REGULATED DEFICIT IRRIGATION (RDI) AND PARTIAL ROOT DRYING (PRD) EFFECTS ON PLANT AND FRUIT GROWTH AND PEDICEL ANATOMY IN TOMATO

Running title: Tomato fruit growth and pedicel anatomy

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A growth chamber experiment was carried out to study the effects of regulated deficit irrigation (RDI) and partial rootzone drying (PRD) on tomato plant and fruit growth and pedicel anatomy. The RDI treatment was 50% of water given to fully irrigated (FI) plants and the PRD treatment was 50% of water of FI plants applied to one half of the root system while the other half dried down, with irrigation shifted when soil water content of the dry side decreased to *ca.* 20%. Plant and fruit growth parameters were measured and sections of fruit pedicels (above, within and below the abscission zone) were made for analysis of xylem and phloem areas. RDI significantly reduced plant and fruit growth, though PRD reduced shoot growth while having no significant effect on fruit growth. PRD treatment increased phloem area and reduced xylem area in earlier stages of fruit development, although RDI reduced xylem area at the abscission zone in all phases of fruit development and this could lead to hydraulic and chemical isolation of fruits. Greater hydraulic isolation of PRD fruits from plant vegetative parts could explain the smaller effect of PRD treatment on fruit growth.

Key words: tomato, partial root drying, pedicel anatomy, regulated deficit irrigation.

EFEKAT REGULISANOG DEFICITA IRIGACIJE (RDI) I DELIMIČNOG SUŠENJA KORENA (PRD) NA RASTENJE PLODOVA PARADAJZA I ANATOMIJU PETELJKE

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Izvod

U cilju proučavanja efekata regulisanog deficita navodnjavanja (RDI) i delimičnog sušenja korena (PRD) na rastenje ploda paradajza i anatomiju peteljke, postavljen je eksperiment u komori za gajenje biljaka. Biljke izložene RDI tretmanu zalivane su sa 50% vode u poređenju sa optimalno navodnjavanim biljkama (FI), dok je kod biljaka izloženih PRD tretmanu polovina korenovog sistema zalivana sa 50% vode dok druga polovina korena nije zalivana, pri čemu je vršena inverzija strana kada se vlažnost supstrata u nezalivanoj strani spusti na oko 20%. Mereni su parametri rastenja biljaka i plodova, a na presecima peteljki ploda (pre, posle i u zoni abscisije) su mereni površina ksilema i floema. RDI tretman je značajno redukovao rastenje biljaka i plodova, dok je PRD tretman redukovao rastenje izdanka, ali nije imao značajan efekat na rastenje ploda. PRD tretman je uticao na povećanje površine floema i redukciju površine ksilema u ranim fazama razvića ploda, dok je RDI tretman redukovao površinu ksilema u zoni abscisije u svim fazama razvića ploda, što bi biti uzrok hidraulične i hemijske izolovanosti plodova. Veća hidraulična izolovanost PRD plodova od ostatka biljke može biti objašnjenje manjeg efekta PRD tretmana na rastenje plodova.

INTRODUCTION

Drought is one of the most common environmental stresses that may limit agricultural production worldwide. Many vegetable crops, including tomato, have high water requirements and in most countries irrigation is necessary for successful vegetable crop production (FERERES and SORIANO 2007). However, in many countries, as a consequence of global climate changes and environmental pollution, amount of water in agriculture is reduced. Therefore, considerable emphasis is placed on crop management for dry conditions with the aim to make plants more efficient in water use (FAO 2002).

RDI is a method that irrigates the entire root zone with an amount of water less than the potential evapotranspiration and the minor stress that develops has minimal effects on yield (ENGLISH and RAJA 1996). Partial root drying (PRD) is a further development of RDI. With the PRD technique half of the plant root zone is irrigated while the other half is allowed to dry out partially (STOLL *et al*. 2000). The treatment is then reversed, allowing the previously well-watered side of the root system to dry down while fully irrigating the previously dry side. Both RDI and PRD were developed on the basis of knowledge of the plant’s reactions to drought. Transport of chemical signals from root to shoot and fruits, as well as transport of water and assimilates, depends also on the vascular characteristics of xylem and phloem elements, especially under drought conditions (LOVISOLO and SCHUBERT 1998).

The effect of PRD appears to be smaller in fruits compared with vegetative parts of PRD-treated plants (DAVIES *et al*. 2000; KANG and ZHANG 2004). DAVIES *et al*. (2000) suggested that xylem area reduction, which occurred during fruit development, might restrict the free movement of ABA from shoot to fruit. Therefore, the ABA chemical signal induced by PRD treatment and transported through the xylem would not accumulate in fruit epidermis as much as in the leaves and, consequently, fruit growth would be less reduced than shoot growth. This hypothesis that PRD may induce relative chemical and hydraulic isolation of tomato fruit is also supported by anatomical observations of xylem tissue within the pedicel of fruiting trusses. LEE (1989) and ANDRÉ *et al*. (1999) demonstrated a reduced xylem cross-sectional area in the abscission zone of tomato pedicel which was interpreted as the cause of a high hydraulic resistance. Direct hydraulic resistance measurements done by VAN IEPEREN *et al*. (2003) showed that overall xylem hydraulic resistance between the shoot and fruit tended to increase with fruit development because of the dominating role of hydraulic resistance in the abscission zone. In contrast, MALONE and ANDREWS (2001) showed that over 90% of the hydraulic resistance between the stem and fruit must reside within the fruit pericarp and not in the abscission zone. However, the effect of a PRD treatment was not considered in these studies. Therefore, because of these contrasting conclusions, we have used the PRD treatment for testing the anatomical basis of the hydraulic isolation hypothesis.

Thus, the aim of this report is to describe the effects of RDI and PRD treatments on tomato plant growth and development as well as on pedicel anatomy, together with their hydraulic implications for the transport of water and assimilates to the developing fruit.

MATERIALS AND METHODS

The experiment was conducted in a growth chamber at the Faculty of Agriculture, University of Belgrade (Serbia). Tomato plants (*Lycopersicon esculentum* L., cv. Sunpak) were raised from seed in compost - (Potground H, Klasmann-Deilmann, Germany) filled seed trays in a growth chamber operating with a 14h photoperiod with light intensity at plant level 300 $\mu molm^{-2}s^{-1}$, temperature 25/18°C and relative humidity 70%. Plants were maintained well-watered until the appearance of the fifth leaf. After that, the root system of each plant was split into two hydraulically separate compartments. Ten days after transplanting the plants, the following three treatments were applied: 1) full irrigation (FI) in which the whole root system was irrigated daily to a soil water content close to field capacity, determined before the experiment to be 35%; 2) regulated deficit irrigation (RDI) in which 50% water of the FI treatment was evenly applied to the whole root system, and (3) partial root drying (PRD) where 50% water of FI was applied to one half of the root system while the other half was allowed to dry, and the irrigation was shifted when soil water content of the dry side had decreased to 15%-20%. Compartments were classified as PRD-L (left side) and PRD-R (right side). Plants were irrigated daily and the amount of water to be applied was calculated on the basis of soil water content readings. The volumetric soil water content was measured daily for both irrigated and non-irrigated compartments by theta probe-type ML2X (Delta-T Device, Ltd, UK). Ten plants per treatment were selected randomly for measurements of growth parameters. Plant growth was characterized by plant height, number of leaves, leaf area, fruit diameters and number of fruits per plant on the end of experiment. Final plant height was measured and final leaf area after destructive sampling. For anatomical measurements pedicels were collected at four stages during fruit development corresponding to the phases defined by GILLASPY *et al*. (1993). Each pedicel was cut 5mm above, 5mm below and at the abscission zone by Leica VT1000 S microtome with vibrating blade and stained for anatomy measurements according to RUZIN (1999). Sections were examined using a Leica DMLS light microscope and documented with a Leica DC 300 digital camera. The number and diameter of xylem elements and total xylem and phloem areas/cross section were measured using an image analysis system connected to the microscope (Leica IM 1000). Student's unpaired t-test (Sigma Plot 6.0 for Windows - SPW 6.0, Jandel Scientific, Erckhart, Germany) was used to test traits for significant differences between irrigation treatments.

RESULTS AND DISCUSSION

Changes of volumetric soil water content in FI, PRD and RDI treated plants during the experimental period are shown in Fig. 1.

Figure 1

Generally, the soil water contents were significantly lower in DI and in the dry side of PRD treatment compared with those of FI where soil water content was maintained close to field capacity (35%). Soil water content of the RDI treatment decreased during the experimental period and after 20 days of treatment was maintained between 15 and 20%. During the first and second cycles of wetting PRD plants, the soil water content of the wet side was kept similar to FI. However, after the second shifting of the PRD irrigation, the soil water content of the wet side was lower than that of FI by 3-10%. 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*. 2004), though others were able to maintain the soil water content of the wet side of PRD-treated tomato plants similar to that of the FI treatment during the whole treatment period (SOBEIH *et al*. 2004). Soil water content results also suggested that water uptake from the irrigated side of the PRD system was greater (as a consequence the soil water content in this side is reduced) than that of a single side of the control plants.

The effect of PRD on plant growth was significant and by the end of experiment plant height of PRD-treated plants was 19% less than that of FI plants and 14.1% than that of RDI-treated plants. A similar decrease was found for number of leaves and for total leaf area in PRD and RDI treated plants compared to FI plants (Table 1), consistent with the results of other tomato PRD experiments (ZEGBE-DOMINGUEZ *et al*. 2003). However, in contrast PRD and RDI treatments had very different effects on fruit growth. Number of fruits and fruit diameter of PRD-treated plants were both similar to those of the FI treatment, whereas fruit diameter and number of fruit of RDI-treated plants were less. PRD reduced fruit fresh wt. although dry weight of PRD fruits was not significantly differed compared to FI treatment, as well as the fruit/shoot DW. However, RDI significantly reduced both the fresh and dry weight of fruit and also the fruit/shoot DW ratio (Table 1). Similar results were also found by ZEGBE-DOMÍNGUEZ *et al*. (2004), KIRDA *et al*. (2004), TOPCU *et al*. (2006).

Table 1

Cross-sections of the pedicels above and below the abscission zone showed an anatomy typical for Solanaceae stems. In all the irrigation treatments there was a tendency to increase xylem areas during fruit formation and growth, especially in the zones near the stem and near the fruit (Table 2). RDI treatment, in comparison with the FI treatment, reduced xylem area during all phases of fruit growth, while xylem area in PRD-treated plants initially declined (at flowering time) but increased in the later phase of fruit growth. At the end of experiment the xylem area of ripe fruits was the smallest in the abscission zone of RDI-treated plants (Table 2). In the abscission zone, compared with the other zones, the xylem area was less developed during all stages of fruit development, as other authors previously reported (LEE 1989, VAN IEPEREN *et al.*2003). According to them the abscission zone is the place of greatest hydraulic resistance in the tomato fruit pedicel. Thus, the xylem area reduction and consequent restriction of the flow of water to the fruit in the abscission zone provide a structural explanation for the high hydraulic resistance of tomato pedicels and hydraulic isolation of fruit from the rest of the shoot (EHRET and HO 1986; LEE 1989; ANDRÉ *et al*. 1999). The reduced xylem area in the abscission zone of PRD-treated plants during flowering and the early phases of fruit development may influence the transport of chemical signals in accordance with the hydraulic hypothesis of DAVIES *et al*. (2000).

Table 2

Phloem areas also increased during development, but in contrast to the xylem, the phloem was much more developed in the abscission zone in comparison with other zones. The effect of RDI treatment on phloem area decreased in most phases of fruit development by around 7-35 %, but RDI had no effect on the phloem in abscission zones (Table 3). PRD treatment increased phloem areas at most positions during fruit development by 40-80%. In the abscission zone during all phases of fruit development the PRD treatment significantly increased the phloem area, especially in the latest phase of fruit development (over 150%) (Table 3).

Table 3

The phloem also contribute to fruit water content and indeed Ho *et al*. (1987) estimated that 90% of the total water content of the fruit is imported *via* the phloem. The gradual and highly significant increase of phloem area in all zones of the pedicel, especially near the fruit, and particularly in PRD-treated plants, might also influence the import of assimilates and consequent source/sink relations between shoot and fruit. For tomato, as for other horticultural plants, photosynthetically-active mature leaves are an active source of assimilates for sink organs, such as flowers, fruits or roots. Among sink organs, fruits are defined as a high priority in the context of competition for assimilates between alternative sinks (WARDLAW 1990), although GAUTIER *et al.* (2001) demonstrated the competition between fruits and leaves of tomato by flower pruning. An increase in phloem area during fruit development would ensure the efficient transport of organic compounds from shoot to fruit that facilitate the metabolic processes necessary for seed and fruit ripening (GILLASPY *et al*. 1993).

CONCLUSION

In conclusion, we have shown that the RDI treatment may reduce the hydraulic connectivity of fruit pedicel and consequently lead to reduced fruit growth and final FW. The anatomy results for the PRD treatment indicated that relative hydraulic isolation of tomato reproductive organs might have occurred but only in the abscission zone and in the earlier stages of flower and fruit development. Increased phloem area and ratio of fruit DW to shoot DW of PRD-treated plants supported the view that changed assimilate partitioning (from shoot to root) could help in explaining the effects of PRD on fruits. Further investigation of functionality of fruit and pedicel vascular systems as well as assimilate partitioning would help in understanding the mechanisms operating in PRD-grown tomato plants.

Acknowledgements. -This study was partly supported by the European Commission FP6 CROPWAT (FP6-2005-INCOWBC/SSA-043526) and Ministry of Science Republic of Serbia (No TR 20025).

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Figure 1

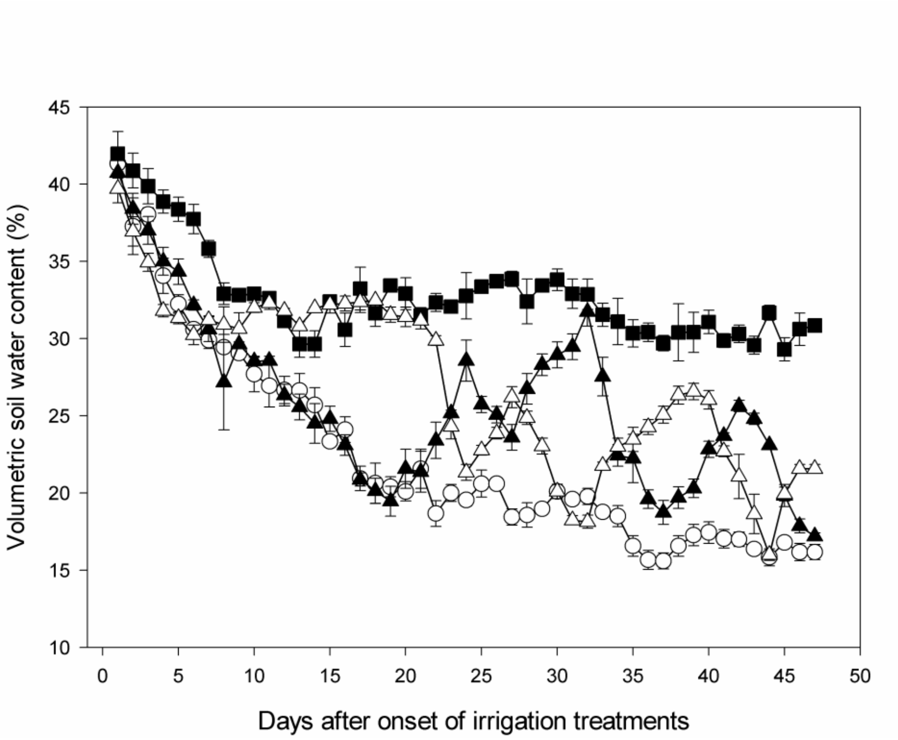
Volumetric soil water content (%)
Days after onset of irrigation treatments
45
40
35
30
25
20
15
10
0
5
10
15
20
25
30
35
40
45
50

Table 1

Trait	Treatments FI	RDI	PRD
Plant height (cm)	87.6 ± 0.9	83.1 ± 1.5	71.3 ± 1.2***
No of leaves per plant	19.3 ± 0.7	16.7 ± 0.3*	15.7 ± 0.3**
Leaves area (dm^2)	111.3 ± 6.6	85.5 ± 2.3*	89.3 ± 2.3*
No of fruits per plant	11.0 ± 1.5	9.7 ± 0.7	11.7 ± 2.0
Average fruit diameter (mm)	73.9 ± 0.2	56.4 ± 0.2***	71.3 ± 0.5
Shoot DW (g)	49.3 ± 2.1	42.9 ± 1.4	47.4 ± 1.1
Average fruit FW (g)	173.7 ± 7.8	75.0 ± 2.5***	137.7 ± 14.9
Average fruit DW (g)	12.2 ± 0.5	6.8 ± 0.2***	11.0 ± 1.2
Fruit DW/Shoot DW	0.60 ± 0.04	0.40 ± 0.04*	0.55 ± 0.04

Table 2

		Xylem area at the pedicel cross section		
Developmental stage	zone	FI	RDI	PRD
Phase I	Near the fruit	0.052±0.010	0.049±0.012	0.043±0.006*
	Abscission zone	0.028±0.008	0.028±0.006	0.021±0.004*
	Near the stem	0.056±0.012	0.048±0.015	0.044±0.007*
Phase II	Near the fruit	0.055±0.014	0.055±0.013	0.113±0.017***
	Abscission zone	0.065±0.019	0.033±0.009*	0.040±0.015*
	Near the stem	0.262±0.053	0.197±0.093	0.482±0.222*
Phase III	Near the fruit	0.097±0.037	0.084±0.020	0.128±0.031
	Abscission zone	0.067±0.019	0.045±0.017*	0.047±0.007*
	Near the stem	0.568±0.169	0.529±0.164	0.651±0.425
Phase IV	Near the fruit	2.947±1.294	3.136±0.638	3.761±1.737
	Abscission zone	0.416±0.098	0.272±0.033*	0.550±0.063
	Near the stem	4.142±0.449	4.964±2.490	5.547±2.789

Table 3

		Phloem area at the pedicel cross section		
Developmental stage	zone	FI	RDI	PRD
Phase I	Near the fruit	0.794±0.144	0.672±0.160**	0.511±0.077***
	Abscission zone	1.681±0.897	1.871±0.483	1.465±0.602
	Near the stem	0.736±0.146	0.573±0.167*	0.511±0.058***
Phase II	Near the fruit	1.219±0.271	1.305±0.212	2.220±0.227***
	Abscission zone	2.591±0.518	2.444±0.646	4.093±0.928*
	Near the stem	1.340±0.165	1.079±0.175*	1.786±0.343**
Phase III	Near the fruit	2.553±0.690	2.091±0.668	3.828±0.784**
	Abscission zone	4.731±1.730	5.530±1.831	6.605±1.419*
	Near the stem	1.501±0.302	1.412±0.252	2.450±0.527**
Phase IV	Near the fruit	5.825±2.300	3.814±1.356	9.804±2.059*
	Abscission zone	20.511±9.220	24.088±14.392	51.782±16.607**
	Near the stem	3.866±0.810	3.147±1.441	3.856±1.423

Tables and figures caption list

Figure 1. Changes in volumetric soil water content for full irrigation-FI (■), partial rootzone drying PRD-L (▲) and PRD-R (Δ), and regulated deficit irrigation-RDI (○) treatments of tomato plants.

Table 1. The effects of full irrigation (FI), regulated deficit irrigation (RDI) and partial root drying (PRD) on parameters of tomato growth. Means are for five plants ± SE (, ** and *** indicate differences between FI and RDI/PRD samples significant at $p \leq 0.05$, $p \leq 0.01$and $p \leq 0.001$, respectively).*

Table 2. Xylem area of flower and fruit pedicels near the stem, at the abscission zone and near the fruit in RDI, PRD treated and control plants (FI). (, ** and *** indicated differences between FI and RDI/PRD samples significant at $p \leq 0.05$, $p \leq 0.01$and $p \leq 0.001$, respectively).*

Table 3. Phloem area of flower and fruit pedicels near the stem, at the abscission zone and near the fruit in, RDI, PRD treated and control plants (FI). (, ** and *** indicated differences between FI and RDI/PRD samples significant at $p \leq 0.05$, $p \leq 0.01$and $p \leq 0.001$, respectively).*