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Physiological and Biochemical Changes of Pepper Cultivars Under Combined Salt and Drought Stress

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Abstract
Drought and salinity have been considered as environmental problems for plant growth and productivity. This study was performed to investigate growth, biochemical and physiological response to interactive salt and drought stress in pepper seedlings with two different cultivars. We examined three different salinity levels (0, 75 and 150 mM NaCl) and three different irrigation levels (100%, 75% and 50% of the water to reach the field capacity). Drought and salt stress were imposed individually and together on Yalova cv. and Maras cv. pepper (*Capsicum annuum* L.). Plant growth, tissue electrolyte leakage, stoma conductivity, relative water content, and antioxidants etc. were significantly degraded by treatments. To tolerate stress conditions, pepper seedlings tried to adapt by changing their antioxidant enzyme activity, proline or sugar content. Severe drought stress caused roughly 55% fresh shoot weight loss for Maras cv. and roughly 65% yield loss for Yalova cv. However severe salt stress caused roughly 70% shoot weight loss for Maras and 78% yield loss for Yalova cv., on the other hand, when two stress factors implemented together the fresh shoot weight reduction were 85% for Maras cv. and 83% for Yalova cv.

Keywords Abiotic Stress · Plant physiology · Water quality · Water deficit

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Physiologische und biochemische Veränderungen von Paprikasorten unter gleichzeitigem Salz- und Trockenstress

Zusammenfassung

Trockenheit und Versalzung werden als Umweltprobleme für das Pflanzenwachstum und die Produktivität angesehen. In dieser Studie wurden das Wachstum sowie die biochemischen und physiologischen Reaktionen auf gleichzeitigen Salz- und Trockenstress bei Paprikasämlingen von zwei verschiedenen Sorten untersucht. Wir untersuchten drei verschiedene Versalzungsgrade (0, 75 und 150 mM NaCl) und drei verschiedene Bewässerungsgrade (100 %, 75 % und 50 % der Wassermenge, um die Feldkapazität zu erreichen). Die Paprikaarten Yalova cv. und Maras cv. (*Capsicum annuum* L.) wurden sowohl einzeln als auch gemeinsam unter Trocken- und Salzstress gesetzt. Das Pflanzenwachstum, der Elektrolytverlust im Gewebe, die stomatäre Leitfähigkeit, der relative Wassergehalt und die Antioxidantien usw. wurden durch die Behandlungen erheblich beeinträchtigt. Um die Stressbedingungen zu tolerieren, versuchten die Paprikasämlinge, sich anzupassen, indem sie ihre antioxidative Enzymaktivität, ihren Prolin- oder Zuckergehalt veränderten. Starker Trockenstress verursachte bei der Sorte Maras einen Verlust von etwa 55 % des Frischgewichts der Triebe und bei der Sorte Yalova einen Verlust von etwa 65 % des Ertrags. Starker Salzstress verursachte bei der Sorte Maras einen Verlust von etwa 70 % des Frischgewichts der Triebe und bei der Sorte Yalova einen Verlust von 78 % des Ertrags. Wurden beide Stressfaktoren kombiniert, so betrug der Rückgang des Frischgewichts der Triebe bei der Sorte Maras 85 % und bei der Sorte Yalova 83 %.

Schlüsselwörter Abiotischer Stress · Pflanzenphysiologie · Wasserqualität · Wasserdefizit

Introduction

Drought and salinity have been considered as environmental problems for plant growth and productivity. Roughly 33% of the world's arable agricultural land is under the influence of cyclic or unpredictable drought, and salinity is a major problem in most of land (Wicke et al. 2011). Cultivated plants often need a large amount of water for their satisfactory growth. The amount and quality of water is becoming increasingly important in order to preserve existing food production and to increase production for the coming years to ensure the continuity of our quality of life. Lack of water often causes significant reduction in quality as well as yield losses (Yildirim et al. 2015, 2021). Therefore, possibility of using low quality water containing salt ions are very important for plant production under drought stress. However, salinity and drought stress conditions affect protein synthesis, photosynthesis, lipid metabolism and proline accumulation (Yolcu et al. 2021). Vegetable crops' exposure to short-term water stress leads them to close stomas. Cell death is caused by a decrease in the stomata which proceed to damage to the membrane systems (Dolferus 2014; Ors et al. 2016).

Plants exposed to osmotic stress try to regulate their osmotic potential by accumulating organic solutions in their cells in order to protect cell turgor. The osmotic states of plants in this situation are called osmotic adaptation (Hamada et al. 1992). Moreover, plants can reduce the harmful effects of stress through antioxidant enzymes (CAT, POD, SOD, etc.) to prevent the destructive effects of oxidative damage. Phytohormones play a crucial role in drought tolerance and affect the physiological processes of plants at low concentrations (De Smet et al. 2006).

Studies exist on the effect of water deficit and salt stress on pepper plant development. However, the effects of these constraints together on pepper have not been subject to much research. Because of the complexity of plants' response to drought and salt stress, exact tolerance mechanisms should be carefully investigated, understood and evaluated before large-scale applications, as they are specific to each plant. The purpose of this study is to gain more insight into the physiological and biochemical changes caused by drought and salt stress as well as their combination in two pepper cultivars during the early vegetative phases.

Materials and Methods

Plant Materials and Growth Conditions

The experiment was conducted in the controlled glass greenhouse at Atatürk University, Erzurum, Turkey. The seeds of the Yalova and Maras pepper cultivars (*Capsicum annuum* L.) were sown into multi-celled trays to a depth of 1–1.5 cm. The seedlings were planted in pots of 50 × 15 × 20 cm, after one month the plants were thinned as each pot had four seedlings. A mixture of soil: sand: manure (2: 1: 1; v/v) were filled in the pots at 1.30 gr. cm^3 bulk density. The relative humidity in the greenhouse was 60–70% and temperatures ranged from 28 to 36 °C during the day and 18 to 21 °C during the night.

Table 1 Pepper plant height, stem diameter, leaf number, leaf area, fresh shoot weight and fresh root weight response to salt and drought stress

NaCl	Drought	Plant height (cm)		Stem diameter (mm)		Leaf number		Leaf area (cm^2)		Fresh shoot weight (g $plant^{-1}$)		Fresh root weight (g $plant^{-1}$)	
		Maras	Yalova	Maras	Yalova	Maras	Yalova	Maras	Yalova	Maras	Yalova	Maras	Yalova
S0	D0	46.97a***	50.57a***	5.63a***	5.54a***	35.67a***	24.60a***	435.21a***	489.06a***	29.50a***	39.44a***	6.59a***	8.56 a***
	D1	36.35 b	46.83 ab	4.67 b	5.24 a	24.73 b	21.73 ab	369.71 b	438.44 b	20.81 b	23.42 b	2.78 b	4.83 b
	D2	29.92 c	39.07 cde	4.40 b	4.17 bc	14.93 c	16.20 bc	324.38 c	313.63 d	13.31 c	14.21 e	1.75 c	2.23 d
S1	D0	27.93 c	45.67 abc	4.19 bc	4.87 ab	15.40 c	18.00 b	264.61 d	368.64 c	11.65 cd	21.34 c	1.44 cd	4.12 c
	D1	28.80 c	41.37 bcd	3.77 cd	3.89 cd	13.20 c	13.13 cd	238.59 e	268.19 e	11.05 d	16.65 d	1.32 de	1.34 ef
	D2	21.20 d	29.07 f	2.98 e	3.20 d	12.27 c	11.33 d	172.16 g	198.29 f	5.70 fg	9.41 f	0.64 fg	0.87 g
S2	D0	25.53 cd	35.67 def	3.56 d	3.63 cd	12.20 c	11.88 d	243.72 e	210.32 f	9.00 e	8.66 f	0.97 ef	1.51 e
	D1	25.53 cd	33.38 ef	3.52 d	3.36 cd	12.40 c	11.38 d	200.34 f	171.44 g	7.54 ef	8.30 f	1.01 ef	0.95 fg
	D2	21.57 d	29.51 f	2.93 e	3.15 d	11.13 c	11.12 d	102.83 h	136.48 h	4.59 g	6.78 g	0.56 g	0.98 fg
S	–	***	***	***	***	***	***	***	***	***	***	***	***
D	–	***	***	***	***	***	**	***	***	***	***	***	***
SxD	–	***	NS	NS	NS	***	NS	***	***	***	***	***	***

NS Not significant; means separation within column by Duncan's multiple range test. $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$

Irrigation and Salinity Treatments

The irrigation water given for each irrigation event was determined by a portable moisture meter (HH2, Delta-T Devices). Soil water content of each pot were measured before each irrigations event and the water required for present pot moisture to reach back to the field capacity applied to the control treatment (full-irrigated; D0). In the drought treatments, the water amounts were adjusted to 75% (D1) and 50% (D2) of the D0 treatment. The pH, EC and sodium absorption ratio (SAR) of tap water used for irrigation were 7.40, 0.220 dS m-1 and 0.42, respectively. Half-strength modified Hoagland's nutrient solution was used to supply nutrients.

NaCl concentrations (0 mM; S0, 50 mM; S1, and 100 mM; S2) were used to obtain different level of salt stress. EC of the irrigation waters were 0.220 dSm^{-1} (tap water), 4.3 $dS\,cm^{-1}$ and 8.47 $dS\,cm^{-1}$ for S0, S1 and S2, respectively. Irrigation performed with three days intervals. Treatments were S0D0, S0D1, S0D2, S1D0, S1D1, S1D2, S2D0, S2D1 and S2D2. The treatments were applied after the seedlings were planted to the pots and the experiment terminated at the end of 45 days.

Plant Harvest and Analysis

Chlorophyll Readings and Leaf Area

CI-202 Portable area meter (CID, Inc USA) was used for leaf area measurements at the harvest. Chlorophyll was determined by SPAD-502 (Konica Minolta) from four different points of three fully expanded leaves.

Measurement of Electrolyte Leakage (EL)

Leaves from two different plants for each replicate were sampled to measure EL. From each leaf, 10 discs (10 mm Ø) were taken and put in 50-mL glass vials and 30 ml distilled water were added. The EC of bathing solution after 24 h at room temperature were recorded as (EC1) and the same vials with leaf discs were kept in a water bath at 95 °C for 20 min. After they were cooled to 23 °C, the EC was measured as EC2. EL was determined as a ratio between EC1 and EC2.

Relative Water Content (RWC)

Sampled leaf discs from each plant were weighted (FW) and they were soaked in the water for 24h h and weighted again (TW). Same leaf discs were kept at 60 °C to air-dry state and weighted (DW). The RWC was determined as follows; 100 * [(FW – DW) / (TW – DW)].

Photosynthetic Activity

Gas exchange parameters were measured one week before the harvest with Li-Cor 6400 (LI-COR, Lincoln, USA). Stomatal conductance (g_s), photosynthetic rate (P_n), intercellular CO_2 content (Ci), and transpiration rate (Tr) of each plant were measured on the third fully expanded upper leaves from between 10:00 am to 1 pm.

Table 2 Pepper dry shoot weight, dry root weight and SPAD response to salt and drought stress

NaCl	Drought (D)	Dry shoot weight (g plant^{-1})		Dry root weight (g plant^{-1})		Chlorphyll reading (SPAD)		RWC		EL	
		Maras	Yalova	Maras	Yalova	Maras	Yalova	Maras	Yalova	Maras	Yalova
S0	D0	3.80 a**	4.68 a***	0.68 a***	0.89 a***	40.27 a***	40.50 a***	87.40 a***	80.49 a***	27.94 g***	17.29 e***
	D1	3.42 ab	4.26 ab	0.46 b	0.53 b	35.90 bc	31.65 c	80.74 b	73.35 b	32.84 f	27.37 d
	D2	2.30 bc	2.66 bc	0.34 c	0.29 d	32.13 de	31.93 c	68.51 c	65.67 c	38.13 e	28.67 d
S1	D0	1.97 bc	2.26 c	0.34 c	0.40 c	37.07 b	34.90 b	82.30 b	73.98 b	55.23 c	41.31 c
	D1	2.24 bc	2.23 c	0.28 d	0.21 e	36.17 b	36.97 b	64.67 de	58.90 d	54.36 c	52.66 b
	D2	1.09 c	1.60 c	0.17 f	0.14 f	35.73 bc	34.22 b	62.27 e	56.05 d	42.02 d	42.33 c
S2	D0	1.77 c	1.50 c	0.22 e	0.21 e	33.77 cd	31.63 c	66.71 cd	71.06 b	59.15 ab	53.47 b
	D1	1.31 c	1.33 c	0.19 ef	0.14 f	32.77 cde	31.20 c	63.91 dee	63.30 c	56.79 bc	56.89 b
	D2	1.07 c	1.26 c	0.16 f	0.13 f	30.20 e	26.07 d	57.84 f	55.54 d	62.47 a	64.22 a
S	–	***	***	***	***	***	***	***	***	***	***
D	–	*	NS	*	***	***	NS	***	***	NS	***
SxD	–	NS	NS	NS	***	**	***	***	*	***	***

NS Not significant; means separation within column by Duncan's multiple range test. *RWC* Relative Water Content, *EL* Electrolyte Leakage. *$P<0.05$, **$P<0.01$, ***$P<0.001$

Harvest and Growth Parameters

Stem diameter, height, number of leaves, fresh-dry weight of the shoot and root were measured from four plants per each replicate. The plant material was kept at 70 °C for 48 h for dry weight. To determine the contents of proline, sucrose, MDA, H_2O_2 and antioxidant enzyme activity roughly 20 g of fresh leaves were frozen in liquid nitrogen and then stored at –80 °C and analysis were conducted later at the laboratory on four replicates. At harvest four plants from each replicate were taken to measure.

Biochemical Measurements

For lipid peroxidation (measurement of malondialdehyde -MDA) the absorbance was measured at 400, 500 and 600 nm and proline concentration was determined spectrophotometrically at 520 nm according to Sahin et al. (2018). Sucrose concentration was measured by a method given by Liu and Huang (2000), and calculation of sucrose content was done according to Ting (1956). H_2O_2 was determined according to Velikova et al. (2000). For determine of H_2O_2, the absorbance was measured at 390 nm by spectrophotometry.5 ml of 100 mM phosphate buffer (pH 7.0) containing 1% (w/v) PVPP at 4 °C were used to homogenize frozen pepper leaves.. This supernatant was used in enzyme assay. SOD and CAD activity was analyzed according to Abedi and Pakniyat (2010). POD activity was measured according to the Angelini et al. (1990).

Completely randomized design was set up with four replications and each replication consists of four plants for two factors. NaCl levels (the first factor) had three levels (0, 50 and 100 mM), and irrigation levels (the second factor) had three levels (100%, 75% and 50%). SPSS were used for analysis of variance (two-way ANOVA).

Results and Discussion

When Tables 1 and 2 are evaluated, both drought and salt stress and their combination had a significant negative effect on plant growth in peppers. Dry shoot weights in the S0D1, S0D2, S1D0, S1D1, S1D2, S2D0, S2D1, and S2D2 treatments were lower by 7.3%, 39.5%, 48.2%, 41.1%, 71.4%, 53.4%, 63.5% and 71.8% for the Maras cv., and 9.0%, 43.2%, 51.7%, 52.4%, 65.2%, 68.0%, 71.6% and 73.1% for the Yalova cv., respectively compared to the S0D0 values. On the other hand, all drought and salinity and their combined treatments were statistically in the same groups for both cultivars. Dry root weight in the S0D1, S0D2, S1D0, S1D1, S1D2, S2D0, S2D1and S2D2 treatments were lower by 32.4%, 50.0%, 50.0%, 59.1%, 75.0%, 67.7%, 72.1% and 76.0% for Maras variety, and 40.5%, 57.4%, 41.1%, 69.1%, 79.4%, 69.1%, 79.4% and 80.9% for the Yalova compared to the peppers in the S0D0 treatment. The lowest results were obtained from S1D2, S2D1 and S2D2 treatments which were in the same statistical groups. The negative impact of salt stress was higher than that of drought stress, while a combination of salt and drought had the most negative effect. As given in Table 1, substantial reductions in plant height, leaf number and leaf area of pepper plants were recorded under stress conditions.

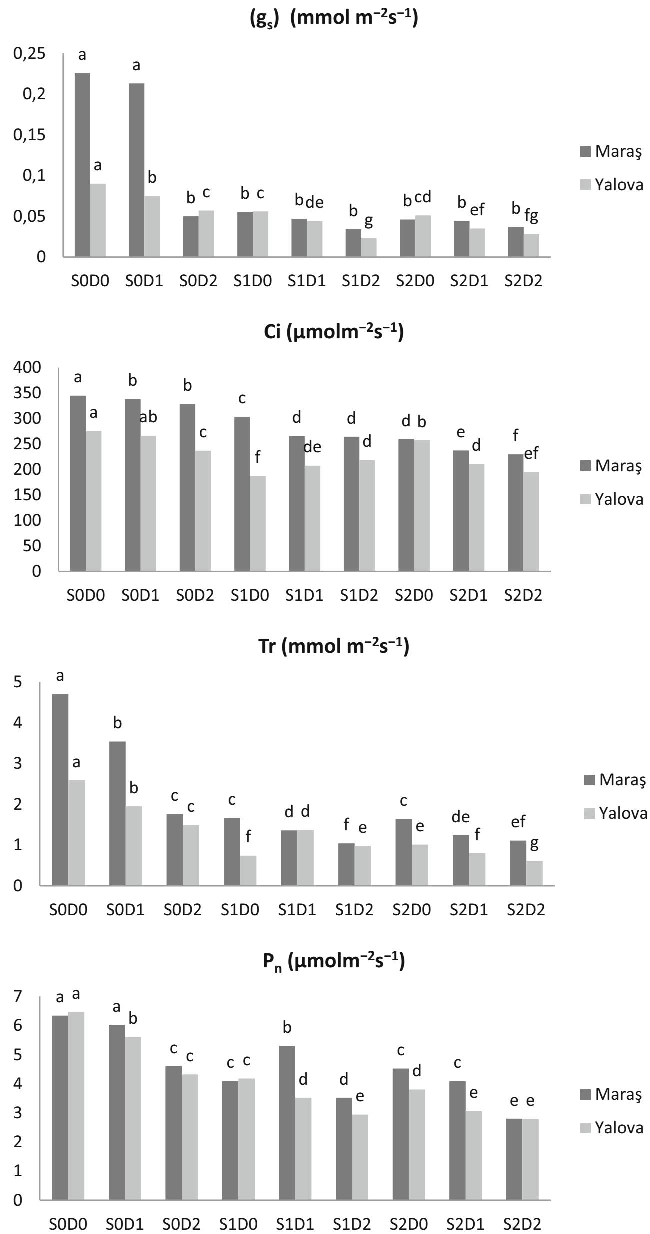

Fig. 1 Pepper photosynthetic rate (Pn), intercellular CO_2 content (Ci), stomatal conductance (gs) and transpiration rate (Tr) response to salt and drought stress. Different letters on top of the bars indicate significant differences according to the Duncan test ($p < 5\%$) for each variety

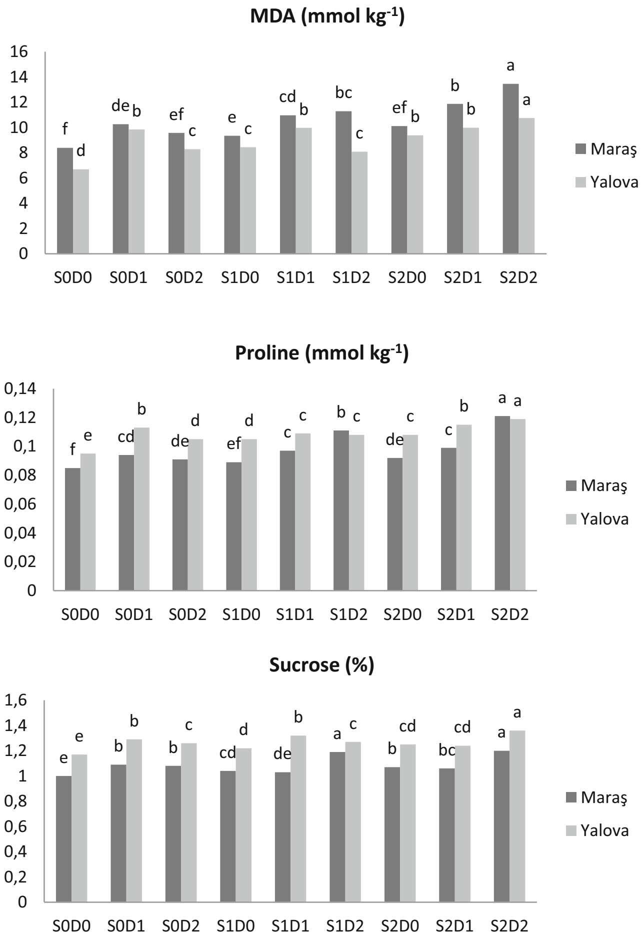

Fig. 2 Pepper H_2O_2 MDA, proline and sucrose content response to salt and drought stress. Different letters on top of bars indicate significant differences according to the Duncan test ($p < 5\%$) for each variety

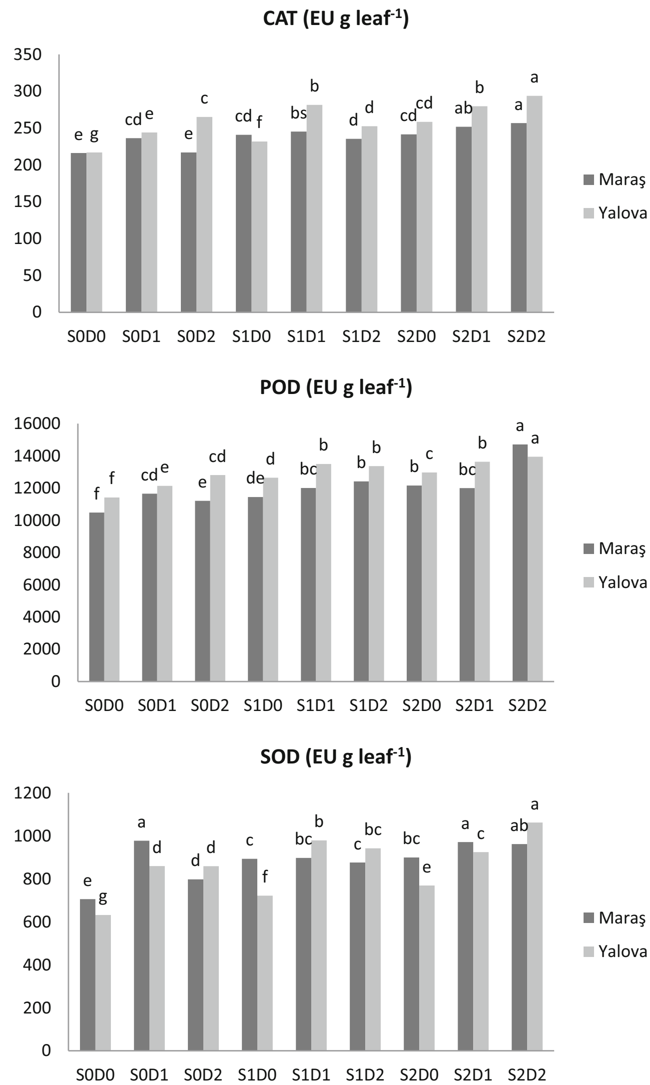

Fig. 3 Pepper CAT, POD and SOD activity response to salt and drought stress. Different letters on top of bars indicate significant differences according to the Duncan test ($p < 5\%$) for each variety

The decrease in leaf area under abiotic stress was evaluated as an avoidance mechanism to minimize transpiration (Blum 1997). Severe drought stress (D2) caused roughly 55% fresh shoot yield loss for Maras cv. and roughly 65% yield loss for Yalova cv. However severe salt stress (S2) caused roughly 70% shoot yield loss for Maras and 78% loss for Yalova cv. These results underline that experimented pepper cultivars developed better tolerance to drought stress and especially Maras cv. were found to be quite drought tolerant. Under mild drought stress conditions (D1) fresh shoot weight reduction of Maras cv. was only 30%, which addresses 25% water deficit throughout the growing period.

The co-occurrence of drought and salinity has been reported to be more detrimental for growth and yield than an individual stress (Umar and Siddiqui 2018). In our experiment, when two stress factors implemented together (S2D2) the fresh shoot weight reduction was 85% for Maras cv., and 83% for Yalova cv. These results show that under combined stress conditions Maras cv. is no longer able to tolerate drought together with salinity, the growth of the plant is almost stopped by the environmental conditions. Similarly, some researchers have reported that the plant growth of onions (Hanci and Cebeci 2015) and soybeans (Khan et al. 2016) were adversely affected by salt and water deficit applied separately or together.

Chlorophyll reading values (SPAD) decreased significantly in all treatments as compared to the control (S0D0). This can be explained by the destruction of chlorophyll pigments, and a minimization of the vulnerability of the pigment-protein complexes and chlorophyll syntheses (Ahmad et al. 2016). Maras had higher SPAD values than Yalova (Table 2).

While there was a decrease in RWC values in pepper plants grown under drought and salt stress conditions, an increase in EL values was observed (Table 2). This increase in EL value is thought to be caused by the damage caused by the stress conditions of the cell membrane. Masoumi et al. (2010) reported that the drought stress caused damage in leaves that resulted as an increased EL from cell membranes. Same findings report earlier for spinach by Ekinci et al. (2015) that EL increased under drought. The decrease in RWC is reported to cause a parallel decrease in photosynthesis rate with closure of stomata (Bhardwaj et al. 2021). Omami and Hammes (2006) also reported that osmotic potential, leaf water potential, and RWC of amaranth plant decreased under salt and water stresses. Reduced leaf area, shoot height, number of leaves and in sensitive genotypes may be explained by the probability of having less RWC in their leaves.

Photosynthetic activity, stomatal conductivity and transpiration rate decreased significantly in the pepper plants under salt and drought stress conditions. The highest reduction in those measured parameters were recorded when both drought and salt stress applied together (Fig. 1).

The reductions in the treatments with increased stress level were sharper in Maras for gs and Tr as compared to Yalova. Previous studies on different plants showed that salinity and drought stress adversely affected the photosynthetic activity in the plant (Farooq et al. 2009; Xu and Leskovar 2014; Ors et al. 2016). The reduction in photosynthesis has been explained due to the decrease in the leaf water potential and RWC (Lawlor and Cornic 2002; Bhardwaj et al. 2021). Under water deficit, drought-tolerant plants able to increase their capability by decreasing stomatal conductance (Oukaltouma et al. 2022). We observed that Maras generally provided better photosynthetic activity than the Yalova under stress conditions (Fig. 1). The genotypes Maras and Yalova showed an 84% and 68% decline respectively in g_s under combined stress as compared to the control plants (Fig. 1). It can be said that Maras mitigate drought and salt by reducing g_s and this improve water use efficiency of plant.

In our study, salinity and drought applications considerably increased the amount of H_2O_2, MDA, proline and sucrose in Yalova and Maras pepper cultivars (Fig. 2). Under severe salt and drought stress, the amount of MDA reached a maximum value (Fig. 2). It has been announced earlier that the amount of MDA increase in plants that exposed to salt and drought stresses (Naveed et al. 2014; Shams et al. 2016; Sahin et al. 2018). Arbona et al. (2008) announced that the oxidative damage of the cell membrane in plant is directly correlated with MDA content.

Reactive oxygen species, such as hydrogen peroxide and O_2 is generally formed in big amounts by plants during variant stress reflex. The proline and sugar content of pepper cultivars elevated depending on stress conditions, the greatest values were observed in combined stress conditions (Fig. 2). Proline increased significantly under both salinity and drought stress as compared to control in onion under drought stress (Hanci and Cebeci 2015). In recent years, studies have also been involved in proline signal transduction, regulation of mitochondrial functions, cell division or death, and regulation of gene expression levels (Liang et al. 2013; Kavi Kishor and Sreenivasulu 2014; Naing and Kim 2021). In this study we obtained the better leaf area, plant height, number of leaves, and RWC in Maras cv. under interactive stress, this can be explained by higher accumulation of proline in plant.

The pepper plants under stress produced more sucrose (Fig. 2). Soluble sugars act as a osmotic protector by performing a significant function in plant metabolism and maintain turgor pressure. Similar results obtained earlier (Krasensky and Jonak 2012) which indicates that plants accumulate proline and sucrose under drought and salt stress.

In this study salt and drought treatments had different effects on the activities of POD, CAT and SOD in pepper cultivars. The activities of POD, CAT and SOD increased significantly under drought and salt stress (Fig. 3). There are many studies suggesting that enzymatic antioxidant mechanisms play a critical role in the defense against ROS in many plants exposed to drought and salinity stress (Naveed et al. 2014; Sahin et al. 2018; Desire and Arslan 2021).

Plants fight against stress with enzymatic antioxidant protective systems consisting of SOD, CAT, POD, APX and GR. Jaleel et al. (2009) announced that plant stress tolerance can be sustained by controlling the ROS production through non-enzymatic mechanisms, such as proline and phenolic compounds or to avoid plants from oxidative damage by the activity of antioxidant enzymes like SOD and CAD (Quan et al. 2008). Our study showed that POD, CAT and SOD activities of pepper cultivars were negatively correlated with H_2O_2 concentrations. CAT is one of the enzymes that detoxify H_2O_2 in plants. CATs use H_2O_2 as a substrate and change it to H_2O and O_2 as products (Umar and Siddiqui 2018).

SOD performs as a main scavenger of ROS under stress. The POD enzyme has a main role in scavenging the H_2O_2 produced under salinity to H_2O and O_2 (Liang et al. 2018; Shams et al. 2016). The increase in enzyme activity and the reduction in H_2O_2 production under stress alert the activation of a plant's defensive system. In this regard, Ma et al. (2017) found that the antioxidant system induced tolerance in sugar beet plants and also decreased the hydrogen peroxide content under salinity stress. In this study, the results of enzyme activity and production of H_2O_2 demonstrated that these cultivars had different responses to salt and drought stress.

Conclusions

The aim of this study was to understand the impact of drought and salt stress individually and their interactions on pepper plant for different cultivars. Both salinity and the drought stress conditions had a negative effect on some properties such as plant growth, photosynthetic activity, chlorophyll content and these effects increased when two stress factors were implemented together. In terms of tolerance to stress, the cultivars initiate to adapt adverse conditions by changing their antioxidant enzyme activity and photosynthetic characteristics. In this study, Maras cv. appeared more tolerant to salt and drought stress than Yalova cv. in terms of having a better physiological performance against either salt and drought or combined stress conditions. Under the conditions of both drought and fresh water absence low quality water usage can be favorable to sustain plant production for some plants, however, in the example of pepper, plant production is more sustained under drought conditions as compared to saline water irrigated conditions. Low quality water caused higher reduction in the measured parameters, thus applying less fresh water can be more practical than using saline irrigation waters.

Conflict of interest E. Yildirim, M. Ekinci, M. Turan, G. Ağar, S. Ors, A. Dursun, R. Kul and G. Akgül declare that they have no competing interests.

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