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Gas exchanges and water use efficiency in the selection of tomato genotypes tolerant to water stress

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ABSTRACT. Water stress can affect the yield in tomato crops and, despite this, there are few types of research aiming to select tomato genotypes resistant to the water stress using physiological parameters. This experiment aimed to study the variables that are related to the gas exchanges and the efficiency in water use, in the selection of tomato genotypes tolerant to water stress. It was done in a greenhouse, measuring 7 x 21 m, in a randomized complete block design, with four replications (blocks), being five genotypes in the F_2BC_1 generation, which were previously obtained from an interspecific cross between *Solanum pennellii* versus *S. lycopersicum* and three check treatments, two susceptible [UFU-22 (pre-commercial line) and cultivar Santa Clara] and one resistant (*S. pennellii*). At the beginning of flowering, the plants were submitted to a water stress condition, through irrigation suspension. After that CO_2 assimilation, internal CO_2, stomatal conductance, transpiration, leaf temperature, instantaneous water use efficiency, intrinsic efficiency of water use, instantaneous carboxylation

efficiency, chlorophyll a and b, and the potential leaf water (Ψf) were observed. Almost all variables that were analyzed, except CO_2 assimilation and instantaneous carboxylation efficiency, demonstrated the superiority of the wild accession, *S. pennellii*, concerning the susceptible check treatments. The high photosynthetic rate and the low stomatal conductance and transpiration, presented by the UFU22/F_2BC_1#2 population, allowed a better water use efficiency. Because of that, these physiological characteristics are promising in the selection of tomato genotypes tolerant to water stress.

Key words: Abiotic stress; Drought tolerance; Tomato; Wild accession

INTRODUCTION

The tomato cropping has an economical and social relevance in Brazil and all over the world. The South American country is among the top 10 tomato producers (AGRIANUAL, 2016), evidencing the relevance of the crop. The tomato [*Solanum lycopersicum* (L.)] adapts to different climatic conditions (Neves et al., 2013), and despite this, the abiotic stress occurrence, like water stress, is one of the biggest problems that the crop presents (Morales et al., 2015b).

Predominantly, in the arid and semi-arid regions, the conflicts for the water use are a limiting factor. However, it is also observed in regions that have abundant water resources but are incapable to supply the high demand (Telles and Costa, 2010). Beyond that, crops that require a large irrigation system present elevated energy costs. In this sense, developing genotypes that are tolerant to water stress has become a low-cost and more efficient strategy in regions with water deficit (Girotto et al., 2012).

The process of tomato domestication caused a shortage of genotypes that are tolerant to water stress (Alvarenga, 2013). However, there are wild species that have a better water use efficiency than the commercial cultivars. The wild accession LA-716 (*S. pennellii*) is one of them and, although it does not present good agronomic characteristics, the wild species uses water more efficiently than the cultivated plants (Rocha et al., 2016). With the plant breeding, it is possible the rescue of important agronomic characteristics, through an interspecific cross followed by backcrossings with a background of interest (Maciel et al., 2011).

Direct methods, used for selection genotypes tolerant to water stress, are expensive and demand more time, which makes the indirect methods more viable. Many types of research have proven the efficiency of genotype selection from different techniques, like visual symptoms, soil water balance, the flow of sap, and gas exchange analyses (Aksic et al., 2011; Celebi, 2014; Begun et al., 2012; Rocha et al., 2016). However, the use of these techniques is scarce.

Because of that, this experiment aimed to study the variables related to gas exchange and the water use efficiency in the selection of tomato genotypes tolerant to water stress.

MATERIAL AND METHODS

The experiment was conducted at the Experimental Horticulture Station (18°42.0'43.19"S and 47°29.0'55.8"W, 873 m above sea level) and at the Genetic Resources Laboratory of the Federal University of Uberlândia - UFU, Monte Carmelo Campus, in the period of May 2013 to August 2016.

The genetic material utilized was originally from the germplasm bank of UFU. The segregating populations evaluated were, previously, obtained from an interspecific cross between UFU-222 (*S. lycopersicum*) versus wild accession LA-716 (*S. pennellii*). UFU-222 is a pre-commercial line that has small fruits (>18 g), 9° Brix and is susceptible to water stress. The wild genotype also presents small fruits (15 g) but is tolerant to water deficit (Morales et al., 2015b; Rocha et al., 2016).

To select genotypes tolerant to water stress, five F_2BC_1 populations, originated from self-fertilization of the first backcrossing, were utilized: UFU22/F_2BC_1#8, UFU22/F_2BC_1#9, UFU47/F_2BC_1#11, UFU22/F_2BC_1#2, UFU22/F_2BC_1# and three check treatments, being two susceptible (*cv*. Santa Clara and UFU-222) and one resistant (*S. pennellii*).

The genotypes were sown on May 5, 2016, in polystyrene trays of 200 cells, filled with commercial coconut fiber substrate. Thirty-five days after sowing, the plants were transplanted into pots (5-L volume), containing the same substrate that was used for seedling's production. The tomato plants were cultivated in a bow-type greenhouse, measuring 7 x 21 m and ceiling 4 m, covered with transparent polyethylene film of 150 microns, protected against ultraviolet rays, and curtain side of white and anti-aphid scream. The cultural dealings were made according to the tomato crop recommendations (Alvarenga, 2013). The experiment was set up in a randomized complete block design, with three replications (blocks), totalizing 24 plots (8 genotypes x 3 blocks). Each plot consisted of one plant.

The climatic conditions, in the greenhouse, were monitored with the aid of an automatic weather station. The flux density (W/m^{-2}) of the global solar radiation was estimated through the equipment Silicon Photodiode Pyranometer (NRLITE - Campbell Sci.), and the temperature (°C) and relative humidity (%) were estimated using the Vaisala Sensor (HMP45C - Campbell Sci.). The equipment was installed in the center of the greenhouse and above the plants, and it was connected to a data acquisition system (Datalogger CR1000 - Campbell Sci.). The data were stored every 15 min.

Tensiometers were installed in each plot, 20 days before the evaluation (98 days after sowing, DAS), to evaluate the water tension on the substrate. The irrigation was done in a controlled manner, keeping the substrate humidity in great conditions (-10 kPa). On the beginning of the flowering (116 DAS), the tomato plants were submitted to a water stress condition, where the water potential was putten closed to -30 kPa through irrigation suspension. The evaluations of the gas exchange, chlorophyll index, and leaf water potential were made on August 31 (118 DAS).

The parameters of the gas exchange were checked using three leaflets of the middle third of each plant, during the morning (approaching 8 h), using the equipment InfraRed Gas Analyzer (IRGA, model LCA-4, analytical development Co., Hoddesdon, England). The parameters obtained were: CO_2 assimilation (A), internal CO_2 (Ci), stomatal conductance (Gs), transpiration (E), and leaf temperature (T). The instantaneous water use efficiency was calculated from the ratio between CO_2 assimilation and leaf transpiration (A/E), the intrinsic efficiency of water use was calculated from the ratio between CO_2 assimilation and the stomatal conductance (A/Gs), and the instantaneous carboxylation efficiency was estimated from the ratio between the CO_2 assimilation and internal CO_2 (A/Ci).

The chlorophyll (a and b) levels were estimated through two leaflets of each plant of the middle third, using a chlorophyll meter (CFL-1030, Falker). The equipment estimates the concentration of photosynthetic pigments with high precision, without needing chemical reagents that are commonly used for this and saving time (Rigon et al., 2012). The values were summed, and the mean of each plot was obtained.

The potential leaf water (Ψf) was measured before sunrise (±5:00 am), with the aid of a pressure chamber, type Scholander (Soil Moisture Model 3000), and five leaflets of the middle third of each plant were used for it. The values were also summed and the mean of each plot obtained. The statistical analyses were done with the aid of the GENES computational program (Cruz, 2013).

RESULTS AND DISCUSSION

The water availability of the substrate was not restrictive for the water demand of the plants (-10 kPa), until the deficit beginning. After 2 days of the water deficit imposition, during the physiologic evaluations, the substrate was submitted to a moderate matricidal potential (below -25 kPa) (Figure 1). Guida et al. (2017), when submitting tomato plants to a water stress, observed that the soil matricidal potential below -28 kPa promotes a reduction in the stomatal conductance, affecting the crop yield.
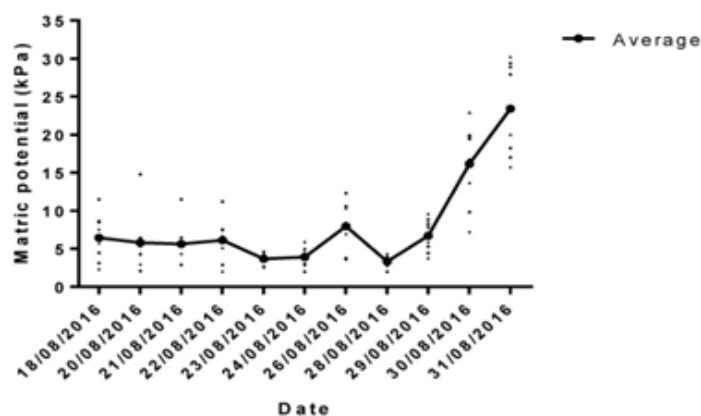
Figure 1. Water matricidal potential (kPa) of the substrate from August 18, 2016 to August 31, 2016.

Analyzing the climatic conditions in the greenhouse, it was found that the average temperature was 23.4°C, which is close to the ideal temperature (18°-24°C), for the tomato crop, according to Duarte et al. (2011). The mean relative humidity of the period was 60.3%, presenting a variation of 33.5-86.4%. The average of the global solar radiation and vapor pressure deficit were, respectively, 167 W/m² and 1.38 kPa (Figure 2).
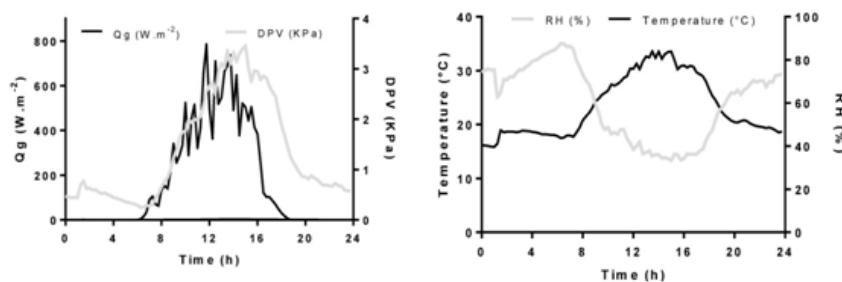
Figure 2. Temperature (°C), relative humidity (RH, %), global solar radiation (Qg, W/m²), and vapor pressure deficit (kPa), monitored on August 31, 2016.

Analyzing the leaf temperature, it was found that the *cv*. Santa Clara showed a temperature 20% higher than the wild accession (*S. pennellii*). The genotypes of the UFU22/F_2BC_1#9 and UFU47/F_2BC_1#11 populations and the pre-commercial line UFU-222 showed a similar behavior to the *cv*. Santa Clara, while the genotypes of the UFU22/F_2BC_1#8 population were similar to the wild accession (Table 1).

Table 1. Averages of leaf temperature (T leaf) (°C), stomatal conductance (Gs) (mol·m^{-2}·s^{-1}), transpiration (E) (mmol·m^{-2}·s^{-1}), internal CO_2 (Ci) (mmol·m^{-2}·s^{-1}), CO_2 assimilation (A) (µmol·m^{-2}·s^{-1}), instantaneous water use efficiency (A/E) (mmol CO_2/mol H_2O), intrinsic efficiency of water use (A/Gs) (mmol·m^{-2}·s^{-1} H_2O), and instantaneous carboxylation efficiency (A/Ci), in tomato genotypes, F_2BC_1, submitted to a water stress.

	Genotype	T leaf		Gs		E		Ci		A		A/E		A/Gs		A/Ci	
T1	UFU22/F_2BC_1#8	25.60	a	0.05	b	2.18	d	370.44	a	1.57	e	0.72	e	40.90	cd	0.001	E
T2	UFU22/F_2BC_1#9	30.37	d	0.09	c	1.25	c	354.22	a	4.84	c	3.84	c	49.00	c	0.013	Bc
T3	UFU47/F_2BC_1#11	30.03	cd	0.09	c	0.76	ab	299.11	bc	1.72	e	2.31	d	20.15	d	0.007	De
T4	UFU22/F_2BC_1#2	28.82	c	0.03	a	0.60	a	251.88	d	3.08	d	5.30	b	119.55	a	0.010	Cd
T5	UFU22/F_2BC_1#3	27.25	b	0.05	b	0.80	b	351.00	a	2.56	de	3.22	cd	58.12	c	0.010	Cd
T6	UFU-222	29.68	cd	0.14	d	2.26	d	258.88	cd	6.51	ab	2.89	cd	45.50	c	0.027	A
T7	*cv*. Santa Clara	30.75	d	0.13	d	2.22	d	234.11	d	6.95	a	3.13	c	55.01	c	0.031	A
T8	*Solanum pennellii*	25.66	a	0.06	b	0.82	b	338.00	ab	5.62	bc	6.76	a	90.36	b	0.018	B
	CV	2.87		15.57		7.70		9.42		19.27		22.88		27.48		28.260	
	Overall average	28.52		0.08		1.36		307.20		4.11		3.52		59.82		0.014	

*Means followed by the same letter in the column do not differ, significantly, from each other by the Tukey test (P < 0.05).

Morales et al. (2015a) affirmed that the variations in the leaf temperature could be used to estimate the water stress of plants. The reduction of water soil availability causes an increase in the leaf temperature, due to a reduction in the transpiration that is the main mechanism responsible for the plant cooling (Morales et al., 2015a), even though this relation was not observed in the present experiment probably due to a disturbance in the plant physiology.

One of the first reactions that plants show in response to water stress is the stomatal closure (Wang et al., 2012). The pre-commercial line UFU-222 presented the higher stomatal conductance (Gs) and did not differ, significantly, from the *cv*. Santa Clara. On the other hand, the wild accession, *S. pennellii*, showed Gs lower (54%) than the *cv*. Santa Clara. The genotypes of the UFU22/F_2BC_1#8, UFU22/F_2BC_1#2, and UFU22/F_2BC_1#3 populations presented Gs similar or higher than the wild species.

The reduction in the stomatal conductance, due to a stomatal closure, reduces the waste of water by transpiration. Even though this strategy affects the photosynthetic rate because it complicates the CO_2 diffusion, which is extremely vital for the process of photosynthesis. Therefore, an effective regulation of the stomatal opening is primordial for the plant's development under water stress conditions (Santos et al., 2013).

The mean transpiration (E) observed was 1.36 mmol·m^{-2}·s^{-1}, and the highest were observed in the genotypes Santa Clara, UFU22/F_2BC_1#8, and UFU-222. The genotypes of the UFU22/F_2BC_1#2 and UFU47/F_2BC_1#11 populations presented the lowest transpiration rate, and the last one did not differ, significantly, from the genotypes of the UFU22/F_2BC_1#3 population and the wild accession *S. pennellii*.

The lowest transpiration rate of the wild accession, *S. pennellii*, makes it capable of tolerating the water stress. Because of this, the wild genotype can develop in arid regions (Easlon and Richards, 2009), being, therefore, a promising material for the tomato breeding that aims to find genotypes tolerant to water stress. Low transpiration (E) might be associated with nonstomatal factors, as variations on the leaf cuticle allow the water loss by transpiration.

The increase in thickness and mesophyll's density are described as adaptive responses to water stress (Poorter et al., 2009).

Evaluating the internal CO_2, it was found that the genotypes of UFU22/F_2BC_1#8, UFU22/F_2BC_1#9, and UFU22/F_2BC_1#3 populations did not differ from each other and had similar behavior to the wild accession *S. pennellii*, presenting an average higher than the overall of the experiment. A significant difference was found between the wild genotype and *cv*. Santa Clara, even though the genotypes UFU22/F_2BC_1#2 and UFU-222 did not differ from *cv*. Santa Clara being all in the worst group.

High values of internal CO_2 indicate that the genotype can provide more CO_2 for the ribulose-1,5-bisphosphate carboxylase-oxygenase (rubisco). However, this did not happen in the present study, probably due to a decrease in the activity of enzymes involved in the CO_2 fixation process (Table 1).

Analyzing the CO_2 assimilation (A) of the genotypes, it was found that the *cv*. Santa Clara was 24% higher than the wild accession *S. pennellii*. However, both check treatments were better than the rest of the genotypes. Furthermore, the other check treatment UFU-222 was also better than the rest of the genotypes and showed a similar behavior to both susceptible and resistant checks. Besides this, the genotype UFU22/F_2BC_1#9 highlighted showing a similar behavior to the wild accession (Table 1).

The mean value of CO_2 assimilation that was observed in the present experiment is lower (4.11 µmol·m^{-2}·s^{-1}) than the results in other experiments under excellent water conditions (15.6 µmol·m^{-2}·s^{-1}) (Galmés et al., 2012). However, it is similar to results found by Morales et al. (2015b), when the photosynthesis decreased from 8.61 to 4.18 µmol·m^{-2}·s^{-1}, when the water stress was submitted. A low CO_2 assimilation proves that the water stress might affect physiological and biochemical processes of the vegetables, such photosynthesis (Farooq et al., 2009; Jaleel et al., 2009).

A higher instantaneous water use efficiency, observed in the wild genotype (*S. pennellii*), about the other treatments, is related to its low transpiration (E). Among the evaluated genotypes, UFU22/F_2BC_1#2 highlighted, being the one that most resembled the wild accession. On the other hand, *S. pennellii* was 2.2 more efficient in water use than the *cv*. Santa Clara, which is possible the main result, proving its resistance to water stress. Similar results were found by Machado et al. (2010), correlating the amount of transpiration water with the dry matter production.

Analyzing the intrinsic efficiency of water use, it was found that the overall average was 59.82 mmol·m^{-2}·s^{-1} and this high value was found in the UFU22/F_2BC_1#2 genotype followed by the wild accession *S. pennellii*. On the other hand, the lowest intrinsic efficiency of water use was found in the UFU22/F_2BC_1#8 and UFU47/F_2BC_1#11genotypes. It was also found that the wild accession was 64% more efficient than the *cv*. Santa Clara. High photosynthetic rate associated with low stomatal conductance (Gs) are characteristics find in plants with tolerance to water stress, which also has a higher intrinsic efficiency of water use (Pazzagli et al., 2016). In environments with limited water resources, the positive magnitude of these parameters becomes essential for the adequate functioning of plants and also for demonstrating the physiological plasticity of the species to abiotic factors (Funk and Vitousek, 2007; Li et al., 2008; Silva et al., 2008).

Evaluating the instantaneous carboxylation efficiency, the check treatment *cv*. Santa Clara highlighted presenting the high value, i.e., 72% higher than the wild accession *S. pennellii*. On the other hand, the lowest instantaneous carboxylation efficiency was observed for the

UFU22/F_2BC_1#8 and UFU47/F_2BC_1#11 genotypes. According Silva et al. (2015), the relation between internal CO_2 (Ci) and CO_2 assimilation (A), which is the instantaneous carboxylation efficiency, is a characteristic that makes possible to estimate non-stomatal factors that could be affecting the photosynthetic process and, consequently, the biological yield.

The potential leaf water (Ψf) indicates the energy status of plants, where values closely to zero indicate that the plant is not under water stress. However, high negative values indicate an intense water stress (Morando et al., 2014). The mean value of leaf water potential, observed in the experiment, was -0.635 mPa (Table 2). The lowest value was found in the *cv*. Santa Clara, being 7.7 times smaller than the wild accession *S. pennellii*, which makes the commercial genotype to be considered susceptible to water stress. The genotypes UFU22/F_2BC_1#8, UFU22/F_2BC_1#9, UFU47/F_2BC_1#11, UFU22/F_2BC_1#2, and UFU-222 were the ones that most approached to the *S. pennellii*, for the potential leaf water, even though they were four times inferior compared to the wild genotype.

Table 2. Potential leaf water (Ψf, mPa), chlorophyll *a,* chlorophyll *b*, and total chlorophyll in tomato genotypes F_2BC_1 submitted to water stress.

	Genotype	Ψf (mPa)		Chlorophyll *a*		Chlorophyll *b*		Total chlorophyll	
T1	UFU22/F_2BC_1#8	-0.536	b	37.68	abc	15.23	ab	52.91	ab
T2	UFU22/F_2BC_1#9	-0.463	b	41.41	a	15.10	ab	56.43	a
T3	UFU47/F_2BC_1#11	-0.560	b	40.70	ab	14.31	ab	55.01	a
T4	UFU22/F_2BC_1#2	-0.626	b	38.43	abc	14.76	ab	53.20	ab
T5	UFU22/F_2BC_1#3	-0.900	c	36.38	bc	13.15	ab	49.53	ab
T6	UFU-222	-0.576	b	30.50	d	8.35	c	38.85	c
T7	*cv*. Santa Clara	-1.253	d	35.48	c	11.50	bc	46.98	b
T8	*Solanum pennellii*	-0.163	a	39.66	abc	17.38	a	57.04	a
	CV	10.11		4.29		10.88		5.36	
Overall	average	-0.635		37.53		13.71		51.24	

*Means followed by the same letter in the column do not differ, significantly, from each other by the Tukey test ($P < 0.05$).

A relation between transpiration and the stomatal opening is related by Firmano et al. (2009), where the higher is the stomatal conductance, stronger is the transpiration. Under moderate stress conditions, plants remain with the stomata closed, to maintain greater water potential and ideal turgor pressure, which is an important indication of tolerance to water stress (Lawlor and Tezara, 2009).

During the experiment, the average chlorophyll *a* content was 37.53 mg/L, with a coefficient of variation relatively low (4.29%) (Table 2). The genotypes UFU22/F_2BC_1#8, UFU22/F_2BC_1#9, UFU47/F_2BC_1#11, and UFU22/F_2BC_1#2 highlighted presenting the highest values and not differing, significantly, from the wild check treatment, *S. pennellii*. The lowest chlorophyll *a* content was observed in the plants of the pre-commercial line, UFU-222. According to Rego and Possamai (2011), the chlorophyll content, in a plant, varies in function of climatic conditions and an increase in this pigment reflects in an increase in the photosynthetic rate.

Almost all the genotypes that were evaluated showed a similar behavior related to the specific chlorophyll *b* content. The lowest value was found in the genotype UFU-222, which did not differ, significantly, from the *cv*. Santa Clara. Furthermore, the genotypes UFU22/F_2BC_1#8, UFU22/F_2BC_1#9, UFU47/F_2BC_1#11, UFU22/F_2BC_1#2, and UFU22/F_2BC_1#3 did not differ, significantly, from the check treatments *cv*. Santa Clara and *S. pennellii* (Table 2).

Analyzing the total chlorophyll, it was found an overall average of 51.24 mg/L. The lowest content was observed in the pre-commercial line UFU-222, which differed significantly

from all the genotypes that were evaluated. On the other hand, the highest values were found in the genotypes *S. pennellii*, UFU22/F$_2$BC$_1$#9, and UFU47/F$_2$BC$_1$#11. Besides that, these three genotypes did not differ, significantly, from the genotypes UFU22/F$_2$BC$_1$#8, UFU22/F$_2$BC$_1$#2, and UFU22/F$_2$BC$_1$#3 (Table 2).

Low chlorophyll content might be associated with climatic conditions, mainly related to high leaf temperature. Plants with a C3 metabolism, like tomato, have a better photosynthetic behavior under temperatures between 20° and 25°C. When submitted to a water stress conditions, the plants may present, in addition to stomatal closure, alterations in the chlorophyll synthesis, functional and structural alterations in chloroplasts, and disturbances in the processes of accumulation, transport, and distribution of assimilates.

CONCLUSIONS

All the variables analyzed, except CO_2 assimilation and instantaneous carboxylation efficiency, evidenced a superiority of the wild accession *S. pennellii*, regarding the susceptible check treatments.

The high photosynthetic rate, low stomatal conductance, and transpiration are promising physiological characteristics that could be used in the selection of tomato genotypes tolerant to water stress.

Conflicts of interest

The authors declare no conflicts of interest.

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