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Nitric Oxide Enhances Salt Tolerance through Regulating Antioxidant Enzyme Activity and Nutrient Uptake in Pea

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ABSTRACT

Background: Salinity is one of the environmental stress factors that restrict the crop production by endangering agricultural areas. Nitric oxide (NO) protects plants from damage caused by oxidative stress conditions in various biological ways.

Methods: In this greenhouse investigation during 2018, pea plants were irrigated with three levels of NaCl (0, 50 and 100 mM) solutions. NO solutions were prepared with three different doses (0, 75 and 100 µM SNP). These solutions were applied to the seeds before sowing and then to the leaves of the pea cultivars. The study was conducted to analyze the impact of NO on growth, malondialdehyde (MDA), hydrogen peroxide (H_2O_2), antioxidant enzyme activity and nutrient uptake in two pea cultivars under salinity conditions.

Result: Salinity reduced fresh-dry weight, relative water content (RWC) and chlorophyll a and b content of pea. However, NO enhanced these parameters under salt stress. Salinity increased tissue electrical conductance (TEC), H_2O_2 and MDA content, which were decreased by combined application of NaCl and NO. Salinity caused an increase in antioxidant enzyme activity in pea, and NO made a significant improvement in their activities under salinity conditions. Salinity treatments decreased the ratio of K^+/Na^+ and Ca^{2+}/Na^+ in both cultivars and application of NO elevated them as compared to the control under salt stress. In conclude, exogenous NO treatment could help pea to tolerate salinity stress by increasing the chlorophyll content and regulating antioxidant enzyme activity and nutrient uptake.

Key words: Enzyme activity, Nitric oxide, Pea, Salt stress.

INTRODUCTION

Salinity is one of the environmental stress factors that restrict crop production. Salinity shows its direct effect on plants by creating osmotic and ion stress, while its indirect effect is shown by structural degradation and synthesis of toxic compounds. Reduction of the amount of water available due to the osmotic effect causes a decrease in cell expansion and a slowing of shoot development. Nutrient deficiency or nutrient imbalance occurs in plants by increasing Na and Cl ions competing with necessary nutrients such as K^+, Ca^{+2} and NO_{-3} (Shams *et al.,* 2019). Much of the cell-level damage caused by salt stress is related to oxidative damage caused by ROS which significantly damages cellular membranes and organelles (Parida and Das 2005). Salinity reduces the leaf number, leaf area, plant fresh weight, dry weight, chlorophyll content and fruit quality (Karlidag *et al.,* 2013).

NO is a signal molecule in plants, which has various metabolic functions. It plays an important role in the growth and development of plants. It is evident that NO protects plants from damage caused by oxidative stress conditions in various biological ways (Shams *et al.,* 2019). Excessive ROS accumulation due to salinity conditions can result in oxidative damage and NO is considered a functional molecule to alleviate salt stress in plants via modifying antioxidant metabolism (Lin *et al.,* 2012). Exogenous NO treatment can cause an increase in antioxidant enzyme activity and salt tolerance genes in plants under salinity stress, this leads to increased plant growth and productivity (Arasimowicz and Floryszak- Wieczorek 2007).

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Pea (*Pisum sativum* L.) belongs to the family Fabaceae and is a low-cost and nourishing food. It is rich in dietary proteins, complex carbohydrates, essential amino acids, vitamins, fiber and minerals. However, its growth, grain yield, and quality and composition of grains significantly were affected by salinity stress (Nenova, 2008). In this regard, it is beneficial to understand the mechanism of NO on the tolerance of *Pisum sativum* L to salinity stress. Here, we report a more detailed study of the influence of NO on plant growth, nutrient uptake, MDA and H_2O_2 content, and enzyme activity in pea cultivars under long-term salt stress.

MATERIALS AND METHODS

The study was done in the greenhouse at Atatürk University,

Turkey in 2018. Plants were maintained under natural light conditions, approximate day/night temperatures of 32/19°C, and 45% relative humidity during the experiment.

Pea (*Pisum sativum* L.cv. Jof and cv. Utrillo) seeds were surface-sterilized with sodium hypochlorite (10% v/v) for 5 min and were well washed with sterilized water. Seeds were then air-dried overnight on sterile Whatman filter paper sheets in the laminar flow hood. The seeds were sown in the pots filled with a mixture of peat: perlite (3:1, v: v) and finally each pot contained four seedlings.

The salinity treatment was established by adding 0, 50 and 100 mM of NaCl to irrigation water and their electrical conductivities were 0.54, 5.23 and 7.61 dS m^{-1} respectively. Salinity treatments were initiated ten days after seedling emergence with an increase of 25 mM NaCl to avoid an osmotic shock for plants. Plants were irrigated with a half-strength Hoagland solution with ten days intervals.

Sodium nitroprusside (SNP), a NO donor, was used as the NO treatment. NO solutions were prepared with three different doses (0, 75 and 100 µM of SNP). These solutions were applied to the seeds before sowing and then to the leaves of the pea cultivars. For this purpose, the seeds were soaked separately in these solutions for 24 h at 20°C then seeds were taken out and air-dried. For foliar application, the solutions of NO were prepared with distilled water containing 0.02% Tween-20 as a surfactant, and they were sprayed on leaves one day before salinity treatment in the late afternoon. The foliar NO treatments were repeated three times at one weekly interval.

The relative water content (RWC), Tissue Electrical Conductivity (TEC) and CRV (Chlorophyll Reading Value) were measured after 52 days of sowing from each pot before harvest. During harvest plants were cut from the soil level, and above ground biomass (shoot) and roots were separated for measurements and analysis.

The leaf area was determined by leaf area meter (CI-202 Portable Laser Leaf Area Meter by CID Bio-Science, USA).

Assays of chlorophyll, MDA, H_2O_2 and antioxidant enzyme activity were performed by UV/Vis spectro-photometer according to Sarafi *et al.* (2018).

For the determination of mineral nutrition content, the leaves of the pea cultivars were dried at 68°C for 48 h and grounded and K, Ca and Na content were analyzed by a coupled plasma spectrophotometer (Optima 2100 DV; Perkin-Elmer, Shelton, CT) (Helrich, 1990). A completely randomized design with three replications was used in the current experiment and we had 12 plants per replicate. Data were subjected to analysis of variance (ANOVA). Means were separated by Duncan's multiple range tests.

Results and Discussion

Salinity stress (100 mM of NaCl) decreased shoot fresh and dry weight, and the root fresh and dry weight by 81, 52, 51 and 52%, respectively in Jof cultivar compared to control. However, in Utrillo, the shoots fresh and dry weight and the root fresh and dry weight were reduced by 32, 33, 16 and 26%, respectively, compared to untreated one (Table 1). These results are similar to the findings of Abdel-Latef and Chaoxing (2014) who reported that salinity stress significantly decreased the plant growth in pea. This inhibition of the growth in pea cultivars can be associated with the adverse effect of salinity stress on water availability, transpiration, carbohydrate fixation and ion balance in plants subjected to salinity stress (Shams *et al.,* 2016).

Based on the results, salinity stresses the biomass values of two pea cultivars, but a different pattern response was found between cultivars. In this respect salinity significantly decreased biomass values in Jof cultivar but it had a slight impact on Utrillo. This might be attributed to differences in salt tolerance across different genotypes. (Sarafi *et al.,* 2018). Based on the data in Table 1. NO treatment (75 µM) was more effective on the growth parameters of Jof than those of Utrillo under salt stress conditions. It increased shoot fresh and dry weight, and root fresh and dry weight by 119, 37, 64 and 31%, respectively in Jof cultivar under 100 mM NaCl. However, it increased shoot fresh and dry weight and root fresh and dry weight in Utrillo cultivar by 15, 26, 13 and 17%, respectively, under 100 NaCl compared to the untreated one. These results pointed out that Jof is more sensitive to salinity than the Utrillo and it is also more responsive to NO treatments (Table 1). These findings are in agreement with those of Hasanuzzaman *et al.* (2011) who reported that NO supplementation ameliorated plant growth under salinity conditions in wheat. Furthermore, it was reported that NO regulated growth under NaCl stress by promoting antioxidant metabolism and maintaining mineral assimilation in chickpea (*Cicer arietinum*) (Ahmad *et al.,* 2018).

Based on the findings, salinity stress caused a significant reduction in CRV, chlorophyll a, chlorophyll b and chlorophyll *a* + *b* (Table 1) and 100 mM NaCl had the highest negative effect. The reduction in chlorophyll content of both pea cultivars under salt stress could be contributed to the adverse effect of NaCl on the chlorophyll pigments and chlorophyll syntheses (Rasoul *et al.,* 2013). However, the simultaneous application of NO and NaCl reversed the adverse effect of salinity. In this regard, 75 µM NO increased the chlorophyll a, chlorophyll b and chlorophyll *a* + *b* content in both cultivars under 100 mM NaCl but it was more effective on Jof cultivar than Utrillo. Similarly, Ahmad *et al.* (2016) determined that salinity decreased chlorophyll content in chickpea, but combined the application of NO and salinity increased chlorophyll content compared to the control.

Cell membrane permeability of pea cultivars used in the study was determined by the measurement of TEC (Table 1). Salinity stress (100 mM NaCl) markedly increased the cell membrane permeability in pea cultivars but it had a lower effect on Utrillo cultivar than the Jof cultivar. The increase in TEC value can be associated with the excessive absorption of Na^+ and Cl^- and consequently disrupting the cell membrane stability by triggering the over-accumulation of reactive oxygen species (ROS) (Mansour, 2013). On the

Table 1: Mitigating effects of NO on plant growth, TEC, RRV, chlorophyll content and RWC of pea plants under different salt stress conditions.

Cultivar	NaCl mM	NO µM	TEC (%)	RWC (%)	CRV (SPAD)	Chl a (mg g $^{-1}$ FW)	Chl b (mg g $^{-1}$ FW)	Chl a+b (mg g $^{-1}$ FW)	Shoot fresh weight (g plant^{-1})	Shoot dry weight (g plant^{-1})	Root fresh weight (g plant^{-1})	Root dry weight (g plant^{-1})
	0	0	4.65 f	88.17 a	38.27 ab	0.147 a	0.054 b	0.200 b	45.78 a	4.58 a	15.70 a	1.14 a
		75	4.77 f	88.71 a	39.33 a	0.152 a	0.061 a	0.213 a	44.63 a	4.58 a	15.73 a	1.15 a
		100	4.60 f	87.24 a	38.30 ab	0.143 a	0.051 bc	0.194 b	28.16 d	3.57 bc	14.21 bc	1.10 ab
JOF	50	0	27.68 d	63.06 c	38.90 a	0.087 d	0.022 g	0.108 f	31.85 c	3.50 c	13.52 c	0.98 c
		75	19.32 e	63.35 c	40.07 a	0.130 b	0.048 cd	0.177 c	38.66 b	3.79 b	14.71 b	1.08 b
		100	29.20 d	77.79 b	38.40 ab	0.112 c	0.045 de	0.158 d	22.86 e	2.50 e	7.21 e	0.72 d
	100	0	70.88 b	45.42 d	32.67 c	0.111 c	0.042 ef	0.153 d	10.50 f	2.21 f	7.64 e	0.54 e
		75	59.70 c	54.64 bc	36.50 b	0.110 c	0.038 f	0.148 d	23.02 e	3.03 d	12.56 d	0.71 d
		100	73.27 a	48.15 d	28.77 d	0.091 d	0.038 f	0.129 e	8.34 f	1.61 g	6.04 f	0.43 f
	NaCl		***	***	***	***	***	***	***	***	***	***
	NO		***	*	***	***	***	***	***	***	***	***
	NaCl × NO		***	ns	***	***	***	***	***	***	***	***
	0	0	6.00 f	89.87 a	39.17 a	0.148 a	0.061 b	0.209 b	62.76 a	5.66 a	24.51 b	1.21 a
		75	6.02 f	91.20 a	37.53 b	0.155 a	0.067 a	0.223 a	61.61 a	5.57 a	25.05 ab	1.23 a
		100	6.16 f	91.24 a	36.20 c	0.151 a	0.058 b	0.210 b	50.97 bc	4.53 c	24.69 ab	1.29 a
UTRILLO	50	0	23.89 d	73.01 c	32.67 e	0.153 a	0.058 b	0.212 b	52.57 b	4.25 d	23.02 c	1.02 b
		75	16.12 e	77.08 b	34.20 d	0.150 a	0.058 b	0.208 b	53.65 b	4.62 bc	25.79 a	0.99 b
		100	25.33 d	75.33 bc	34.63 d	0.123 c	0.057 b	0.180 c	49.11 c	4.16 d	16.85 e	0.82 c
	100	0	57.46 a	66.98 d	30.93 f	0.096 d	0.042 d	0.138 d	42.74 d	3.80 e	20.54 d	0.84bc
		75	32.97 c	76.65 b	33.83 de	0.133 b	0.050 c	0.183 c	49.12 c	4.78 b	23.21 c	0.98 b
		100	47.73 b	73.52 c	30.20 f	0.102 d	0.042 d	0.144 d	41.74 d	3.59 f	19.72 d	0.85 bc
	NaCl		***	***	***	***	***	***	***	***	***	***
	NO		***	***	***	***	***	***	***	***	***	**
	NaCl × NO		***	***	***	***	*	***	***	***	***	**

Data followed by a different letter in column were significantly different according to the DMRT ($p<0.001$), *:$p<0.05$; **:$p<0.01$; ***: $p<0.01$; ns: $p>0.05$

other hand, 75 µM NO treatment decreased TEC values compared to the control in both cultivars (Table 1). This means that NO treatment mitigated the harmful effect of NaCl on cell membranes. Similarly, it had been shown that oxidative damages in rice seedlings were mitigated by NO applications under salt stress (Wu *et al.,* 2011)

The RWC value was decreased in pea cultivars by salinity stress, but the strongest effect of salinity was observed in Jof under 100 mM NaCl. NO treatments had no significant on RWC in all cultivars compared to control. However, in the presence of salinity stress, NO treatment (75 µM) significantly increased RWC in all pea cultivars compared to the plants subjected to NaCl and without NO (Table 1). The findings were similar to those of Shams *et al.* (2019) who demonstrated that salinity stress decreased RWC and increased TEC, but the application of NO ameliorated the adverse effect of salinity stress. Ahmad *et al.* (2018) also reported that NaCl negatively affected RWC and chlorophyll content while NO treatments improved RWC and chlorophyll content of tomato.

NaCl treatment significantly caused an increase in H_2O_2 and MDA contents in pea cultivars (Table 2). The highest H_2O_2 and MDA content were observed in Jof cultivar under 100 mM NaCl. However, the application of NO reduced the H_2O_2 and MDA content in both cultivars under salinity stress. This increase in H_2O_2 and MDA content can be related to the role of NaCl on the over-accumulation of ROS and stimulation of oxidative stress which causes injury to membranes and other cellular structures (Parida and Das 2005). In harmony with our results, salinity increased the MDA and H_2O_2 content in tomato, but NO treatment decreased MDA and H_2O_2 content (Ahmad *et al.,* 2018).

APX, POD and SOD enzymes by scavenging ROS perform a crucial role in the antioxidant defense system to remove oxidative damage under environmental stresses in plants. The salinity induced a significant increase in the SOD, APX and POD activities in Utrillo and Jof (Table 2). To mitigate the hazardous effect of NaCl stress, plants can produce higher levels of antioxidant enzyme activities in the cytosol and other organs of the cells. In this experiment, a similar higher activity trend of APX, SOD and POD was detected in pea cultivars under salinity stress (Table 2). The increased enzyme activities in response to salinity stress were reported by Shams *et al.* (2019) in *Capsicum annum*.

NO is considered a functional molecule in alleviating salt stress in plants through NO modifying antioxidant metabolism (Lin *et al.,* 2012). In the current study, NO (75 µM) increased the POD, SOD and APX activities in both cultivars compared to control in the absence of salinity

Table 2: Mitigating effects of NO on MDA, H_2O_2, POD, APX, SOD and K^+/Na^+ and Ca^{+2}/Na^+ ratios of pea plants under different salt stress conditions.

Cultivars	NaCl mM	NOµM	MDA	H_2O_2	POD	APX	SOD	K/Na	Ca/Na
	0	0	13.30 f	116.83 gh	34.88 f	4.72 f	386.20 f	51.81 a	34.91 a
		75	13.46 f	119.23 fg	67.64 d	10.35 cd	406.72 e	51.16 a	33.38 a
		100	13.93 f	114.20 h	38.83 f	8.87 de	478.88 c	47.13 b	30.84 b
	50	0	28.88 b	144.96 b	47.81 e	7.51 e	479.39 c	27.48 d	17.46 d
		75	24.80 c	131.96 d	70.73 d	12.84 b	467.97 c	31.02 c	18.90 cd
JOF		100	22.24 d	124.67 e	76.28 c	7.46 e	430.40 d	32.80 c	20.46 c
	100	0	34.24 a	175.29 a	127.35 a	11.53 bc	524.47 b	6.52 e	4.59 e
		75	21.60 d	139.99 c	66.84 d	11.46 bc	555.47 a	7.22 e	4.97 e
		100	19.58 e	120.86 f	105.19 b	17.53 a	464.12 c	7.98 e	5.38 e
	NaCl	***	***	***	***	***	***	***	
	NO	***	***	***	***	***	***	***	
	NaCl × NO	***	***	***	***	***	ns	ns	
	0	0	20.38 de	122.62 d	44.31 g	9.75 f	470.35 d	54.61 a	35.88 a
		75	20.24 e	112.95 e	47.80 f	18.39 e	394.18 e	53.21 a	34.31 a
		100	21.33 d	110.09 e	52.81 e	24.77 b	535.96 bc	48.70 b	31.69 b
	50	0	24.43 b	131.75 b	53.02 e	21.72 cd	547.01 b	28.39 d	17.94 d
		75	22.70 c	120.69 d	56.81 cd	21.03 d	522.58 c	31.02 cd	19.42 cd
UTRILLO		100	20.77 de	119.43 d	59.45 bc	25.43 b	308.09 f	33.89 c	21.03 c
	100	0	29.05 a	146.84 a	61.07 b	25.21 b	544.45 b	6.94 e	4.72 e
		75	22.43 c	132.62 b	54.06 de	23.66 bc	566.02 a	7.58 e	5.11 e
		100	23.85 b	126.40 c	82.16 a	28.40 a	467.18 d	8.28 e	5.53 e
	NaCl	***	***	***	***	***	***	***	
	NO	***	***	***	***	***	***	***	
	NaCl × NO	***	*	*	***	***	ns	ns	

Data followed by a different letter in column were significantly different according to the DMRT (p<0.001)*:p<0.05; **:p<0.01; ***: p<0.01; ns: p>0.05.

stress. Also, the application of NO to salinity-stressed pea cultivars stimulated a significant increase in enzyme activities. Similarly, it was reported that NO caused an increase in the activities of SOD, CAT, APX and GR in tomato under salinity stress (Ahmad *et al.,* 2018). This can be attributed to the crucial role of NO on the regulation of genes responsible for the enzyme activities (Ahmad *et al.,* 2016).

Salinity stress markedly affected the Na^+, K^+ and Ca^{2+} uptake and, consequently, the ratio of K^+/Na^+ and Ca^{2+}/Na^+ significantly was decreased in leaves of pea cultivars (Table 2). The decrease in K^+/Na^+ and Ca^{2+}/Na^+ ratios can be linked to the over-accumulation of Na^+ and the decrease in Ca^{2+} and K^+ concentration in leaves of pea cultivars under NaCl stress. Nonetheless, increase in K^+/Na^+ and Ca^{2+}/Na^+ by exogenous NO to salt-stressed plants (50 mM) was reported by Shams *et al.* (2019), which is similar to our results. Gadelha *et al.* (2017) reported that NO priming limited the accumulation of toxic ions and ROS by inducing an effective antioxidant system and thus, improving salt tolerance during seedling development.

CONCLUSION

In conclusion, our study shows that exogenous NO treatment mitigates the adverse effect of salinity stress on pea cultivars by improving the antioxidant enzyme activities and nutrient uptake. In conclusion, the exogenous NO can have an essential role as a growth enhancer for the pea under salinity conditions.

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