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# Growth, photosynthesis and ion balance of sesame (*Sesamum indicum* L.) genotypes in response to NaCl concentration in hydroponic solutions

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## Abstract

A hydroponic, greenhouse experiment was conducted to assess the effects of NaCl on growth, gas-exchange parameters, chlorophyll (Chl) content, and ion distribution in seven sesame (*Sesamum indicum* L.) genotypes (Ardestan, Varamin, Naz-Takshakhe, Naz-Chandshakhe, Oltan, Yekta, Darab). The plants were grown in 4-L containers and subjected to varying levels of salinity (0, 30, and 60 mM NaCl). After 42 days, salt treatments induced decreases of plant fresh and dry mass, total leaf area, and plant height in all genotypes. Increasing NaCl concentration caused significant, genotype-dependent decrease in the net photosynthetic rate, stomatal conductance, Chl content, and maximum quantum efficiency of photosystem II, while it increased the intercellular $CO_2$ concentration. Based on the dry matter accumulation under salinity, the genotypes were categorized in two groups, *i.e.*, salt-tolerant and salt-sensitive. The impact of salt on plant ion concentrations differed significantly among the sesame genotypes and between both two groups. The plant $Na^+$ concentrations were significantly lower in Ardestan, Darab, and Varamin genotypes than those found in the remaining genotypes. The highest plant $K^+$ and $Ca^{2+}$ concentrations together with the lowest $Na^+/K^+$ and $Na^+/Ca^{2+}$ ratios were observed in Ardestan, Varamin, and Darab genotypes. Our results indicated the presence of differences in salt response among seven sesame genotypes. It suggested that growth and photosynthesis could depend on ion concentrations and ratios in sesame.

*Additional key words*: chlorophyll fluorescence; gas exchange; potassium; salinity; sodium.

## Introduction

*Sesamum indicum* (L.) is an ancient, oil seed crop, which origin is probably in East Africa and India (Bedigian 2003, Anilakumar *et al.* 2010). Sesame seed is widely used in food, pharmacy, and industry in many countries (Bedigian 2003), since it contains a considerable amount of oil (50–60%), proteins (18–25%), carbohydrates (13.5%), and fibre (11.8%) (Were *et al.* 2006, Anilakumar *et al.* 2010). Sesame oil, compared to polyunsaturated oils of other crops, has proven to be more stable due to the natural antioxidants, sesamin and sesamolin, preserving the integrity of double bonds of unsaturated fatty acids (Uzun *et al.* 2002, Anilakumar *et al.* 2010). The beneficial effects of sesame oil on human health have been documented (Sankar *et al.* 2006). The most recent data on sesame production (FAOSTAT 2010) indicate that the average grain yield per ha is less than 1,000 kg $ha^{-1}$, which is quite low in comparison with most other oilseed crops. In addition to a dehiscent capsule and, therefore, seed loss through shattering, abiotic stresses are among the major factors contributing to the low grain yield.

Salt stress is one of the major environmental constraints for crop plants, particularly in arid and semiarid regions (Kaymakanova and Stoeva 2008, Turan *et al.* 2009). Salinization is quickly expanding on a global scale (Turkan and Demiral 2009) and currently more than 800 million ha of the cultivated lands are affected by salinity (FAOSTAT 2010). Salinity reduces the soil water potential which can lead to osmotic stress (Winicov 1998, Tejera *et al.* 2006). Osmotic effect exposes the plants to secondary stresses, such as drought stress and nutrient deficiency due to a decrease in the plant ability to obtain nutrients from root (Sairam *et al.* 2002). Furthermore,

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*Abbreviations:* Chl – chlorophyll; $C_i$ – intercellular $CO_2$ concentration; DM – dry mass; FM – fresh mass; $F_v/F_m$ – quantum efficiency of PSII; $g_s$ – stomatal conductance; LNP – leaf number per plant; PH – plant height; $P_N$ – net photosynthetic rate; PPFD – photosynthetic photon flux density; PS – photosystem; TLA – total leaf area per plant.
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salinity can directly affect nutrient uptake. Increase in the accumulation of specific ions, such as $Na^+$ and $Cl^-$, can reduce the uptake of $K^+$, $Ca^{2+}$, and $Mg^{2+}$ ions. The latter impact is called ion-excess effect of salinity (Soussi *et al.* 2001, Desingh and Kanagaraj 2007). The continuing salt accumulation in the soils brings about alterations in many physiological processes of the plant, including increased respiration rate and ion toxicity, decreased growth and change in mineral distribution (Munns and Termaat 1986, Genc *et al.* 2007). A depletion in Chl content along with reduction in the photosynthetic rate and efficiency have been also observed (Munns 2002, Sayed 2003).

In order to cope with the osmotic and ionic effects caused by salinity stress, some plant species have developed an array of up- and down-regulations (Delgado and Sánchez-Raya 1999, Sairam *et al.* 2002). They include osmotic adjustment by accumulation of compatible solutes, such as proline, polyols, amino acids, and proteins and regulatory mechanisms for ion transport (Chen and Murata 2002, Ashraf and Harris 2004).

Sensitivity of *S. indicum* to salinity (Yahya 1998) and some varietal differences in its response to salinity were documented (Gehlot *et al.* 2005, Koca *et al.* 2007, Yahya 2010). Disturbances in K, Ca, and P nutrition of the sesame plants were proposed to be the main reason for the negative effects of NaCl on sesame (Yahya 1998). Differences in the response of sesame genotypes to NaCl were associated with the differences in their ability to inhibit $Na^+$ translocation and accumulation in the shoots and leaves (Yahya 1998, 2010).

Despite the high nutritional value, health benefits, and economic importance in many countries, data on the effect of biotic and abiotic stresses on sesame plant are scarce. The present study evaluates some growth characteristics, and photosynthetic and ion attributes of sesame genotypes in hydroponic solutions under NaCl treatment.

## Materials and methods

**Plants and growth conditions**: Experiments were carried out in a greenhouse equipped with a partial canopy shading at the Isfahan University of Technology, Isfahan, Iran, in 2010. Seeds of seven *S. indicum* genotypes, namely Naz-Takshakhe, Naz-Chandshakhe, Ardestan, Varamin, Yekta, Darab, and Oltan were sown into 20 × 30 × 5 cm plastic trays filled with washed sand and grown under controlled conditions (light/dark regime of 12/12 h at 25/20°C, relative humidity of 60–70%). Some characteristics of the genotypes are given in Table 1. After emergence, seedlings were watered every day with half-strength Hoagland's solution (Hoagland and Arnon 1950). Four healthy, 5-week-old seedlings from each genotype were selected and transferred to the containers filled with 4 L of aerated Hoagland's nutrient solution. In total, 63 containers were used in the experiment. Salt treatment started when the plants were 40 d old. In order to avoid osmotic shock, 3 d after transplantation, salt solutions were added in two equal portions of 30 mM on alternate days until the concentrations of 30 and 60 mM were achieved, while only the nutrient solution was used in the control treatment. Nutrient solutions were collected every 24 h from each container and electric conductivity (EC) and pH were measured with conductivity meter (*Cond7110, InoLab*, Germany) and pH meter (*PHM3030, Jenway*, UK), respectively. The pH of the solutions was maintained at 6.0–6.5 throughout the experiment. The nutrient solution was renewed every 2 weeks and the amount of evaporated water was replenished with distilled water every day.

**Leaf gas exchange, Chl fluorescence, and Chl content**: Net photosynthetic rate ($P_N$), intercellular $CO_2$ concentration ($C_i$), and stomatal conductance to water vapour ($g_s$) were measured on 3 healthy leaves in each container with a calibrated portable gas-exchange system (*LCA4, ADC Bioscientific Ltd.,* UK) at 5 weeks after application of NaCl. All measurements were made at the leaf temperature of 26–33°C, $CO_2$ concentration of 370–390 mg $kg^{-1}$, and photosynthetic photon flux density (PPFD) of 350–500 μmol $m^{-2}$ $s^{-1}$. Chl fluorescence parameters, including maximum ($F_m$) and minimum ($F_0$) fluorescence along with the maximum efficiency of photosystem (PS) II ($F_m - F_0/F_m$, *i.e.*, $F_v/F_m$), were measured on 3 young, fully expanded, attached leaves per container (dark-adapted for 20 min). The fluorescence parameters were measured 6 weeks after the NaCl application, using a portable Chl fluorometer (*Opti-Sciences, Inc.,* Hudson, NH, USA). Each data set represented the mean of 3 measurements.

Table 1. Sesame genotypes and their agronomic properties.

| Genotype | Local region | Branching status | Relative height | Seed color | Lodging status | Silique status | Maturity status |
|---|---|---|---|---|---|---|---|
| Naz-Takshakhe | Northern Iran | low | tall | white | intermediate | intermediate | early |
| Ardestan | Central Iran | high | tall | brown | sensitive | sensitive | late |
| Naz-Chandshakhe | Northern Iran | high | tall | white | intermediate | sensitive | early |
| Yekta | Central Iran | low | tall | white | resistant | intermediate | semi-early |
| Varamin | Central Iran | low | tall | brown | resistant | intermediate | semi-late |
| Darab | Southern Iran | high | intermediate | brown | intermediate | sensitive | semi-late |
| Oltan | North-east Iran | high | tall | brown | sensitive | intermediate | semi-early |

The leaf Chl content of the sesame genotypes was determined 6 weeks after salt treatment using fully expanded, young leaves. A fresh leaf sample of 0.5 g was ground and extracted with 15 mL of 80% (v/v) acetone. The slurry was filtered and absorbance was determined at 645 and 663 nm for Chl *a* and Chl *b*, respectively, using the spectrophotometer (*PD-303S, APEL, Co., Ltd.,* Japan). Concentrations of Chl *a* and Chl *b* were calculated according to Arnon (1949).

**Growth parameters**: All four plants from each experimental unit were subjected to the following measurements, and then harvested after 6 weeks of the salt treatment. Mean leaf area per plant was calculated after measuring total leaf area (TLA) of all plants in each container, using a portable area meter (*Li 3000A, LI-COR, Inc.,* Lincoln, Nebraska, USA). Plant heights (PH) were measured and fresh (FM) and dry mass (DM) of shoots and roots were determined. For DM determination, the samples were oven-dried at 70°C for 72 h and then weighed.

**Ion determinations**: For determination of inorganic ion concentrations, plant aerial parts (stem and leaves) were dried at 70°C for 72 h and pulverized. One gram of the powdered sample was kept at 560°C for 4 h during ash preparation. Then 10 mL of 2 N HCl was added and the mixture was heated at 90°C to remove HCl. The digested ash was dissolved in 100 mL of distilled water and then filtered. The filtrate was refrigerated until analysis. The $K^+$ and $Na^+$ concentrations were measured using a flame photometer (*Corning Flame Photometer 410, Corning Medical and Scientific*, Halstead Essex, UK). Concentrations of $K^+$ and $Na^+$ ions were estimated by referring to the standard working solution. The $Ca^{2+}$ concentration was estimated by atomic absorption spectrometry (*Perkin-Elmer, Analyst 200,* Waltham, Massachusetts, USA) according to Chapman and Pratt (1961).

**Experimental design and statistical analysis**: A factorial experiment (salinity at 3 levels and genotype at 7 levels) was conducted using a randomized complete block design with three replications. All data were subjected to analysis of variance (*ANOVA*) using a *Statistical Analysis Software Version 9.1* (*SAS Institute Inc.,* Cary, North Carolina, USA). Based on the data obtained from FM and DM accumulation, the genotypes were divided into two groups: *i.e.*, salt-tolerant (Ardestan, Varamin, and Darab) and salt-sensitive (Naz-Takshakhe, Naz-Chandshakhe, Yekta, and Oltan). Orthogonal independent comparisons were conducted for differences within and between the two groups and for their interaction with the salt treatment. The means were separated using *Fisher's* protected least significant differences (LSD). Differences were considered significant at $p \leq 0.05$.

## Results

**Growth**: FM and DM were significantly affected by salt, genotype, tolerant *vs*. sensitive type, and the interaction effect of group × salt (Table 2). PH was significantly affected by salt, genotype, salt sensitive group, and tolerant *vs.* sensitive. TLA was significantly affected by salt, genotype, salt sensitive group, tolerant *vs*. sensitive, and the interaction effect of group × salt. The leaf number per plant (LNP) was significantly affected by salt, genotype, and tolerant *vs*. sensitive (Table 2).

FM and DM of the sesame genotypes decreased on average by 66.5 and 66.7%, respectively, in the plants subjected to the 60 mM NaCl in comparison with the control (Table 3). Averaged over genotypes, reductions of 29.8 and 73.5% in the means of TLA were observed in the plants grown under 30 and 60 mM of NaCl, respectively, compared with the control. Significant genotypic variation was observed in the growth parameters of the genotypes in response to NaCl (Table 2). This difference was mainly due to the difference between two groups of genotypes. The highest means for FM, DM, and TLA were observed in Varamin followed by Ardestan and Darab (Table 4), all representing the tolerant group. FM and DM were not different in both groups in the absence of any salt stress, but the tolerant group showed comparatively higher values of FM and DM under 30 and 60 mM NaCl (Fig. 1*A,B*). TLA in both groups differed under the control and saline conditions, but the extent of their difference increased with salinity, *i.e.*, 30 and 60 mM led to a more pronounced decrease in mean TLA in the sensitive group (Fig. 1*E*). Averaged over genotypes, 60 mM NaCl decreased mean PH and LNP by 47.8 and 41%, respectively, in comparison with the control (Table 3). The means with the highest PH and LNP values were recorded in the tolerant genotypes (Table 4, Fig. 1*C*,*D*).

**Gas exchange, Chl fluorescence, and Chl content**: Gas-exchange parameters were significantly affected by salt, genotype, tolerant *vs*. sensitive, and the interaction effects of salt × genotype and salt × group (Table 2). Averaged over the genotypes, $P_N$ decreased by 64% as NaCl concentration raised from 0 to 60 mM in the nutrient solution (data not shown). The NaCl presence decreased the $P_N$ of all seven genotypes. However, the magnitude of the reduction varied considerably among the genotypes in general (Fig. 2*A*) and between the two groups in particular (Fig. 3*A*). Among the genotypes studied in this experiment, $P_N$ showed a greater decrease at 60 mM NaCl in the sensitive group of the genotypes (*i.e.,* Naz-Takshakhe, Naz-Chanshakhe, Yekta, and Oltan), compared with those in the tolerant group (Fig. 2*A*). The $g_s$ response of sesame to NaCl seemed to be the genotype- and group-dependent (Table 2). Although the genotypes (Fig. 2*B*) and both two

Table 2. A synopsis of analysis of variance (*AVOVA*) for fresh mass (FM), dry mass (DM), plant height (PH),total leaf area per plant (TLA), leaf number per plant (LNP), net photosynthetic rate ($P_N$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration($C_i$), and quantum efficiency of PSII ($F_v/F_m$) of 7*S. indicum* genotypes when 40-d-old seedlings were allowed to grow for 6 weeks under normal or saline conditions.*–$p \leq 0.05$,** –$p \leq 0.01$,*** –$p \leq 0.001$, ns – nonsignificant, df – degrees of freedom.

| Source of variation | df | Mean square FM | DM | PH | TLA | LNP | $P_N$ | $g_s$ | $C_i$ | $F_v/F_m$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Replication | 2 | $61.512^{ns}$ | $0.632^{ns}$ | $41.921^{ns}$ | $11.977^{ns}$ | $6.798^{ns}$ | $1.56^{ns}$ | $0.0001^{ns}$ | $49.29^{ns}$ | $0.0004^{ns}$ |
| Salt treatment | 2 | $7625.592^{***}$ | $86.982^{***}$ | $5208.192^{***}$ | $2972.561^{***}$ | $570.619^{***}$ | $268.83^{***}$ | $0.0133^{***}$ | $10376.83^{***}$ | $0.05^{***}$ |
| Genotype | 6 | $472.223^{***}$ | $5.068^{***}$ | $205.099^{***}$ | $53.659^{***}$ | $11.661^{***}$ | $16.78^{** *}$ | $0.0008^{***}$ | $1440.85^{***}$ | $0.003^{***}$ |
| Sensitive group | 3 | $16.696^{ns}$ | $0.333^{ns}$ | $64.912^{*}$ | $24.117^{*}$ | $2.851^{ns}$ | $4.96^{*}$ | $0.0001^{ns}$ | $573.37^{*}$ | $0.003^{*}$ |
| Tolerant group | 2 | $242.526^{ns}$ | $2.114^{ns}$ | $22.980^{ns}$ | $5.535^{ns}$ | $4.314^{ns}$ | $0.126^{ns}$ | $0.00005^{ns}$ | $42.40^{ns}$ | $0.0008^{ns}$ |
| Between group | 1 | $2298.201^{***}$ | $25.181^{***}$ | $989.898^{***}$ | $238.533^{***}$ | $52.783^{***}$ | $85.55^{***}$ | $0.004^{***}$ | $6840.18^{***}$ | $0.100^{***}$ |
| Genotype× Salt treatment | 12 | $101.973^{ns}$ | $0.909^{ns}$ | $44.599^{ns}$ | $6.763^{ns}$ | $1.844^{ns}$ | $4.21^{**}$ | $0.0002^{*}$ | $356.85^{*}$ | $0.0003^{ns}$ |
| Sensitive × Salt treatment | 6 | $18.240^{ns}$ | $0.408^{ns}$ | $49.051^{ns}$ | $5.252^{ns}$ | $1.523^{ns}$ | $2.692^{ns}$ | $0.0001^{*}$ | $171.60^{ns}$ | $0.0004^{ns}$ |
| Tolerant × Salt treatment | 4 | $66.369^{ns}$ | $0.379^{ns}$ | $33.523^{ns}$ | $2.125^{ns}$ | $1.211^{ns}$ | $0.57^{ns}$ | $0.00001^{ns}$ | $14.45^{ns}$ | $0.0001^{ns}$ |
| Groups× Salt treatment | 2 | $424.382^{**}$ | $3.473^{*}$ | $53.393^{ns}$ | $20.567^{*}$ | $4.074^{ns}$ | $16.07^{***}$ | $0.0006^{***}$ | $1597.41^{***}$ | $0.0005^{ns}$ |
| Error | 40 | 65.697 | 0.925 | 23.488 | 4.932 | 3.259 | 1.35 | 0.00008 | 159.63 | 0.0006 |

Table 4. Effect of *S. indicum* genotypes on fresh mass (FM), dry mass (DM), plant height (PH), total leaf area per plant (TLA), leaf number per plant (LNP), chlorophyll (Chl) *a*, Chl *b*, total Chl ($Chl_{tot}$),Chl *a*/*b*, and quantum efficiency of PSII ($F_v/F_m$). Data are means ± SE ($n = 9$). Values followed by the same letter(s) within a row are not significantly different at $p \leq 0.05$ (LSD test).

| Parameters | Genotypes Naz-Chandshakhe | Ardestan | Naz-Takshakhe | Yekta | Varamin | Darab | Oltan |
|---|---|---|---|---|---|---|---|
| FM [g plant$^{-1}$] | $30.90 \pm 6.7^{d}$ | $44.72 \pm 4.69^{ab}$ | $31.80 \pm 7.284^{cd}$ | $33.90 \pm 6.34^{cd}$ | $49.02 \pm 4.88^{a}$ | $38.68 \pm 5.86^{bc}$ | $31.15 \pm 6.95^{cd}$ |
| DM [g plant$^{-1}$] | $3.29 \pm 0.742^{c}$ | $4.74 \pm 0.53^{ab}$ | $3.32 \pm 0.781^{c}$ | $3.64 \pm 0.661^{c}$ | $5.07 \pm 0.543^{a}$ | $4.11 \pm 0.64^{bc}$ | $3.20 \pm 0.705^{c}$ |
| PH [cm] | $50.23 \pm 3.784^{bc}$ | $57.16 \pm 4.96^{a}$ | $43.82 \pm 3.62^{d}$ | $48.23 \pm 4.83^{cd}$ | $54.56 \pm 4.70^{ab}$ | $54.25 \pm 6.15^{ab}$ | $46.94 \pm 5.55^{cd}$ |
| TLA [cm$^2$ plant$^{-1}$] | $18.64 \pm 3.553^{de}$ | $23.17 \pm 3.27^{a}$ | $20.48 \pm 3.58^{cd}$ | $21.02 \pm 3.71^{bc}$ | $24.19 \pm 3.56^{a}$ | $22.65 \pm 3.74^{ab}$ | $17.48 \pm 3.45^{e}$ |
| LNP | $20.02 \pm 1.688^{bc}$ | $21.8\ 3\pm 1.48^{a}$ | $19.13 \pm 1.63^{c}$ | $19.92 \pm 1.68^{c}$ | $20.55 \pm 1.68^{abc}$ | $21.65 \pm 1.59^{ab}$ | $18.90 \pm 1.48^{c}$ |
| Chl *a* [mg g$^{-1}$(FM)] | $0.40 \pm 0.014^{c}$ | $0.45 \pm 0.027^{ab}$ | $0.41 \pm 0.016^{bc}$ | $0.44 \pm 0.021^{abc}$ | $0.46 \pm 0.022^{a}$ | $0.41\pm 0.020^{bc}$ | $0.40 \pm 0.026^{c}$ |
| Chl *b* [mg g$^{-1}$(FM)] | $0.26 \pm 0.027^{ab}$ | $0.27 \pm 0.035^{a}$ | $0.21 \pm 0.0170^{c}$ | $0.26 \pm 0.024^{ab}$ | $0.25 \pm 0.017^{ab}$ | $0.26 \pm 0.029^{ab}$ | $0.23 \pm 0.026^{bc}$ |
| $Chl_{tot}$[mg g$^{-1}$(FM)] | $0.66\pm 0.038^{bcd}$ | $0.72 \pm 0.057^{a}$ | $0.63 \pm 0.031^{d}$ | $0.70 \pm 0.041^{ab}$ | $0.71 \pm 0.038^{ab}$ | $0.68 \pm 0.046^{abc}$ | $0.64\pm 0.045^{cd}$ |
| Chl *a*/*b* | $1.66 \pm 0.176$ | $1.83 \pm 0.210$ | $2.02 \pm 0.108$ | $1.76 \pm 0.145$ | $1.83 \pm 0.079$ | $1.69 \pm 0.180$ | $1.86 \pm 0.173$ |
| $F_v/F_m$ | $0.75 \pm 0.016^{c}$ | $0.79 \pm 0.011^{a}$ | $0.76 \pm 0.16^{bc}$ | $0.79 \pm 0.015^{a}$ | $0.78 \pm 0.015^{ab}$ | $0.80 \pm 0.017^{a}$ | $0.76 \pm 0.020^{bc}$ |

Table 3. Effect of different salt concentrations on fresh mass (FM), dry mass (DM), plant height (PH), total leaf area per plant (TLA), leaf number per plant (LNP), chlorophyll (Chl) *a*, Chl *b*, total Chl ($Chl_{tot}$), Chl *a*/*b*, and quantum efficiency of PSII ($F_v/F_m$), of *S. indicum* genotypes. Data are means ± SE ($n$ = 21). Values followed by *the same letter(s)* within a row are not significantly different $p \leq 0.05$ (LSD test).

| Parameters | NaCl [mM] | | |
|---|---|---|---|
| | 0 | 30 | 60 |
| FM [g plant$^{-1}$ ] | 57.09 ± 1.84$^a$ | 35.30 ± 2.94$^b$ | 19.12 ± 2.03$^c$ |
| DM [g plant$^{-1}$] | 6.07 ± 0.22$^a$ | 3.64 ± 0.30$^b$ | 2.02 ± 0.21$^c$ |
| PH [cm] | 65.42 ± 1.55$^a$ | 52.71 ± 1.60$^b$ | 34.11 ± 1.28$^c$ |
| TLA [cm$^2$ plant$^{-1}$] | 32.17 ± 0.61$^a$ | 22.58 ± 0.93$^b$ | 8.52 ± 0.47$^c$ |
| LNP | 24.55 ± 0.51$^a$ | 21.83 ± 0.37$^b$ | 14.48 ± 0.39$^c$ |
| Chl *a* [mg g$^{-1}$(FM)] | 0.46 ± 0.011$^a$ | 0.46 ± 0.011$^a$ | 0.36 ± 0.005$^b$ |
| Chl *b* [mg g$^{-1}$(FM)] | 0.29 ± 0.011$^a$ | 0.30 ± 0.010$^a$ | 0.16 ± 0.005$^b$ |
| $Chl_{tot}$ [mg g$^{-1}$(FM)] | 0.75 ± 0.012$^a$ | 0.77 ± 0.019$^a$ | 0.52 ± 0.008$^b$ |
| Chl *a*/*b* | 1.65 ± 0.091$^b$ | 1.52 ± 0.052$^b$ | 2.25 ± 0.077$^a$ |
| $F_v/F_m$ | 0.82 ± 0.006$^a$ | 0.78 ± 0.006$^b$ | 0.72 ± 0.007$^c$ |

groups (Fig. 3*B*) did not vary significantly in their $g_s$ under the control conditions, the sensitive group indicated a greater decrease in the $g_s$ at 60 mM NaCl concentration compared with the control. On the other hand, the tolerant group (*i.e.*, Ardestan, Varamin, and Darab) showed a smaller decrease in the $g_s$ under the 30 mM NaCl compared with the sensitive group. $C_i$ was significantly affected by the salt concentration of the nutrient solution in the genotype and group-dependent manner (Table 2). Although the increase in salt concentration led to a raise in $C_i$ of all genotypes (Fig. 2*C*) and both groups (Fig. 3*C*), the magnitude of the increase was remarkably greater in the sensitive group compared with the tolerant group.

$F_v/F_m$ was significantly affected by salt, genotype, and tolerant *vs*. sensitive (Table 2). At 60 mM NaCl, 11.8% decrease was observed in mean $F_v/F_m$, relative to the control (Table 3). The highest and lowest mean values of $F_v/F_m$ were found in Darab (0.80) and Naz-Chandshakhe (0.75), respectively (Table 4). Both groups did not differ in their $F_v/F_m$ under the control conditions, but the tolerant group indicated greater $F_v/F_m$ under 30 and 60 mM NaCl concentrations (Fig. 3*D*).

Leaf Chl *a*, Chl *b*, and total Chl contents were significantly affected by the effects of salt, genotype, and tolerant *vs.* sensitive (Table 5). Chl *a* was significantly affected by the interaction effect of salt × group. Chl *a/b* was significantly affected by salt. The means of Chl *a*, Chl *b*, and total Chl content appeared to be greater in the plants grown under 30 mM NaCl than those grown under the control conditions (Table 6). The plants growing under the 60 mM NaCl showed means of Chl *a*, Chl *b*, and total Chl lowered by 21.7, 44.8, and 30.6%, respectively, compared with the control (Table 3). Varamin, Ardestan, and Yekta genotypes indicated the greatest means of Chl *a*, Chl *b*, and total Chl (Table 4). The tolerant group of genotypes exceeded the sensitive group in Chl concentrations under 30 mM NaCl (Table 6).

Overall, increasing salinity level up to 60 mM raised the Chl *a/b* ratio by 36.3%, compared with the control (Table 3).

**Plant ion concentrations**: Shoot $Na^+$ and $K^+$ concentrations and the $Na^+/K^+$ and $Na^+/Ca^{2+}$ ratios of sesame were significantly affected by salt, genotype, tolerant *vs*. sensitive, and the interaction effects of salt × genotype and salt × group (Table 5). The shoot $Ca^{2+}$ concentration was affected by the salt, genotype, salt sensitive group, and group effects. The shoot $Na^+$ concentrations did not differ significantly under the control conditions in sesame genotypes and both two groups. Under both 30 and 60 mM NaCl, the shoot $Na^+$ concentrations increased appreciably in all genotypes, though, the extent of the enhancement was significantly different among the genotypes in general (Fig. 4*A*) and between both two groups in particular (Table 6). The greatest increases were observed in the $Na^+$ concentrations of 60 mM NaCl in the genotypes of Oltan, Naz-Chandshakhe, Naz-Takshakhe, and Yekta, which represented the sensitive group (Fig. 4*A*).

The shoot $K^+$ concentrations of sesame decreased significantly in response to the increasing salt concentration. Averaged over the genotypes, the shoot $K^+$ concentrations decreased by 34 and 54% in the plants subjected to 30 and 60 mM NaCl, respectively, relative to the control condition (data not shown). The shoot $K^+$ concentrations of the Naz-Chandsakhe, Naz-Takshakhe, Oltan and Yekta genotypes, all belonging to the sensitive group, decreased significantly at 30 mM NaCl, whereas, in the tolerant group of the genotypes, it remained unaffected and decreased significantly when the salt concentration increased to 60 mM (Fig. 4*B*). The shoot $K^+$ concentrations also decreased remarkably in all genotypes under 60 mM NaCl.

The shoot $Ca^{2+}$ concentrations decreased significantly with the increasing salt content in the nutrient solution in both sensitive and tolerant groups (Table 6). Averaged over the genotypes and groups, the shoot $Ca^{2+}$ concentrations decreased by 44% in the plants grown under the 60 mM NaCl, compared with those grown under the control condition (data not shown). The greatest means of shoot $Ca^{2+}$ concentrations were observed under both 30 and 60 mM NaCl in the genotypes of Darab and Ardestan from

the tolerant group, compared with the rest of the genotypes (Fig. 4*C*).

Averaged over the genotypes and groups, the means of the $Na^+/K^+$ and $Na^+/Ca^{2+}$ ratios under the 60 mM NaCl were nearly 15.3 and 12.3 fold of those of the control, respectively (data not shown). Both ratios of $Na^+/Ca^{2+}$ and $Na^+/K^+$ increased in all genotypes and in both groups with increasing salt concentration, though the magnitude of the increase differed with the genotype (Fig. 5*A*,*B*) and group (Table 6). The greatest increases in the $Na^+/Ca^{2+}$ and $Na^+/K^+$ ratios were observed with those in the sensitive group, *i.e.*, Naz-Chandshakhe, Naz-Chandshakhe, Oltan, and Yekta treated with 60 mM NaCl.

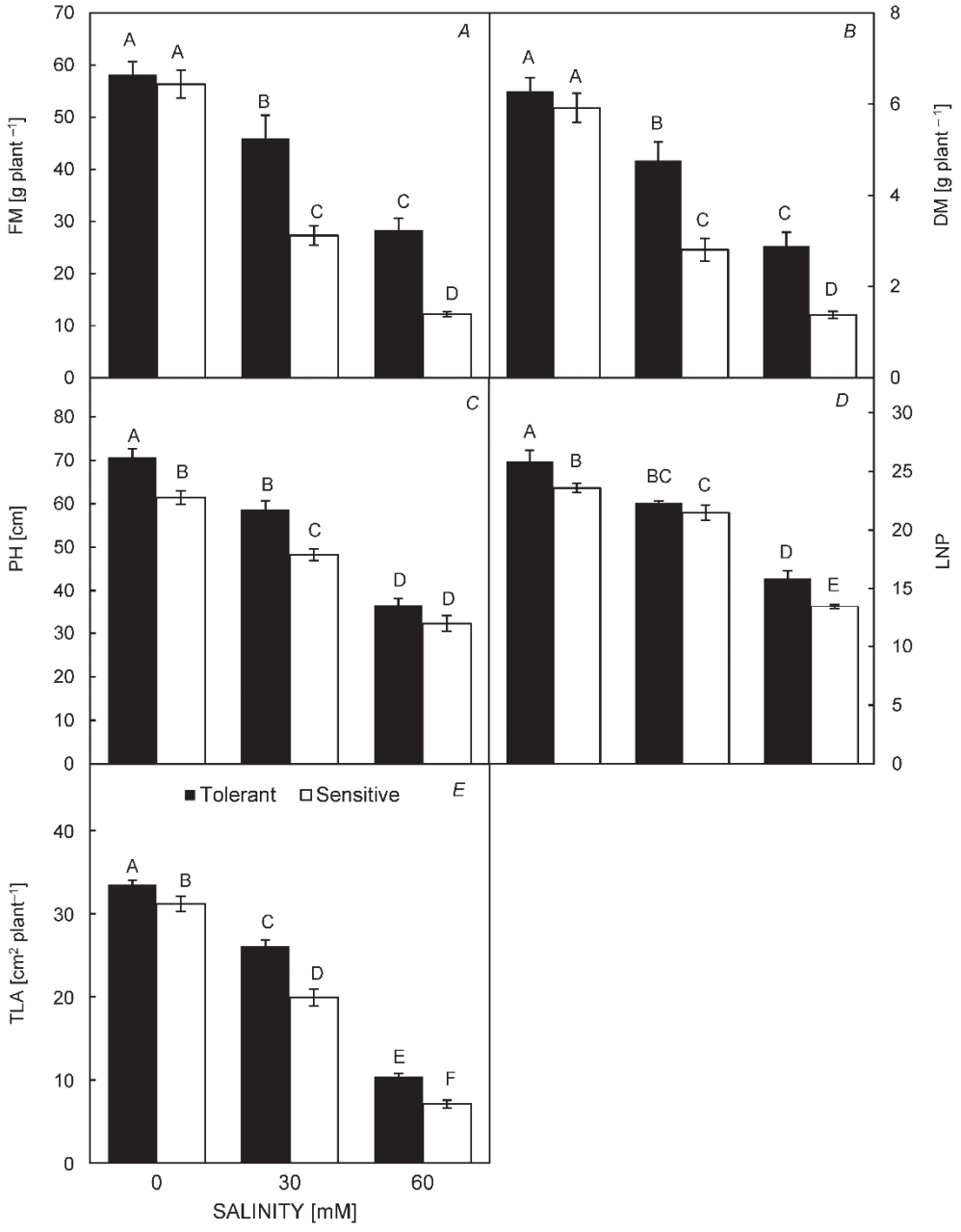


Fig. 1. Fresh mass (FM) (*A*), dry mass (DM) (*B*), plant height (PH) (*C*), leaf number per plant (LNP) (*D*), and total leaf area per plant (TLA) (*E*) of sensitive (Naz-Takshakhe, Naz-Chandshakhe, Oltan, Yekta) and tolerant (Varamin, Darab, Ardestan) genotypes of *Sesamum indicum* when grown for 6 weeks under different level of salinity (0, 30, and 60 mM). Data are the mean ± SE ($n$ = 9 for tolerant; $n$= 12 for sensitive). Means with *the same letter(s)* are not significantly different from each other (according to pairwise comparison based on $t$-test; $p \leq 0.05$).

## Discussion

Salt stress is a complex phenomenon with 3 components: osmotic, specific ion, and nutrient deficiency effects (Blum 1988, Munns and Tester 2008). Different plant species have evolved various mechanisms to cope with these effects (Munns 2002, Ashraf and Harris 2004, Genc *et al.* 2007). Then, genetic variations among the various crop species and genotypes are useful in providing a valuable tool for the selection of genotypes with favourable salt stress–related characteristics (Misra and Dwivedi 2004). We demonstrated that some salt-induced, differential responses existed among sesame genotypes in terms of biomass production, mineral ions accumulation, and photosynthetic-related traits.

Our results revealed that increasing salinity in the

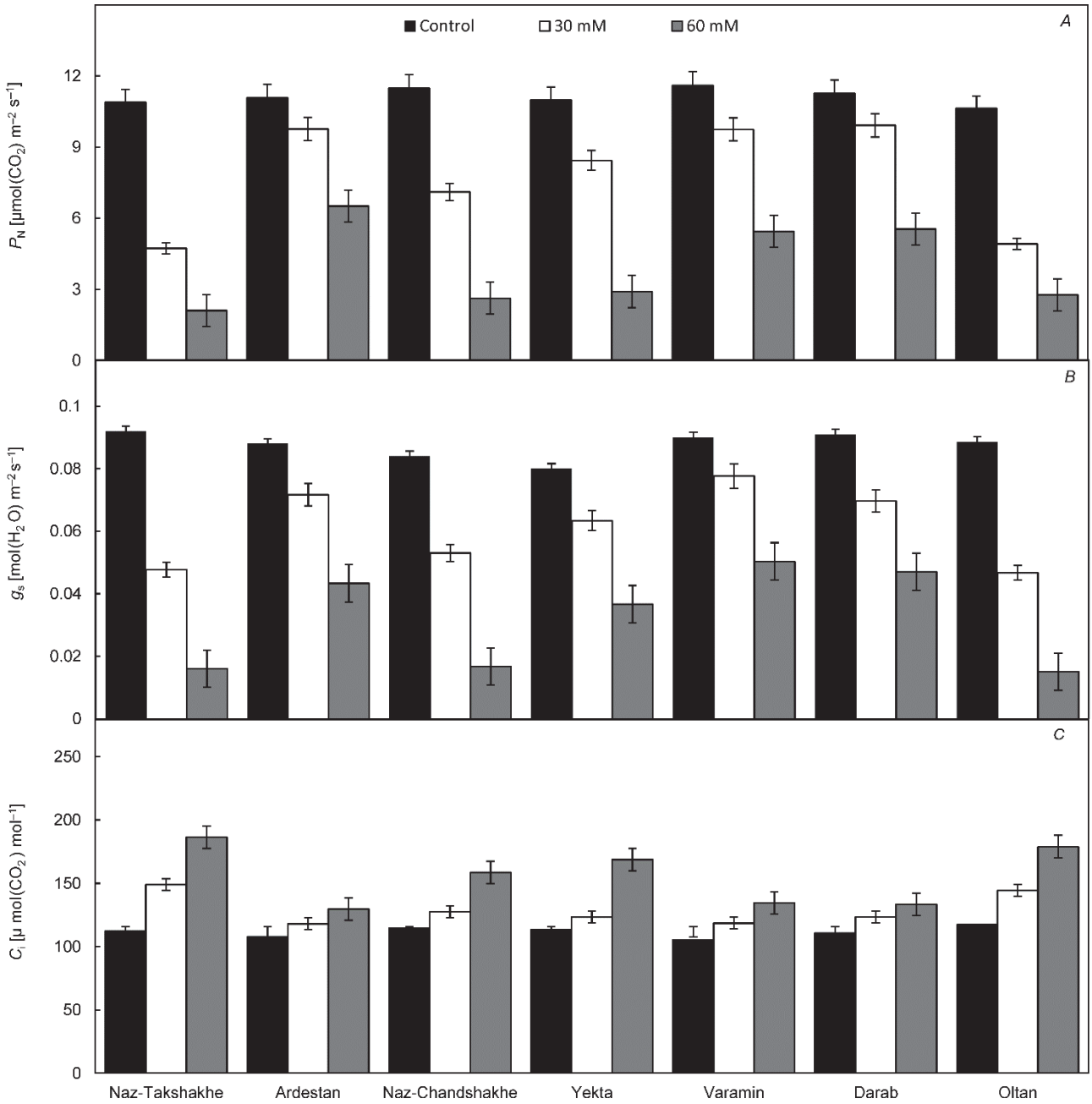


Fig. 2. Net photosynthetic rate ($P_N$) (*A*), stomatal conductance ($g_s$) (*B*), and intercellular $CO_2$ concentration ($C_i$) (*C*) of 7 genotypes of *Sesamum indicum* when grown for 6 weeks under 0, 30, and 60 mM NaCl. Data are the mean ± SE ($n$ = 3). LSDs (0.05) for $P_N$, $g_s$, and $C_i$ are 1.92, 0.015, and 20.47, respectively.

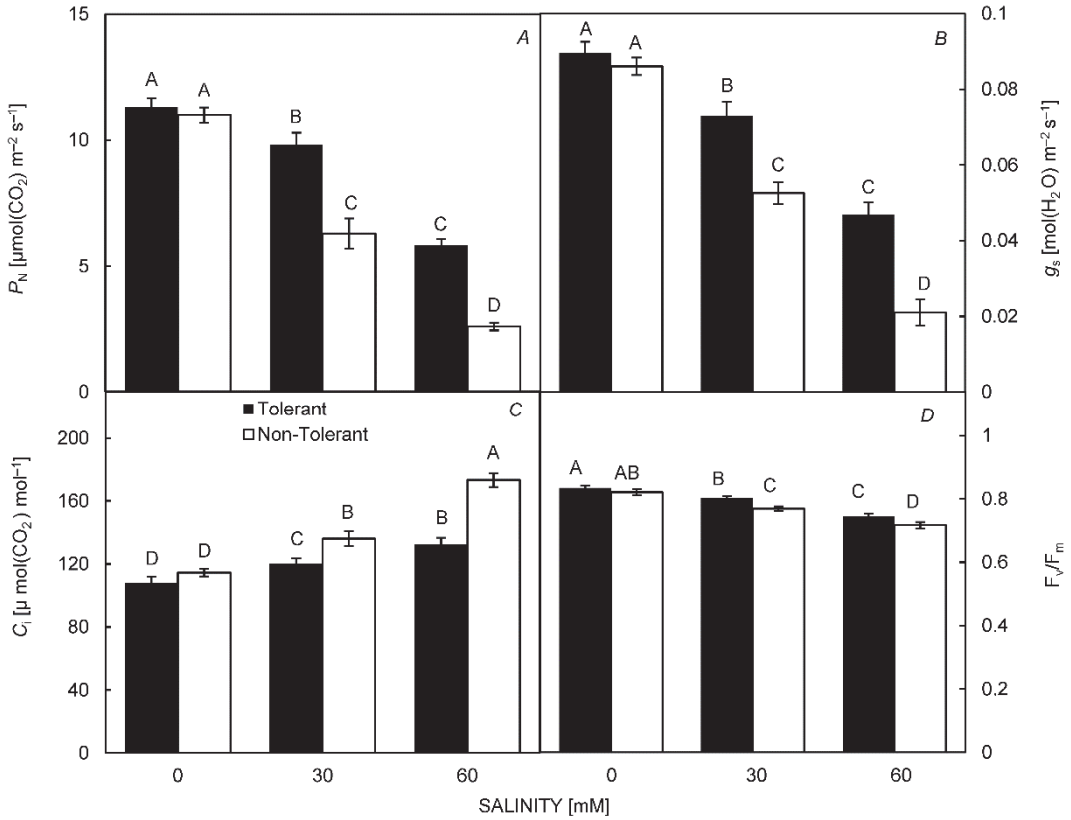


Fig. 3. Net photosynthetic rate ($P_N$) (*A*), stomatal conductance ($g_s$) (*B*), intercellular $CO_2$ concentration ($C_i$) (*C*), and quantum efficiency of PS-II ($F_v/F_m$) (*D*) of sensitive (Naz-Takshakhe, Naz-Chandshakhe, Oltan,Yekta) and tolerant (Varamin, Darab, Ardestan) genotypes of *S. indicum* when grown for 6 weeks under different level of salinity (0, 30, and 60 mM). Data are the mean ± SE ($n$ = 9 for tolerant; $n$= 12 for sensitive). Means with *the same letter(s)* are not significantly different from each other (according to pairwise comparison based on *t*-test; $p \leq 0.05$).

nutrient solution led to the decrease in plant growth characteristics, such as FM, DM, PH, TLA, and LNP, but the declines were the genotype- (Table 4) and group-dependent (Fig. 1). The observed reduction in FM and DM might be due to the reduced photosynthetic activity per unit of leaf area (Netondo *et al.* 2004), additional cost to exclude or compartmentalize salts within the cells, and also the salt-induced damage to the tissues (Munns 2005). In the present study, 6 weeks after the salt treatment, the injury was visible as yellowing and death of older leaves in different sesame genotypes, more notably in the sensitive group. When a species is less tolerant to salt, *i.e.*, it has the high rate of salt uptake or it is unable to compartmentalize salt once it has built up in the leaves, the effects of salinity may become obvious for weeks (Munns 2002). Leaf area appears to be one of the first plant characteristics affected by salinity. Plants with lesser tolerance to salinity have often fewer and smaller leaves, because salt may lead to the leaf death or, more frequently, to haltered leaf expansion (Munns and Termaat 1986). Furthermore, the reduction in leaf area due to salt stress has been considered an avoidance mechanism to reduce water loss through transpiration (Blum 1988). In the salt-sensitive species, where salt is not considerably excluded from the transpiration stream, salt builds up to toxic concentrations, particularly in the leaves that have been transpiring for a longer time (Munns 2002). This leads to the death of the older leaves eventually. If new leaves are produced faster than old leaves die, there is a sufficient leaf area for photosynthesis. In the present study, the salt-tolerant genotypes were able to minimize an adverse effect of NaCl on their growth.

In contrast to $C_i$, which significantly increased with increasing salinity, $P_N$ and $g_s$ of all sesame genotypes significantly decreased. Thus, the extent of the decrease in $P_N$ (Fig. 2*A*) and $g_s$ (Fig. 2*B*) and the magnitude of the increase in $C_i$ (Fig. 2*C*) were strongly genotype- and group-dependent. Salt effects on photosynthetic processes may be classified as: (*1*) the response of stomata to salt, and (*2*) the diffusion-independent effects of salt on the photosynthetic capacity of the plant. Stomata closure in response to salt is commonly seen in salt-sensitive species. The data presented here for sesame indicated that stomata opening and, hence conductance, decreased due to the presence of NaCl in the nutrient solution. However, the extent, to which stomata closure affects photosynthetic

Table 5. A synopsis of analysis of variance (*AVOVA*) for chlorophyll (Chl) *a*, Chl *b*, total Chl ($Chl_{tot}$), Chl *a/b*, $Na^+$, $K^+$, $Ca^{2+}$, $Na^+/K^+$, and $Na^+/Ca^{2+}$of 7*S. indicum* genotypes when 40-d-old seedlings were allowed to grow for 6-weeks under normal or saline conditions. *–$p \leq 0.05$, ** –$p \leq 0.01$, *** –$p \leq 0.001$, ns – nonsignificant, df – degrees of freedom.

| Source of variation | df | Mean square Chl *a* | Chl *b* | $Chl_{tot}$ | Chl *a/b* | $Na^+$ | $K^+$ | $Ca^{2+}$ | $Na^+/K^+$ | $Na^+/Ca^{2+}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Replication | 2 | $0.0004^{ns}$ | $0.0002^{ns}$ | $0.0006^{ns}$ | $0.04^{ns}$ | $1.87^{ns}$ | $10.97^{ns}$ | $10.26^{ns}$ | $0.003^{ns}$ | $0.03^{ns}$ |
| Salt treatment | 2 | $0.068^{**}$ | $0.12^{***}$ | $0.38^{***}$ | $3.19^{***}$ | $787.87^{***}$ | $4683.08^{***}$ | $312.12^{***}$ | $0.99^{***}$ | $11.36^{***}$ |
| Genotype | 6 | $0.004^{*}$ | $0.004^{*}$ | $0.012^{**}$ | $0.12^{ns}$ | $19.14^{***}$ | $123.91^{**}$ | $16.17^{*}$ | $0.03^{***}$ | $0.53^{***}$ |
| Sensitive group | 3 | $0.002^{ns}$ | $0.005^{**}$ | $0.009^{*}$ | $0.203^{ns}$ | $0.92^{ns}$ | $100.31^{ns}$ | $16.21^{*}$ | $0.006^{ns}$ | $0.294^{***}$ |
| Tolerant group | 2 | $0.004^{ns}$ | $0.001^{ns}$ | $0.004^{ns}$ | $0.058^{ns}$ | $8.91^{ns}$ | $83.82^{ns}$ | $2.83^{ns}$ | $0.006^{*}$ | $0.06^{ns}$ |
| Between group | 1 | $0.105^{*}$ | $0.007^{*}$ | $0.036^{*}$ | $0.023^{ns}$ | $94.24^{***}$ | $274.90^{***}$ | $42.73^{***}$ | $0.205^{***}$ | $2.17^{***}$ |
| Genotype× salt treatment | 12 | $0.003^{ns}$ | $0.002^{ns}$ | $0.004^{ns}$ | $0.12^{ns}$ | $11.34^{**}$ | $96.47^{**}$ | $0.97^{ns}$ | $5.41^{***}$ | $0.211^{***}$ |
| Sensitive × salt treatment | 6 | $0.0006^{ns}$ | $0.001^{ns}$ | $0.001^{ns}$ | $0.097^{ns}$ | $3.03^{ns}$ | $19.23^{ns}$ | $1.54^{ns}$ | $0.003^{ns}$ | $0.106^{ns}$ |
| Tolerant × salt treatment | 4 | $0.001^{ns}$ | $0.003^{ns}$ | $0.006^{ns}$ | $0.189^{ns}$ | $2.95^{ns}$ | $21.47^{ns}$ | $2.43^{ns}$ | $0.001^{ns}$ | $0.01^{ns}$ |
| Groups× salt treatment | 2 | $0.007^{*}$ | $0.0005^{ns}$ | $0.010^{ns}$ | $0.051^{ns}$ | $53.04^{***}$ | $478.19^{***}$ | $1.401^{ns}$ | $0.087^{***}$ | $0.918^{***}$ |
| Error | 40 | 0.001 | 0.001 | 0.002 | 0.12 | 3.80 | 35.63 | 5.50 | 0.003 | 0.05 |

Table 6. Effect of different salinity on chlorophyll (Chl) *a*, Chl *b*, total Chl ($Chl_{tot}$), $Na^+$, $K^+$, $Ca^{2+}$, $Na^+/K^+$, and $Na^+/Ca^{2+}$ in sensitive (Naz-Takshakhe, Naz-Chandshakhe, Oltan,Yekta) and tolerant (Varamin, Darab, Ardestan) genotypes of *S. indicum* when grown for 6 weeks under 0, 30, and 60 mM NaCl. Data are means ± SE ($n$ = 9 for tolerant; $n$ = 12 for sensitive). Values followed by *the same letter(s)* within a row are not significantly different at $p \leq 0.05$ (according to pairwise comparison based on $t$-test). FM – fresh mass, DM – dry mass.

| Parameters | Tolerant [mM NaCl] | | | Sensitive [mM NaCl] | | |
|---|---|---|---|---|---|---|
| | 0 | 30 | 60 | 0 | 30 | 60 |
| Chl *a* [mg $g^{-1}$(FM)] | $0.45 \pm 0.015^{b}$ | $0.50 \pm 0.017^{a}$ | $0.37 \pm 0.009^{c}$ | $0.46 \pm 0.017^{b}$ | $0.43 \pm 0.009^{b}$ | $0.35 \pm 0.006^{c}$ |
| Chl *b* [mg $g^{-1}$(FM)] | $0.30 \pm 0.018^{ab}$ | $0.32 \pm 0.015^{a}$ | $0.17 \pm 0.010^{c}$ | $0.27 \pm 0.014^{b}$ | $0.29 \pm 0.013^{b}$ | $0.15 \pm 0.006^{c}$ |
| $Chl_{tot}$ [mg $g^{-1}$(FM)] | $0.76 \pm 0.012^{b}$ | $0.82 \pm 0.015^{a}$ | $0.54 \pm 0.010^{c}$ | $0.74 \pm 0.020^{b}$ | $0.72 \pm 0.016^{b}$ | $0.51 \pm 0.010^{c}$ |
| $Na^+$ [mg $g^{-1}$(DM)] | $2.40 \pm 0.359^{d}$ | $7.84 \pm 0.808^{c}$ | $10.98 \pm 0.689^{b}$ | $1.92 \pm 0.221^{d}$ | $9.84 \pm 0.563^{b}$ | $16.87 \pm 0.714^{a}$ |
| $K^+$ [mg $g^{-1}$(DM)] | $58.12 \pm 3.270^{b}$ | $53.82 \pm 1.512^{b}$ | $33.84 \pm 0.496^{d}$ | $63.58 \pm 2.282^{a}$ | $40.00 \pm 1.788^{c}$ | $29.53 \pm 0.626^{d}$ |
| $Ca^{2+}$ [mg $g^{-1}$(DM)] | $18.11 \pm 0.939^{a}$ | $12.25 \pm 0.770^{c}$ | $10.08 \pm 0.653^{cd}$ | $15.86 \pm 0.751^{b}$ | $10.73 \pm 0.732^{c}$ | $8.84 \pm 0.488^{d}$ |
| $Na^+/K^+$ | $0.04 \pm 0.004^{e}$ | $0.14 \pm 0.016^{d}$ | $0.32 \pm 0.019^{b}$ | $0.03 \pm 0.003^{e}$ | $0.25 \pm 0.020^{c}$ | $0.57 \pm 0.026^{a}$ |
| $Na^+/Ca^{2+}$ | $0.13 \pm 0.023^{d}$ | $0.65 \pm 0.070^{c}$ | $1.12 \pm 0.111^{b}$ | $0.12 \pm 0.018^{d}$ | $0.96 \pm 0.084^{b}$ | $1.95 \pm 0.113^{a}$ |

capacity, can be conferred by the magnitude of the alteration in $C_i$ (Seemann and Critchley 1985). Our results indicated that the reduction in $g_s$ did not lead to the depletion of the intercellular $CO_2$ (due to photoassimilation) of sesame genotypes studied in this experiment. The decline of $P_N$ associated with the increase in $C_i$ has been frequently interpreted as the direct effect of the stress factor on the photosynthetic capacity. Such changes in the apparent photosynthetic capacity that are not proportional to diffusional limitations could be attributed to either a change in the concentration of photosynthetic machinery and/or an alteration in the efficiency of operation of this machinery (Seemann and Critchley 1985). Our results, therefore, indicated that the declined photosynthetic rate in sesame genotypes in response to the salinity could only be partly explained by the decreased $g_s$. It seems that a decreased mesophyll conductance, which is suggestive of inhibition of photosynthetic activity at the biochemical level, contributed to the lowered photosynthetic performance of the sesame genotypes. In addition to the decrease in $g_s$, the increase in $C_i$ of the salt-tolerant genotypes was as severe as that of the salt-sensitive group. Both stomatal and nonstomatal components of photosynthesis were less affected by the salt concentration in the salt-tolerant genotypes. Decrease in photosynthesis associated with stomatal and/or nonstomatal inhibition of photosynthesis by salt stress have been reported in a number of other salt-sensitive species (Downton 1977, Seemann and Critchley 1985, Lloyd *et al.* 1990, García-Legaz *et al.* 1993, Gucci and Tattini 2010).

Chl *a*, Chl *b*, and total Chl of all sesame genotypes were reduced, while the Chl *a/b* ratio increased with the salinity, albeit at the 60 mM concentration (Table 3). The decrease in leaf Chl concentration could be due to changes in the lipid protein ratio of pigment-protein complexes (Rao and Rao 1981), increased chlorophyllase activity and degradation (Singh and Dubey 1995) and an inhibition in the synthesis of photosynthetic pigments (García-Sánchez *et al.* 2002). The decrease in Chl *a* and Chl *b* in wheat (Ehsanzadeh *et al.* 2009, Li *et al.* 2010) and increase in the ratio of Chl *a/b* in wheat (Azizpour *et al.* 2010) and sunflower (Santos 2004) were reported under saline conditions. During the process of Chl degradation, Chl *b* is converted into Chl *a* (Azizpour *et al.* 2010) and this might explain the increase of Chl *a/b* ratio under 60 mM NaCl. The decrease in the leaf Chl concentration of the sesame genotypes could be an important factor contributing to the previously discussed alterations in their $P_N$. Moreover, since the decreased Chl concentration was accompanied by a concomitant decrease in $F_v/F_m$ (Table 3), this could be considered as a further evidence of the fact that $g_s$ was not the sole factor responsible for the decrease in the $P_N$ of the sesame genotypes studied. Consistent with our results, Masojidek and Hall (1992) reported that $Cl^-$ ions at toxic concentrations can affect reaction centers of PSII either directly or *via* accelerated leaf senescence. Increases in Chl *a* and total Chl could be attributed in the salt-tolerant group treated with 30 mM NaCl to the fact that a cell size decreases in some species and genotypes under moderate levels of salinity and it leads to an increase in chloroplast concentration per leaf area (Li *et al.* 2010, Rivelli *et al*. 2010).

In the present study, the concentration of $Na^+$ in the shoots increased with genotype- and group-dependent manners. The salt-sensitive group of genotypes indicated the greatest increases in their $Na^+$ concentrations (Fig. 4*A*). In contrast, the concentration of $K^+$ decreased in sesame genotypes, the extent of the decrease being the function of the genotype and the group. The salt-tolerant group maintained the higher concentration of $Ca^{2+}$ (Fig. 4*C*) and $K^+$ (Fig. 4*B*) under the saline conditions. It is believed that with high NaCl concentrations in the rhizosphere, root capacity for $Na^+$ accumulation is saturated and, consequently, excess $Na^+$ is translocated to the aerial tissues. This may lead to decline in the uptake of $K^+$ and $Ca^{2+}$ in different plant species (Desingh and Kanagaraj 2007, Turan *et al.* 2009). Salt injury develops due to inability of the cells to compartmentalize an excess of $Na^+$ or $Cl^-$ in the vacuole. Consequently, ions may build up in the cytoplasm and inhibit enzyme activities or they may accumulate in

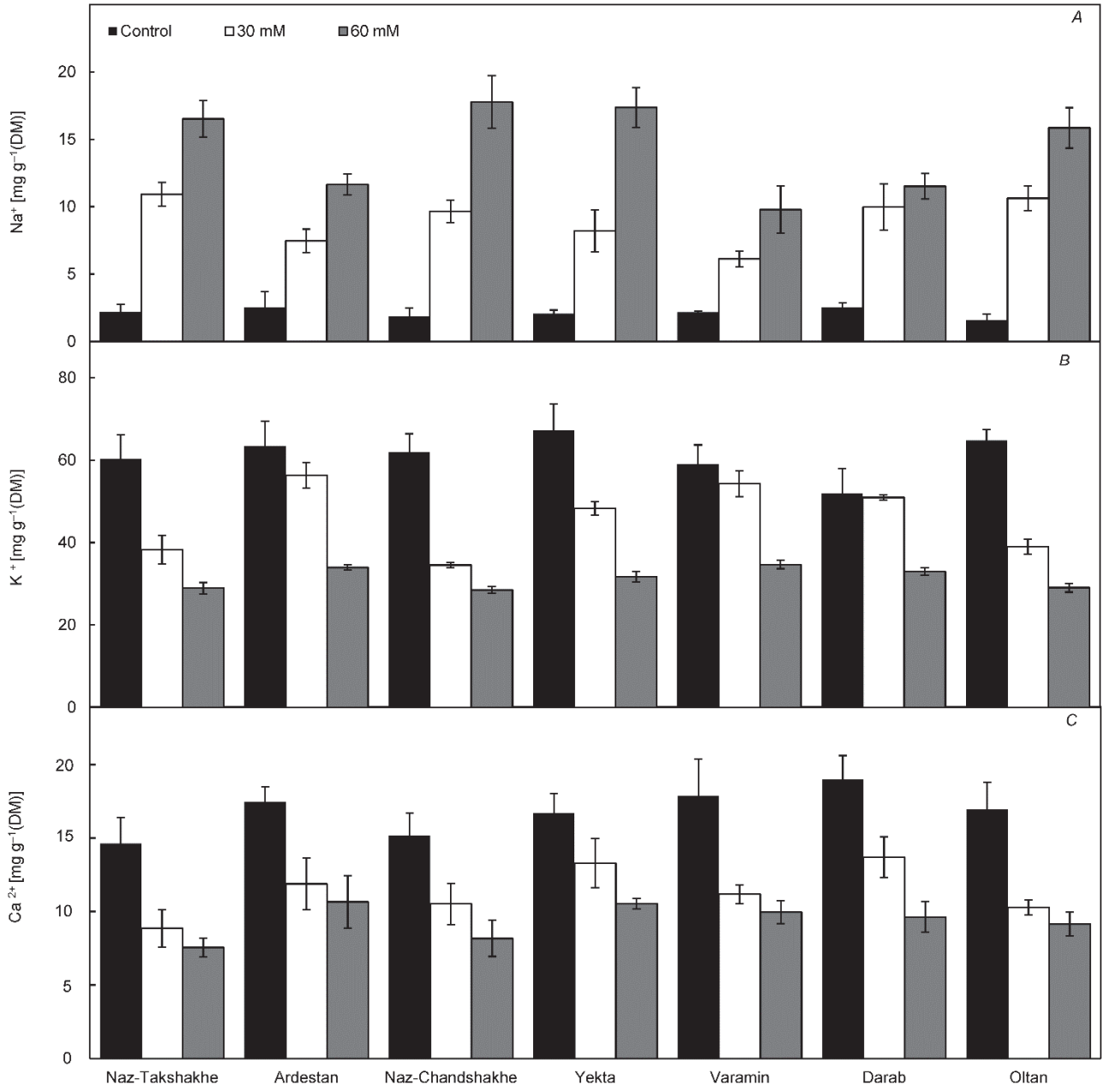


Fig. 4. $Na^+$ (*A*), $K^+$ (*B*), and $Ca^{2+}$ (C) concentrations of 7 genotypes of *S. indicum* when grown for 6 weeks under 0, 30, and 60 mM NaCl. Data are the mean ± SE ($n$ = 3). LSDs (0.05) for $Na^+$, $K^+$, and $Ca^{2+}$ concentrations are 3.17, 9.67, and 3.94, respectively.

the cell walls and facilitate the cellular dehydration (Munns 2002). Osmotically driven removal of water from cells may happen as the result of high $Na^+$ concentrations in the leaf apoplast, since $Na^+$ enters leaves by the transpiration stream and is left behind as water evaporates (Parvaiz and Satyawati 2008). However, appropriate amounts of both $K^+$ and $Ca^{2+}$ are needed to maintain the integrity of cell membranes and normal functioning of all metabolic processes (Debez *et al.* 2004). Small $Na^+/K^+$ and $Na^+/Ca^{2+}$ ratios are essential for normal cellular functions under saline conditions, and these ratios have been repeatedly shown as reliable parameters for salt tolerance estimation (Soussi *et al.* 2001, Chen and Murata 2002, Sairam *et al.* 2002). The high $Na^+$concentration or $Na^+/K^+$ ratio may interfere with a number of enzymatic processes in the cytoplasm. The maintenance of $Ca^{2+}$ acquisition and transport under salt stress is also the important component of salinity tolerance (Debez *et al.* 2004). The maintenance of enough $K^+$ in plant tissue under salinity seems to be related to the selective $K^+$ uptake, the appropriate cellular $K^+$ and $Na^+$ compartmentation and distribution in the shoots (Munns 2002). To maintain desirable $Na^+/K^+$

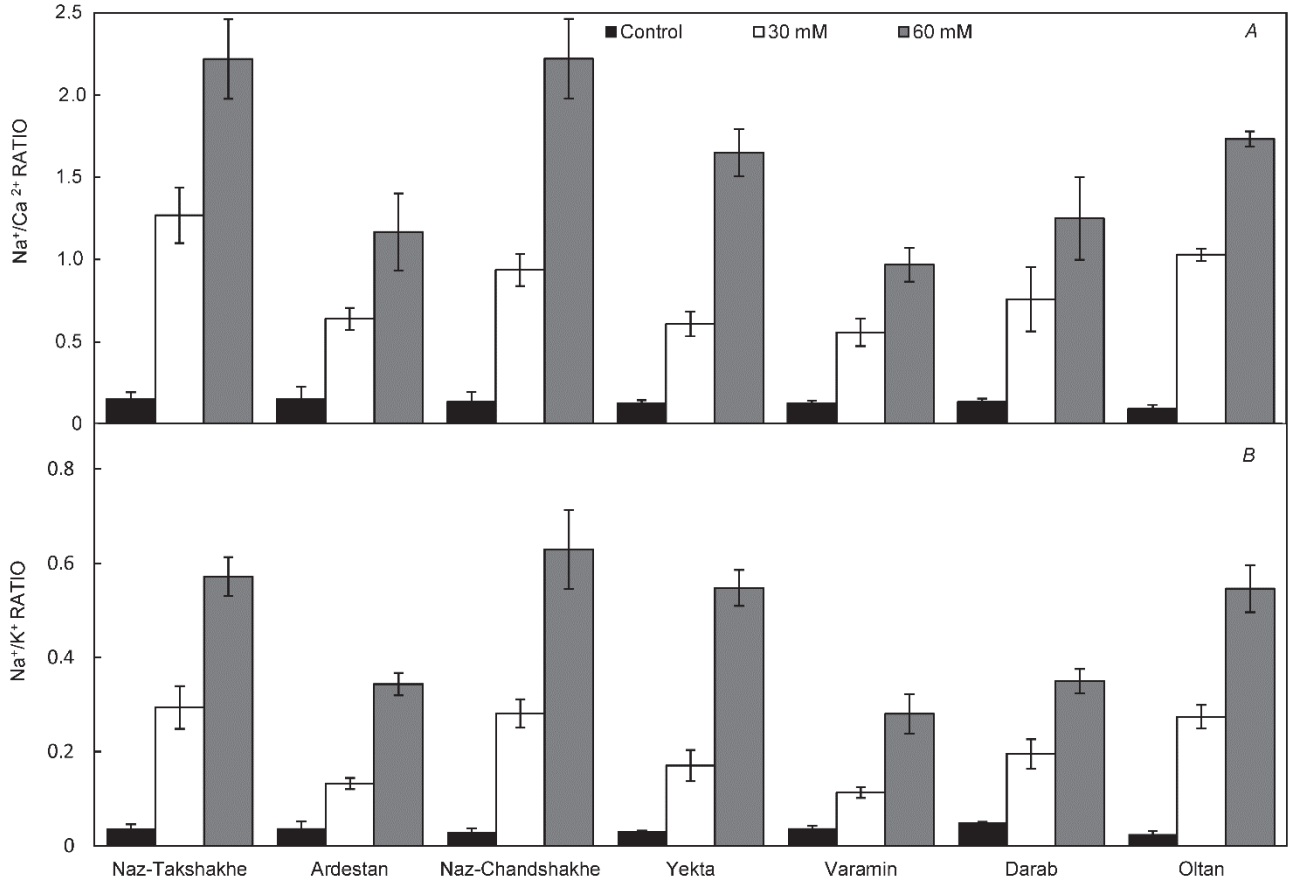


Fig. 5. $Na^+/Ca^{2+}$ (*A*) and $Na^+/K^+$(*B*) ratios of 7 genotypes of *S. indicum* when grown for 6 weeks under 0, 30, and 60 mM NaCl. Data are the mean ± SE ($n$ = 3). LSDs (0.05) for $Na^+/Ca^{2+}$and $Na^+/K^+$ ratios are 0.38 and 0.09, respectively.

ratios in the cytosol, plants commonly regulate $K^+$ and $Ca^{2+}$ uptake, prevent $Na^+$ influx, enhance its efflux from the cell and utilize $Na^+$ for osmotic adjustment. Some species and genotypes can maintain higher growth rates under saline conditions by accumulating fewer toxic ions and maintaining high tissue $Ca^{2+}$ and $K^+$ concentrations (Chen and Murata 2002). We found smaller $Na^+/Ca^{2+}$ and $Na^+/K^+$ ratios under salinity in the salt-tolerant group of sesame genotypes (Fig. 5*A*,*B*), which indicated their ability to maintain a more appropriate ionic balance and normal physiological functioning.

The increase in $Na^+$ along with the decrease in $K^+$ and $Ca^{2+}$ in cells and tissues was reported previously, *e.g.*, in chickpea (Soussi *et al.* 2001), wheat (Sairam *et al.* 2002, Genc *et al.* 2007), cotton (Desingh and Kanagaraj 2007), and rice (García-Morales *et al.* 2012). Other authors have confirmed that the deleterious effects of salinity on plant growth may occur through a ion imbalance, specific ion effects, and nutrient deficiency (Munns and Termaat 1986, Winicov 1998, Soussi *et al.* 2001). Greenway and Munns (1980) proposed that salt tolerance in plants is associated with the ability to prevent entry and/or translocation of saline ions (mainly $Na^+$ and $Cl^-$) from the root zone to the aerial parts. Therefore, salt-tolerant genotypes and/or species may have a more efficient mechanism for regulating salt translocation from the roots to the shoots. Since we did not measure ion distribution and/or translocation, we were unable to determine the dominant component of tolerance in the salt-tolerant genotypes. Furthermore, despite a great number of studies on the mechanisms of salinity tolerance of plants, neither the metabolic sites at which salt stress damages plants nor the adaptive components of salt tolerance are fully understood (Ashraf and Harris 2004). In fact, salt-stress physiology is so complex that in addition to variation among species it could vary also among genotypes within a single species and even with physiological age.

**Conclusion**: The differences in response to NaCl seemed to stem from different capabilities of the genotypes in terms of ion (*i.e.*, $Na^+$, $K^+$, and $Ca^{2+}$) concentrations and ion ratios. Associated with the smaller increases of $Na^+/K^+$ and $Na^+/Ca^{2+}$ in some sesame genotypes, there was the smaller decrease in the photosynthetic parameters and, hence, growth parameters. These findings provided new perspectives on the salt responses of sesame, as no such

previous reports on this oilseed crop were published before (at least from a physiological stand-point). A fair degree of consistency was observed between different traits, such as gas-exchange parameters, ion concentrations and ratios, and growth attributes. Thus, responses at the other growth phases (*e.g.*, reproduction and grain filling) could be different from those observed in the vegetative phase. Therefore, this consistency did not rule out the necessity for further testing by using larger populations and the entire growth cycle. Further research should focus on identifying mechanisms of differential ion distributions and dissecting $Na^+$ exclusion and tissue salt tolerance in sesame genotypes.

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