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Influence of severe drought on leaf response in ABA contrasting tomato genotypes (wild type and *flacca* mutant)

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Abstract: The reaction of leaf growth to drought stress is controlled by various hormones, among which ABA is one of the most important. The aim of this study was to examine the effects of ABA deficiency on tomato leaf response under severe drought stress. Therefore, ABA-mutant (*flacca*) and wild type (Ailsa Craig) were selected for research and in the stage of 2nd flower truss anthesis plants were exposed to the severe water deficit. The effects of severe drought on wild-type leaves and *flacca* mutant showed that, as a result of reduced ABA concentrations, *flacca* plants were exposed to a higher degree of stress than wild-type leaves, which had a negative impact on the examined physiological and biochemical parameters. Severe drought caused stomatal closure, decreased water potential, specific leaf area, and chlorophyll concentrations in the leaves in both genotypes, but this was more pronounced in the mutant. Wild-type plants have accumulated more vitamins C and ABA and have a higher total antioxidant capacity in the leaves in dry conditions than *flacca* mutants, which contribute to their better adaptive response to stress. Based on this, it can be assumed that the ABA mutation has led to a decrease in the capacity for oxidative stress products caused by severe drought stress.

Keywords: tomato; *flacca*; Ailsa Craig; severe drought; leaf

1. Introduction

Drought is one of the most abiotic stress factor which affects plants in physiological, biochemical and molecular level, triggers a different plant defence mechanisms as a reduction of transpiration, increase of water absorption, osmotic adjustment, increased antioxidant system and drought tolerance [1]. The impact of drought on the tomato growth and development largely depends on the stage of ontogenesis when exposed to water deficit [2]. Leaf growth is one of the most drought sensitive processes in plants leading to a reduced leaf area, but also induces changes in parameters related to the leaf area-leaf dry mass ratio [3]. Drought-induced stomatal closure has an impact on net photosynthesis, but it also adversely affects the pigment system and photosynthetic electron transport and increases the risk of photooxidative stress [4].

Abscisic acid (ABA) as a "stress" hormone whose concentration increases under abiotic stresses, especially drought, plays an important role in regulating growth and development of plants that affect water regime, stoma reactions and photosynthesis, leaf and root growth, and changes in gene expression that control plant adaptive response [5]. In the study of the role and mechanisms of plant hormones in plants, mutants with reduced hormone biosynthesis are usually used. The aim of

presented study is to analyze the leaf response in ABA contrasting tomato genotypes by following physiological and biochemical changes under severe drought conditions. In order to reveal role of hormone ABA in plant reactions to drought, two tomato genotypes were used: wild type Ailsa Craig and ABA-deficient mutant *flacca* with reduced amount of ABA due to the changes in the activity of ABA-aldehyd oxidase [6].

2. Experiments

2.1. Experiment

The seeds of tomato wild-type Ailsa Craig and ABA-deficient mutant *flacca* were obtained from IPK Gatersleben Genebank and germinated in substrate Potgrond H-Klasmann (Germany). In the phase of the 5th leaf, plants were planted into pots filled with the mixture of substrate (Terracult "Blue line", Germany) and perlite. The plants were grown in controlled conditions in plant growth chamber at the Faculty of Agriculture, University of Belgrade, Serbia at following conditions: daily temperature between 25–28°C, in 16/8 light regimens, at 250 $\mu\text{molm}^{-2}\text{s}^{-1}$ PAR. Plants were fertilized every 14 days with liquid fertilizers.

In the phase of anthesis of the 2nd flower truss, plants were divided in two treatments (9 plants per treatment and genotype):

1. Control group—plants were fully irrigated from beginning to the end of experiment (36% of volumetric water content)
2. Severe drought—plants were fully irrigated to the phase of the 2nd flower truss, when severe drought treatment started (10–11% of volumetric water content) until the end of experiment.

Water content of the substrate was measured daily by ML3 ThetaProbe Soil Moisture sensor (Delta-T Device, Ltd., UK), in order to obtain amount of water for irrigation.

2.2. Physiological Parameters

Stomatal conductance was measured by AP4 Leaf Porometer (Delta-T Device, Ltd., UK), while the leaf water potential was measured by using a pressure chamber [7]. At the end of experiment, leaves were dried and dry matter content was determined. Leaf area was measured by LI-3100 areameter (LI-COR, USA) and specific leaf area (SLA) was calculated according to Hunt [8]. Leaf chlorophyll content was measured in the phases of anthesis, mature green and turning phase of fruit development by Dualex Force-A device.

2.3. Biochemical Analysis

For biochemical analysis, leaves were grounded to powder in liquid nitrogen. Analysis of ascorbic acid was done following the protocol of Stevens et al. [9]. Antioxidant capacity was measured by modified protocol [10]. Abscisic acid (ABA) concentration was measured by ELISA test following the protocol of Asch [11].

3. Results

3.1. Physiological Parameters

3.1.1. Stomatal Conductance and Leaf Water Potential

Obtained results showed that stomatal conductance and leaf water potential were not statistically different among investigated tomato genotypes under control conditions, while under drought stress were expressed genotype-related differences (Table 1). Severe drought caused the decrease of stomatal conductance in both genotypes, but the effect was more expressed in wild type Ailsa Craig compared to mutant *flacca* (for 83% and 62%, respectively). On the contrary, the decrease

of water potential values under drought was more expressed in mutant *flacca* (from -0,33 to -1,55 MPa) compared to wild type (from -0,31 to -1,22 MPa).

Table 1. Stomatal conductance and leaf water potential under optimal and drought conditions (Mean \pm SE; level of significance *** $p \leq 0.001$).

Genotype	Stomatal Conductance (mmol m ⁻² s ⁻¹)		Leaf Water Potential (-MPa)	
	Control	Drought	Control	Drought
Ailsa Craig	961,25 \pm 7,66	160,37 \pm 2,05 ***	-0,31 \pm 0,01	-1,22 \pm 0,04 ***
<i>flacca</i>	1038,75 \pm 7,66	396,87 \pm 7,84 ***	-0,33 \pm 0,01	-1,55 \pm 0,06 ***

3.1.2. Specific Leaf Area and Dry Matter Content

Genotype-specific differences among specific leaf area (SLA) values were expressed in both, control and drought conditions (Table 2). Under control conditions mutant *flacca* had 32% lower SLA in compare to wild type. Severe drought caused SLA higher reduction of SLA in mutant *flacca* (27%) than in wild type (15 %). Leaf dry matter content was not statistically different among genotypes in control conditions (Table 2), but under drought stress reducing effect was more expressed in mutant *flacca* (49%) compared to Ailsa Craig (36%).

Table 2. Specific leaf area and leaf dry matter content under optimal and drought conditions (Mean \pm SE; level of significance *** $p \leq 0.001$).

Genotype	Specific Leaf Area—SLA (cm ² /g)		Dry Matter Content (%)	
	Control	Drought	Control	Drought
Ailsa Craig	158,83 \pm 9,66	135,58 \pm 10,12 ***	9,93 \pm 0,17	13,51 \pm 0,33 ***
<i>flacca</i>	108,54 \pm 3,71	78,84 \pm 2,76 ***	10,39 \pm 0,19	15,53 \pm 0,30 ***

3.1.3. Chlorophyll Content

Analysis of chlorophyll content in the leaves at different stages of fruit development in optimal conditions showed that both genotypes in anthesis stage had similar amounts of chlorophyll, while in later stages, chlorophyll accumulated more in *flacca* leaves (Table 3). Severe drought stress induced the decrease of leaf chlorophyll content in mature green phase (*flacca* for 15%, Ailsa Craig for 6%), while pronounced effect was observed in turning phase of fruit development (12% for wild type and 19% for *flacca* mutant).

Table 3. Chlorophyll content in the leaves at different stage of tomato fruit development under optimal and drought conditions (Mean \pm SE; levels of significance * $p < 0.05$, ** $p < 0.01$, *** $p \leq 0.001$).

Genotype	Phase of Fruit Development	Chlorophyll Content ($\mu\text{g}/\text{cm}^2$)	
		Control	Drought
Ailsa Craig	Anthesis	32,58 \pm 0,87	
	Mature green	36,15 \pm 0,92	33,90 \pm 0,81 *
	Turning phase	39,70 \pm 0,84	34,88 \pm 0,71 *
<i>flacca</i>	Anthesis	33,18 \pm 0,70	
	Mature green	41,23 \pm 0,93	35,14 \pm 0,87 **
	Turning phase	48,88 \pm 0,63	39,49 \pm 0,95 ***

3.2. Biochemical Parameters

3.2.1. Vitamin C, Antioxidant Capacity and ABA Content

Analysis of vitamin C content showed significant differences among genotypes under control and stress conditions (Table 4). Severe drought induced accumulation of vitamin C in both genotypes (Ailsa Craig for 21%, and *flacca* for 9%) in comparing to control. Under stress conditions the increase of antioxidant capacity was more pronounced in the leaves of wild type (51%) than in *flacca* mutant (30%). Specific genotypic differences was observed in leaf ABA content under control conditions, since ABA-deficient mutant *flacca* had 37% less ABA than wild type (Table 4). Severe drought induced the accumulation of ABA that was more expressed in wild type (increase for 242%) compared to the mutant *flacca* (123 %).

Table 4. Vitamin C content, antioxidant capacity and ABA content under optimal and drought conditions (Mean \pm SE; levels of significance *** $p \leq 0.001$).

Genotype	Vitamin C (mg/100 g FW)		Antioxidant Capacity (μ mol TEAC/100 g FW)		ABA (ng/g FW)	
	Control	Drought	Control	Drought	Control	Drought
Ailsa Craig	70,53 \pm 2,35	85,47 \pm 2,30 ***	79,66 \pm 1,93	120,45 \pm 1,60 ***	387,93 \pm 8,26	1326,99 \pm 42,6 ***
<i>flacca</i>	55,39 \pm 1,35	60,61 \pm 1,57	81,96 \pm 1,56	106,70 \pm 2,11 ***	243,36 \pm 8,57	541,70 \pm 17,87 ***

4. Discussion

4.1. Physiological Processes

Stomatal conductance and leaf water potential are the indicators of plant water regime, but also can be used for selection of tomato-resistant genotypes to drought conditions [12]. Literature data confirm that drought stress induced stomatal closure and causes decrease of turgor and water potential in tomato plants [13,14]. Our results of stomatal conductance are in correspondence with data reported by Nankishore i Farrell [15] in different tomato genotypes under severe drought stress. Previous studies have confirmed that genotype *flacca* was more affected by dehydration compared to Ailsa Craig [16] and our results are in agreement with this, since the mutant have lower water potential than wild type under drought (Table 1). Investigation of leaf tomato response under severe drought showed that the decrease of stomatal conductance was followed by increased accumulation of ABA in the leaves [17]. Differences in stomatal conductance between the investigated genotypes under stress conditions in our experiment could be related to different accumulation of ABA in the leaves (Table 4), where the reactions of mutant are related to lower ABA concentration compared to wild type.

Our results also showed that severe drought induces decrease of specific leaf area, which is in correspondence with literature data [18]. The effect was more pronounced in *flacca* mutants (Table 2) that could be related with smaller leaf area due to less growth and curling of leaves [19,20]. The increase of the dry matter content in the leaves under severe drought was significantly higher in the *flacca* genotype than in wild type (Table 2). The application of different degrees of drought stress in tomatoes showed that the leaves have a higher dry matter content under severe stress [21], which is in line with the data obtained in our experiment. An increase in the dry matter content in the leaves indicates changes in hydration in the leaf tissues that could be a consequence of the concentration effect, but also the effect of osmotic adjustment [22].

Chlorophyll content is a parameter which indicates the efficiency of photosynthesis process. Severe drought stress had a negative effect on the accumulation of chlorophyll in the leaves in both

genotypes at different stages of fruit development (Table 3) which is in agreement with literature data [23]. The greatest effect in both genotypes was observed in the earlier phase of fruit ripening (the turning phase) which indicates the relation between chlorophyll biosynthesis and fruit ripening process [24]. A greater decrease in the chlorophyll content in mutant *flacca* indicates a greater sensitivity of this genotype to drought stress. These data are consistent with data of Sivakumar et al. [25], who showed that drought stress induced a greater decrease in chlorophyll content in sensitive genotypes than in tolerant genotypes. Exogenous application of low concentrations of ABA in different tomato genotypes led to an increase in the content of chlorophylls in the leaves [26]. Therefore, it can be assumed that the increase in ABA content in the leaves of both genotypes resulted in a small increase in chlorophyll content under severe drought in the turning phase (Table 3), compared to the green fruit phase.

4.2. Biochemical and Metabolic Processes

Severe drought stress is often accompanied with oxidative stress, the production of reactive oxygen species (ROS) and activation of antioxidant defense systems. Our results showed that an increase of vitamin C as well as antioxidant activity in the leaves, was more pronounced in the wild type than in the *flacca* mutant. Severe drought stress often increases the activity of the enzymes superoxide dismutase, peroxidase and catalase as well as the antioxidative activity in tomato plants [23,27].

The capacity for antioxidant defense is closely related to ABA accumulation. ABA-deficient tomato mutants (*notabilis* and *sitiens*) are characterized by increased peroxidase activity, which indicates the association between this enzyme and ABA concentration [28]. Ünyayar and Çekic [29] also showed that in the leaves of the *notabilis* antioxidant activity can be increased by applying drought stress or by exogenous ABA. The relation between antioxidative activity and ABA may explain genotypic response in our experiments, since ABA-mutation in *flacca* could be responsible for reduced antioxidant activity and limited the capacity for ROS removal under severe stress (Table 4).

One of the first biochemical changes in plants under drought stress is accumulation of ABA as a chemical signal of drought that affects plant response. Moles et al. [14] found an increase in ABA concentration in leaves and roots in different tomato genotypes under drought stress conditions. Our results showed that drought-induced accumulation of ABA in the leaves was more pronounced in wild type compared to *flacca* mutant (Table 4) that could be explained a specific stomata and leaf response. Investigation of gene expression in Ailsa Craig leaves indicate a synergistic effect of signaling pathways for ABA and ethylene, while in *flacca* the expression of the NCED gene was reduced and EIL1 was increased, which indirectly imply an increase in the concentration of ethylene [30]. Therefore, the explanation for the smaller leaf area and mass of *flacca* mutant or specific leaf response compared to the wild type may be due to decreased ABA production or increased ethylene concentration.

5. Conclusions

Investigations of the effect of severe drought on tomato leaf indicated specific genotypic response. Leaves of *flacca* mutant had lower water potential and higher stomatal conductance in drought conditions and where therefore exposed to a higher degree of water stress compared to the wild type. Under severe drought, a decrease in specific leaf area as an indicator of leaf growth, and chlorophyll concentration was found in the leaves in both genotypes, but the effect was more pronounced in the mutant than in wild-type. Water deficit induced an increase in total antioxidant capacity, vitamin C and ABA content, which was more pronounced in the leaves of wild-type. These results indicated that the ABA-mutation led to a reduced capacity for defense against oxidative stress that could be occurring during severe drought.

Author Contributions: Z.J. and R.S. conceived and designed the experiments; I.P. and S.S. performed the experiments; Z.J., I.P. and M.M. analyzed the data; M.M. contributed analysis tools; Z.J. and I.P. wrote the paper. All authors have read and agreed to the published version of the manuscript.

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Abbreviations

The following abbreviations are used in this manuscript:

ABA	Abscisic acid
FW	Fresh weight
SLA	Specific leaf area
ROS	Reactive oxygen species
TEAC	Trolox equivalent antioxidant capacity

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