CAPÍTULO 7

ECOPHYSIOLOGICAL CHARACTERIZATION OF SORGHUM GENOTYPES SUBMITTED TO WATER DEFICIT TOLERANCE

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ABSTRACT: Sorghum [*Sorghum bicolor* (L.)] is one of the most drought tolerant cereal and many studies have been done to understand the mechanisms involved in this process. In this work, we evaluated in the greenhouse the effects of different levels of water stress on the ecophysiological characteristics and accumulation of soluble sugars in two contrasting sorghum [*Sorghum bicolor* (L.) Moench] inbred lines for drought tolerance: 9910032 (tolerant) and 9618158 (sensitive). Water stress was imposed in both genotypes at pre-flowering growth stage for two different time exposure: mild (6 days of drought); severe (12 days). Recovery treatments for each drought treatment were also done at six days after the stress. Sensitive and tolerant genotypes showed lower stomatal conductance and leaf water potential for all types of stress when compared to irrigated treatments. An increase in total soluble sugar content was observed in leafs of the two sorghum genotypes however higher in the tolerant line. Overall, the genotype 9910032 presented higher photosynthetic rate and grain yield in relation to the sensitive genotype 9615818, in the same water condition. These results indicated that sugar content is modified under water deficit conditions indicating that if might be involved in plant protection.
KEYWORDS: Drought tolerance, evapotranspiration rate, photosynthetic rate, soluble sugars, grain yield.

RESUMO: O sorgo [Sorghum bicolor (L.)] é um dos cereais mais tolerantes à seca e muitos estudos têm sido realizados para entender os mecanismos envolvidos neste processo. Neste

trabalho, avaliamos em casa de vegetação os efeitos de diferentes níveis de estresse hídrico sobre as características ecofisiológicas e acúmulo de açúcares solúveis em duas linhagens contrastantes de sorgo [Sorghum bicolor (L.) Moench] para tolerância à seca: 9910032 (tolerante) e 9618158 (sensível). O estresse hídrico foi imposto em ambos os genótipos na fase de crescimento pré-floração para dois tempos de exposição diferentes: leve (6 dias de seca); grave (12 dias). Tratamentos de recuperação para cada fase também foram feitos seis dias após o estresse. Os genótipos sensível e tolerantes apresentaram menor condutância estomática e potencial hídrico foliar para todos os tipos de estresse quando comparados aos tratamentos irrigados. Um aumento no teor de açúcar solúvel total foi observado nas folhas dos dois genótipos de sorgo, porém maior na linha tolerante. De maneira geral, o genótipo 9910032 apresentou maior taxa fotossintética e rendimento de grãos em relação ao genótipo sensível 9615818, na mesma condição hídrica. Esses resultados indicaram que o teor de açúcar é modificado sob condições de déficit hídrico, indicando que ele pode estar envolvido na proteção da planta.

PALAVRAS - CHAVE: Tolerância a seca, taxa de evapotranspiração, taxa fotossintética, açúcares solúveis, rendimento de grãos.

INTRODUCTION

Global climate has been causing changes in the period and the distribution of the rainfall bringing deep consequences to the agriculture. Besides that, the competition and use of the water by other sources have restricted the water mainly in the irrigated areas (Osakabe et al. 2014). Due to complex traits, a lot of research has been done to understand plant responses to water deficit; however, the combined responses describing the effects of drought and re-watering are limited (Filippou et al. 2011, Devnarain et al. 2016). Some plant adaptation to abiotic stresses is associated with metabolic adjustments that lead to the accumulation of organic solutes including soluble carbohydrates (Rosa et al. 2009). Carbohydrates in different forms are known to serve in diverse functions. Soluble sugars do not only function as metabolic resources and structural constituents of cells but also act as signals regulating various processes associated with plant growth and development (Loreti et al. 2001 and Slewinski 2012). Responses of carbohydrate metabolism to drought stress vary with forms of carbohydrates, plant species, and stress duration or severity (Yang et al. 2013). The accumulation of SS has been considered one of the major traits for improving drought resistance in some plant species such as reported in durum wheat *Triticum durum* (AL Hakimi et al. 1995) and other studies (Yang et al. 2013, Boyles et al., 2019).

Sorghum bicolor (L.) Moench is the fifth most important grain crop of the world, with 67 million tons produced during 2014 (FAO 2015) and constitute the major source of proteins for millions of people from African and Asia (Dicko et al., 2006). In Brazil, the production is used mainly for animal feeding (McCuistion et al., 2019). The sorghum crop is one of the most water deficit tolerant among other cereals. It is a C4 plant of short day and high photosynthetic rates. Sorghum responds to drought stress through various biochemical

metabolic adjustments (Araya et al. 2018). Water deficit tolerance of sorghum has been attributed to morphological and physiological factors such as the dense roots system, the ability to maintain stomatal opening and photosynthesis at low water potentials. For this reason, the sorghum has been a good choice for grain and forage in situations where the water deficit offers more risks to other crops, such as maize. The objective of this study is to associate ecophysiological characteristics and soluble sugars of sorghum genotypes under water stress and re-watering and use it for identification of sorghum genotypes more tolerant to water deficit stress of a breeding program.

MATERIAL AND METHODS

The experiments were carried out in Sete Lagoas - MG (19º28 'S, 44º15'08' 'W, 732 m altitude). The plant material consisted of two contrasting sorghum genotypes for drought tolerance, genotype 9910032 tolerant and genotype 9618158 sensitive. These genotypes were previously tested and selected by the group of researchers from the Embrapa (SOUZA et al. 2013). The experimental design was completely randomized with four treatments (genotype 9910032 irrigated and under water deficit, genotype 9618158 irrigated and under water deficit).

The plants were cultivated in 20 L plastic pots containing Typical Dystrophic Red Latosol. The soil water content was monitored daily between 9 AM and 3 PM using a GB Reader N1535 moisture sensors (Measurement Engineering, Australia) installed in the center of each pot at the 20 cm depth. The irrigation water replecement was performed based on the readings with the sensor and the water returned to the field capacity during the period before the imposition of the treatments. The water replecement calculations were performed according to the water retention curve of the soil. In parallel, all the necessary cultural and phytosanitary treatments were carried out, according to the demand of the sorghum crop. The experimental unit was composed of the pot, containing two plants and four replicates per treatment.

Upon reaching pre-flowering growth stage, half of each initial treatment was submitted to water deficit (WD) and the other half continued to receive irrigation daily in order to maintain soil moisture near field capacity (FC), with soil water tension of -18 kPa. Exposure to WD was imposed by the daily supply of 50% of the total available water until the water tension in the soil reached a minimum of -138 kPa, which was maintained for a period of twelve days. During this period four evaluations were performed at 6 and 12 days of stress. After this period, the rehydration was accomplished up to field capacity, after 24h the last physiological evaluation was carried out. Irrigation was maintained until the end of the crop cycle to obtain growth and yield data.

Biophysical analyzes

The gas exchange and photosystem II efficiency evaluations occurred between

9h and 10h with an infrared gas analyzer (IRGA), model LI 6400 (LI-COR, Lincoln, NE, USA), equipped with with a fluorometer (LI-6400-40, LI-COR Inc.) on the second leaf below the flag leaf. The relative chlorophyll content and/or SPAD index was determined using the chlorophyllometer (MODEL SPAD 502, Minolta, Japan). Leaf water potential was also measured using a Scholander pressure pump at noon (Ψmd).

Carbohydrate Analysis

For the quantification of soluble sugars, 5 mm leaf discs from the third leaf of sorghum plants, for each stress period and controls, were ground in liquid nitrogen, and fifty mg of frozen tissue powder was extracted in 395 µL methanol. The extracts were incubated at 70 ºC for 15 min with continuous shaking at 4,000 rpm followed by the addition of 200 µl chloroform and, a new incubation at 37 ºC for 5 min in continuous shaking at 4,000 rpm. After the incubation, 1400 µL of ultrapure water were added to the extracts and the samples were then vortexed and centrifuged at 13,000 g for 5 min. The aqueous phase was filtered through PTFE membranes of 0.45 μm and transferred to vials with a capacity of 2 mL, which were analyzed by HPLC (Waters 2695 Alliance, Milford, MA, USA) using a Phenomenex column (RCM-Ca). The mobile phase used was ultrapure water flow of 0.6 mL min^{-1} and column temperature at 65ºC. The detector was the Refractive Index (Milford, MA, USA) working at 40 °C. Analytical curves were produced by using sucrose, glucose and fructose as standards (Sigma-Aldrich) with 99.5% purity, respectively. Sucrose, glucose and fructose in the samples were detected by comparison to standard retention time.

Agronomic parameters

At the end of the plant cycle (physiological maturity), the height of the plants, the length of the panicle and the diameter of the stem were measured. Later, the panicles were harvested and dried in a stove with air circulation, at 65ºC, for 72h. The dry grain biomass was obtained using 100 grains.

Statistical analysis

The data was analyzed by preliminary statistical tests applied to match or not the results to analysis of variance (ANOVA). The Scott-Knott test at 5% probability was used to test all contrast between treatments within each time of evaluation with Sisvar software (Ferreira, 2008).

RESULTS

Leaf water potential reduced with water deficit independent of genotype (Figure 1-A). The lowest values were verified at 12 days of stress. After the rehydration, there was a recovery of the leaf water potential of the plants that was under stress, but it was not enough to reach the values exhibited by the plants that were under field capacity. In all the analyzed periods no statistical differences between the genotypes in this water condition

were verified. At 12 days, the plants that were in field capacity presented a reduction in leaf water potential, but in the fourth evaluation, when the plants that were under water deficit were rehydrated, these values were already similar to those of the first evaluation. However, it is important to note that in this condition, plants of the tolerant genotype 9618158 exhibited higher values of this variable.

The foliar temperature (Figure 1-B) showed results inverted compared to that the water potential. There was an increase in leaf temperature at 12 days of treatment, being the highest values found in the genotypes that were under water deficit, which did not differ among them. On the other hand, in field capacity, the highest leaf temperature was verified in genotype 9910032. After rehydration, the genotypes that were under water deficit reduced the leaf temperature, so that the drought tolerant 9910032 matched its control under field capacity, and the drought-sensitive 9618158 showed the lowest temperature among all treatments.

The chlorophyll index (Figure 2-A) decreased in both genotypes under water deficit after twelve days of treatment, with the lowest values of these variables being verified in the drought-sensitive genotype 9618158. With rehydration, the chlorophyll index was similar between the plants which were under water deficit, but still remained below those of their controls, which remained throughout the experimental period under field capacity. The Fv'/Fm' ratio (Figure 2-B) with up to twelve days of treatment exhibited the same behavior as the chlorophyll index. However, with rehydration the genotypes that were under water deficit increased the values of the Fv'/Fm' ratio, but it was not sufficient to match the plants that remained the entire experimental period under field capacity. Among the genotypes that were under water deficit, the drought tolerant 9910032, exhibited higher Fv'/Fm' ratio when compared to the sensitive genotype 9618158.
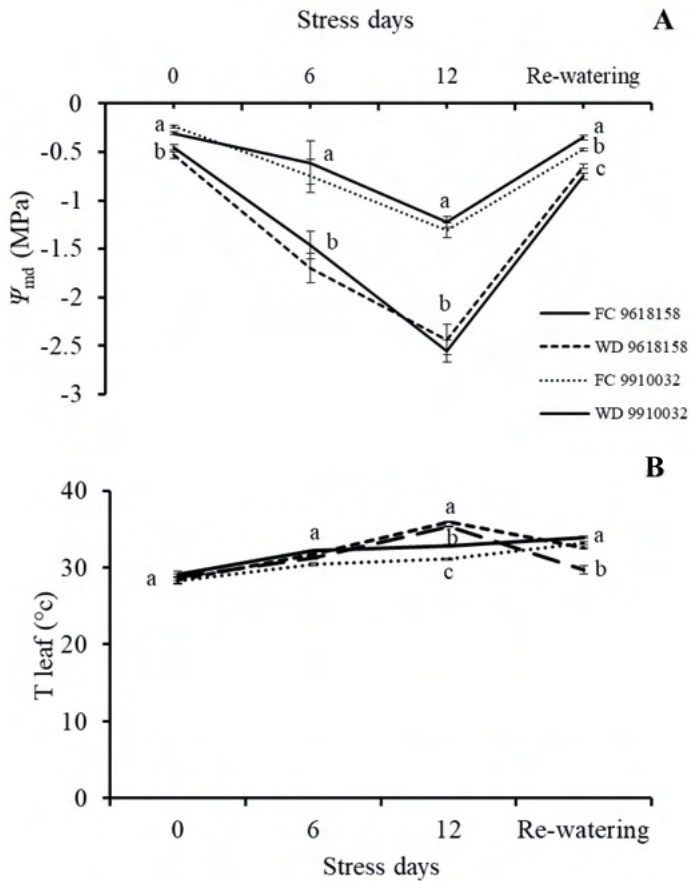
Figure 1- Temporal analysis of water potential at noon (Ψmd) (A) and foliar temperature in two sorghum genotypes (B), contrasting for drought tolerance, cultivated under different levels of water in the soil. FC = field capacity. WD = water deficit. Averages followed by the same letter at each evaluation time do not differ statistically from each other by the Scott-Knott test at 5% probability. The bars represent the standard error of the means of four replicates.

For the photosynthetic rate (Figure 3-A), it was verified that the begin of treatment, the genotype 9910032, under field capacity, exhibited the highest values among the other treatments, which did not differ among themselves. In the 6th day of treatment, the plants in field capacity showed values similar and superior to those that were under water deficit. In this last water condition, the plants of the drought tolerant genotype 9910035 exhibited a higher photosynthetic rate. With twelve days of treatment the genotypes that were under water deficit had the lowest photosynthetic rates observed during the whole experimental period.
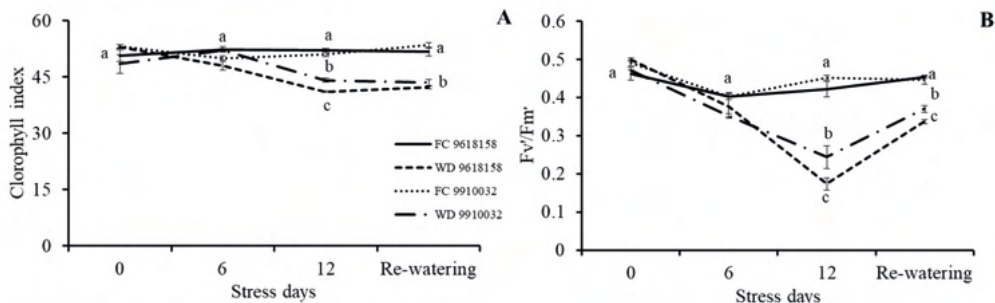
Figure 2 - Temporal analysis of the chlorophyll index (A) and the Fv '/Fm' (B) ratio in two sorghum genotypes contrasting for drought tolerance cultivated under different soil water levels. FC = field capacity. WD = water deficit. Means followed by the same letter at each sampling time do not differ statistically by the Scott-Knott test at 5% probability. The bars represent the standard error of the means of five replicates.

In this period, both in field capacity and in water deficit, the plants of the drought tolerant genotype 9910032 exhibited a higher photosynthetic rate. In the rehydration, the plants of the genotypes that were under water deficit increased the photosynthetic rate, but still presented lower values than the plants in field capacity. At this time of evaluation there was no differentiation between genotypes within the same water condition.

The stomatal conductance (Figure 3-B) at time zero did not vary significantly between treatments. On the other hand, transpiration (Figure 3-C) was higher in plants that were under field capacity compared to those under water deficit. Within the same soil water level, there were no differences for this variable among the genotypes. From the sixth day of treatment, the plants under water deficit maintained the stomatal conductance and the transpiratory rate lower than the plants under field capacity. On the sixth day specifically, the genotype plants in field capacity did not differ from each other. On the other hand, among the plants under water deficit, those of the drought tolerant genotype 9910032 exhibited greater stomatal conductance and transpiratory rate.
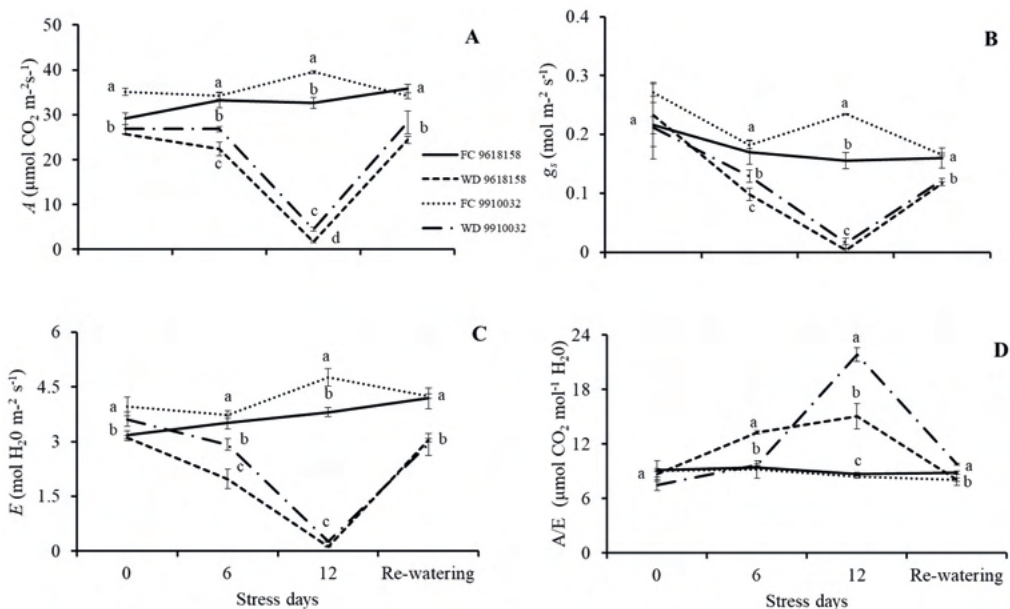
Figure 3 - Temporal analysis of photosynthetic rate (A), stomatal conductance = gs (B), transpiration rate = E and water use efficiency = A / E (D) in two sorghum genotypes contrasting for drought tolerance cultivated under different under different soil water levels . FC = Field capacity. WD = Water deficit. Means followed by the same letter at each evaluation time do not differ statistically from each other by the Scott-Knott test at 5% probability. The bars represent the standard error of the means of four replicates.

After twelve days of treatment, genotypes under water deficit reached the lowest stomatal conductance and transpiratory rate, but there were no differences among the genotypes for these variables. In contrast, among the plants in field capacity, those of the tolerant genotype 9910032 exhibited greater stomatal conductance and transpiration. After rehydration, plants that were under water deficit increased the values of these variables, but still maintained values lower than their controls in field capacity. At this time of analysis there were no differences between genotypes within the same soil water level for stomatal conductance and transpiration.

Water use efficiency (Figure 3-D) did not differ between genotypes at the time zero. With six days of treatment, the plants of the genotype susceptible to drought 9618158 that were under water deficit increased the efficiency in the use of water, while the other treatments remained constant. With twelve days of treatment the highest values of this variable were observed in plants of the genotype tolerant to drought 9910032 followed by those of genotype 9618158, both under water deficit. Among the genotypes that were in field capacity there were no differences. With rehydration, plants of genotype 9618158 that were under water deficit reduced water use efficiency to levels similar to those of the control. This reduction was also verified in genotype 9910032, however, they still had higher values

in relation to the other treatments.

The sucrose content (Figure 4-A) at time zero was higher in the genotype 9910032 plants in field capacity, followed by those of the genotype 9618158 under water deficit and did not differ in the other treatments. With six and twelve days of treatment, there was an expressive increase in the content of this disaccharide in the plants that were under water deficit in relation to those that remained in the field capacity. Regarding the plants that were under water deficit, those of the tolerant genotype 9910032 were those that presented the highest content of sucrose. In contrast, in the field capacity, the highest sugar content was verified in plants of the sensitive genotype 9618158.

The content of glucose (Figure 4-B), fructose (Figure 4-C) and total sugars (Figure 4-D) exhibited the same behavior for all genotypes throughout the experimental period. For this, it was verified that with zero and twelve days of water treatment, the highest contents of these carbohydrates were verified in the tolerant genotype 9910032 under field capacity, in relation to the other treatments, which did not differ among them. With six days of treatment and in rehydration the content of these sugars was higher in plants of the tolerant genotype 9910032 under water deficit, followed by their respective control in field capacity. At these evaluation times, the sensitive genotype 9618158 did not show differences between the water treatments.

Plant height and panicle length were not influenced by water deficit (Table 1). For this it was found that the plants of the tolerant genotype 9910032 exhibited higher plant height and panicle length relative to the plants of the sensitive genotype 9618158. In contrast, the stem diameter was higher in plants of the susceptible genotype 9618158 at field capacity, followed by plants of genotype 9618158 under water deficit and those genotype 9910032.
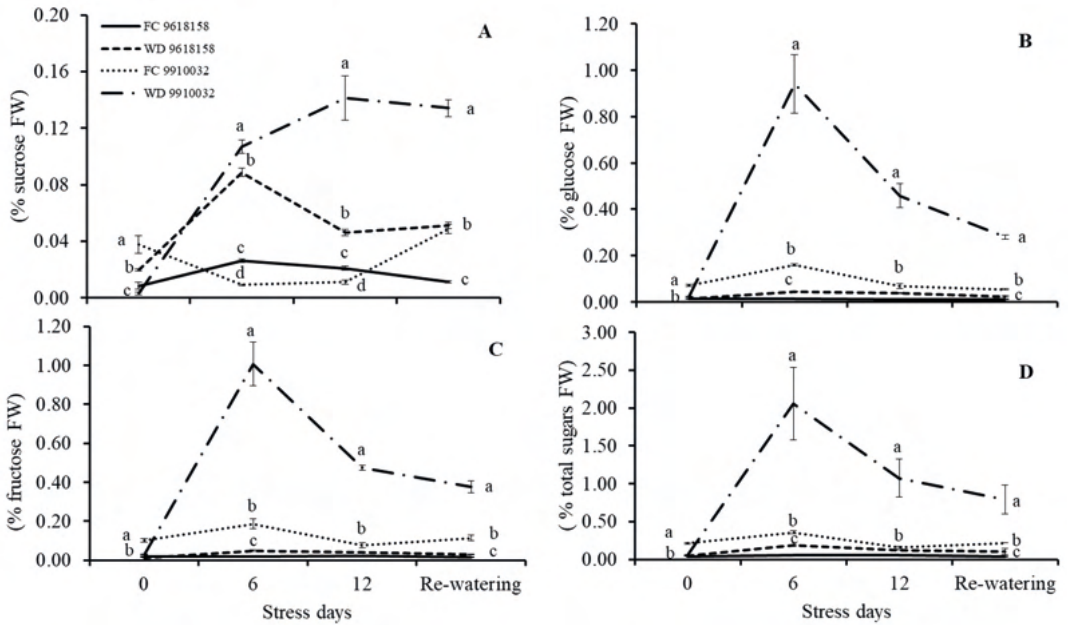
Figure 4 - Temporal analysis of the sucrose gradient (A), glucose (B), fructose (C) and total sugars (D) in two sorghum genotypes, contrasting for drought tolerance cultivated under different soil water levels. FC = Field capacity. WD = Water deficit. Means followed by the same letter at each evaluation time do not differ statistically from each other by the Scott-Knott test at 5% probability. The bars represent the standard error of the means of four replicates.

Panicle diameter was significantly influenced by drought. A reduction of 20.77% in panicle diameter in plants of genotype susceptible to drought 9618158 and only 7.71% in plants of the tolerant genotype 9910032 was observed. Among the treatments at field capacity there were no significant differences.

Panicle dry mass and grain dry mass were influenced by both genotype and drought. Thus, it was verified that the highest grain dry biomass and panicle were verified in the genotype plants in field capacity and that, in this water condition, the tolerant genotype 9910032 presented the highest values for this variable. Comparing the same genotype between the two water levels in the soil, there was a reduction of 38.45% in the panicle dry biomass and 41.02% in the grain dry biomass for the plants of the drought-sensitive genotype 9618158 and 24.94% and 24.81 %, respectively, in the plants of the drought-tolerant genotype 9910032.

	9618158		9910032	
	FC	**WD**	**FC**	**WD**
PH (cm)	65.94 b	66.56 b	70.46 a	70.62 a
SD (cm)	20.91 a	19.95 b	19.86 b	18.41 c
PL (cm)	18.84 b	18.81 b	24.40 a	25.40 a
PD (cm)	43.46 a	34.43 c	44.31 a	40.89 b
PDM (g)	52.34 b	32.20 c	70.00 a	52.54 b
GDM (g)	35.42 b	20.89 c	47.75 a	35.90 b
M100G (g)	2.15 a	1.64 b	1.95 a	1.56 b

FC: Field capacity. WD: water deficit.

The means followed by the same letter in the line do not differ statistically from one another by the Scott-Knott test at the 5% probability level.

Table 1 - Plant height (PH), stem diameter (SD), panicle length (PL), panicle diameter (PD), panicle dry mass (PDM), dry grain mass (GDM) and dry mass of 100 grains (M100G) from drought contrast sorghum plants submitted to water stress at pre-flowering.

In this way, it can be noticed that the greatest droughtinduced reductions on these variables occurred in the plants of the sensitive genotype 9618158. The dry matter of 100 grains was higher in the genotypes in field capacity in relation to those under water deficit.

DISCUSSION

The genotype 9910032 confirmed its drought tolerance behavior, exhibiting a reduction in grain yield of only 24.81%, a value significantly lower than the 41.02% observed in the susceptible genotype 9618158. It is worth mentioning that genotype 9910032 exhibited a higher yield also in the field capacity. Therefore, in order to verify which genotype maintained a more stable production after the period of water deficit in the pre-flowering, we worked with the percentage of reduction in grain production.

One of the main reasons of the reduction in grain production caused by drought is due to the entropy that this stressful environmental factor causes in the gas exchanges (Lavinsky et al. 2015). With the onset of stress, plants alter their metabolism making their water management more effective. For this, is observed, an increase in the biosynthesis of abscisic acid, a plant hormone highly responsive to drought, which regulates, among others, the stomatal closure (Sharp and Lenoble 2002).

The strategy of reducing stomatal opening and consequently stomatal conductance is highly feasible in a water deficit scenario, since it reduces leaf water loss by reducing the transpiration rate (Chaves et al. 2002). However, with stomatal closure, plants lose their efficiency in dissipating latent heat and reducing the absorption of carbon dioxide (CO_2) (Avila et al. 2017). Therefore, the internal concentration of CO_2 near the catalytic sites of ribulose-1,5-bisphosphate carboxylase / oxigenase (Rubisco) is reduced and the plant has

its photosynthesis affected, in a process known as stomatal limitation (Ghannoum, 2008). In this work, it was verified that as the days of stress increased, the genotypes that were under water deficit reduced their stomatal conductance, transpiratory rate and photosynthetic rate. In this sense, upon reaching 12 days of treatment, they exhibited the lowest values of these variables, but a higher leaf temperature.

It is important to emphasize that in this physiological state, the Calvin clic operates at a lower rate and therefore, consumes less NADPH reducing power, causing chloroplasts to become highly reduced and conducive to the formation of reactive oxygen species (ROS). The ROS at low concentrations are signaling molecules, however, at high concentrations they can promote the oxidation of chlorophyll, membrane and protein molecules, among them the D1 proteins of photosystem II (Edreva, 2005; Gill and Tuteja 2010). With the oxidation of the chlorophyll molecules and the D1 protein, the photochemical apparatus has its reduced efficiency which incisively compromises the transport of electrons. With lower electron transport rate, there is a lower production of the energy molecules, ATP and NADPH, which are essential for various processes in the plant, including CO_2 assimilation. In this state, photosynthesis is reduced by a process referred to biochemical limitation, which can be observed by the reduction in the photosynthetic rate and the Fv/Fm and/or Fv'/Fm' ratio.

In this work, it was verified that stress-treated plants, regardless of genotype, showed a marked reduction in chlorophyll content and in the Fv'/Fm' ratio, as there was an increase in days of stress and reduction in potential leaf water. However, the plants of the tolerant genotype 9910032 with twelve days of stress had a higher Fv'/Fm' ratio and higher photosynthetic rate, indicating a lower biochemical damage (Grassi and Magnani, 2005).

Therefore, it is suggested that during stress, the plants of the drought-tolerant genotype 9910032 maintained a greater production of photoassimilates, which are important, among others, for the maintenance of the development of the reproductive organs. Thus, it may be related to the larger panicle diameter and grain yield observed in the plants of this genotype. In fact, the ability to maintain high photosynthesis values is a striking feature of drought tolerant genotypes (Cattivelli et al. 2008). This hypothesis can be sustained by verifying that the in general genotype 9910032 irrigated, also presented higher photosynthetic rate and grain yield in relation to the sensitive genotype 9615818, in the same water condition.

In addition to their contribution to grain filling, sugars produced during drought can contribute to drought tolerance, acting as compatible osmoregulatory agents (Mohammadkhani and Heidari, 2008). In fact, during water stress a drastic reduction in the cellular water potential occurs. In response, the cell changes the levels of ionic solutes in the vacuole, such as potassium, chlorine and calcium, as a strategy to maintain the rate of water absorption. However, for a water balance to occur between vacuoles and cytosols, there is a need to produce and accumulate compatible organic compounds, such as proline and soluble sugars in cytosol. The accumulation of sugars in the leaves may also

have a protective effect against ROS, especially $^1O_2$ and OH- formed during processes with electron transfer in leaf and root tissues, since these ROS are not eliminated enzymatically (Sami et al. 2016) .

In view of the significant increase in sugar content in leaves of the tolerant genotype 9910032 during drought, it is suggested that this is a physiological mechanism used by this genotype to protect the photosynthetic apparatus from the deleterious effects of drought and thus tolerate it. In this context, they deserve more studies, since in the future it can be inserted in breeding programs in order to develop sorghum plants with a higher degree of tolerance to drought.

CONCLUSIONS

The drought-tolerant genotype 9910032 showed a higher sugar biosynthesis suggesting that this may be one of the mechanisms of protection of the photosynthetic apparatus during the water deficit. This mechanism gives it a higher photosynthetic rate and grain yield during drought when compared to the drought-sensitive genotype 9618158, which does not have this mechanism.

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