Root and leaf abscisic acid concentration impact on gas exchange in tomato (*Lycopersicon esculentum* Mill.) plants subjected to partial root-zone drying

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Abstract

Partial root-zone drying (PRD) is a deficit irrigation technique with great potential for water saving. A split-root experiment was conducted on tomato in controlled environment in order to test the response of two long-time storage cultivars to PRD. *Ponderosa* tomato, a cultivar with yellow fruits, was compared to *Giallo tondo di Auletta*, a local cultivar from southern Campania (Italy). Plants were subjected to three irrigation treatments: plants receiving an amount of water equivalent to 100% of plant evapotranspiration (V100); plants in which 50% of the amount of water given to V100 was supplied (V50); and plants where one root compartment was irrigated at 50% of water requirements and the other compartment was allowed to dry, and thereafter every side was rewetted alternatively (PRD). The highest levels of leaf abscisic acid (ABA) [on average equal to 104 ng g^{-1} fresh weight FW)] were measured in PRD and V50, at 70 days after transplantation. Root ABA concentration in both PRD and V50 reached mean values of 149 ng g^{-1} FW. There were differences for the irrigation regime in root ABA biosynthesis and accumulation under partial root-zone drying and conventional deficit irrigation (V50). Assimilation rate, stomatal conductance and intercellular CO_2 concentration decreased in relation to the irrigation regime by 22, 36 and 12%, respectively, in PRD, V50 and V100 at 50 days after transplantation. *Ponderosa* variety accumulated 20% more dry matter than *Auletta* and significant differences were observed in leaf area. In both PRD and V50 of the two varieties, it was possible to save on average 46% of water. Our results indicate that there is still space to optimise the PRD strategy, to further improve the cumulative physiological effects of the root-sourced signaling system.

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Key words: *Lycopersicon esculentum*; Partial root drying (PRD); Conventional deficit irrigation; Water use efficiency; ABA concentration.

Acknowledgements: the authors wish to thank Prof. Candido V. for invaluable scientific assistance and Mr. Giuseppe Mercurio for invaluable technical assistance.

Received for publication: 21 April 2016.
Revision received: 3 October 2016.
Accepted for publication: 3 October 2016.

Italian Journal of Agronomy 2017; 12:788
doi:10.4081/ija.2016.788

Introduction

The continuous raise in world population, combined with the increase in food consumption, especially in emerging countries, highlights the urgent need to produce more food to meet the growing demand. Agricultural fields irrigation plays and will continue to play a major role in food production and the livelihoods of the world's population. The availability of water varies considerably from region to region, and the competition for water can become very severe in arid and semi-arid areas. No economic sector uses as much water as agriculture, with an estimated value of 1300 m^3 per person per year (de Fraiture *et al.,* 2007). Due to climate-change related issues, in semi-arid Mediterranean areas, the frequency and severity of prolonged periods of drought may also increase in the future (Lovelli *et al.,* 2012; Giorgi and Lionello, 2008). Hence, the need to apply innovative irrigation techniques able to increase the efficiency of water use is urgent. Research in the last two decades showed the importance of root-sourced chemical signals in modulating the growth and physiology of plants in drought conditions (Campos *et al.,* 2009; Davies *et al.,* 2002; Sauter *et al.,* 2001). Results of these studies were applied to the development of innovative irrigation techniques known as deficit irrigation practices. One of these is the partial root-zone drying (PRD), consisting in keeping half of the root system near to field capacity, while the other half is under water deficit (Campos *et al.,* 2009). In this way, only half of the root system is intermittently in dry conditions (Loveys *et al.,* 2000) and triggers the production of abscisic acid (ABA), which in turn reduces leaf growth and stomatal conductance. At the same time, roots in the wet side of the soil take up enough water to maintain high leaf water potential in the leaves and sustain plant growth (Zegbe *et al*., 2006; Ahmadi *et al.,* 2010). PRD irrigation technique has been shown to improve tomato water use efficiency (WUE) and fruit quality (Bravdo, 2005; Davies *et al.,* 2000; Zegbe-Domínguez *et al.,* 2003; Nardella *et al*., 2012). Notwithstanding, there is still little understanding on the mechanisms of PRD in different tomato cultivars, and therefore procedures for scheduling the optimum timing of irrigation for each root side still need research (Sepaskhan and Ahmadi, 2010). In this work, ABA levels in both roots and leaves were analysed in two cultivated genotypes of tomato submitted to PRD and conventional deficit irrigation (V50) to study the effects of these irrigation techniques on leaf and root ABA concentration, gas exchange and WUE. The aim of the work was also to analyse the response of two different tomato genotypes to the PRD technique application.

Materials and methods

The experiment was conducted at the University of Basilicata (Potenza, Italy), under controlled conditions, in a growth chamber from 9 October 2014 to 18 December 2014. The day/night temperatures were 26/23°C, relative humidity 70% and mean photon flux density was about 1000 μmol m^{-2} s^{-1} at plant height with a 16-h photoperiod. After the germination of seeds of *Lycopersicon esculentum* Mill. cv *Ponderosa* and cv *Giallo tondo di Auletta,* seedlings were transferred into plastic boxes (40 cm length×10 cm width×60 cm height) filled with field soil with the following characteristics: sand 76.5%, silt 16.2%, clay 6.7%; pH 6.8; N 1.9 g kg^{-1}; phosphates (P_2O_5) 50.3 g kg^{-1}; potassium oxide (K_2O) 1430 g kg^{-1}. Gravimetric soil water was 29.5% dry weight (DW) at field capacity and 11.7% DW at the theoretical wilting point (determined in the lab at -0.03 and -1.5 MPa, respectively). Two cultivars and three irrigation treatments were compared in a completely randomised factorial experimental design with three replications. The cultivars were both yellow tomatoes with long-time storage: *Ponderosa* and *Giallo tondo di Auletta*. Irrigation treatments were the following: a control-full irrigation, in which 100% of evapotranspiration was restored (V100); a conventional deficit irrigation in which 50% of the amount of water supplied to V100 was supplied (V50); and plants where the root system was split into two parts, such that each half was planted in a plastic-bag compartment (PRD). In PRD, one compartment was watered as in V50 and the other compartment was allowed to dry, and thereafter irrigation was switched between sides. Plants were kept fully watered (field capacity) for about two weeks until five leaves were fully expanded and roots well established. Plants were fertilised with Hoagland solution (2.53 mM KNO_3, 0.75 mM $Ca(NO_3)_2{\cdot}4H_2O$, 0.50 mM $NH_4H_2PO_4$, 0.50 mM $MgSO_4{\cdot}7H_2O$, 4.10 mM $FeSO_4{\cdot}7H_2O$, 2.03 mM Na_2-EDTA, 11.58 mM H_3BO_3, 2.28 mM $MnCl_2{\cdot}4H_2O$, 0.08 mM $CuSO_4{\cdot}5H_2O$, 0.15 mM $H_2MoO_4{\cdot}H_2O$, 0.40 mM $ZnSO_4{\cdot}7H_2O$). During the crop cycle, soil water content was monitored by gravimetric method. Evapotranspiration was calculated from the difference in pot weights between successive days, and tomato plants were watered twice a week. All pots were rotated within the growth chamber to prevent microclimate effects. Leaf water potential (Ψ) was measured from the beginning of the irrigation treatments on the youngest uppermost fully expanded leaf of three plants per treatment at midday using the pressure chamber technique (Scholander pressure chamber), according to Scholander *et al*. (1965). Measurements of leaf area, dry matter (DM) and chlorophyll content were made at the end of the experiment [70 days after transplanting (DAT)]. In particular, leaf area was measured by a surface electronic detector (Model 3100; LI-COR Inc., Lincoln, NE, USA) and DM was obtained drying the samples in a ventilated oven at 75°C until constant weight. Water use efficiency (expressed in g L^{-1}) at the plant level was calculated as the ratio between DM and plant water use obtained from total irrigation volume applied to each irrigation treatment. Chlorophyll content was measured by a chlorophyll meter soil-plant analyses development (SPAD)-502 (Konica Minolta, Osaka, Japan) at 50 DAT, from the apical leaflet of the youngest fully expanded leaf. The mean values were calculated using the internal function of the chlorophyll meter and expressed in SPAD units. In all cases, the value of three replicates (n=3) for each experimental treatment was taken. The correlation between total chlorophyll content and SPAD was verified in plants grown under experimental radiation conditions. Net photosynthesis (A), transpiration (E), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) were measured using a LI-6400 portable photosynthesis system equipped with a 2-cm^2 chamber and 6400-40 LED light source (LI-COR Inc.), operating at 380 ppm ambient CO_2 concentration. Analyses were carried out between 12:00 and 14:00 h (solar time) under saturating light conditions (photosynthetic active radiation, PAR about 1500 μmol photons m^{-2} s^{-1}). These measurements were made on 22 and 50 days after transplantation (DAT) concomitant with the measurements of leaf water potential (Ψ). Instantaneous water use efficiency (WUE_i) was calculated as the ratio between assimilated CO_2 and transpiration flow (Medrano *et al.*, 2015).

The measurement of ABA level was made in leaves and roots at 50 and 70 DAT. Frozen foliage and root samples (75 mg) were grounded into powder with liquid nitrogen with a mortar and pestle, and put in a tube. To each tube, 0.75 mL, extraction solvent (2-propanol/H_2O/HCL 37%; 2:10:002, v/v/v) was added. The tubes were shaken at a speed of 100 rpm for 30 min at 4°C. To each tube, 0.75 mL, of dichloromethane was added, and then the samples were shaken for 30 min at 4°C and centrifuged at 13,000 g for 5 min. After centrifugation two phases were formed, with plant debris between the two layers, so 400 µL of the solvent from the lower phase was transferred using a Pasteur pipette into a screw-cap vial, and the solvent mixture was concentrated using a evaporator with nitrogen flow. Finally, the samples were re-dissolved in 0.210 mL methanol and stored at -20°C before quantitative analysis. To quantify the ABA content, known amounts of pure standard were injected into the HPLC system and an equation, correlating peak area to ABA concentration, was formulated.

Data were analysed using analysis of variance (ANOVA) and treatment means were separated by Tukey's Student range test at $P \leq 0.05$. All analyses were performed by the Minitab (version 17.1.0) software.

Results

Leaf abscisic acid

Leaf ABA content is reported in Figure 1. At the first measurement (50 days after transplanting), the cultivar effect was significant. In *Ponderosa*, ABA content was lower than in *Auletta* (Figure 1A). Significant differences were also observed as a function of irrigation treatment: the highest ABA values were observed in PRD and V50, compared to V100 (Figure 1B). At 70 days after transplanting, irrigation significantly affected leaf ABA. Higher levels of ABA were measured in PRD compared to V100, while V50 showed intermediate values, not significantly different from either of the other treatments (Figure 1C).

For root abscisic acid concentration (Figure 1D), the interaction between variety and irrigation treatment was significant. In the *Auletta* cultivar, root ABA content in V100 was significantly lower than in the deficit irrigation treatments, which were not different from each other. For *Ponderosa*, root ABA concentration in PRD reached significantly higher values than both V50 and V100, and a lower value of V100 was not significantly different from that of V50.

Gas exchange

Measurements of single-leaf gas exchange (assimilation rate, CO_2 concentration stomatal, conductance to H_2O and transpiration rate) were taken at 22 DAT (Figure 2) and 50 DAT (Figure 3) after transplanting. According to two-way ANOVA test, at 22 DAT (Figure 2), V50 in *Ponderosa* showed lower values of photosynthetic rate than in PRD, and intermediate values between PRD and V100 for transpiration and conductance. In *Auletta*, PRD showed lower stomatal conductance and transpiration rate than V100, and this caused a higher WUE_i. Successively, at 50 DAT (Figure 3), as regards photosynthetic rate (*a*) and conductance, only the effect of irrigation treatments was significant. The lowest values of photosynthesis, stomatal conductance (Figure 3A and B) and intercellular CO_2 concentration (Table 1) were observed in PRD and V50, compared to V100. Assimilation rate, stomatal conductance and intercellular CO_2 concentration decreased by 22, 36 and 12%, respectively, in PRD, V50 and V100 (Figure 3 and Table 1). At 50 DAT, the highest transpiration values were observed in V100 for both varieties (*Ponderosa* and *Auletta*), but they were significantly different only in V50 in *Ponderosa*, and in PRD in *Auletta* (Figure 3C). Regarding WUE_i, the interaction between irrigation treatment and varieties was significant. In *Auletta*, WUE_i was significantly higher for the PRD treatment with respect to V100, whereas in *Ponderosa* it was significantly higher in V50 with respect to PRD (Figure 3D).

Figure 4 shows the relationship between ABA concentration and stomatal conductance. A significant inverse correlation was found between the leaf ABA concentration and g_s (r^2=0.4; P<0.01). Referring to total chlorophyll content (SPAD values) measured at 50 DAT, the effects of irrigation treatments and variety were both significant. The higher value of total chlorophyll content was observed in *Ponderosa* variety (Table 1), while, as regards deficit irrigation treatments, the highest value was detected in PRD e V50 (50 and 51 SPAD values, respectively) (Table 1).

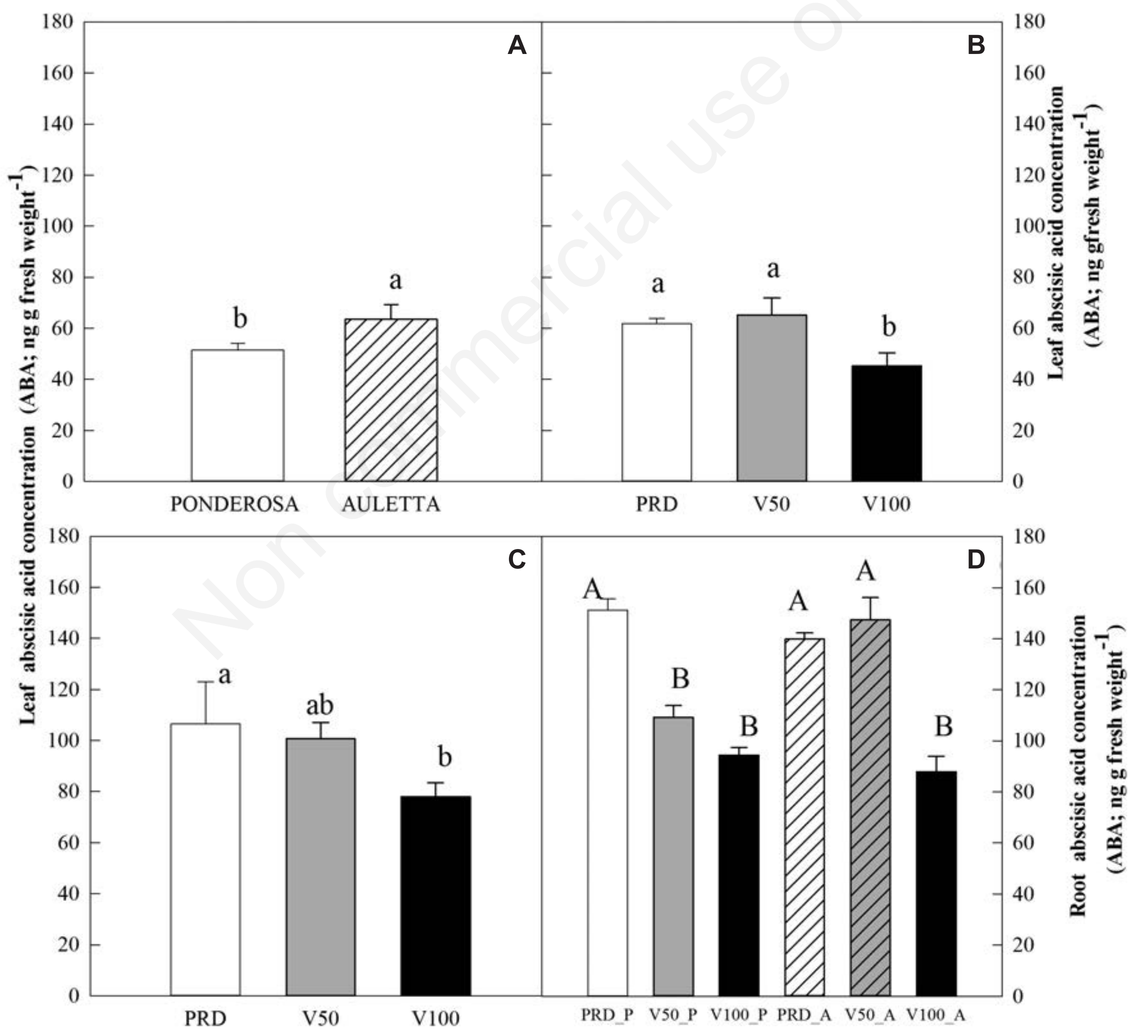

Figure 1. Abscisic acid (ABA) concentration in leaves measured 50 days (A and B) and 70 days (C) after transplantation and ABA concentration in roots measured 70 days (D) after transplantation in tomato plants subjected to partial root drying (PRD) and deficit irrigation (V50). Mean values (n=3) within a column followed by different lowercase and uppercase letters are significantly different at P<0.05 and P<0.01, respectively, according to Tukey's Student range test.

Leaf water potential

Leaf Ψ was measured twice during the experiment (at 50 and 70 DAT). The value of Ψ at 50 DAT was lower in V100, but differences were not significant (Figure 5A), while the values at 70 DAT in PRD and V50 were significantly higher than in V100 (Figure 5B).

Water use efficiency and soil water content

Significant differences were also observed on WUE calculated at the plant level (g L^{-1}) (Table 2). PRD and V50 in *Ponderosa* showed the highest values, and PRD the lowest in *Auletta* significantly different from *Ponderosa* value (Table 2). In both PRD and V50, for both varieties it was possible to save on average 46% of water, compared to V100 (Table 2). At the end of the experiment, the highest soil water content was measured in V100, while the lowest value was measured in V50 for both varieties (data not shown).

Leaf area and dry matter

Significant differences were observed in the leaf area (LA) related to both varieties and irrigation treatments. Leaf area was significantly higher in V100, compared to deficit irrigation treatments, and it was always higher in *Ponderosa* (Table 3). Irrigation treatments and variety significantly affected above-ground plant dry biomass, that was significantly reduced in PRD and V50, compared to V100. Differences in DM were related to the variety, as *Ponderosa* accumulated 20% more DM than *Auletta* (Table 3). There were also great differences between the two variety in relation to the water regime in terms of DM (Table 3).

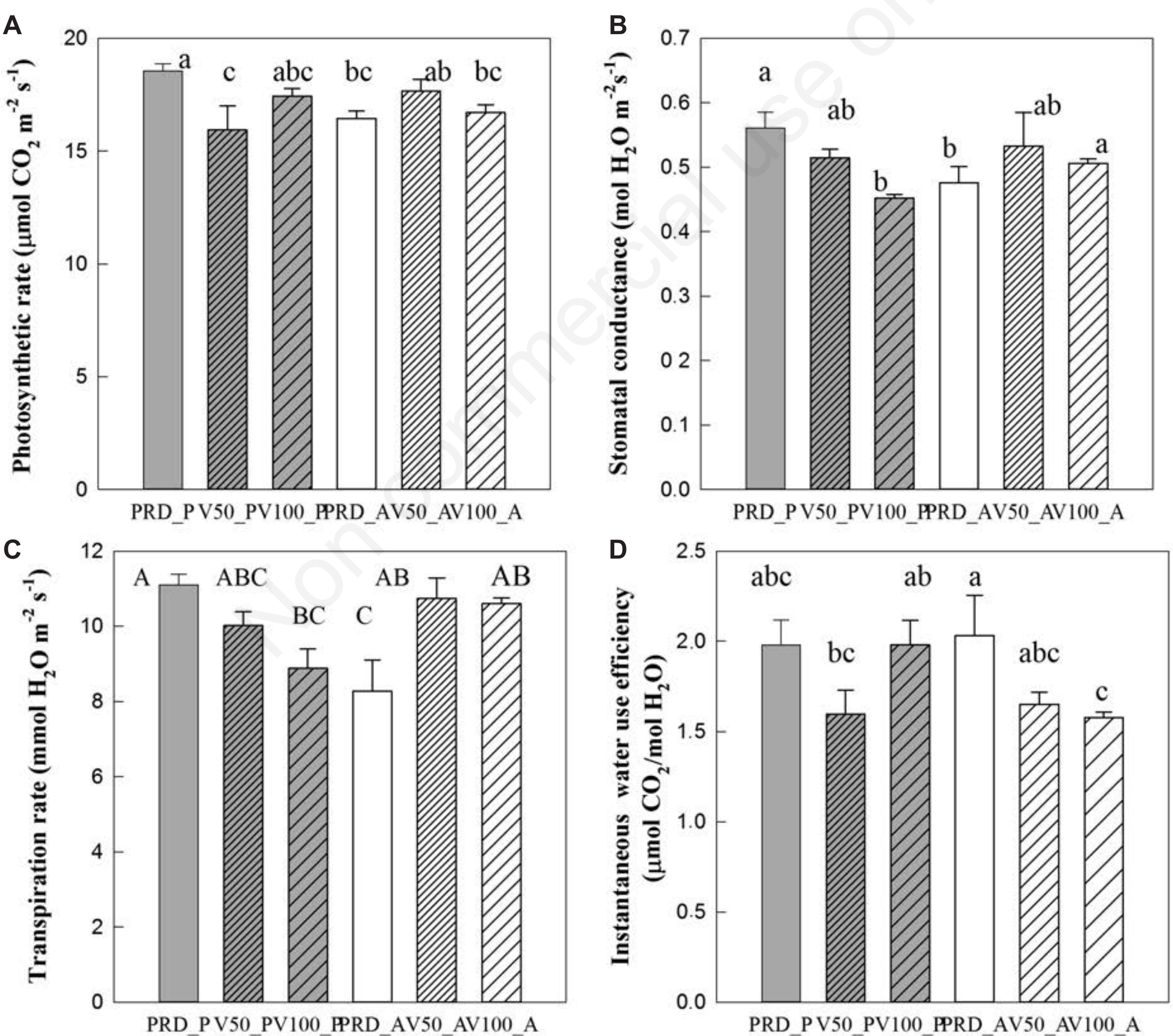

Figure 2. Photosynthetic rate (A), stomatal conductance (B), transpiration rate (C) and instantaneous water use efficiency (D) measured 22 days after transplanting in leaves of tomato plants subjected to partial root drying (PRD) and deficit irrigation (V50). Mean values (n=3) within a column followed by different lowercase and uppercase letters are significantly different at P<0.05 and P<0.01, respectively, according to Tukey's Student range test.

Table 1. Intercellular CO_2 concentration and chlorophyll content measured at 50 days after transplanting.

	Ci (μmol CO_2 m^2 s^{-1})			SPAD		
	Ponderosa	*Auletta*	Mean	*Ponderosa*	*Auletta*	Mean
PRD	309.3	256.7	283^b	52.9	47.5	50.2^{ab}
V50	261.3	307.3	284.3^{ab}	52.7	49.6	51.1^a
V100	318.7	325.3	322^a	48.7	45.1	46.9^b
Mean	296.4	296.4	-	51.4^a	47.4^b	-

C_i, intercellular CO_2 concentration; SPAD, soil-plant analyses development; PRD, partial root drying; V50, plants in which 50% of the amount of water given to V100 was supplied; V100, plants receiving an amount of water equivalent to 100% of plant evapotranspiration. [a,b]Values within and between columns followed by different letters are significantly different at P<0.01 and P<0.05 according to Tukey method. Number of replicates=3.

Table 2. Irrigation water use and water use efficiency.

	Irrigation water use (L $plant^{-1}$)			WUE (g L^{-1})		
	Ponderosa	*Auletta*	Mean	*Ponderosa*	*Auletta*	Mean
PRD	10	9	9.5^a	1.5^a	1.1^b	1.3
V50	10	9	9.5^a	1.5^a	1.3^{ab}	1.4
V100	18	17	17.5^b	1.2^{ab}	1.3^{ab}	1.3
Mean	14	13	-	1.4	1.2	-

C_i, intercellular CO_2 concentration; SPAD, soil-plant analyses development; PRD, partial root drying; V50, plants in which 50% of the amount of water given to V100 was supplied; V100, plants receiving an amount of water equivalent to 100% of plant evapotranspiration. [a,b]Values between columns followed by different letters are significantly different at P<0.01 and P<0.05 according to Tukey method. Number of replicates=3.

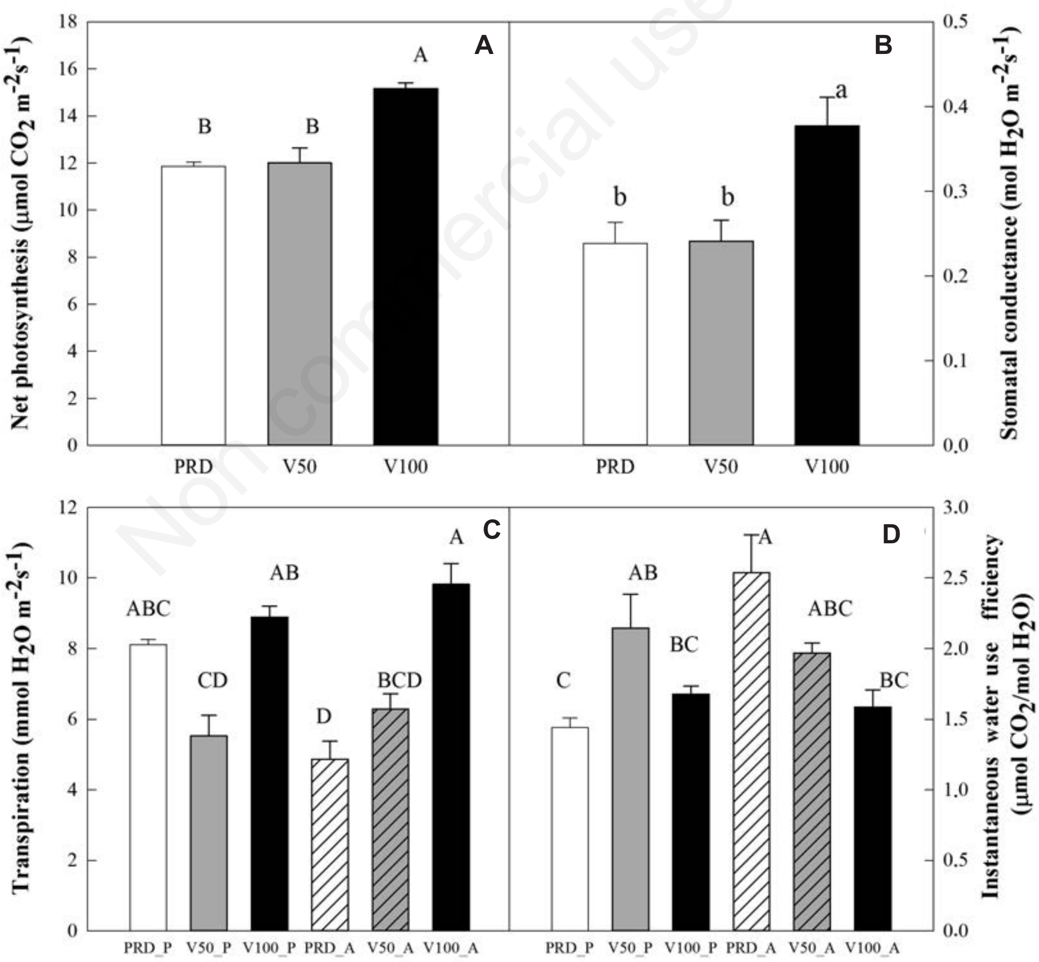

Figure 3. Net photosynthesis (A), stomatal conductance (B), transpiration (C) and instantaneous water use efficiency (D) measured 50 days after transplanting in leaves of tomato plants subjected to partial root drying (PRD) and deficit irrigation (V50). Mean values (n=3) within a column followed by different lowercase and uppercase letters are significantly different at P<0.05 and P<0.01, respectively, according to Tukey's Student range test.

Discussion

This study confirmed several previous papers (Kirda *et al.,* 2004; Mingo *et al.,* 2003) about PRD irrigation technique on tomato. ABA levels in both roots and leaves were analysed in two cultivated genotypes submitted to partial root-zone drying (PRD) and conventional deficit irrigation (V50). Our results showed the crucial role of chemical signaling in PRD treatment, being leaf ABA concentration at 50 DAT already higher in both PRD and V50 treatments, compared to V100 (Figure 1B), as observed also by other authors (Davies *et al.,* 2002; Dodd, 2003; Taiz and Zeiger, 2006). The high leaf ABA can move to stomata through the transpiration flow. It was also underlined that xylem sap pH in tomato increased as soil water content decreased and this change is correlated to increased ABA concentration in the xylem sap (Holbrook *et al.,* 2002; Mingo *et al.*, 2003; Tahi *et al*., 2007). In this work, it was observed a higher leaf ABA concentration in the *Auletta* variety

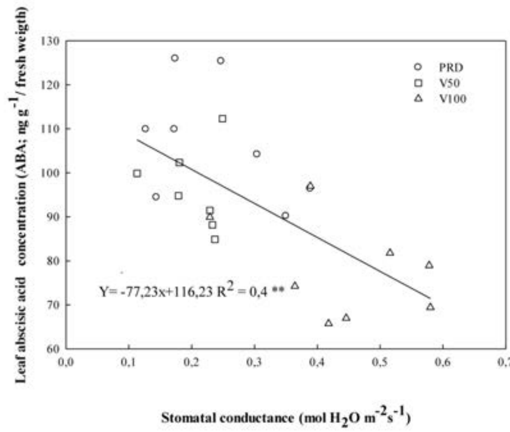

Figure 4. Relationship between leaf abscisic acid and stomatal conductance: values measured at 50 days after transplanting.

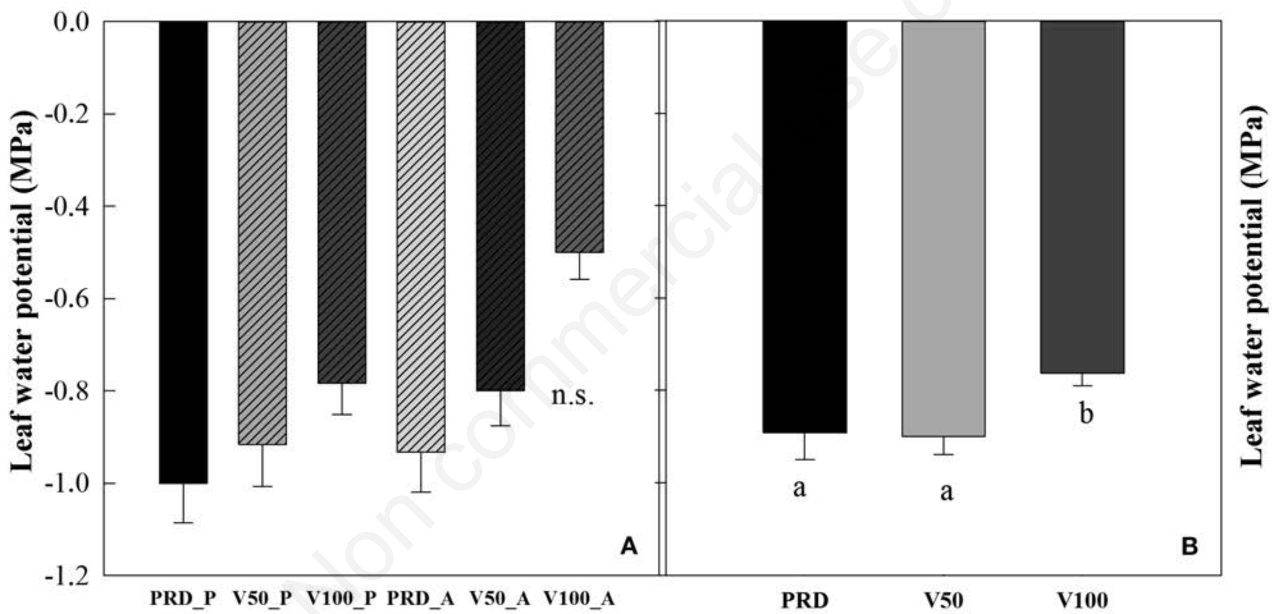

Figure 5. Leaf water potential measured 50 (A) and 70 days (B) after transplantation. Bars are mean values (n=3)±standard error, different lowercase and uppercase letters on bars indicate significant difference at P<0.05 and P<0.01, respectively, according to Tukey's Student range test.

Table 3. Leaf area and above ground dry matter measured at 70 days after transplanting.

	LA (cm^2)			DM (g $plant^{-1}$)		
	Ponderosa	*Auletta*	Mean	*Ponderosa*	*Auletta*	Mean
PRD	722[bc]	607[c]	665	14.7	8.4	11.5[b]
V50	660[bc]	585[c]	622	14.8	11.6	13.2[b]
V100	1456[a]	754[b]	1105	21.9	21.3	21.6[a]
Mean	946	649	-	17.1[a]	13.8[b]	-

LA, leaf area; DM, dry matter; PRD, partial root drying; V50, plants in which 50% of the amount of water given to V100 was supplied; V100, plants receiving an amount of water equivalent to 100% of plant evapotranspiration. [a-c]Values within and between columns followed by different letters are significantly different at P<0.01 and P<0.05 according to Tukey method. Number of replicates=3.

with respect to *Ponderosa* variety, and this likely means that there is a different behavior between tomato cultivar as regards to leaf ABA accumulation into leaf tissue (Figure 1A). Roots in tomato submitted to PRD and V50 treatments produced more ABA than under normal condition, as also shown by other authors (Davies and Zang, 1991), but we also showed the interaction effect irrigation×variety (Figure 1D). This result confirms our hypothesis that there are varietal differences in root ABA biosynthesis and accumulation under conventional deficit irrigation (V50). Some authors (Topcu *et al*., 2007) showed that ABA xylem concentration is actually higher in deficit irrigation treatment than in PRD plants before irrigation events, while after irrigation the opposite occurs. It seems that ABA xylem concentration and accumulation into leaf and root tissue of PRD and V50 plants are very dynamic, the results being very much dependent on the sampling time. Gas exchange parameters were affected less during initial part of the experiment (22 DAT; Figure 2), while later (50 DAT; Figure 3) both photosynthesis and stomatal conductance where significantly affected. Our results on photosynthesis are in disagreement with Campos *et al.* (2009) and Zegbe *et al.* (2004), who found only a small reduction in the assimilative process under PRD conditions. These discrepancies might be related to the different experiment conditions: it is known that cultivar and weather conditions significantly impact the results of PRD experiments (Zegbe and Behboudian, 2008). Notwithstanding the great reduction of stomatal conductance that we measured at 70 DAT is in agreement with other studies on tomato (Campos *et al.,* 2009; Zegbe *et al.,* 2004; Nardella *et al*., 2012). Moreover it is related to the leaf ABA accumulation as shown by the linear regression between these two parameters (Figure 4). Due to stomatal closure we measured a significant reduction in transpiration rate, which was more pronounced in the *Auletta* variety under PRD conditions. As a direct effect of this reduction WUE_i was higher in *Auletta* variety than in *Ponderosa*, expecially at 70 DAT, and this result shows in clear way the existence of differences between cultivars in terms of response to PRD irrigation technique. As expected we did not measure any change of plant water status during the initial part of the experiment, when tomato plant were subjected only to a mild stress, while later plant water status was affected (Figure 5A and B) by treatments. In addition to the chemical signal, hydraulic signal is also involved, but usually a balance between them occur in PRD treatments since tomato roots on the wetted side absorb enough water to keep high shoot water potential while tomato roots in the dry side produce ABA to allow a reduction in stomatal conductance. In this way WUE_i increases, as shown also by other authors (Zegbe *et al.,* 2004; Tahi *et al.,* 2007). Our results on PRD impact on leaf area development and plant growth (Table 3) are consistent with other studies (Campos *et al.,* 2009; Sobeih *et al.,* 2004). Greater Leaf Area in *Ponderosa* than *Auletta* variety is also related to the genotype. *Ponderosa* has a typical habit characterised by a high leaf number and leaf area (Perniola *et al.,* 1993; Miccolis *et al.,* 1999). Leaf area was lower in PRD and V50 treatment than fully irrigated treatment as was total DM. Water use efficiency – expressed as total DM produced per L of irrigation water applied – was higher in *Ponderosa* cultivar under PRD treatment than *Auletta* cultivar (Table 2). There is discrepancy between WUE_i and water use efficiency calculated at the plant level on *Ponderosa* due to the different nature of the two indices: the former is an instantaneous measurement at leaf level, whereas the latter represents the integration of leaf area development, leaf photosynthesis and crop growth over all the experiment period. In both cultivars the increase in WUE_i with PRD reflects the integration of instantaneous gas exchange measurements, which showed a larger decrease in transpiration relative to the decrease in CO_2 assimilation in accompanying stomatal closure. The reduction in the water applied by irrigation, which was of 46% in both PRD and V50 treatment, was a consequence of the water regime applied, and it is of great importance for irrigation in semi-arid environment. The use of methods of controlled irrigation, as PRD, leads to optimised water use by stomata that means an increase of WUE without a significant decrease in growth of tomato (Chaves and Oliveira, 2004) as we observed in our experiment. However, equal improvement of WUE by PRD and DI treatments means that irrigation volume rather than irrigation methods is more important in determining crop growth, as was also suggested by several authors (Fernández *et al.,* 2006; Tahi *et al.,* 2007; Nardella *et al*., 2012). The *Ponderosa* yellow long-storage tomato variety is known as moderately resistant to water deficit (Perniola *et al.,* 1993; Miccolis *et al.*, 1999) and perhaps for this moderate drought resistance it lends itself to the application of deficit irrigation. Values of WUE of the local *Auletta* variety and of *Ponderosa* variety were not significantly different from those in well watered and conventional deficit irrigation, nevertheless, *Auletta* showed lower values of WUE in PRD conditions which means that compared to *Ponderosa*, it lends itself less to the application of this irrigation technique (Table 2).

Conclusions

It can be concluded that PRD presented some advantages in regulating leaf gas exchange and crop growth, compared to conventional deficit irrigation (V50). These short-term positive aspects at the leaf level did not cause marked differences at the whole-plant level in the long term, as both treatments resulted in similar crop growth and WUE. Moreover, differences between tomato cultivars, in terms of WUE to PRD irrigation technique, highlighted that the choice of variety is crucial for the success of this irrigation technique. Our results indicate that there is still space to optimise the PRD strategy, so improving the cumulative physiological effects of the root-sourced signaling system. Further studies with different varieties and sampling time for ABA accumulation into crop tissue are therefore required.

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