The study of benzidine peroxidase activity of tomato (*Solanum lycopersicum* L.) varieties under drought conditions followed by recovery

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Drought is one of the most severe conditions that limit the growth and productivity of plants. This issue is important when considering economically relevant crops, including tomato plants. Therefore, research into the effects of drought on tomato plants is critical. The antioxidant system is known to play a key role in plant responses to drought. The benzidine peroxidase (BPO, EC 1.1.11.1.7) activity and its isoenzyme spectrum have been studied in ten local tomato varieties (Elim, Azerbaijan 94, Nuru, Ilyas, Yubiley 60, Mirvari, Zarrabi, Elnur, Khazar, Shakar). The benzidine peroxidase activity was found to increase in all studied genotypes under drought compared to the control variants. However, the activity of benzidine peroxidase decreased significantly in all varieties except the Elim variety after 3 days and 7 days of rehydration. Furthermore, it was determined 5 isoforms of BPO for the Khazar Elnur, Nuru, Miravari, Ilyas, and Yubiley 60 genotypes, 4 isoforms for the Elim genotype, and 3 isoforms for the Azerbaijan-94 genotype.

Keywords: *Solanum lycopersicum* L., *reactive oxygen species, benzidine peroxidase, drought stress*

INTRODUCTION

Recently, an increase in the frequency and severity of drought due to the effects of global climate change, with varying degrees of drought threat present in most countries and regions (Fullana-Pericas et al., 2018; Lesk et al., 2016). Limited water supply all over the world is a major problem in irrigated agriculture (Dasgan & Koc, 2009). The progressive desertification of irrigated agricultural areas threatens the future of agricultural lands. Crop losses caused by drought are the highest in comparison with the losses caused by all abiotic stresses (Placide et al., 2014). Drought stress negatively affects plant growth and yield, water competition between the vegetative and generative organs of the plant, and intracellular structures, thereby impairing plant metabolism and causing significant changes in plant morphology, physiology, and biochemistry (Torres-Ruiz et al., 2015; Kocaçalışkan, 2003).

Tomato (*Solanum lycopersicum* L.), with annual global production of around 182.3 million tons, is the second top tonnage-produced vegetable worldwide (FAOSTAT 2018). Amongst some of the summer vegetable species, tomato (*Solanum lycopersicum* L.) is grown intensively in the open and under cover in many of our country's semi-arid regions. Tomato is not classified as a tolerant plant, and its growth and productivity are hampered by unfavorable environmental conditions such as drought and salinity (Dong et al., 2020). Drought stress has diverse negative effects on all stages of development of tomato cultivars during their ontogeny (Jiang et al., 2019). The yield of tomatoes cultivated in drought and/or heat-prone areas can be decreased due to their drought and heat sensitivity (Pervez et al., 2009; Zhou et al., 2016), which could cause serious economic and societal impacts. From this perspective, the selection and breeding of tomato cultivars that can grow and produce economic yield under saline and drought conditions are low costings, permanent, and complementary alternative solutions to minimize their detrimental effects on production (Dasgan et al., 2002; Dasgan and Koc, 2009). Therefore, more research into the study of stress effects on physiological and biochemical processes and the responses and adaptation mechanisms of tomato varieties to drought stress is needed to develop drought tolerance and productivity in tomatoes.

Drought stress negatively affects many physiological and cellular processes, by acting at the molecular level (e.g., by inducing protein denaturation), at the cellular level (cell collapse), and at the level of the entire plant (wilting) by altering the water balance of cells and tissues (Joshi et al., 2016). Decreased water availability has an

immediate impact on water status and affects plant growth via detrimental effects on water absorption, photosynthesis, and the transport of water and solutes to growing organs like fruit. Drought leads to oxidative stress in the plant cell by increasing electron leakage towards O_2 during photosynthetic and respiratory processes, resulting in an increase in reactive oxygen species (ROS) generation (Asada, 1999; Sánchez-Rodríguez et al., 2012). ROS, such as hydrogen peroxide (H_2O_2), hydroxyl radical (HO^-), and singlet oxygen ($^1O_2$), damage cellular structures and macromolecules (Smirnoff, 1993; Ahmad et al., 2011), causing peroxidation of membrane lipids, inactivation of metabolic enzymes, inhibition of cell cycle and damaging the nucleic acids leading to cell death (Mittler, 2002; Gill and Tuteja, 2010; Ahmad et al., 2011). Moreover, reactive oxygen species act a signaling role in plants in response to abiotic stresses (Miller et al., 2008; Hasanuzzaman et al., 2012). The response of plants to drought stress varies depending on the species, the phase of development, the severity of the drought, and the duration of the impact (Stagnari et al., 2014; Bahadur et al., 2011). Plants douse the ROS through their antioxidant defense system with enzymatic and non-enzymatic components (Li, 2008; Simova-Stoilova, 2008; Hussain et al., 2008).

The main purpose of the study is to investigate the effects of water deficit on physiological markers such as RWC and the activity and isoenzyme spectrum of benzidine peroxidase, one of the enzymatic components of the antioxidant defense system, in ten tomato genotypes differing in their tolerance to drought stress followed by recovery.

MATERIALS AND METHODS

The study objects were local tomato varieties (Elim, Azerbaijan 94, Nuru, Ilyas, Yubiley 60, Mirvari, Zarrabi, Elnur, Khazar, Shakar) from the experimental base of the Research Institute of Vegetable-Growing under the Ministry of Azerbaijan Agriculture. The plants were cultivated in an artificial climate chamber at 65 ± 5% relative humidity, 25°C/20° C temperature regime, and a photoperiod of 16h/8h. Drought was imposed by withdrawing watering for 10 days. Plants were rehydrated after drought exposure. Leaf samples taken from control, drought-exposed, rewatered (after 3 days and 7 days of rehydration) plants were ground in liquid nitrogen in the laboratory and kept at a temperature of −80°C until use.

Determination of relative water content in leaves. The relative water content (RWC) was determined in the tomato leaves according to Turner (1981). Medium-sized fresh tomato plant leaves were weighed on an electronic scale and stored in distilled water for 24 hours. Following the determination of the turgor weight, the samples were dried in an 80°C thermostat and re-weighed. RWC was calculated by the following formula:

RWC = [(FW - DW) / (TW - DW)] x100

where, FW – fresh weight, TW – turgid weight, and DW – dry weight.

Extraction of enzymes. 0.5 g of leaf samples were ground in liquid nitrogen and homogenized in 100 mM Na-phosphate (pH 7.8) buffer solution containing 1 mM EDTA, 2 mM PMSF, 1% PVP and 0.1% Triton X-100. Samples were centrifuged at 4°C at a rate of 15,000 g for 20 minutes. The obtained supernatant was used to analyze the activity of benzidine peroxidase and the isoenzyme content.

Determination of the benzidine peroxidase activity. The activity of the benzidine peroxidase enzyme (BPO, EC 1.1.11.1.7) was determined by the increase in optical density of the reaction mixture for 2 minutes at a wavelength of 590 nm (Gechev et al., 2002). The reaction medium consisted of 50 mM Na-phosphate buffer (pH 5.0), 0.01% benzidine, 0.3% H_2O_2, and 20 µl of enzyme extract in a final volume of 1 ml. Taking ε=39 mM^{-1} cm^{-1} as the molar extinction coefficient, enzyme activity was expressed in µmol benzidine/mg protein min.

Determination of the isoenzyme spectrum of benzidine peroxidase. Qualitative changes in the enzyme activity were determined using native PAGE electrophoresis according to the method of Davis (Davis, 1964). A separating gel of 7 % acrylamide was used for the visualization of BPO isoenzymes. The enzyme extract in 50 % glycerol with 1 % bromophenol blue was applied to the gel. Electrophoresis was carried out for 3h at 4°C with a steady current of 30 mA, using the device SE 250 (Amersham Biosciences, USA). For determining benzidine peroxidase isoenzymes by the method of Cuypers et al. (2002), the gel was stored for 1 hour at 37°C in a 50 mM Na-acetate (pH 5.0) solution containing 10% benzidine and 1% H_2O_2.

Statistical analysis: The obtained results were subjected to a one-way analysis of variance (ANOVA) procedure.

RESULTS AND DISCUSSION

Water deficit causes disruptions in the plant cell's metabolic processes, and plants respond to stress with alterations in physiological, molecular, and biochemical changes. Relative water content is an indicator of water status (or availability) within

the plant, and any reduction in RWC can cause loss of turgidity, which in turn affects cell size and shape of plants, and itself induces many metabolic responses (Siddique et al., 2000). Relative water content was measured in ten tomato varieties (*Solanum lycopersicum* L.) after drought exposure and three and seven days of rehydration (Table 1). The study revealed that the relative water content decline was slightly different among the Elnur, Ilyas, Azerbaijan 94, Nuru, and Elm varieties by 25.4%, 24.7%, 26.8%, 23.9%, and 25%, respectively, after 10 days of drought exposure. These genotypes slightly recovered between 8.5%-11.5% in the following three days of rehydration. After 7 days of re-watering, a significant increase was observed in the Elnur, Ilyas, Azerbaijan 94, Nuru, and Elm varieties by 20.2%, 14.2%, 22.2%, 16.9%, and 21.2%, respectively. Compared to these five varieties, the rate of water loss was 35.6%, 41%, 32.9%, 30%, and 33% higher in the Zarrabi, Yubiley 60, Khazar, Miravari, and Shakar varieties. The table shows that the measured RWC in the leaves of Zarrabi, Yubiley 60, Khazar, Miravari, and Shakar cultivars after 7 days of rehydration was 25.8%, 19.7%, 20.55%, 20.4%, and 26.09%, respectively. While the minimum increase was observed in the Khazar variety by 4.8%, the maximum rise was in the Zarrabi variety by 14.3% after 3 days of water treatment.

Table. RWC in leaves of tomato plants cultivated under normal and drought conditions and re-watering.

Varieties	Variants	RWC (%)
Elim	Watered	70% ±2.0
	Drought-exposed	44.58%±0.6
	After 3 days of rehydration	53.87%±3.102
	After 7 days of rehydration	65.67%±2.517
Elnur	Watered	84.67%±5.508
	Drought-exposed	59.30%±4.351
	After 3 days of rehydration	68.78%±5.480
	After 7 days of rehydration	79.53%±5.220
Zarrabi	Watered	79.00%±2.000
	Drought-exposed	43.63%±2.876
	After 3 days of rehydration	57.93%±1.888
	After 7 days of rehydration	69.47%±2.829
Miravari	Watered	81.33%±5.132
	Drought-exposed	51.33%±3.512
	After 3 days of rehydration	60.70%±3.996
	After 7 days of rehydration	71.73%±5.605
Ilyas	Watered	81.50%±3.775
	Drought-exposed	56.805±3.617
	After 3 days of rehydration	65.31%±3.392
	After 7 days of rehydration	70.97%±3.392
Shakar	Watered	87% ±1.0
	Drought-exposed	54.58%±1.4
	After 3 days of rehydration	66.43%±3.881
	After 7 days of rehydration	80.67%±3.055
Azerbaijan 94	Watered	73.97%±3.950
	Drought-exposed	47.15%±2.335
	After 3 days of rehydration	58.67%±3.512
	After 7 days of rehydration	69.33%±2.517
Nuru	Watered	75.17%±6.252
	Drought-exposed	51.20%±5.068
	After 3 days of rehydration	61.85%±5.147
	After 7 days of rehydration	68.08%±6.956
Khazar	Watered	71.60%±3.143
	Drought-exposed	38.72%±3.104
	After 3 days of rehydration	43.50%±4.500
	After 7 days of rehydration	59.27%±4.606
Yubiley 60	Watered	70% ±2.0
	Drought-exposed	29.1%±0.8
	After 3 days of rehydration	40.73%±2.483
	After 7 days of rehydration	50.33%±2.517

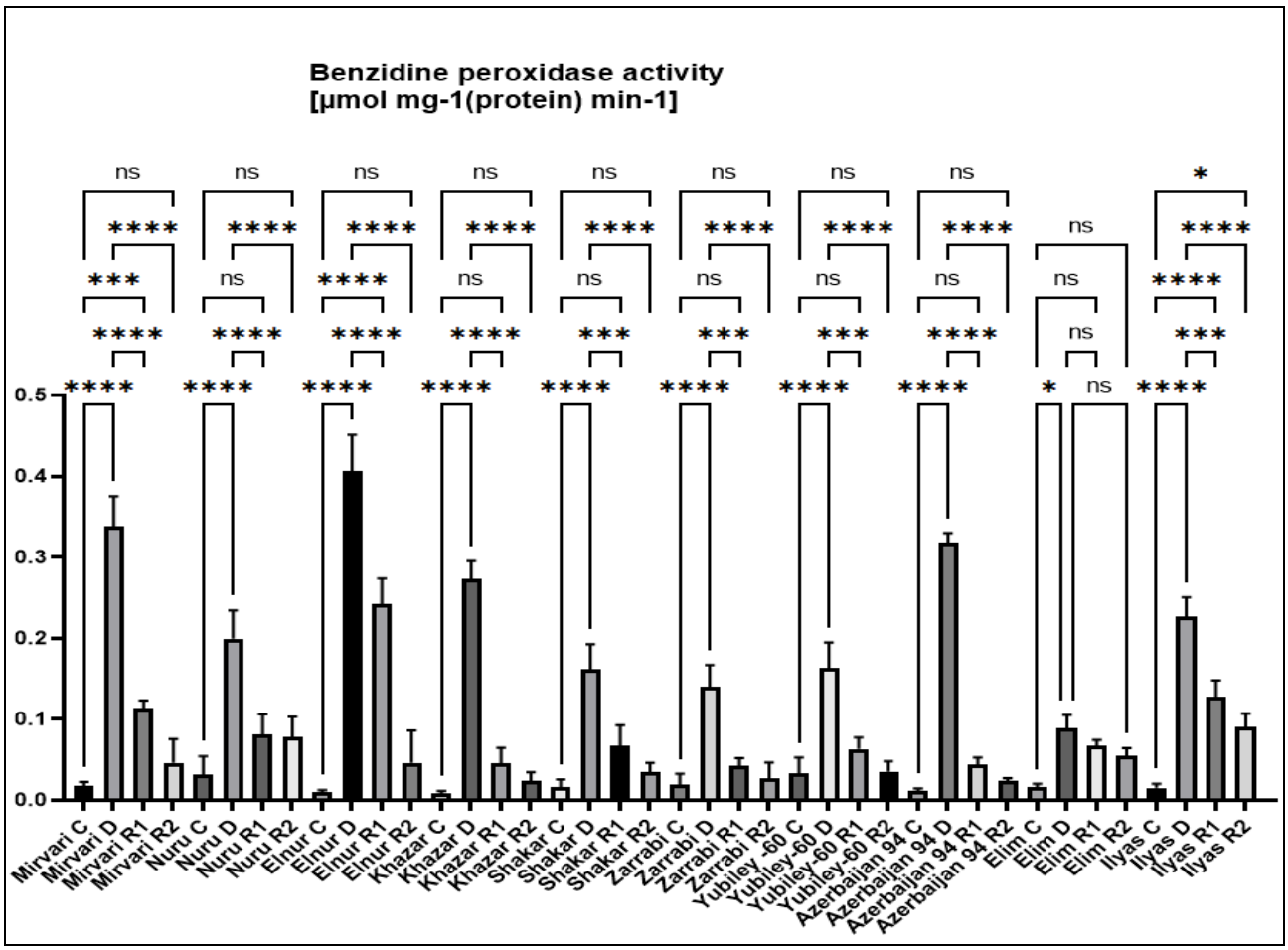

Fig. 1. Benzidine peroxidase (BPO, EC 1.1.11.1.7) activity in leaves of tomato plants (Elim, Yubiley 60, Shakar, Mirvari, Nuru, Elnur, Ilyas, Khazar, Zarrabi, Azerbaijan 94) under the drought and re-watering periods. Results of statistical test: **** - significance at P<0.0001, *** - significance at P>0.0001, * - significance at P=0.05.

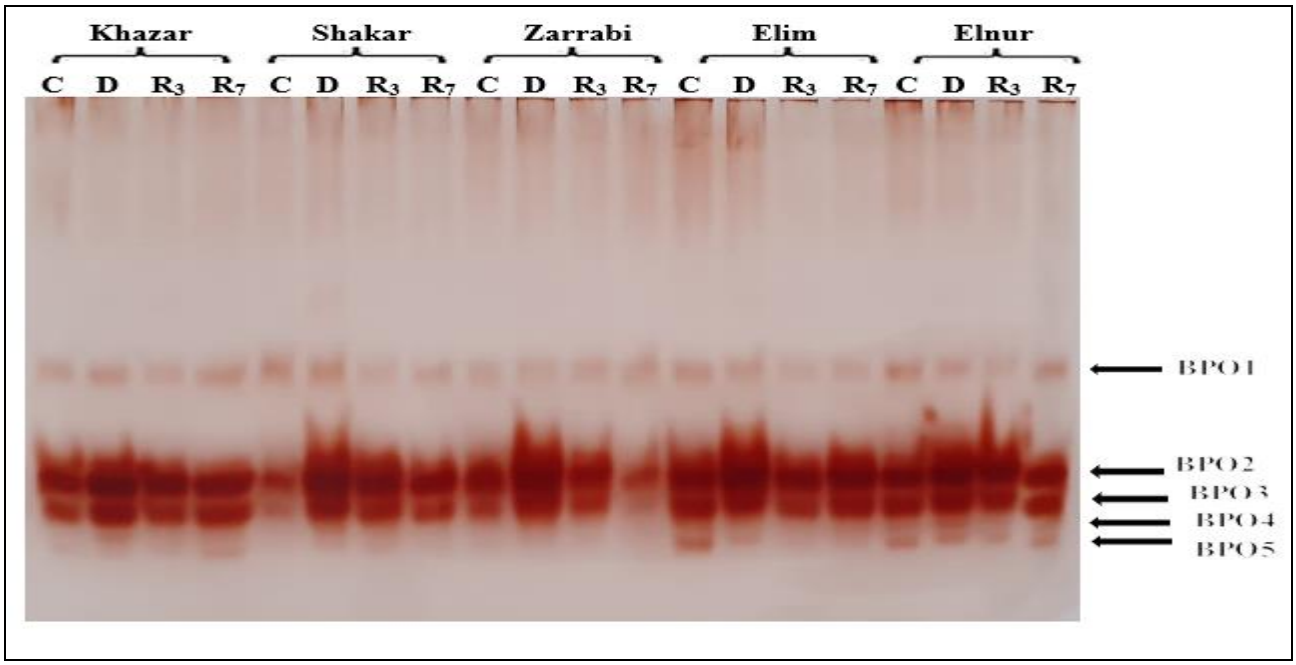

Fig. 2. The isoenzyme content of benzidine peroxidase (BPO, EC 1.1.11.1.7) in ten tomato genotypes during drought and re-watering periods. C, – control, D, – drought, R_3, – 3 days of rehydration, R_7, – 7 days of rehydration.

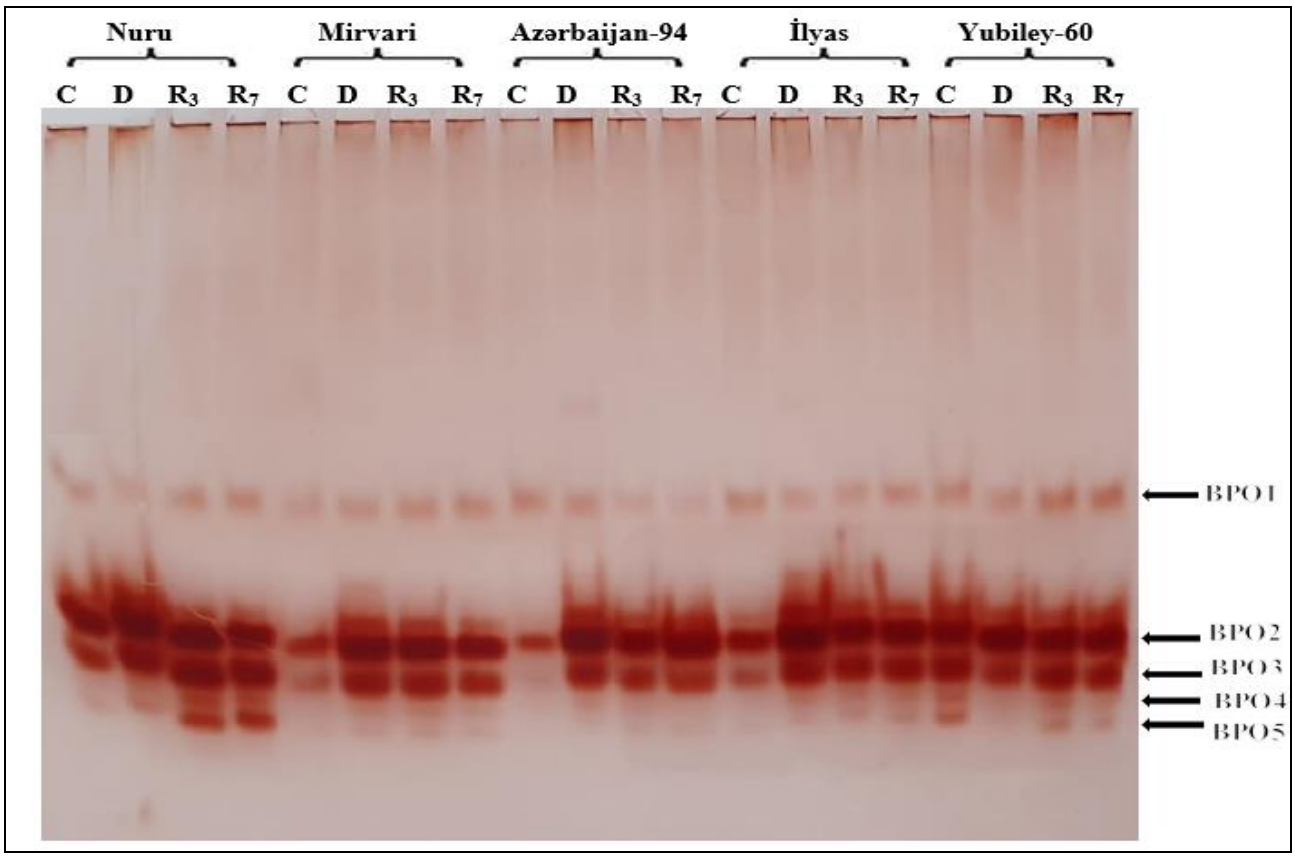

Fig. 3. The isoenzyme content of benzidine peroxidase (BPO, EC 1.1.11.1.7) in ten tomato genotypes during drought and re-watering periods. C, – control, D, – drought, R_3, – 3 days of rehydration, R_7, – 7 days of rehydration.

Under normal conditions, non-enzymatic and enzymatic antioxidants tightly control the balance between ROS formation and consumption in plants. Whereas, drought stress causes an imbalance between the production and scavenging of ROS (Ajithkumar and Panneerselvam, 2014). The activity of enzymatic antioxidants and components of the antioxidant defense system changes to suppress toxic levels of ROS within the cell (Ahmad et al., 2010; Hasanuzzaman et al., 2012). Therefore, in this study, the changes in the activity of benzidine peroxidase were determined by the spectrophotometric assay and the gel electrophoresis method. The enzyme activity increased significantly in all drought-exposed tomato varieties. When compared to control variants, a higher rate of increase was observed by 0.35 µmol/mg protein min in the Mirvari cultivar, 0.40 µmol/mg protein min in the Elnur cultivar, 0.27 µmol/mg protein min Khazar cultivar, 0.31 µmol/mg protein min in the Azerbaijan-94 cultivar, and 0.22 µmol/mg protein min in the Ilyas cultivar. The lowest rate of increase was found to be 0.09 µmol/mg protein min for the Elim cultivar. The enzyme activity increased 6.4, 9.7, 7.3, 5.1, and 5.6 folds, in the Nuru, Shakar, Zarrabi, and Yubiley 60 genotypes, respectively. After 3 days of water treatment, benzidine peroxidase activity decreased significantly compared to the drought-exposed variants, and following 7 days of rehydration, the enzyme activity approached to control variants in all varieties except the Elim variety. There were no significant changes in the activity of benzidine peroxidase in the Elim variety after both 3 days and 7 days of re-watering compared to the drought variant (Fig 1.).

At the next step of the research, native PAGE analysis was applied to identify the isoenzyme content of benzidine peroxidase using enzyme extract obtained from leaf samples of ten tomato genotypes. In the electropherogram results of Shakar and Zarrabi varieties, 3 isoforms of BPO (BPO1, BPO2, BPO3) were observed. The intensity of medium-molecular-mass BPO2 and BPO3 isoforms increased in the drought-exposed variants of these genotypes. After 3 and 7 days of re-watering, the intensity of these isoforms decreased. Furthermore, 5 isoforms of BPO were determined for the Khazar, Elnur, Nuru, Miravari, Ilyas, and Yubiley 60 genotypes, 4 isoforms for the Elim genotype, 3 isoforms for the Azerbaijan 94 genotype. Due to the effects of water deficiency, the low-molecular-weight BPO4 isoform was observed in the drought variants of the Khazar cultivar and after 7 days of the water treatment, another low-molecular-weight BPO5 isoform was

synthesized. According to the electropherogram results, after the drought treatment, the intensity of the BPO5 isoforms reduced and disappeared after 3 and 7 days of the water treatment in the Elim variety. The synthesis of BPO2, BPO4, and BPO5 isoforms slightly decreased after the 3 and 7 days of rehydration compared to drought-exposed variants of the Elnur variety (Fig. 2.).

As a result of the water treatment, the low-molecular-mass isoforms (BPO4 and BPO5) were synthesized intensively in the Nuru variety. Although the same isoforms were not found in the control variant of the Mirvari and Ilyas genotypes, they were synthesized both in the drought-exposed variant of genotypes and after the 3 and 7 days recovery at different intensity levels. Compared to the control variant of the Azerbaijan-94 variety, the medium-molecular-mass BPO3 isoform was detected during scarcity of water and after the rehydration. Additionally, while, the low-molecular-mass isoforms (BPO4 and BPO5) disappeared after drought treatment in the Yubliey-60 genotype, the bands of isoforms recovered after re-watering (Fig. 3.)

The result of the native PAGE analysis demonstrated that the heavy-molecular-mass isoform (BPO1) and the medium-molecular-mass isoform (BPO2) were synthesized in all variants of the studied ten genotypes.

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Quraqlıq və təkrar suvarma şəraitində tomat (*Solanum lycopersicum* L.) sortlarında benzidin peroksidaza fermentinin fəallığının tədqiqi

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Quraqlıq stresi bitkilərin böyüməsini və məhsuldarlığını məhdudlaşdıran ən şiddətli şəraitlərdən biridir. Bu məsələ tomat bitkisi də daxil olmaqla iqtisadi əhəmiyyətli məhsullar nəzərə alındığında böyük əhəmiyyət kəsb edir. Buna görə də quraqlığın tomat bitkiləri üzərindəki təsirinin öyrənilməsinə istiqamətlənmiş tədqiqatların aparılması vacibdir. Antioksidant sistem bitkilərin quraqlığa cavab reaksiyalarında əhəmiyyətli rol oynayır. Təqdim olunan işdə yerli tomat sortlarında (Elim, Azərbaycan-94, Nuru, İlyas, Yubiley-60, Mirvari, Zərrabi, Elnur, Xəzər, Şəkər) benzidinperoksidaza (BPO, EC 1.1.11.1.7) fermentinin fəallığı və izoferment tərkibi öyrənilmişdir. Benzidin peroksidaza fermentinin fəallığı tədqiq olunan bütün genotiplərdə nəzarət variantla müqayisədə artırmışdır. Lakin 3 gün və 7 gün rehidratasiyadan sonra benzidinperoksidazanın fəallığı Elim sortu istisna olmaqla, tədqiq olunan digər bütün sortlarda quraqlıq variantla müqayisədə əhəmiyyətli dərəcədə azalmışdır. Bundan əlavə Xəzər Elnur, Nuru, Miravari, İlyas və Yubiley-60 genotipləri üçün benzidinperoksidaza fermentinin 5, Elim genotipi üçün 4, Azərbaycan-94 genotipləri üçün isə 3 izoforması müəyyən edilmişdir.

Açar sözlər: *Solanum lycopersicum* L., *oksigenin fəal formları, benzidin peroksidaza, quraqlıq stresi*