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IAA-induced alteration in growth and photosynthesis of pea (*Pisum sativum* L.) plants grown under salt stress

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Abstract

The present study investigates the role of foliar application of indole acetic acid (IAA) in mitigating the loss caused by salinity stress in terms of plant growth and leaf characteristics in pea plants (*Pisum sativum* L. cv. Adi). Potted plants were grown on amended soil (75% soil and 25% farmyard manure), and IAA (0, 15, and 30mg l^{-1}) was applied to 30-day-old plants as foliar spray for 15 days. Three levels of NaCl (0, 50 and 100mM) were then used for salt-stress treatment and pots were watered regularly with 100% field capacity. Two-month-old plants were sampled for recording data on growth measurements, dry mass production, relative water content and leaf characteristics such as pigment concentration, maximum quantum yield of PSII (*Fv/Fm*), stomatal conductance (*gs*), net photosynthetic rate (*Pn*) transpiration rate (*E*) and water use efficiency (WUE). All these parameters were suppressed under salinity; the effect of salinity was greater on plants receiving no IAA treatment than on those treated with IAA. Of the salt doses used, 100mM NaCl was most effective. IAA application (30mg IAA l^{-1}) to plants growing under stress of 50mM NaCl reduced the expected loss by about 13% in leaf area, 20% in number of leaves, 6% in RWC, 47% in root dry mass (DM), 30% in stem DM, 9% in leaf DM, 27% in total DM, 11% in total chlorophyll, 10% in carotenoids, 15% in *Fv/Fm*, 20% in *gs*, 15% in *Pn*,11% in *E* and 4% in WUE. However, the same IAA concentration, when applied to plants grown under 100mM NaCl stress, reduced the expected loss by about 25% in leaf area, 24% in number of leaves, 12% in RWC, 65% in root DM, 22% in stem DM, 25% in leaf DM, 30% in total DM, 30% in total chlorophyll, 16% in carotenoids, 17% in *Fv/Fm*, 32% in *gs*, 19% in *Pn,* 14% in *E* and 6% WUE . On the whole, exogenous IAA application significantly reduced the salinity-induced loss by enhancing plant capacity to withstand the salt stress.

Key words

Chlorophyll fluorescence, Photosynthetic efficiency, Plant-water relationship, Stomatal conductance, Stress tolerance

Introduction

Soil salinity is a major limiting factor for sustainable agriculture. It inhibits plant growth via interplay with a variety of physiological and biochemical attributes, and strongly influences plant distribution, survival and productivity. As per the FAO estimates, 34 million ha (11% of irrigated area) are affected globally by the varied level of salinization, and an additional 60-80 million ha by waterlogging (FAO, 2012). Enhanced salt stress disrupts homeostasis in plant water potential and ion distribution at cellular, as well as, whole-plant level. This damages biological molecules, causing arrest of growth and even death of the plant (Munns and Tester, 2008). Ability of plants

to counteract the adverse effects of salinity can be assessed by examining its water relations level of inorganic nutrients and compatible solutes, hormonal regulation, and antioxidative defence activity (Munns and Tester, 2008; Qureshi *et al.,* 2005, 2013; Yousuf *et al.*, 2015).

Water use efficiency (WUE) is a fine indicator of the status of growth and yield of crop plants growing under abiotic stress (Getnet *et al.,* 2015). If water use and salt uptake are indeed linked (Moya *et al.,* 2003), increased WUE should result in reduced rate of salt accumulation in leaves. Photosynthetic efficiency is hampered under stress through limited CO_2 diffusion through stomata and mesophyll and the biochemical impairment of photosynthetic apparatus (Chaves *et al.,* 2009; Bashir *et al.,* 2015), and fluctuates with severity and duration of stress (Husen, 2010; Wargent *et al.,* 2013; Hakim *et al.,* 2014; Husen *et al.,* 2014). Efficiency of photosystem II (PSII), measured as chlorophyll fluorescence (maximum quantum yield, *Fv/Fm*), has been used extensively as a diagnostic tool in studies of environmental stress and seedling-stock quality (Husen, 2009; Hanachi *et al.,* 2014; Husen *et al.,* 2014). Glycinebetaine and proline are known for effecting osmotic adjustment and protecting subcellular structures in stressed plants (Hare *et al.,* 1998; Yamaguchi-Shinozaki, 2001; Getnet *et al.,* 2015). Increased activity of antioxidant enzymes also help in raising plant tolerance to stress and keeping PSII activity high (Foyer and Shigeoka, 2011; Cristina *et al.,* 2013). Enhanced salinity causes imbalance of nutrients in most crop plants and disturbs plant growth (Arshi *et al*., 2006, 2010; Turan *et al.,* 2010). Accumulation of sodium and chloride ions in chloroplast inactivates electron transport and photophosphorylation of thylakoid membranes (Bazrafshan and Ehsanzadeh, 2014; Feng *et al.,* 2014). On the other hand, plants adapted to salinity stress generally maintain a low concentration of Na^+ in cytosol by excluding Na^+ into apoplast or vacuole due to specific Na^+/H^+ antiporters and tonoplast, respectively (Ratajczak, 2000).

Auxin, a group of phytohormones, has long been recognized for its essential role in growth and development of plants facing abiotic stress, including salinity (Iqbal and Ashraf, 2007; Javid *et al.,* 2011). Indole-3-acetic acid (IAA), which can be synthesized from tryptophan -dependent and -independent pathways, is the main auxin in plants, producing majority of auxin effects in plants and participating in modulation of several plant processes (Zhao, 2010). Exogenous application of IAA alleviates the adverse effect of salt stress (Javid *et al.,* 2011; Guru Devi *et al.,* 2012). IAA-producing bacterial strains significantly increased root growth, up to 25% in non-saline conditions and 52% at 100mM NaCl, which markedly alleviated the adverse effects of salinity on wheat seedlings (Egamberdieva, 2009).

Pea (*Pisum sativum* L.), an important leguminous crop and an excellent source of proteins, carbohydrates, vitamins, minerals, salts and antioxidants (Noreen and Ashraf, 2009), has been reported to be more salt sensitive than other common legumes, like broad bean (*Vicia faba*), common bean (*Phaseolus vulgaris*) and soybean (*Glycine max*) (Zahran, 1999). Salinity impact on growth, physiology, and antioxidant system of pea plant has been subject of several investigations (Noreen and Ashraf, 2009; Martí *et al.,* 2011; Pandolfi *et al.,* 2012; Shahid *et al.,* 2012), but the role of IAA in modulating these impact in salinity-affected pea plant remains little explored. This study on *Pisum sativum* L. cv. Adi is an attempt towards filling this void.

Materials and Methods

Experimental site : Experiments were conducted at the Tewodros campus of the University of Gondar located at 12° 35' 14.19" N, 37° 26' 29.53"E at 2143m above mean sea level. The annual average of the maximum and minimum daily temperature at Gondar lies around 27°C and 16°C, respectively. March to May is the hottest period, with average maximum temperature 29°C. Average precipitation in Gondar is about 1161mm per annum, which means a monthly precipitation of 96.75mm. The annual average of daily relative humidity (RH) is about 56%, lowest (40%) occurring in January and February and highest (79%) in July. During the entire experimental period RH was 50%, maximum and minimum daily temperature was recorded as 29 ± 1 and 18 ± 1°C, respectively, and no rainfall took place.

Plant material and pot media: Seeds of pea (*Pisum sativum* L. cultivar Adi) were obtained from Gondar Agricultural Research Centre, Gondar, Ethiopia. Seed surface was sterilized with 80% ethanol for 15 min, followed by repeated washing with distilled water. Clean seeds were dipped in distilled water for 12 hrs and then sown in plastic tray containing 75% soil and 25% farmyard manure (FYM). After 2 weeks of germination, uniform seedlings were chosen and transferred separately to plastic pots (8cm width x 16cm height) filled with 1.5 kg soil and 500g FYM in 3:1 ratio, sown at a depth of 2 cm and irrigated daily with tap water for the next 2 weeks with 100% field capacity (FC), supposedly a period of plant acclimatization. Each pot contained one seedling only. Sandy loam (62.56% sand, 14.88% clay and 22.56% silt) with pH 7.23 and EC 0.69 ms cm^{-1} was used.

Experimental design, IAA application and salt treatments: After acclimatization, one-month-old seedlings were divided in 7 groups to assess the role of IAA and salt-stress treatments (T1-T7). The pots were arranged in a simple randomized design. Prior to the commencement of salt stress treatments, foliar spray of 0, 15 and 30mg l^{-1} IAA (HiMedia Laboratories Pvt. Ltd., Mumbai, India) was done daily for

150 days. Thereafter, salt treatments (0, 50 and 100mM NaCl) were given through irrigation on alternate days for a period of 10 days (*i.e.,* on 2nd, 4th, 6th, 8th and 10th day). Five replications of five plants each were arranged for the following (T1-T7) treatments. ·T1: No IAA + No NaCl (Control); T2: No IAA + 50mM NaCl; T3: No IAA + 100mM NaCl; T4: 15mg IAA l^{-1} + 50mM NaCl; T5: 15mg IAA l^{-1} + 100 mM NaCl; T6: 30mg IAA l^{-1} + 50mM NaCl; T7: 30mg IAA l^{-1} + 100mM NaCl. Seedlings were allowed to adjust with soil salinity for 5 more days and watered regularly with 100% field capacity (FC). Sampling was done when plants were 2-month old.

Plant growth, leaf characteristics and water status: Plant-growth parameters and leaf traits were measured for each treatment. Seedlings were uprooted gently for recording the length of root and shoot (cm), and the size, area and number of opened leaves. Ground-line basal diameter (mm) of stem was measured with electronic digital calliper. The length (mm) and area (mm^2) of individual leaves were measured using AM300 leaf area meter (ADC Bio Scientific Limited, U.K.). Roots, stems and leaves were separated to obtain their total dry mass (g) on a CY510 electronic digital balance (Citizen Scale, Poland). Five replications were used for each parameter. Water status of leaf was determined for each treatment (T1-T7) by measuring the relative water content (RWC) of fully-developed leaves. Leaves were weighed (FW) and then kept in distilled water overnight at 5°C in the dark, before obtaining their turgid weight (TW). It was then oven-dried at 80°C for 12 hr and weighed again to obtain dry weight (DW). RWC was calculated as:

$$RWC = \{(FW - DW) \div (TW - DW)\} \times 100$$

Photosynthetic pigments : Chlorophyll (a, b and total) and caroteniod contents were analyzed for each treatment. Following the method of Hiscox and Israelstam (1979), test tubes containing 0.5g green-leaf tissue in 10ml dimethyl sulfoxide (DMSO) were kept in oven at 65°C for 2hrs and 3ml of DMSO was then added to 1ml of aliquot. Optical density (OD) was read at 663nm, 643nm, 510nm and 480 nm, using a T60 UV/VIS spectrophotometer (PG Instruments Limited, England). Chlorophyll *a* and *b*, total chlorophyll and carotenoid contents were estimated by the formulae of Duxbury and Yentsch (1956) and MacLachlan and Zalick (1963).

Chlorophyll fluorescence : Chlorophyll fluorescence of leaves was recorded in the forenoon (10 to 11 AM) for each treatment with the help of a portable Multi-Mode OS5p Chlorophyll Fluorimeter (Opti-Sciences, Inc., USA). Prior to fluorescence measurements, the upper surface of the leaf was pre-darkened with leaf clips for 30 min to ensure complete relaxation of all reaction centres. The basal non-variable chlorophyll fluorescence (*Fo*), maximal fluorescence induction (*Fm*), and variable fluorescence (*Fv*) were determined. The maximum quantum yield of PSII (*Fv/Fm*) was estimated by *Fv/Fm* = (*Fm* – *Fo*)/ Fm ratio (Genty *et al.,* 1989).

Foliar gas exchange and water-use efficiency: Leaf gas exchange was measured between 10 to 11 am for each treatment. Stomatal conductance (*gs*), net photosynthetic rate (*Pn*) and transpiration rate (*E*) were measured using a portable leaf gas exchange system (ADC BioScientific Limited, U.K.) on fully expanded attached leaves. The equipment was used with the following specifications/ adjustments: leaf surface area 6.25 cm^2, ambient CO_2 concentration (C_{ref}) 371µmol mol^{-1}, temperature of leaf chamber (Tch) 25 to 28°C, molar air flow per m^2 of leaf surface (Us) 296mol m^{-2} s^{-1}, leaf chamber volume gas flow rate (v) 400ml m^{-1}, ambient pressure (P) 97.95kPa, PAR (Q_{leaf}) at leaf surface up to 770µmol m^{-2} s^{-1}. Water use efficiency (WUE) of photosynthesizing leaf, defined as ratio of photosynthesis (*Pn*) to water loss in transpiration (*E*), was calculated by the formula :

$$WUE = Pn/E.$$

Statistical analysis : Statistical analysis of data was performed using version 16.0 of SPSS software (SPSS Inc., Illinois, USA). Data were subjected to one-way analysis of variance (ANOVA) to determine significant difference among the treatments. Means were compared by Duncan test at significance level of $P < 0.05$ (values marked with same letter within a row or column were not significantly different at $P > 0.05$ level).

Results and Discussion

The effect of IAA application on growth characteristics of pea plants grown under control (without IAA) and salt stress conditions (with and without IAA) was assessed (Table 1). Root length, shoot length, basal diameter of stem, length, area and number of leaves and level of relative water content (RWC) decreased significantly with salinity treatments. Statistically, dimension of root, stem and leaves responded similarly at both concentrations of NaCl, while leaf area, leaf abundance and RWC decreased more significantly with higher (100mM) concentration. In terms of percentage, leaf area, leaf number and RWC decreased by 39%, 12% and 16% respectively due to 50mM NaCl (T2) and by 53%, 33%, and 23%, respectively, at 100mM NaCl (T3), compared to the control (T1) (Fig. 1). Salt stress had a negative impact on all these parameters, but foliar application of IAA significantly reduced the negative impact of salinity. As compared to T1 (control), leaf area, leaf number and RWC were reduced by 13%, 20% and 6% for T6 (30mg IAA l^{-1} +

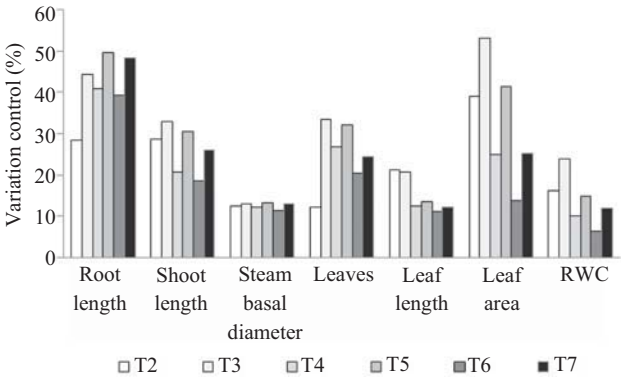

Fig. 1 : Percent variation from the control (T1 = No IAA + No NaCl) with reference to various growth parameters of Pisum sativum. T2 = No IAA + 50 mM NaCl, T3 = No IAA + 100 mM NaCl, T4 = 15 mg IAA l-1 + 50 mM NaCl, T5 = 15 mg IAA l-1 + 100 mM NaCl, T6 = 30 mg IAA l-1 + 50 mM NaCl and T7 = 30 mg IAA l-1 + 100 mM NaCl

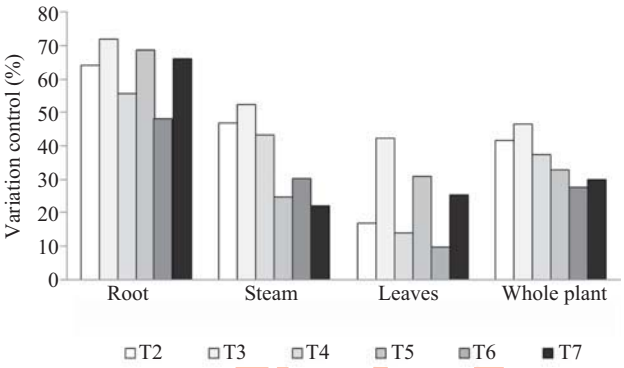

Fig. 2 : Percent variation from the control with reference to the dry mass of root, stem, leaves and whole plant of Pisum sativum. Details of treatments (T1 to T7) are given in the legend of Fig. 1

Table 1: IAA-induced alteration in growth parameters of *Pisum sativum* plants grown under normal and salt-treated conditions

Growth and leaf parameters	T1 Mean ±SE	T2 Mean ±SE	T3 Mean ±SE	T4 Mean ±SE	T5 Mean ±SE	T6 Mean ±SE	T7 Mean ±SE
Root length (cm)	8.62±0.28^{a}	6.17±0.68^{b}	4.79±0.11^{bc}	5.10±0.52^{bc}	4.35±0.22^{c}	5.23±0.64^{bc}	4.46±0.29^{c}
Shoot length (cm)	26.34±0.81^{a}	18.82±1.18^{bcd}	17.67±0.89^{d}	20.92±1.06^{bc}	18.29±0.39^{cd}	21.42±0.86^{b}	19.47±1.01^{bcd}
Stem basal diameter (mm)	2.42±0.02^{a}	2.17±0.01^{bc}	2.16±0.01^{bc}	2.18±0.02^{bc}	2.15±0.01^{c}	2.20±0.01^{b}	2.16±0.01^{bc}
Number of leaves	112.47±6.37^{a}	98.65±0.76^{b}	74.87±1.45^{d}	82.39±0.88^{cd}	76.31±0.68^{d}	89.48±0.42^{c}	84.87±1.13^{c}
Leaf length (mm)	167.67±4.97^{a}	133.07±0.52^{c}	132.25±0.93^{c}	146.72±0.59^{b}	144.96±0.58^{b}	149.13±0.19^{b}	147.13±0.59^{b}
Leaf area (mm^2)	15241.19 ±169.85^{a}	9293.39 ±196.05^{d}	7162.87 ±166.74^{e}	11438.07 ±293.87^{c}	8895.44 ±506.63^{c}	13146.23 ±478.34^{b}	11396.10 ±133.10^{c}
Relative water content (%)	92.27±0.29^{a}	77.37±0.85^{e}	70.31±0.65^{f}	83.08±0.51^{c}	78.67±0.88^{e}	86.44±0.29^{b}	81.18±0.60^{d}

T1: No IAA + No NaCl (Control), T2: No IAA + 50 mM NaCl, T3: No IAA + 100 mM NaCl, T4: 15 mg IAA l^{-1} + 50 mM NaCl, T5: 15 mg IAA l^{-1} + 100 mM NaCl, T6: 30 mg IAA l^{-1} + 50 mM NaCl and T7: 30 mg IAA $^{l-1}$ + 100 mM NaCl. Values followed by the same letter indicate no significant differences at $P < 0.05$ level according to the Duncan test. Each value represents the mean ± SE of five replicates

50mM NaCl) and by 25%, 24% and 12%, respectively, for T7 (30mg IAA l^{-1} + 100mM NaCl) (Fig. 1). The effect of foliar IAA and NaCl applications on dry mass (DM) production was also examined (Table 2). Salt stress caused a significant suppressive effect on DM production, but it could not undo completely the stimulatory effect of IAA, which continued even under salinity effect. At 50mM NaCl (T2), dry matter was reduced by about 64% for roots, 46% for stem, 16% for leaves and 41% for whole plant, whilst at 100mM NaCl (T3) these parameters were suppressed by 71%, 52%, 42% and 46%, respectively (Fig. 2). Foliar application of IAA significantly reduced the decline caused by salinity. In comparison with T1 (control), reduction in DM of roots, stem, leaves and the whole plant was 47%, 30%, 9% and 27%, respectively, at T6 (30mg IAA l^{-1} + 50mM NaCl) and 65%, 22%, 25% and 30%, respectively, at T7 (30mg IAA l^{-1} + 100mM NaCl) (Fig. 2).

Suppression of plant growth due to salinity, as observed in the present study, could be due to changes in ion equilibrium, water status, mineral nutrition, efficiency of photosynthesis and the quantum of carbon as CO_2 (Munns, 2005; Munns *et al.,* 2006). A decrease in leaf RWC with increase in salinity stress is indicative of loss of turgor, showing limited water availability for cell extension processes (Katerji *et al.,* 1997). Low photosynthetic rate, possibly due to disturbed turgor maintenance, sodium/chloride ion toxicity and hampered metabolic activities, becomes limiting for leaf area and biomass. Significant losses in growth and yield of crop plants due to salinity have been reported earlier (Astolfi and Zuchi, 2013; Zahra *et al.,* 2014). However, foliar IAA application to *P. sativum* minimized the loss due to salt stress, possibly because auxin enhances the plant's ability to adapt to abiotic stresses, mediating a wide range of adaptive responses

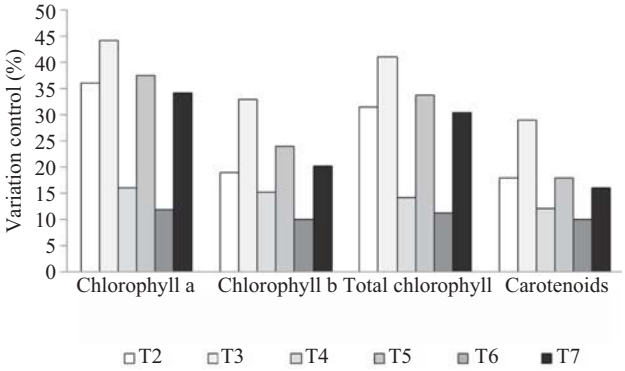

Fig. 3 : Percent variation from the control with reference to pigment concentration in the leaves of Pisum sativum. Details of treatments (T1 to T7) are given in the legend of Fig. 1.

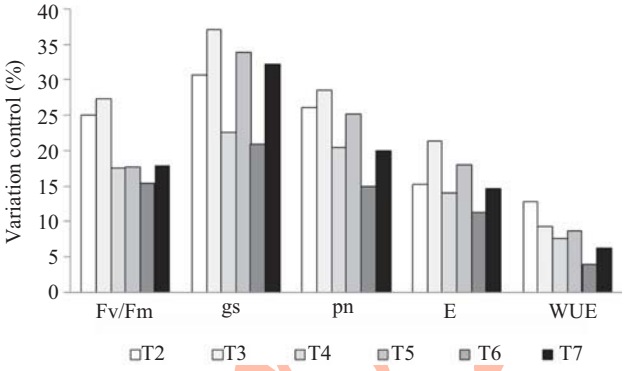

Fig. 4 : Percent variation from the control with reference to some photosynthetic traits of Pisum sativum. Details of treatments (T1 to T7) are given in the legend of Fig. 1.

Table 2 : IAA-induced alteration in dry mass (g) of *Pisum sativum* L. grown under normal and salt-treated conditions

Dry mass (g)	T1 Mean ±SE	T2 Mean ±SE	T3 Mean ±SE	T4 Mean ±SE	T5 Mean ±SE	T6 Mean ±SE	T7 Mean ±SE
Roots	0.39±0.006^{a}	0.14±.007^{d}	0.11±.005^{f}	0.17±.003^{e}	0.12±0.004^{ef}	0.20±0.003^{b}	0.13±0.003^{de}
Stem	1.62±0.01^{a}	0.86±0.02^{d}	0.77±0.01^{f}	0.92±0.03^{e}	1.22±0.01^{b}	1.13±0.02^{c}	1.26±0.03^{b}
Leaves	0.71±0.01^{a}	0.59±0.02^{d}	0.41±0.03^{g}	0.61±0.03^{c}	0.49±0.02^{f}	0.64±0.02^{b}	0.53±0.01^{e}
Whole plant	2.73±0.02^{a}	1.59±0.03^{c}	1.49±0.01^{f}	1.71±0.01^{d}	1.83±0.02^{c}	1.98±0.02^{b}	1.91±0.03^{b}

Details of T1-T7are given in the footnote of Figure 1. Values followed by the same letter indicate no significant differences at $P < 0.05$ level according to the Duncan test. Each value represents the mean ± SE of five replicates

Table 3 : IAA-alteration in photosynthetic pigments in leaves of *Pisum sativum* L. grown under normal and salt-treated conditions

Photosynthetic pigments	T1 Mean ±SE	T2 Mean ±SE	T3 Mean ±SE	T4 Mean ±SE	T5 Mean ±SE	T6 Mean ±SE	T7 Mean ±SE
Chlorophyll *a* (mg g^{-1} FW)	2.11±0.09a	1.35±0.08c	1.18±0.08^{d}	1.77±0.05^{b}	1.32±0.05^{c}	1.86±0.01^{b}	1.39±0.02^{c}
Chlorophyll *b* (mg g^{-1} FW)	0.79±0.05a	0.64±0.08d	0.53±0.02^{f}	0.67±0.03^{e}	0.60±0.03^{e}	0.71±0.01^{b}	0.63±0.02^{d}
Total Chlorophyll (mg g^{-1} FW)	2.90±0.09a	1.99±0.01d	1.71±0.02^{e}	2.45±0.03^{c}	1.92±0.01^{d}	2.57±0.04^{b}	2.02±0.01^{d}
Carotenoids (mg g^{-1} FW)	0.48±0.01a	0.39±0.01d	0.34±0.03^{e}	0.42±0.03^{b}	0.39±0.02^{d}	0.43±0.05^{bc}	0.40±0.01^{c}

Details of T1-T7are given in the footnote of Figure 1. Values followed by the same letter indicate no significant differences at $P < 0.05$ level according to the Duncan test. Each value represents the mean ± SE of five replicates

(Wolters and Jurgens, 2009; Liu *et al.,* 2014). Our findings on the effects of auxin application under salinity stress substantiate some earlier studies (Iqbal and Ashraf, 2007; Guru Devi *et al.,* 2012; Kaya *et al.,* 2013)

Our salt treatments caused a significant decrease in the concentration of photosynthetic pigments of *P. sativum* (Table 3). Chlorophyll *a,* chlorophyll *b,* total chlorophyll and carotenoid contents of leaves were reduced by 36%, 18%, 31% and 18%, respectively, due to 50mM NaCl (T2) and by 44%, 32%, 41% and 29%, respectively, at 100mM NaCl (T3) in comparison to control (T1). However, IAA exposure reduced the extent of salinity-induced decline in concentration of these pigments. In comparison with T1 (control), chlorophyll *a*, chlorophyll *b*, total chlorophyll and carotenoids content of leaves were reduced by 11%, 10%, 11% and 10%, respectively, at T6 (30mg IAA l^{-1} + 50mM NaCl) and by 34%, 20%, 30% and 16%, respectively, at T7 (30mg IAA l^{-1} + 100mM NaCl) (Fig. 3). The maximum PSII efficiency (*Fv/Fm),* stomatal conductance (*gs*), net photosynthetic rate (*Pn*), transpiration rate (*E) and* water use efficiency (WUE) decreased significantly under salt stress (Table 4). In terms of percentage, *Fv/Fm*, *gs*, *Pn*, *E* and WUE decreased by 25%, 30%, 26%, 15% and 12%, respectively, due to 50mM NaCl (T2) and by 27%, 37%, 28%, 21% and 9%, respectively, due to 100mM NaCl (T3), as compared to

Table 4: IAA-induced alteration in photosynthetic traits of *Pisum sativum* L. grown under normal and salt-treated conditions

Physiological activities	T1 Mean ±SE	T2 Mean ±SE	T3 Mean ±SE	T4 Mean ±SE	T5 Mean ±SE	T6 Mean ±SE	T7 Mean ±SE
Maximum quantum yield of PSII	0.84±.005^{a}	0.63±.006^{c}	0.61±0.004^{c}	0.69±0.008^{b}	0.69±0.01^{b}	0.71±0.005^{b}	0.69±0.006^{b}
Stomatal conductance (mol m^{-2} s^{-1})	0.06±0.003^{a}	0.04±0.002^{c}	0.04±0.003^{c}	0.05±0.003^{b}	0.04±0.00^{d}	0.05±0.003^{b}	0.04±0.002^{cd}
Net photosynthetic rate (µmol CO_2 m^{-2} s^{-1})	5.52±0.26^{a}	4.08±0.04^{cd}	3.94±0.09^{d}	4.39±0.02^{bc}	4.13±0.02^{cd}	4.69±0.06^{b}	4.42±0.04^{bc}
Transpiration rate (mmol m^{-2} s^{-1})	1.50±0.01^{a}	1.27±.02^{c}	1.18±.01^{e}	1.29±0.03^{c}	1.23±0.01^{d}	1.33±0.01^{b}	1.28±0.02^{c}
Water use efficiency (WUE)	3.68±0.18^{a}	3.21±0.08^{c}	3.34±0.12^{d}	3.40±0.16^{cd}	3.36±0.07^{d}	3.53±0.11^{b}	3.45±0.09^{b}

Details of T1-T7are given in the footnote of Fig. 1. Values followed by the same letter indicate no significant differences at $P < 0.05$ level according to the Duncan test. Each value represents the mean ± SE of five replicates

control (T1). However, variation in *Fv/Fm* and *Pn* at these two salt concentration was not significant. Foliar IAA application significantly reduced the adverse effects of salinity at both these concentrations. In comparison with T1 (control), *Fv/Fm, gs*, *Pn*, *E,* WUE were reduced by 15%, 20%, 15%, 11% and 4% at T6 (30 mg IAA l^{-1} + 50 mM NaCl) and by 17%, 32%, 19%, 14% and 6%, respectively, at T7 (30 mg IAA l^{-1} + 100 mM NaCl) (Fig. 4).

Quite often, photosynthetic pigments are directly related to growth and productivity of plants. The decreased content of chlorophyll *a* and *b*, total chlorophyll and carotenoids under salinity stress, as observed by us, might be an outcome of possible NaCl intervention in chlorophyll synthesis, which in turn depends on adequate ion balance. Excess of salt creates an imbalance in ion homeostasis, leading to decrease in synthesis of chlorophyll (Agastian *et al.,* 2000). Insufficient chlorophyll content under stress may cause malfunctioning of photosystem and increase the leakage of electrons to O_2, resulting in a decline of total CO_2 fixation (Woodward and Bennett, 2005). However, IAA exposure improves the concentration of photosynthetic pigments under salinity, as reported earlier by Kaya *et al.* (2013).

Photochemical efficiency of PSII (*Fv/Fm*) can be used as a criterion for evaluating plant performance under stressful conditions (Husen *et al.,* 2014; Oukarroum *et al.,* 2015; Getnet *et al.,* 2015), and hence for determining the seedling-stock quality (Husen, 2009, 2013). Generally, *Fv/Fm* in higher plants is close to 0.83 (Bjorkman and Demmig, 1987). A decreased *Fv/Fm* value was noted under salinity stress, which is quite common (Kalaji *et al.,* 2011; Li *et al.,* 2013). In the present study, *Fv/Fm* ratio value showed statistically uniform response at 50 and 100 mM NaCl treatment. The negative influence of salinity on PSII activity in barley plants was found to be dependent on stress duration and the cultivar used (Kalaji *et al.,* 2011). The *Fv/Fm* decreased by about 9 and 10%, while electron-transport rate by 20 and 25% in two sorghum varieties grown under 250mM NaCl; however, photosynthesis rate was affected primarily by stomatal closure (Netondo *et al.,* 2004). In *Sphaerophysa kotschyana* plants, *Fv/Fm* ratio was not affected under mild (150mM) salt stress, but declined significantly at higher (300mM NaCl) level (Yildiztugay *et al.,* 2014).

Our findings suggest that salinity influenced some process(es) related to the photochemistry of photosynthesis and perhaps the reaction centres were injured (photochemically inactive), thus reducing the electron-transport capacity in PSII. Similarly, inhibition of PSI and PSII activities under salinity stress, leading to a drop in the overall activity of electron-transport chain and a rise in reactive oxygen species (ROS) production, was observed in *Lemna gibba* by Oukarroum *et al.* (2015). In short, the net photosynthetic rate (*Pn)*, stomatal conductance (*gs*) and transpiration rate (*E*) *in P sativum* declined under saline condition as observed earlier in many other species (Arshi *et al.,* 2004, 2006; Jiang *et al.,* 2006; Shahbaz *et al.,* 2011; Hakeem *et al.,* 2012; Hakim et al., 2014). In addition, water-use efficiency (WUE) decreased with increase in salt concentration, showing that *P. sativum* has a low WUE when irrigated with saline water. Salinity stress often disturbs water balance and reduces WUE of plants (Syvertsen *et al.,* 2010; Huez-López *et al.,* 2011), which could be due to inhibition of absorption and translocation of water from root system to aerial plant parts. However, Ashraf (2001) observed increased WUE in some salt-tolerant *Brassica* species under high external salt concentration. Nonetheless, foliar spray of IAA on *P. sativum* partially overcame the adverse effect of salt stress, significantly improving the photosynthetic parameters.

Since salinity is deleterious for photosynthesis, one of the strategies that plants adopt to avoid/withstand stress is growth reduction by lowering photosynthesis (Matsui *et al.,* 2008) in order to to be able to reallocate the limited energy resources from developmental processes towards defence pathways to combat harmful stresses (Chaves *et al.,* 2009; Ha

et al., 2012). Low CO_2 concentration in chloroplasts and reduced photosynthetic carbon assimilation under salt stress normally correlate to a reduced stomatal conductance (Brugnoli and Lauteri, 1991). However, Parida *et al.* (2004) reported that the photosynthetic rate increased at a low salinity level but decreased at a higher one, whereas stomatal conductance remained unchanged at low level but declined at high salinity level in *Bruguiera parviflora*. This could well be a case of hormesis, thus showing a small rise in metabolic activities under low level of stress (Aref *et al.,* 2016). IAA application can partially mitigate the stress-caused losses in plants with a variety of adaptive strategies (Wolters and Jurgens, 2009; Peleg and Blumwald, 2011), which might involve inducing transcriptional regulators or preventing their degradation *via* the ubiquitin-proteasome system (Santner and Estelle, 2010). A study of *Arabidopsis thaliana* mutant phenotypes (Santner and Estelle, 2009) has provided evidence in support of a hormonal cross talk in this context. The synergistic or antagonistic hormonal action and the coordinated regulation of hormone-biosynthesis pathways play crucial role in making plants adapt to abiotic stresses (Peleg and Blumwald, 2011).

In conclusion, salinity applied through irrigation inhibited the vegetative growth of *P. sativum* by suppressing dry mass production, water status, photosynthetic pigments, photochemical efficiency, gaseous exchange and water use efficiency of the plant. In terms of percentage, these parameters were reduced more at higher salt concentration (100mM NaCl). On the contrary, foliar application of 30mg IAA l^{-1} considerably promoted the above parameters and alleviated the negative impact of salinity.

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