Plant Science 178 (2010) 30–40

Contents lists available at ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

Genotypic differences in some physiological parameters symptomatic for oxidative stress under moderate drought in tomato plants

Eva Sánchez-Rodríguez *, MªMar Rubio-Wilhelmi, Luis M. Cervilla, Begoña Blasco, Juan J. Rios, Miguel A. Rosales, Luis Romero, Juan M. Ruiz

Department of Plant Physiology, Faculty of Science, University of Granada, Fuentenueva SN, 18071 Granada, Spain

ARTICLE INFO

Article history:
Received 27 July 2009
Received in revised form 28 September 2009
Accepted 3 October 2009
Available online 14 October 2009

Keywords:
Water stress
Solanum lycopersicum
Osmoprotective compounds
Oxidative stress

ABSTRACT

Water stress strongly affects horticultural cultivars, reducing yield and fruit quality. Also the physiological functions of the plant are altered by this stress, due fundamentally to the formation of reactive oxygen species and water relationships. This study examines the response of five cherry tomato varieties to oxidative stress generated by moderate water deficit. Our results indicate that the cultivar Zarina is more tolerant to this stress, registering greater biomass and leaf relative water content (LRWC), associated with high antioxidant activity and low content in osmoprotective compounds. Also, we found a positive correlation of relative growth rate (RGR) total and foliar with LRWC, and a negative one with the parameters malondialdehyde (MDA), H_2O_2, test antioxidants, phenolic content, proline and quaternary ammoniums compounds (QAC), indicating the importance of lipid peroxidation as the determinant physiological process in selecting tomato plants tolerant to water stress.

1. Introduction

Plants, when subjected to environmental stress, undergo alterations in their growth, metabolism, and production. Among these, drought is the most adverse environmental factor regarding growth and productivity of cultivars. Losses in agricultural yield due to water stress probably exceed the losses inflicted by all other causes combined [1]. It is known that drought has a profound impact on agricultural and ecological systems, and thus the capacity of plants to withstand this stress is of great economic importance [2]. Therefore, at present, with the aim of improving agricultural yield within the earth's limited resources, it is necessary to develop crops able to give a high yield when growing in stressed environments.

Water stress influences plant growth in several ways. For example, shoot biomass significantly decreased in wheat under drought conditions [3]. In potato plants, stem length and dry weight diminished under water stress [4,5], and in tomato plant, shoot weight and total leaf area were lower than well-watered [6]. Also, water deficit diminishes leaf size, longevity, and number of leaves per plant [2].

The damage caused by water stress has two primary causes: first, the formation of reactive oxygen species (ROS) and, second, the alteration of water relationships within the plant. The extent to which plants can avoid or buffer these physiological processes determines the degree of resistance to water stress. Therefore the study of the metabolic and biochemical responses to water deficit is vital to present-day agriculture in order to select plants with high yield and stability under this type of stress [7].

Plants respond to water stress by producing abscisic acid (ABA), which stimulates the closure of the guard cells of the stomata to reduce water loss [8]. This process decreases CO_2 availability for photosynthesis, resulting in an imbalance between the generation and the use of electrons, provoking the overproduction of ROS. Free ROS attack biological structures, damaging DNA, prompting the oxidation of amino acids and proteins, and provoking lipid peroxidation [9,10]. To avoid such damage, plants have developed ROS-detoxification mechanisms that can be divided into enzymatic and non-enzymatic systems. The enzymatic systems comprise superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutation reductase (GR), dehydroascorbate reductase (DHAR), and monodehydroascorbate reductase (MDHAR). The non-enzymatic systems are composed of antioxidants such as phenols (flavonoids, anthocyanins, carotenoids, etc.), ascorbic acid (AsA) and glutation (GSH) [11]. Currently, there is clear evidence that many stress situations raise total foliar

Abbreviations: ABA, abscisic acid; APX, acorbate peroxidase; AsA, ascorbate; CAT, catalase; DHAR, dehydroascorbate reductase; GSH, glutation; GR, glutation reductase; LRWC, leaf relative water content; LOX, lipooxygenase; MDA, malondialdehyde; MDHAR, monodehydroascorbate reductase; QAC, quaternary ammoniums compounds; RGR, relative growth rate; ROS, reactive oxygen species; SOD, superoxidedismutase.

* Corresponding author.
E-mail address: evasr@ugr.es (E. Sánchez-Rodríguez).

0168-9452/$ – see front matter © 2009 Elsevier Ireland Ltd. All rights reserved.
doi:10.1016/j.plantsci.2009.10.001

antioxidant activity. Dhindsa and Matowe [12] demonstrated that water-stress-tolerant *Tortula ruralis* registered low lipid-peroxidation levels together with higher SOD and CAT activities. Also, Fazeli et al. [13] studied the behaviour of antioxidant enzymes under water stress in two sesame cultivars, observing that the SOD and CAT activities were higher in the most tolerant cultivar.

In plant cells, the components of the Halliwell–Asada cycle, which involves AsA, GSH, APX, MDHAR, and GR, represent the primary H_2O_2-detoxification mechanism. It has been confirmed that water-stressed *Hordeum* species show high GR and APX activities [14]. Furthermore, the activities of MDHAR, GR, and DHAR show a significant increased in rice plants subjected to water deficit [15]. Also, high GR and DHAR levels were found in lettuce leaves under drought [16]. Within the non-enzymatic systems, AsA is the main antioxidant synthesized in plant cells, which reacts chemically with $^1O_2$, O_2^-, OH and the radical thiol and which acts as a natural substrate for many plant peroxidases [9,17]. A high ratio of reduced AsA to oxidized AsA is essential to eliminate ROS in cells. It has been confirmed that these compounds increase in plants acclimated to drought stress [18]. Also, it has been concluded that the buffering capacity provided by AsA generates stress resistance in plants [19].

Finally, with respect to ROS detoxification under water-stress conditions, the role of phenols is also noteworthy. These compounds present two functions with the aim of preventing ROS formation. First, it has been verified that water deficit intensifies blue fluorescence provoked by the accumulation of phenolic compounds [20]. By radiation absorption, phenolic compounds transform highly destructive low-wavelength radiation (λ) into blue radiation of greater λ and therefore less destructive to leaf-cell structures, including the photosynthetic apparatus [21]. Also, Hura et al. [22,23] found a positive correlation between the emission of blue fluorescence and the total phenol content in *Triticale* plants subjected to water stress. These results were found also in maize, where the emission was greater in cultivars sensitive to water stress. Secondly, phenolic compounds also show an antioxidant action, which depends principally on the number and position of the hydroxyl groups and their structure [24]. Antioxidant activity has been demonstrated in flavonoids, mainly for their ability to sequester ROS, such as the anion superoxide, and the radicals hydroxyl and peroxyl [24].

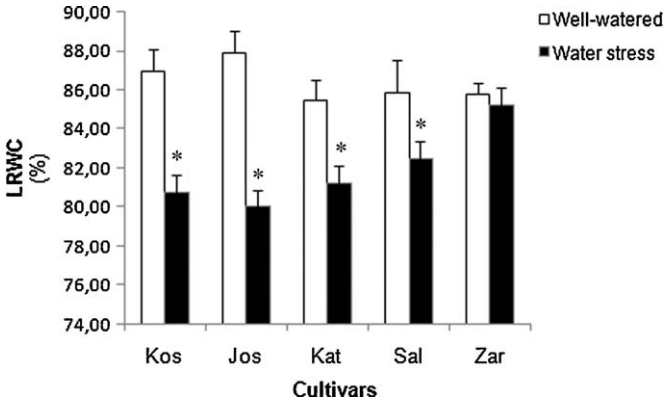

Fig. 1. Effect of moderate water stress on LRWC in leaves of five tomato cultivars: 'Kosaco', 'Josefina', 'Katalina', 'Salomé' and 'Zarina'. Columns are mean ± S.E. ($n = 9$) and differences between means were compared by Fisher's least-significant difference test (LSD; $P = 0.05$). *Significant difference with control groups (well-watered).

As indicated above, one of the main ways in which water deficit harms plants is by altering the water relationships under this type of stress. In this regard, water stress causes water loss within the plant and therefore a reduction in its relative content. In this sense, one of the most reliable and widely used indicators for defining both the sensitivity and/or the resistance to water stress in plants is leaf relative water content (LRWC) [25]. One of the most common strategies of plants for avoiding water stress is the accumulation of the so-called compatible solutes, also called osmoprotectors or osmolytes [26]. During osmotic stress, plant cells accumulate solutes to prevent water loss and re-establish cell turgour. The solutes that accumulate during osmotic adjustment include ions such as K^+, Na^+, and Cl^-, or organic solutes that include compounds that contain N, such as proline and other amino acids, polyamines, and QAC [27]. Proline accumulates in a great variety of plant species in response to stress such as drought, salinity, and extreme temperatures. Although its osmotolerant role in plants is not

Table 1
Dry weight and RGR in plants of 5 cultivars of cherry tomato plants well-watered and subjected to moderate water stress.

Cultivar/water treatment	Total biomass (g DW)	Total RGR (mg g^{-1} day^{-1})	Foliar biomass (g DW)	Foliar RGR (mg g^{-1} day^{-1})
Kosaco				
Well-watered	12.83 ± 1.15	87.02 ± 1.22	11.76 ± 0.72	87.23 ± 1.25
Water stress	8.40 ± 0.57*	68.15 ± 2.30*	7.54 ± 0.91*	64.74 ± 0.65*
$LSD_{0.05}$	3.58	8.02	3.25	1.54
Josefina				
Well-watered	12.76 ± 1.46	84.21 ± 5.02	11.66 ± 0.57	82.05 ± 3.20
Water stress	7.63 ± 0.71*	61.65 ± 0.32*	6.77 ± 1.15*	54.84 ± 0.21*
$LSD_{0.05}$	4.51	16.10	3.59	8.12
Katalina				
Well-watered	13.29 ± 1.09	83.41 ± 0.51	11.85 ± 0.50	87.25 ± 0.62
Water stress	8.51 ± 0.57*	63.95 ± 1.00*	7.65 ± 0.43*	64.38 ± 1.71*
$LSD_{0.05}$	3.44	5.15	1.84	5.10
Salomé				
Well-watered	12.17 ± 0.64	100.21 ± 0.75	11.22 ± 0.87	100.09 ± 0.75
Water stress	7.51 ± 0.57*	78.25 ± 0.51*	6.77 ± 0.45	76.25 ± 0.91*
$LSD_{0.05}$	2.39	2.53	2.74	3.09
Zarina				
Well-watered	11.38 ± 0.62	93.52 ± 8.11	10.87 ± 0.57	93.85 ± 2.33
Water stress	8.83 ± 0.68	79.23 ± 9.27	7.95 ± 0.63*	80.28 ± 0.34*
$LSD_{0.05}$	2.58	14.01	2.38	6.87

Values are mean ± S.E. ($n = 9$) and differences between means were compared by Fisher's least-significance test (LSD; $P = 0.05$).
* Significant difference with controls groups (well-watered).