Drought stress affects physiological parameters but not tuber yield in three Andean potato (*Solanum tuberosum* L.) cultivars

El estrés por sequía afecta los parámetros fisiológicos, pero no el rendimiento de los tubérculos en tres cultivares andinos de papa (*Solanum tuberosum* L.)

Loyla Rodríguez-Pérez[1], Carlos Eduardo Ñústez L.[2], and Liz Patricia Moreno F.[2]

ABSTRACT

This study evaluated the effect of water deficit on the physiological response and yield of three Andean potato cultivars. Leaf water potential (Ψ_w), soil matric potential (SMP), photosynthesis (A), stomatal conductance (g_s), transpiration (E), intrinsic water use efficiency (WUEi), leaf temperature (LT), chlorophyll fluorescence parameters, chlorophyll (Chl), carotenoids (Car), electrolyte leakage (EL), growth and yield (Y). Parameters were determined in well-watered (WW) and drought-stressed (DS) plants. The three DS cultivars showed a decrease in leaf Ψ_w from the first day of treatment and reached values close to -2.00 MPa 4 days after treatment (DAT) for the Diacol Capiro (DC) cultivar, 5 DAT for the Pastusa Suprema (PS) cultivar and 6 DAT for the Esmeralda (Es) cultivar. The values of A, g_s and E in the DS cultivars decreased from the first DAT. The LT reached the highest values when g_s showed the lowest values for the three DS cultivars. WUEi was higher in Es under DS plants but lower in DC under DS. The PSII photochemical efficiency (F_v/F_m) showed values greater than 0.8 for all DS cultivars under DS, suggesting the absence of non-stomatal limitations for A. The Chl content increased in the Es cultivar under DS from 5 to 7 DAT compared to WW plants. Carotenoids (Ca) contents, the Car/Chl ratio, and EL increased in the three DS cultivars. There were no differences in yield and growth parameters between WW and DS cultivars. These results suggest that the three cultivars developed mechanisms to overcome the stress. One of these mechanisms could be the early synthesis of Car, which may maintain photosystem II function under water stress.

Key words: carotenoid/chlorophyll ratio, electrolyte leakage, photoprotection, water deficit tolerance, leaf temperature.

RESUMEN

Este estudio evaluó los efectos del déficit hídrico sobre la respuesta fisiológica y el rendimiento de tres cultivares andinos de papa. Potencial hídrico foliar (Ψ_w), potencial mátrico del suelo (SMP), fotosíntesis (A), conductancia estomática (g_s), transpiración (E), la eficiencia en el uso del agua intrínseca (WUE_i), la temperatura de la hoja (LT), los parámetros de la fluorescencia de la clorofila (Chl), carotenoides (Car), pérdida de electrolitos (EL), parámetros de crecimiento y rendimiento (Y) en plantas bien irrigadas (WW) y sometidas a estrés por sequía (DS). Los tres cultivares DS mostraron una disminución de Ψw de la hoja desde el primer día de tratamiento y alcanzaron valores cercanos a -2,00 MPa a los 4 días después del tratamiento (DAT) para el cultivar Diacol Capiro (DC), a 5 DAT para el cultivar Pastusa Suprema (PS) y a los 6 DAT para el cultivar Esmeralda (Es). Los valores de A, g_s y E en los cultivares bajo DS disminuyeron desde el primer DAT. La LT alcanzó los valores más altos cuando g_s mostró los valores más bajos para los tres cultivares DS. WUE_i fue más alta en las plantas de Es bajo DS, pero menor en DC bajo DS. La eficiencia fotoquímica PSII (F_v/F_m) presentó valores superiores a 0,8 para todos los cultivares bajo DS, lo que sugiere la ausencia de limitaciones no estomáticas para la A. El contenido de Chl aumentó en el cultivar Es bajo DS entre el 5 y 7 DAT en comparación con el de plantas WW. El contenido de Car, el radio Car/Chl, and EL incrementaron en los tres cultivares bajo DS. No hubo diferencias en los parámetros de rendimiento y crecimiento entre los cultivares WW y los sometidos a DS. Estos resultados sugieren que los tres cultivares desarrollaron mecanismos para superar el estrés. Uno de estos mecanismos podría ser la síntesis temprana de Car, que puede mantener la función del fotosistema II bajo estrés hídrico.

Palabras clave: radio carotenoides/clorofila, pérdida de electrolitos, fotoprotección, tolerancia al déficit hídrico, temperatura foliar.

Abbreviations: A, photosynthesis; ABA, abscisic acid; ABG, above-ground mass; Car, carotenoids; Chl, chlorophyll; DAP, days after planting; DAT, days after treatment; DAP, days after planting; DC, Diacol Capiro; DS, drought-stressed; E, transpiration; EL, electrolyte leakage; Es, Esmeralda; ETR, electron transport rate; F_v/F_m, maximum quantum yield of PSII photochemistry; FW, fresh weight; g_s, stomatal conductance; LA, leaf area; LT, leaf temperature; NPQ, non-photochemical quenching; PS, Pastusa Suprema; qP, photochemical quenching; RDM, root dry mass; R/S, root/shoot ratio; ROS, reactive oxygen species; SMP, soil matric potential; VPD, vapor pressure deficit; Ψ_w, water potential; WW, well-watered; WUEi, intrinsic water use efficiency; Y, tuber yield; Y(II), effective photochemical quantum yield of photosystem II.

Received for publication: 24 June, 2017. Accepted for publication: 20 July, 2017

Doi: 10.15446/agron.colomb.v35n2.65901

[1] Biology Department, Pontificia Universidad Javeriana, Bogota (Colombia). loyla.rodriguez@javeriana.edu.co

[2] Agronomy Department, Faculty of Agricultural Sciences, Universidad Nacional de Colombia, Bogota (Colombia).

Introduction

The climate change has generated an increase in the environmental temperature and this has resulted in modifications of the water regimes and the precipitation patterns worldwide (Hitz and Smith, 2004). This situation has made drought stress one of the principal limiting abiotic stresses for agricultural production (Zoebl, 2006). Water stress reduces plant growth through a reduction in photosynthesis, mainly caused by a stomatal limitation (Liu *et al*., 2005; Parent *et al*., 2014). A decrease in the plant water potential (Ψ_w) caused by water deficit, increases the levels of abscisic acid (ABA) in the plants, which induces a stomatal closure as an early response in the defense against stress (Lim *et al*., 2015). Decreases in stomatal conductance (g_s) reduce water loss through transpiration, but it also decrease carbon dioxide uptake, reducing the production of photoassimilates and, therefore, plant growth (Lahlou *et al*., 2003; Tourneux *et al*., 2003a). This decrease in the photosynthetic rate under water deficit conditions has been reported in plants such as potato (*Solamun tuberosum* L.) (Moorby *et al*., 1975 Schapendonk *et al*., 1989; Ierna and Mauromicale, 2006; Liu *et al*., 2006; Ramírez *et al*., 2016). With severe water stress, in addition to the stomatal limitation of photosynthesis, the presence of non-stomatal limitations related to damage to the photosynthetic apparatus has been reported (Sanda *et al*., 2011; Noctor *et al*., 2014). These limitations can be measured with different variables such as the maximum photochemical efficiency of photosystem II (F_v/F_m) (Xu *et al*., 2010). The photosynthetic rate in many cases is also affected by the chlorophyll (Chl) content (Obidiegwu *et al*., 2015).

Stomatal and non-stomatal limitations cause an imbalance between the two phases of photosynthesis and an increase in the production of reactive oxygen species (ROS) (Sanchez-Rodríguez *et al*., 2010; Farhad *et al*., 2011). ROS can alter the normal functioning of plants due to the damage caused to lipids, proteins, nucleic acids, photosynthetic pigments and enzymes (Kar, 2011). The principal damage caused by ROS during water stress is lipid peroxidation, which decreases the stability of cellular membranes and increases their permeability, thereby modifying cellular metabolism (Yordanov *et al*., 2003). In order to overcome oxidative stress, plants have developed enzymatic and non-enzymatic antioxidants (Cruz de Carvalho, 2008). Among the non-enzymatic antioxidants, carotenoids (Car) are particularly important because they decrease ROS contents and thereby protect the photosynthetic machinery (Cazzonelli, 2011). Car may also act as a defensive response by reducing thermal effects of drought stress (Farooq *et al*., 2009).

The decrease in photosynthesis resulting from drought stress reduces growth, affecting parameters such as foliar area, total dry mass, and distribution of photoassimilates within the plants (Chaves *et al*., 2002; Lahlou *et al*., 2003). This negative effect on growth has been reported for plants including potato (Lahlou *et al*., 2003; Ierna and Mauromicale, 2006) and sorghum (*Sorghum bicolor* L.) (Zegada-Lizarasu and Monti, 2013). However, differences have been observed in the effects caused by drought stress related to morphological, physiological, biochemical, and molecular changes among species and cultivars (Tourneux *et al*., 2003a; Liu *et al*., 2005; Liu *et al*., 2006; Graca *et al*., 2010). Likewise, under drought stress, the tolerance of some genotypes has been associated with rapid recuperation after rehydration (Hu *et al*., 2010; Zegada-Lizarazu and Monti, 2013).

Solanum tuberosum L. is a species originated in the Andean region of South America, cultivated worldwide and very important for food security in Colombia (Devaux *et al*., 2014). Potato plants are very sensitive to drought stress compared to other species (Porter *et al*., 1999). It has been reported that drought stress considerably decreases yield, making water availability a limiting factor in the production of this crop (Lahlou *et al*., 2003; Tourneux *et al*., 2003a; Obidiegwu *et al*., 2015). In South American countries, potato is cultivated in highly mountainous areas with few or no available water, suggesting that this crop is often subjected to drought stress conditions.

It has been shown that the magnitude of drought stress in potato production depends on the plant phenology, duration, and severity of the stress (Jefferies, 1995). Potato plants are susceptible to soil matric potentials (SMP) lower than -25 kPa and SMP values near -45 kPa, causing water stress in this crop (Wang *et al*., 2007). Thus far, there is not information available about the physiological effects of short periods of water deficit on Colombian potato cultivars. Potato plants could respond to drought stress very early and develop strategies to cope with it (Farhad *et al*., 2011; Monneveux *et al*., 2013). Therefore, physiological behavior of the plants under this stress could provide information on their capacity to tolerate drought stress.

This study aimed to evaluate leaf Ψ_w, gas exchange behavior, leaf temperature (LT), chlorophyll fluorescence parameters, photosynthetic pigment content, membrane permeability, growth parameters, and yield in three potato (*S. tuberosum* L.) cultivars that are commercially used in Colombia under a short period of water stress and recovery, aiming to expand knowledge on this topic of interest.

Materials and methods

Plant material and experimental design

This study was carried out in 2013 in the greenhouses of the Facultad de Ciencias Agrarias of the Universidad Nacional de Colombia, located at 2,600 m a.s.l. A seed tuber with a weight of 50 (±10) g of the potato tubers of Diacol Capiro (DC), Pastusa Suprema (PS), and Esmeralda (Es) cultivars were planted in black plastic bags that contained 5 kg of silty loam soil with pH 6.3. The plant materials were arranged in plots. Each plot consisted of 12 plants distributed in an area of 4.80 m^2, 0.80 m, and 0.40 m apart. Considering the results of the soil analysis, each plant was fertilized with 20 g of Abocol® 10-30-10 (N-P-K) and 5 g of Agrimins®, applied at planting. Foliar applications of Omex Bio 8®, which provide macroelements and chelated microelements were applied at doses of 1 cm^3 L^{-1} 60 d after planting (DAP). Since planting time, plants were irrigated with 800 mL of water every third day; the SMP was maintained at 0.00 MPa to guarantee plant emergence and growth. During the experiment, the maximum and minimum temperatures and relative humidity were registered daily with a weather station (MCR200 µMetos®, Pessl Instruments, Weiz, Austria) (Fig. 1a). The mean vapor pressure deficit (VPD) (Fig. 1b) also was calculated.

The treatments were distributed in a split-plot arrangement under a randomized complete block design with three replications; the cultivars were placed in the main plots, and the water states were in the sub-plots – drought-stressed (DS) or well-watered (WW) plants. In the DS treatment, irrigation was suspended at 74 DAP, at the beginning of tuberization stage in the three cultivars; several studies report that when the water deficit is applied in this phenological stage generates a reduction in crop yield (Liu *et al.*, 2005; Liu *et al.*, 2006; Ahmadi *et al.*, 2010). Drought stress was applied for 4 to 6 d, until the SMP reached values below -45 kPa, which is considered to cause water stress in potato crops (Wang *et al.*, 2007; Aksić *et al.*, 2014). The stress level also was defined according to the permanent wilting point reported for potato crops, in which the leaf Ψ_w reaches a less negative value than -1.60 MPa (Vos and Haverkort, 2007; Rolando *et al.*, 2015). After this period of stress, the plants were irrigated for recovery.

Leaf water potential and soil matric potential

The leaf Ψ_w was measured from 12:00 h to13:00 h in 3 or 4 completely expanded leaves from top to bottom of six plants per treatment. Ψ_w was measured with a Scholander pressure chamber (PMS Model 615, Fresno, CA, USA). SMP was measured at 6:00 h with a tensiometer (Tensiorun®, Unidrench, Bogota, Colombia).

Gas exchange, water use efficiency, and leaf temperature

For the three cultivars, the photosynthetic rate (A), g_s, and transpiration rate (E) were registered using a photosynthesis measurement system (LCpro-SD, Portable BioScientific, Hoddesdon, UK). The measurements were taken on 3 or 4 completely expanded leaves of six plants per treatment from 9:00 h to 11:30 h with a CO_2 concentration of 400 µL L^{-1} and a photosynthetic photon flux density of 900 µmol m^{-2} s^{-1}. The intrinsic water use efficiency (WUEi) was calculated with A and g_s data (A/g_s). The leaf temperature (LT) was measured using a manual infrared thermometer (HD550, Extech®, Waltham, Ma, USA). Five measurements were taken per leaf of six plants per treatment.

Chlorophyll fluorescence parameters

In order to determine the photoinhibition of photosynthesis, F_v/F_m was measured in dark-adapted leaves for 45 min using a MINI-PAM modulated fluorometer (Walz®, Effeltrich, Germany). The measurements were carried out on the same leaves that were used to measure A. The Chl molecules were excited for 0.80 s with 1,500 µmol m^{-2} s^{-1} of actinic light. The parameters photosynthetic electron transport rate (ETR), effective quantum efficiency of PSII (Y[II]), photochemical quenching (qP), and non-photochemical quenching (NPQ) were registered.

Photosynthetic pigments

Leaf pigments were extracted in accordance with Lichtenthaler (1987). The upper-third portion (equal to three or four expanded leaves) of six plants per treatment was homogenized in 80% acetone. The absorbance was determined at an optical density of 663 nm and 647 nm for Chl and 470 nm for Car. The Chl and Car contents were determined, and a carotenoid/chlorophyll ratio (Car/Chl) was calculated using these values.

Membrane permeability

Permeability of cellular membranes was measured by the amount of electrolyte leakage (EL) (Valentovic *et al.*, 2006). Ten 2.5-mm-diameter leaf discs were placed in Falcon tubes with 2 mL of deionized water at 25°C. The electrical conductivity (EC) was determined with a conductometer (HI 9835 Hanna® - ICT, SL, Bogota, Colombia) at 24 h. The EC values were expressed as a percentage with respect to the highest value using the equation PE = (EC1 * EC2) * 100; where PE = percentage of lost electrolytes, EC1 = EC at 24 h, and EC2 = EC after heating up 80°C.

Growth and yield parameters

At 123 DAP, the stem length was measured from the base to the apical meristem; the leaf area (LA) was measured with a LI-3000C portable leaf area meter (LI-COR Inc., Lincoln, NE, USA). The plants were individually separated into above-ground mass (ABG), roots (R) and tubers, which were subsequently dried in a 70 °C oven at constant weight. The root/shoot ratio (R/S) was determined using dry weight data. At 164 DAP, the tuber yield (Y) was determined as tuber fresh weight per plant using 10 plants per treatment at the time of harvest for the three varieties.

Data analysis

The data of each parameter were analyzed with analysis of variance (ANOVA) and presented as the mean value for each treatment and cultivar. A Tukey test ($P \leq 0.01$) was performed to evaluate the treatment effects. Each treatment value is the average of six replicates. Statistical analyses were performed using the R software program (R Development Core Team, 2010).

Temperature, relative humidity, and vapor pressure deficit

During the experiment period, the minimum air temperature was between 9.7°C and 12.8°C, and the maximum temperature was between 31.3°C and 38.5°C; the mean temperature was between 18.6°C and 20.6°C. The mean relative air humidity oscillated between 69.4% and 89.3%; the mean minimum and maximum relative humidity values were 44.2±10.20% and 98.8±1.6%, respectively (Fig. 1A). During the evaluation period, the VPD varied between 0.30 kPa and 0.50 kPa (Fig. 1B).

Results

Leaf water potential and soil matric potential

Leaf Ψ_w was significantly different ($P \leq 0.01$) between the WW and the DS cultivars from 1 to 6 d after treatment (DAT) and between the DS cultivars from 3 to 6 DAT (Fig. 2A). From 2 DAT, a significant decrease in the leaf Ψ_w was recorded in the DS cultivars. A leaf Ψ_w close to -2.00 MPa was observed at 4 DAT for DC (-1.99 MPa), at 5 DAT for PS (-2.15 MPa), and at 6 DAT for Es (-2.00 MPa). One day after recovery, the DC and PS cultivars showed a significantly lower leaf Ψ_w (-0.46 MPa and -0.51 MPa, respectively) compared to the WW cultivars (-0.28 MPa and -0.23 MPa, respectively), while Es had leaf Ψ_w values equal to those of the WW cultivars (-0.26 MPa) (Fig. 2a). The leaf Ψ_w was significantly different ($P < 0.01$) between the WW and DS cultivars, from 1 to 4 DAT; however, there weres no significant differences between WW cultivars at any day. The SMP was reduced from 1 DAT and reached the most negative values in the DC (-54 kPa), PS (-56 kPa), and Es (-61 kPa) cultivars at 4, 5, and 6 d, respectively (Fig. 2B). However, after 1 d of recovery, the SMP of DS treatments reached the value of WW treatments (-0.00 kPa). Analyzed together, these results indicate the plants of the three cultivars experimented water deficit at different times, which decreased the leaf Ψ_w to values associated with water stress in plants.

Gas exchange, water use efficiency, and leaf temperature

The photosynthetic rate was statistically significant ($P \leq 0.01$) between the WW and DS cultivars from 1 to 6 DAT. The physiological parameters g_s and E were statistically significant ($P \leq 0.01$) between the WW and DS cultivars from 2 to 6 DAT. Among the DS cultivars, there was a statistically significant difference in A from 1 to 6 DAT; in g_s between 2 and 6 DAT; and in E at 2 DAT, 5 DAT, and 6 DAT (Fig. 3A-C). A, g_s, and E were significantly different ($P \leq 0.01$) between the WW and DS cultivars from 1 DAT (A) and from 2 DAT (g_s and E) until the leaf Ψ_w of the plants reached their lowest values (Fig. 3A, C). The highest

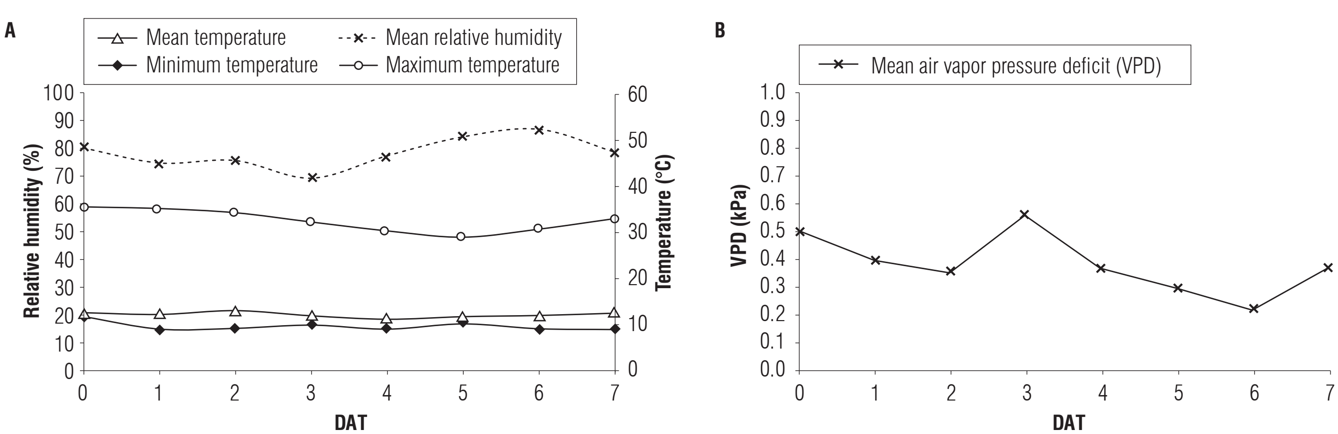

FIGURE 1A. Mean temperature, maximum and minimum temperatures (°C) and mean relative humidity (%); B. Average vapor pressure deficit (VPD) (kPa) in the greenhouse during the days of the period in which the potato plants were subjected to water deficit. DAT: days after treatment.

A values in the DS cultivars were recorded in the Es cultivar from 1 to 4 DAT (4.49-22.56 μmol CO_2 m^{-2} s^{-1}) (Fig. 3A). The g_s only presented significant differences between the DS cultivars at 2 DAT, and the Es cultivar showed the highest value (0.09 mmol H_2O m^{-2} s^{-1}). The lowest values for A (0.56-1.17 μmol CO_2 m^{-2} s^{-1}), g_s (0.01 mmol H_2O m^{-2} s^{-1}), and E (0.40–0.53 mmol H_2O m^{-2} s^{-1}) were recorded in all cultivars when they reached the lowest Ψ_w. One day after recovery, only the PS cultivar showed significant differences in A with the WW treatment (24.21 μmol CO_2 m^{-2} s^{-1}), while for g_s and E all cultivars reached the values of the WW treatments.

LT showed the significantly higher values in the DS cultivars at 2 DAT for plats of Es (18.01°C) and at 3 DAT for all cultivars (Fig. 3D). The maximum values for the DC (21.48°C) and PS (23.19°C) cultivars were recorded when the lowest leaf Ψ_w values were reached, while in the Es cultivar the maximum value was observed at 5 DAT (22.29°C). One day after recovery, the LT for the three cultivars reached the values of the WW cultivars (9.53-14.02°C). These results indicate that in the three cultivars under DS, there was a gradual stomatal closure which was higher when the plants reached a leaf Ψ_w close to -2.00 MPa, and this decrease in stomatal conductance reduced the CO_2 input for photosynthesis as well.

WUEi in the DS cultivars was significantly higher at 3 DAT for PS (181.37 μmol CO_2 mol^{-1} H_2O) and Es (218.09 μmol CO_2 mol^{-1} H_2O) and at 4 DAT for Es (261.52 μmol CO_2 mol^{-1} H_2O) compared with the plants of WW cultivars (Fig. 4). These results showed that the PS and Es cultivars subjected to water deficit have a higher WUEi, which could be related to drought tolerance.

Chlorophyll fluorescence parameters

F_v/F_m has been widely used to detect stress-induced alterations in the photosynthetic apparatus (Zegada-Lizarasu and Monti, 2013). In this study, we found that F_v/F_m recorded values greater than 0.80 for the DS and WW cultivars (Fig. 5A). Y(II) and ETR presented significant differences between the WW and DS cultivars at 4 DAT and 5 DAT (Fig. 5B, C). The DC and PS cultivars presented the lowest values for Y(II) and ETR when they reached the lowest leaf Ψ_w, while the Es cultivar presented the lowest value for both parameters 1 d before reaching the lowest of leaf Ψ_w. One day after recovery, the three DS cultivars did not show significant differences in Y(II) and ETR compared to the WW cultivars. qP exhibited a significant decrease in Es (0.37) and PS (0.37) cultivars at 5 DAT; during the other days (from day 1 to 4), qP did not show differences between the WW and DS cultivars (Fig. 5D). NPQ was significantly higher in DS cultivars at 4 DAT and 5 DAT, with the highest value in PS (0.44) at 5 DAT (Fig. 5E). One day after recovery, the variables F_v/F_m, Y(II), and ETR reached the values of those of WW plants in the three cultivars, while for NPQ the cultivars did not reach the values of the WW plants. These results indicate the absence of any major impairment of the photosynthetic apparatus during leaf water deficit.

Photosynthetic pigments

Chl for Es cultivar under DS was significantly higher from 5 to 7 DAT compared to WW plants (Fig. 6A). For the other cultivars, there were no significant differences in Chl between the plants under DS and WW. The Car presented a significantly higher value in DS cultivars from 2 DAT for DC and Es and from 4 to 6 DAT for PS compared to WW plants. From 4 DAT, Es presented the highest values for

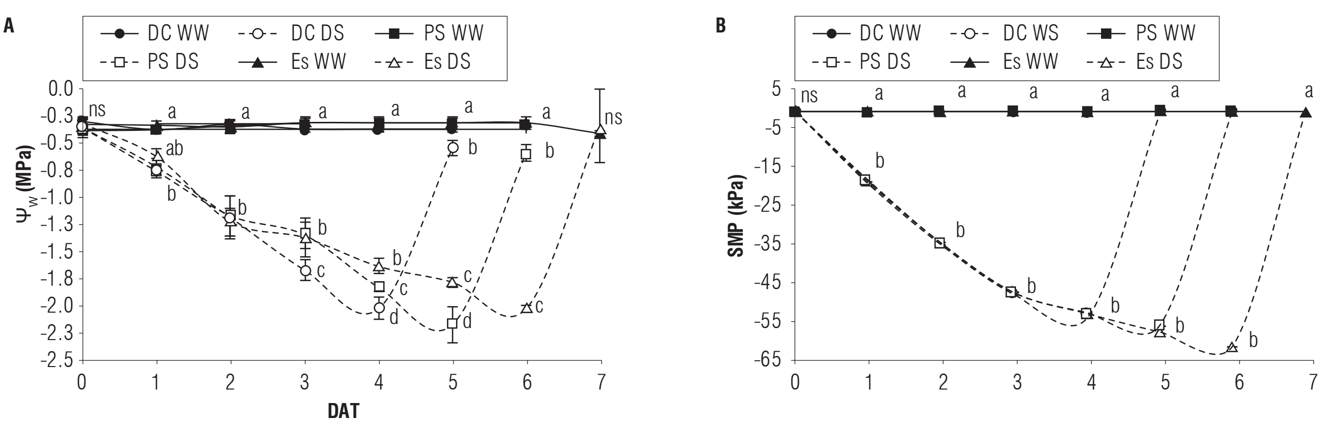

FIGURE 2. Effects of drought stress and subsequent recovery in three potato cultivars (DC: Diacol Capiro, PS: Pastusa Suprema, Es: Esmeralda). WW: well-watered, DS: drought-stressed, DAT: days after treatment. A. Leaf water potential (Ψ_w); B. Soil matric potential (SMP). The data shown are the averages of six replicates, with the standard deviations indicated by the vertical bars. Means denoted by the same letter do not significantly differ at $P \leq 0.01$ according to the Tukey test.

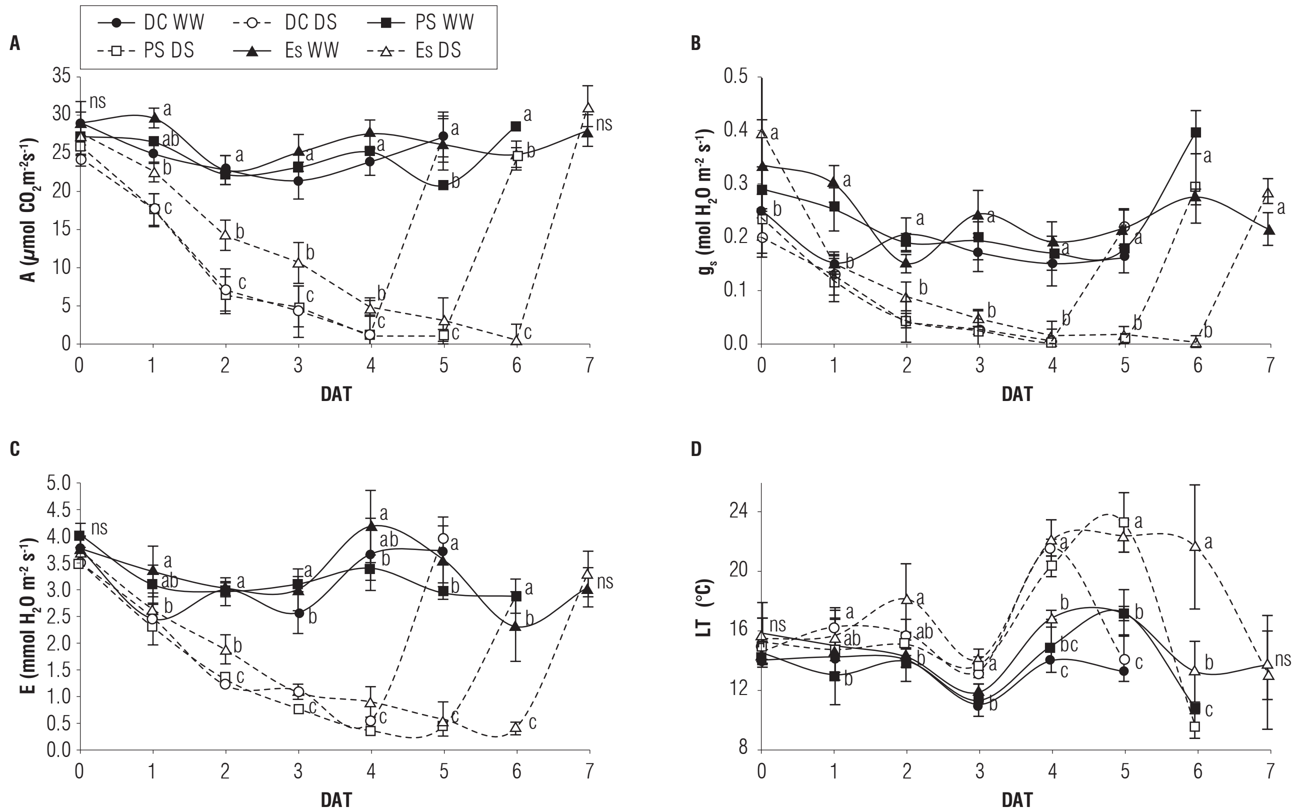

FIGURE 3. Effects of water deficit and subsequent recovery in three cultivars of potato (DC: Diacol Capiro, PS: Pastusa Suprema, Es: Esmeralda). WW: well-watered, DS: drought-stressed, DAT: days after treatment. A. Photosynthesis (A); B. Stomatal conductance (g_s); C. Transpiration (E); D. Leaf temperature (LT). The data shown are the means of six replicates, with the standard deviations indicated by the vertical bars. Means denoted by the same letter do not significantly differ at $P\leq0.01$ according to the Tukey test.

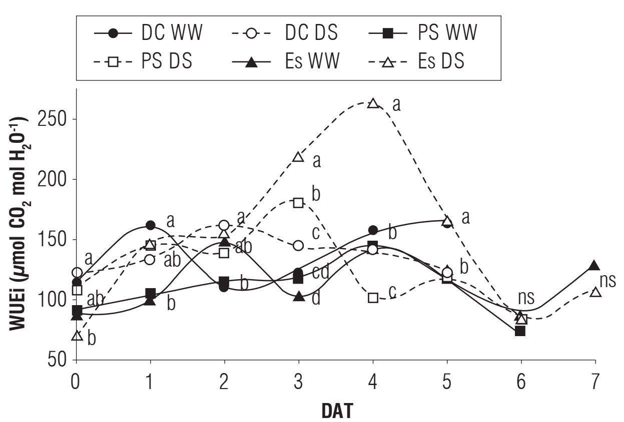

FIGURE 4. Effects of water deficit and subsequent recovery on the intrinsic water use efficiency (WUEi) in three cultivars of potato (DC: Diacol Capiro, PS: Pastusa Suprema, Es: Esmeralda). WW: well-watered, DS: drought-stressed, DAT: days after treatment. The data shown are the means of six replicates, with the standard deviations indicated by the vertical bars. Means denoted by the same letter do not significantly differ at $P\leq0.01$ according to the Tukey test.

Car content (0.36-0.40 mg g^{-1} fresh weight [FW]), while DC presented the lowest values at 5 DAT (0.27 mg g^{-1} FW) (Fig. 6B). The Car/Chl ratio was higher for DS plants (Fig. 6C); the ratios increased from 2 DAT for DC and Es and from 4 DAT for PS. These results suggest that the three varieties exhibit a strong photoprotective system against water stress.

Membrane permeability

The DS cultivar plants presented a significant increase in EL from 2 DAT (Fig. 7). The Es cultivar presented the highest values at 5 DAT and 6 DAT (62.36 % and 55.29%, respectively). One day after recovery, none of the DS cultivars reached the EL values of WW plants (Fig. 7). These data suggest that the three DS cultivars exhibit an increase in membrane permeability, although this increase was higher in the Es cultivar.

Growth and yield parameters

ABG was significantly greater in WW plants across all cultivars (Fig. 8A), while for the RDM there were no significant differences between the DS and the WW cultivars (Fig. 8B). Regarding the R/S, the DS Es cultivar presented a significant increase (1.5) due to a lower ABG compared to the analogous WW cultivar (1.3) (Fig. 8C). The LA did not show differences between the DS and WW cultivars

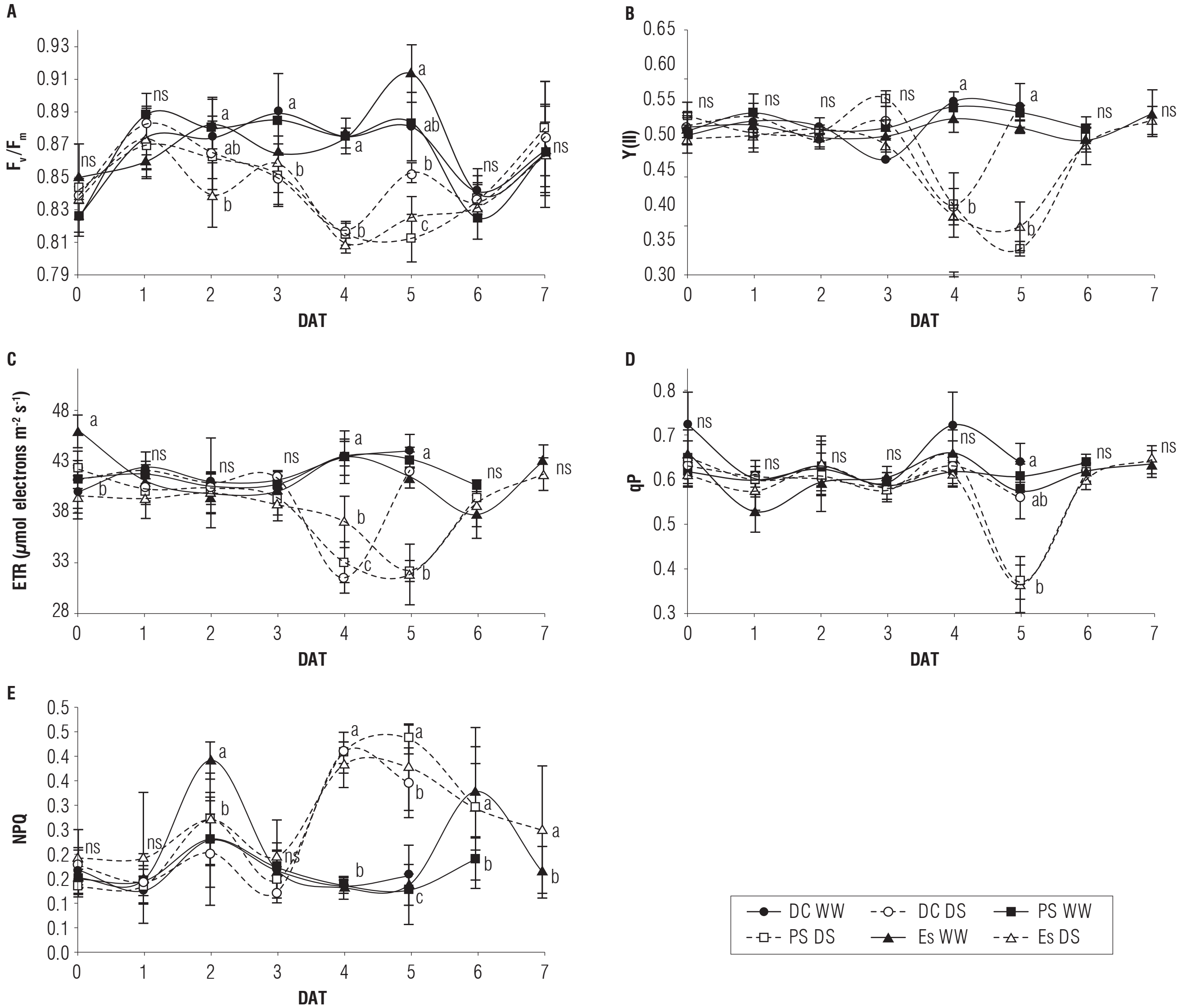

FIGURE 5. Effects of water deficit and subsequent recovery on the variables derived from chlorophyll fluorescence in three cultivars of potato (DC: Diacol Capiro, PS: Pastusa Suprema, Es: Esmeralda). WW: well-watered, DS: drought-stressed, DAT: days after treatment. A. Maximum quantum yield of photosystem II (F_v/F_m); B. Effective quantum efficiency of PSII (Y[II]); C. Photosynthetic electron transport rate (ETR); D. Photochemical quenching (qP); E. Non-photochemical (NPQ). The data shown are the averages of six replicates, with the standard deviations indicated by the vertical bars. Means denoted by the same letter do not significantly differ at $P \leq 0.01$ according to the Tukey test.

(Fig. 8D). There were no differences in Y between the DS and WW cultivars (Fig. 8E). Taken together, these data suggest that the three cultivars were tolerant to the drought stress.

Discussion

Drought stress is one of the most common stresses limiting crop productivity (Chaves *et al*., 2003). Cultivars can differ in their sensitivity to water deficit, being classified as tolerant or sensitive (Cabello *et al*., 2013; Obidiegwu *et al*., 2015). A few studies have been conducted on the physiological characterization of potato cultivars that are currently cultivated in the Andean region, under either irrigated or water deficit conditions (Tourneux *et al*., 2003a, b; Ramírez *et al*., 2014; Rolando *et al*., 2015; Ramírez *et al*., 2016). Neither is information available about the physiological effects of short periods of water deficit on potato. In his study we evaluated physiological parameters, and yield in three potato (*S. tuberosum* L.) cultivars commercially used in Colombia under a short period of water stress and recovery. One measurement related con the tolerance of the plants to water stress is leaf Ψ_w, because it indicates the water state and, therefore, the ability of the plant to take

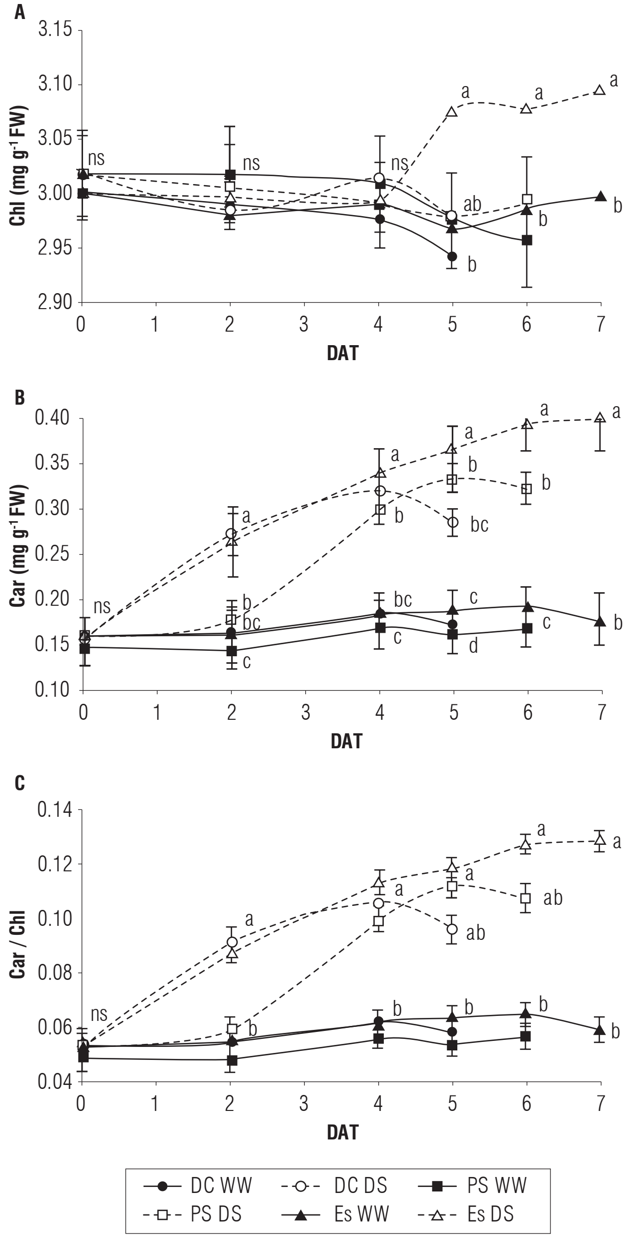

FIGURE 6. Effects of water deficit and subsequent recovery in three cultivars of potato (DC: Diacol Capiro, PS: Pastusa Suprema, Es: Esmeralda). WW: well-watered, DS: drought-stressed, FW: fresh weight, DAT: days after treatment. A. Chlorophyll (Chl); B. Carotenoids (Car); C. Carotenoids/chlorophyll ratio (Car/Chl). The data shown are the means of six replicates, with the standard deviations indicated by the vertical bars. Means denoted by the same letter do not significantly differ at $P \leq 0.01$ according to the Tukey test.

up water or conserve the amount it has (Hsiao, 1973). In this study, it was recorded that the three cultivars, DC, PS, and Es, presented a leaf Ψ_w close to -2.00 MPa in a short period of time. The Es cultivar took more time to reach this Ψ_w (6 d), followed by PS (5 d) and DC (4 d). The Es cultivar was the only one to equal the Ψ_w of the WW plants after 1 day of recovery (Fig. 2a). The values of leaf Ψ_w for

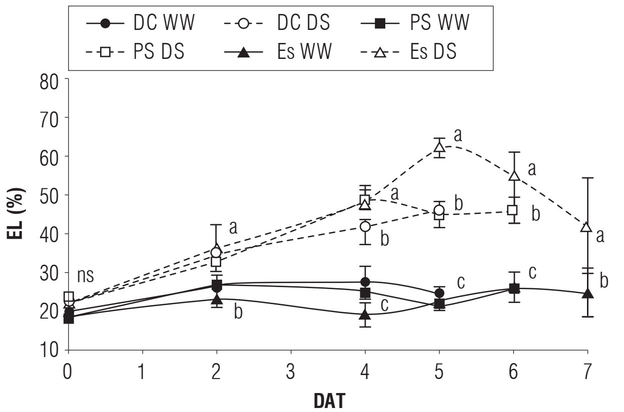

FIGURE 7. Effects of water deficit and subsequent recovery on electrolyte leakage (EL) in three cultivars of potato (DC: Diacol Capiro, PS: Pastusa Suprema, Es: Esmeralda). WW: well-watered, DS: drought-stressed, DAT: days after treatment. The data shown are the means of six replicates, with the standard deviations indicated by the vertical bars. Means denoted by the same letter do not significantly differ at $P \leq 0.01$ according to the Tukey test.

the three cultivars were below those reported for potato crops at the permanent wilting point (-1.60 MPa) (Vos and Haverkort, 2007; Rolando *et al.*, 2015). In many plants, the degree of decrease in leaf Ψ_w under drought stress conditions is related to the regulation of water loss through a reduction in g_s (Liu *et al.*, 2006; Osakabe *et al.*, 2014). There was a decrease in g_s in the three DS cultivars from 2 DAT below 0.05 mol H_2O m^{-2} s^{-1} (Fig. 3B), wich suggests a regulation of water loss through a decrease in stomatal conductance, as has been observed in other plants, such as wheat (*Triticum aestivum* L.) (Siddique *et al.*, 2000), cotton (*Gossypium hirsutum* L.) (Pallas *et al.*, 1967), and sugarcane (*Saccharum* spp.) (Graca *et al.*, 2010). The g_s values we recorded are below the values that have been associated with metabolic impairment affecting photochemical and biochemical components of photosynthesis (Flexas *et al.*, 2004, 2006). LT is usually negatively correlated with g_s and E (Pallas *et al.*, 1967; Graca *et al.*, 2010). An increase in LT in the three DS cultivars was recorded when the values of g_s and E were lowest (Fig. 3D). Differences in water stress tolerance between cultivars may be due in part to differential sensitivities of the photosynthetic process to water deficit (Chaves *et al.*, 2002; Tourneux *et al.*, 2003b; Ierna and Mauromicale, 2006). A and E were greatly influenced by stomatal behavior, decreasing in the DS cultivars (Fig. 3A, C), as has been described previously (Tourneux *et al.*, 2003b; Liu *et al.*, 2005; Ierna and Mauromicale, 2006). The fast recovery of the photosynthetic rate to values of WW plants (DC and Es cultivars) or very close to those values (PS cultivar) suggests that stomatal closure is the earliest response to water deficit and the dominant limitation of photosynthesis. The Es cultivar showed the lowest decrease

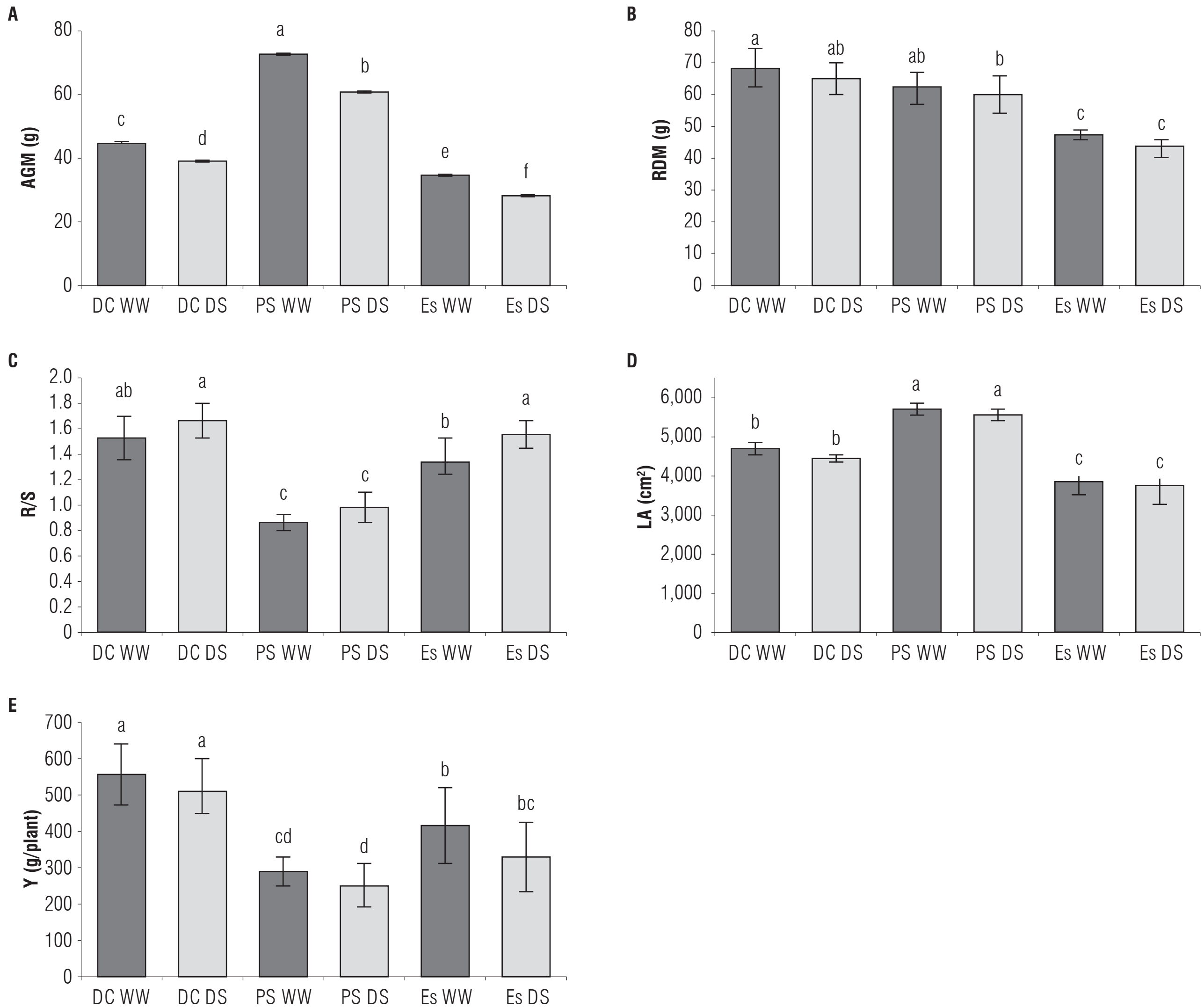

FIGURE 8. Effects of water deficit and subsequent recovery in three cultivars of potato (DC: Diacol Capiro, PS: Pastusa Suprema, Es: Esmeralda). WW: well-watered, DS: drought-stressed. A. Above-ground mass (ABG); B. Root dry mass (RDM); C. Root/shoot ratio (R/S); D. Leaf area (LA); E. Tuber yield (Y). The data shown are the averages of six replicates, with the standard deviations indicated by the vertical bars. Means denoted by the same letter do not significantly differ at $P \leq 0.01$ according to the Tukey test.

in A under drought stress, wich suggests a lower sensitivity of its photosynthetic process to water deficit (Fig. 3A). A fast, full recovery of photosynthesis after re-watering has been reported in potato after irrigation deficit (Van Loon, 1981; Vos and Groenwold, 1989; Ramírez *et al.*, 2016). It also was found that some drought stress-tolerant cultivars showed an increase in WUEi (Gago *et al.*, 2014). The higher values of WUEi in DS Es (Fig. 4) are due to the lower reduction in photosynthesis that was recorded in this cultivar and could be related to tolerance (Liu *et al.*, 2006; Ahmadi *et al.*, 2010). The F_v/F_m values (0.81-0.91) observed in all cultivars (Fig. 5A) suggest the absence of any major impairment of the photosynthetic apparatus in the plants under DS and indicate resistance of the photosynthetic apparatus, as has been reported in previous studies (Moorby *et al.*, 1975; Schapendonk *et al.*, 1989; Tourneux *et al.*, 2003b). However, the decrease in ETR, Y(II), and qP and the increase in NPQ in all DS cultivars (Fig. 5B-E) suggest a possible mild alteration in the phase of light-dependent reactions, which did not have a significant effect on the photosynthetic rate. Consequently, the main limitation was due to stomatal closure and not to an impairment of the photosynthetic apparatus (Ierna and Mauricale, 2006; Ahmadi *et al.*, 2010).

It was observed that the DS Es cultivar showed an increase of Chl (Fig. 6A). Drought stress can reduce the final size of leaves of potato, and this effect varies among cultivars (Jefferies, 1993). The increase in Chl content found in Es could be associated with the decrease in leaf growth and water turgor loss, as has been described in potato (Teixeira and Pereira, 2007; Ramírez *et al*., 2014; Rolando *et al*., 2015). The DC and PS cultivars under drought stress did not exhibit differences in Chl compared to WW plants. These data could suggest that in these cultivars leaf growth and leaf turgor were less affected by water deficit, likely as result of the osmotic adjustment (Sánchez-Rodríguez *et al*., 2010; Farhad *et al*., 2011).

Carotenoids pigments are essential in photosynthesis. At the same time, they have a protective role in their ability to reduce the thermal effects of drought stress, and these pigments are also non-enzymatic antioxidants (Cruz de Carvalho, 2008; Farooq *et al*., 2009). An increase in Car content has been reported in many plants under stress conditions (Efeoglu *et al*., 2009; Ghobadi *et al*., 2013). Here, we found that all cultivars showed an increase in the Car content, which was highest in the Es cultivar under DS (Fig. 6B). The Car/Chl ratio in all cultivars under drought stress was also higher than that in WW plants. The Car content and Car/Chl ratio are correlated with the capacity of light protecting mechanisms (Boardman, 1977). These results suggest that the three cultivars have a strong photoprotective system against water stress, as has been described in other plants (Efeoglu *et al*., 2009; Ghobadi *et al*., 2013).

Another important parameter that is negatively affected during drought stress is the permeability of membranes, which is widely used to evaluate drought tolerance (Blum and Ebercon, 1981; Premachandra *et al*., 1991). For plants such as maize (*Zea mays* L.) (Quan *et al*., 2004) and wheat (Bajji *et al*., 2002), an increase in membrane permeability under drought stress has been reported, measured as EL. Here, an increase in EL from the second day of drought stress was recorded, which was greater when plants exhibited a more negative leaf Ψ_w (Fig. 7). This increase could be due to the peroxidation of lipids caused by an increase in ROS, as has been reported for plants such as tomato (*Lycopersicon esculentum* Mill.) (Sanchez-Rodríguez *et al*., 2010), cotton (Deeba *et al*., 2012), and potato (Farhad *et al*., 2011). It has been found that EL under stress conditions is mainly due to K^+ and anion efflux (Bajji *et al*., 2002; Demidchik *et al*., 2014). Also, it has been hypothesized that the decrease in cytosolic K^+ may be involved in metabolic adjustment, which is essential for adaptation to any stress factor (Demidchik *et al*., 2014).

Finally, drought stress can alter carbon allocation to different tissues (Chaves *et al*., 2002; Shao *et al*., 2008). This alteration in carbon partitioning could be related to mechanisms developed by the plant to cope with the stress, such as the increase in root size or the increase in the synthesis of different compounds involved in osmotic adjustment or in protection (Schafleitner *et al*., 2007; Obidiegwu *et al*., 2015). Some potato genotypes have the capacity to increase root size under drought stress, which might lead to a reduction in the canopy size and also to an increase in R/S (Steckel and Gray, 1979). We recorded that there was a decrease in the ABG in PS and Es cultivars under drought stress but not in the LA (Fig. 8A). We also found an increase in R/S in the Es cultivar under water deficit but not in RDM (Fig. 8c). These results show that the patterns of biomass partitioning among plants under DS and WW were not very different. In potato, severe water deficit can negatively affect Y if the stress occurs just before or during tuber initiation (Mackerran and Jefferies, 1986; Monneveux *et al*., 2013). Although the SMP reached values near -45 kPa for the three cultivars evaluated, which has been reported to cause water stress in this crop (Wang *et al*., 2007), Y was not reduced. The capacity to maintain Y under drought stress showed by the three cultivars suggests that these cultivars were tolerant to the drought stress (Obidiegwu *et al*., 2015).

Conclusion

It has been shown that the magnitude of drought stress on potato production depends on the phenological timing, duration, and severity of the stress (Jefferies, 1995; Monneveux *et al*., 2013). In this study the three cultivars showed physiological responses similar to those reported for potato plants subjected to longer periods of drought stress. The plants presented values of g_s that have been associated with impairment of the photosynthetic apparatus (Flexas *et al*., 2004, 2006; Ramírez *et al*., 2016). However, we have not find a major impairment of the photosynthetic apparatus, and the plants showed a fast recovery of photosynthetic rate after 1 day of rehydration. We also observed in the plants of the three cultivars that under drought stress conditions there was not a reduction of Y. These results suggest that the three cultivars developed very early mechanisms to overcome the stress. One of these mechanisms could be the early synthesis of Car that we recorded in these cultivars. This could be an indicator of the high capacity of potato plants to maintain a functional photosystem II under drought stress with a photoprotective system. Although the exposure time to water stress was short, the plants showed indicators of stress and developed very early mechanisms associated with protection. Other experiments are needed to identify whether other mechanisms are present that might explain the response showed by these cultivars under water deficit, such as proline or antioxidant synthesis, both of which have already been described in potato (Schafleitner *et al*., 2007; Farhad *et al*., 2011). It is also necessary to explore the response of these cultivars to a longer period of water deficit to evaluate if they maintain the tolerance traits that they showed in this study.

Acknowledgments

We would like to thank Darwin Moreno for his technical assistance and Danny Sanjuanelo for the statistical analysis. This work was supported by the Ciencias Agrarias graduate program of the Facultad de Ciencias Agrarias of the Universidad Nacional de Colombia; and the Vicerrectoría de Investigación of the Pontificia Universidad Javeriana, Bogota.

Literature cited

Aksić, M., S. Gudzic, N. Deletic, N. Gudzic, S. Stojkovic, and J. Knezevic. 2014. Tuber yield and evapotranspiration of potato depending on soil matric potential. Bulgarian J. Agric. Sci. 20(1), 122-126.

Ahmadi, S.H., M.N. Andersen, F. Plauborg, R.T. Poulsen, C.R. Jensen, A.L. Sepaskhah, and S. Hansen. 2010. Effects of irrigation strategies and soils on field-grown potatoes: gas exchange and xylem [ABA]. Agr. Water Manag. 97, 1486-1494. Doi: 10.1016/j.agwat.2010.05.002

Bajji, M., J.M. Kinet, and S. Lutts. 2002. The use of the electrolyte leakage method for assessing cell membrane stability as a water stress tolerance test in durum wheat. Plant Growth Regul. 36(1), 61-70. Doi: 10.1023/A:1014732714549

Blum, A. and A. Ebercon. 1981. Cell membrane stability as a measure of drought and heat tolerance in wheat. Crop Sci. 21, 43-47. Doi: 10.2135/cropsci1981.0011183X002100010013x

Boardman, N.K. 1977. Comparative photosynthesis of sun and shade plants. Ann. Rev. Plant Physiol. 28, 355-377. Doi: 10.1146/annurev.pp.28.060177.002035

Cabello, R., P. Monneveux, F. De Mendiburu, and M. Bonierbale. 2013. Comparison of yield-based drought tolerance indices in improved cultivars, genetic stocks, and landraces of potato (*Solanum tuberosum* L.). Euphytica 193, 147-156. Doi: 10.1007/s10681-013-0887-1

Cazzonelli, C. 2011. Carotenoids in nature: insights from plants and beyond. Funct. Plant Biol. 38, 833-847. Doi: 10.1071/FP11192

Chaves, M.M., J.P. Maroco, and J.S. Pereira. 2003. Understanding plant responses to drought: from genes to the whole plant. Funct. Plant Biol. 30, 239-264. Doi: 10.1071/FP02076

Chaves, M.M., J.S. Pereira, J. Maroco, M.L. Rodrigues, C.P.P. Ricardo, M.L. Osorio, I. Carvalho, T. Faria, and C. Pinheiro. 2002. How plants cope with water stress in the field. Photosynthesis and growth. Ann. Bot. 89, 907-916. Doi: 10.1093/aob/mcf105

Cruz de Carvalho, M.H. 2008. Drought stress and reactive oxygen species: production, scavenging and signaling. Plant Signal. Behav. 3, 156-165. Doi: 10.4161/psb.3.3.553

Deeba, F., A.K. Pandey, S. Ranjan, A. Mishra, R. Singh, Y.K. Sharma, P.A. Shirke, and V. Pandey. 2012. Physiological and proteomic responses of cotton (*Gossypium herbaceum* L.) to drought stress. Plant Physiol. Bioch. 53, 6-18. Doi: 10.1016/j.plaphy.2012.01.002

Demidchik, V., D. Straltsova, S.S. Medvedev, G.A. Pozhvanov, A. Sokolik, and Y. Vladimir. 2014. Stress-induced electrolyte leakage: the role of K^+-permeable channels and involvement in programmed cell death and metabolic adjustment. J. Exp. Bot. 65(5), 1259-1270. Doi: 10.1093/jxb/eru004

Devaux, A., P. Kromann, and O. Ortiz. 2014. Potatoes for sustainable global food security. Potato Res. 57(3), 185-199. Doi: 10.1007/s11540-014-9265-1

Efeoglu, B., Y. Ekmekci, and N. Cicek. 2009. Physiological responses of three maize cultivars to drought stress and recovery. S. Afr. J. Bot. 75(1), 34-42. Doi: 10.1016/j.sajb.2008.06.005

Farhad, M.S., A.M. Babak, Z.M. Reza, R.S.M. Hassana, and T. Afshin. 2011. Response of proline, soluble sugars, photosynthetic pigments, and antioxidant enzymes in potato (*Solanum tuberosum* L.) to different irrigation regimes in greenhouse condition. Aust. J. Crop. Sci. 5(1), 55-60.

Farooq, M., A. Wahid, N. Kobayashi, D. Fujita, and S.M. Basra. 2009. Plant drought stress: effects, mechanisms, and management. Agron. Sustain. Dev. 29, 185-212. Doi: 10.1051/agro:2008021

Flexas, J., J. Bota, J. Cifre, J. Mariano Escalona, J. Galmés, J. Gulías, E.K. Lefi, S. Martínez-Canellas, M. Teresa Moreno, and M. Ribas-Carbó. 2004. Understanding down-regulation of photosynthesis under water stress: future prospects and searching for physiological tools for irrigation management. Ann. Appl. Biol. 144, 273-283. Doi: 10.1111/j.1744-7348.2004.tb00343.x

Flexas, J., J. Bota, J. Galmés, H. Medrano, and M. Ribas-Carbó. 2006. Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. Physiol. Plant. 127, 343-352. Doi: 10.1111/j.1399-3054.2006.00621.x

Gago, J., C. Douthe, I. Florez-Sarasa, J.M. Escalona, J. Galmes, A.R. Fernie, J. Flexas, and H. Medrano. 2014. Opportunities for improving leaf water use efficiency under climate change conditions. Plant Sci. 226, 108-119. Doi: 10.1016/j.plantsci.2014.04.007

Ghobadi, M., S. Taherabadi, M.E. Ghobadi, G.R. Mohammadi, and S. Jalali-Honarmand. 2013. Antioxidant capacity. Photosynthetic characteristics and water relations of sunflower (*Helianthus annuus* L.) cultivars in response to drought stress. Ind. Crop. Prod. 50, 29-38. Doi: 10.1016/j.indcrop.2013.07.009

Graca, J.P., F.A. Rodrigues, J.R.B. Farias, M.C.N. Oliveira, C.B. Hoffmann-Campo, and S.M. Zingaretti. 2010. Physiological parameters in sugarcane cultivars submitted to water deficit. Braz. J. Plant. Physiol. 22, 189-197. Doi: 10.1590/S1677-04202010000300006

Hitz, S. and J. Smith. 2004. Estimating global impacts from climate change. Global. Environ. Chang. 14, 201-218. Doi: 10.1016/j.gloenvcha.2004.04.010

Hu, L., Z. Wang, and B. Huang. 2010. Diffusion limitations and metabolic factors associated with inhibition and recovery of photosynthesis from drought stress in a C_3

perennial grass species. Physiol. Plant. 139, 93-106. Doi: 10.1111/j.1399-3054.2010.01350.x

Hsiao, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24(1), 519-570. Doi: 10.3389/fpls.2014.00086

Ierna, A. and G. Mauromicale. 2006. Physiological and growth response to moderate water deficit of off-season potatoes in a Mediterranean environment. Agr. Water Manag. 82, 193-209. Doi: 10.1016/j.agwat.2005.05.005

Jefferies, R.A. 1993. Responses of potato genotypes to drought. I. Expansion of individual leaves and osmotic adjustment. Ann. Appl. Biol. 122, 93-104. Doi: 10.1111/j.1744-7348.1993.tb04017.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. Wageningen Academic Publishers, The Netherlands. Doi: 10.1007/978-94-011-0051-9

Kar, R.K. 2011. Plant responses to water stress: role of reactive oxygen species. Plant Signal. Behav. 6, 1741-1745. Doi: 10.4161/psb.6.11.17729

Lahlou, O., S. Ouattar, and J.F. Ledent. 2003. The effect of drought and cultivar on growth parameters, yield, and yield components of potato. Agron. 23, 257-268. Doi: 10.1051/agro:2002089

Lichtenthaler, H.K. 1987. Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. Methods Enzymol. 148, 350-382. Doi: 10.1016/0076-6879(87)48036-1

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, 831-836. Doi: 10.1016/j.plantsci.2004.10.016

Liu, F., A. Shahnazari, M.N. Andersen, S.E. Jacobsen, and C.R. Jensen. 2006. Effects of deficit irrigation (DI) and partial root drying (PRD) on gas exchange, biomass partitioning, and water use efficiency in potato. Sci. Hortic. 109, 113-117. Doi: 10.1016/j.scienta.2006.04.004

Lim, C.M., W. Baek, J. Jung, J.H. Kim, and S.H. Lee. 2015. Function of ABA in stomatal defense against biotic and drought stresses. Int. J. Mol. Sci. 16, 15251-15270. Doi: 10.3390/ijms160715251

Mackerran, D.K.L. and R.A. Jefferies. 1986. The influence of early soil moisture stress on tuber numbers in potato. Potato Res. 299-312. Doi: 10.1007/BF02359959

Monneveux, P., A.D. 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

Moorby, J., R. Munns, and J. Walcott. 1975. Effect of water deficit on photosynthesis and tuber metabolism in potatoes. Aust. J. Plant Physiol. 2, 323-333. Doi: 10.1071/PP9750323

Noctor, G., A. Mhamdi, and C.H. Foyer. 2014. The roles of reactive oxygen metabolism in drought: not so cut and dried. Plant Physiol. 164, 1636-1648. Doi: 10.1104/pp.113.233478

Obidiegwu, J.E., G.J. Bryan, H.G. Jones, and A. Prashar. 2015. Coping with drought: stress and adaptive responses in potato and perspectives for improvement. Front. Plant Sci. 6(542), 1-23. Doi: 10.3389/fpls.2015.00542

Osakabe, Y., K. Osakabe, K. Shinozaki, and L.S.P. Tran. 2014. Response of plants to water stress. Front. Plant Sci. 5, 1-8. Doi: 10.3389/fpls.2014.00086

Pallas, J.E., B.E. Michel, and D.G. Harris. 1967. Photosynthesis, transpiration, leaf temperature, and stomatal activity of cotton plants under varying water potentials. Plant Physiol. 42, 76-88. Doi: 10.1104/pp.42.1.76

Parent, B., C. Hachez, E. Redondo, T. Simonneau, F. Chaumont, and F. Tardieu. 2014. Drought and abscisic acid effects on aquaporin content translate into changes in hydraulic conductivity and leaf growth rate: a trans-scale approach. Plant Physiol. 149, 2000-2012. Doi: 10.1104/pp.108.130682

Porter, G.A., G.B. Opena, W.B. Bradbury, J.C. McBurnie, and J.A. Sisson. 1999. Soil management and supplemental irrigation effects on potato: I. Soil properties, tuber yield, and quality. Agron. J. 91, 416-425. Doi: 10.2134/agronj1999.00021962009100030010x

Premachandra, G.S., H. Saneoka, M. Kanaya, and S. Ogata. 1991. Cell membrane stability and leaf surface wax content as affected by increasing water deficits in maize. J. Exp. Bot. 42, 167-171. Doi: 10.1093/jxb/42.2.167

Quan, R., M. Shang, H. Zhang, Y. Zhao, and J. Zhang. 2004. Engineering of enhanced glycinebetaine synthesis improves drought tolerance in maize. Plant Biotechnol. J. 2(6), 477-486. Doi: 10.1111/j.1467-7652.2004.00093.x

Ramírez, D.A., W. Yactayo, R. Gutiérrez, V. Mares, F. De Mendiburu, A. Posadas, and R. Quiroz, R., 2014. Chlorophyll concentration in leaves is an indicator of potato tuber yield in water-shortage conditions. Sci. Hortic. 168, 202-209. Doi: 10.1016/j.scienta.2014.01.036

Ramírez, D.A., W. Yactayo, R.L. Rens, J.J. Rolando, S. Palacios, F. De Mendiburu, V. Mares, C. Barreda, H. Loayza, P. Monneveux, L. Zotarelli, A. Khan, and R. Quiroz. 2016. Defining biological thresholds associated to plant water status for monitoring water restriction effects: stomatal conductance and photosynthesis recovery as key indicators in potato. Agr. Water Manag. 177, 369-378. Doi: 10.1016/j.agwat.2016.08.028

R Development Core Team. 2010. A language and environment for statistical computing. R foundation for statistical computing. Viena, Austria.

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

Sánchez-Rodríguez, E., M.M. Rubio-Wilhelmi, L.M. Cervilla, B. Blasco, J.J. Rios, M.E. Rosales, L. Romero, and J.M. Ruiz. 2010. Genotypic differences in some physiological parameters symptomatic for oxidative stress under moderate drought in tomato plants. Plant Sci. 178, 30-40. Doi: 10.1016/j.plantsci.2009.10.001

Sanda, S., K. Yoshida, M. Kuwano, T. Kawamura, Y. Nakajima, K. Akashi, and Y. Yokota. 2011. Responses of the photosynthetic electron transport system to excess light energy caused by water deficit in wild watermelon. Physiol. Plant. 142, 247-264. Doi: 10.1111/j.1399-3054.2011.01473.x

Schafleitner, R., A. Gaudin, R.O. Gutierrez Rosales, C.A. Alvarado Aliaga, and M. Bonierbale. 2007. Proline accumulation and real-time PCR expression analysis of genes encoding enzymes of proline metabolism in relation to drought tolerance in

Andean potato. Acta Physiol. Plant. 29, 19-26. Doi: 10.1007/s11738-006-0003-4

Schapendonk, A.H.C.M., J.J. Spitters, and P.J. Groot. 1989. Effects of water stress on photosynthesis and chlorophyll fluorescence of five potato cultivars. Potato Res. 32, 17-32. Doi: 10.1007/BF02365814

Shao, H.B., L.Y. Chu., C.A. Jaleel, and C.X. Zhao. 2008. Water-deficit stress-induced anatomical changes in higher plants. C. R. Biol. 331, 215-225. Doi: 10.1016/j.crvi.2008.01.002

Siddique, M.R.B., A. Hamid, and M.S. Islam. 2000. Drought stress effects on water relations of wheat. Bot. Bull. Acad. Sin. 41, 35-39.

Steckel, J.R.A., and D. Gray. 1979. Drought tolerance in potatoes. J. Agric. Sci. 92, 375-381. Doi: 10.1016/j.plantsci.2013.01.011

Teixeira, J., and S. Pereira. 2007. High salinity and drought act in 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

Tourneux, C., A. Devaux, M. Camacho, P. Mamani, and J.F. Ledent. 2003a. Effects of water shortage on six potato genotypes in the highlands of Bolivia I: morphological parameters, growth, and yield. Agron. 23, 169-179. Doi: 10.1051/agro:2002079

Tourneux, C., A. Devaux, M. Camacho, P. Mamani, and J.F. Ledent. 2003b. Effect of water shortage on six potato genotypes in the highlands of Bolivia II: water relations, physiological parameters. Agron. 23(2), 181-190. Doi: 10.1051/agro:2002080

Valentovic, P., M. Luxová, L. Kolarovic, and O. Gasparíková. 2006. Effect of osmotic stress on compatible solutes content, membrane stability, and water relations in two maize cultivars. Plant Soil Environ. 52, 186-191.

Van Loon, C.D. 1981. The effect of water stress on potato growth, development and yield. Am. Potato J. 58, 51-69. Doi: 10.1007/BF02855380

Vos, J. and J. Groenwold. 1989. Characteristics of photosynthesis and conductance of potato canopies and the effects of cultivar and transient drought. Field Crops Res. 20(237), 237-250. Doi: 10.1016/0378-4290(89)90068-3

Vos, J. and A.J. Haverkort. 2007. Water availability and potato crop performance. pp. 333-351. In: Vreugdenhil, D., J. Bradshaw, C. Gebhardt, F. Govers, D.K.L. Mackerron, M.A. Taylor and H.A. Ross (eds.). Potato biology and biotechnology: Advances and perspectives. Elsevier, Italy. Doi: 10.1016/B978-044451018-1/50058-0

Wang, F.X., Y. Kang, S.P. Liu, and X.Y. Hou. 2007. Effects of soil matric potential on potato growth under drip irrigation in the North China Plain. Agr. Water Manag. 88(1), 34-42. Doi: 10.1016/j.agwat.2006.08.006

Xu, Z., G. Zhou, and H. Shimizu. 2010. Plant responses to drought and rewatering. Plant Signal. Behav. 5, 649-654. Doi: 10.4161/psb.5.6.11398

Yordanov, I., V. Velikova, and T. Tsonev. 2003. Plant responses to drought and stress tolerance. Bulg. J. Plant Physiol. Special Issue, 187-206. Doi: 10.1023/A:1007201411474

Zegada-Lizarazu, W. and A. Monti. 2013. Photosynthetic response of sweet sorghum to drought and re-watering at different growth stages. Physiol. Plant. 149, 56-66. Doi: 10.1111/ppl.12016

Zoebl, D. 2006. Is water productivity a useful concept in agricultural water management? Agr. Water Manag. 84, 265-273. Doi: 10.1016/j.agwat.2006.03.002