

EFFECT OF PARTIAL ROOT DRYING ON
GROWTH AND PHOTOSYNTHESIS OF TOMATO
(*Lycopersicon esculentum L.*)

Sladjana Savic¹

Abstract: Tomato plants were grown in commercial compost with the root system divided equally in two parts (PRD technique). At the end of vegetative and during generative stage of development, half of the root system was exposed to drought, while the remainder of the root system was irrigated. One PRD treatment took c.10 days and during this period the soil water content in the dry root side was reduced to 30%. After this, the treatment was reversed, allowing the previously dry compartment to be well-watered and the well-watered compartment to dry down. In control plants both compartments were watered daily to drip point throughout the experimental period.

During experimental period the following measurements were done: plant height, leaf number and area, number of flower trusses, number and diameter of fruit, leaf gas exchange (photosynthesis and transpiration), leaf water potential, leaf apoplastic pH and water-use efficiency (WUE). Obtained results of plants height and leaf number and area showed that, as a consequence of PRD treatment, the growth of whole plants was reduced, but not fruit, although WUE was increased. These results pointed out that with PRD technique it is possible to reduce irrigation water without significant reduction effect on tomato yield.

Key words: partial root drying (PRD), tomato, growth, photosynthesis, transpiration, water use efficiency (WUE).

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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 supplemental irrigation is necessary for successful vegetable crop production. However, in many countries as a consequence of global climate changes and environmental pollution, water use for agriculture is reduced. Therefore, great emphasis is placed in the area of crop physiology and crop management for dry conditions with the aim to make plants more efficient in water use.

Partial root drying is an irrigation technique where half of the root zone is irrigated while the other half is allowed to dry out. 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. Implementing the PRD technique is simpler, requiring only the adaptation of irrigation systems to allow alternate wetting and drying of part of the rootzone (Loveys et al. 2000). The PRD technique was developed on the basis of knowledge of root-to-shoot chemical signalling in drying soil and, therefore, understanding of this process is essential for successful application of the PRD technique.

It is a new method whose application in the world started several years ago. Until now, the greatest success in PRD application was in Australia where the drought effect is very outstanding. In vineyard irrigation in Australia, it was shown that this process of plant growing increases the yield and quality of fruits (Dry et al., 2000); besides, it enlarges the efficiency of water absorption. Until now, the process of partial root drying has not been applied in an agricultural practice in our country. In the present paper we review some of the recent data concerning the theoretical background of the PRD technique and we also present some of our own data concerning the effects of PRD treatment on tomato plants grown and leaf gas exchange in control conditions. This knowledge will be valuable in making modifications to our irrigation and, possibly, fertilization strategies in tomato and other horticultural plants in the future.

Material and Methods

Seeds of tomato (*Lycopersicon esculentum* L.) line L-4 were germinated in commercial compost in a growth cabinet (photoperiod was 14h; light intensity at plant level 250 molm⁻² s⁻¹, temperature 28/20°C and relative humidity 70%) until the emergence of the fifth leaf. The plants were then removed from their pots and the root system of each plant was divided into two and repotted into two separate plastic bags (volume 3.0 dm³ each) containing the same compost. The bags were joined by plastic tape and placed together into a big pot. Thereby, the root system of each plant was split into two hydraulically separate compartments.

Pots were watered daily to drip point for 1 week until the root systems were established in both compartments and before the PRD regime was started. For PRD treatment we repeated the Davies et al. (2000) experiment in such a way that during the vegetative and generative stages of tomato development, half of the root system of PRD was maintained in a dry state, while the remainder of the root system was watered. One PRD treatment took *c.* 10 days and during this period the soil water content in the dry root side was reduced to 30%. After this, the treatment was reversed, allowing the previously dry compartment to be well-watered and the well-watered compartment to dry down. In control plants both compartments were watered daily to drip point throughout the experimental period.

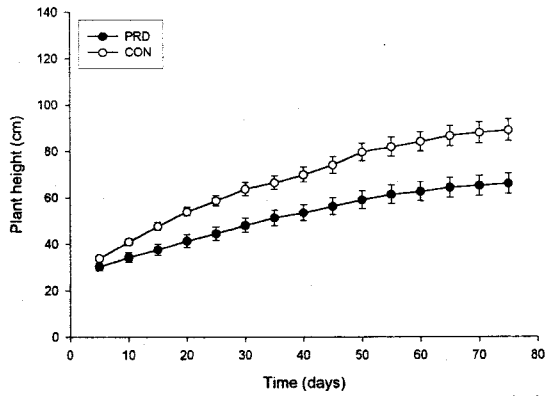
For measurements of the investigated parameters ten plants per treatment were selected randomly. Plant height, leaf number and leaf area (Džamić et al., 1999) were determined every 5 days, as well as number of flower trusses per plants. At the end of the experiment, measurements of shoot and root dry weight were done and root/shoot ratio was calculated. Number and diameter of fruit were also monitored during the same time course. In the distal part of the youngest fully expanded leaf, measurements of leaf gas exchange (photosynthesis and transpiration) were done by infrared gas analyzer (Waltz, Germany). Measurements of leaf water potential (by pressure probe) and leaf apoplastic pH, by the centrifugation method (Dannel et al. 1995) and water use efficiency (WUE), were done several times during the experimental period.

Results and Discussion

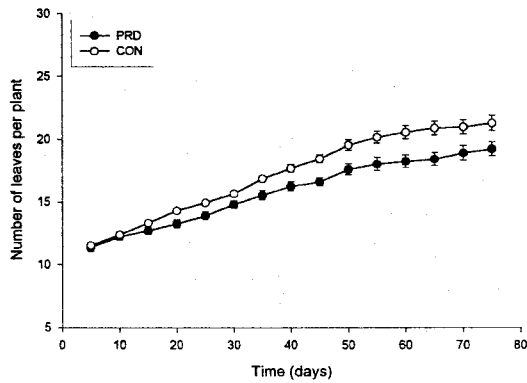
Effect of the PRD on the growth vegetative organs

The results showed that the effect of PRD on the growth of the whole plant was significant and the decline in plant height at the end of the experiment was (c.26%) compared to well-watered plants (Graph.1.).

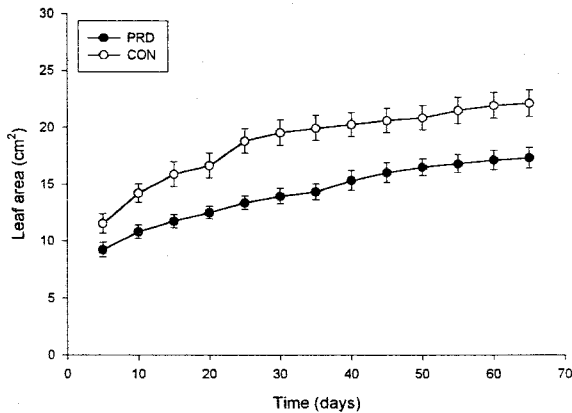
Leaf growth reduction was the result of both decrease of the number of leaves (c.10%) (Graph.2.) and leaf area (c.22%) (Graph.3.). Biomass results also showed, similarly to Davies et al. (2000), a significant PRD effect on shoot and root growth (Tab.1.). Root/shoot ratios were similar in both treatments (*c.* 0.08) and they didn't confirm that PRD treatment enhanced root growth (Tab.1.). Therefore, our results confirmed that applied partial root drying of the root system was sufficient to trigger a shoot response. Consistent with the evidence from other split root procedures (Davies et al. 2000; Dry et al. 2000), water potentials of PRD plants did not differ significantly from those of well-watered plants. During the whole experimental period bulk values were *c.* 0.38 MPa (Tab. 1.). These results support the hypothesis that a root-sourced signal and not a leaf-sourced signal may be responsible for triggering growth reduction in these PRD plants.



Graph. 1. - The effect of PRD treatment on the plant height



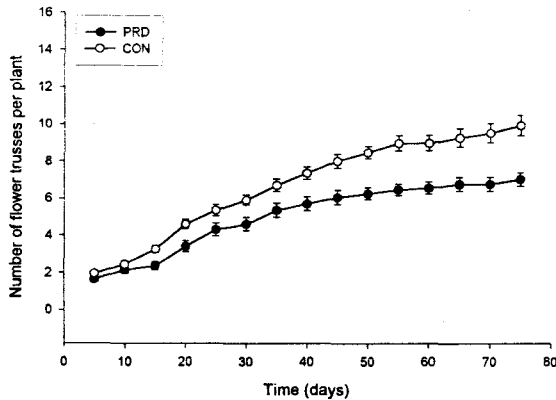
Graph. 2. - The effect of PRD treatment on the number of leaves



Graph. 3. - The effect of PRD treatment on the leaf area

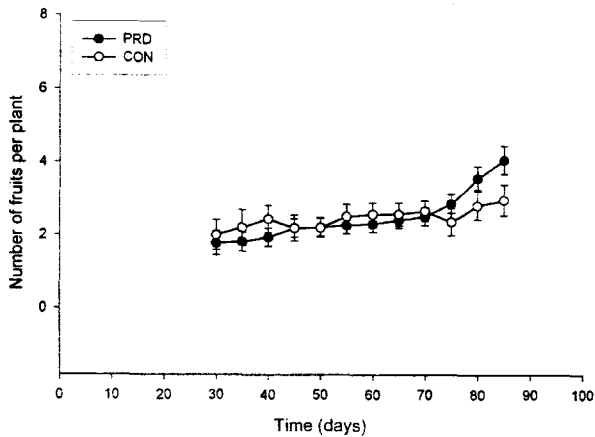
Effect of the PRD on the growth generative organs

Comparing to the PRD effect on vegetative parts, the effects on generative plants organ was smaller. Obtained results showed that PRD caused a significant reduction in flower trusses but not in fruits numbers and diameters. The results showed that the effect of PRD on number of flower trusses was significant and the decline in at the end of the experiment was c.28.8% compared to well-watered plants (Graph.4.).



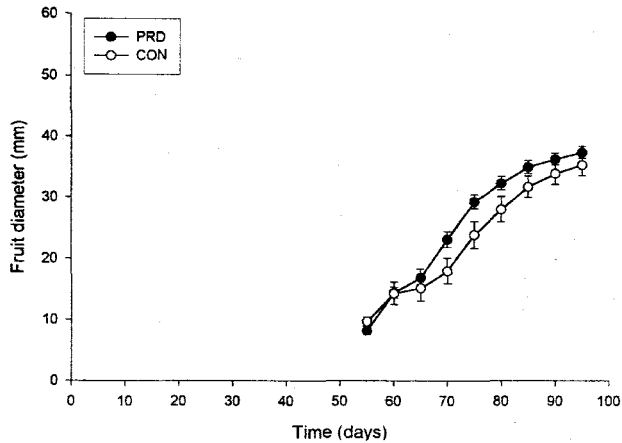
Graph. 4. - The effect of PRD treatment on the number of flower trusses

Our results showed that the effect of PRD on number of fruits was significant and the increase at the end of the experiment was c.23% compared to well-watered plants (Graph.5.), but this effect was not significant for fruit diameter (Graph.6.).



Graph. 5. - The effect of PRD treatment on the number of fruits

As a result of PRD treatment, it came to the changing of the hormonal status of the examined plants and the synthesis of the growth retardants (abscission acid probably) that led to the growth reduction of the vegetative organs and flowers but not the fruits. It indirectly shows that PRD treatment can lower the abortificiency and flower abscission by changing the hormonal balance and assimilates transportation. Dry et al. (1996) state that the reduction of shoot strength (of trunk and leaves) brought to the relative increasing of sink fruit strength, therefore, the carbohydrates, previously directed toward the shoot, are redirected toward the fruit now.



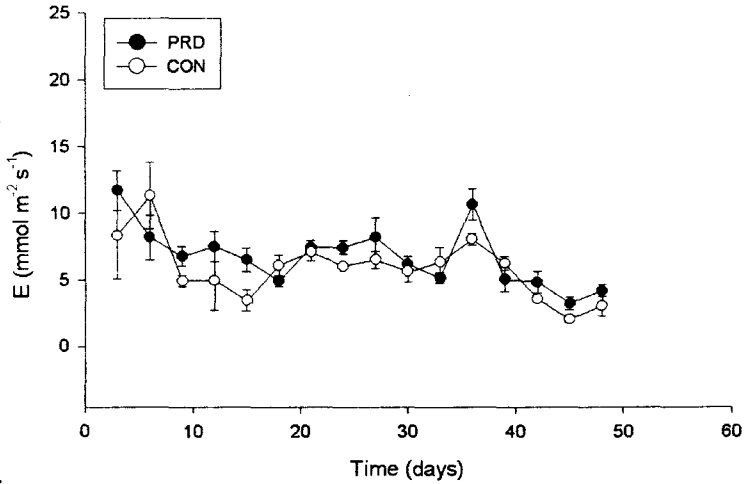
Graph. 6. - The effect of PRD treatment on the fruits diameter

Effect of the PRD on the leaf gas exchange parameters

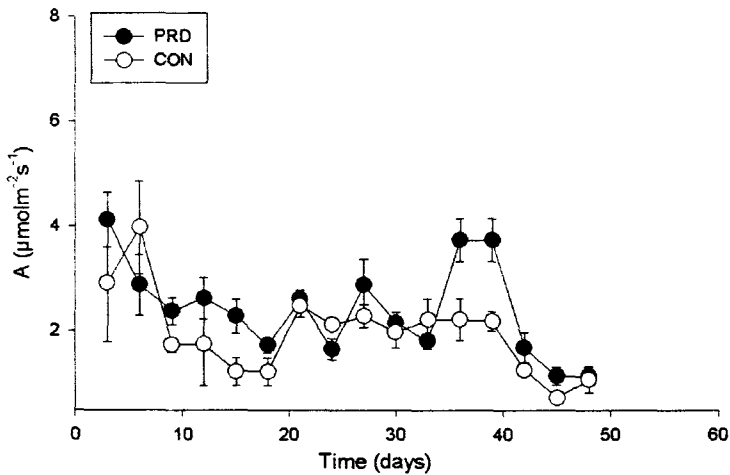
In our study, the change in gas exchange was less than expected. We found no effect of PRD on stomatal conductance or transpiration (Graph.7.) and photosynthesis (Graph.8.). This differed from several reports that attributed stomatal closure to chemical signals from roots in drying soil (Davies et al., 2000; Holbrook et al., 2002).

However, Saab and Scharp (1989) also failed to record a change in stomatal conductance, while observing a highly significant reduction in growth rate due to drying soil around split root maize plants. An explanation of such reactions might be that stomatal sensitivity to chemical signals such as ABA is modulated by differences in xylem pH (Wilkinson and Davies, 2002). Our results didn't confirm any significant differences in apoplastic pH values that in turn might cause changes in stomatal conductance (Tab.1.). Croker et al. demonstrated significant genotypic differences in stomatal sensitivity to non-

hydraulic signaling between six deciduous tree species. Therefore, an alternative explanation is that stomata of the tomato genotype we used were less sensitive to the root-sourced chemical signal in PRD grown tomato plants.



Graph. 7. - The effect of PRD treatment on the transpiration



Graph. 8. - The effect of PRD treatment on the photosynthesis

Effect of the PRD on the water use efficiency (WUE)

Water use efficiency (WUE) was calculated as a fruit dry weight per unit evapotranspired water. PRD plants produced more fruit biomass per dm⁻³ water (0.340) compared to control plants (0.214). It is clear that highly significant

increases in WUE have been achieved. What is not so clear is the mechanism whereby this has been achieved. The increasing efficiency of water use for fruit biomass production might be due to increasing assimilate allocation to the fruit of PRD plants, but this hypothesis should be investigated further.

T a b.1.- The effect of partial root drying on shoot and root growth, root/shoot ratio, water use efficiency (WUE), leaf apoplastic pH and leaf water potential (Ψ_l).

Trait	CON	s.e.	PRD	s.e.	Significance
Shoot DW (g)	18.66	0.74	13.16	0.51	P<0.001
Root DW (g)	1.05	0.07	0.81	0.04	P<0.01
Ratio root/shoot	0.06	4.89e ⁻³	0.07	4.18e ⁻³	Ns
WUE (gdm ⁻³)	0.214	-	0.340	-	P<0.001
Apoplastic pH	6.18	0.12	6.11	0.07	Ns
Water potential (-MPa)	0.38	0.026	0.40	0.027	Ns

Conclusion

Partial root drying significantly reduced shoot growth as well as leaf expansion of tomato plants in the absence of any changes in shoot water status. Therefore, it clearly indicates involvement of chemical root-to-shoot signals.

Comparing to the PRD effect on vegetative parts, the effects on generative plants organ was smaller. Obtained results showed that PRD caused a significant reduction in fruit trusses but not in fruits numbers and their diameters.

In our investigations we found no effect of PRD on stomatal conductance (or transpiration and photosynthesis), probably because our results didn't confirm any significant differences in apoplastic pH values that in turn might cause changes in stomatal conductance.

Water-use efficiency was significantly higher in PRD than in control plants. PRD plants produced *c.*30% more fruit biomass per dm⁻³ water compared to control plants. It is clear that highly significant increases in crop WUE have been achieved. These results pointed out that with PRD technique it is possible to reduce irrigation water without significant reduction effect on tomato yield.

This knowledge will be valuable in making modifications to our irrigation and, possibly, fertilization strategies in tomato and other horticultural plants in the future.

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UTICAJ DELIMIČNOG SUŠENJA KORENOVA NA RASTENJE I
FOTOSINTEZU PARADAJZA
(*Lycopersicon esculentum L.*)

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Re z i m e

U ovom radu predmet istraživanja bio je efekat delimičnog sušenja korenova (DSK) na rastenje i razmenu gasova kod biljaka paradajza (*Lycopersicon esculentum L.*). Biljke su gajene u komercijalnom supstratu sa korenovim sistemom podeljenim u dve plastične kese (svaka zapremine 3.0 dm³) - DSK tehnika. Kese su spojene lepljivom trakom i zajedno stavljene u velike posude. Tako je korenov sistem svake biljke bio razdvojen u dva hidraulično izolovana odeljka. U toku vegetativne i generativne faze razvića paradajza polovina korenovog sistema je zasušivana, dok je druga polovina optimalno zalivana. Jedan DSK ciklus traje oko deset dana i u toku tog perioda vlažnost supstrata u zasušivanom delu korenovog sistema se spušta na 30% optimalnog vodnog kapaciteta. Zatim se vrši inverzija, tako da se zasušivana polovina korena zaliva, a zalivana polovina zasušuje. Kod kontrolnih biljaka ceo koren je optimalno zalivan tokom celog eksperimentalnog perioda.

Za merenje ispitivanih parametara odabrano je deset biljaka po tretmanu. Visina biljaka, broj i površina listova su mereni svakih 5 dana kao i broj cvetnih grana. U toku istog vremenskog intervala mereni su i broj i prečnik ploda. U distalnom delu najmlađeg razvijenog lista izvršena su merenja razmene gasova (fotosinteze i transpiracije - pomoću infracrvenog gasnog analizatora), potencijala vode u listovima (pomoću komore pritiska) i apoplastičnog pH (metodom centrifugiranja). Efikasnost korišćenja vode (WUE) je obračunata kao odnos suve mase plodova po jedinici evapotranspirisane vode. Merenja suve mase izdanka i korena su obavljena na kraju eksperimenata i na osnovu tih podataka izračunat je odnos koren/izdanak.

Rezultati merenja visine i suve mase su pokazali da je kao posledica DSK tretmana došlo do redukcije rastenja celih biljaka. Redukcija rastenja listova je bila posledica opadanja i broja i površine listova. Odnos koren/izdanak je bio sličan u oba tretmana i stoga nije potvrdio da je DSK tretman ubrzao rastenje

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korenovog sistema. Vrednosti potencijala vode DSK biljaka nisu se značajno razlikovale od onih koje su izmerene kod optimalno zalivanih biljaka. To je potvrdilo hipotezu da su za redukciju rasteanja kod DSK biljaka bili odgovorni signali poreklom iz korena a ne iz lista. U našim istraživanjima nije utvrđen efekat DSK tretmana na provodljivost stoma (transpiraciju) i fotosintezu, verovatno zbog toga što nije utvrđen efekat na pH apoplasta, koji bi sa svoje strane mogao da utiče na provodljivost stoma. Alternativno objašnjenje bi moglo da bude u neosetljivosti stominih ćelija ovog genotipa na hemijske signale korena. U poređenju sa efektom na vegetativne organe, DSK efekat na generativne organe je bio manji. Dobijeni rezultati su pokazali da je DSK tretman izazvao značajnu redukciju broja cvetnih grana, ali ne i broja plodova, njihove biomase i dijametra. Efikasnost korišćenja vode (WUE) bila je značajno veća kod DSK u odnosu na kontrolne biljke. DSK biljke su obrazovale c. 30% više biomase plodova po dm^{-3} vode u odnosu na kontrolne biljke. Ti rezultati ukazuju da je primenom DSK tehnike moguća redukcija količine vode za navodnjavanje, a da se pri tome ne redukuje prinos paradajza.

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