

# Interactive effects of salinity and ozone pollution on photosynthesis, stomatal conductance, growth, and assimilate partitioning of wheat (*Triticum aestivum* L.)

I.A. HASSAN

Department of Botany, Faculty of Science, Alexandria University, 21526 El-Shatby, Alexandria, Egypt

## Abstract

Plants of an Egyptian cultivar of wheat (*Triticum aestivum* L. cv. Giza 63) were exposed in open-top chambers (OTCs) for 8 h d<sup>-1</sup> for up to 75 d to a factorial combination of two levels of salinity (0 and 50 mM NaCl) and two levels of O<sub>3</sub> (filtered air and 50 mm<sup>3</sup> m<sup>-3</sup>). Exposure to 50 mm<sup>3</sup> m<sup>-3</sup> O<sub>3</sub> significantly decreased stomatal conductance (g<sub>s</sub>), net photosynthetic rate (P<sub>N</sub>), and chlorophyll (Chl) content by 20, 25, and 21 %, respectively. This reduction resulted in a change in assimilate allocation in favour of shoot growth leading to a decrease in root to shoot ratio and eventually to a decrease in relative growth rate (RGR) of both root and shoot. There was a very large reduction in yield parameters, especially in the number of ears/plant and 1 000-grain mass. Soil salinity significantly reduced P<sub>N</sub> and g<sub>s</sub> by 17 and 15 %, respectively, while Chl content was increased by 17 %. Root growth was decreased leading to an increase in root/shoot ratio. Yield parameters were decreased due to salt stress. There was antagonistic interaction between salinity (50 mM NaCl) and O<sub>3</sub> (50 mm<sup>3</sup> m<sup>-3</sup>) showing that salinity effectively protects against the adverse effects of O<sub>3</sub> by increasing g<sub>s</sub> during O<sub>3</sub> fumigation.

*Additional key words:* chlorophyll; ear; NaCl; O<sub>3</sub>; relative growth rate; shoot/root ratio; 1 000 grain mass.

## Introduction

Many studies deal with the impact of air pollutants on different plant species in terms of growth, yield (dose-response relationship), and physiology (Baker *et al.* 1986, Ashmore *et al.* 1988, Malik and Bell 1993, Hassan *et al.* 1994, 1995, 1999, Huang *et al.* 1994, Malik 2000). However, plant response to air pollutants such as O<sub>3</sub>, SO<sub>2</sub>, and NO<sub>2</sub> may be modified by coexisting environmental factors, such as nutrient availability (e.g. Cowling and Lockyer 1978), drought (e.g. Hassan *et al.* 1999), and soil salinity (e.g. Huang *et al.* 1994, Welfare *et al.* 1996). Influences of these interactive effects on the responses of plant growth, physiology, and biochemistry may result in a lack of consistent relationships between gaseous air pollutant doses and plant growth and yield (Bell 1982, 1993).

Soil salinity is a major constraint of agricultural production in many arid and semi-arid regions of the world. About 950 million hectares are affected to varying degrees by salinity (Stoner 1988). This problem is particularly severe in the Middle East, Northern Africa, and

Indian Sub-Continent, where agricultural land suffers from salinisation largely due to inadequately managed irrigation schemes.

Soil salinity and/or air pollution may cause physiological and biochemical changes leading to changes in growth and assimilate partitioning. Air pollution causes a reduction in photosynthetic capacity and biomass accumulation, and alters carbon allocation pattern in plants grown in areas with bad air quality (Bytnerowicz and Taylor 1983, Mooney and Winner 1987, Huang *et al.* 1994, Hassan *et al.* 1995, 1999). Increasing soil salinity imposes dramatic osmotic stress and specific ion toxicity (e.g. Na<sup>+</sup>, Cl<sup>-</sup>) upon growth and metabolic processes of non-halophytes causing excessive accumulation of salt ions (Na<sup>+</sup>, Cl<sup>-</sup>) in the leaves with subsequent increase in stomatal resistance, g<sub>s</sub> (Downton 1977, Huang *et al.* 1994, El-Shintinawy 2000).

In developing countries, salt-affected agricultural lands may also be exposed to other stress, such as air

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Fax: +0203 39 11 794, e-mail: i\_hassan82@hotmail.com

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pollution, and their number grows where the rapidly increasing population is paralleled with urbanisation, industrialisation, and increased number of motor vehicles (WHO/UNEP 1992). Furthermore, the climatic conditions in such countries are frequently favourable for the formation of high concentrations of  $O_3$  (Hassan 1999, El-Khatib 2003).

Studies on the interaction between  $SO_2$  and soil salinity have been done with many plant species (e.g. Qifu and Murray 1991, Huang and Murray 1993, Huang *et al.* 1994). These studies showed no protective or antagonistic effect of salt stress on vegetative growth of  $SO_2$ -fumigated plants. In contrast to  $SO_2$ , the combined effects of soil salinity and  $O_3$  on crops have not been examined thoroughly, although this is potentially important (Malik and

Bell 1993).

The mean 8-h (09:00–17:00 of Egyptian local time) concentrations of ambient  $O_3$  in Egypt ranged from 77 at a “suburban” site to 155  $mm^3 m^{-3}$  at an “urban site” in Northern Egypt (Hassan 1999). These concentrations exceeded the WHO guidelines of 70–100  $mm^3 m^{-3}$  (UNEP 1991, WHO/UNEP 1992), and may occur in other developing countries which also have soil salinisation problems (UNEP 1991, Malik and Bell 1993).

The objective of the present study was to investigate the responses of wheat plants in terms of physiology, growth, yield, and assimilate partitioning to the combined effect of  $O_3$  and/or mild  $NaCl$  salinity stress, in order to understand whether this combined effect could antagonistically interact and affect growth and yield parameters.

## Materials and methods

**Plants:** Grains of an Egyptian cultivar of wheat (*Triticum aestivum* L. cv. Giza 163) were washed with distilled water to remove excess fungicides and imbibed overnight in a beaker filled with tap water. Grains were sown in pots filled with washed sand in a glasshouse housed in Alexandria University on 5 April 2003; there were 15 seeds/pot and the total number of pots was 60. All pots were irrigated with a nutrient Hoagland solution (Hewitt and Smith 1975). After emergence of the flag leaf, 25 d after sowing (DAS) (*i.e.* on 1 May 2003) the seedlings were thinned to three plants per pot and transferred to open-top chambers (OTCs) of the design of Treshow and Stewart (1973). Each chamber was 1 m long, 2 m wide, and 2 m tall, consisting of an iron framework and covered with polyethylene plastic. Air was distributed into these chambers through two perforated semi-circular annuli attached to the wall of the chambers at heights of 50 and 100 cm above ground level.  $O_3$  fumigation and salinity treatment started 25 DAS.

**Experiment design:** Four OTCs were used in this experiment in a split plot design: two chambers received charcoal-filtered air (FA) and the other two received 50  $mm^3 m^{-3}$   $O_3$  (8 h  $d^{-1}$  between 09:00 and 17:00 for 75 d). Half of the pots (randomly chosen) inside each chamber received 50 mM  $NaCl$  every other day while control pots received the unamended nutrient solution. Both the control and salt solutions were adjusted to pH 7.2–7.8. There were 7 pots/treatment/chamber.

Ozone ( $O_3$ ) was generated from dry air using an  $O_3$  generator (*SANDORS 200*); the air was passed through a water trap to remove free radicals (*e.g.*  $N_2O_5$ ).  $O_3$  was monitored with a UV photometer (*DAISBI* model 1003-AH).

## Results

**Gas exchange and Chl:** The mean reductions in  $g_s$  and  $P_N$  of wheat plants after fumigation with 50  $mm^3(O_3) m^{-3}$

**Net photosynthetic rate ( $P_N$ ) and total  $CO_2$  g<sub>s</sub>** were measured on the youngest fully expanded leaf of the main stem. Gas exchange measurements were carried out fifteen times at 5 d intervals to cover all growth stages (from early tillering to anthesis) using a *LI-6200* portable IRGA (*LI-COR*, Lincoln, USA) between 10:00 and 14:00 h (Egyptian Local time). All plants were measured on each day.

**Chlorophyll** was extracted in acetone from all leaves in the main stems of three plants (*i.e.* one pot) and six plants per treatment (*i.e.* two pots), and determined according to Khan and Khan (1994).

**Growth analysis:** Five destructive harvests were carried out on 25 (early tillering), 45 (late tillering), 60 (early anthesis), 80 (mid-anthesis), and 100 (late anthesis) DAS. Two pots were harvested per treatment in each harvest. Plants were separated into main organs and dried at 100 °C for 5 d and relative growth rate (RGR) for shoot and root was calculated according to the formula:

$$RGR = \ln(DM_n) - \ln(DM_{n-1})/T$$

where  $DM_n$  = the average dry mass of plant organ at harvest (n),  $DM_{n-1}$  = the average dry mass of the plant organs at the preceding harvest, and T = time interval between the harvests [d].

**Data** were log-transformed prior to analysis to ensure that they were normally distributed. Then they were subjected to two-way ANOVA (using *STATGRAF* statistical package) based on chamber means, using  $O_3$  and  $NaCl$  as factors. PAR irradiance was used as a covariate in ANOVA of gas exchange measurements. There was no covariate used in ANOVA of RGR and Chl contents.

were 20 and 25 %, respectively (Fig. 1). Chl  $a$  content decreased following  $O_3$  fumigation by 21 %, while salt

stress increased it by 17 %. On the other hand, Chl *b* showed no significant response to O<sub>3</sub> and/or NaCl treatments ( $p>0.005$ ) (Table 1). Treatment with 50 mM NaCl reduced P<sub>N</sub> and g<sub>s</sub> by 17 and 15 %, respectively (Fig. 1).

Wheat plants subjected to salt stress had slightly reduced g<sub>s</sub> in response to O<sub>3</sub> in comparison with the non-

saline ones; moreover, there was a corresponding interaction with P<sub>N</sub> (Fig. 1). However, the interaction between salt stress and O<sub>3</sub> had no significant effect on Chl contents (Table 1).

**Assimilate partitioning and growth:** Both O<sub>3</sub> and NaCl significantly reduced plant dry mass. Shoot growth was more sensitive to NaCl than to O<sub>3</sub>, while root growth was more sensitive to O<sub>3</sub> than to salinity (Table 2).

The mean reduction in root dry mass (RDM) after fumigation with 50 mm<sup>3</sup>(O<sub>3</sub>) m<sup>-3</sup> was significantly higher (45 %) than in salt stressed plants (35 %). In contrast, the mean decrease in shoot growth (16 %) due to O<sub>3</sub> was lower than that in salt stressed plants (22 %) (Table 2).

RGR of root and shoot decreased in response to 50 mM NaCl and 50 mm<sup>3</sup>(O<sub>3</sub>) m<sup>-3</sup>, both singly and in combination (Table 3). The percent reduction in shoot RGR (average 47 %) was larger than that in root RGR (average 30 %) in response to 50 mM NaCl (Table 3). In contrast, the percent decrease in root RGR (average 44 %) was greater than in shoot RGR (average 27 %) due to fumigation with 50 mm<sup>3</sup>(O<sub>3</sub>) m<sup>-3</sup>. Shoot RGR was not affected by soil salinity at the early growth stage (45–60 DAS) but significantly ( $p\leq 0.001$ ) decreased during the other stages

Fig. 1. Effects of O<sub>3</sub> and salinity on (A) net photosynthetic rate, P<sub>N</sub> [μmol m<sup>-2</sup> s<sup>-1</sup>] and (B) stomatal conductance, g<sub>s</sub> [mmol m<sup>-2</sup> s<sup>-1</sup>]. Bars represent  $\pm 1$  SE.

Table 1. Changes in chlorophyll (Chl *a*, *b*, and Chl *a/b*) content [g kg<sup>-1</sup>] in response to different treatments. Means $\pm$ SD of 6 replications. FA = filtered air. Means in each column not followed by the same letter are significantly different from each other at  $p\leq 0.05$ .

Parameter	Treatment			
	FA $\times$ 0 mM NaCl	O <sub>3</sub> $\times$ 0 mM NaCl	FA $\times$ 50 mM NaCl	O <sub>3</sub> $\times$ 50 mM NaCl
Chl <i>a</i>	7.80 <sup>b</sup> ( $\pm 1.1$ )	6.20 <sup>a</sup> ( $\pm 0.9$ )	9.20 <sup>c</sup> ( $\pm 1.5$ )	7.70 <sup>b</sup> ( $\pm 0.8$ )
Chl <i>b</i>	5.70 <sup>a</sup> ( $\pm 0.9$ )	5.80 <sup>a</sup> ( $\pm 0.8$ )	5.60 <sup>a</sup> ( $\pm 0.9$ )	5.80 <sup>a</sup> ( $\pm 1.1$ )
Chl <i>a/b</i>	1.35 <sup>a</sup> ( $\pm 0.2$ )	1.11 <sup>a</sup> ( $\pm 0.3$ )	1.64 <sup>b</sup> ( $\pm 0.5$ )	1.33 <sup>a</sup> ( $\pm 0.3$ )

(60–80 and 80–100 DAS) (Table 3). The non-significant effect of NaCl treatment at the stage the 45–60 DAS may be due to early maturation, especially ear heading occurred earlier in saline plants than in the non-saline ones (values not shown). Moreover, root RGR decreased earlier than shoot RGR in response to O<sub>3</sub>. The interaction between O<sub>3</sub> and NaCl was less than additive (Table 3).

O<sub>3</sub> had a greater effect on the number of ears per plant and the number of grains/ear than NaCl salinity, as these parameters were reduced by 20 and 22 % due to O<sub>3</sub> and

by 14 and 20 % due to NaCl, respectively (Table 4). Moreover, the percent reduction in 1 000-grain mass due to O<sub>3</sub> (38 %) was greater than that due to salinity (30 %), and this accounted for the large effect on yield estimated by dry mass of grains per plant (51 and 38 % reduction due to O<sub>3</sub> and salinity, respectively).

The interaction between both stresses was less than additive for all parameters and this confirms the results of gas exchange measurements, namely that salinity has an antagonistic effect on the phytotoxic effect of O<sub>3</sub>.

## Discussion

O<sub>3</sub> concentration used in this experiment (50 mm<sup>3</sup> m<sup>-3</sup>) has been found in Egyptian ambient atmosphere (e.g. Nasralla 1990, WHO/UNEP 1992, Hassan 1999). It decreases yield and growth and alters physiological and biochemical processes of many agricultural crops including wheat (e.g. Kress *et al.* 1985, Fuhrer *et al.* 1989, 1990, 1992, Schenone *et al.* 1992, Wahid *et al.* 1995, Malik 2000). O<sub>3</sub> fumigation caused significant reductions

in P<sub>N</sub>, g<sub>s</sub>, and plant growth and yield in the present study.

The reduction in P<sub>N</sub> may be partially responsible for the reduction in growth and yield; the reduction in P<sub>N</sub> is highly correlated with the decrease in g<sub>s</sub>. This is consistent with the results of Huang *et al.* (1994) who exposed wheat plants to SO<sub>2</sub>. Fuhrer *et al.* (1992) and Malik (2000) reported that photosynthetic inhibition was largely related to O<sub>3</sub>-caused decrease in g<sub>s</sub>. However, prolonged

Table 2. Interactive effects of  $O_3$  [ $\text{mm}^3 \text{ m}^{-3}$ ] and  $\text{NaCl}$  [mM] on dry mass accumulation and root/shoot ratio (RSR). Means of 6 plants (3 plants/chamber). Legends as in Table 1.

Parameter	Days after sowing (DAS)					
		25	45	60	80	100
Shoot dry mass (SDM) [g]	FA $\times$ 0 mM NaCl	0.314 <sup>d</sup>	0.653 <sup>d</sup>	1.257 <sup>c</sup>	2.074 <sup>c</sup>	3.277 <sup>c</sup>
	$O_3$ $\times$ 0 mM NaCl	0.243 <sup>b</sup>	0.554 <sup>b</sup>	1.012 <sup>a</sup>	1.974 <sup>b</sup>	2.914 <sup>b</sup>
	FA $\times$ 50 mM NaCl	0.212 <sup>a</sup>	0.503 <sup>a</sup>	1.000 <sup>a</sup>	1.832 <sup>a</sup>	2.751 <sup>a</sup>
	$O_3$ $\times$ 50 mM NaCl	0.268 <sup>c</sup>	0.601 <sup>c</sup>	1.103 <sup>b</sup>	1.999 <sup>b</sup>	3.002 <sup>b</sup>
	LSD at $p = 0.05$	0.019	0.031	0.015	0.023	0.089
Root dry mass (RDM) [g]	FA $\times$ 0 mM NaCl	0.033 <sup>c</sup>	0.057 <sup>c</sup>	0.085 <sup>c</sup>	0.118 <sup>c</sup>	0.153 <sup>d</sup>
	$O_3$ $\times$ 0 mM NaCl	0.019 <sup>a</sup>	0.029 <sup>a</sup>	0.042 <sup>a</sup>	0.068 <sup>a</sup>	0.090 <sup>a</sup>
	FA $\times$ 50 mM NaCl	0.022 <sup>b</sup>	0.032 <sup>b</sup>	0.051 <sup>b</sup>	0.079 <sup>b</sup>	0.099 <sup>b</sup>
	$O_3$ $\times$ 50 mM NaCl	0.023 <sup>b</sup>	0.030 <sup>b</sup>	0.054 <sup>b</sup>	0.083 <sup>b</sup>	0.104 <sup>c</sup>
	LSD at $p = 0.05$	0.002	0.002	0.006	0.007	0.004
Root/shoot ratio (RSR)	FA $\times$ 0 mM NaCl	0.105 <sup>c</sup>	0.087 <sup>c</sup>	0.068 <sup>c</sup>	0.057 <sup>c</sup>	0.047 <sup>c</sup>
	$O_3$ $\times$ 0 mM NaCl	0.078 <sup>a</sup>	0.052 <sup>a</sup>	0.042 <sup>b</sup>	0.035 <sup>b</sup>	0.031 <sup>a</sup>
	FA $\times$ 50 mM NaCl	0.104 <sup>c</sup>	0.064 <sup>b</sup>	0.051 <sup>a</sup>	0.043 <sup>a</sup>	0.036 <sup>b</sup>
	$O_3$ $\times$ 50 mM NaCl	0.086 <sup>b</sup>	0.050 <sup>a</sup>	0.050 <sup>a</sup>	0.042 <sup>a</sup>	0.036 <sup>b</sup>
	LSD at $p = 0.05$	0.004	0.002	0.004	0.005	0.004

Table 3. Interactive effects of  $O_3$  and  $\text{NaCl}$  on relative growth rate (RGR) of shoot and root [ $\text{kg kg}^{-1} \text{ d}^{-1}$ ]. Legends as in Table 1.

	Treatment	45–25 DAS	60–45 DAS	80–60 DAS	100–80 DAS
Shoot RGR	FA/0 NaCl	1.983 <sup>c</sup> ( $\pm 0.115$ )	1.337 <sup>c</sup> ( $\pm 0.121$ )	0.647 <sup>c</sup> ( $\pm 0.215$ )	0.353 <sup>c</sup> ( $\pm 0.015$ )
	FA/50 NaCl	1.065 <sup>a</sup> ( $\pm 0.097$ )	1.055 <sup>a</sup> ( $\pm 0.096$ )	0.315 <sup>a</sup> ( $\pm 0.017$ )	0.149 <sup>a</sup> ( $\pm 0.007$ )
	$O_3$ /0 NaCl	1.331 <sup>b</sup> ( $\pm 0.115$ )	1.136 <sup>b</sup> ( $\pm 0.102$ )	0.402 <sup>b</sup> ( $\pm 0.063$ )	0.186 <sup>b</sup> ( $\pm 0.033$ )
	$O_3$ /50 NaCl	1.421 <sup>b</sup> ( $\pm 0.132$ )	1.205 <sup>b</sup> ( $\pm 0.087$ )	0.426 <sup>b</sup> ( $\pm 0.102$ )	0.208 <sup>b</sup> ( $\pm 0.076$ )
Root RGR	FA/0 NaCl	0.611 <sup>c</sup> ( $\pm 0.034$ )	0.296 <sup>c</sup> ( $\pm 0.085$ )	0.152 <sup>c</sup> ( $\pm 0.011$ )	0.085 <sup>c</sup> ( $\pm 0.005$ )
	FA/50 NaCl	0.410 <sup>a</sup> ( $\pm 0.028$ )	0.217 <sup>c</sup> ( $\pm 0.035$ )	0.103 <sup>c</sup> ( $\pm 0.008$ )	0.071 <sup>c</sup> ( $\pm 0.004$ )
	$O_3$ /0 NaCl	0.305 <sup>b</sup> ( $\pm 0.031$ )	0.178 <sup>a</sup> ( $\pm 0.015$ )	0.072 <sup>c</sup> ( $\pm 0.007$ )	0.043 <sup>c</sup> ( $\pm 0.003$ )
	$O_3$ /50 NaCl	0.457 <sup>a</sup> ( $\pm 0.032$ )	0.225 <sup>c</sup> ( $\pm 0.047$ )	0.091 <sup>c</sup> ( $\pm 0.010$ )	0.055 <sup>c</sup> ( $\pm 0.004$ )

Table 4. Effect of  $O_3$  and/or salinity on yield parameters. Legends as in Table 1; \*  $p \leq 0.05$ ; \*\*  $0.05 \leq p \leq 0.01$ ; \*\*\*  $p \leq 0.001$ .

Parameter	Treatment			
	FA/0 NaCl	$O_3$ /0 NaCl	FA $\times$ 50 NaCl	$O_3$ $\times$ 50 NaCl
No. of ears/plant	3.72	3.00 <sup>**</sup>	3.21 <sup>*</sup>	3.35 <sup>*</sup>
No. of grains/ear	41.40	32.10 <sup>***</sup>	33.24 <sup>**</sup>	34.51 <sup>**</sup>
1 000-grain mass [g]	51.60	32.07 <sup>***</sup>	36.14 <sup>***</sup>	36.89 <sup>***</sup>
Dry mass of grains/plant [g]	3.92	1.93 <sup>***</sup>	2.42 <sup>***</sup>	2.61 <sup>***</sup>

exposure to  $O_3$  causes more  $O_3$  to be absorbed into mesophyll cells and  $O_3$  becomes toxic to  $\text{CO}_2$  fixation enzymes. In the present study,  $O_3$  increased leaf senescence, which decreased the available photosynthetic area and carbon gain in combination with the decrease in  $P_N$  and the content of Chl  $a$ . This reduction in Chl  $a$  might cause the inhibition of  $P_N$  and eventually the reduction in growth and yield of the plants. This is in agreement with the results of Milthorpe and Moorby (1974) and Huang *et al.* (1994) who reported that the reduction in  $P_N$  and Chl content of flag leaves causes reductions in photosynthate production, ear growth, and grain yield as flag leaves are important suppliers of assimilates to ears.

The reduction in  $P_N$  can change assimilate partitioning between shoot and root (Huang *et al.* 1994, Davison and Barnes 1998). I found that  $O_3$  reduced the dry mass and RGR in roots earlier than in shoots, resulting in an initial increase in the root/shoot ratio. This may reduce the ability and capacity of roots to absorb nutrients from soil, ultimately affecting shoot growth adversely. The decrease in RGR indicates severe resource limitation or resource imbalance in plants (Coleman *et al.* 1989, Huang *et al.* 1994).

My results indicated that treating the plants with 50 mM NaCl had a smaller adverse impact on  $P_N$  and  $g_s$  than  $O_3$ . Munns *et al.* (1982) suggested that saccharide

use and not their production (from photosynthesis) limited the growth of plants grown in saline soils. On the other hand, Yeo *et al.* (1985) found that salinity reduced  $P_N$  in older leaves where sodium was accumulated. Nevertheless, salinity stress can cause osmotic stress and salt toxicity in plants leading to a reduction in growth and ultimately in yield (Greenway and Munns 1990). NaCl salinity significantly reduced plant growth and yield in the present study. Furthermore, El-Shintinawy (2000) reported a reduction in Hill reaction in salt stressed chloroplasts isolated from wheat plants (19 and 40 % inhibition in tolerant and sensitive cultivar, respectively).

On the contrary, salinity had a smaller effect on root growth than on shoot growth, leading to an initial reduction in root/shoot ratio. Owing to increased leaf senescence and decrease in photosynthetic area caused by salt stress, saccharide supply for root growth would be limited and net carbon gain by plant would be reduced (Munns and Termaat 1986, Huang *et al.* 1994). I found that by the expansion of flag leaf, the most actively growing regions were stem internodes and ears, with a diminution of root growth which caused an increase in shoot to root ratio at 80 DAS. Moreover, yield potential (number of spikelets, number of grains per spike, and 1 000-grain mass) was strongly affected by salinity. This is in agreement with the results of Malik and Bell (1993) and Grieve *et al.* (1992), who reported that treating wheat plants with NaCl significantly reduced the yield potential of wheat.

My results showed that the interaction between salinity and O<sub>3</sub> was less than additive (*i.e.* antagonistic effect). Malik and Bell (1993) reported protective effects of salinity on the number of spikelets and number of grains per spike in wheat plants exposed to 60 or 90 mm<sup>3</sup>(O<sub>3</sub>) m<sup>-3</sup> (8 h d<sup>-1</sup> for 12 d). They concluded that salinity diminished  $g_s$  and O<sub>3</sub> diffusion into leaves. Ogata and Maas (1973) observed similar changes in salt-tolerant garden beet (*Beta vulgaris* L.) when they exposed plants to 200 mm<sup>3</sup>(O<sub>3</sub>) m<sup>-3</sup> for 3 h d<sup>-1</sup>. Moreover, Bytnerowicz and Taylor (1983) showed that salinity alleviated leaf injury by O<sub>3</sub> due to reduction in  $g_s$  but the interaction between them on growth was additive. Similar combined effects were reported with SO<sub>2</sub> and NaCl in wheat and soybean plants by Huang *et al.* (1994) and Qifu and Murray (1991). My results contradicted the findings of Hoffman

*et al.* (1973) that the effects of O<sub>3</sub> and salinity on growth and yield of pinto bean (*Phaseolus vulgaris* L.) were additive.

It is difficult to separate the effect of O<sub>3</sub> on growth from salinity stress as the latter alone can produce severe osmotic stress and growth reductions. Nevertheless, the mechanism by which salinity (osmotic stress) increases plant tolerance to O<sub>3</sub> is speculative.

The antagonistic interaction between O<sub>3</sub> and salinity may be due to the effect of NaCl on O<sub>3</sub> uptake and toxicity as well as the effect of O<sub>3</sub> on salt uptake and accumulation. Salinity reduces SO<sub>2</sub> uptake and sulphur concentrations in leaves due to increased  $g_s$  (*e.g.* Qifu and Murray 1991, Huang and Murray 1993, Huang *et al.* 1994). The significant reduction in  $g_s$  in the present study could be responsible for this antagonistic effect, as this would cause a decrease in  $P_N$  and consequently saccharide production, which together with the toxic effect of O<sub>3</sub> might severely reduce growth and yield. However, the final growth response to both stresses may depend on the balance between benefits (*e.g.* the reduction in O<sub>3</sub> absorption and salt uptake in leaves) and detriments (*e.g.* the reduction in saccharide production and increased maintenance energy cost). Any factor, including salinity that increases water stress in the plant, can increase both stomatal and mesophyll resistances to gas exchange and presumably reduce O<sub>3</sub> flux into the leaves (Mansfield 1973, Kingsbury *et al.* 1984, Welfare *et al.* 1996).

However, this antagonistic interaction on growth may have resulted from an impact of O<sub>3</sub> on ion (Na<sup>+</sup> and Cl<sup>-</sup>) uptake and concentration in the shoot, due to O<sub>3</sub> impact on  $g_s$ . The negative impact of O<sub>3</sub> on shoot mass of plants grown in saline conditions may in turn have a growth dilution effect on salt concentration (*e.g.* Na<sup>+</sup> and Cl<sup>-</sup>) (Huang *et al.* 1994).

My results demonstrated that salinity might provide some protection against the toxic effects of O<sub>3</sub>. However, this is likely to be offset by the detrimental impact on yield by salinity alone (Malik and Bell 1993).

In conclusion, the benefit from the antagonistic interaction between 50 mm<sup>3</sup>(O<sub>3</sub>) m<sup>-3</sup> and 50 mM NaCl on plant physiology, growth, and yield should be taken into account for agricultural purposes not only in Egypt but also in other developing countries and parts of the world with similar conditions.

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