Physiological mechanism contributing to efficient use of water in field tomato under different irrigation

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ABSTRACT

An open field experiment was conducted under furrow irrigation with 3 treatments: CK (control), PRD (partial root drying) and RDI (regulated deficit irrigation). The results showed that water potential, water content of the leaf and growth were decreased under PRD and RDI and the plants met stronger water stress under RDI than under PRD regime. The water use efficiency (WUE) based on fruit yield reached to 10.95 kg/m^3 and 15.33 kg/m^3, i.e. 17.1% and 63.9% increase over CK under RDI and PRD, respectively. The transpiration efficiency in RDI was kept at the same level as CK, whereas it was promoted by 32.4% under PRD condition. CAT, SOD and POD activities were more active under RDI and especially under PRD than under CK. Therefore, following conclusions could be made: moderate water stress induced osmotic regulation under PRD conditions, leading to normal water status, higher antioxidant enzymes activities, the same level of biomass and lower water use, thus providing some part of mechanism to higher WUE under PRD condition.

Keywords: partial root drying; transpiration efficiency; antioxidant enzymes activities; biomass partition

It is all known that water supply is limited in the world and irrigation of agricultural lands accounts for over 85% of water usage worldwide (van Schilfgaarde 1994), so how to increase water use efficiency becomes a key issue for research and more emphasis is put on developing thrifty irrigation systems.

In last decades, partial root drying (PRD) was invented and a lot of work was done on it (Davies et al. 2000, Tahi et al. 2007). The early experiments showed that PRD reduced irrigation water amount by 30–50%; it had no conspicuous yield reduction and fruit quality was improved, so it meant the water use efficiency was improved. It was also demonstrated that alternation of wet and dry zones was vital to initiate the continuous production of root-to-shoot signal because the root system is not able to maintain root ABA production for long periods.

Tomato is one of the most widely grown vegetables in the world. A lot of research (Kirda et al. 2004, Claussen 2005, Tahi et al. 2007) was done on it under irrigation in pot or greenhouse experiments. However, few researches were conducted focused on the effect of PRD on physiological response in open field conditions. Moreover, the advantage of PRD over other deficit irrigation method such as regulated deficit irrigation (RDI) is still not very clear.

In this study, an open field experiment was conducted to investigate the effects of PRD and RDI on plant growth, biomass, water relations, yield, water use efficiency, photosynthesis rate, transpiration rate, osmotic regulation, membrane integrality and the activity of antioxidant enzymes of tomato in North China. The objectives were to study the physiological mechanism of PRD on improving water use efficiency (WUE).

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MATERIAL AND METHODS

Experimental design. Field experiment was conducted between April 27 and August 1, 2007 at the Luancheng Agro-Ecological Experimental Station (37°53′N, 114°40′E), Chinese Academy of Sciences. The experimental design consisted of three furrow irrigation treatments: (i) CK (control): irrigation was given on both sides of the plants; (ii) PRD (partial root drying): irrigation in the amount of 50% of CK was given on one side of the plants and switched to the other side next time; and (iii) RDI (regulated deficit irrigation): irrigation in the amount of 50% of CK was given on both sides of the plants. Nine plots with plot area of 24 m^2 (4 m × 6 m) were arranged in a randomized block design with three replicates per treatment. A flow meter was installed on the end of plastic pipes to control the irrigation amount. The irrigation was applied six times in the growth period. In total, 0.42 m^3/m^2 of water was given to CK, and 0.21 m^3/m^2 of water was given to PRD and RDI. Precipitation between April 27, 2007 and August 1, 2007 amounted to 0.21m^3/m^2; water consumption in PRD and RDI treatments was therefore 0.42 m^3/m^2 and total water consumption in CK was 0.63 m^3/m^2. The treatment was specified in Figure 1.

Crop management. Manure (60 m^3/ha) and fertilizer (N15-P10-K15 600Kg/ha) were applied before ploughing. Tomato plants were transplanted on April 27, 2007 with the density of 50 000 plants/ha.

Soil moisture measurement. Neutron probes were installed in the middle row of each plot (Figure 1) to determine the soil water content at depth intervals of 0.1 to 1.5 m for each 7 days.

Physiological measurements and sampling

Midday leaf water potential (Ψ_p) was determined with WP4 Dewpoint Meters (Decagon, Pullman, WA DC, and USA) from the third leaf from the top. Relative water content (RWC) was determined by weighting method according to Gao (2000).

Leaf area (LA, cm^2) was calculated according to the formula of Van der Varst and Postel (1972): LA = 0.25 (L × W)/(1 – 1.48 L × W), where L is the leaf length (cm) and W the leaf width (cm).Three plants of each treatment were randomly selected to measure leaf area. Pn and Tr of the third leaf from top were measured every 10 days between 10:00 am and 12:00 am by using the Licor-6400 (LI-COR, Lincoln, NE, USA), transpiration efficiency (TE) was determined by Pn/Tr. At the same time, 3 plants were collected to measure biomass (leaf, stem, root and fruit). Harvest index (Hi) was calculated at harvest, Hi = fruit dry biomass/dry biomass above-ground.

Evapotranspiration (ET) was calculated from the water balance equation: ET = I + P – R – D – ΔW (Mao et al. 2003), where P is precipitation (mm), I is the irrigation water (mm), R is the surface runoff (mm), ΔW is the soil water content changes (mm), and D is the deep water percolation and drainage. At the study site, R and D could be neglected and there was no change in the soil water content changes, therefore ET = I + P. Water use efficiency (WUE) was calculated as Y/ET, Y being the fruit yield.

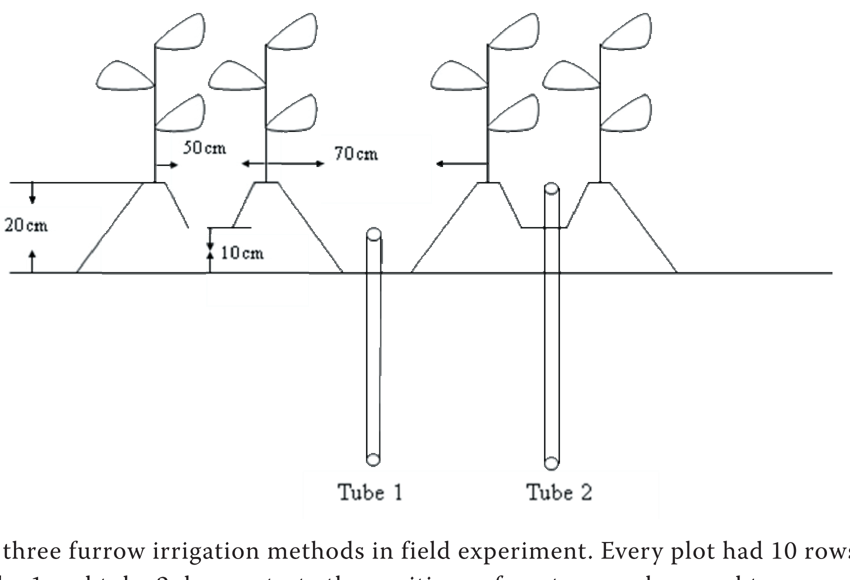

Figure 1. Layout of three furrow irrigation methods in field experiment. Every plot had 10 rows with plants interval of 40 cm. Tube 1 and tube 2 demonstrate the positions of neutron probes used to measure soil moisture

Leaf samples were taken at the interval of 10 days after irrigation treatment, frozen in liquid nitrogen and then stored at –40°C; 0.5 g frozen leaves were ground in an ice-cold mortar with 10 ml extraction phosphate acid buffer (pH 7.8), centrifuged for 15 min at 10 000 × g at 4°C. Crude extract was collected for measurement of corresponding absorption by UV-vis spectrophotometer (UV2450, Japan). POD (POD, EC 1.11.1.7) activity was determined using the guaiacol test according to Bacon et al. (1997). Catalase (CAT, EC 1.11.1.6) activity was measured as described by Havir et al. (1987). Superoxide dismutase (SOD, EC 1.15.1.1) activity, MDA content and proline content were determined by referring to Gao (2000).

Data analysis. The data were analyzed by one-way analysis of variance (ANOVA) followed by LSD test at $P = 0.05$ level to compare the means using SPSS 13.0 for Windows.

RESULTS

Leaf water potential and relative water content

Leaf water potential (ψ_p) and relative water content (RWC) decreased with the plants growth (Figure 2). Compared with CK, ψ_p and RWC under PRD were slightly lower; under RDI, they were significantly ($P < 0.05$) lower, which means that plants met slight water stress under PRD and strong stress under RDI.

Plant height and leaf area

Plants were significantly (5–12 cm) higher in CK than in PRD and RDI. Leaf area was affected significantly under RDI, per plant it was 296.48 to 1147.50 cm^2 less than leaf area in CK; under PRD it was affected moderately, 40.42–899.46 cm^2 less per plant than in CK.

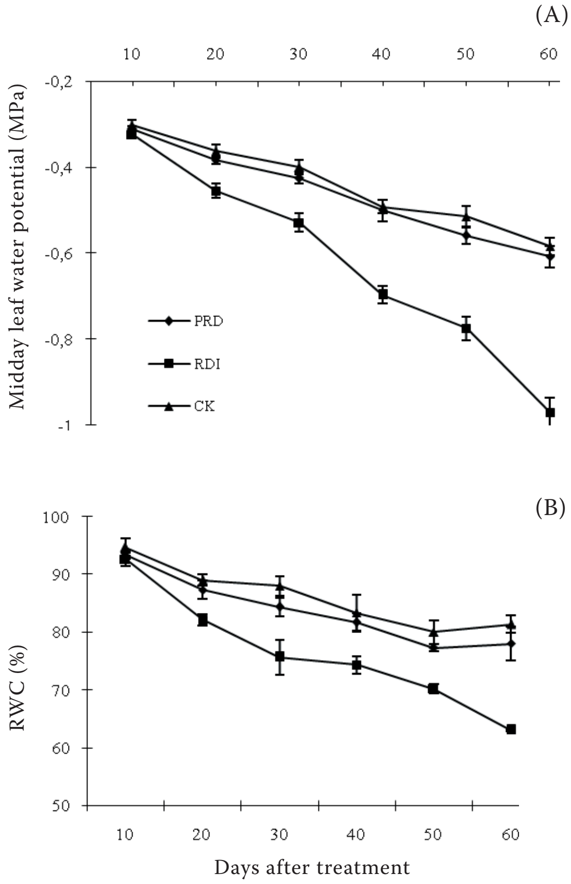

Figure 2. Time courses of midday leaf water potential (2A), relative water content (2B) of tomato plants in CK, RDI and PRD. Data are means of 3 replicates

Biomass

As Table 1 shows, there was no significant difference in total dry biomass and harvest index between CK and PRD, but total dry biomass significantly decreased by 22.8% and harvest index reduced by 9.3% under RDI. PRD and RDI increased roots dry biomass distribution by 40.4% and 57.1%, respectively.

Water use and water use efficiency based on fresh yield. Table 1 shows the total water use (ET), yield and WUE of all treatments. Yield under PRD

Table 1. Yield, WUE, harvest index and dry biomass partition of different irrigation treatments

Treatment	Yield (kg/m^2)	Total water consumption (m^3/m^2)	WUE (kg/m^3)	Total dry biomass (g per plant)	Harvest index	Dry biomass partition (%)			
						leaves	stems	roots	fruits
PRD	6.44^a	0.42	15.33^a	209.87 ± 10.1^a	0.45^a	0.42^b	0.121	0.017^a	0.44^a
RDI	4.60^b	0.42	10.95^b	171.98 ± 0.3^b	0.39^b	0.47^a	0.133	0.019^a	0.38^b
CK	5.89^a	0.63	9.35^b	222.78 ± 6.1^a	0.43^a	0.45^{ab}	0.114	0.012^b	0.43^a

Lowercase letters mean difference at $P < 0.05$ level; values are means of three plots of each treatment

Table 2. Physiological indexes of different treatments

Treatment	Pn (μmol/m²·s)	Tr (mmol/m²·s)	Transpiration efficiency	MDA (μmol/g fw)	
				40 DAT	80 DAT
PRD	26.44 ± 1.07 [a]	6.68 ± 0.18 [b]	3.96 [a]	5.27 [b]	3.34 [b]
RDI	17.03 ± 0.71 [c]	5.44 ± 0.11 [c]	3.12 [b]	6.46 [a]	3.53 [a]
CK	21.92 ± 0.73 [b]	7.34 ± 0.18 [a]	2.99 [b]	5.04 [c]	3.16 [c]

Lowercase letters mean difference at $P < 0.05$ level; values are means of three plots of each treatment

was increased by 9.34% over CK, however, it was not significant at $P = 0.05$ level. Yield of RDI was significantly reduced. Total water use of PRD and RDI was by 32.3% lower than CK. WUE of RDI increased by 1.60 kg/m^3, however it was not significant at $P = 0.05$ level; the WUE under PRD was much higher than CK, it increased by 63.9%.

Photosynthetic rate, transpiration rate and transpiration efficiency

Photosynthesis rate (Pn), transpiration rate (Tr) and transpiration efficiency (TE) of three irrigation treatments on June 19 are presented in Table 2. Pn in PRD was by 20.4% higher than CK; under RDI it was by 22.3% lower than CK. Tr under PRD and RDI decreased by 9.0% and 35.9%, respectively. Therefore, TE under PRD and RDI was increased by 32.4% and 4.3% over CK, respectively.

Proline concentration

Proline concentration first increased with the plant development, reached the peak on 40 days after treatment beginning, then decreased in all treatments. Compared with CK, it was at higher level under PRD and RDI, especially under RDI at late growth stage. Proline content in PRD was on average by 5.88 μg/g FW higher than in CK; in RDI it was on average by 5.98 μg/g FW higher than in CK. It can be indicated that osmotic regulation was induced by water stress.

MDA concentration. Lipid peroxidation was measured in terms of MDA concentration. It was determined at 40DAT and 80DAT; the data in Table 2 show that MDA concentration was increased by 4.6% and 5.7% under PRD, and by 28.2% and 11.7% under RDI, respectively. It was indicated that plants under PRD had better membrane integrality than under RDI.

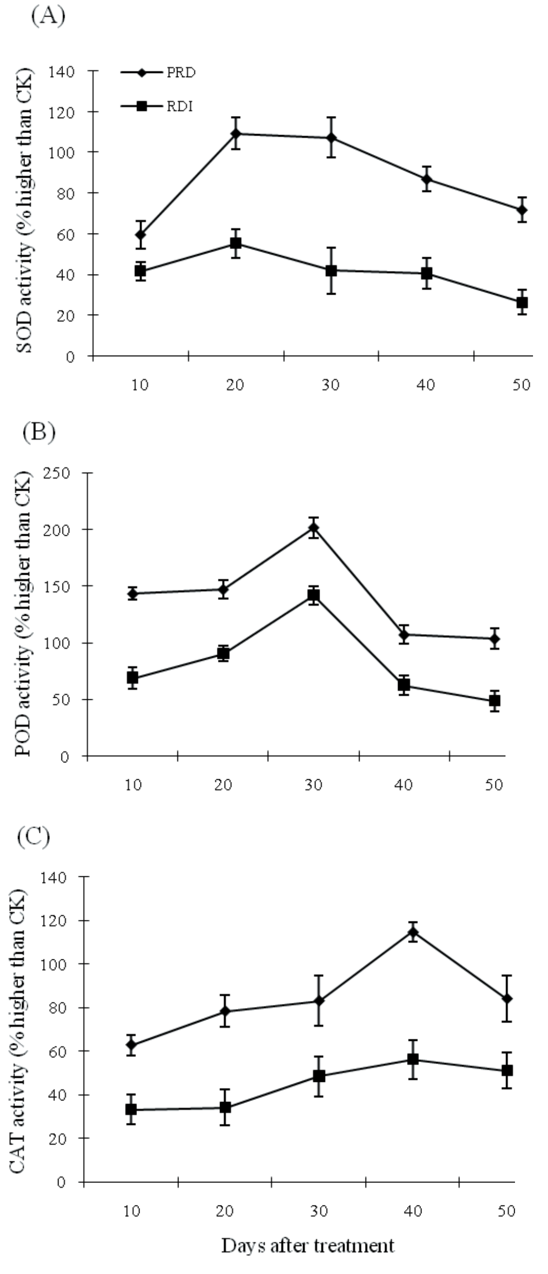

Figure 3. Activities of SOD (A), CAT (B) and POD (C) under PRD and RDI. All enzymatic activities are expressed as % higher than the control. Symbols are the mean values. Asterisks denote significant differences at $P < 0.05$

Antioxidant enzymes activity

Both PRD and RDI treatments promoted the activities of SOD, POD and CAT, and they were more increased under PRD than under RDI during the experimental period (Figure 3), which indicated that the plant had a higher antioxidant ability than in CK, especially under PRD condition.

DISCUSSION AND CONCLUSION

Water status of the plant is the main factor affecting the plants' growth and development. Water use efficiency (WUE) is the key indicator of plant water relation and is regulated by physiological process.

The data from this experiment showed that leaf water potential and relative water content were decreased under PRD and RDI, especially under RDI condition. Similar result was observed by Sobeih et al. (2004) in tomato plants, De Souza et al. (2005) in grapevine and by Aganchich (2007) in olive. PRD had weaker vegetative growth inhibition compared with RDI and CK, and this conclusion was in agreement with the evidence of Kirda et al. (2004) and Tahi et al. (2007). The plants meet water stress because of less irrigation water; the water stress was moderate under PRD and severe under RDI.

Recently, the proline content of tomato leaves was shown to be strongly related to the relative water content of leaves (Claussen 2005) and water potential; it is thus a useful indicator of the plant's water status. The proline content in this experiment increased under PRD and RDI, which means that osmotic regulation occurred.

The magnitude of oxidative damage is usually measured by MDA (an end product of membrane lipid peroxidation). MDA content in PRD was lower than in RDI, which also demonstrated that plants in PRD had better membrane integrality than in RDI.

Water stress activates oxygen species (AOS) (Mittler et al. 2004); AOS can be controlled through the mobilization of antioxidant reserves, which react enzymatically or non-enzymatically with the AOS and their products (De Gara 2003). The role of the antioxidant system is not confined to the elimination of AOS, but it is also involved in the adjustment of the redox balance and the regulation of gene expression in plant cells (Wingate et al. 1988). Plants enhance antioxidant enzymes (POD, SOD and CAT) activities to protect themselves. Our results on the evolution of CAT, POD and SOD activities confirm previous findings in olive plants under drought stress (Sofo et al. 2005, Aganchich et al. 2007). The results indicate that both PRD and RDI treatments possibly induced oxidative stress, which resulted in up-regulated activities of CAT, POD and SOD under water deficits. Some authors suggested that an increase in POD could be correlated with drought adaptation (Sofo et al. 2005, Dong et al 2008). Overall, we could speculate that in response to PRD, which is generally considered a moderate drought-stress treatment, tomato could activate an antioxidant system (particularly POD and SOD) more than under RDI.

Under PRD, the leaf could have higher photosynthesis and lower transpiration, leading to more biomass and lower water usage. While the plant could be also kept at high level of harvest index as under CK, it was in accordance with the result from Theobald et al. (2007). Higher fruit yield and lower water use made the WUE improving.

Therefore, following conclusions could be made: moderate water stress induced osmotic regulation under PRD condition, leading to normal water status of the plants, higher activity of antioxidant enzymes, membrane integrality, higher Pn and lower Tr, the same level of biomass, lower water use, high level of the harvest index, thus providing some part of mechanism to higher WUE under PRD condition.

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