J. Agr. Sci. Tech. (2015) Vol. 17: 1839-1849

Potassium Nutritional Status Affects Physiological Response of Tamarillo Plants (*Cyphomandra betacea* Cav.) to Drought Stress

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ABSTRACT

***Cyphomandra betacea* (*Cav.)* is a native species from South America that is cultivated because its fruits have a high content of vitamins. In Colombia, it is common to find periods of drought between the rainy seasons or during ENSO events such as El Niño. An adequate nutritional status of K^+ in plants helps to increase the chance of tolerating the negative effects of drought stress. Regarding this situation, a study was conducted to determine the effect of the interaction between the nutritional status of potassium (K^+) and the levels of water availability in the soil. Twenty-week-old Tamarillo seedlings were transplanted into 1 L plastic pots containing peat as substrate. Fifteen Days After Transplanting (DAT), the plants were irrigated with nutrient solutions with two different concentrations of K^+ (0.05 and 2.5 mM KCl) until the end of the experiment. When differences in growth due to the two levels of K^+ were observed, drought stress treatments were established during two drought periods of two weeks. The results showed that plants under drought stress and/or a lack of K^+ had a lower growth rate, total plant dry weight, transpiration (E), and stomatal conductance (g_s). Plants grown with an optimal nutritional status of K^+ showed a better performance under drought conditions, as their Water Use Efficiency (WUE) did not fall sharply despite having low E and g_s. These results suggest that a good supply of K^+ can improve the acclimation of plants of *C. betacea* during periods of drought stress.**

Keywords: Acclimation of plants, Leaf Dehydration Speed, Transpiration, Water use efficiency.

[DOR: 20.1001.1.16807073.2015.17.7.21.4]

INTRODUCTION

The Tamarillo (*Solanum betaceum Cav.*) is a native fruit species from South America (Andean regions of Bolivia, Colombia, Chile, Ecuador and Peru) which belongs to the Solanaceae family (Enciso-Rodríguez *et al.*, 2010) and is widely cultivated in Colombia for its fruits, as these have a high content of vitamins, minerals, carotenoids, and phenolic compounds (Correia and Canhoto, 2012; Osorio *et al.*, 2003). Also, this crop occupied an area of 8,371 hectares and had a production of 129,492 tons in 2011 in Colombia (Ministry of Agriculture and Rural Development, 2011).

Crop production is strongly influenced by environmental conditions, which affect the physiology of the cultivated plant and the efficiency of the production systems (Pinilla-Herrera *et al.*, 2012). Consequently, the agricultural areas of Colombia, principally the Andean region, can show a bimodal rain fall pattern throughout the year, resulting in periods of water shortage in some specific months (June to September and December to March) (Mejia *et al.*, 1999). Also, ENSO events (El Niño/Southern Oscillation) dramatically affect the availability of water,

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which affects crop production negatively (Poveda, 2004).

The plants undergo physiological changes caused by drought stress (Sun *et al.,* 2013). In addition, drought stress conditions cause a reduction in vegetative plant growth and leaf expansion rate in tomato and potato (Potters *et al.*, 2007; Jensen *et al.*, 2010). It has also been reported in lupins (*Lupinus angustifolius* L.) and blue storksbill (*Erodium crinitum* Carolin) that drought stress can alter the morphological characteristics, especially; the shoot: root ratio (French and Turner, 1991; Cox and Conran, 1996, Turner, 1997). Furthermore, drought stress has a negative effect on the leaf gas exchange (Medrano *et al.*, 2002). Potato plants (*Solanum tuberosum* L.) close their stomata under low soil moisture conditions (Liu *et al.*, 2005). Also, tomato plants (*Solanum lycopersicum*) respond the same way to drought stress conditions by reducing stomatal conductance (Jensen *et al.*, 2010).

Potassium (K^+) is an essential nutrient for growth and development because it is the main osmotic solute in plants (Marschner, 2012). On the other hand, the positive effect of K^+ in the amelioration of the negative effects of drought stress on plants by favoring the Water Use Efficiency (WUE) has been widely reported (Cakmak, 2005). Studies developed by Arquero *et al.* (2006), Egilla *et al.* (2001) and Egilla *et al.* (2005) showed that olive trees (*Olea europaea*) and Chinese hibiscus (*Hibicusrosa sinensis*), cultivated with an optimal level of potassium (2.5 mM KCl) and subsequently subjected to prolonged periods of drought stress had better WUE compared to plants of the same species grown with a low concentration of potassium (0.05 mM KCl) and subjected to periods of drought stress. Little is known about the response of Tamarillo plants to environmental stresses mainly in the Andean region; studies have focused on estimating the effect of the relationships among abiotic stresses. Therefore, this study was performed as an approach to estimate the effect of the relationship between the nutritional status and drought stress on growth, gas exchange properties of the leaf, and water use efficiency in Tamarillo plants.

MATERIALS AND METHODS

Plant Material and Growth Conditions

The experiment was developed under greenhouse conditions for a period of sixteen weeks (August-December 2011) at the Universidad Nacional de Colombia campus in Bogotá. Twenty-week-old Tamarillo seedlings were transplanted into 1 L plastic pots containing peat without nutrients (Base 1 substrate, Klasman-Deilmann GmbH, Geeste, Germany) as substrate. The environmental conditions in the greenhouse during the experiment were the following: an average temperature of 22±4°C, a relative humidity of 40 to 90%, a photosynthetically active radiation at midday of 1,500 μmol m^{-2} s^{-1} and a natural photoperiod of 12 hours. After transplanting, the plants were subjected to an acclimation period of 14 days. During this period, the plants were watered three times a week with 100 mL of distilled water. After this acclimation period, treatments of K^+ nutritional status were established by fertigation with 200 mL of a nutrient solution containing the following composition: 2.5 mM $Ca(NO_3)_2$, 0.25 mM $Ca(H_2PO_4)_2$, 1.0 mM $MgSO_4$, 12.5 mM H_3BO_3, 1.0 mM $MnSO_4$, 1.0 mM $ZnSO_4$, 0.25 mM $CuSO_4$, 0.2 mM $(NH_4)_6Mo_7O_{24}$, 10 mM Fe-ethylenediamine-di-o-hydroxyphenylacetic acid and 0.05 or 2.5 mM KCl, respectively, for each nutritional status. In all cases, $Ca(OH)_2$ was used to adjust pH to 5.5 when necessary. The plant height was determined at 21, 31, 59 and 112 Days After Transplantation (DAT).

Drought Stress Treatments

Drought stress treatments were established at 59 DAT when differences in plant height occurred because of two fertigation treatments (0.05 and 2.5 mM KCl). The plants were split into K-starved plants (low K^+) and well-nourished plants (normal K^+). Then, a group of 24 plants (twelve for each nutritional status) was maintained without irrigation for two periods of time, whereas the previous growth conditions were maintained for the other group of plants (control). Drought stress periods were performed by withholding irrigation for 15 days, and these periods were carried out at 59-74 and 96-112 DAT, respectively. The drought-stressed plants were re-watered between the stress periods with the same daily amount of water used in the control plants. The stress experiment lasted for a total of 112 DAT.

Determined Variables

Stomatal Conductance (g_s)

This parameter was measured between 09:00-10:00 hour using a porometer (SC-1, Decagon Devices Inc., Pullman, WA, USA). Two completely developed leaves from the upper third part of the plant were selected for the measurements. g_s was estimated between 96-112 DAT.

Total Plant Transpiration (E)

This parameter was determined daily during the second last period of drought stress (96-112 DAT) using the gravimetric technique described by Ferrara and Flore (2003), which consists of estimating the difference of the weight of the plants in their respective pots every 24 hours. Previously, the pots had been tightly covered with plastic, in order to prevent water loss through evaporation.

Leaf DeHydration Speed (LDHS)

It is a technique used to estimate leaf water status (Melgar *et al.,* 2007). It was obtained by collecting two mature leaves from the middle portion of the canopy. LDHS was determined at the end of the experiment (112 DAT), using a halogen moisture analyzer (Mettler Toledo HB43, Greifensee, Switzerland) at 50°C, when the percentage of water loss was recorded at 5, 10, and 15 minutes.

Water Use Efficiency (WUE)

This parameter was calculated at the end of the experiment (112 DAT), using the total plant dry weight on the total amount of water supplied to each plant (Raviv and Blom, 2001).

Growth Variables

At the end of the experiment (112 DAT), Leaf Area (LA) was also determined using a leaf area meter (LI-3100, LI -COR Inc., Lincoln, NE, USA). Then, leaves, stems, and roots were collected in order to estimate growth variables such as stem diameter and fresh weights. Finally, dry weights were obtained by placing the plant tissues in a drying oven at 80°C until a constant weight was achieved.

Experimental Design and Data Analysis

The data were analyzed using a factorial design by two-way ANOVA. One factor was the two concentrations of potassium (0.05 mM KCl, vs. 2.5 mM KCl) and the other one was the irrigation (irrigation vs. drought). Twelve repetitions (plants) were used for each experimental unit. All percentage values were transformed using the arcsine transformation before analysis where a significant F-test was observed, a separation of means between treatments was obtained using Tukey’s test. The data were analyzed using the program Statistixv 8.0 (AnalyticalSoftware, Tallahassee, FL, US).

[DOR: 20.1001.1.16807073.2015.17.7.21.4]

RESULTS

Growth Variables

The two levels of potassium (0.05 and 2.5 mM KCl) and water regimes (with and without irrigation) affected plant height. Significant differences were observed at 59 DAT due to potassium fertilization. The fertigated plants with an optimum K^+ nutrient solution (2.5 mM KCl) showed a higher plant height compared to the plants treated with a low concentration of potassium (0.05 mM KCl) (Figure 1). This showed that there were two K^+ nutritional statuses before starting the drought stress treatments, since one of the main symptoms of lack of K^+ is a lesser shoot length (Restrepo-Diaz *et al.*, 2009). On the other hand, drought stress also affected negatively the plant height in both concentrations of potassium at 112 DAT. The plants that were grown at a concentration of 2.5 mM KCl without being subjected to two periods of drought stress had the highest plant height at the end of the experiment.

Some differences were observed separately in the nutritional status and drought stress factors in stem diameter, leaf dry weight, stem, root, and also the total plant dry weight and the relationship between the aerial part and the root (Table 1). Accordingly, it could be observed that plants that were grown in a medium rich in K^+ (2.5 mM KCl) had a higher accumulation of dry matter in their different organs. In general, potassium deficiency reduced by ~36% the total plant dry weight compared to that of the well-nourished plants. In addition, the two periods of drought stress also caused a reduction of ~16% of the total dry weight. Regarding the shoot/root relationship, we found that this ratio was lower under conditions of lack of K or drought stress. Similarly, significant differences were also observed in the interaction of nutritional status (0.05 vs. 2.5 mM KCl) and hydric state (irrigated vs. drought) on the leaf area (Figure 2). The largest leaf area was obtained in well-nourished plants without drought regimens.

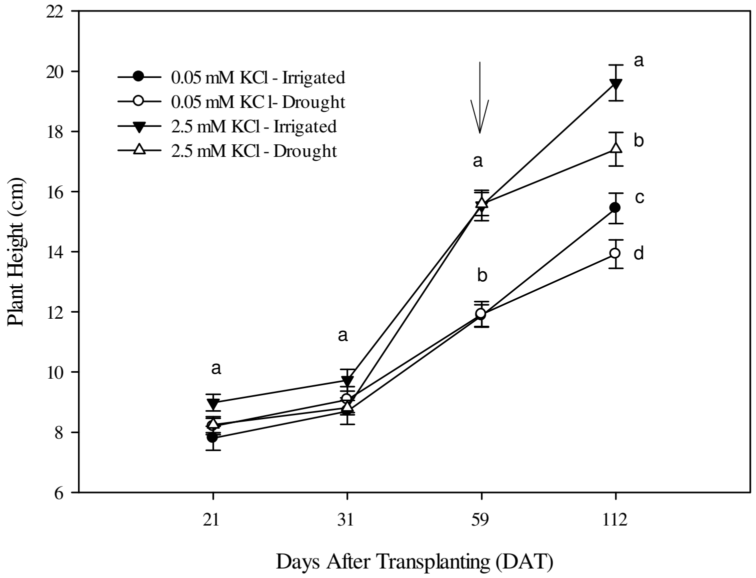

Figure 1. Effect of the relationship between two levels of potassium (0.05 vs. 2.5 mM KCl) and water regimes (irrigated vs. drought stressed) on plant height of Tamarillo plants. Arrow indicates when drought stress periods started at 59 DAT. Vertical bars represent the SE of 12 replicates. Means followed by the same letter did not show significant differences (Tukey $P \leq 0.05$).

Table 1. Effect of the relationship between two levels of potassium (0.05 vs. 2.5 mM KCl) and water regimes (Irrigation vs. Drought) on Stem Diameter (SD), Leaf Dry Weights (LDW), Stem Dry Weights (SDW), Root Dry Weights (RDW), Total plant Dry Weight (TDW), and Shoot:Root ratio (S/R) of Tamarillo plants.[a]

Treatment	*SD* (mm)	*LDW* (g)	*SDW* (g)	*RDW* (g)	*TDW* (g)	*S/R*
Interaction						
2.5 KCl/Irrigated	85.83	1.94	1.64	0.98	4.55	3.79
2.5 KCl/Drought	80.42	1.29	1.36	1.23	3.85	2.25
0.05 KCl/Irrigated	67.50	1.22	0.99	0.74	2.95	3.08
0.05 KCl/Drought	62.08	0.83	0.70	0.92	2.43	1.88
Significance	NS	NS	NS	NS	NS	NS
Concentration, mM						
2.5 KCl	83.12 a	1.61 a	1.49 a	1.10 a	4.20 a	3.02 a
0.05 KCl	64.8 b	1.02 b	0.84 b	0.83 b	2.69 b	2.48 b
Significance	***	***	***	*	***	*
Water availability						
Irrigated	76.67 a	1.58 a	1.31 a	0.86 b	3.75 a	3.43 a
Drought	71.25 b	1.06 b	1.03 b	1.07 a	3.14 b	2.07 b
Significance	*	***	**	*	*	***
CV (%)	11.37	27.95	27.77	36.64	25.33	26.06

[a] The data represent the average of 12 plants per treatment (*n*= 12). Averages followed by the same letter didn't show significant differences from $P < 0.05$.

*, **, and ***: Differ significantly at 0.05, 0.01 and 0.001 probability levels respectively. NS: Not Significant at $P \leq 0.05$.

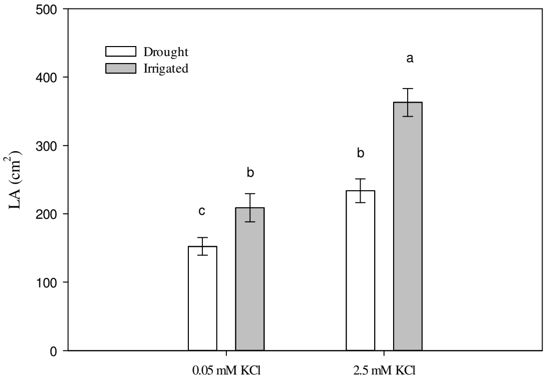

Figure 2. Effect of the relationship between two levels of potassium (0.05 vs. 2.5 mM KCl) and water regimes (irrigated vs. drought stressed) on Leaf Area (LA) at 112 DAT in Tamarillo plants. Vertical bars represent the SE of 12 replicates. Means followed by the same letter did not show significant differences (Tukey $P \leq 0.05$).

Similarly, water stress treatments reduced by ~30% the leaf area in Tamarillo plants under high potassium conditions, reaching similar values to the Tamarillo plants grown with low potassium and without drought periods. On the other hand, a smaller leaf area was found when the Tamarillo plants were grown in a medium with low levels of K^+ and subjected to two periods of drought stress. In this group of plants, leaf area was reduced by ~60% compared to the well-nourished plants without periods of water scarcity.

[DOR: 20.1001.1.16807073.2015.17.7.21.4]

Leaf Dehydration Speed

Some differences were found on Leaf DeHydration Speed (LDHS) in the interaction K^+ nutritional status and irrigation regimens (with or without drought) at 5, 10, and 15 minutes, respectively. The control plants grown with normal potassium showed a higher LDHS at the three different periods of time than the ones with the other treatments (Figures 3-A, -B and -C). Additionally, the drought stress treatments caused a decrease ~29% on LDHS in the well-nourished plants. Similar trends were observed in the K-starved plants due to irrigation treatments while the plants cultivated with low K^+ under drought conditions showed the lowest LDSH in all cases. As it was mentioned above, LDHS is a technique that helps to indicate leaf water status (Melgar*et al.*, 2007), hence, this measurement showed that a group of plants were under water stress conditions.

Stomatal Conductance and Transpiration

Some differences between the effects of nutritional and the hydric status on stomatal conductance (g_s) and transpiration (E) were observed (Figures 4-A and -B). In both variables, the values were significantly higher in plants under good potassium nutritional conditions without deprivation of water. Additionally, the plants under poor irrigation conditions decreased their transpiration in both nutritional statuses in response to the low water availability. In general, the decrease of g_s and E was about 40% compared to the control plants (Tamarillo plants cultivated with a high content of K^+ and without drought stress). The ratio between total plant transpiration and leaf area was also estimated. The Tamarillo plants grown under low K^+ conditions had a higher ratio in both irrigation regimens, mainly the plants without drought conditions (Figure 5). Also, this relationship showed how a good K^+ status helped to regulate the water loss per unit leaf area, especially under drought stress conditions.

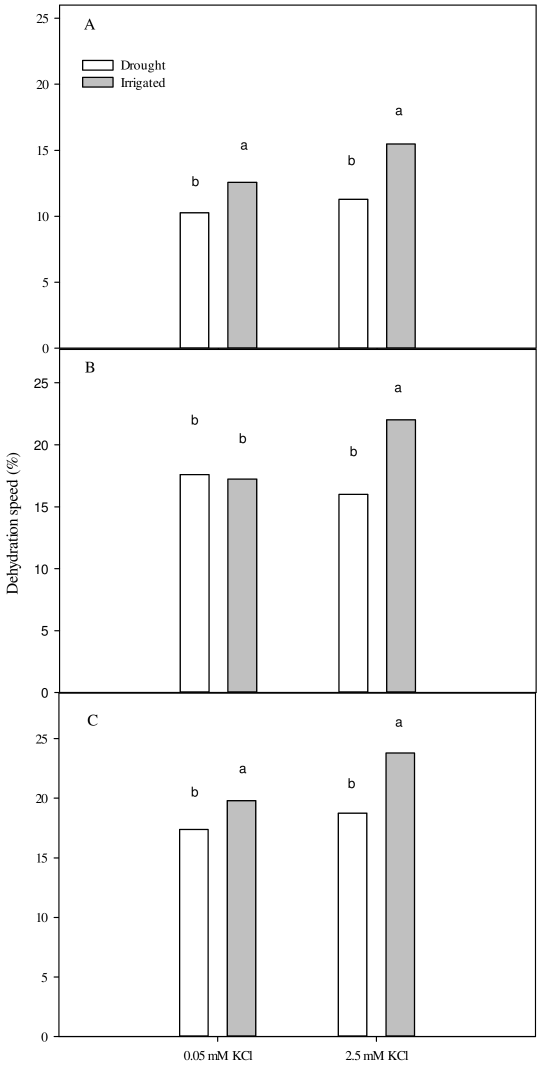

Figure 3. Effect of the relationship between two levels of potassium (0.05 vs. 2.5 mM KCl) and water regimes (irrigated vs. drought stressed) on the dehydration speed at five (A) ten (B) and fifteen minutes (C) of leaf tissue discs of Tamarillo plants at 112 DAT. Means followed by the same letter did not show significant differences (Tukey $P \leq 0.05$).

Water Use Efficiency (WUE)

The plants adequately supplied with potassium (2.5 mM KCl) and without

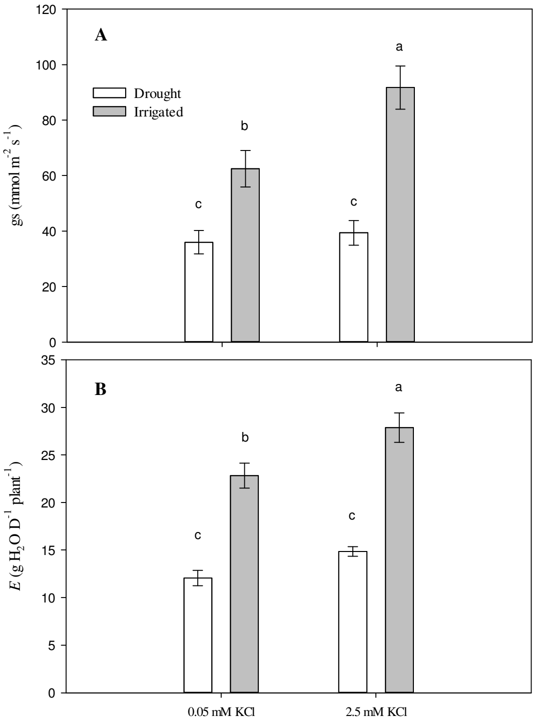

Figure 4. Effect of the relationship between two levels of potassium (0.05 vs. 2.5 mM KCl) and water regimes (irrigated vs. drought stressed) on stomatal conductance (A), and transpiration (B) at 112 DAT in leaves of Tamarillo plant. Vertical bars represent the *SE* of 12 replicates. Means followed by the same letter did not show significant differences (Tukey P≤ 0.05).

periods of drought stress had the greatest *WUE*, with a greater biomass production per mL of water (Figure 6). Also, the nutritional status had a positive influence under the two conditions of lack of irrigation. The plants grown with low potassium (0.05 mM KCl) and under two irrigation conditions showed no difference compared to the Tamarillo plants under drought stress but grown in a high potassium medium.

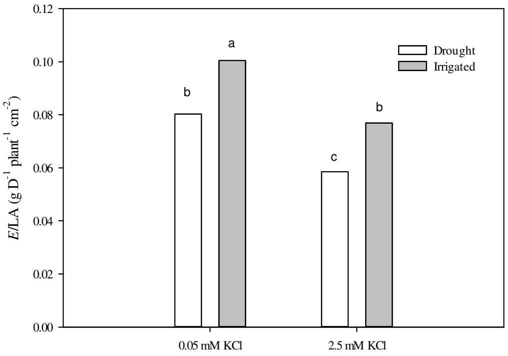

Figure 5. Effect of two levels of potassium (0.05 vs. 2.5 mM KCl) and water regimes (irrigated vs. drought stressed) on transpiration:leaf area ratio in Tamarillo plants. Means followed by the same letter did not show significant differences (Tukey P≤ 0.05).

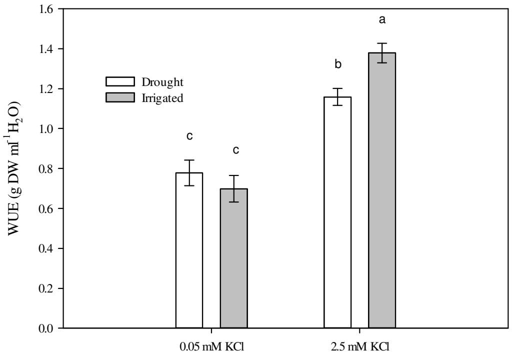

Figure 6. Effect of the relationship between two levels of potassium (0.05 vs. 2.5 mM KCl) and water regimes (irrigated vs. drought stressed) on Water Use Efficiency (WUE) in Tamarillo plants. Vertical bars represent the *SE* of 12 replicates. Means followed by the same letter did not show significant differences (Tukey P≤ 0.05).

DISCUSSION

Reduced shoot length and dry matter accumulation was observed in the plants cultivated with a low concentration of K^+ (0.05 mM KCl) (Figure 1 and Table 1.). This may be due to a deficiency of K^+, since one of the main symptoms present in plants grown for long periods of deficiency of this element is a significant reduction in both the plant growth and the total dry matter of the plant (Restrepo Diaz *et al*., 2009). Similar effects were reported in tomato plants by Kanai *et al*. (2011). They also observed that a deficiency of K^+ reduced growth due to alteration of the water relationship of the plant, which affected the source:sink relationship.

After analyzing the influence of the two irrigation treatments i.e. plants with periods of no irrigation vs. plants with continuous irrigation, it was observed that drought stress also affected the shoot length and dry matter production, especially in plants with potassium deficiency. It is well known that drought stress affects growth and dry weight of plants (Restrepo-Diaz *et al*., 2010). Taiz and Zeiger (2006) link these effects mainly to the reduction of cell elongation due to the loss of cellular turgor. Egilla *et al*. (2001) reported similar results about the effect of the interaction of the nutritional status of potassium and levels of drought stress on the shoot length and total plant dry weight in plants of *H. rosa-sinensis*. Similarly, they also observed an analogous behavior in the increase of root dry weight in drought stressed plants, like the results obtained in the present study. This increase of the dry mass of the root may be the result of an increase of the carbon allocation to root production as an acclimation mechanism to cope with the adverse conditions of low soil moisture (Malik *et al*., 1979; Steinberg *et al*., 1990). Besides, potassium starvation causes a lower uptake of CO_2 which could result in reduced allocation of biomass to the shoot, leading to a decrease in the shoot:root ratio (Ericsson, 1995).

Total plant transpiration (E) and stomatal conductance (g_s) were negatively affected by both the nutritional status of plants and the effect of drought stress (Figure 4). According to the results obtained in this study, no differences were found on *E* and g_s in Tamarillo plants subjected to two periods of drought stress in both nutritional states (0.05 and 2.5 mM KCl). However, the values of these variables were lower (50%) compared to the plants grown in these two levels of K^+ and without any period of stress. This decrease in the gas exchange of the leaves (E and g_s) due to low soil moisture conditions is commonly associated with stomatal closure, which can probably lead to an increase in the Abscisic Acid content (ABA) in the plant (Liu *et al*., 2005). The effect of the nutritional status of K^+ on g_s has been well documented (Arquero *et al*., 2006; Jin *et al.,* 2011; Andrés *et al.,* 2014). However, the results in this area can be somehow contradictory. While some authors report that potassium deficiency may promote stomatal opening and thus increase respiration (Sudama *et al*., 1998; Arquero *et al*., 2006), others have found that lack of potassium promotes stomatal closure (Egilla *et al*., 2005; Kanai *et al*., 2011). The latter agrees with the findings in the present work in which stomatal conductance in Tamarillo was affected negatively under conditions of deficiency of K^+. A plausible explanation why the deficiency of K^+ reduces the (g_s) is due to the fact that K^+ is an osmolyte that actively participates in the regulation of stomatal opening and closing (Marschner, 2012).

The dehydration speed of the leaves has been used as an indirect measure to assess the hydric status of plants (Melgar *et al*., 2007). Our results showed mainly that the plants nourished with good levels of potassium showed differences in their dehydration speed between the two irrigation treatments compared to the malnourished plants which showed no significant variation in their dehydration speed due to the two levels of irrigation during the experiment (Figure 3). As it was previously mentioned, the K^+, being an osmolyte, participates in the hydric relationships through the control of the turgor of guard cells of stomata (Taiz and Zeiger, 2006)

On the other hand, differences in the differences in the interaction of potassium nutritional status and drought conditions on the ratio among total plant transpiration and leaf area, and water use efficiency were observed and Water Use Efficiency (WUE) were observed (Figures 5 and 6). Based on the results of this experiment, it was observed that a good supply of K^+ helps to regulate the water loss per unit leaf area and the accumulation of dry matter under drought stress conditions. Similar observations were found by Egilla *et al.* (2005) and Arquero *et al.* (2006) in *H. rosa-sinensis* and *O. europaea,* respectively. They concluded that a good level of K^+ (2.5 mM KCl) helped to maintain a high *WUE* under drought stress conditions. In our study, despite the decrease in plants g_s in adequate and deficient K^+ conditions, it was observed that *WUE* under drought stress was enhanced by a good supply of K^+. This may be due to the fact that an adequate concentration of potassium in the leaf can promote carboxylation efficiency of CO_2 under low soil moisture conditions (Bednarz *et al.*, 1998; Egilla *et al.,* 2005).

To sum up, the results of this study show that K^+ plays an important role in regulating the water status of Tamarillo plants because a deficiency of this element causes a substantial reduction in the transpiration rates and the stomatal conductance of the leaf. Also, an adequate level of K^+ helps to improve the acclimation process in plants subject to conditions of low availability of soil moisture because it can promote better *WUE*. This allows us to conclude that adequate potassium fertilization may be essential for this species to overcome specific periods of drought stress during its development process.

Abbreviations

Dry Weight (DW), DeHydration Speed (DHS), stomatal conductance (g_s), Transpiration (E), Water Use Efficiency (WUE).

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تاثیر وضعیت تغذیه پتاسیم بر واکنش های فیزیولوژیکی گیاه Tamarillo (*Cyphomandra betacea* Cav.)به تنش خشکی

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چکیده

گیاه Tamarillo (*Cyphomandrabetacea*Cav.) یک گونه بومی امریکای جنوبی است که به خاطر میوه هایش که سرشار از ویتامین است کاشت می شود. در کلمبیا، بین فصل های بارانی یا طی رخداد هایی مشهور به ENSO از قبیل النینو، به طور معمول دوره های خشکی وجود دارد. از سویی، وجود پتاسیم کافی در گیاه شانس تحمل اثرات منفی تنش خشکی را افزایش می دهد. با توجه به این موارد، هدف پژوهش حاضرتعیین اثر برهمکنش وضعیت تغذیه پتاسیمی گیاه و مقدار آب قابل دسترس در خاک بود. به این منظور، گیاهچه های ۲۰ هفته ای Tamarilloدر گلدان های یک لیتری پلاستیکی که حاوی پیت به عنوان بستر بودند نشاء شدند. پانزده روز بعد از نشاکاری، گیاهان تا آخر آزمایش با محلول های غذایی آبیاری شدند که دو غلظت متفاوت K^+(۰/۰۵ و ۲/۵ میلی مول KCl) داشتند. سپس، در هنگامی که گیاهان به لحاظ سطوح مختلف غلظت های پتاسیم تفاوت رشد نشان دادند، تیمارهای تنش خشکی طی دو دوره دوهفته ای اعمال شد.نتایج نشان داد که گیاهانی که تحت تنش خشکی و/یا کمبود K^+پتاسیم بودند رشد کمتری داشتند و وزن کل ماده خشک ، تعرق(E)، و هدایت روزنه ای آن ها(g_s) هم کمتر بود. اما، گیاهانی که تغذیه پتاسیمی آن ها بهینه بود، در شرایط تنش خشکی عملکرد بهتری داشتند و با وجود کاهش (E) و (g_s)، کارآیی مصرف آب آن ها (WUE)کاهش تندی نداشت. بر پایه این نتایج می توان گفت که تامین K^+کافی می تواند سازگاری گیاه *C. betacea* را در دوره های تنش خشکی بهبود بخشد.