

Effect of water deficit on some physiological and biochemical responses of the yellow diploid potato (*Solanum tuberosum* L. Group Phureja)

Efecto del déficit hídrico sobre algunas respuestas fisiológicas y bioquímicas en papa amarilla diploide (*Solanum tuberosum* L. Group Phureja)

Wilmar Ariza¹, Luis Ernesto Rodríguez¹, Darwin Moreno-Echeverry¹, Carlos Arturo Guerrero², and Liz Patricia Moreno^{1*}

ABSTRACT

Water availability is one of the main limitations of potato yields due to the high sensitivity of this crop to water deficit. The objective of this study was to determine the effect of water deficit on some physiological and biochemical responses in yellow diploid potato plants (*Solanum tuberosum* L. Group Phureja) of the cultivars Criolla Colombia, Criolla Dorada and Criolla Ocarina. Plants at tuber initiation were subjected to two treatments: continuous irrigation and water deficit imposed by withholding water at tuber initiation for 17 d. The results showed that plants under water deficit increased chlorophyll concentration, malondialdehyde and proline content. However, these plants showed a decrease in stomatal conductance, leaf area, total dry mass and exhibited a higher root/shoot ratio in all potato cultivars. In addition, all the cultivars also showed a decrease in yield, which was associated with sensitivity to water stress. Although the high content of proline and high root/shoot ratio may be associated with tolerance to water deficit, this association was not observed in these cultivars, probably due to the high reduction of stomatal conductance, which limited the production of photoassimilates, plant growth, and, therefore, the yield.

Key words: leaf area, membrane stability, malondialdehyde, proline.

RESUMEN

La disponibilidad hídrica es uno de las principales limitantes del rendimiento en papa debido a la alta sensibilidad de este cultivo al déficit hídrico. El objetivo de este estudio fue determinar el efecto del déficit hídrico sobre algunas respuestas fisiológicas y bioquímicas en plantas de papa amarilla diploide (*Solanum tuberosum* L. Group Phureja) de los cultivares Criolla Colombia, Criolla Dorada y Criolla Ocarina. Las plantas al inicio de la tuberización fueron sometidas a dos tratamientos: riego continuo y déficit hídrico por suspensión de riego al inicio de la tuberización durante 17 días. Los resultados mostraron que las plantas con déficit hídrico aumentaron la concentración de clorofila y el contenido de malondialdehído y prolina. Sin embargo, estas plantas también mostraron una disminución en la conductancia estomática, el área foliar y la masa seca total, y presentaron una mayor relación raíz/parte aérea en todos los cultivares. Además, todos los cultivares mostraron una disminución en el rendimiento, que se asoció con su sensibilidad al déficit hídrico. Aunque el alto contenido de prolina y la alta relación raíz/parte aérea pueden estar asociados con la tolerancia al déficit hídrico, esta asociación no se observó en estos cultivares, probablemente debido a la alta reducción de la conductancia estomática, que limitó la producción de fotoasimilados, el crecimiento de la planta y por tanto el rendimiento.

Palabras clave: área foliar, estabilidad de membranas, malondialdehído, prolina.

Introduction

The potato (*Solanum tuberosum* L.) is the fourth most important crop in planted areas worldwide and the third most important food for human consumption after rice and wheat (Devaux *et al.*, 2014; Hardigan *et al.*, 2017; Kam-moun *et al.*, 2018). Potatoes are among the plants that are susceptible to water deficit causing a decrease in both yield

and quality of tubers (Monneveux *et al.*, 2013). The effect of water deficit on the yield of this crop depends on the stage of plant development at which it occurs and also on the duration and severity (Jefferies, 1995).

Tuber initiation is one of the most sensitive stages to water deficit, since the development of the plant is affected, as well as the supply of photoassimilates to the tuber

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¹ Departamento de Agronomía, Facultad de Ciencias Agrarias, Universidad Nacional de Colombia, Bogota (Colombia).

² Departamento de Ciencias Fisiológicas, Facultad de Medicina, Universidad Nacional de Colombia, Bogota (Colombia).

* Corresponding author: lpmorenof@unal.edu.co



(Dallas-Costa *et al.*, 1997). Water deficit in the potato (*S. tuberosum* L.) reduces stomatal conductance (g_s), resulting in a decrease in the photosynthetic rate and an increase of reactive oxygen species (ROS) (Shi *et al.*, 2015). ROS cause the degradation of macromolecules such as chlorophylls, proteins, nucleic acids and lipids (Mahmud *et al.*, 2015). In addition, increasing ROS can produce photoinhibition affecting the functionality of photosystems. This is observed in potatoes under severe stress conditions (Li *et al.*, 2017). Another target of ROS is the cell membranes due to lipid peroxidation that modifies their permeability (Lima *et al.*, 2002). The modifications already mentioned cause a decrease in the growth of the plant since cell expansion processes are limited by the decline in water content and the loss of turgor pressure (Rolando *et al.*, 2015; Kesiime *et al.*, 2016). One of the first responses to water deficit is osmotic adjustment due to the accumulation of osmotically active molecules that allow plants to absorb water and maintain cellular turgor pressure (Singh *et al.*, 2000). In potatoes, the increase in proline accumulation is associated with osmoregulation under water deficit (Mahmud *et al.*, 2015).

The yellow diploid potato (*S. tuberosum* L. Group Phureja) is widely cultivated in the Andes from western Venezuela to central Bolivia with an important center of diversity in southern Colombia and northern Ecuador (Ghislain *et al.*, 2006). A great variability in response to water deficit is found in diploid varieties (Coleman, 2008; Anithakumari *et al.*, 2012; Cabello *et al.*, 2012). The sensitivity of yellow potato to water deficit limits its distribution to areas with optimal levels of precipitation and irrigation, and this reduces the potential area of cultivation. New diploid yellow potato cultivars have been recently developed in Colombia with high levels of tolerance to the pathogen *Phytophthora infestans* (Mont.) de Bary and with better nutritional characteristics regarding levels of iron, zinc and proteins, such as Criolla Ocarina (UN 64) and Criolla Dorada (UN 04) (Peña *et al.*, 2015). The objective of this research was to determine the effect of water deficit on some physiological and biochemical responses of the cultivar (cv.) Criolla Colombia (Colombia), the most commercially important cultivar nowadays, as well on the new cultivars Criolla Dorada (Dorada) and Criolla Ocarina (Ocarina).

Materials and methods

Plant material and growth conditions

This research was carried out in 2016 under greenhouse conditions at Facultad de Ciencias Agrarias, Universidad Nacional of Colombia, at 2,600 m a.s.l. Potato tubers of

cultivars *S. tuberosum* L. Group Phureja, Colombia, Dorada and Ocarina, were planted in black plastic bags that contained 7 kg of soil. Plants were irrigated every day from the time of planting. During the experiment, daily records of temperature and relative humidity (average temperature of 19.7°C and an average relative humidity of 68.1%) were registered with a weather station (EL-USB-2, China).

Plants of the three cultivars were subjected to two treatments: well-watered (WW) maintaining a volumetric soil water content (VSWC) of 30% and water-deficit (WD) by withholding water for 17 d from 48 d after sowing, at tuber initiation. After the stress period, the plants were re-watered for recovery until the end of the crop cycle. A completely randomized design (CRD) with three replications was used. The measurements of the variables were taken at 5, 8, 11, 14 and 17 d after treatment (DAT) from completely expanded leaves of the upper third of the plant. For biochemical parameters, three technical replicates were used.

Field sampling and processing

Volumetric soil water content and leaf water status

The VSWC was measured at dawn with a time domain reflectometer (TDR-300, USA) at 20 cm depth. The leaf water potential (Ψ_w) was measured at dawn with a Scholander pressure chamber (PMS Model 615, CA, USA). Relative water content (RWC) was determined according to Anithakumari *et al.* (2012). At each point, leaves of the upper third of the plant were sampled and their fresh weight (FW) immediately recorded. Subsequently, the turgid weight (TW) was recorded after overnight rehydration at 4°C. For dry weight (DW) determination, samples were dried to constant weight at 75°C. Relative water content was calculated with the following equation:

$$\text{RWC (\%)} = (\text{FW} - \text{DW} / \text{TW} - \text{DW}) \times 100 \quad (1)$$

Stomatal conductance and chlorophyll a fluorescence

The stomatal conductance (g_s) was measured with a porometer (SC-1, Decagon Device, USA) from 9.00 am to 11.00 am. The chlorophyll a fluorescence (Fv/Fm) was measured in dark-adapted leaves for 30 min using a MINI-PAM modulated fluorometer (Walz®, GmbH Effeltrich, Germany). The chlorophyll molecules were excited for 0.80 s with 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of actinic light. The parameter of maximum quantum yield of photosystem II (Fv/Fm) was registered. Fv/Fm is a ratio that indicates the quantum efficiency of photosystem II (PSII).

Chlorophyll concentration

Chlorophyll concentration (Chl_{SPAD}) was measured in leaves using a portable chlorophyll meter (SPAD-502 model, Konica Minolta, Sakai, Osaka, Japan) from 8.00 am to 11.00 am.

Malondialdehyde and proline content

The leaf samples were ground to a fine powder in liquid nitrogen and were stored at -80°C until the determinations were performed. Lipid peroxidation was measured as the amount of malondialdehyde (MDA) determined by the thiobarbituric acid (TBA) reaction (Wang *et al.*, 2013). The leaf sample (0.4 g) was homogenized in 2 ml of 10% (w/v) trichloroacetic acid (TCA). The homogenate was centrifuged at 4126 xg for 30 min. Then, 4 ml of TCA (10%) containing 0.5% (w/v) of TBA were added to 1 ml of the supernatant. The mixture was heated at 95°C for 30 min and then quickly cooled on ice. The extracts were centrifuged at 4126 xg for 15 min, and the absorbance was measured at 450, 532 and 600 nm. The concentration of MDA was calculated by applying the formula proposed by Wang *et al.* (2013), $\text{CMDA} (\mu\text{mol ml}^{-1}) = 6.45 \times (\text{A}532 - \text{A}600) - 0.56 \times \text{A}450$. Proline content was determined based on the proline reaction with ninhydrin. For the proline determination, a 1:1:1 solution of proline, ninhydrin and glacial acetic acid was incubated at 97°C for 1 h. The reaction was arrested in an ice bath, the chromophore was extracted with toluene, and its absorbance was measured at 520 nm. The proline content is determined using a standard curve and is expressed as $\mu\text{mol proline g}^{-1}$ fresh weight (FW) (Bates *et al.*, 1973)

Growth parameters, dry-mass partitioning and yield

The leaf area (LA) was determined using a portable leaf area meter (LICOR Li 3100C, USA). The plants were individually separated into roots, stems and leaves and dried at 70°C until the weight became constant. The dry-mass (D-M) partitioning and the root/shoot ratio (R/S) were determined. These measurements were taken at the end of the stress treatment (17 DAT). The tuber yield was determined as tuber fresh weight per plant at the end of the crop cycle. The decrease in yield in plants under WD was calculated in comparison to the yield of WW plants.

Data analysis

The effects of irrigation treatments and time on the physiological parameters and yield were assessed by an analysis of variance (ANOVA) with repeated measures over time using a PROC MIXED procedure (Littell *et al.*, 1998) of SAS 9.4 software (SAS institute). A one-way ANOVA was carried out to determine the effect of the treatments per day. The comparison of the means was performed with a Tukey multiple range test ($P < 0.05$).

Results and discussion

Volumetric soil water content and leaf water status

VSWC remained close to 30% in WW treatments; these values were similar to those reported for well-watered plants under semi-controlled conditions (Banik *et al.*, 2016). In the WD treatment, VSWC decreased significantly for all cultivars from 5 DAT (47%) to 17 DAT (72%) (Fig. 1). In this study, the irrigation suspension led to a high drop in the VSWC from 5 DAT to 17 DAT, which indicated that the plants had water deficit.

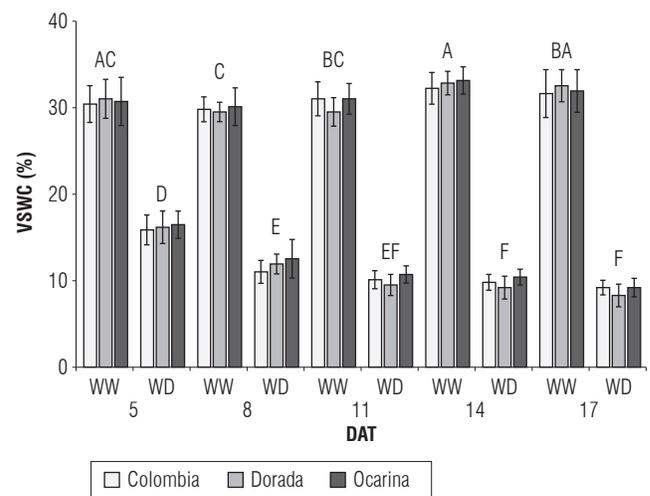


FIGURE 1. Volumetric soil water content (VSWC) in three yellow diploid potato cultivars. WW: well-watered, WD: water-deficit, DAT: days after treatment. Values represent means \pm SD, $n=6$. Capital letters indicate the differences between treatments in time. Means denoted by the same letter do not significantly differ at $P < 0.05$ according to the Tukey test.

The Ψ_w in plants subjected to WD was significantly lower (-0.57 MPa to -1.74 MPa) than in WW plants (-0.20 MPa to -0.24 MPa). In plants with WD at 8 DAT the lowest Ψ_w was observed in the cv. Colombia (-0.86 MPa) compared with cv. Dorada and Ocarina (-0.71 MPa). At 11 DAT water potential of the cv. Colombia was similar to cv. Ocarina (-1.31 MPa) but lower than in the cv. Dorada (-1.18 MPa). At 14 and 17 DAT there were no differences in Ψ_w between cultivars (Fig. 2A). RWC in plants subjected to WD (81% - 57%) was significantly lower than in WW plants (90%) without differences between cultivars.

In plants with WD, the RWC decreased at 5 DAT (81%), at 8 DAT (70%), at 11 DAT (64%), and at 17 DAT (57%) in comparison to irrigated plants. From 5 DAT, both Ψ_w and RWC gradually decreased in plants under WD (Fig. 2B). Both the RWC and the Ψ_w are variables that indicate the hydric state of the plant as well as the level of stress that it

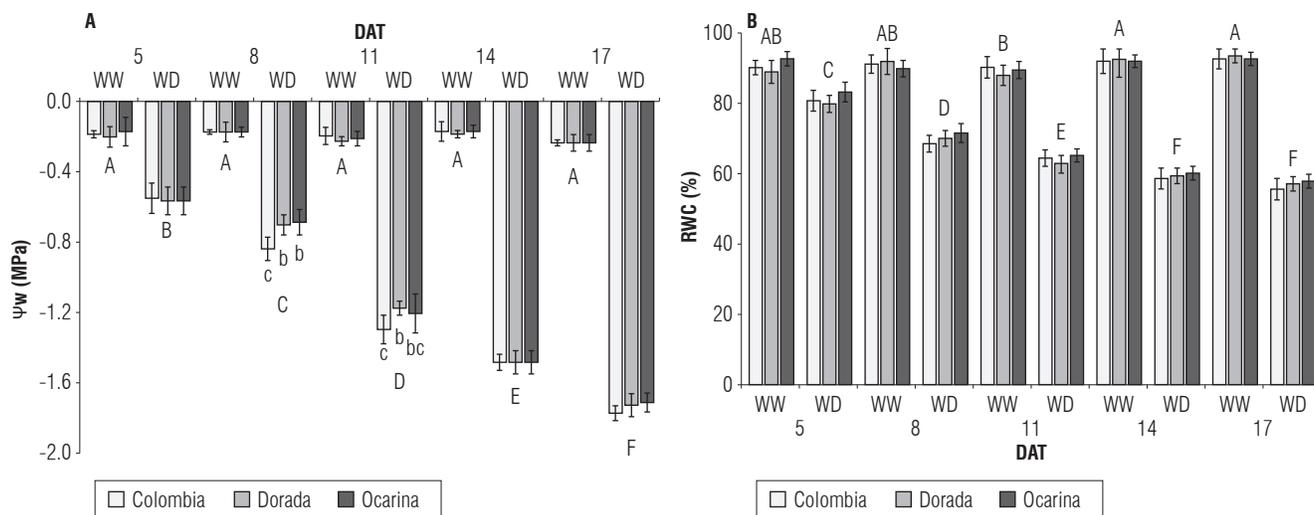


FIGURE 2. Changes in (A) leaf water potential (Ψ_w) and (B) relative water content (RWC) in three yellow diploid potato cultivars. WW: well-watered, WD: water-deficit, DAT: days after treatment. Values represent means \pm SD, $n=6$. Capital letters indicate the differences between treatments in time. Lowercase letters indicate the differences per day. Means denoted by the same letter do not significantly differ at $P<0.05$ according to the Tukey test.

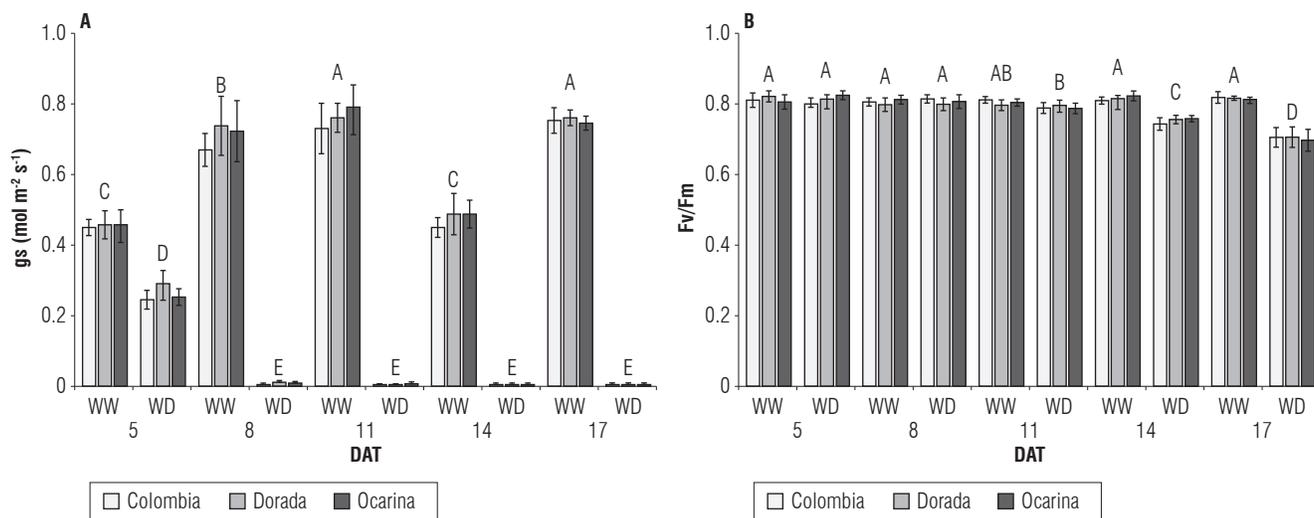


FIGURE 3. Changes in (A) stomatal conductance (g_s) and (B) chlorophyll a fluorescence (Fv/Fm) in three yellow diploid potato cultivars. WW: well-watered, WD: water-deficit, DAT: days after treatment. Values represent means \pm SD, $n=6$. Capital letters indicate the differences between treatments in time. Means denoted by the same letter do not significantly differ at $P<0.05$ according to the Tukey test.

shows (Hsiao, 1973; Soltys-Kalina *et al.*, 2016). Plants of all cultivars subjected to WD showed a reduction in both the RWC and Ψ_w . Based on the decrease in the RWC compared with well-watered plants, and according to the criteria established by Hsiao (1973), the three cultivars showed a mild water deficit at 5 DAT, while the stress was severe after 8 DAT. The RWC presented a pattern of decrease similar to that of the drop observed in the VSWC, while the Ψ_w showed a greater decrease, mainly at 17 DAT. These data suggest that the cultivars developed mechanisms to retain or absorb water. These mechanisms include the synthesis of different osmolytes such as proline.

Stomatal conductance and Chlorophyll a fluorescence

Stomatal conductance was significantly lower in plants under WD ($0.265 \text{ mol m}^{-2} \text{ s}^{-1}$ - $0.008 \text{ mol m}^{-2} \text{ s}^{-1}$) compared with WW plants ($0.456 \text{ mol m}^{-2} \text{ s}^{-1}$ - $0.761 \text{ mol m}^{-2} \text{ s}^{-1}$). The highest decrease in g_s in plants subjected to WD was at 5 DAT, while the stress was severe after 8 DAT ($0.265 \text{ mol m}^{-2} \text{ s}^{-1}$) and at 8 DAT ($0.012 \text{ mol m}^{-2} \text{ s}^{-1}$). From 8 DAT to 17 DAT, g_s did not show significant differences in plants under WD (Fig. 3A). Due to the decrease of VSWC in the first days of irrigation suspension, the plants showed a high decrease in g_s , indicating that g_s in these cultivars is very sensitive to the reduction in water availability (Stiller *et al.*, 2008; Timothy *et al.*, 2018). The observed

stomatal closure was related to an isohydric behavior as a strategy to avoid losing water under conditions of water deficit as has already been described for tetraploid potato cultivars (Liu *et al.*, 2005). The stomatal closure observed also suggests an early stomatal limitation of photosynthesis in the three cultivars. Decreases in stomatal conductance cause an imbalance between light harvesting, electron transport and carbon assimilation, which leads to the production of ROS resulting in damage to PSII.

Fv/Fm was higher than 0.8 in WW plants and in plants subjected to WD until 11 DAT. In plants under WD, Fv/Fm values were lower than 0.8 at 14 DAT (0.75) and 17 (0.70) (Fig. 3A). Neither g_s nor Fv/Fm showed differences between cultivars (Fig. 3B). As a consequence of the stomatal closure induced by water deficit, the intercellular CO₂ concentration decreases causing an imbalance between the phases of photosynthesis and an increase in ROS that leads to photoinhibition (Lima *et al.*, 2002; Rudack *et al.*, 2017; Timothy *et al.*, 2018). An indicator of the functionality of the photosynthetic apparatus is the quantum efficiency of photosystem II, determined by the Fv/Fm ratio (Lu and Zhang, 1998). Here, an Fv/Fm value of 0.7 was found at 17 DAT, suggesting the presence of mild PSII damage, since in plants with values higher than 0.75 there is an absence of damage in the PSII (Van der Mescht *et al.*, 1999). The presence of Fv/Fm values higher than 0.8 at 8 DAT and 14 DAT, when severe stress and a high reduction in g_s are observed, suggests that these plants present early defense mechanisms to deal with oxidative stress caused by water deficit, which prevents or diminishes the damage of the PSII (Mane *et al.*, 2008).

Chlorophyll concentration

Chl_{SPAD} was significantly higher in plants subjected to WD (46 SPAD Units - 57 SPAD Units) than in WW plants (41 SPAD Units - 43 SPAD Units) throughout the experimental period, without differences between cultivars (Fig. 4). Another factor that affects the photosynthetic capacity of plants is the content of the chlorophylls, since they are essential in the capture of light. An increase in Chl_{SPAD} was found in plants under water deficit in all the cultivars. These results contrast with what was reported in other diploid and tetraploid cultivars in which a reduction in the chlorophyll content under water deficit is found (Anithakumari *et al.*, 2012). The increase in Chl_{SPAD} was observed from 5 DAT and was related to the severity of the stress and the reduction in the growth of the leaf. The increase in Chl_{SPAD} is also observed in tetraploid cultivars of potato under water deficit conditions (Ramírez *et al.*, 2014; Rolando *et al.*, 2015). Therefore, the increase in the content of chlorophylls

observed is associated with the susceptibility of these cultivars to water deficit (Ramírez *et al.*, 2014).

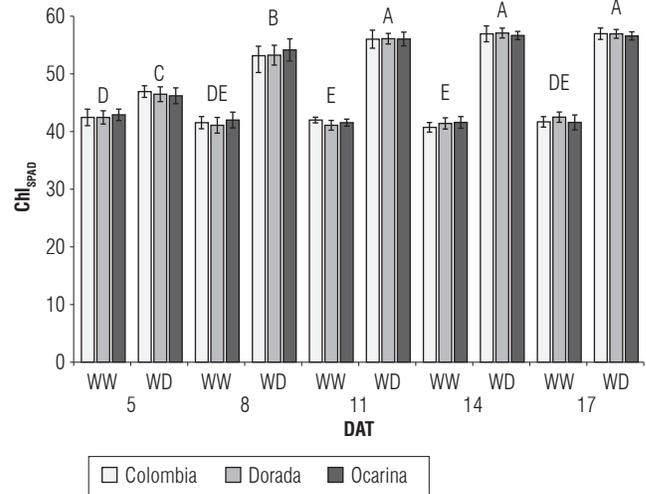


FIGURE 4. Chlorophyll concentration (Chl_{SPAD}) in three yellow diploid potato cultivars. WW: well-watered, WD: water-deficit, DAT: days after treatment. Values represent means \pm SD, n=6. Capital letters indicate the differences between treatments in time. Means denoted by the same letter do not significantly differ at $P < 0.05$ according to the Tukey test.

Malondialdehyde and proline content

MDA content in plants under WD increased significantly from 8 DAT (1.32 $\mu\text{mol g}^{-1}$ FW - 1.46 $\mu\text{mol g}^{-1}$ FW) to 17 DAT (3.05 $\mu\text{mol g}^{-1}$ FW - 3.24 $\mu\text{mol g}^{-1}$ FW) in comparison to WW plants (1.03 $\mu\text{mol g}^{-1}$ FW - 1.13 $\mu\text{mol g}^{-1}$ FW) (Tab. 1). Another effect of water deficit is cell membrane damage due to an increase in ROS (Shi *et al.*, 2015). In potatoes, the increment in MDA under water deficit conditions is considered an indicator of the loss of membrane stability caused by lipid peroxidation (Li *et al.*, 2017; Kammoun *et al.*, 2018). There was an increase in MDA content in the three cultivars under WD. The data suggests an increase in oxidative stress that alters cellular metabolism, reducing plant performance in these cultivars (Anithakumari *et al.*, 2012).

The proline content in plants subjected to WD also showed an increase at 8 DAT (1268 $\mu\text{g g}^{-1}$ FW) and 17 DAT (1868 $\mu\text{g g}^{-1}$ FW), reaching values 55 and 73 times higher than in WW plants (Tab. 1). Neither MDA nor proline content showed differences between cultivars. One of the first responses of the plant to water deficit is the synthesis of osmolytes in order to make an osmotic adjustment and absorb water (Shao *et al.*, 2009). We found that the three cultivars under WD showed an increase in the proline content compared with WW plants. The data suggested that the synthesis of proline in the three cultivars contributed

TABLE 1. Malondialdehyde (MDA) and proline content in three yellow diploid potato cultivars.

DAT	Treatment	Cultivars	MDA $\mu\text{mol g}^{-1}$ FW	Proline $\mu\text{g g}^{-1}$ FW
8	WW	Colombia	1.06 ± 0.05	23.5 ± 4.1
		Dorada	1.13 ± 0.15	22.3 ± 4.8
		Ocarina	1.11 ± 0.11	22.4 ± 2.1
		Means	1.10 C	22.8 C
	WD	Colombia	1.46 ± 0.05	1181.8 ± 121.6
		Dorada	1.32 ± 0.12	1366.5 ± 85.8
		Ocarina	1.35 ± 0.18	1256.1 ± 107.6
		Means	1.38 B	1268.1 B
17	WW	Colombia	1.03 ± 0.15	26.5 ± 2.3
		Dorada	1.09 ± 0.09	23.3 ± 1.7
		Ocarina	1.10 ± 0.27	26.5 ± 2.8
		Means	1.08 C	25.4 C
	WD	Colombia	3.09 ± 0.05	1830.1 ± 111.1
		Dorada	3.05 ± 0.06	1833.1 ± 84.7
		Ocarina	3.24 ± 0.14	1943.4 ± 101.7
		Means	3.12 A	1868.9 A

WW: well-watered, WD: water-deficit, DAT: days after treatment, Treatment, FW: fresh weight. Values represent means ± SD, n=6. Capital letters indicate the differences between treatments in time. Means denoted by the same letter do not significantly differ at $P < 0.05$ according to the Tukey test.

to the maintenance of water status during the water deficit period, preventing the RWC from being lower than 57%, even though the VSWC was low (9%). In potatoes, the presence of osmoregulation due to the increase in proline accumulation under water deficit is known (Teixeira and Pereira, 2007). The data also suggest that the increase in proline is one of the protection mechanisms of these cultivars in response to water deficit, and may partly explain the lack of damage observed in photosystem II (Mane *et al.*, 2008).

Growth parameters, dry-mass partitioning and yield

The plants under WD at 17 DAT showed a significant decrease in LA (1426 cm²) and in the total dry mass (TDM) (53 g) compared with WW plants (Figs. 5A-B). The plants with WD showed a higher fraction of D-M partitioning to the roots (35% - 40%) and a lower fraction of D-M partitioning to the leaves (17% - 22%) and the tubers (13% - 12%) in comparison to WW plants (Fig. 5C). The R/S ratio was significantly higher in plants subjected to WD (0.81 - 0.69) compared with WW plants (0.38 - 0.50) (Fig. 5D). The yield decreased significantly under WD for the cultivars Colombia (37%), Dorada (45%) and Ocarina (41%) compared to WW plants (Tab. 2). There were no differences between cultivars in the LA, DTM, D-M partitioning and yield (Fig. 5, Tab. 2). Water deficit in potatoes reduces

the growth and yield (Jefferies, 1993; Lahlou *et al.*, 2003; Kammoun *et al.*, 2018). The high reduction of VSWC affects the water intake generating a decrease in the RWC and a loss of turgor pressure that limits the cellular elongation process (Rolando *et al.*, 2015). Besides the high decrease of g_s observed after 8 DAT, the water deficit causes an increase in the resistance to the diffusion of CO₂ inside the leaf, reducing the production of photoassimilates required for growth (Dallas-Costa *et al.*, 1997).

Yield in potatoes is considered as an indicator of tolerance to water deficit (Tourneux *et al.*, 2003; Timothy *et al.*, 2018). Here, a decrease in yield in plants under WD in the three cultivars was observed (Tab. 2). This reduction in yield was attributed mainly to the high sensitivity of g_s to the water deficit that limits the production of photoassimilates and the growth. Other parameter associated with a decrease in yield under water deficit is the D-M partitioning (Jefferies, 1993). In the evaluated cultivars, water deficit caused an increase in the D-M partitioning to the roots, generating a higher R/S ratio. Although the increase in the R/S ratio is a defense mechanism to cope with water deficit, it is considered as an indicator of susceptibility to water deficit of these cultivars since the partitioning of photoassimilates into tubers decreased (Jefferies, 1993; Tourneux *et al.*, 2003).

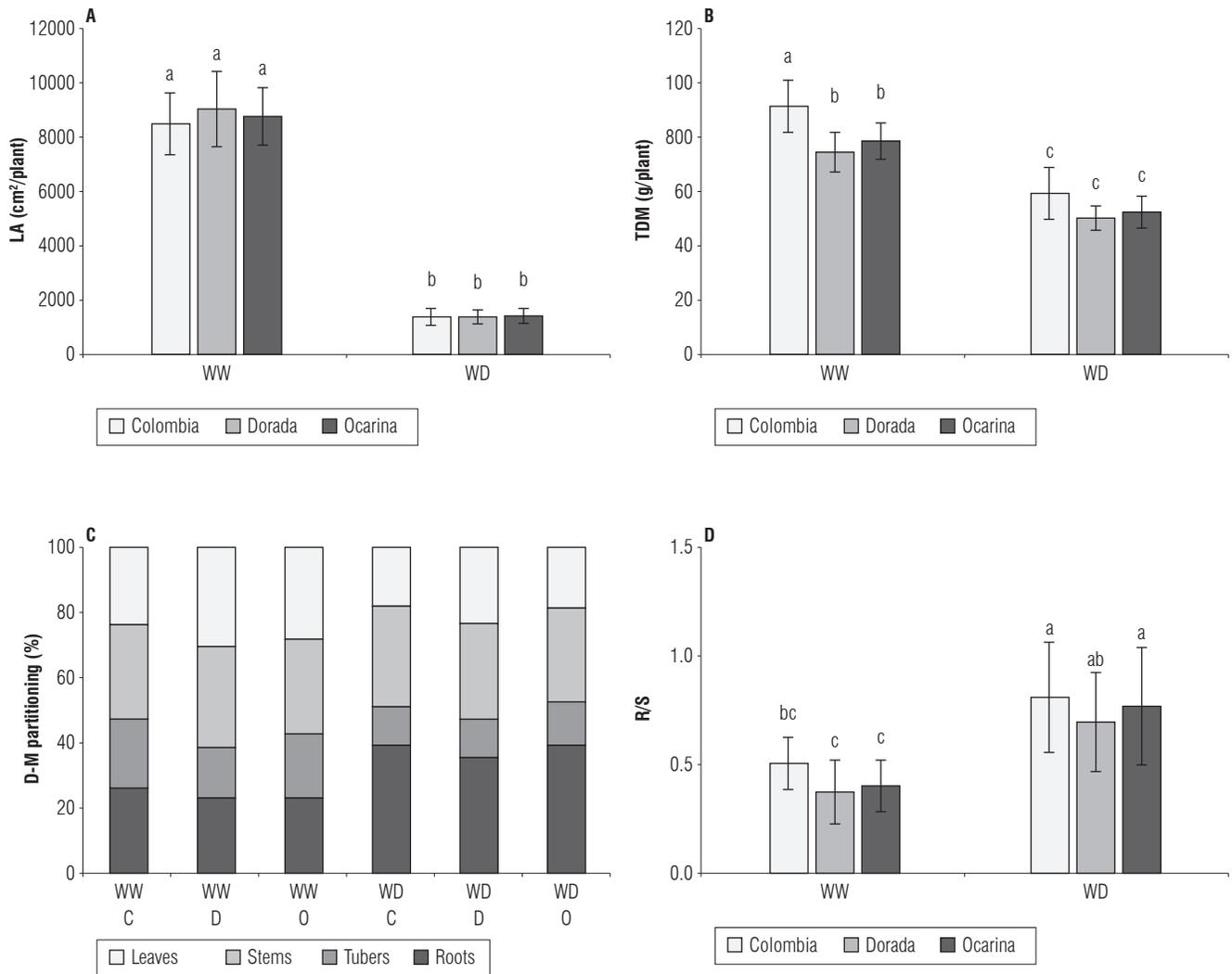


FIGURE 5. Changes in (A) leaf area (LA), (B) total dry mass (TDM), (C) dry-mass (D-M) partitioning and (D) root/shoot ratio (R/S) in three yellow diploid potato cultivars. WW: well-watered, WD: water-deficit, O: Ocarina, D: Dorada, C: Colombia. Values represent means \pm SE, $n=12$. Means denoted by the same letter do not significantly differ at $P<0.05$ according to the Tukey test.

TABLE 2. Yield and reduction in yield (RY) in three yellow diploid potato cultivars.

Cultivars	Yield (g/plant)		RY (%)
	WW	WD	
Colombia	600 \pm 59	378 \pm 42	37
Dorada	613 \pm 53	339 \pm 32	45
Ocarina	624 \pm 64	366 \pm 31	41

WW: well-watered, WD: water-deficit. Values represent means \pm SE, $n=12$. Means denoted by the same letter do not significantly differ at $P<0.05$ according to the Tukey test.

In conclusion, the drop in yield observed in the three cultivars may have also been related to the severity of the stress and to the defense mechanisms that the plants exhibited, such as the increase in proline. In this research, a high production of proline in all cultivars was observed in WD

conditions. Proline synthesis requires both carbon skeletons and nitrogen that are also needed for plant growth. The development of defense mechanisms may be associated with tolerance to water deficit; however, this association was not observed in these cultivars due to the reduction of g_s and a limited production of photoassimilates. Although the three cultivars evaluated in this research showed sensitivity to water deficit, according to the percentage of reduction in yield compared to WW plants, the most sensitive to the water deficit imposed was cv. Dorada and the least sensitive was cv. Colombia.

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Literature cited

- Anithakumari, A.M., K.N. Nataraja, R.G.F. Visser, and C.G. Van der Linden. 2012. Genetic dissection of drought tolerance and recovery potential by quantitative trait locus mapping of a diploid potato population. *Mol. Breed.* 30(3), 1413-1429. Doi: 10.1007/s11032-012-9728-5
- Banik, P., W. Zeng, H. Tai, B. Bizimungu, and K. Tanino. 2016. Effects of drought acclimation on drought stress resistance in potato (*Solanum tuberosum* L.) genotypes. *Environ. Exp. Bot.* 126, 76-89. Doi: 10.1016/j.envexpbot.2016.01.008
- Bates, L.S., R.P. Waldren, and I.D. Teare. 1973. Rapid determination of free proline for water-stress studies. *Plant and Soil* 39, 205-207. Doi: 10.1007/BF00018060
- Cabello, R., F. De Mendiburu, M. Bonierbale, P. Monneveux, W. Roca, and E. Chujoy. 2012. Large-Scale evaluation of potato improved varieties, genetic stocks and landraces for drought tolerance. *Amer. J. Pot. Res.* 89, 400-410. Doi: 10.1007/s12230-012-9260-5
- Coleman, W.K. 2008. Evaluation of wild *Solanum* species for drought resistance: 1. *Solanum gandarillasii* Cardenas. *Environ. Exp. Bot.* 62(3), 221-230. Doi: 10.1016/j.envexpbot.2007.08.007
- Dallas-Costa, L., G. Vedove-Delle, G. Gianquinto, R. Giovanardi, and A. Peressotti. 1997. Yield, water use efficiency and nitrogen uptake in potato: influence of drought stress. *Pot. Res.* 40, 19-34. Doi: 10.1007/BF02407559
- Devaux, A., P. Kromann, and O. Ortiz. 2014. Potatoes for sustainable global food security. *Pot. Res.* 57, 185-199. Doi: 10.1007/s11540-014-9265-1
- Ghislain, D., M. Andrade, F. Rodríguez, R.J. Hijmans, and D.M. Spooner. 2006. Genetic analysis of the cultivated potato *Solanum tuberosum* L. Phureja Group using RAPDs and nuclear SSRs. *Theor. Appl. Genet.* 113, 1515-1527. Doi: 10.1007/s00122-006-0399-7
- Hardigan, M.A., F.P.E. Laimbeer, L. Newton, E. Crisovan, J.P. Hamilton, B. Vaillancourt, K. Wiegert-Rininger, J.C. Wood, D.S. Douches, E.M. Farré, R.E. Villeux, and C.R. Buell. 2017. Genome diversity of tuber-bearing *Solanum* uncovers complex evolutionary history and targets of domestication in the cultivated potato. *Proc. Natl. Acad. Sci.* 114, 1-10. Doi: 10.1073/pnas.1714380114
- Hsiao, T.C. 1973. Plant responses to water stress. *Ann. Rev. Plant Physiol.* 24, 519-570. Doi: 10.1146/annurev.pp.24.060173.002511
- Jefferies, R.A. 1993. Cultivar responses to water stress in potato: effects of shoot and roots. *New Phytologist* 123, 491-498. Doi: 10.1111/j.1469-8137.1993.tb03761.x
- Jefferies, R.A. 1995. Physiology of crop response to drought. pp. 61-74. In: Haverkort, A.J. and D.K.L. Mackerron (eds.). *Potato ecology and modeling of crops under conditions limiting growth*. Proceedings of the Second International Potato Modeling Conference. 1994, May 17-19, Wageningen, Netherlands. Netherlands, Springer. Doi: 10.1007/978-94-011-0051-9_4
- Kammoun, M., O. Bouallous, M.F. Ksouri, and R. Gargouri-Bouزيد. 2018. Agro-physiological and growth response to reduced water supply of somatic hybrid potato plants (*Solanum tuberosum* L.) cultivated under greenhouse conditions. *Agr. Water. Manage.* 203, 9-19. Doi: 10.1016/j.agwat.2018.02.032
- Kesiime, V.E., G. Tusiime, I.N. Kashaija, R. Edema, P. Gibson, P. Namugga, and R. Kakuhenzire. 2016. Characterization and evaluation of potato genotypes (*Solanum tuberosum* L.) for tolerance to drought in Uganda. *Amer. J. Pot. Res.* 93, 543-551. Doi: 10.1007/s12230-016-9533-5
- Lahlou, O., S. Ouattar, and J.F. Ledent. 2003. The effect of drought and cultivar on growth parameters, yield and yield components of potato. *Agronomie* 23, 257-268. Doi: 10.1051/agro:2002089
- Li, J., Z. Cang, F. Jiao, X. Bai, D. Zhang, and R. Zhai. 2017. Influence of drought stress on photosynthetic characteristics and protective enzymes of potato at seedling stage. *J. Sau. Soc. Agr. Sci.* 16, 82-88. Doi: 10.1016/j.jssas.2015.03.001
- Lima, A.L.S., F.M. DaMatta, H.A. Pinheiro, M.R. Totola, and M.E. Loureiro. 2002. Photochemical responses and oxidative stress in two clones of *Coffea canephora* under water deficit conditions. *Environ. Exp. Bot.* 47(3), 239-247. Doi: 10.1016/S0098-8472(01)00130-7
- Littell, R.C., P.R. Henry, and C.B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. *J. Anim. Sci.* 76(4), 1216-1231. Doi: 10.2527/1998.7641216x
- Liu, F., C.R. Jensen, A. Shahanzari, M.N. Andersen, and S.E. Jacobsen. 2005. ABA regulated stomatal control and photosynthetic water use efficiency of potato (*Solanum tuberosum* L.) during progressive soil drying. *Plant Sci.* 168(3), 831-836. Doi: 10.1016/j.plantsci.2004.10.016
- Lu, C. and J. Zhang. 1998. Effects of water stress on photosynthesis, chlorophyll fluorescence and photoinhibition in wheat plants. *Aust. J. Plant Physiol.* 25(8), 883-892. Doi: 10.1071/PP98129
- Mahmud, A.A., M. Hassain, M.S. Kadian, and Md.A. Hoque. 2015. Physiological and biochemical changes in potato under water stress condition. *Ind. J. Plant Physiol.* 20(4), 297-303. Doi: 10.1007/s40502-015-0173-4
- Mane, S.P., C.V. Robinet, A. Ulanov, R. Schafleitner, L. Tincopa, A. Gaudin, and R. Grene. 2008. Molecular and physiological adaptation to prolonged drought stress in the leaves of two Andean potato genotypes. *Funct. Plant Biol.* 35(8), 669. Doi: 10.1071/FP07293
- Monneveux, P., D.A. Ramírez, and M.T. Pino. 2013. Drought tolerance in potato (*S. tuberosum* L.): can we learn from drought tolerance research in cereals? *Plant Sci.* 205-206, 76-86. Doi: 10.1016/j.plantsci.2013.01.011
- Peña, C., L.P. Restrepo-Sánchez, A. Kushalappa, L.E. Rodríguez-Molano, T. Mosquera, and C.E. Narváez-Cuenca. 2015. Nutritional contents of advanced breeding clones of *Solanum tuberosum* Group Phureja. *LWT - Food Sci. Technol.* 62, 76-82. Doi: 10.1016/j.lwt.2015.01.038
- Ramírez, D.A., W. Yactayo, R. Gutiérrez, V. Mares, F. De Mendiburu, A. Posadas, and R. Quiroz. 2014. Chlorophyll concentration

- in leaves is an indicator of potato tuber yield in water-shortage conditions. *Scientia Hort.* 168, 202-209. Doi: 10.1016/j.scienta.2014.01.036
- Rolando, J.L., D.A. Ramírez, W. Yactayo, P. Monneveux, and R. Quiroz. 2015. Leaf greenness as a drought tolerance related trait in potato (*Solanum tuberosum* L.). *Environ. Exp. Bot.* 110, 27-35. Doi: 10.1016/j.envexpbot.2014.09.006
- Rudack, K., S. Seddig, H. Sprenger, K. Köhl, R. Uptmoor, and F. Ordon. 2017. Drought stress-induced changes in starch yield and physiological traits in potato. *J. Agron. Crop Sci.* 203, 494-505. Doi: 10.1111/jac.12224
- SAS Institute. 2014. Base SAS 9.4 procedures guide: statistical procedures. SAS Institute Inc., Cary, USA.
- Shao, H.B., L.Y. Chu, C.A. Jaleel, P. Manivannan, R. Panneerselvam, and M.A. Shao. 2009. Understanding water deficit stress-induced changes in the basic metabolism of higher plants - biotechnologically and sustainably improving agriculture and the ecoenvironment in arid regions of the globe. *Crit. Rev. Biotechnol.* 29, 131-151. Doi: 10.1080/07388550902869792
- Shi, S., M. Fan, K. Iwama, F. Li, Z. Zhang, and L. Jia. 2015. Physiological basis of drought tolerance in potato grown under long-term water deficiency. *Int. J. Plant Prod.* 9(2), 305-320. Doi: 10.22069/IJPP.2015.2050
- Singh, D.K., P.W.G. Sale, C.K. Pallaghy, and V. Singh. 2000. Role of proline and leaf expansion rate in the recovery of stressed white clover leaves with increased phosphorus concentration. *New Phytol.* 146, 261-269. Doi: 10.1046/j.1469-8137.2000.00643.x
- Soltys-Kalina, D., J. Plich, D. Strzelczyk-Żyta, J. Śliwka, and W. Marezewski. 2016. The effect of drought stress on the leaf relative water content and tuber yield of a half-sib family of 'Katahdin'-derived potato cultivars. *Breed. Sci.* 66(2), 328-331. Doi: 10.1270/jsbbs.66.328
- Stiller, I., S. Dulai, M. Kondrák, R. Tarnai, L. Szabó, O. Toldi, and Z. Bánfalvi. 2008. Effects of drought on water content and photosynthetic parameters in potato plants expressing the trehalose-6-phosphate synthase gene of *Saccharomyces cerevisiae*. *Planta* 227(2), 299-308. Doi: 10.1007/s00425-007-0617-9
- Teixeira, J. and S. Pereira. 2007. High salinity and drought act on an organ-dependent manner on potato glutamine synthetase expression and accumulation. *Environ. Exp. Bot.* 60, 121-126. Doi: 10.1016/j.envexpbot.2006.09.003
- Timothy, S.G., M.A. Taylor, I.C. Dodd, and P.J. White. 2018. Climate change and consequences for potato production: a review of tolerance to emerging abiotic stress. *Potato Res.* 60, 239-269. Doi: 10.1007/s11540-018-9366-3
- Tourneux, C., A. Devaux, M.R. Camacho, P. Mamani, and J.F. Ledent. 2003. Effect of water shortage on six potato genotypes in the highlands of Bolivia (II): water relations, physiological parameters. *Agronomie* 23(2), 169-179. Doi: 10.1051/agro:2002080
- Van der Mescht, A., J.A. De Ronde, and F.T. Rossouw. 1999. Chlorophyll fluorescence and chlorophyll content as a measure of drought tolerance in potato. *S. Afr. J. Sci.* 95(9), 407-412.
- Wang, Y., M. Ding, X. Gu, J. Wang, Y. Pang, L. Gao, and T. Xia. 2013. Analysis of interfering substances in the measurement of malondialdehyde content in plant leaves. *Amer. J. Biochem. Biotechnol.* 9(3), 235-242. Doi: 10.3844/ajbbsp.2013.235.242