

EFFECTS OF DIFFERENT DROUGHT TREATMENTS ON ROOT AND SHOOT DEVELOPMENT OF THE TOMATO WILD TYPE AND *FLACCA* MUTANT

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Abstract - The effects of drought and partial root drying (PRD) on shoot and root growth was assessed in the wild type Ailsa Craig (WT) and the *flacca* tomato mutant deficient in the plant hormone ABA. Our results show that drought had an inhibitory effect on shoot growth in *flacca* and especially in WT; the most profound effect was observed in FI (full irrigation), then PRD and the smallest in D plants. Root development in both WT and *flacca* was stimulated after the 3rd day of the experiment following a decrease in the soil water content. On the 11th day of the experiment, when the soil water content was reduced by about 50% of full irrigation (FI), the root density was increased in the drying part of the PDR and on both sides of the drought treatment. On the basis of these results it can be assumed that increased root density and root length represent an adaptation or root adjustment to drought conditions.

Key words: WT, *flacca*, root, shoot growth, drought

UDC 635.64:632.112:575

INTRODUCTION

The partial root drying (PRD) technique is a water-saving irrigation technique which was first applied in Australia for vineyard irrigation. As a result, the water use efficiency (dry biomass production per unit of used water) was increased by 30% although the yield was sustained (Loveys, 1991). At present, the PRD method is in use for the irrigation of many other cultures, including apple, pear, peach, olive, strawberry, corn, cotton, tomatoes, potatoes, peppers (Kang and Zhang, 2004). The theoretical basis of the PRD method is based on our understanding of plant reactions to drought and especially the so-called "chemical signals of drought" where the key role is that of their plant hormone abscisic acid (ABA). It is well known that an increased concentration of ABA in plants under drought conditions has an inhibitory effect on shoot growth (Chapin, 1991, Achard et al., 2006). The PRD results obtained on different species such as tomatoes (Stikic et al., 2003), vines (du Toit

et al., 2003) and potatoes (Dasgan and Kirda, 2007) also showed a similar reduction on the growth of stems and leaves, while the development of the roots was generally increased, as well as their hydraulic conductivity.

Water transport follows the water potential gradient in the soil-plant-atmosphere continuum (SPAC). The flow rate of water from the soil to the root could be calculated by dividing the gradient in water potential by the sum of resistance, including those between the bulk soil to the root surface, and those between the root surface and the root interior. Some of the presented hydraulic models suggest that both types of resistance decrease if the dry mass of the root is increased (Johnson et al., 1991).

According to Steudle (2000), the water flow differed between young and older roots, and younger roots in optimal conditions have a smaller apoplastic resistance than older ones. The exposure of roots

to drought stress reduces by 50% the water uptake compared to young unstressed roots (Lauenroth et al., 1987). Depending on the resistance and shoot mass, water movement continues through the shoot following the gradient of water potential, which is to be expected is usual in a hydraulic model (Johnson et al., 1991).

PRD irrigation must be switched regularly from one side of the root to the other to maintain the roots in the dry soil alive and fully functional and to sustain the supply of root signals, including ABA. The time of switching and number of applied watering/drying cycles are essential for plant reactions to PRD. Most of the published papers about the effects of PRD on root or shoot growth are based on several longer-term cycles. The aim of the present paper was to assess the effects of the first wet/dry cycle on the root and shoot development of the tomato which could be significant for the understanding of the reactions of plants to PRD under longer-term cycling. Our aim was also to compare the reactions under PRD between a wild type tomato cultivar, Ailsa Craig, and tomato mutant *flacca*. The mutant *flacca* is deficient in ABA and its response could improve our understanding of the role of ABA in PRD short-term effects. The root and shoot development was followed by a visual estimation of the plants in non-destructive experimental conditions.

MATERIALS AND METHODS

Seeds of tomato species *Lycopersicon esculentum* Mill. cv. Ailsa Craig and mutant *flacca* (Lancaster Environment Centre, UK) were sown in a commercial substrate. The plants were grown under controlled conditions in a growth chamber (day/night temperature 26/18°C, relative humidity of 70% and light of 300 µmol/m²s). The primary root was removed from the plants at the 4th leaf stage, and the root system divided equally between two transparent pots. Pots 24 cm in height were filled with 800g of substrate (*Klasman Postgraund-H*), and wrapped with aluminum foil. The tomato was sown in the pots and after 5 days (recovering period) the plants were exposed to drought.

For the PRD treatment, half of the root system was maintained in a dry state, while the other half was watered. In the drought treatment (variant D), both sides of the root zone were maintained in a dry state, while in the PRD system, drought was induced only in one side of the root zone. One drying cycle at PRD lasted until the soil water content decreased by 50% of the field capacity of the substrate (Gowing et al., 1990). In our experiments this was achieved on the 11th day of the experiment when the volumetric soil water content (SWC) decreased by half, from 37% to 17%. Assessment of the development and growth of the shoot and root was done by constant visual observations of the plants that were maintained in transparent pots.

RESULTS AND DISCUSSION

Figs. 1A and 2A show the shoot and root growth and development of Ailsa Craig (*WT*) and *flacca* on the 3rd and 11th days of treatment. After 3 days of treatment, the visual estimation did not show any differences between the investigated plants. This uniformity in development was expressed in both organs, i.e. the roots and shoots (shoot height and leaf number). During this period, in both *WT* and *flacca* the majority of the roots were at a depth of 7-10 cm. Furthermore, significant differences between *WT* and *flacca* were not expressed in the root level, while in the *WT* plants shoot development was more obvious than in the *flacca* plants (Figs. 1A and 2A). Differences between the treatments in the shoots were the greatest at the end (after 11 days). Maximal shoot growth was attained by the FI plants, then the PRD, while it was smallest in and the D plants (Figs. 1B and 2B).

Although our experiment did not include ABA measurements, differences in shoot growth could be explained by the effects of ABA that was induced by our treatments. The roots in the drying soil produce chemical signals such as ABA, that restrict plant water use by partially closing the stomata and restricting vegetative growth (Davies and Zhang, 1991; Dodd, 2005). Similar inhibitory effects of ABA on leaf and stem growth were confirmed by the exogenous application of ABA (Trewaves and Jones, 1991). The ef-

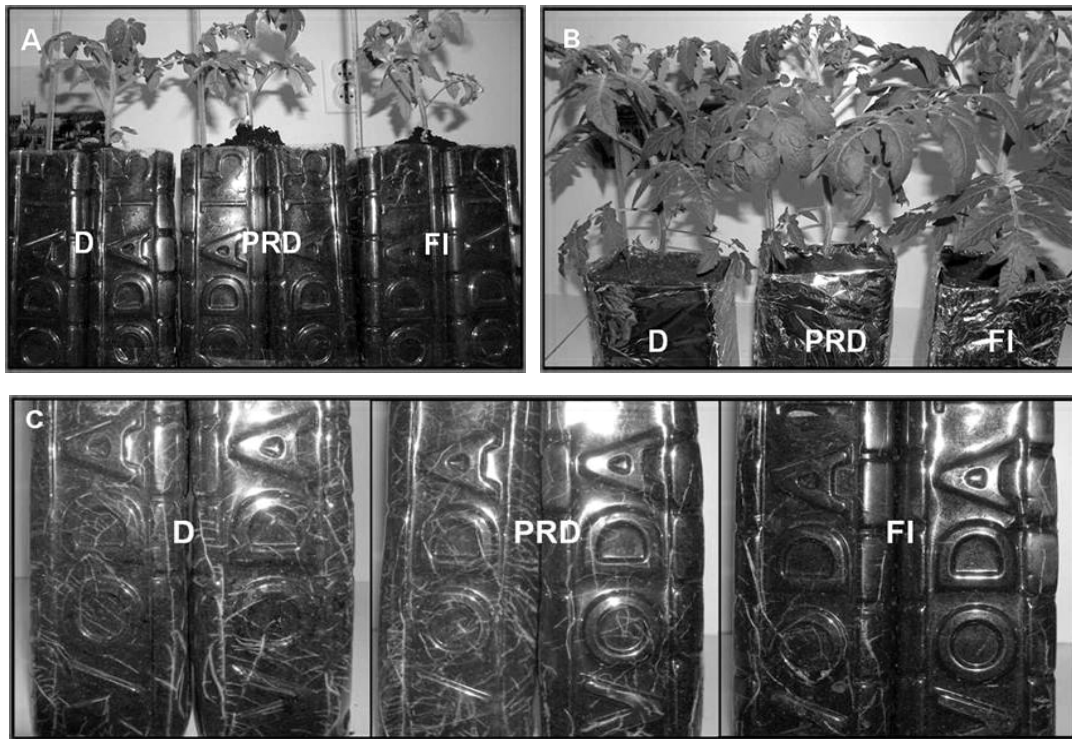


Fig 1. The effect of different treatments on the root and shoot of Ailsa Craig (*WT*) on the third (A) and on the eleventh days (B, C).

fects of ABA were further confirmed by the results of transgenic tomato lines with high expression *NCED* gene. This gene encodes the enzyme *9cis epoxy carotenoid-dioxygenase* which affects the rate of ABA synthesis. Results of Thompson et al., (2007) showed that under conditions of optimal irrigation, in transgenic plants the concentration of ABA was increased and the biomass reduced compared to the wild type. Results of Creelman et al. (1990) showed that in soybean plants under drought conditions the synthesis of ABA is increased and that this was in correlation with a reduced shoot/root ratio. This reduced ratio indicated that the root growth was increased in relation to the shoot.

Comparison of root development between *WT* and *flacca* and applied treatments during the 3rd day of experiment did not show any significant differences (Figs. 1A and 2A). However, the differences were expressed on the 11th day when the root density increased in the drying part of the PDR and in both

sides exposed to the drought treatment. Increased root development was observed in both the *WT* and *flacca* plants (Figs. 1C and 2C). A similar tendency to increase the length and density of the roots has been previously detected in tomatoes under PRD treatment as well (Mingo, 2003). Furthermore, exogenously applied ABA also leads to the development of root hairs and initiation of lateral primordia in the top of young seminal roots (Chen et al., 2006). The results of Yoshimura et al., (2008) showed that the reactions of watermelon depend on the severity of stress. During the early stages of drought increases in root length were noticed, while in more serious drought (after the reduction of soil water content by more than 20%), both root and shoot growth was reduced.

On the basis of the results that concern the time-course of the applied treatments, we assumed that the root growth response is not static, but is modified during the treatment, which could present an adap-

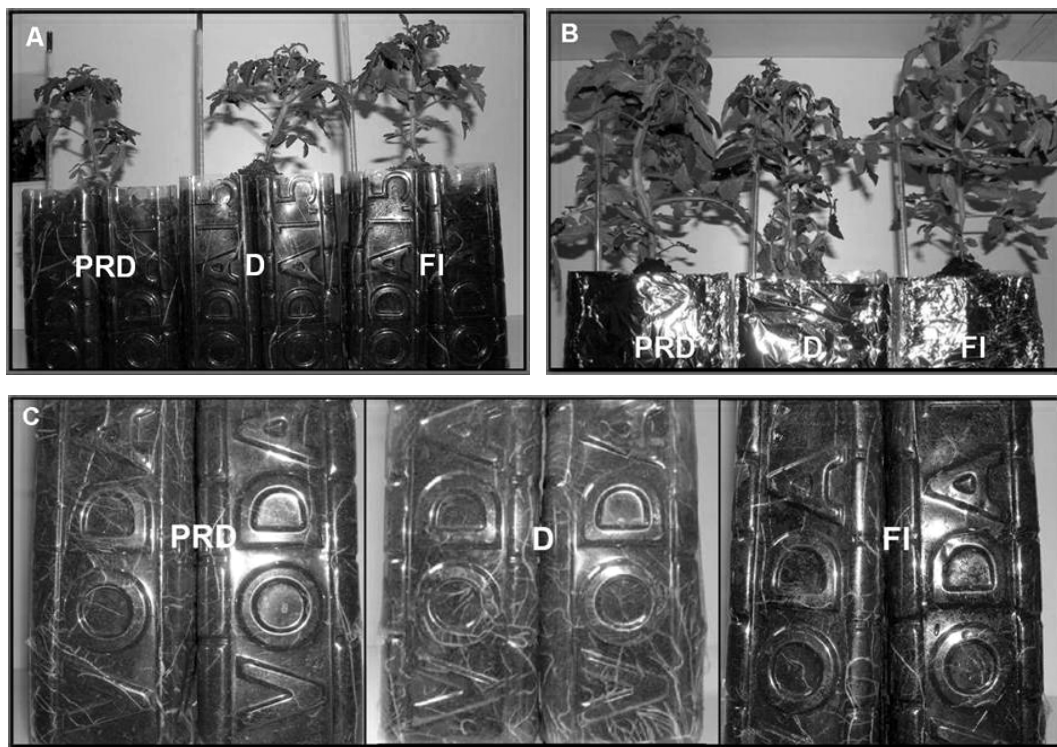


Fig 2. The effect of different treatments on the root and shoot of *flacca* on the third (A) and on the eleventh days (B, C).

tive reaction (Dinneny et al., 2008). Our results with *flacca*, and especially with the *WT* plants, showed that drying in the during drought and the PRD treatment leads to increased root development. The increased density and root length could be a type of adaptation or root adjustment to the drought conditions. The PRD treatment with one/several shiftings could be commensurable with amplitude/modified oscillatory kinetics. We can assume that the first wet/dry cycle leads to improved development in the half of the root exposed to drying during the PRD treatment, while the next alternation had the same effect in the second half of the root, and so on. Thus, the PRD technique could be treated as an irrigation strategy in which drought stress is applied as a modified oscillatory kinetics contributing to the development of roots, i.e. the development of a certain type of plant adaptation.

Acknowledgments - This work was supported by Serbian Ministry of Education and Science, projects TR 31005 and II₃ 43010.

REFERENCES

- Bohnert, H. J., Nelson, D.E. and R.G. Jensen (1995). Adaptation to environmental stress. *The Plant Cell* **7**: 1099-1111.
- Borsani, O., Cuartero, J., Fernandez, J. A., Valpuesta, V. and M.A. Botella (2001). Identification of two loci in tomato reveals distinct mechanisms for salt tolerance. *The Plant Cell* **13**: 873-888.
- Borsani, O., Cuartero, J., Valpuesta, V. and M.A. Botella (2002). Tomato *tos1* mutation identifies a gene essential for osmotic tolerance and abscisic acid sensitivity. *The Plant Journal* **32**: 905-914.
- Chapin, F.S. (1991). Integrated responses of plants to stress. A centralized system of physiological responses. *BioScience* **40**: 29-31.
- Chen, C.W., Yang, Y.W., Lur, H.S., Tsai, Y.G. and M.C. Chang (2006). A novel function of abscisic acid in the regulation of rice (*Oryza sativa* L.) root growth and development. *Plant and Cell Physiology* **47**: 1-13.
- Creelman, R.A., Mason, H.S, Bensen, R.J, Boyer, J.S. and J.E. Mullet (1990). Water deficit and abscisic acid cause differential

- inhibition of shoot versus root growth in soybean seedlings. *Plant Physiology* **92**: 205-214.
- Dasgan, H.Y and C. Kirda (2007). Partial root drying (PRD) is a new technique for soilless grown vegetables. *Acta Horticulturae* **747**: 433-440. *ISHS symposium on Advances in Soil and Soilless Cultivation under Protected Environment, Morocco, 2006*
- Davies, W.J. and J. Zhang (1991). Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Plant Molecular Biology* **42**, 55-76.
- Dinnyen, J.R., Long, T.A., Wang, J.Y., Jung, J.W., Mace, D., Pointer, S., Barron, C., Brady, M.S., Schiefelbein, J and P.N. Benfey (2008). Cell Identity Mediates the Response of *Arabidopsis* Root to Abiotic Stress. *Science* **320**, 942-945.
- Dodd, I.C. (2005). Root-to-shoot signalling: assessing the roles of "up" in the up and down world of long-distance signalling in plants. *Plant and Soil* **274**, 251-270.
- Dodd, I.C., Tan, L.P. and J. He (2003). Do increases in xylem sap pH and/or ABA concentration mediate stomatal closure following nitrate deprivation? *Journal of Experimental Botany* **54**, 1281-1288.
- Drew, M.C. (1997). Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. *Annual Review Plant Physiology and Plant Molecular Biology* **48**, 223-250.
- du Toit, P.G, Dry, P.R. and B.R. Loveys (2003). A preliminary investigation on Partial Rootzone Drying (PRD) effects on grapevine performance, nitrogen assimilation and berry composition. *South African Journal for Enology and Viticulture* **24**, 43-54.
- Gowing, D.J., Davies, W.J. and H.G. Jones (1990). A root-sourced signal of drying soil in apple (*Malus domestica*) Borkh. In Importance of Root to Shoot Communication in the Responses to Environmental Stress (eds W. J. Davies and B. Jeffcoat). *BSPGR Monograph* **21**, 274-277.
- Johnson, I.R., Melkonian, J.J., Thornley, J.H.M. and S.J. Riha (1991). A model of water of water flow through plants incorporating shoot/root message control of stomatal conductance. *Plant, Cell and Environment* **14**:531±544
- Kang, S. and J. Zhang (2004). Controlled alternate partial root zone irrigation: its physiological consequences and impact on water use efficiency. *Journal of Experimental Botany* **55**, 2437-2446.
- Kim, S-H., Arnold, D., Lloyd A. and S.J. Roux (2001). Antisense expression of an *Arabidopsis* Ran binding protein renders transgenic roots hypersensitive to auxin and alters auxin-induced root growth and development by arresting mitotic progress. *The Plant Cell* **13**, 2619-2630.
- Lauenroth, W.K., Sala, O.E., Milchunas, D.G. and R.W. Lanthrop (1987). Root dynamics of *Bouteloua gracilis* during short-term recovery from drought. *Functional Ecology* **1**, 117-124.
- Leung, J. and J. Giraudat (1998). Abscisic acid signal transduction. *Annual Review Plant Physiology Plant and Molecular Biology* **49**, 199-222.
- Liu, J. and J. K. Zu (1997). An *Arabidopsis* mutant that requires increased calcium for potassium nutrition and salt tolerance. *Proceedings of the National Academy of Sciences, USA* **94**, 14960-14964.
- Lopez-Bucio, J., Cruz-Ramirez, A. and L. Herrera-Estrella (2003). The role of nutrient availability in regulating root architecture. *Current Opinion Plant Biology* **6**, 280-287.
- Loveys, B.R.. (1991). Water use is knowledge of ABA physiology for crop improvement. In: Abscisic acid. (Eds. W. J. Davies and H.G. Jones), 245-259. Bios Scientific Publishers, Oxford.
- Mingo, M.D. (2003). Regulation of vegetative and reproductive growth in plants exposed to Partial Root-Zone Drying. *Thesis*. Lancaster University.
- Steudle, E. (2000). Water uptake by roots: effects of water deficit. *Journal of Experimental botany* **51**: 1531-1542.
- Stikic, R., Popovic, S., Srdic, M., Savic D., Jovanovic, Z. and Lj. Prokic (2003). Partial root drying (PRD): a new technique for growing plants that saves water and improves the quality of fruit. *Bulgarian Journal Plant Physiology*, special issue: 164-171.
- Thompson, A.J., Andrews, J., Mulholland, B.J., McKee, J.M.T., Hilton, H.W., Black, C.R. and I.B. Taylor (2007). Overproduction of abscisic acid in tomato increases transpiration efficiency and root hydraulic conductivity and influences leaf expansion. *Plant Physiology* **143**, 1905-1917.
- Trewaves, A.J. and H.G. Jones (1991). An assessment of the role of ABA in plant development In: Davies W.J., Jones H.G., eds *abscisic acid: physiology and biochemistry*. Oxford Bios Scientific Publishers: 169-188.
- Wang, X., Xu, Y., Han, Y., Bao, S., Du, J., Yuan, M., Xu, Z. and K. Chong (2006). Overexpression of RAN1 in rice and *Arabidopsis* alters primordial meristem, mitotic progress, and sensitivity to auxin. *Plant Physiology* **140**, 91-101.
- Yoshimura, K., Masuda, A., Kuwano, M., Yokota, A and K. Akashi (2008). Programmed Proteome Response for Drought Avoidance/Tolerance in the Root of a C3 Xerophyte (*Wild Watermelon*) Under Water Deficits. *Plant Cell Physiology* **49**(2), 226-241.

