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## Research Article

# Plant Organ Sensitivity to Water Stress: The Case of Roma Tomato (*Solanum Lycopersicum*)

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## Abstract

The Ferry Morse heirloom seeds of the Roma tomato variety were germinated in the greenhouse at Texas A&M University, Kingsville, TX. The seedlings were used to study the effects of water stress or deficit irrigation (DI) on organ cell wall and lumen development in *Solanum lycopersicum*. The seedlings were pre-acclimated to four DI treatments of 100% (control), 75%, 50%, and 25% in a randomized complete block experiment and grown until flowering occurred. The seedlings were watered only when the control needed watering, and the amount of water used on the treatments was a fraction of the quantity required to saturate the control treatment pots. The results indicate that DI impacted plant organ cell wall and lumen development but had no effect on the stem lumen. A pooled data analysis of the organ measurements to understand the effect of DI on the species anatomical structures indicates that DI had an effect on cell wall development of the whole plant, but no effect on the lumen of the species.

## Introduction

Irrigation is one of the crucial components of agricultural production, making agriculture a major user of freshwater, estimated at 70% of total available freshwater resources [1]. Irrigated land alone accounts for approximately 40% of global food production [2]. Water scarcity and food insecurity are intricately linked; hence, the agricultural sector is among the first to be impacted by freshwater depletion [3]. Lascano and Sojka [4] stressed the need to increase both irrigated land under agriculture and crop yield to sustain global food demand for the growing human population. Despite the need for sustainable human food security, irrigation practices in the agricultural industry are economically inefficient as a result of low irrigation water use efficiency [5].

The future of agriculture lies in the optimization of the available freshwater resources. As water shortages become a global problem, the use of alternative irrigation strategies becomes inevitable to optimize freshwater resources [6]. Also,

other pressing factors of the 21<sup>st</sup> century necessitate water conservation in all agricultural practices. The Organization for Economic Co-operation and Development [7] reported an urgent need to double food production to meet human demands by 2050. Climate change has accelerated groundwater depletion, creating an intense freshwater competition between agriculture and other sectors [8]. Trenberth [9] reported that unpredictable weather conditions, drought, and climate change would exacerbate the pressure on global freshwater resources. Forouzani and Karami [10] and Chai, et al. [11] noted that regional water scarcity throughout the globe is clearly evident and poses major problems, especially in arid agriculture and areas where water has been vigorously extracted for various uses.

One of many freshwater conservation strategies that has been widely studied in crop irrigation is deficit irrigation (DI) [12–14], the practice of irrigating a crop with less water than the evapotranspiration requirements of the species. Most of these studies focused on the morphological and physiological

growth characteristics of DI crops [12–14], with a significant knowledge gap left on the anatomical characteristics of such crops. This study focuses on the anatomical growth and development of Roma tomato (*Solanum lycopersicum*) grown under different DI prime acclimations to determine the extent to which the evapotranspiration requirement of the species can be reduced without compromising its anatomical development.

## Materials and methods

The Ferry Morse heirloom seeds of the Roma tomato variety were sown in trays containing a 1:1 mixture of topsoil and perlite in the Department of Agriculture, Agribusiness & Environmental Sciences greenhouse at Texas A&M University-Kingsville. Upon germination in seven days, the seedlings were transplanted into celled trays containing topsoil and perlite in a 2:1 ratio, and fertilized with Miracle-Gro (NPK 30:10:10) applied at 13.75 g/liter to facilitate vegetative and root growth. After 21 days of growth, the seedlings were again transplanted into 20 cm diameter pots containing a mixture of topsoil and perlite in a 5:1 ratio.

A total of 200 pots were transplanted and arranged in a randomized complete block design (RCBD). The pots were divided into four watering treatment groups of 100%, 75%, 50% and 25% such that each treatment group contained 50 plants. The treatments were replicated five times, such that each block contained 10 treatments of each group. The pots were watered only when plants in the 100% treatment (Control) needed water. The amount of irrigation water given for each treatment was computed as a fraction of the irrigation water required by the control. For example, if 600 ml of water was applied to the control (100% treatment) to attain potting soil saturation, the 75%, 50%, and 25% irrigation water were computed as 450 ml, 300 ml, and 150 ml, respectively. The plants were grown and treatments maintained until flowering occurred.

At flowering, randomly selected leaves of each treatment were collected from the third phyllochron below the stem apex of the sample plant in each block. The leaves were detached and fixed in formalin-acetic acid solution prepared according to Berlyn and Miksche [15] for further laboratory preparation and cellular measurement. Also, randomly selected stems from each treatment block were excised at 2.54 cm from the stem collar. The samples were fixed and transported to the lab for anatomical preparation for cellular measurement according to the protocols of Berlyn and Miksche [15]. Twenty measurements of each treatment per block for a total of 100 measurements per treatment group were made with a 40X objective calibrated with a stage micrometer.

Roots of all plants in the study were carefully removed from the pots and washed using a water emitter with a pressured nozzle set at slow speed to avoid loss of root parts. Also, randomly selected samples of the washed roots from each block and treatment were fixed and transported to the lab for anatomical preparation and measurement as previously described. Twenty cellular measurements of each treatment per block for a total of 100 measurements per treatment were made to compare the effects of primed DI treatment on the

anatomical development of Roma tomato. Leaf, stem, and root cell wall thickness was measured with the light microscope calibrated with a stage micrometer. Also, the lumen diameter of the three organs was measured with the same microscope to understand the effect of DI on the cellular development of Roma tomato. The analysis of variance (ANOVA) and post-hoc pairwise t-test statistical analyses were performed for each organ (leaf, stem, root) to understand the effect of DI on cellular development of the organ. Paired t-test allows comparison of two treatment groups per block for the pooled five replications under the tolerance and/or severity of water stress on the anatomical structure compared to the control. Also, the data of identical anatomical structures of each organ were pooled and analyzed to understand the effect of DI on the anatomical development of the whole organism. Thus, the cell wall thickness of the root, stem, and leaf was pooled and analyzed to understand the DI effect on the anatomical development of the Roma tomato cell wall. Also, a similar analysis was performed to understand the lumen development of the species under greenhouse conditions. Lumen diameter measurement was computed as an average of two diameter measurements taken at right angles to each other [16].

## Results

The ANOVA of Roma tomato cell wall and lumen development shows that DI significantly impacted cell wall synthesis ( $p = 0.0046$ ) but did not affect lumen development ( $p = 0.4091$ ). Table 1 indicates that cell wall thickness decreased at 50% reduction in the evapotranspiration water requirement of the species, but increased at a severe reduction of 25%. The implication of increased cell wall synthesis by the species under severe drought conditions will be discussed later.

Because DI affected the anatomical development of the Roma tomato cell wall, we adopted the post-hoc paired t-test to explore crop organ sensitivity to DI. We used  $p$ -value as a measure of sensitivity, such that a more sensitive organ to the DI treatment would show a  $p$ -value of less than, equal to, or closer to  $p = 0.05$ . Table 2 shows the effects of DI treatments on cell wall development of the root, stem, and leaf of the species. We used the mean  $p$ -values of 75%, 50%, and 25% DI treatments to compare organ sensitivity to water stress; the comparison shows that the Roma tomato root is the most sensitive organ to water stress relative to the stem and leaf (Table 2). Organ sensitivity to DI tends to be acropetal from the root through the stem to the leaf. Thus, mean  $p$ -values of the DI treatments are less, equal, or closest to  $p = 0.05$  at the root compared to the stem and leaf values (Table 2).

Although DI showed no statistical effect on whole plant lumen development, the study still highlights significant lumen effect of the organs. Leaf and root lumen dimeters are

**Table 1:** Effects of DI on cell wall and lumen development in *Solanum lycopersicum*.

Anatomical Characteristics	100%	75%	50%	25%
Cell wall thickness, mm	0.00044 <sup>a</sup>	0.00038 <sup>ab</sup>	0.00029	0.00034 <sup>b</sup>
Lumen diameter, mm	0.004 <sup>a</sup>	0.005 <sup>a</sup>	0.004 <sup>a</sup>	0.004 <sup>a</sup>

Numbers with the same letter superscripts are not statistically significantly different.

significantly different from the control (100% treatment)  $p = 0.0004$  and  $p = 0.0003$  respectively, while stem lumen diameter is not ( $p = 0.2685$ ). This is a consequential result about the use of DI information as a water conservation strategy in irrigation management. Also, DI effect on lumen development follows a similar pattern as in cell wall development with crop root lumen being the most sensitive to water stress followed by the stem and leaf (Table 3).

## Discussion

Deficit irrigation has been widely studied and recommended as an irrigation management technique for crop production in areas with limited water resources and in arid agriculture [5,13]. Most of the recommendations are based on morphological and physiological crop studies hence the different opinions about using DI as crop irrigation management for water conservation. Also, the interaction of DI as irrigation management strategy is influenced by both biotic (crop factor) and abiotic (environmental) factors hence study results vary by location and region.

We used the anatomical development of cell wall and lumen of Roma tomato seedlings prime acclimated to a range of DI treatments to study plant organ sensitivity to water stress. The study suggests that root anatomical development is very sensitive to water stress making root the most sensitive plant organ to water stress. Also, we report an increased cell wall synthesis of the species subjected to a severe water stress of 25% reduction in the evapotranspiration requirement of the species. Shi, et al. [17] noted that improved resilience to water stress was correlated to thicker cell walls and this increased the water-retaining capacity for growth under suboptimal conditions. Also, Tenhaken [18] noted that water stress could result in cell wall thickening by deposition of cell wall components. This could be the reason for the improved cell wall development at a severe water reduction treatment in this study. Also, evidence in this study and those of Shi, et al. [17]

and Tenhaken [18] suggest that improved cell wall synthesis is an adaptation strategy for drought tolerance by plants.

Tyree and Ewers [19] previously reported that tomato plants are sensitive to water stress and suggested genetic breeding programs that regulation vein development to improve the hydraulic efficiency of the species. We report that Roma tomato root is the most sensitive organ of the species to water stress. The species root anatomical structures show sensitivity to water stress even when no discernible morphological and physiological growth delays are apparent [12]. This finding is totally not surprising since roots are the primary organs for water uptake so anatomical traits like xylem vessel diameter and thickness play a crucial role in determining a crop's potential to withstand water stress. Organ sensitivity to water stress in the species is most severe in the root and progresses acropetally through the stem to the leaf. Because the effect of DI is not uniform through the species organ systems, DI inferences based on whole plant morphological and physiological characteristics could be misleading because of delay in the manifestation of drought acclimated anatomical structures which eventually determine the morphological and physiological growth and development of a plant species. It is easy to miss the effect of DI on the anatomy of annual agricultural crops because these crops are harvested before any abnormal anatomical characteristics manifest in the morphology and physiology of the crop. However, this may not be case with perennials since they live long enough for any anatomical deformity to manifest in the morphological architecture.

The response of plant organ lumen to DI treatment in this study highlights the danger in drawing inference on the effects of DI on a whole plant as an organism. The results indicate that DI had no effect no lumen development when lumen measurements of the organs (root, stem and leaf) were combined but when each organ's lumen measurements were analyzed individually, DI had a clear impact on the root and leaf lumen. Because DI did not show any effect on the stem

**Table 2:** Effects of water stress on cell wall development of Roma tomato organs.

Treatment %	Call the wall thickness at 100 % treatment (Control) (p-value)			Call the wall thickness at 75% treatment (p-value)			Call wall thickness at 50% treatment (p-value)			Call wall thickness at 25 % treatment (p-value)		
	Root	Stem	Leaf	Root	Stem	Leaf	Root	Stem	Leaf	Root	Stem	Leaf
100	-	-	-	0.0786	0.0437	0.3069	0.0016	0.0007	0.6304	0.0070	0.0078	0.6804
75	0.0786	0.0437	0.3069	-	-	-	0.0008	0.2614	0.1066	0.0245	0.3596	0.4493
50	0.0016	0.0007	0.6304	0.0008	0.2614	0.1066	-	-	-	0.0195	0.0964	0.2631
25	0.0070	0.0078	0.6804	0.0245	0.3596	0.4493	0.0195	0.0964	0.2631	-	-	-
Mean	0.0291	0.0174	0.5392	0.0346	0.2216	0.2876	0.0073	0.1195	0.3334	0.0170	0.1546	0.4643

**Table 3:** Lumen development sensitivity to deficit irrigation (water stress).

Treatment %	Lumen diameter at 75% treatment (p-value)			Lumen diameter at 50 % treatment (p-value)			Lumen diameter at 25 % treatment (p-value)		
	Root	Stem	Leaf	Root	Stem	Leaf	Root	Stem	Leaf
100	0.2588	0.3103	0.6297	0.0142	0.4138	0.1431	0.0001	0.0318	0.4326
75	-	-	-	0.0066	0.3486	0.4523	0.0001	0.7973	0.9801
50	0.0066	0.3486	0.4523	-	-	-	0.3525	0.0581	0.3236
25	0.0001	0.7973	0.9801	0.3525	0.0581	0.3236	-	-	-
Mean	0.0885	0.4854	0.6874	0.1244	0.2735	0.3063	0.1176	0.2957	0.5788

lumen in this study, combining the lumen measurements of all the organs to understand the impact of DI gave the misleading result that DI has no effect on lumen development of a whole plant. It is important to understand that plant lumen is subject to a variety of external factors that affect its growth and these factors impact the organs differently. Cavitation and development of embolism are factors that affect lumen formation and could influence lumen measurement if these factors impacted the organs unequally. Trifilò, et al. [20] noted that xylem cavitation and embolism were induced by drought. These anatomical abnormalities could cause partial reduction in lumen size which could lead to error in lumen diameter measurement. They could also cause complete lumen closure resulting in reduced lumen density and water conduction efficiency in drought conditions. It is important to note that DI treatment affected the species lumen acropetally with the root being the most sensitive organ to water stress followed by the stem and leaf. A similar effect was observed with the species cell wall development.

## Conclusion

Anatomical structures of Roma tomato are impacted by irrigation management and the impact can differentially affect the anatomy of the organs. The effect of DI management on an organ can dilute its impact on the whole plant as was the case with the stem lumen measurements in this study. Also, plant organ sensitivity to water stress is differentially felt with the root as the most sensitive organ to water stress. Results of this study indicate that organ sensitivity to water stress is acropetally progressive from root-stem-leaf with leaf as the least sensitive. We conclude that the use of leaf limp as indication of a plant's need of water is erroneous since leaf limp is a sign of a resource that has been in demand for a long time.

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## References

1. Huffaker R, Hamilton JR. The role of crop yield response and economic returns in deficit irrigation decision-making. *Irrig Sci.* 2007;25(3):251–261.
2. Food and Agriculture Organization of the United Nations. The state of food and agriculture 2007: paying farmers for environmental services. Rome: FAO; 2007. Available from: <https://www.fao.org/4/a1200e/a1200e00.htm>
3. Carrijo DR, Lundy ME, Linquist BA. Rice yields and water use under alternate wetting and drying irrigation: a meta-analysis. *Field Crops Res.* 2017;203:173–180. Available from: <https://doi.org/10.1016/j.fcr.2016.12.002>

4. Lascano RJ, Sojka RE, editors. Irrigation of agricultural crops. 2nd ed. Agronomy Monograph No. 30. Madison (WI): ASA-CSSA-SSSA; 2007.
5. Fereres E, Evans RG. Irrigation of fruit trees and vines: an introduction. *Irrig Sci.* 2006;24(2):55–57. Available from: <https://link.springer.com/article/10.1007/s00271-005-0019-3>
6. Swaminathan MS. An evergreen revolution. *Crop Sci.* 2006;46(5):2293–2303. Available from: <https://doi.org/10.2135/cropsci2006.9999>
7. Organisation for Economic Co-operation and Development. OECD environmental outlook to 2050. Paris: OECD Publishing; 2010. Available from: <https://www.oecd.org/en/html>
8. Hatfield JL. Agriculture and the environment: climate change and water. *Agric Water Manag.* 2015;147:1–3.
9. Trenberth KE. Changes in precipitation with climate change. *Clim Res.* 2011;47(1–2):123–138. Available from: [https://www.int-res.com/articles/cr\\_oa/c047p123.pdf](https://www.int-res.com/articles/cr_oa/c047p123.pdf)
10. Forouzani M, Karami E. Agricultural water poverty index and sustainability. *Agron Sustain Dev.* 2011;31(2):415–431. Available from: <https://link.springer.com/article/10.1051/agro/2010026>
11. Chai Q, Gan Y, Zhao C, Xu H, Waskom RM, Niu Y, Siddique KHM. Regulated deficit irrigation for crop production under drought stress: a review. *Agron Sustain Dev.* 2016;36(1):3. Available from: <https://link.springer.com/article/10.1007/s13593-015-0338-6>
12. Gadde N, Anoruo A, Turner B, Holland P, Nelson S. Using Roma tomato to study the limits of deficit irrigation. *Int J Appl Agric Res.* 2025;11(4):120–125. Available from: <https://www.sciencepublishinggroup.com/article/10.11648/j.ijaas.20251104.12>
13. Morgan E, Zamora E, Nelson SD, Consuelo-Molia M, Anoruo A. Effects of deficit irrigation in pepper plants (*Capsicum annuum*) grown under greenhouse conditions. *World J Agric Soil Sci.* 2024;9(2):1–7. Available from: <https://irispublishers.com/wjass/pdf/WJASS.MS.ID.000705.pdf>
14. Mitchell JP, Shennan C, Grattan SR, May DM. Tomato fruit yields and quality under water deficit and salinity. *J Am Soc Hortic Sci.* 1991;116(2):215–221. Available from: <https://doi.org/10.21273/JASHS.116.2.215>
15. Berlyn GP, Miksche JP. Botanical microtechnique and cytochemistry. Ames (IA): Iowa State University Press; 1976. Available from: <https://www.scrip.org/reference/referencespapers?referenceid=1236631>
16. Anoruo AO, Turner BL, Garcia MR, Nelson SD, Donato-Molina MC. Morphological and anatomical development of *Solanum lycopersicum* seedlings grown with non-conventional water. *Int J Agric Res Environ Sci.* 2024;5(1):1–4. Available from: <https://skeenapublishers.com/journal/ijares/IJARES-05-00039.pdf>
17. Shi Y, Li BJ, Grierson D, Chen KS. Tomato cell wall and its role in fruit softening. *J Exp Bot.* 2017;68(16):3977–3989.
18. Tenhaken R. Cell wall remodeling under abiotic stress. *Front Plant Sci.* 2015;5:771. Available from: <https://doi.org/10.3389/fpls.2014.00771>
19. Tyree MT, Ewers FW. The hydraulic architecture of trees and other woody plants. *New Phytol.* 1991;119(3):345–360. Available from: <https://doi.org/10.1111/j.1469-8137.1991.tb00035.x>
20. Trifilò P, Barbera PM, Raimondo F, Nardini A, Lo Gullo MA. Coping with drought-induced xylem cavitation: coordination of embolism repair and ionic effects in three Mediterranean evergreens. *Tree Physiol.* 2014;34(2):109–122. Available from: <https://doi.org/10.1093/treephys/tpt119>