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COMPARATIVE EFFECTS OF PARTIAL ROOTZONE DRYING AND DEFICIT IRRIGATION ON GROWTH AND PHYSIOLOGY OF TOMATO PLANTS

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Abstract — The effects of partial rootzone drying (PRD), deficit irrigation (DI), and full irrigation (FI) on tomato physiology were investigated. In PRD and DI plants, leaf water potential values and stomatal conductance were significantly lower, while xylem ABA concentration was greater compared to FI plants. Photosynthesis was similar for all treatments. Water use efficiency was improved by PRD and DI, which reduced fruit dry weight, but had no effect on dry weight of leaves and stems.

Key words: Tomato, partial root drying, deficit irrigation, soil and leaf water status, gas exchange, water use efficiency

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INTRODUCTION

Many vegetable crops (including tomatoes) require irrigation in order to achieve high yield and good quality. However, irrigation water resources have become limited as a consequence of the increased incidence of drought in many countries. It is therefore of strategic importance to increase plant water use efficiency (WUE), thereby saving water resources in agriculture.

Partial rootzone drying (PRD) and deficit irrigation (DI) are water-saving irrigation strategies. Deficit irrigation is a method that irrigates the entire rootzone with an amount of water less than potential evapotranspiration, and the minor stress that develops has minimal effects on the yield (English et al., 1996). Partial rootzone drying is a further development of DI; it involves irrigating only part of the rootzone, leaving the other part to dry to a predetermined level before the next irrigation. In such a way PRD allows induction of the ABA-based root-to-shoot chemical signaling system to regulate growth and water use and thereby increase WUE (Davies et al., 2002). Use of PRD has been shown to be successful in fruit trees, some field crops, and vegetables (including tomatoes) (Kirda et al., 2004). Compared to full irrigation (FI), PRD can save 30-50% of irrigation water and increase WUE by 50-100% (Loveys et al., 2000). Most importantly, it has been reported by several authors that, given the same amount of irrigation volume, PRD is superior to DI in terms of maintaining crop yield and increasing WUE (Kirda et al., 2004; Du et al., 2006; Topcu et al., 2007). However, recent evidence suggests that PRD has no advantages over DI for crop species like grapevine (Gu et al., 2002, 2004; dos Santos et al., 2003; Pudney and McCarthy, 2004; Collins et al., 2005), olive (Fernández et al., 2006), apple (Leib et al., 2005), peach, common bean (Wakrim et al., 2005), and potato (Liu et al., 2006a). These authors observed that it is the amount of irrigation rather than the type of irrigation that determined crop response. It is apparent that more experiments comparing PRD and DI are required.

Therefore, the objective of present study was to compare the effects of PRD and DI on soil and plant water status, leaf gas exchange, xylem ABA concentration, and WUE of tomato plants. This should help to elucidate the relative advantages of the two water-saving irrigation techniques.

MATERIALS AND METHODS

Tomato plants (*Lycopersicon esculentum* L., cv. Sunpak) were raised from seed and transplanted into 10-L pots (one plant per pot) filled with 4.9 kg of commercial compost (PINSTUP, Denmark) in a glasshouse. The pots were specially designed for PRD experiments in such a way that they were separated with plastic sheets into two equally sized compartments. Roots of the seedlings were equally distributed between the two hydraulically separated compartments. The glasshouse was supplied with supplementary lighting (metal-halide lamps) providing photosynthetically active radiation (PAR) of above 500 µmol m^{-2} s^{-1} and a photoperiod of 18 h. The day/night temperature regime was 19/17 ± 2°C.

After transplantation, all plants were irrigated daily to full pot holding capacity, viz., a volumetric soil water content (θ) of 33%, with nutrient solution (Pioneer NPK Macro 14-3-23 + Mg combined with Pioneer Micro; pH = 5.5; EC = 1.3). The θ of both compartments of each pot was measured daily using TDR probes (time domain reflectometer, TRASE, Soil Moisture Equipment Corp., USA) with a length of 33 cm. Ten days after transplantation, plants were subjected to three irrigation treatments: 1) full irrigation (FI), in which the whole root system was irrigated daily at 9:00 h to a θ of 33%; 2) deficit irrigation (DI), in which 70% of FI water was evenly applied to the whole root system; and 3) partial root drying (PRD), where 70% of FI water was applied to one half of the root while the other half was allowed to dry, and the irrigation was shifted when θ of the dry side had decreased to 10%.

For measurements of investigated parameters, 4-10 plants per treatment were selected randomly. Stomatal conductance (g_s) and photosynthesis (A) were measured daily on the second fully expanded upper canopy leaflets (one leaflet per plant) from 11:00 to 12:00 h with an LI-6200 portable photosynthesis system (LiCor Inc., Lincoln, NE, USA). The intrinsic water use efficiency (WUE_i) was calculated as the ratio between A and g_s, i.e., A/g_s. The midday leaf water potential (Ψ_l) was measured with a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) on the same leaves as for leaf gas exchange measurements from 11:00 to 12:00 h every two days after the onset of treatment (DAT).

Plant biomass was characterized by plant dry weight (DW). At the onset of treatments, five plants were harvested to get their initial information (H0). After the onset of treatments, plants were harvested three times, viz., H1, H2, and H3 at the end of the first, third, and fifth shifts, respectively, in the PRD treatment. At each harvest, shoots and fruits (if available) were collected. The DW values of leaves, stems, and fruits were determined after oven drying for 48 h at 80°C. Plant water use (PWU) during the treatment period was calculated as the sum of daily irrigation plus the depletion of water from the soil fund. Plant water use efficiency (WUE) was calculated as the increment of fruit DW divided by PWU during the treatment periods.

At each harvest, xylem sap was collected by pressurizing roots of the potted plants in a Scholander-type pressure chamber. The entire pot was sealed into the pressure chamber and the shoot was detopped at 15-20 cm from the stem base. With the stem stump protruding outside the chamber, pressure was applied until the root water potential (Ψr) was equalized. The cut surface was cleaned with pure water and dried with blotting paper. The pressure was then increased by 2-3 bars greater than Ψ_r and a 0.5-1.0-ml aliquot of sap was collected using a pipette from the cutting surface into an Eppendorf. The sap was immediately stored at -80°C for ABA analysis. The concentration of ABA in the xylem ($[ABA]_{xylem}$) was analyzed without further purification by an enzyme-linked immunosorbent assay (ELISA) using a monoclonal antibody for ABA (MAC 252) according to Asch (2000). No cross-reaction of the antibody with other compounds in the xylem sap was detected when tested according to Quarrie et al. (1988).

To facilitate data comparison, the values of WUE_i in PRD and DI plants were further expressed relative to those of FI plants and plotted as a function of relative gs (i.e., gs of PRD and DI plants relative to that of FI plants). Data were subjected to analysis of variance (ANOVA) procedures (SAS Institute Inc., 1988). Appropriate standard errors of the means (S.E.) were calculated. Differences between irrigation treatments were distinguished with Student's unpaired *t*-tests (when two treatments were being compared). Tukey's Studentized Range (HSD) Test was applied to separate measured parameters of plants that experienced the three irrigation regimes.

RESULTS AND DISCUSSION

Changes of soil water content (θ) in FI, PRD, and DI-treated plants during the experimental period are shown in Fig. 1. Generally, the θ values were significantly lower in DI and on the dry side of PRD treatment compared to those of FI. The daily θ of FI after irrigation remained close to pot capacity (33%), while θ of DI decreased during the first 21 days and remained at 14-16% thereafter.

The difference of θ between the PRD wet and dry sides was significant during the whole experimental period. Despite considerable differences of θ between the two sides of the PRD plants, the average θ of the whole pot was very similar to that of DI plants, indicating that the rates of water use were very similar between the two treatments. It was also noticed that θ of the PRD wet side was maintained similar to that of FI only in the initial phase after the onset of treatment; after the first shifting of PRD irrigation, the θ value of the wet side was lower than that of FI by 3-8%. A similar pattern of soil water dynamics has also been observed in PRD-treated tomato and other crops (Kirda et al., 2004; Zegbe-Domínguez et al., 2006). However, some other authors showed that θ of the wet side of PRD tomato plants was for the most part maintained during the whole treatment period (Sobeih et al., 2004). One explanation of this discrepancy between different studies may be that there are genotypic differences in the response of tomato plants to PRD such that some genotypes (like our variety Sunpak) after the shifting period adapt to PRD treatment by extracting much more water from the wet side and, as a consequence, the θ of this side is reduced. A higher rate of water

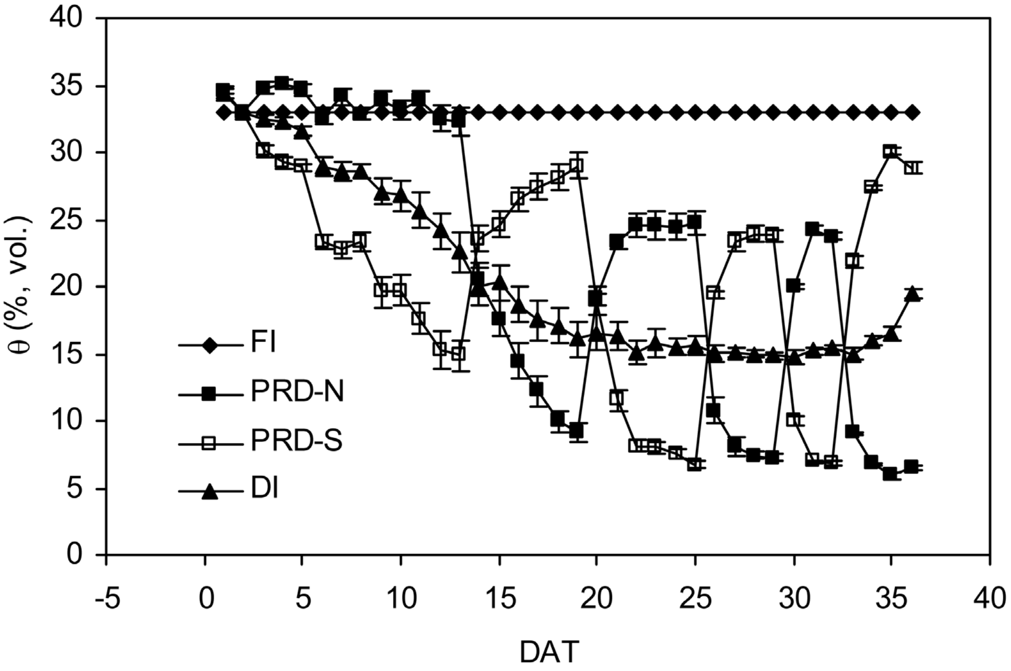

Fig. 1. Changes of volumetric soil water content (θ) in tomato plants treated by full irrigation (FI), partial rootzone drying (PRD-N and PRD-S), and deficit irrigation (DI).

uptake could be a result of increased root contact area or improved root hydraulic conductivity after re-watering the dry side, as was shown by Kang et al. (2002). All these results imply the need for further investigation on the effects of PRD on root development and water uptake mechanism.

Figure 2 shows the Ψ_l of tomatoes under the three irrigation treatments. It was clear that, except for one case, Ψ_l was similar in all treatments up to day 17. Thereafter, Ψ_l began to decrease in PRD and DI plants compared to FI, indicating that those plants experienced shoot water stress. Thus, maintenance of Ψ_l in PRD plants as high as in FI plants was not achieved during the later phase of the experimental period.

Similarly, Zegbe-Domínguez et al. (2006) demonstrated that in some phenological phases of tomato growth, Ψ_l values were lower in PRD than in FI-treated plants. Liu et al. (2006a, 2006b) suggested that retaining high θ of the PRD wet side is crucial in maintaining a high Ψ_l. Also the ability to maintain higher Ψ_l in plants under PRD may be species dependent, and anisohydric species probably can maintain leaf water potential better than isohydric ones at similar levels of soil water deficit (Liu et al., 2006b).

The response of g_s and *A* to PRD and DI as compared to FI is presented in Fig. 3. The average g_s and *A* of FI plants during the treatment period was about 1.41 mol m^{-2} s^{-1} and 12.9 μmol m^{-2} s^{-1}. Compared to FI, g_s was significantly lower in PRD and DI plants in eight and 12, respectively, out of 31 instances.

However, it is noteworthy that g_s decreased earlier in PRD than in DI plants at a time when Ψ_l had not been affected (Figs. 2 and 3A), indicating chemical signals from the dry roots of PRD plants are likely responsible for g_s reduction, as reported elsewhere for tomato (Sobeih et al., 2004). However, further exposure (after 15 DAT) of plants to the investigated treatments showed that g_s in both PRD and DI plants are in good accordance with lowered Ψ_l (Figs. 2 and 3A). This indicates that significant reduction in leaf water status may override chemical signals produced by drying roots. It follows that in later phases of the experimental period, changes in stomatal response to the applied treatments were

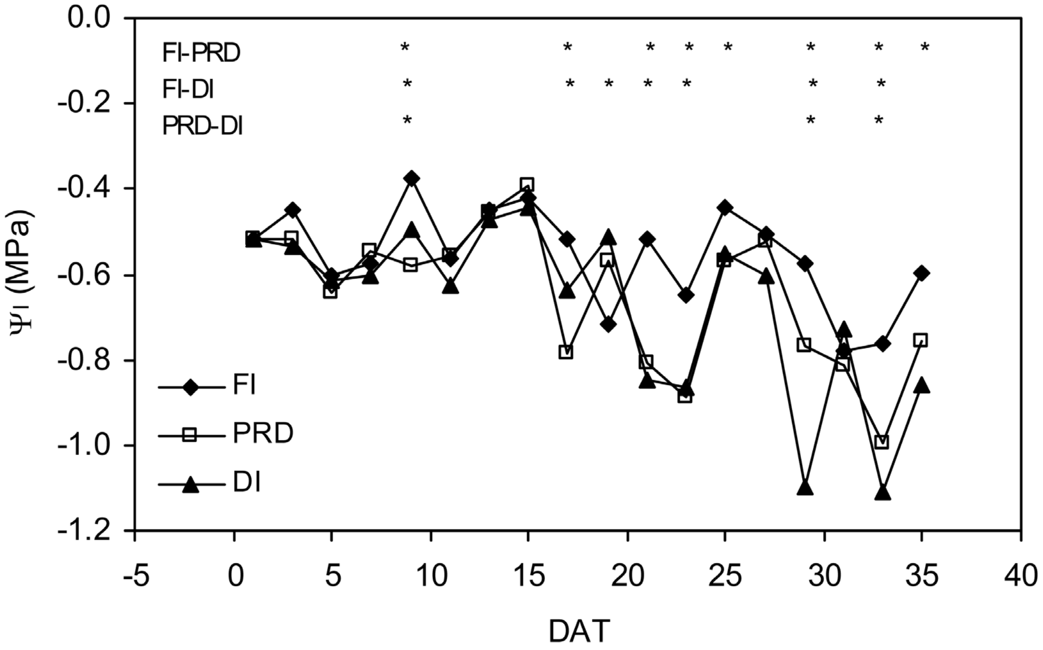

Fig. 2. Effect of full irrigation (FI), partial rootzone drying (PRD), and deficit irrigation (DI) on midday leaf water potential (ψ_l) of tomato plants.

associated with hydraulic signals related to soil water content (Liu et al., 2005).

Compared with g_s, *A* was insensitive to water deficit treatments and in only one out of 31 cases was it lower in PRD and DI than in FI plants (Fig. 3B). Thus, WUE_i was improved in both PRD and DI treatments, and was negatively correlated with g_s (Fig. 4).

This result is in line with earlier findings in PRD-treated grapewine (de Souza et al., 2003) and potatoes (Liu et al., 2006b). It is a well-known fact that stomatal closure can be the main factor responsible for reduction of CO_2 assimilation under mild stress (Chaves et al., 2002). However, our results showed that decreased g_s as an early event in the plant response to PRD treatment did not have a

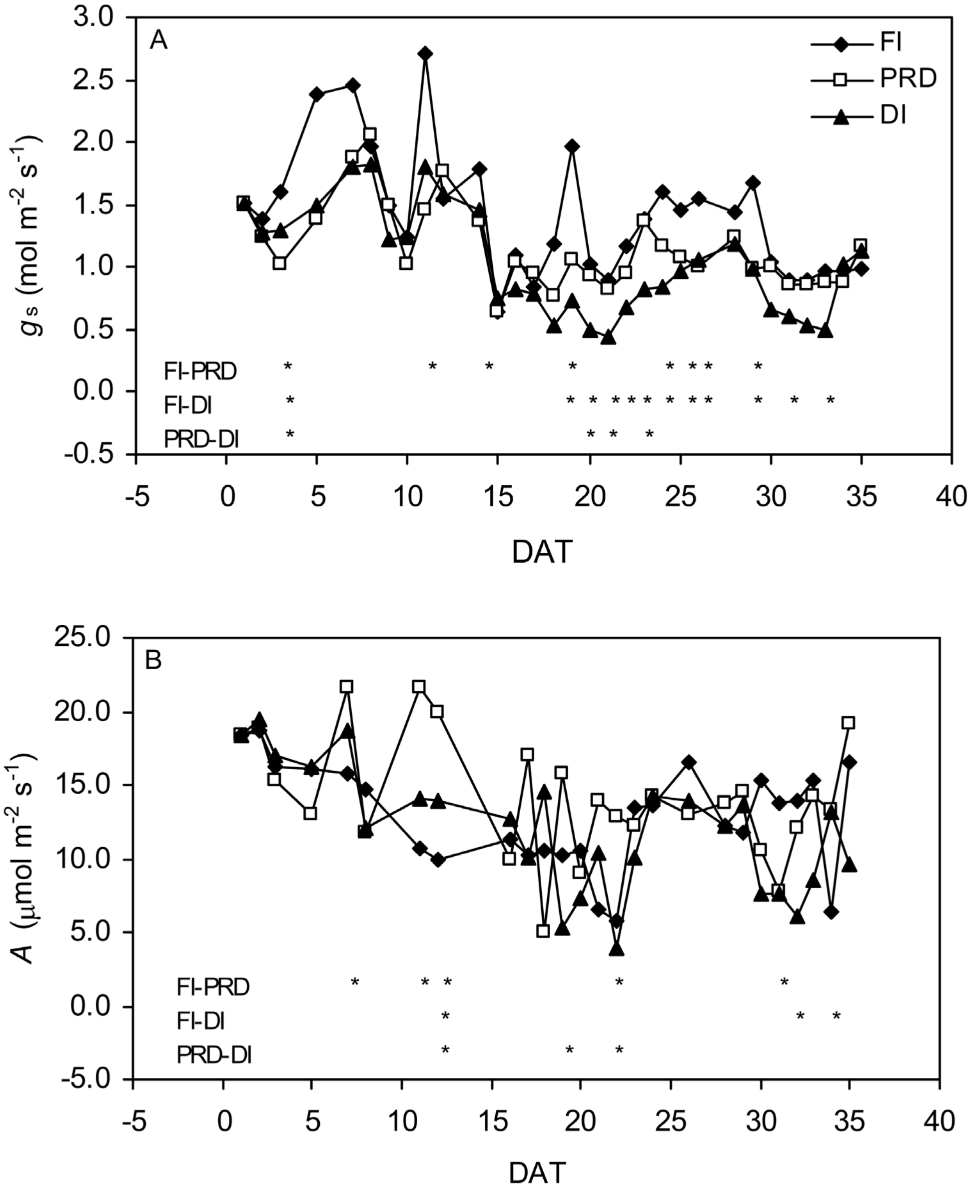

Fig. 3. Effect of partial rootzone drying (PRD) and deficit irrigation (DI) as compared to full irrigation (FI) on stomatal conductance (gs) (A) and photosynthesis (A) (B) in tomato plants.

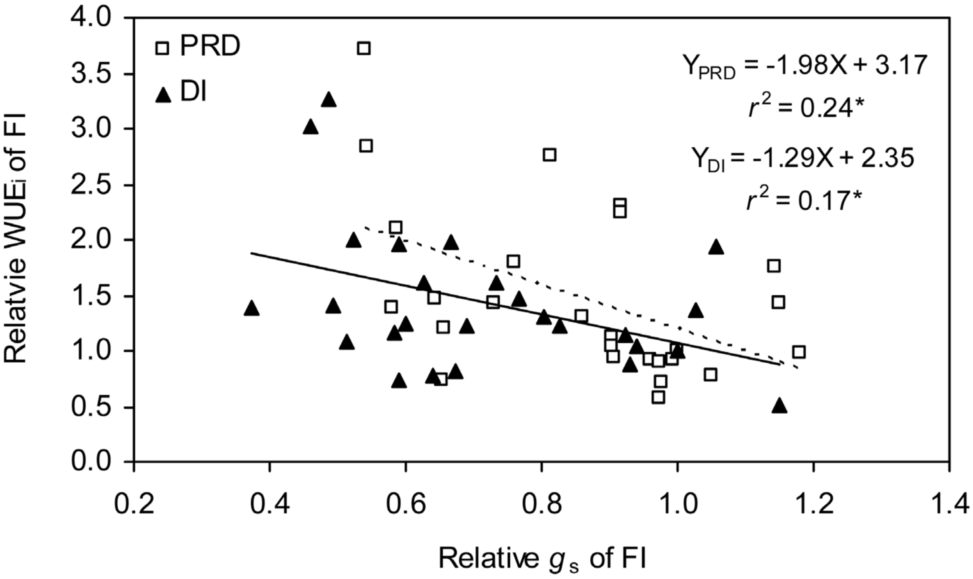

Fig. 4. Relationship between relative intrinsic water use efficiency (WUEi) (i.e., WUEi of PRD and DI plants relative to that of FI plants) and relative gs (i.e., gs of PRD and DI plants relative to FI plants) (C) in tomato plants.

depressive impact on *A*. This is in agreement with de Souza et al. (2003), who pointed out that triggering of partial stomatal closure under PRD irrigation may prevent excessive water loss and lead to a better water balance of the plants; it also may prevent the metabolic inhibition of CO_2 assimilation that otherwise would occur if drought stress were allowed to develop extensively (Chaves et al., 2002).

Of the three harvests after the onset of treatment, only at the final harvest was $[ABA]_{xylem}$ sig-

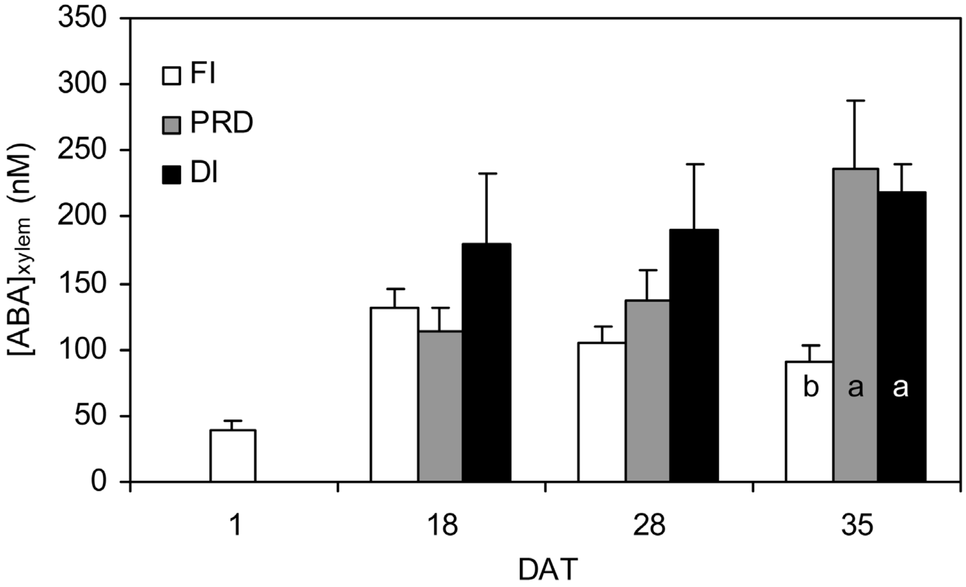

Fig. 5. Effect of partial rootzone drying (PRD) and deficit irrigation (DI) as compared to full irrigation (FI) on xylem sap ABA concentration ([ABA]xylem) in tomato plants.

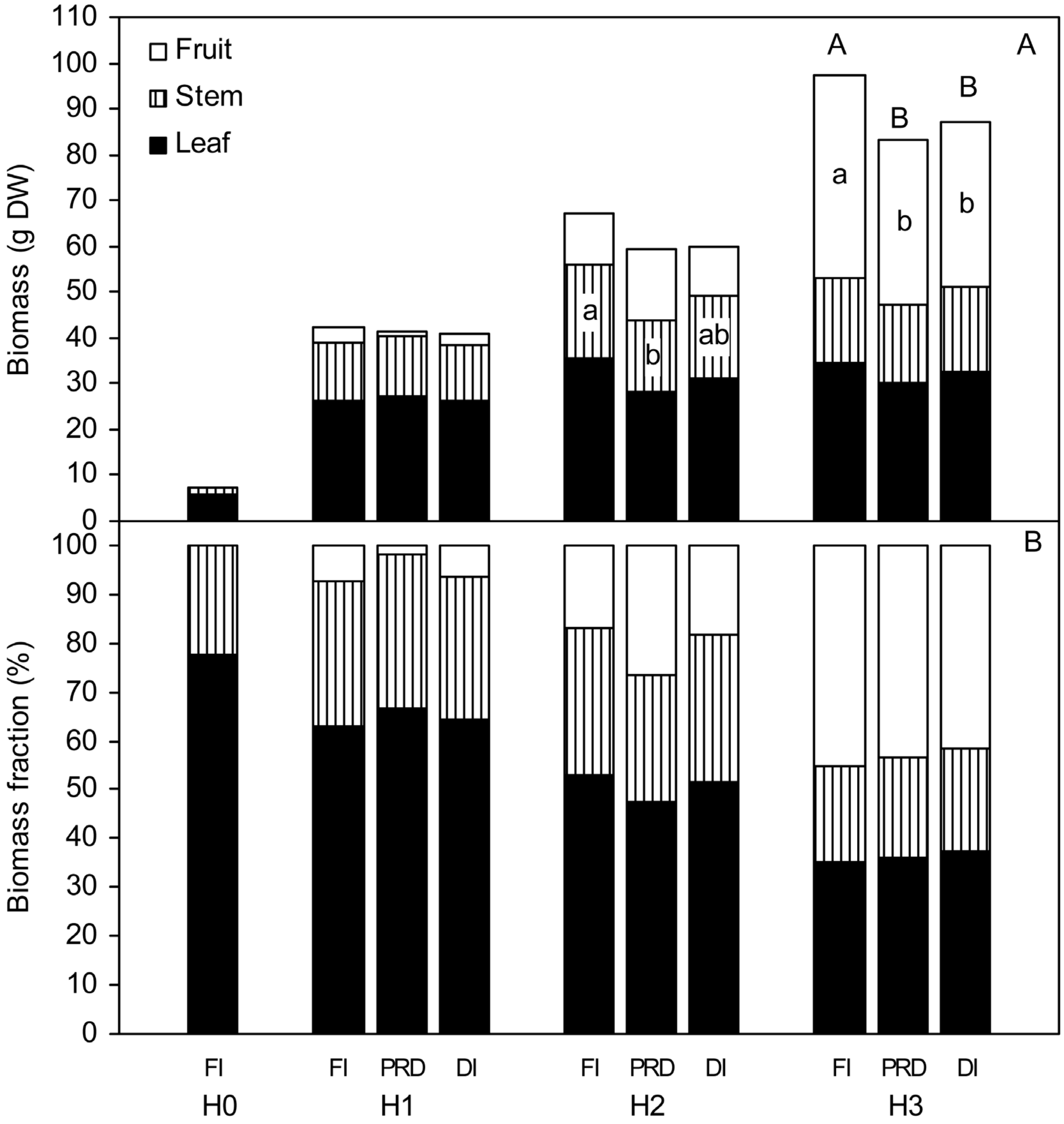

Fig. 6. Effect of partial rootzone drying (PRD) and deficit irrigation (DI) as compared to full irrigation (FI) on dry weight (DW) of leaves, stems, and fruits and DW partitioning of tomato plants.

nificantly higher in PRD and DI plants than in FI plants (Fig. 5).

In accordance with the results reported by Sobeih et al. (2004), we also observed that prior to significant increase in $[ABA]_{xylem}$, g_s decreased substantially in PRD and DI plants (Figs. 3A and 5). This may indicate that other signalling molecules rather than xylem ABA induce stomatal closure in the absence of decreasing Ψ_l (Sobeih et al., 2004). However, Dodd et al. (2006) recently observed that compared to FI plants, $[ABA]_{xylem}$ was significantly increased in PRD-treated tomatoes and greater than in ones treated with DI; they also pointed out that comparison of irrigation treatments relatively recently after an alternation event may produce this result, whereas comparison much later after such an event may result in no differences between PRD and DI treatments. Interestingly, Topcu et al. (2007) observed that $[ABA]_{xylem}$ is actually higher in DI than in PRD plants before irrigation events, while

Table 1. Effects of full irrigation (FI), partial rootzone drying (PRD), and deficit irrigation (DI) on plant water use (PWU), fruit DW, and plant water use efficiency (WUE) of tomatoes. Different letters within columns indicate significant different difference by Tukey's Studentized Range (HSD) Test at $P \leq 0.05$.

Treatment	PWU (L plant^{-1})	Fruit DW (g plant^{-1})	WUE (g L^{-1})
FI	29.56a	44.05a	1.49b
PRD	21.19b	36.08b	1.70a
DI	21.19b	36.03b	1.70a

after irrigation the reverse is true. It is apparent that $[ABA]_{xylem}$ values of PRD and DI plants are very dynamic, the results being very much dependent on the sampling time. Further studies with more frequent xylem sap sampling are therefore required. Such studies would make it possible to reveal concomitant development of $[ABA]_{xylem}$ and g_s acting to optimize the ABA signalling system under PRD and DI treatment, thereby maximizing WUE (Dodd et al., 2006).

Our results also show that, given a similar soil water deficit in the whole pot, there was a general trend for Ψ_l, g_s, and A to be lower in DI than in PRD plants, although for only two, three, and three events, respectively, was the difference significant (Figs. 1, 2, and 3). These results indicate that PRD may be superior to DI in maintaining leaf gas exchange and shoot water status. Similar results were reported in tomato by Topcu et al. (2007).

Plant biomass (DW of leaves, stems, and fruits) of tomatoes under the three irrigation treatments is presented in Fig. 6A. At the last two harvests, total plant DW was higher in FI compared to PRD and DI plants, even though the difference was significant only at the final harvest (Fig. 6A). Greater plant DW at the final harvest in FI than in PRD and DI plants is due to higher fruit DW and not to an increase of leaf and stem DW. Figure 6B shows biomass partitioning among leaves, stems, and fruits of tomatoes under FI, PRD, and DI treatments.

Basically, there was no significant effect of irrigation treatments on the biomass allocation among aboveground plant organs. However, in all treatments there was a clear trend of increasing allocation of biomass from vegetative parts to the fruits, as the highest sink for assimilates in tomato (Ho et al., 1987; Ho, 1996). Root biomass was not determined in the present study, although Mingo et al. (2004) showed that PRD induced increase of root growth in tomato. It was also observed that fruit water content was lower in DI and PRD than in FI treatment (data not shown). Lower water content in tomato fruit could be advantageous for the tomato-processing industry because less energy would be needed to evaporate water from the fruit during the processing procedure (Zegbe-Dominguez et al., 2003).

Crop water use efficiency (WUE) was defined as DW of produced fruit per liter of applied irrigation water. The results show that PRD and DI plants produced more fruit biomass per liter of water (1.70) compared to FI plants (1.49), thus significantly increasing WUE (Table 1).

These results confirmed benefits of the PRD technique as a means of increasing WUE in tomato that were also found in other studies (Davies et al., 2002; Zegbe-Dominguez et al., 2003). However, similar improvement of WUE by PRD and DI treatments implies that irrigation volume rather than irrigation methods is more important in determining crop yield, as was recently suggested by several authors (Fernández et al., 2006; Tahi et al., 2007).

It can be concluded that compared to DI, PRD has some advantages in regulating leaf gas exchange and maintaining shoot water status. However, these advantages at the leaf level in the short term did not bring about any benefits at the whole plant level in the long term, as both treatments resulted in similar fruit yield and WUE. On the other hand, this may indicate that the PRD strategy can be optimized so as to maximize cumulative physiological effects of the root-sourced signaling system, thereby achieving maximal crop yields and WUE values.

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ЕФЕКТИ ДЕЛИМИЧНОГ СУШЕЊА КОРЕНОВА И ДЕФИЦИТА НАВОДЊАВАЊА НА ФИЗИОЛОГИЈУ И РАСТЕЊЕ ПАРАДАЈЗА

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У раду су истраживани ефекти делимичног сушења коренова (PRD), дефицита наводњавања (DI) и пуног наводњавања (ФИ) на физиологију парадајза. Код PRD и DI биљака водни потенцијал листова и проводљивост стома су били значајно нижи, док је концентрација ABA у ксилему била већа у поређењу са FI биљкама. Фотосинтеза је била слична код свих третмана. PRD и DI третмани су значајно повећали ефикасност коришћења воде, редуковали су суву масу плодова, али нису имали утицаја на суву масу листова и стабла.