

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

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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⁻¹ for up to 75 d to a factorial combination of two levels of salinity (0 and 50 mM NaCl) and two levels of O₃ (filtered air and 50 mm³ m⁻³). Exposure to 50 mm³ m⁻³ O₃ significantly decreased stomatal conductance (g_s), net photosynthetic rate (P_N), 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_N and g_s 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 O₃ (50 mm³ m⁻³) showing that salinity effectively protects against the adverse effects of O₃ by increasing g_s during O₃ fumigation.

Additional key words: chlorophyll; ear; NaCl; O₃; 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 O₃, SO₂, and NO₂ 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⁺, Cl⁻) upon growth and metabolic processes of non-halophytes causing excessive accumulation of salt ions (Na⁺, Cl⁻) in the leaves with subsequent increase in stomatal resistance, g_s (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

Received 29 September 2003, accepted 15 January 2004.

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Acknowledgements: I thank Prof. H.-J. Weigel and Dr. J. Bender of the Institute of Agroecology (FAL), Braunschweig, Germany for lending the O₃ generator, and Prof. D.A. Grantz, Director of Kearney Agricultural Centre at California University, USA, for lending the LI-COR. I also express my deepest thanks to Prof. S. Barakat, Professor of Plant Physiology at Alexandria University, for revising the manuscript and his valuable comments.

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 $155 \text{ mm}^3 \text{ m}^{-3}$ at an “urban site” in Northern Egypt (Hassan 1999). These concentrations exceeded the WHO guidelines of $70\text{--}100 \text{ mm}^3 \text{ m}^{-3}$ (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 $50 \text{ mm}^3 \text{ m}^{-3} O_3$ (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 $50 \text{ mm}^3(O_3) \text{ m}^{-3}$

Net photosynthetic rate (P_N) and total CO_2 g_s 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:

$$\text{RGR} = \ln(\text{DM}_n) - \ln(\text{DM}_{n-1})/T$$

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 O₃ and/or NaCl treatments ($p > 0.005$) (Table 1). Treatment with 50 mM NaCl reduced P_N and g_s by 17 and 15 %, respectively (Fig. 1).

Wheat plants subjected to salt stress had slightly reduced g_s in response to O₃ in comparison with the non-

saline ones; moreover, there was a corresponding interaction with P_N (Fig. 1). However, the interaction between salt stress and O₃ had no significant effect on Chl contents (Table 1).

Assimilate partitioning and growth: Both O₃ and NaCl significantly reduced plant dry mass. Shoot growth was more sensitive to NaCl than to O₃, while root growth was more sensitive to O₃ than to salinity (Table 2).

The mean reduction in root dry mass (RDM) after fumigation with 50 mm³(O₃) m⁻³ was significantly higher (45 %) than in salt stressed plants (35 %). In contrast, the mean decrease in shoot growth (16 %) due to O₃ 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 mm³(O₃) m⁻³, 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 mm³(O₃) m⁻³. 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

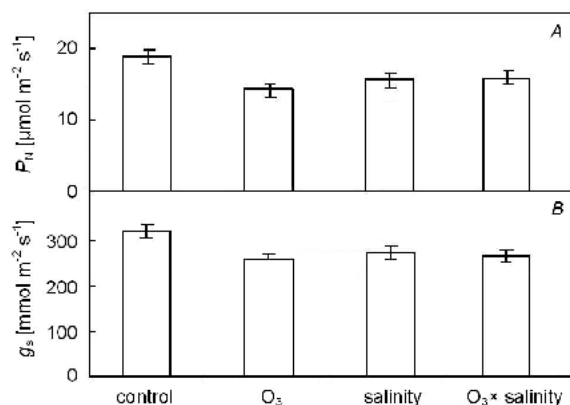


Fig. 1. Effects of O₃ and salinity on (A) net photosynthetic rate, P_N [$\mu\text{mol m}^{-2} \text{s}^{-1}$] and (B) stomatal conductance, g_s [$\text{mmol m}^{-2} \text{s}^{-1}$]. Bars represent ± 1 SE.

Table 1. Changes in chlorophyll (Chl *a*, *b*, and Chl *a/b*) content [g kg^{-1}] 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×0 mM NaCl	O ₃ ×0 mM NaCl	FA×50 mM NaCl	O ₃ ×50 mM NaCl
Chl <i>a</i>	7.80 ^b (± 1.1)	6.20 ^a (± 0.9)	9.20 ^c (± 1.5)	7.70 ^b (± 0.8)
Chl <i>b</i>	5.70 ^a (± 0.9)	5.80 ^a (± 0.8)	5.60 ^a (± 0.9)	5.80 ^a (± 1.1)
Chl <i>a/b</i>	1.35 ^a (± 0.2)	1.11 ^a (± 0.3)	1.64 ^b (± 0.5)	1.33 ^a (± 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 O₃. The interaction between O₃ and NaCl was less than additive (Table 3).

O₃ 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 O₃ and

by 14 and 20 % due to NaCl, respectively (Table 4). Moreover, the percent reduction in 1 000-grain mass due to O₃ (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 O₃ 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 O₃.

Discussion

O₃ concentration used in this experiment (50 mm³ m⁻³) 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). O₃ fumigation caused significant reductions

in P_N , g_s , and plant growth and yield in the present study.

The reduction in P_N may be partially responsible for the reduction in growth and yield; the reduction in P_N is highly correlated with the decrease in g_s . This is consistent with the results of Huang *et al.* (1994) who exposed wheat plants to SO₂. Fuhrer *et al.* (1992) and Malik (2000) reported that photosynthetic inhibition was largely related to O₃-caused decrease in g_s . However, prolonged

Table 2. Interactive effects of O₃ [mm³ m⁻³] and 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×0 mM NaCl	0.314 ^d	0.653 ^d	1.257 ^c	2.074 ^c	3.277 ^c
	O ₃ ×0 mM NaCl	0.243 ^b	0.554 ^b	1.012 ^a	1.974 ^b	2.914 ^b
	FA×50 mM NaCl	0.212 ^a	0.503 ^a	1.000 ^a	1.832 ^a	2.751 ^a
	O ₃ ×50 mM NaCl	0.268 ^c	0.601 ^c	1.103 ^b	1.999 ^b	3.002 ^b
	LSD at <i>p</i> = 0.05	0.019	0.031	0.015	0.023	0.089
Root dry mass (RDM) [g]	FA×0 mM NaCl	0.033 ^c	0.057 ^c	0.085 ^c	0.118 ^c	0.153 ^d
	O ₃ ×0 mM NaCl	0.019 ^a	0.029 ^a	0.042 ^a	0.068 ^a	0.090 ^a
	FA×50 mM NaCl	0.022 ^b	0.032 ^b	0.051 ^b	0.079 ^b	0.099 ^b
	O ₃ ×50 mM NaCl	0.023 ^b	0.030 ^b	0.054 ^b	0.083 ^b	0.104 ^c
	LSD at <i>p</i> = 0.05	0.002	0.002	0.006	0.007	0.004
Root/shoot ratio (RSR)	FA×0 mM NaCl	0.105 ^c	0.087 ^c	0.068 ^c	0.057 ^c	0.047 ^c
	O ₃ ×0 mM NaCl	0.078 ^a	0.052 ^a	0.042 ^b	0.035 ^b	0.031 ^a
	FA×50 mM NaCl	0.104 ^c	0.064 ^b	0.051 ^a	0.043 ^a	0.036 ^b
	O ₃ ×50 mM NaCl	0.086 ^b	0.050 ^a	0.050 ^a	0.042 ^a	0.036 ^b
	LSD at <i>p</i> = 0.05	0.004	0.002	0.004	0.005	0.004

Table 3. Interactive effects of O₃ and NaCl on relative growth rate (RGR) of shoot and root [kg kg⁻¹ 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 ^c (± 0.115)	1.337 ^c (± 0.121)	0.647 ^c (± 0.215)	0.353 ^c (± 0.015)
	FA/50 NaCl	1.065 ^a (± 0.097)	1.055 ^a (± 0.096)	0.315 ^a (± 0.017)	0.149 ^a (± 0.007)
	O ₃ /0 NaCl	1.331 ^b (± 0.115)	1.136 ^b (± 0.102)	0.402 ^b (± 0.063)	0.186 ^b (± 0.033)
	O ₃ /50 NaCl	1.421 ^b (± 0.132)	1.205 ^b (± 0.087)	0.426 ^b (± 0.102)	0.208 ^b (± 0.076)
Root RGR	FA/0 NaCl	0.611 ^c (± 0.034)	0.296 ^c (± 0.085)	0.152 ^c (± 0.011)	0.085 ^c (± 0.005)
	FA/50 NaCl	0.410 ^a (± 0.028)	0.217 ^c (± 0.035)	0.103 ^c (± 0.008)	0.071 ^c (± 0.004)
	O ₃ /0 NaCl	0.305 ^b (± 0.031)	0.178 ^a (± 0.015)	0.072 ^c (± 0.007)	0.043 ^c (± 0.003)
	O ₃ /50 NaCl	0.457 ^a (± 0.032)	0.225 ^c (± 0.047)	0.091 ^c (± 0.010)	0.055 ^c (± 0.004)

Table 4. Effect of O₃ and/or salinity on yield parameters. Legends as in Table 1; * *p* ≤ 0.05; ** 0.05 ≥ *p* ≤ 0.01; *** *p* ≤ 0.001.

Parameter	Treatment			
	FA/0 NaCl	O ₃ /0 NaCl	FA×50 NaCl	O ₃ ×50 NaCl
No. of ears/plant	3.72	3.00 ^{**}	3.21 [*]	3.35 [*]
No. of grains/ear	41.40	32.10 ^{***}	33.24 ^{**}	34.51 ^{**}
1 000-grain mass [g]	51.60	32.07 ^{***}	36.14 ^{***}	36.89 ^{***}
Dry mass of grains/plant [g]	3.92	1.93 ^{***}	2.42 ^{***}	2.61 ^{***}

exposure to O₃ causes more O₃ to be absorbed into mesophyll cells and O₃ becomes toxic to CO₂ fixation enzymes. In the present study, O₃ 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 O₃ 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 O₃. 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_3 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 $mm^3(O_3) m^{-3}$ (8 h d^{-1} for 12 d). They concluded that salinity diminished g_s and O_3 diffusion into leaves. Ogata and Maas (1973) observed similar changes in salt-tolerant garden beet (*Beta vulgaris* L.) when they exposed plants to 200 $mm^3(O_3) m^{-3}$ for 3 h d^{-1} . Moreover, Bytnerowicz and Taylor (1983) showed that salinity alleviated leaf injury by O_3 due to reduction in g_s but the interaction between them on growth was additive. Similar combined effects were reported with SO_2 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_3 and salinity on growth and yield of pinto bean (*Phaseolus vulgaris* L.) were additive.

It is difficult to separate the effect of O_3 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_3 is speculative.

The antagonistic interaction between O_3 and salinity may be due to the effect of NaCl on O_3 uptake and toxicity as well as the effect of O_3 on salt uptake and accumulation. Salinity reduces SO_2 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_3 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_3 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_3 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_3 on ion (Na^+ and Cl^-) uptake and concentration in the shoot, due to O_3 impact on g_s . The negative impact of O_3 on shoot mass of plants grown in saline conditions may in turn have a growth dilution effect on salt concentration (*e.g.* Na^+ and Cl^-) (Huang *et al.* 1994).

My results demonstrated that salinity might provide some protection against the toxic effects of O_3 . 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 $mm^3(O_3) m^{-3}$ 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.

References

- Ashmore, M.R., Bell, J.N.B., Mimmack, A.: Crop growth along a gradient of ambient air pollution. – *Environ. Pollut. A* **53**: 99-121, 1988.
- Baker, C.K., Colls, J.J., Fullwood, A.E., Seaton, G.C.R.: Depressions of growth and yield in winter barley exposed to SO_2 in the field. – *New Phytol.* **104**: 233-241, 1986.
- Bell, J.N.B.: SO_2 and the growth of grasses. – In: Unsworth, M.H., Ormrod, D.A. (ed.): *Effects of Gaseous Air Pollution in Agriculture and Horticulture*. Pp. 225-247. Butterworth, London 1982.
- Bell, J.N.B.: Biotic and abiotic interactions with air pollutants. – In: Jäger, H.J., Unsworth, W., De Temmerman, L., Mathy, P. (ed.): *Effects of Air Pollution on Agricultural Crops in Europe*. Air Pollution Res. Rep. **46**: 383-408, 1993.
- Bytnerowicz, A., Taylor, O.C.: Influence of ozone, sulphur dioxide, and salinity on leaf injury, stomatal resistance, growth, and chemical composition of bean plants. – *J. environ. Qual.* **12**: 397-405, 1983.
- Coleman, J.S., Mooney, H.A., Gorham, J.N.: Effects of multiple stresses on leaf injury, stomatal resistance, growth and chemi-

- cal composition of bean plants. – J. environ. Qual. **81**: 115-119, 1989.
- Cowling, D.W., Lockyer, D.R.: The effect of SO₂ on *Lolium perenne* L. grown at different levels of sulphur and nutrition. – J. exp. Bot. **29**: 257-265, 1978.
- Davison, A.W., Barnes, J.D.: Effects of O₃ on wild plants. – New Phytol. **139**: 135-151, 1998.
- Downton, W.J.S.: Photosynthesis in salt-stressed grapevines. – Aust. J. Plant Physiol. **4**: 183-192, 1977.
- El-Khatib, A.A.: The response of some common Egyptian plants to O₃ and their use as bioindicators. – Environ. Pollut. **124**: 419-428, 2003.
- El-Shintinawy, F.: Photosynthesis in two wheat cultivars differing in salt susceptibility. – Photosynthetica **38**: 615-620, 2000.
- Fuhrer, J., Egger, A., Lehnher, B., Grandjean, A., Tschannen, W.: Effects of O₃ on the yield of spring wheat (*Triticum aestivum* L. cv. Albis) grown in open-top field chambers. – Environ. Pollut. **60**: 273-289, 1989.
- Fuhrer, J., Egger, A., Lehnher, B., Moeri, P.B., Tschannen, W., Shariat-Madari, H.: Effects of O₃ on the grain composition of spring wheat grown in open-top field chambers. – Environ. Pollut. **65**: 181-192, 1990.
- Fuhrer, J., Grandjean, A., Tschannen, W., Shariat-Madari, H.: The response of spring wheat (*Triticum aestivum* L.) to O₃ at higher elevations. II. Changes in yield, yield composition and grain quality in response to O₃ flux. – New Phytol. **121**: 211-219, 1992.
- Greenway, H., Munns, R.: Mechanisms of salt tolerance in non-halophytes. – Annu. Rev. Plant Physiol. **31**: 49-150, 1990.
- Grieve, C.M., Lesch, S., Francois, L.E., Maas, V.A.: Analysis of main spike yield components in salt-stressed wheat. – Crop Sci. **32**: 697-703, 1992.
- Hassan, I.A.: Air pollution in Alexandria region-Egypt. I: An investigation of air quality. – Int. J. environ. Educ. Inform. **18**: 67-78, 1999.
- Hassan, I.A., Ashmore, M.R., Bell, J.N.B.: Effects of O₃ on the stomatal behaviour of Egyptian varieties of radish (*Raphanus sativus* L. cv. Baladey) and turnip (*Brassica rapa* L. cv. Sultani). – New Phytol. **128**: 243-249, 1994.
- Hassan, I.A., Ashmore, M.R., Bell, J.N.B.: Effects of ozone on radish and turnip under Egyptian field conditions. – Environ. Pollut. **89**: 107-114, 1995.
- Hassan, I.A., Bender, J., Weigel, J.H.: Effects of ozone and drought stress on growth, yield and physiology of tomatoes (*Lycopersicon esculentum* Mill. cv. Baladey). – Gartenbauwissenschaft **64**: 152-157, 1999.
- Hewitt, E.J., Smith, T.A. (ed.): Plant Mineral Nutrition. – English Universities Press, London 1975.
- Hoffman, G.J., Maas, E.V., Rawlins, S.L.: Salinity O₃ interactive effects on yield and water relations of pinto bean. – J. environ. Qual. **2**: 148-152, 1973.
- Huang, L., Murray, F.: Effects of sulphur dioxide fumigation on growth and sulphur accumulation in wheat [*Triticum aestivum* L. cv. Wilgoyne (Ciano/Gallo)] under salinity stress. – Agr. Ecosyst. Environ. **43**: 285-300, 1993.
- Huang, L., Murray, F., Yang, X.: Interaction between mild NaCl salinity and sub-lethal SO₂ pollution on wheat *Triticum aestivum* cultivar "Wilgoyne" (Ciano/Gallo). I. Responses of stomatal conductance, photosynthesis, growth and assimilate partitioning. – Agr. Ecosyst. Environ. **48**: 163-178, 1994.
- Kingsbury, R.W., Epstein, E., Percy, R.W.: Physiological responses to salinity in selected lines of wheat. – Plant Physiol. **74**: 417-423, 1984.
- Khan, M.R., Khan, M.W.: Single and interactive effects of O₃ and SO₂ on tomato. – Environ. exp. Bot. **34**: 461-469, 1994.
- Kress, L.W., Miller, J.E., Smith, H.J.: Impact of O₃ on winter wheat yield. – Environ. exp. Bot. **25**: 211-228, 1985.
- Malik, I.: Effects of Ozone and Salinity on Pakistani Wheat (*Triticum aestivum* L. cvs. Pak-81 and Rowal-87). – Ph.D. Thesis. Imperial College of Science, Technology & Medicine, London University, London 2000.
- Malik, I., Bell, J.N.B.: The effects of salinity and O₃ on wheat. – In: Jäger, H.J., Unsworth, M., De Temmerman, L., Mathy, P. (ed.): Effects of Air Pollution on Agricultural Crops in Europe. Air Pollution Res. Rep. **46**: 575-578, 1993.
- Mansfield, T.A.: The role of stomata in determining the response of plants to air pollutants. – Curr. Advan. Plant Sci. **2**(4): 11-20, 1973.
- Milthorpe, F.L., Moorby, J. (ed.): An Introduction to Crop Physiology. – Cambridge Univ. Press, Cambridge 1974.
- Mooney, H.A., Winner, W.E.: Carbon gain, allocation and growth as affected by atmospheric pollutants. – In: Schulte-Hostede, S., Darrall, N.M., Blank, L.W., Wellburn, A.R. (ed.): Air Pollution and Plant Metabolism. Pp. 272-287. Elsevier, London 1987.
- Munns, R., Grenway, H., Delane, R., Gibbs, J.: Ion concentration and carbohydrate status of the elongating leaf tissue of *Hordeum vulgare* growing at high external NaCl. II. Cause of the growth reduction. – J. exp. Bot. **33**: 574-583, 1982.
- Munns, R., Termaat, A.: Whole plant response to salinity. – Aust. J. Plant Physiol. **13**: 143-160, 1986.
- Nasralla, M.M.: Air Pollution in Cairo Metropolitan Area. – National Research Centre, Cairo 1990.
- Ogata, G., Maas, E.V.: Interactive effects of salinity and O₃ on growth and yield of garden beet. – J. environ. Qual. **2**: 518-520, 1973.
- Qifu, M., Murray, F.: Soil salinity modifies SO₂ sensitivity in soybean. – New Phytol. **119**: 269-274, 1991.
- Schenone, G., Botteschi, G., Fumagalli, I., Mignanego, L., Montinaro, F.: Physiological effects of ambient air pollution in OTCs on winter wheat. – In: Jäger, H.J., Unsworth, M., De Temmerman, L., Mathy, P. (ed.): Effects of Air Pollution on Agricultural Crops in Europe. Air Pollution Res. Rep. **46**: 597-600, 1992.
- Stoner, R.: Engineering a solution to the problem salt-laden soils. – New Scientist **3**: 42, 1988.
- Treshow, M., Stewart, D.: O₃ sensitivity of plants in natural communities. – Biol. Conserv. **5**: 209-214, 1973.
- UNEP: United Nations Environment Programme. Data Report. 3rd Ed. – Blackwell, Oxford 1991.
- Wahid, A.R., Maggs, R., Shamsi, R., Ashmore, M.R., Bell, J.N.B.: Air pollution and crop yield in Punjab, Pakistan. I: Effects on wheat. – Environ. Pollut. **88**: 147-154, 1995.
- Welfare, K., Flowers, T.J., Taylor, G., Yeo, A.R.: Additive and antagonistic effects of O₃ and salinity on the growth, ion contents and gas exchange of five varieties of rice (*Oryza sativa* L.). – Environ. Pollut. **92**: 257-266, 1996.
- WHO/UNEP: Urban Air Pollution in Megacities of the World. – Blackwell, Oxford 1992.
- Yeo, A.R., Capron, S.J.M., Flowers, T.J.: The effect of salinity upon photosynthesis in rice (*Oryza sativa* L.): gas exchange by individual leaves in relation to their salt content. – J. exp. Bot. **36**: 1240-1248, 1985.