

PARTIAL ROOT DRYING (PRD): A NEW TECHNIQUE FOR GROWING PLANTS THAT SAVES WATER AND IMPROVES THE QUALITY OF FRUIT

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Summary. Partial root drying (PRD) is a new irrigation and plants growing technique which improves water use efficiency without significant yield reduction. In the present paper some of the recent data concerning PRD effects on crop plants are presented as well as some of our own results of PRD grown tomato plants. Tomato plants (*Lycopersicon esculentum* Mill.) were grown in commercial compost with the root system divided equally between two plastic pots. During the vegetative and generative stage of development, half of the root system of PRD was maintained in a dry state, while the remainder of the root system was irrigated. After c.10 days (when soil water content was reduced to 30%) the treatment was reversed, allowing the previously well-watered side of the root system to dry down while fully irrigating the previously dry side. Therefore, PRD plants received half of the amounts of water used by plants in the control treatment. During the experimental period the analyses of several plant growth and productivity and gas exchange parameters were done. The results obtained showed that as a consequence of PRD treatment the growth of whole plants was reduced with increased crop water use efficiency and sugar content.

Key words: *Lycopersicon esculentum* Mill., partial root drying, plant growth, tomato, water use efficiency

Abbreviations: PRD – partial root drying; WUE – water use efficiency; ABA – abscisic acid

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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. Recent results demonstrated that regulated deficit irrigation (RDI) and partial root drying (PRD) are the irrigation methods that tend to decrease agricultural use of water. RDI is the method where the control and management of water stress was achieved by irrigating at less than the full requirement of the plants and, thus, maintaining soil moisture at a relatively dry level. RDI significantly limits leaf growth and this treatment generally results in yield reductions (Matthews and Anderson, 1988). Partial root drying (PRD) 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. Compared to RDI, 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. In this 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 under control conditions.

The occurrence of root-to-shoot chemical signaling

The conventional view of drought is that soil drying induces restriction of water supply and this results in a sequential reduction of tissue water content, growth and stomatal conductance. While this is definitely the case, it appears that in some cases changes in leaf physiology are more closely linked to the changes in soil water content (Pasioura, 1988). This kind of reaction requires that the plants have some mechanism for sensing the availability of water in the soil and regulating stomatal conductance and leaf growth accordingly. Jones (1980) has suggested that this might involve transfer of chemical information from the roots to shoots *via* the xylem. Such control has been termed non-hydraulic or chemical signalling. This distinguishes it from hydraulic signalling, which represents transmission of reduced soil water availability *via* changes in the xylem sap tension.

For demonstration of the effects of chemical signals two different methods were frequently used. In the so-called "Passioura method" the whole plant is grown and exposed to drought in a pressure chamber in a pot to which a balancing pressure can be applied to the roots to maintain shoots at full turgor (Passioura, 1988). Another method is split root techniques where the plant root system is divided between two containers so that some roots are exposed to drying soil (and hence generate a chemical signal) while others remain under well watered conditions to supply the shoot's water requirements. Using this technique Gowing et al. (1990) apparently confirmed the existence of chemical signals in droughted roots of apple. They demonstrated that excision of drying roots (removing the putative stimulus) allowed the shoots to recover and continue to grow.

There is much interest on the nature of chemical signals produced by drying roots since this knowledge is important for understanding the mechanisms of chemical signalling. Chemical signals, according to the terminology of Jackson and Kowalevska (1983) can be negative or positive messages. Negative messages are supplied by turgid roots and promote stomatal opening and shoot growth. Therefore the production and transport of these messages decrease as the soil dries. The best example of this kind of message is reduced supply of cytokinins from dehydrated roots. Positive messages, whose production increases as the soil dries, may be an inhibitor such as abscisic acid (ABA). Changes in mineral composition and pH of xylem sap may provide additional signals.

Stoll et al. (2000) investigated the hormonal changes induced by partial rootzone drying of irrigated grapevine. Their results showed that PRD treatment increased xylem sap ABA concentration and pH, and as a result stomatal conductance was reduced. In addition, there was a reduction in the cytokinin content in roots, shoot tips and buds and as a consequence reduction of shoot growth occurred, although apical dominance of vines was intensified. Davies et al. (2000) investigated shoot-to-fruit signalling in PRD grown tomato plants and founded significant accumulation of ABA in expanded and mature leaves, but not in the fruit epidermis. They pointed out that this difference in ABA accumulation as a signal molecule may lie partly in the relative hydraulic and chemical isolation of the tomato fruit.

Agricultural benefit of root-to-shoot chemical signaling

In the past decade a large number of field studies have validated the existence of chemical signalling in the field, supporting the more artificial studies in control conditions. Loveys (1991) was the first who applied the split-root technique for inducing chemical signals in the root system of grapevine grown in field conditions and these results showed that PRD reduced vine vigour and increased the quality and yield of fruit. Excessive plant vigour is a major problem for many fruit crops, since the use of assimilates in leaf growth restricts fruit set and development. The PRD field

results, mainly from the vineyards of Southern Australia, demonstrated that in addition to the benefit in terms of reduced canopy density and consequent improvement of fruit quality, the benefit comes also in the form of improved water-use efficiency (Loveys et al., 2000).

Alternating wet and dry zones of the root system are essential to trigger the continuous root-to-shoot signal. This is necessary because the root system is not able to maintain root ABA production for long periods (Loveys et al., 2000). The frequency of the switch is determined according to soil type and other factors such as rainfall and temperature. In most of the published data the PRD cycle includes 10 to 15 days (Davies et al., 2000; Stoll et al., 2000).

Material and Methods

Tomato PRD experiment

Seeds of tomato (*Lycopersicon esculentum* Mill.) line L-4 were germinated in commercial compost in a growth cabinet (photoperiod was 14 h; light intensity at plant level $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, temperature 28/20°C and relative humidity 70%) until the appearance of the fifth leaf. The plants were then removed from their pots and the root system of each plant was divided in two and repotted into two separate plastic bags (volume 3.0 dm^{-3} each) containing the same compost. The bags were joined by plastic tape and placed together in 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. Therefore, PRD plants received half of the amounts of water used by plants in the control treatment.

For measurements of the investigated parameters ten plants per treatment were selected randomly. Plant height, leaf number and leaf area (measured by planimeter) 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, measure-

ments of leaf gas exchange (photosynthesis and transpiration) were done by infrared gas analyzer (Waltz, Germany). On the same leaf, measurements of leaf water potential (by pressure probe) and leaf apoplastic pH, by the centrifugation method (Muhling and Sattelmacher, 1995), were done several times during the experimental period. At the end of the experimental period, fruit yield and dry weight were measured as well as the content of total minerals, sugars and lycopene (Lacatus et al., 1995).

Results and discussion

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 (Table 1). Leaf growth reduction was the result of both a decrease in the number of leaves (c.10%) and leaf area (c.22%). Biomass results also showed, similarly to Davies et al. (2000), a significant PRD effect on shoot and root growth as well as flower formation. Therefore, our results confirmed that applied partial root drying of the root system was sufficient to trigger a shoot response. Root/shoot

Table 1. Investigated traits of the tomato crop grown under PRD and well-watered regime

Trait	Control	s.e.	PRD	s.e.	Significance
Plant height (cm)	88.92	4.68	66.01	4.33	P<0.001
No of leaves per truss	21.26	0.60	19.19	0.55	P<0.05
Leaf area (cm ²)	22.12	1.17	17.33	2.90	P<0.01
Water potential (-MPa)	0.38	0.03	0.40	0.03	Ns
Apoplastic pH	6.18	0.12	6.11	0.07	Ns
No of flower trusses	9.90	0.54	7.00	3.36	P<0.001
No of fruits	2.95	0.42	4.05	0.38	Ns
Fruit diameter	35.15	1.73	37.19	0.97	Ns
Fruit g DW	1.70	0.10	1.88	0.15	Ns
Shoot g DW	18.66	0.74	13.16	0.51	P<0.001
Root g DW	1.05	0.07	0.81	0.04	P<0.01
R/S ratio	0.06	4.89x10 ⁻³	0.07	4.18x10 ⁻³	Ns
Crop WUE (g fruit DWdm ⁻³)	0.21	0.02	0.34	0.03	P<0.001
Photosynthesis (μmol.m ⁻² .s ⁻¹)	1.08	0.25	1.39	0.15	ns
Transpiration (mmol.m ⁻² .s ⁻¹)	3.06	0.72	4.20	0.44	ns
Leaf WUE (mmol CO ₂ / mmol H ₂ O)	0.35	6.13x10 ⁻⁴	0.35	1.52x10 ⁻⁵	ns

ratios were similar in both treatments (*c.* 0.08) and they didn't confirm that PRD treatment enhanced root growth and, therefore, explored a higher amount of available water in the soil.

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 (Table 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.

In our study, the change in gas exchange was less than expected. We found no effect of PRD on stomatal conductance (or transpiration) and photosynthesis (Table 1). 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 Sharp (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 (Table 1). Croker et al. (1998) demonstrated significant genotypic differences in stomatal sensitivity to non-hydraulic signalling 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. Further investigation of the relevance of these data for PRD treatment would be very worthwhile.

Our results also showed that PRD caused a significant reduction in fruit numbers (*c.* 30%) but this effect was not significant for fruit biomass and fruit diameter (Table 1). Investigations of some biochemical traits (Table 2) showed a significantly increased PRD effect on sugar content (*c.* 13%) and, therefore, crop nutritional value. Davies et al. (2000) pointed out that reduction of carbohydrate strength (side shoots) in PRD treated plants resulted in a relative increase in the sink strength of tomato fruit, such that carbohydrate previously partitioned towards the side shoots is redirected towards the fruit.

Table 2. Biochemical characteristics of tomato fruits grown under PRD and well-watered regime

Trait	Control	s.e.	PRD	s.e.	Significance
Dry weight (%)	10.73	0.19	10.05	0.14	ns
Sugars (%)	3.70	0.14	4.20	0.10	P<0.05
Lycopene (mg %)	3.43	0.13	3.18	0.12	ns
Total minerals (%)	1.03	0.03	1.09	0.02	ns

Here, water-use efficiency (WUE) was calculated on a leaf level (as the ratio between photosynthetic rate and transpiration rate) and on a crop level (as a fruit dry weight per unit evapotranspired water of pot grown plants). Leaf WUE depends on transpiration and since stomatal conductance was unaffected by PRD treatment, leaf WUEs were not significantly different between treatments (Table 1). In contrast to crop water-use efficiency, 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 crop 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.

In conclusion, continuing physiological studies will help to understand the mechanisms operating in PRD grown tomato plants. 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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