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Salt-induced changes in photosynthetic activity and growth in a potential medicinal plant Bishop's weed (*Ammi majus* L.)

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Abstract

Sixty seven-days-old plants of *Ammi majus* L. were subjected for 46 d to sand culture at varying concentrations of NaCl, *i.e.* 0 (control), 40, 80, 120, and 160 mM. Increasing salt concentrations caused a significant reduction in fresh and dry masses of both shoots and roots as well as seed yield. However, the adverse effect of salt was more pronounced on seed yield than biomass production at the vegetative stage. Calculated 50 % reduction in shoot dry mass occurred at 156 mM (*ca.* 15.6 mS cm^{-1}), whereas that in seed yield was at 104 mM (*ca.* 10.4 mS cm^{-1}). As in most glycophytes, Na^+ and Cl^- in both shoots and roots increased, whereas K^+ and Ca^{2+} decreased consistently with the successive increase in salt level of the growth medium. Plants of *A. majus* maintained markedly higher K^+/Na^+ ratios in the shoots than those in the roots, and the ratio remained more than 1 even at the highest external salt level (160 mM). Net photosynthetic (P_N) and transpiration (E) rates remained unaffected at increasing NaCl, and thus these attributes had a negative association with salt tolerance of *A. majus*. Proline content in the shoots increased markedly at the higher concentrations of salt. Essential oil content in the seed decreased consistently with increase in external salt level. Overall, *A. majus* is a moderately salt tolerant crop whose response to salinity is associated with maintenance of high shoot K^+/Na^+ ratio and accumulation of proline in shoots, but P_N had a negative association with the salt tolerance of this crop.

Additional key words: net photosynthetic rate; salt tolerance; stomatal conductance; transpiration; water use efficiency.

Introduction

Cultivation of medicinal plants is gaining ground in many countries where farmers have been cultivating since very long the conventional crops such as cotton, rice, wheat, *etc*. In fact, switching over to medicinal plants is due to considerably low output of the conventional crops in comparison with high inputs in the form of fertilizers and pesticides to these crops. In addition, the rapid progress in use of herbal medicine during the last two decades has motivated the farmers to grow medicinal plants on a large scale. Of the potential medicinal plants being cultivated these days, Bishop's weed (*Ammi majus* L.), belonging to family Apiaceae, is a traditional medicinal herb which is also known as gout weed, ajowain, Ethiopian cumin-seed, or ground elder (Purohit *et al.* 1995, Ekiert and Gomolka 2000). Bishop's weed seed imparts a specific aroma and taste to a wide variety of foods. The plant produces small white flowers in umbels similar in form to Queen Ann's Lace (*Daucus carota*, wild carrot), but not as showy, that bloom in mid summer and produce small round seeds that are hot and bitter to taste. It is an aromatic spice closely resembling thyme in flavour. It also has excellent preservative and medicinal properties (Abraham *et al.* 1996). Traditional usage of *A. majus* is in bruises, digestive problems, gas, hypoglycemia, preservative, psoriasis, snake bites, and water retention (Lipp 1996, Kiistala *et al.* 1999).

The seeds and plants of Bishop's weed contain furanochromones and khellin most concentrated in the seeds. The seeds also contain approximately 22.4 % cellulose, ammajin, ammifurin, ammirin, bergapten, calcium oxalate, 1 % essential oil, 13 % fat, 1 % glycosides, heraclenin, imperatorin, 1.5–2.0 % psoralens, and 14 % protein (El Gamal *et al.* 1993, Lipp 1996, Singab 1998, Ekiert and Gomolka 2000).

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High concentration of salts is an important characteristic of the soils of semi-arid and arid regions of the world and is a continuing threat to crop production (Ashraf 2002, Munns 2002, Tester and Romola 2003). However, such soils can be utilized by growing salt tolerant crops. Since *A. majus* is a potential medicinal crop, it could be grown on salt-affected lands if it possesses high degree of salt tolerance. Keeping this in mind the present study was carried out to assess the degree of salt tolerance of this crop and draw relationship with photosynthetic capacity.

Materials and methods

The seeds of a local race of *Ammi majus* L. were obtained from the Department of Botany, University of Agriculture, Faisalabad, Pakistan, which were originally collected from Pakistan Forest Institute Peshawar, Pakistan. The experiment was conducted in a netting house supplied with natural sunlight in the Botanic Garden, University of Agriculture, Faisalabad, Pakistan, from October 2002 to May 2003. The average day and night temperatures were 29±9 and 15±7 °C, respectively. The average relative humidity ranged from 41 to 69 % and natural photoperiod from 10.0 to 12.5 h. The experiment was laid out in a completely randomized design with four replications and five salt treatments including control. The earthen pots of 30 cm diameter lined with polythene sheets were filled with 9.0 kg of well washed pure river sand. Fifty seeds were sown in each pot. After 15 d of germination, plants were thinned to 6 plants per pot. Two litres of full strength Hoagland's nutrient solution were applied to each pot every week before the start of salt treatments. Plants were allowed to establish for further 52 d (67 d after germination) after which time NaCl treatment in Hoagland's nutrient solution was initiated. The NaCl treatments used were 0, 40, 80, 120, and 160 mM ($NaCl_0$, $NaCl_{40}$, $NaCl_{80}$, $NaCl_{120}$, and $NaCl_{160}$).

2 000 cm^3 of solution with appropriate treatment were applied every week to each pot. This volume was sufficient to wash the salt already present in the sand. During the week the pots were regularly kept moist by adding 200 cm^3 distilled water to each pot.

Proline in fresh shoot samples was determined according to Bates *et al.* (1973). Fresh leaves (1.0 g) were homogenized in 10 cm^3 of 3 % sulfosalicylic acid. This extract was used for spectrophotometric estimation of proline.

Gas exchange characteristics: Net photosynthetic (P_N) and transpiration (E) rates and stomatal conductance (g_s) were measured on a fully expanded youngest leaf of each plant using an open system *LCA-4 ADC* portable infrared gas analyzer (*Analytical Development Company*, Hoddesdon, England). Measurements were performed from 09:30 to 11:30 with the following specifications and adjustments: leaf chamber area was fixed as 6.25 cm^2, ambient CO_2 concentration (C_{ref}) 295.35 µmol mol^{-1}, temperature in leaf chamber in the range 25.67–38.24 °C, leaf chamber gas flow rate (V) 4.20–4.26 cm^3 s^{-1}, molar flow of air per unit leaf area (Us) 404.8 mmol m^{-2} s^{-1}, ambient pressure (P) 99.9 kPa, water vapour pressure in chamber (e_{ref}) 1.24–1.45 kPa, PAR at leaf surface (Q_{leaf}) up to 1 473 µmol m^{-2} s^{-1}.

Two plants were harvested from each pot 46 d after the start of NaCl treatments. Plants were uprooted carefully and washed with distilled water. After recording the fresh masses (FM) of both shoots and roots, they were oven-dried at 65 °C for one week and their dry masses (DM) recorded. The remaining four plants were used for attaining seed yield.

Determination of ions in shoots and roots: The dried ground shoot and root material (0.1 g) was digested with sulphuric acid-hydrogen peroxide according to Wolf (1982). Na^+, K^+, and Ca^{2+} were determined with a flame photometer (*Jenway PFP7, Gransmore Green*, Dunmow, UK). For the determination of Cl^-, shoot and root samples (100 mg each) were ground and extracted in 10 cm^3 of distilled water by heating at 80 °C for 3 h. Cl^- content in the extracts was determined with a chloride meter (*Sherwood Chloride Analyzer 926*, Tokyo, Japan). At maturity all plants were harvested and seed yield per plant was recorded for each salt treatment.

Extraction of oil from seed: The seeds of each treatment were sieved to remove any foreign material. The seeds were dried in an oven at 50 °C for 4 h. The dried seeds were ground to a uniform powder and oil was extracted in *n*-hexane. A weighed quantity (15 g) of the seed powder was placed in an extraction thimble and extraction was carried out for 6 h in a Soxhlet extractor, after which time the oil containing solvent was filtered through *Whatman No.42* filter paper. The oil was heated in an oven at 60 °C to remove last traces of the solvent.

Statistical analysis: Analyses of variance of data for all attributes were computed using the *COSTAT* computer package (*Cohort Software*, Berkeley, USA). The mean values were compared with the least significant difference test (LSD) following Snedecor and Cochran (1980).

Results

Imposition of salt stress on 67 d-old plants of *A. majus* for 46 d had a significant inhibitory effect on FM of both shoots and roots, but the effect of salt stress was non-significant for DM of shoots and roots (Table 1). However, there was a consistent decrease in both FM and DM of the shoots and roots with an increase in salt concentration of the growth medium (Fig. 1). Maximum reduction in biomass was observed at $NaCl_{160}$.

Salt stress had a significant ($p<0.001$) increasing effect on Na^+ and Cl^- concentrations in both shoots and roots (Table 1). The contents of both ions in the shoots and roots increased with increasing supply of NaCl and they were maximal at $NaCl_{160}$ (Fig. 2). A consistent decrease in the concentrations of K^+ and Ca^{2+} in both shoots and roots of *A. majus* was found with increasing supply of NaCl in the root medium, and maximum reduction in both ions was observed at $NaCl_{160}$ (Fig. 3). At this concentration, the reduction in shoot K^+ content was greater than that in the roots.

Table 1. Mean squares from analyses of variance of data for growth and gas exchange attributes and ion contents in shoots and roots of *Ammi majus* when 67-d-old plants were subjected for 46 d to varying NaCl treatments. For abbreviations see the text. Four degrees of freedom for salt concentration, 14 or 15 for error. *, **, *** = significant at 0.05, 0.01, and 0.001 levels, respectively; ns = non-significant.

	NaCl	Error
Shoot fresh mass [g]	59.69***	6.58
Shoot dry mass [g]	2.16ns	0.90
Root fresh mass [g]	2.14*	0.57
Root dry mass [g]	0.04ns	0.02
Seed yield [g per plant]	3.51***	0.18
Oil [%]	0.054*	0.003
P_N	1.78ns	1.86
E	0.47ns	0.23
g_s	250045.00***	409.58
Sub-stomatal CO_2 concentration	2927.44***	8.26
Water use efficiency	0.22ns	0.71
C_i/C_a	0.024***	0.012
Proline	2.97***	0.19
Shoot Na^+	13.95**	3.57
Root Na^+	175.51***	2.37
Shoot Cl^-	568.02***	12.78
Root Cl^-	166.81***	2.16
Shoot K^+	677.65***	19.68
Root K^+	57.50*	14.58
Shoot Ca^{2+}	30.2***	0.65
Root Ca^{2+}	10.33***	1.55

As expected, there was a consistent decrease in K^+/Na^+ and Ca^{2+}/Na^+ ratios in the shoots and roots of *A. majus* with increase in NaCl concentration of the rooting medium (Table 2). The plants maintained considerably higher K^+/Na^+ ratios in the shoots as compared to those in the roots, whereas Ca^{2+}/Na^+ ratios in both shoots and roots were similar.

Effect of salinity was non-significant on P_N, E, and water use efficiency (P_N/E) (Table 1). The pattern of increase or decrease in P_N and E was not consistent at varying NaCl concentrations of the medium (Fig. 4). However, a significant effect of salt stress was observed on sub-stomatal CO_2 concentration (C_i) and relative sub-stomatal CO_2 concentration (sub-stomatal CO_2 concentration/ambient CO_2 concentration = C_i/C_a) (Table 1), but the pattern of increase or decrease in sub-stomatal CO_2 concentration and C_i/C_a was not consistent at increasing contents of NaCl in the growth medium (Fig. 4).

Leaf proline content did not vary up to $NaCl_{80}$, but thereafter there was a sharp rise in its content at $NaCl_{120}$ and $NaCl_{160}$ (Fig. 5). A maximum increase in proline content was observed at $NaCl_{160}$.

A marked inhibitory effect of salt stress was observed on seed yield per plant (Table 1). However, seed yield started decreasing from $NaCl_{80}$ onwards. Yield reduction was maximal at $NaCl_{120}$ and $NaCl_{160}$ (Fig. 6).

Seed oil content decreased consistently with increasing salt concentration of the rooting medium, and the maximum reduction in oil was found at $NaCl_{80}$ (Fig. 6). Seed oil of plants subjected to $NaCl_{120}$ and $NaCl_{160}$ could not be determined because of very few seeds produced by these plants.

Table 2. K^+/Na^+ and Ca^{2+}/Na^+ ratios in shoot and roots of *Ammi majus* when 67-d-old plants were subjected for 46 d to varying concentrations of NaCl salinity in sand culture. Means with the same letters within each row do not differ significantly at the 5% level.

	$NaCl_0$	$NaCl_{40}$	$NaCl_{80}$	$NaCl_{120}$	$NaCl_{160}$	LSD 5 %
Shoot K^+/Na^+	8.46±1.01 a	6.93±0.78 b	3.58±0.43 c	2.82±0.22 c	1.29±0.12 d	1.36
Root K^+/Na^+	5.89±0.61 a	6.16±0.56 a	3.55±0.41 b	1.80±0.21 c	0.87±0.06 d	0.91
Shoot Ca^{2+}/Na^+	1.48±0.12 a	1.29±0.09 b	0.50±0.04 c	0.39±0.04 c	0.20±0.03 d	0.16
Root Ca^{2+}/Na^+	1.93±0.23 a	1.46±0.11 b	0.79±0.06 c	0.31±0.02 d	0.15±0.02 d	0.18

Discussion

Increasing salt concentration of the growth medium generally caused a significant suppression of vegetative growth and seed yield in *A. majus*. Such an inhibitory effect of salt stress on the growth, seed yield, and yield components has also been reported in alfalfa (Serraj and Drevon 1998, Esechie *et al.* 2002), carrot (Gibberd *et al.* 2002), fennel (Graifenberg *et al.* 1996), and kalonji (Hajar *et al.* 1996). However, the reduction in seed yield due to salt stress was more marked than that in vegetative growth of *A. majus*. For example, 50 % reduction in

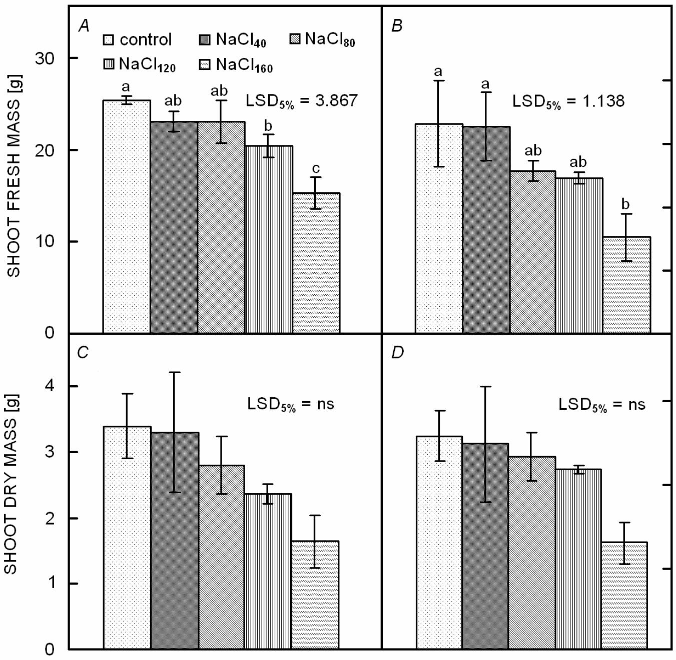

Fig. 1. Growth attributes of *Ammi majus* when 67-d-old plants were subjected for 46 d to varying NaCl salinity. *Bars* with the same letters are non-significant at 5 % level.

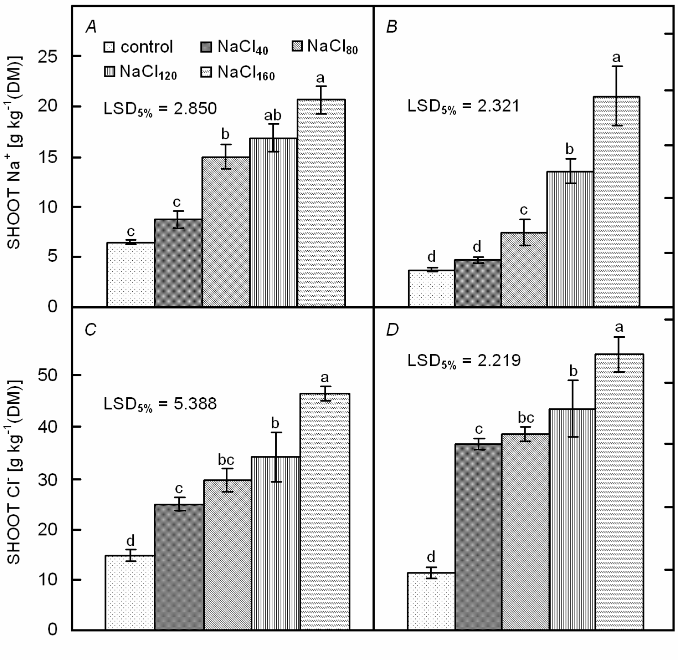

Fig. 2. Contents of Na^+ and Cl^-[g kg^{-1}(DM)] in shoots and roots of *Ammi majus* when 67-d-old plants were subjected for 46 d to varying NaCl salinity. *Bars* with the same letters are non-significant at 5 % level.

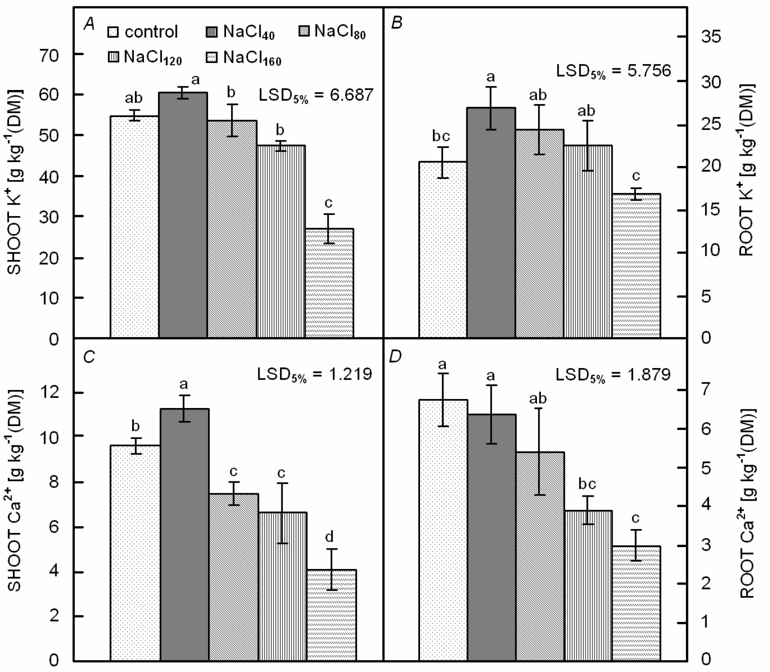

Fig. 3. Contents of K^+ and Ca^{2+} [g kg^{-1}(DM)] in shoots and roots of *Ammi majus* when 67-d-old plants were subjected for 46 d to varying NaCl salinity. *Bars* with the same letters are non-significant at 5 % level.

biomass at the vegetative stage, calculated by drawing a regression line, occurred at 156 mM of NaCl (almost equal to 15.6 mS cm^{-1}), and that in seed yield at 104 mM of NaCl (almost equivalent to 10.4 mS cm^{-1}). According to Maas and Hoffman (1977) this crop can be categorized as moderately salt tolerant. The difference in degree of salt tolerance at different growth stages of *A. majus* is parallel to what has earlier been observed in studies showing that salt tolerance in most of crop species varies with the change in stage of plant life cycle (Ashraf 1994, Sharma and Manchanda 1997).

As in most other glycophytes, a consistent increase in Na^+ and Cl^- and a decrease in K^+ and Ca^{2+} contents in both shoots and roots of *A. majus* with increase in salt concentration of the rooting medium was found. Accumulation of Na^+ and Cl^- in the shoots was greater than that in the roots. Such pattern of accumulation of these toxic ions has earlier been reported in a number of plants referred to as salt includers (accumulators). For example, most dicotyledonous halophytes are salt includers, and some salt tolerant glycophytes such as barley fall into this category (Greenway and Munns 1980, Munns *et al.* 2000).

Plants exposed to a saline environment generally take up high amounts of Na^+, whereas the uptake of K^+ and Ca^{2+} is significantly reduced. However, reasonable amounts of both K^+ and Ca^{2+} are required by plants to maintain the integrity and functioning of cell membranes (Marschner 1995, Davenport *et al.* 1997, Wenxue *et al.* 2003). The pertinent mechanism for maintenance of adequate K^+ in plant tissue under salinity seems to be dependent upon selective K^+ uptake and selective cellular K^+ and Na^+ compartmentation and distribution in the shoots (Munns *et al.* 2000, Carden *et al.* 2003). However, high K^+/Na^+ selectivity in plants under salt stress is an important selection criterion of salt tolerance (Gorham *et al.* 1997, Ashraf 2002, Wenxue *et al.* 2003). Although both K^+/Na^+ and Ca^{2+}/Na^+ ratios decreased consistently in the shoots and roots of *A. majus* with increase in salt content of the growth medium, K^+/Na^+ ratio was markedly higher in shoots than in roots. Even at $NaCl_{160}$ the shoot K^+/Na^+ ratio was more than 1, a minimum level suggested for the normal functioning of most mesophytes under saline conditions (Wyn Jones 1981).

Salinity reduces P_N, E, and g_s in most plant species (Gibberd *et al.* 2002, Tezara *et al.* 2002, Ashraf and Shahbaz 2003). Salt-induced reduction of P_N can be caused by stomatal limitation with stomatal closure (Pascale and Barbieri 1995, Goldstein *et al.* 1996), non-stomatal limitation or both limitations with stomatal closure at low tissue salt content, and a disturbance of photosynthetic activity at high tissue salt content (Downton *et al.* 1990, Yeo *et al.* 1991). We did not find any significant effect of salt stress on P_N or any of the attributes related to gas exchange in *A. majus*. Similarly, there are many earlier reports in which no or little association between growth and photosynthetic capacity is evident, *e.g. Hibiscus cannabinus* (Curtis and Läuchli 1986), *Hordeum vulgare* (Rawson *et al.* 1988), *Trifolium repens* (Rogers and Noble 1992), *Triticum aestivum* (Hawkins and Lewis 1993, Ashraf and O'Leary 1996), and *Olea europea* (Loreto *et al.* 2003).

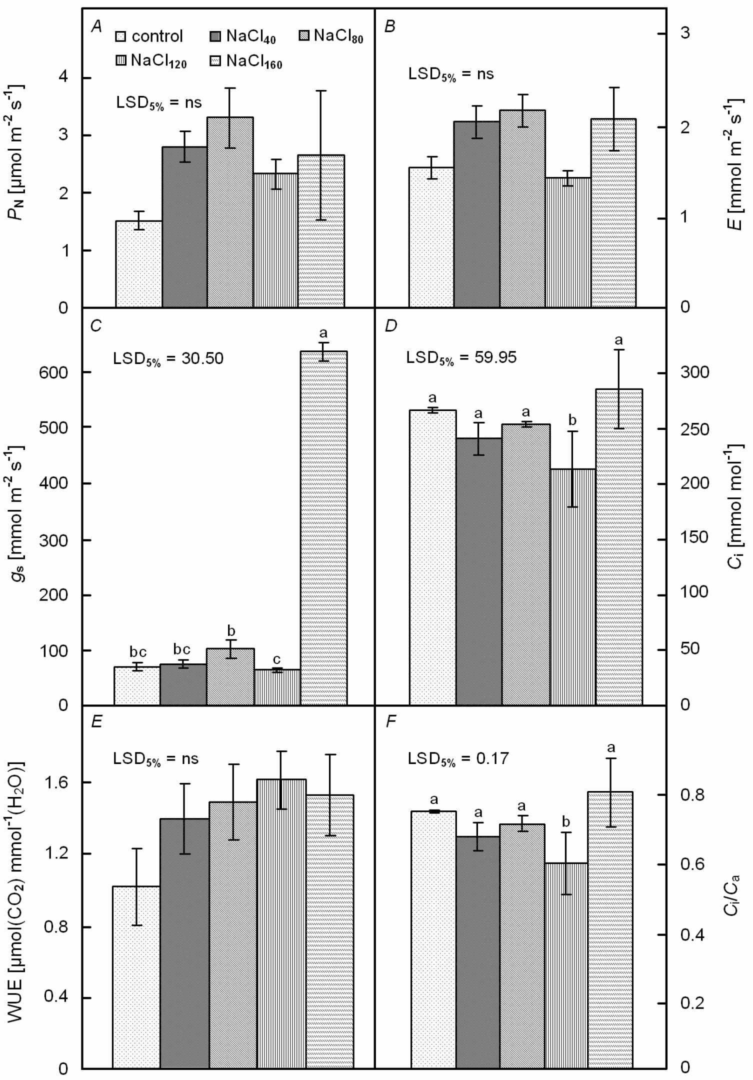

Fig. 4. Gas exchange characteristics of *Ammi majus* when 67-d-old plants were subjected for 46 d to varying NaCl salinity. *Bars* with the same letters are non-significant at 5 % level.

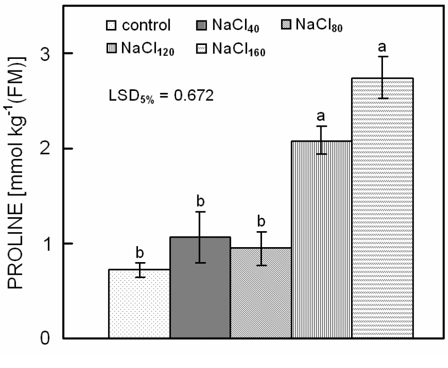

Fig. 5. Proline content [mmol kg^{-1}(FM)] of *Ammi majus* when 67-d-old plants were subjected for 46 d to varying NaCl salinity. *Bars* with the same letters are non-significant at 5 % level.

In the present study, accumulation of proline in the shoots of *A. majus* was enhanced particularly at the higher external salt concentrations, thus showing the positive role of proline in the salt tolerance of this crop because proline contributes to membrane stability (Rudolph *et al.* 1986, Hanson and Burnet 1994, Gadallah 1999) and reduces the effect of NaCl on cell membrane disruption (Mansour 1998). Furthermore, proline may act as a signalling/regulatory molecule able to activate multiple responses that are component of the adaptation to abiotic stresses including salt stress (Maggaio *et al.* 2002). Our findings for proline can be explained in view of some earlier reports that proline accumulation is one of the common characteristics in many plants under salinity (Storey *et al.* 1977, Wyn Jones and Storey 1978). Increase in proline content due to salinity has also been reported in some medicinal plants, *e.g.* black cumin

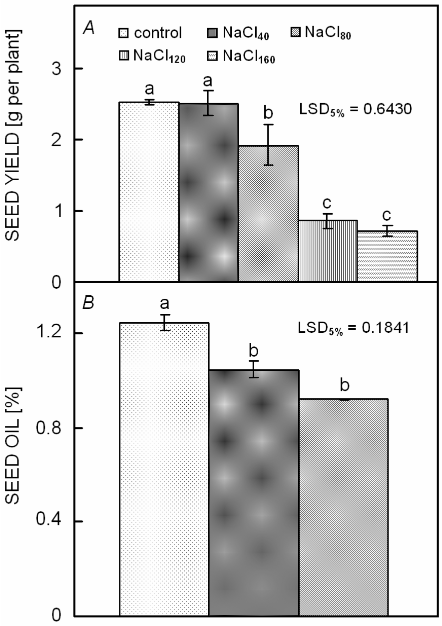

Fig. 6. Seed yield and oil percentage of *Ammi majus* when 67-d-old plants were subjected for 46 d to varying NaCl salinity. *Bars* with the same letters are non-significant at 5 % level.

(Hajar *et al.* 1996), anise and coriander (Zidan and Elewa 1995).

In conclusion, *A. majus* is a moderately salt tolerant crop whose response to salinity is associated with maintenance of high K^+/Na^+ ratio and accumulation of proline in shoots. However, P_N showed a negative association with the salt tolerance of this crop.

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