recent decades, there has been growing concern about the effects of human activities on the increase in average global temperatures, especially in more sensitive areas, such as regions with arid and semi-arid climates. Regarding climate change, projections regarding the Brazilian semiarid region are worrying because, in addition to the increase in temperature, there should be an increase in the frequency, as well as in the duration, of dry periods (LACERDA et al., 2016; MARENGO, TORRES, ALVES, 2017), placing the Caatinga as one of the most vulnerable ecological regions on the planet (CAVALCANTE; FERNANDES; SILVA, 2020).

In general, the species of the Caatinga present morphological modifications that guarantee their survival under the severe environmental conditions common to this biome, such as the presence of xylopodia in the roots, cut leaves, leathery leaves, etc. (LARCHER, 2000).

When subjected to water deficit conditions, plants promote stomatal closure, directly compromising processes such as stomatal conductance, transpiration and photosynthesis, affecting their growth (CHAVES, MAROCO, PEREIRA, 2003; CHAVES, OLIVEIRA, 2004; SOUZA et al., 2015). However, the control on stomatal opening can be intensified by the use of

(CaCl ₂ 0.01 M)	μg dm ⁻³	-----cmol _c dm ⁻³ -----					-----%-----	
5.00	4.50	5.10	1.90	0.17	0.57	3.10	10.84	71.40
Physical analysis								
Sand		Silt		Clay		Texture Classification		
-----g kg ⁻¹ -----		-----g kg ⁻¹ -----		-----g kg ⁻¹ -----		-		
780		100		120		Sand loam		

During the experimental period, the irrigation of the pots was done trying to keep the humidity close to 80% of the substrate retention capacity, obtained through weighing. To determine this retention capacity, five pots were submerged in a bucket with water until the substrate was completely soaked. Then, they were removed and, after complete leaching, weighed. This value corresponded to their weight with 100% of the vessel capacity (cv) and, based on it, the weight it should have when reaching 80% of the holding capacity was calculated.

The treatments were distributed in a completely randomized design (DIC), consisting of a 4 x 4 factorial, with four levels of potassium (K) (0, 50, 100 and 150 mg dm⁻³ K) and four water turning (ID - daily irrigation (control), and every 5 (5D), 10 (10D) and 15 days (15D)), with five replications and two plants per sampling unit, totaling 160 plants.

Water regimes were started at 25 days after seedlings were transferred to pots (plants at 30 days of age). On that day, the height of the plants (initial height) was measured. This measurement was also performed at the end of the experiment, which occurred 90 days after the start of water treatments [120 days after emergence (DAE)].

2.1 Evaluated parameters

a) Relative water content (RWC): at the end of the experiment, two leaves per plant were collected, taken to the Laboratory of Plant Physiology (CSTR), from which 5 disks of 1 cm² per leaf were removed and subjected to weighing, obtaining if the fresh mass (FM). Then, they were placed under two sheets of hydrated germination paper, in Petri dishes, and placed in a refrigerator (5 °C) until complete hydration. Upon reaching this point, they were removed, lightly dried and weighed to determine the turgid mass (TM). Subsequently, they were placed in an oven for drying (±65 oC), until reaching constant mass, to determine the dry mass (DM). The relative water content was calculated using the Weatherley (1950) formula:

$$RWC = \left(\frac{FM-DM}{TM-DM} \right) \times 100$$

(1)

b) Stomatal evaluations: at the end of the experiment, readings of transpiration (*E*) and photosynthesis (*A*), stomatal conductance (*gs*) and internal concentration of CO₂ (*C_i*) were performed with the aid of a portable LCpro-SD photosynthesis (ADC BioScientific Ltd.). These readings were taken on fully expanded leaves, two per plant, inserted at the third and fourth nodes from the apex of the plants, between 9 am and 10 am. From the values of *A* and *gs*, the intrinsic efficiency in water use (*EUA_i*) was calculated and, with the data of *A* and *C_i*, the carboxylation efficiency (*A/C_i*).

The data were submitted to analysis of variance by the F test, and the means were compared by the Tukey test, at 5% of significance, using the statistical program *Assiste*® (SILVA; AZEVEDO, 2002).

3. RESULTS AND DISCUSSION

There was a significant interaction of the treatments in the parameters *RWC*, *gs*, *E*, *A* and *EUA_i* and isolated effect in the water turning in *C_i* and *A/C_i*.

Comparing the K doses in each water turning treatment (Table 2), it was verified that there was no significant effect of potassium fertilization on the *RWC* when the plants received water daily (ID) and every 5 days (5D). However, despite the water turning increasing to 10 (10D) and 15

days (15D), the use of 100 and 150 mg dm⁻³ of K enabled higher *RWC*, compared to 0 and 50 mg dm⁻³ of K.

In the analysis of the *RWC* in the water regimes at each dose of K, there was statistical equality between treatments ID and 5D, which were superior to 10D and 15D, both at 0 and 50 mg dm⁻³ of K. 100 and 150 mg dm⁻³ of K provided statistical equality between water turning.

Table 2. Relative water content (*RWC*) (%) of *M. rigida* plants, as a function of potassium fertilization and water turning.

Water turning	K (mg dm ⁻³)			
	0	50	100	150
ID	77.1 aA	73.3 aA	74.6 aA	78.9 aA
5D	82.1 aA	74.2 aA	76.1 aA	75.5 aA
10D	54.8 bB	65.4 bB	79.6 aA	74.8 aA
15D	46.5 bC	54.8 bB	77.0 aA	77.1 aA

*Means followed by equal letters, uppercase in the lines and lowercase in the columns, do not differ statistically from each other ($P \leq 0.05$).

It can be seen from the data contained in Table 2 that, even under irrigation every five days, the oiticica plants were able to maintain a high *RWC*, regardless of potassium supply, evidencing the species' resistance to water deficit. However, the positive effect of provisioning with this nutrient, specifically 100 and 150 mg dm⁻³ of K, became evident when the plants were irrigated at longer intervals (10D and 15D), which allowed the maintenance of high *RWC*. According to Prado (2010), *RWC* values below 50% are considered critical and can lead to tissue death, with the exception of some xerophilous species, which can withstand this value without tissue loss.

Reduction in *RWC* due to water deficit has been reported in other studies (WANG, 2014; ATAÍDE et al., 2018; LEITE et al., 2018; ALMEIDA et al., 2020). However, in aroeira (*Myracrodruon urundeuva* Fr. Allem) and jucá (*Libidibia ferrea* (Mart. ex Tul) under moderate and severe water deficits, Almeida et al. (2020) found an increase in *RWC* when they supplied potassium to the plants. Presented by plants, when supplied with K, demonstrates its ability to provide drought tolerance, helping to carry out photosynthesis and transport carbohydrates from leaves to roots (MARTINEAU et al., 2017), and the osmotic effect exerted on plants. Roots, contributing to water absorption and maintenance of high *RWC* (PREMACHANDRA et al., 1992).

Low *RWC* causes numerous damages to various physiological processes, from the arrest of cell growth, the closing of stomata and the reduction in photosynthesis, in addition to impairing basic metabolic processes in plants, such as the production and degradation of proteins and carbohydrates and the accumulation of solutes, which may compromise plant growth (KUMAR; SING, 1998; FRANCO et al., 2005).

RWC value below the critical (46.5%) mentioned above was verified only in the plants of the 15D treatment, which did not receive the K supply, evidencing once again the role of this nutrient in the absorption and maintenance of tissue water in the species here studied. Potassium is the ion found in the highest concentration in the vacuole of cells, being closely related to osmotic balance, thus acting in the maintenance of cell turgidity (KERBAUY, 2013; TAIZ et al., 2017). The accumulation of osmotically active solutes in the cell is an important strategy developed by plants that tolerate drought, promoting a reduction in water potential (CHAVES FILHO; STACCIARINI-SERAPHIN, 2001).

As the dose of K supplied increased, there was a progressive decrease in stomatal conductance (*gs*) in all water turning evaluated (Table 3). Analyzing the water turning within the K doses provided, it was found that, in unfertilized plants (0 mg dm⁻³ of K), the highest *gs* values were recorded in plants under 5D and 10D. However, in plants fertilized with 50 mg dm⁻³ of K, those maintained in water turning 10D and 15D stood out, and at 100 mg dm⁻³ of K there was no significant difference between water turning. Providing 150 mg dm⁻³ of K, plants under daily irrigation have lower stomatal conductance, statistically different from other water turning.

Table 3. Stomatal conductance (g_s) ($\text{mmol H}_2\text{O dm}^{-2} \text{ s}^{-1}$) of *M. rigida* plants, as a function of potassium fertilization and water turning.

Water turning	K (mg dm^{-3})			
	0	50	100	150
ID	0.79 bA	0.37 bB	0.26 aB	0.12 bB
5D	1.08 aA	0.43 bB	0.18 aC	0.29 aC
10D	0.95 aA	0.57 aB	0.19 aC	0.24 aC
15D	0.67 bA	0.53 aA	0.21 aB	0.25 aB

*Means followed by equal letters, uppercase in the lines and lowercase in the columns, do not differ statistically from each other ($P \leq 0.05$).

Potassium fertilization did not positively influence g_s , regardless of the water turning, with an average reduction of 74% between the treatment without K and the one that received the highest dose (150 mg dm^{-3}). Similar results were obtained in *Mimosa tenuiflora*, when submitted to 100% and 25% of vessel capacity (cv), in which the g_s reduced with the increase of the amount of K (ALMEIDA et al., 2020). In contrast, Costa, Carvalho and Pinto (2019) reported that the highest dose of potassium contributed to greater stomatal conductance, adding that it provided a greater balance between the turgor of the guard cells and the control of the osmotic potential of the plant.

Reduction in stomatal conductance is probably associated with the adaptation mechanism of the plant when exposed to water deficit conditions, since, under these circumstances, plants tend to close their stomata, causing a decrease in leaf transpiration and, consequently, in water loss. (TAIZ et al., 2017). The reduction of g_s is a mechanism for evaluating the degree of water stress to which the seedling is exposed due to the sensitivity of the stomata to changes in water availability (EKSTEEN et al., 2013). According to Pita et al. (2005), this aspect can be used in genetic improvement, aiming at increasing productivity, even in drought conditions.

Regarding the transpiration rate (E) (Table 4), comparing the K treatments in each water turning, there was an increase in the values as the supplied dose increased, except in plants kept under daily irrigation (ID), which showed lower E when they received 150 mg dm^{-3} of K. Comparing the water turning, at each dose of K, the highest transpiration rate occurred in plants irrigated every five days (5D), when they received 0. 50 and 100 mg dm^{-3} of K, higher than water turning ID, 10D and 15D.

Table 4. Transpiration rate (E) ($\mu\text{mol H}_2\text{O dm}^{-2} \text{ s}^{-1}$) of *M. rigida* plants, as a function of potassium fertilization and water turning.

Water turning	K (mg dm^{-3})			
	0	50	100	150
ID	3.82 bA	3.92 bA	4.85 bA	3.27 bB
5D	4.53 aB	5.88 aA	6.36 aA	5.42 aA
10D	3.23 bB	3.11 bB	4.82 bA	5.00 aA
15D	3.08 bB	3.16 bB	4.77 bA	5.75 aA

*Means followed by equal letters, uppercase in the lines and lowercase in the columns, do not differ statistically from each other ($P \leq 0.05$).

In a parallel between treatments 5D and 10D, reductions in E of 29% (0 mg dm^{-3} of K), 47% (50 mg dm^{-3} of K) and 24% (100 mg dm^{-3} of K) were observed. While in the 15D treatment, the reductions were, respectively, 32%, 46% and 25%. In plants fertilized with 150 mg dm^{-3} of K, statistical equality was verified between the 5D, 10D and 15D water turning, which were statistically superior to the ID treatment. There is, therefore, a positive effect of potassium fertilization in the attenuation of water deficit on plant transpiration.

The reduction in water availability that occurred in plants irrigated at longer water turning (10D and 15D) had direct consequences on the RWC (Table 1) and on plant transpiration (Table 3). It can be seen that plants from treatments 10D and 15D, fertilized with K at doses of 0 and 50 mg dm^{-3} , showed lower values of RWC and, therefore, greater stomatal closure and lower E . According to Chaves, Flexas and Pinheiro (2009), this stomatal closure resulting from water deficit is a strategy to reduce water loss through transpiration. With this, the plant guarantees the maintenance of an adequate state of hydration and, consequently, of activities vital to its

growth. Stomatal closure due to water deficit was also reported by Albuquerque et al. (2013), França et al. (2017), Campelo et al. (2018) and Almeida et al. (2020), among others. The increase in water turning and consequent decrease in soil moisture content may have resulted in the production of abscisic acid (ABA) in the roots and its transport to the leaves, resulting in the closing of the stomata (INÁCIO et al., 2011; VALADARES, PAULA, PAULA, 2014). This, in turn, limits the loss of water by the plant, preventing tissue dehydration and consequent death of the plant (CHAVES et al., 2002; CHAVES et al., 2016).

The increase in plant transpiration with the increase in the dose of K supplied (100 and 150 mg dm⁻³) evidences the beneficial effect of potassium for plants, especially under water deficit conditions, through a possible cellular osmotic adjustment, ensuring greater water absorption and perspiration. Silva et al. (2013) reinforced the role of potassium as an osmotic agent, ensuring the maintenance of water absorption by plants. Subjecting acerola plants to saline stress, Dias et al. (2019) reported that low transpiration was a direct reflection of stomatal behavior and that the use of potassium in plants promoted osmotic adjustment, ensuring greater water uptake and increases in transpiration and CO₂ assimilation rate.

Regarding the photosynthesis rate (A) (Table 5), there was a gradual reduction as the water turning increased, regardless of the amount of K supplied. This effect was more severe in plants that did not receive potassium, with A values reducing from 31.26 μmol dm⁻² s⁻¹ (ID) to 5.08 μmol dm⁻² s⁻¹ (15D), equivalent to 84% decrease, while in the other K treatments, there was an average decrease of 60%.

Table 5. Photosynthesis (A) (μmol CO₂ dm⁻² s⁻¹) of *M. rigida* plants, as a function of potassium fertilization and water turning.

Water turning	K (mg dm ⁻³)			
	0	50	100	150
ID	31.26 aA	25.68 aA	35.92 aA	37.99 aA
5D	17.74 bB	17.82 bB	20.91 bB	26.82 bA
10D	12.12 bB	10.88 bB	13.50 bA	14.62 cA
15D	5.08 cC	10.80 bB	13.72 bA	14.75 cA

*Means followed by equal letters, uppercase in the lines and lowercase in the columns, do not differ statistically from each other (P ≤ 0.05).

Comparing K doses, in each water turning, in plants irrigated daily (ID), no significant difference was detected between treatments. However, in the 5D water turning, there was an elevation in A when they received 150 mg dm⁻³ of K and, in the 10D and 15D water turning, in which there was an elevation in A from 100 mg dm⁻³ of K, with the most pronounced effect in plants irrigated every 15 days (15D), with a 66% increase in this variable when comparing plants that did not receive K (0 mg dm⁻³) with those that received 150 mg dm⁻³ of K.

The increase in the water turning imposed a water deficit condition on the plants, causing the stomata to close, with consequent decreases in transpiration (Table 4) and photosynthesis (Table 5) rates. Such a response is a common fact to plants, and its intensity varies with the species and with the degree of water condition imposed.

For some authors, photosynthesis is directly impaired by the limitation of gas exchange that occurs in the stomata, since it reduces the availability of CO₂ to the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (FLEXAS et al., 2004; PITA et al., 2005; SIRCELJ et al., 2007; CHAVES, FLEXAS, PINHEIRO, 2009; PINHEIRO, CHAVES, 2011; JACINTO JÚNIOR et al., 2019), which consequently affects their activity (PARRY et al., 2002). However, this process may originate from other non-stomatal factors, such as the impairment of the photosynthetic system, through the disruption of thylakoid membranes (DIAS; BRÜGGERMANN, 2010), decrease in ATP synthesis, electron transport in photosystem II (PSII), the capacity and speed of regeneration of Rubisco (FLEXAS; MEDRANO, 2002; FLEXAS et al., 2004; CHAVES; FLEXAS; PINHEIRO, 2009) and the regeneration of RuBP (BOUSSADIA et al., 2008).

Silveira et al. (2021) point out that resistances related to water flow in the soil-plant-atmosphere system cause disharmony between water absorption and transpiration. These authors also

emphasize that the partial closure of the stomata is a maneuver to prevent excessive dehydration or a leaf water imbalance, which, consequently, would lead to a reduction in the photosynthetic rate. Several studies relate the decrease in stomatal conductance and in transpiration and photosynthesis rates with soil water deficit in arboreal species of the caatinga, such as aroeira (*Myracrodruon urundeuva* Allemão) (COSTA et al., 2015), ipê-roxo (*Handroanthus impetiginosus* (Mart. ex DC.) Mattos) (PESSOA; FREIRE; COSTA, 2017) and faveleira (*Cnidocolus quercifolius* Pohl.) (RAMOS; FREIRE, 2019).

Despite the reduction in the photosynthetic rate, due to the increase in the water turning, it can be seen that this effect is attenuated by the use of potassium, especially at doses of 100 and 150 mg dm⁻³ of K (Table 5). A positive effect of potassium in maintaining a high RWC and increasing stomatal conductance, transpiration and photosynthesis was also obtained by Almeida et al. (2020) in *Myracrodruon urundeuva*, *Libidibia ferrea* and *Mimosa tenuiflora* under conditions of low water availability. These authors attributed these results to the osmotic action of this nutrient, providing cellular osmoregulation and greater water absorption by plants, corroborating the statements by Mendes et al. (2013), Battie-Laclau et al. (2014), Zahoor et al. (2017) and Dias et al. (2019).

Due to the decrease in *g_s* (Table 3) and the increase in *A* (Table 5), the intrinsic water use efficiency (*EUA_i*) (Table 6) decreased as the interval between water turning, at all levels of K evaluated. Comparing the ID and 15D treatments, the decreases were 81%, 71%, 53% and 81%, respectively, at the levels of 0, 50, 100 and 150 mg dm⁻³ of K.

Table 6. Intrinsic efficiency in water use (*EUA_i*) of *M. rigida* plants, as a function of potassium fertilization and water turning.

Water turning	K (mg dm ⁻³)			
	0	50	100	150
ID	39.6 aD	69.7 aC	138.1 aB	316.6 aA
5D	16.4 bD	41.4 bC	116.2 bA	92.5 bB
10D	12.7 bC	19.1 cB	71.0 cA	60.9 cA
15D	7.58 cC	20.4 cB	65.3 dA	59.0 cA

*Means followed by equal letters, uppercase in the lines and lowercase in the columns, do not differ statistically from each other (*P* ≤ 0.05).

In each water turning, there was an increase in *EUA_i*, with the increase in the amount of K supplied to the plants (Table 5), and between treatments 0 and 150 mg dm⁻³ of K, the values obtained in this variable were about 8, 5.6, 4.8 and 7.8 times, respectively, in the ID, 5D, 10D and 15D water turning.

Therefore, *EUA_i* was strongly affected by water stress caused by water turning, regardless of potassium dose. Furthermore, it was found that the supply of K (100 and 150 mg dm⁻³) enabled the attenuation of the effects of eventual water deficit in the plants under the water turning evaluated. The values presented in Table 5 are mainly due to the positive effect exerted by K on photosynthesis *A* (Table 4) and negative effect on stomatal conductance (Table 2). This statement corroborates the studies by Tsonev et al. (2011), who reported that the reduction in *g_s* and not in *A* can explain the higher *EUA_i* values of plants when submitted to water deficit. This is because, when under water stress, a small reduction in *g_s* can have a protective effect against water stress, allowing plants to reduce water consumption and thus improve water use efficiency (CHAVES; FLEXAS; PINHEIRO, 2009). A negative effect of water deficit on water use efficiency and photosynthesis rate was also reported by Hommel et al. (2014), when evaluating the stomatal and mesophilic conductances of forest species under conditions of low water availability.

According to Dias et al. (2019), potassium is essential for enzyme activation, carbohydrate translocation and water regulation. Taiz et al. (2017) emphasize that, as a result of gas exchange, during the absorption of carbon dioxide from the external environment, the plant loses water to the atmosphere and, in order to reduce this loss, it reduces the entry of CO₂.

Figures 1 and 2 show the data for *C_i* and *A/C_i*, respectively.

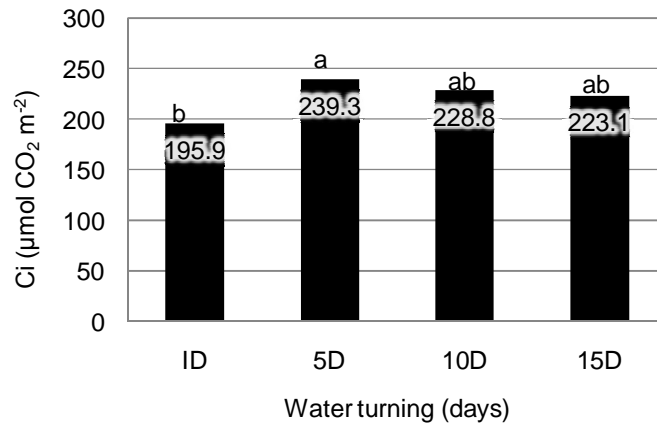


Figure 1. Internal CO_2 (C_i) concentration of *M. rigida* leaves at 120 DAE, as a function of water turning.

*Means followed by equal letters do not differ statistically from each other ($P \leq 0.05$).

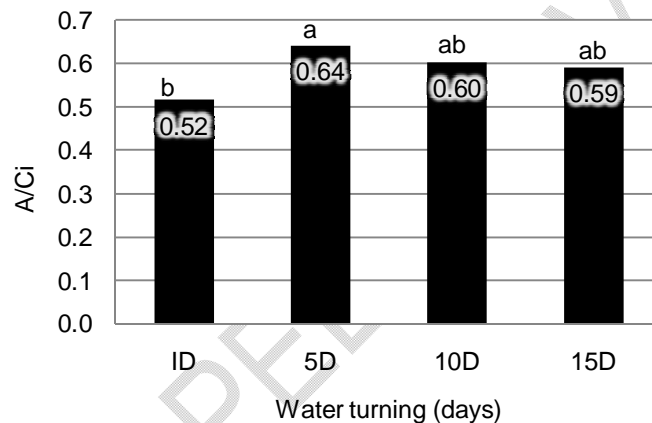


Figure 2. Carboxylation efficiency (A/C_i) of *M. rigida* leaves at 120 DAE, as a function of water turning.

*Means followed by equal letters do not differ statistically from each other ($P \leq 0.05$).

Regarding the internal concentration of CO_2 (C_i), the highest value was observed in plants irrigated every 5 days. However, there was statistical equality between this and treatments 10D and 15D (Figure 2). The same behavior was verified in the carboxylation efficiency (A/C_i). Fernandes et al. (2011) explain that, during gas exchange, as the stomata are responsible for regulating the substomatic concentration of CO_2 , the C_i remains slightly constant, a similar behavior observed in this research.

4. CONCLUSION

Water stress impaired gas exchange in *M. rigida* seedlings. Daily irrigation or every five days provided the maintenance of higher water status and better stomatal behavior, and they were sensitive to water stress caused by longer water turning (10D and 15D). Potassium fertilization proved to be effective in mitigating the negative effects caused by water deficiency on gas exchange and $EUAI$ of plants, especially at doses of 100 and 150 mg dm^{-3} of K.

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