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# Effects of Ozone and Soil Salinity, Singly and in Combination, on Growth, Yield and Leaf Gas Exchange Rates of Two Bangladeshi Wheat Cultivars

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**ABSTRACT**

In Bangladesh, increases in the tropospheric ozone ($O_3$) concentration and in soil salinization may lead to crop damage. To clarify the effects of $O_3$ and/or soil salinity on Bangladeshi wheat cultivars, BAW1059 (salt-tolerant) and Shatabdi (salt-sensitive) were exposed to 70-day treatments with $O_3$ (charcoal-filtered air (CF), $1.0\times O_3$, and $1.5\times O_3$) and different levels of soil salinity (0, 4, and 8 dS $m^{-1}$). In both cultivars, the whole-plant dry mass and grain yield were significantly reduced by exposure to $O_3$. Increased soil salinity caused significant reductions in whole-plant growth and yield in Shatabdi, but the reductions were negligible in BAW1059. No significant interactions between $O_3$ and salinity were detected for growth, yield, and leaf gas exchange parameters in both cultivars. We concluded that the effects of $O_3$ are not ameliorated by soil salinity in two Bangladeshi wheat cultivars, regardless of their salinity tolerance.

**Key words:** Ozone, Salinity, *Triticum aestivum* L., Yield, Leaf gas exchange rates

## 1. INTRODUCTION

The tropospheric ozone ($O_3$) concentration is rising because of increasing anthropogenic emissions of several $O_3$-forming precursors (Ainsworth, 2008; Kostiainen *et al*., 2006). Ozone is produced in the troposphere as a secondary air pollutant via photochemical reactions between nitrogen oxides ($NO_x$) and volatile organic compounds in the presence of sunlight (Ashmore, 2005). According to the Fourth Assessment Report (AR4) of Intergovernmental Panel on Climate Change (IPCC), $O_3$ concentration could rise by 20%-25% between 2015 and 2050, and further increase by 40%-60% by 2100, if the current trends in precursor emissions continue (IPCC, 2007). Worryingly for the South Asian region, the projections of future global $O_3$ trends show that atmospheric $O_3$ concentrations will increase rapidly over the next 20 to 30 years, with the greatest increase in surface $O_3$ in South Asia (Dentener *et al*., 2006). In India, ozone levels have risen from a preindustrial atmospheric $O_3$ concentration of 10 nL $L^{-1}$ (ppb) to 50-60 ppb at present (Van Dingenen *et al*., 2009). If emissions of $O_3$ precursors in the northern hemisphere do not decrease, the $O_3$ concentration in India is predicted to increase by 5-11 ppb, depending on the season, by 2030 (Van Dingenen *et al*., 2009). Peak $O_3$ concentrations have exceeded 100 ppb during the summer season in the Indo-Gangetic region (Mishra *et al*., 2013; Tiwari *et al*., 2010).

Ozone has detrimental effects on the growth and productivity of crops (Tiwari *et al*., 2010). After entering the leaves through stomata, $O_3$ induces the formation of highly reactive oxygen species (ROS) and free radicals (Foyer and Noctor, 2005), which interact with cellular components to reduce the net photosynthetic rate (Dermody *et al*., 2006; Skotnica *et al*., 2005; Morgan *et al*., 2003) and stomatal conductance (Gerosa *et al*., 2014; Calatayud *et al*., 2003). Relatively high concentrations of $O_3$ cause visible foliar injury, accelerate leaf senescence (Massman *et al*., 2000), and affect biochemical and physiological processes (Rai *et al*., 2011; Betzelberger *et al*., 2010; Sarkar *et al*., 2010). Ozone exposure adversely affects whole-plant growth (Akhtar *et al*., 2010a; Biswas *et al*., 2008), nutrient uptake, and translocation of assimilates (Tiwari *et al*., 2010), leading to inferior quality and reduced yield of many crops (Sarkar and Agrawal, 2010; Fuhrer, 2009). Crop yield losses due to $O_3$ have been estimated by 5%-35% in agriculturally important locations across South Asia (Emberson and Büker, 2008). However, limited information is available on the effects of $O_3$ on crops cultivated in Bangladesh (Saitanis *et al*., 2014; Akhtar *et al*., 2010a, b).

Soil salinity is a major environmental stress that drastically affects crop productivity worldwide (Zhu, 2001). Out of 2.85 million hectares in the coastal area of Bangladesh, approximately 1 million ha (30% of the cultivable area) is affected by salinity to some extent, and the salt-affected area has increased by approximately 26.7% over the last 36 years (Ahsan and Sattar, 2010). Salt-stress inhibits plant growth in four major ways; salt-induced osmotic stress, specific ion toxicity, oxidative stress, and hormonal imbalance (Ashraf, 2009). Salt-stress decreases relative water content, chlorophyll content, membrane stability, ascorbic acid content, and the activities of several antioxidant enzymes in the leaves of crops at the seedling stage (Ozturk *et al*., 2012; Hameed *et al*., 2008; Shim *et al*., 2003) and at the heading and grain-filling stages (Bai *et al*., 2013; Burcu *et al*., 2009).

In many parts of the world, tropospheric $O_3$ and soil salinity are limiting factors in agriculture (Gerosa *et al*., 2014; FAO, 2007; Fuhrer and Booker, 2003; Qadir *et al*., 2000). There is a possibility that the combined effects of $O_3$ and soil salinity will adversely affect crops cultivated in South Asian countries such as Bangladesh (Titumir and Basak, 2012; Welfare *et al*., 2002, 1996). However, very limited information is available on the combined effects of $O_3$ and salinity on crops (Gerosa *et al*., 2014; Zheng *et al*., 2012; Welfare *et al*., 2002, 1996). Welfare *et al*. (2002, 1996) reported additive effects of $O_3$ and salinity on leaf gas exchange rates of rice and chickpea. Stomatal closure is one of the plant responses that limits damage under stress conditions (Maggio *et al*., 2009; Ma *et al*., 2006; Warren and Dreyer, 2006). Therefore, salinity-induced stomatal closure might reduce stomatal $O_3$ flux into the intercellular spaces and protect crops from $O_3$ damage.

In Bangladesh, wheat has become the second most important cereal crop after rice (Akhtar *et al*., 2010a). The total area under wheat cultivation in Bangladesh during 2011-2012 was estimated to be 400,000 hectares, and 1.1 million metric tons of wheat was produced (Anonymous, 2012). Wheat has been shown to be the most $O_3$-sensitive crop (Mills *et al*., 2007), and Asian wheat cultivars are more sensitive to $O_3$ than are other tropical and temperate cultivars (Akhtar *et al*., 2010a; Emberson *et al*., 2009; Van Dingenen *et al*., 2009; Rai *et al*., 2007). However, little is known about the responses of salt-tolerant and salt-sensitive Bangladeshi wheat cultivars to $O_3$ under salt-stress. The objective of the present study was to clarify the effects of $O_3$ and soil salinity, singly and in combination, on the growth, yield, and leaf gas exchange rates of two Bangladeshi wheat cultivars with different salt sensitivities.

## 2. MATERIALS AND METHODS

### 2. 1 Gas Exposure Chambers

Nine gas exposure chambers located in the Field Museum Tamakyuryo, Tokyo University of Agriculture and Technology (Hachioji, Tokyo), were used in the present study. The latitude, longitude and above sea level at the experimental site are 35°38′ N, 139°22′ E and 144.1 m, respectively. Ambient air was introduced into the chambers at a flow rate of 1.03 $m^3$ $s^{-1}$ after it had passed through an activated charcoal filter in the fan box to remove ambient $O_3$. In the chambers assigned to the $O_3$-treatments, $O_3$ was added to the charcoal-filtered air introduced into the chambers. The ambient $O_3$ concentration was used as the standard concentration for controlling of $O_3$ concentration in the $O_3$-exposure chambers. The concentrations of $O_3$ in each chamber and in ambient air were independently and continuously monitored at 30-min and 10-min intervals, respectively, using a UV absorption $O_3$ analyzer (Model-1210; Dylec Inc., Ibaraki, Japan). Details of the construction of the gas exposure chambers and the $O_3$-exposure system are described in Kinose *et al*. (2014). Mean removal efficiency, mean concentration, and accumulated $O_3$ exposure over a threshold of 40 ppb (AOT40) during the $O_3$-exposure period were calculated based on $O_3$ concentration in the chambers and ambient air. The photosynthetic photon flux density (PPFD) under ambient conditions was measured at 1-min intervals using a quantum sensor (LI-190SA; Li-Cor Inc., Lincoln, NE, USA). The mean light transmissibility of the chambers during the gas treatment period was approximately 73%. In three of the nine chambers, air temperature and relative air humidity were continuously measured at 10-min intervals using a TR-72U Thermo Recorder (T&D Corporation, Nagano, Japan).

### 2. 2 Plant Materials

Two Bangladeshi cultivars of spring wheat (*Triticum aestivum* L.), BAW1059 and Shatabdi, were used as plant materials. Seeds of the two wheat cultivars were obtained from the Bangladesh Agricultural Research

Institute (BARI). BAW1059 is salt-tolerant and Shatabdi is salt-sensitive (Wheat Atlas CYMMYT, 2014; Barma *et al*., 2011). The yield potential of the both cultivars is 3.6-5.0 ton $ha^{-1}$ in Bangladesh (Saitanis *et al*., 2014; Barma *et al*., 2011). Both wheat cultivars are heat tolerant (Barma *et al*., 2011).

On 23 April 2013, seeds of the two Bangladeshi wheat cultivars were sown in Wagner pots (volume: 12 L, diameter: 240 mm, depth: 258.5 mm) filled with horticultural soil. Three hills were formed in each pot, and three seeds were sown per hill. The seedlings were grown from 23 April to 20 May under field conditions. Average 12-h $O_3$ concentration and daylight AOT40 under field conditions were 39.4 nL $L^{-1}$ (ppb) and 3.9 μL $L^{-1}$ h (ppm h), respectively. Under field conditions, air temperature and relative air humidity fluctuated from 9.5 to 22.1°C and from 72 to 98%, respectively. The seedlings were thinned to leave one seedling per hill on 10 and 17 May. Because the potting soil was slightly acidic, $CaCO_3$ was added at a rate of 5 g per pot and mixed thoroughly to a depth of 15 cm before sowing seeds. As a result, initial pH of the soil was 5.73. The N, P, and K contents in the potting soil were all 384 mg $L^{-1}$, which maintained the optimum nutrient range for growth and development of wheat. According to Miah *et al*. (2005), the optimum N, P, and K concentrations for growth of Bangladeshi wheat are 40, 10, and 30 kg $ha^{-1}$, respectively. Although the soil contained optimum nutrients for wheat growth, to enhance growth at the tillering stage and to prompt booting, two-split applications of fertilizer (N : P : K = 8 : 8 : 8; 0.83 g per pot) were administered. In wheat, the nutrient use efficiency of nitrogenous fertilizer ranges from 14.1% when applied at sowing to 54.8% when applied as a topdressing at the beginning of stem elongation (Bellido *et al*., 2005).

## 2. 3 Gas and Salinity Treatments

The experiment was organized in a split-split plot design with three chamber replications. The whole-plot treatment comprised three levels of $O_3$, the two contrasting cultivars as a sub-plot treatment, and soil salinity (at three salt concentrations) as a sub-sub plot treatment. The gas and salinity treatments started on 21 May at the third-leaf stage of the two wheat cultivars, which coincided with the tillering stage, and continued until harvest as reported by El-Hendawy *et al*. (2005). For 70 days from 21 May to 29 July 2013, the two wheat cultivars were exposed to charcoal-filtered air (mean $O_3$ removal efficiency: 54%) or $O_3$ at 1.0- and 1.5-times the ambient concentration ($1.0 \times O_3$ and $1.5 \times O_3$ treatments, respectively). For each cultivar, four pots (i.e., 12 plants) were assigned to each soil salinity treatment in each chamber. The salinity treatment consisted of three levels of soil salinity; 0, 4, and 8 dS $m^{-1}$ electrical conductivity (EC). To maintain the soil salinity at 0, 4, or 8 dS $m^{-1}$ EC, 0, 75, or 150 mM NaCl solution (corresponding to 0, 4.383, and 8.766 g $L^{-1}$ of NaCl solution, respectively) was applied to each pot at 4-day intervals for a total of 15 applications during the 70-day gas and salinity treatments. To avoid osmotic shock and to allow the plants to adapt to salt-stress, the two salt concentrations were initially divided into three portions and applied at 3-day intervals before imposing the final concentrations. Deionized water was added to each pot between salt applications to maintain soil moisture and prevent salt accumulation.

## 2. 4 Measurements of Growth and Yield Parameters

Twelve plants of each cultivar were harvested from each treatment-chamber combination on 26 July (67 days after treatment, DAT) for BAW1059 and 29 July 2013 (70 DAT) for Shatabdi. The harvested plants were divided into leaves, stems, spikes, and roots. The plant organs were dried at 80°C for 5 days and then weighed. Yield parameters were assessed at harvest. The harvest index is the weight of harvested product as a percentage of the total plant weight of crop. We calculated the harvest index as the ratio of grain yield to the whole-plant dry mass. The number of filled and unfilled grains per plant and 1000-grain weight were determined. The grains were separated from spikes and manually categorized into two groups; filled and unfilled. The 1000-grain weight was calculated from the dry mass of filled grains per plant and the number of filled grains per plant. Yield per plant was expressed as the dry mass of filled grains per plant.

## 2. 5 Measurements of Leaf Gas Exchange Rates

The gas exchange rates of flag leaves in BAW1059 and Shatabdi were measured on 26-30 June (36-40 DAT) and 2-6 July 2013 (42-46 DAT) using a portable photosynthetic measurement system (LI-6400, Li-Cor Inc., Lincoln, NE, USA), respectively. For measurements of net photosynthetic rate ($A$), stomatal conductance to $H_2O$ ($G_s$) and intercellular $CO_2$ concentration ($C_i$), three plants per cultivar-treatment-chamber combination were randomly selected (nine measurements per treatment for each cultivar). During the measurements of $A$, $G_s$, and $C_i$, the conditions in the leaf chamber were maintained as follows: atmospheric $CO_2$ concentration, 390 μmol $mol^{-1}$; air temperature, $25 \pm 1$°C; relative air humidity, 70% ± 5%; and photosynthetic photon flux density (PPFD), 1500 μmol $m^{-2}$ $s^{-1}$. Once conditions for gas exchange measurements were stable, light-saturated $A$, $G_s$, and $C_i$ were recorded simultaneously.

## 2. 6 Measurements of Soil Salinity

The initial and residual soil salinities in each whole pot were determined by measuring the electrical conductivity of a 1 : 5 soil : water extract (ECe1 : 5) with a conductivity meter (SS974, Horiba Korea Ltd., Korea). The soil was initially non-saline ($EC = 0.71$ dS $m^{-1}$).

## 2. 7 Statistical Analyses

The data of growth parameters, yield, yield components, and leaf gas exchange parameters were subjected to three-way analysis of variance (ANOVA) to examine the individual effects of $O_3$, soil salinity, and cultivar (CV). In the ANOVA, chamber replication was set as a random factor. We confirmed that there were no significant interactions between $O_3$ and chamber replication for any of the parameters. All statistical analyses were performed with the SPSS statistical package (SPSS 11.5, SPSS Inc., USA).

# 3. RESULTS

## 3. 1 Environmental Parameters

Table 1 summarizes the air temperature, relative air humidity, and cumulative solar radiation in the gas-exposure chambers during the gas and salinity treatments for 70 days from 21 May to 29 July 2013. The mean 12-h (6:00-18:00) air temperature and relative air humidity were 24.7°C and 78.7%, respectively. The mean daily air temperature and relative air humidity during the harvest period of the two wheat cultivars (1-29 July) were 25.2°C and 88.1%, respectively, which were similar to those during the harvest period of wheat in Bangladesh (BBS, 2004). The cumulative PPFD during the gas and salinity treatments for 70 days was 1473 mol $m^{-2}$.

Table 2 shows the mean concentration, AOT0, and AOT40 of $O_3$ in each gas treatment during the gas treatments for 70 days from 21 May to 29 July 2013. The mean 24-h concentrations of $O_3$ in the charcoal-filtered air (CF), $1.0 \times O_3$, and $1.5 \times O_3$ treatments were 10, 24, and 34 nL $L^{-1}$ (ppb), respectively. The daylight AOT40 of $O_3$ in the CF, $1.0 \times O_3$, and $1.5 \times O_3$ treatments were 0, 2.9, and 8.9 μL $L^{-1}$ h (ppm h), respectively.

## 3. 2 Soil Salinity Concentration

Table 3 shows the EC of the potting soil at final harvest of BAW1059 and Shatabdi. The three-way ANOVA revealed that the salinity treatment significantly increased the soil EC of potting soil for both culti-

**Table 1.** Mean daily, maximum, minimum and 12-h mean of air temperature and relative air humidity, and cumulative PPFD inside the chambers during the gas and salinity treatments for 70 days from 21 May to 29 July 2013.

| Period (2013) | Air temperature (°C) | | | | Relative air humidity (%) | | | | Cumulative PPFD[d] (mol $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|
| | Daily mean | Daily maximum[a] | Daily minimum[b] | 12-h mean[c] | Daily mean | Daily maximum[a] | Daily minimum[b] | 12-h mean[c] | |
| 21-31 May | 20.4 (1.0) | 27.1 (3.2) | 16.0 (1.9) | 22.8 (1.9) | 80.9 (8.1) | 98.3 (1.3) | 53.1 (18.5) | 68.7 (14.0) | 268 |
| 1-30 June | 21.0 (1.7) | 26.5 (3.4) | 17.4 (2.5) | 22.8 (2.1) | 88.1 (8.2) | 98.8 (0.7) | 67.0 (20.1) | 80.4 (13.8) | 560 |
| 1-29 July | 25.2 (2.0) | 31.4 (4.1) | 21.6 (1.7) | 27.3 (2.8) | 88.1 (6.0) | 98.7 (1.0) | 67.0 (13.7) | 80.7 (9.4) | 645 |
| 21 May-29 July | 22.7 (2.8) | 28.5 (4.3) | 18.9 (3.1) | 24.7 (3.2) | 87.0 (7.7) | 98.6 (1.0) | 64.8 (17.9) | 78.7 (12.8) | 1473 |

Each value of air temperature and relative air humidity is the mean of 3 chambers, and the standard deviation is shown in parenthesis.
[a]Mean of daily 1-h maximum value.
[b]Mean of daily 1-h minimum value.
[c]12-h: 6:00-18:00.
[d]Each value of cumulative PPFD is the sum of 1-h average PPFD.

**Table 2.** The mean concentration, AOT0 and AOT40 of $O_3$ in three gas treatments during the exposure period for 70 days from 21 May to 29 July 2013.

| Period (2013) | Gas treatment | Concentration (nL $L^{-1}$) | | AOT0[c] (μL $L^{-1}$ h) | | AOT40[d] (μL $L^{-1}$ h) | |
|---|---|---|---|---|---|---|---|
| | | 24-h | 12-h[a] | 24-h | Daylight[b] | 24-h | Daylight[b] |
| 21-31 May | CF | 14 (0.2) | 16 (0.4) | 3.6 (0.1) | 1.8 (0.1) | 0.0 (0.0) | 0.0 (0.0) |
| | $1.0\times O_3$ | 32 (0.5) | 39 (0.7) | 8.5 (0.1) | 4.4 (0.1) | 1.1 (0.1) | 0.8 (0.0) |
| | $1.5\times O_3$ | 46 (0.2) | 56 (0.3) | 12.2 (0.1) | 6.3 (0.1) | 4.0 (0.0) | 2.4 (0.1) |
| 1-30 June | CF | 10 (0.3) | 11 (0.3) | 7.0 (0.3) | 3.3 (0.1) | 0.0 (0.0) | 0.0 (0.0) |
| | $1.0\times O_3$ | 29 (0.4) | 34 (0.8) | 20.6 (0.4) | 9.6 (0.2) | 2.8 (0.1) | 1.7 (0.1) |
| | $1.5\times O_3$ | 42 (0.1) | 49 (0.1) | 33.6 (0.1) | 14.0 (0.0) | 8.9 (0.1) | 4.9 (0.1) |
| 1-29 July | CF | 10 (0.8) | 12 (0.9) | 6.7 (0.6) | 5.4 (0.3) | 0.0 (0.1) | 0.0 (0.0) |
| | $1.0\times O_3$ | 17 (0.4) | 21 (0.5) | 11.9 (0.3) | 10.5 (0.1) | 0.7 (0.1) | 0.4 (0.1) |
| | $1.5\times O_3$ | 22 (0.1) | 27 (0.5) | 15.6 (0.0) | 14.2 (0.0) | 2.6 (0.0) | 1.6 (0.1) |
| 21 May-29 July | CF | 10 (0.5) | 12 (0.5) | 17.4 (0.8) | 10.5 (0.3) | 0.0 (0.0) | 0.0 (0.0) |
| | $1.0\times O_3$ | 24 (0.1) | 29 (0.3) | 41.0 (0.3) | 24.5 (0.1) | 4.6 (0.1) | 2.9 (0.0) |
| | $1.5\times O_3$ | 34 (0.0) | 41 (0.3) | 57.7 (0.1) | 34.5 (0.1) | 15.5 (0.1) | 8.9 (0.1) |

[a]12-h: 6:00-18:00.
[b]Daylight hours: global radiation $>50$ W $m^{-2}$
[c]AOT0: Accumulated exposure over a threshold of 0 nL $L^{-1}$.
[d]AOT40: Accumulated exposure over a threshold of 40 nL $L^{-1}$.

**Table 3.** Electrical conductivity (EC, dS $m^{-1}$) of residual soil after final harvest of two Bangladeshi wheat cultivars (BAW 1059 and Shatabdi).

| Treatment | | Soil EC (dS $m^{-1}$) | |
|---|---|---|---|
| Salinity | Gas | BAW1059 | Shatabdi |
| 0 dS $m^{-1}$ | CF | 0.84 (0.07) | 0.76 (0.07) |
| | $1.0\times O_3$ | 0.75 (0.16) | 0.78 (0.06) |
| | $1.5\times O_3$ | 0.81 (0.06) | 0.79 (0.06) |
| 4 dS $m^{-1}$ | CF | 3.32 (0.67) | 3.72 (0.26) |
| | $1.0\times O_3$ | 3.70 (0.54) | 3.98 (0.16) |
| | $1.5\times O_3$ | 3.50 (0.46) | 3.63 (0.13) |
| 8 dS $m^{-1}$ | CF | 5.71 (0.13) | 5.55 (0.40) |
| | $1.0\times O_3$ | 5.93 (0.54) | 6.15 (0.33) |
| | $1.5\times O_3$ | 5.45 (0.48) | 5.86 (0.49) |
| ANOVA | $O_3$ | $0.0602^{n.s.}$ | |
| | Salinity | $0.0000^{***}$ | |
| | $O_3\times$ Salinity | $0.3720^{n.s.}$ | |
| | Cultivar (CV) | $0.1213^{n.s.}$ | |
| | $O_3\times$ CV | $0.7867^{n.s.}$ | |
| | Salinity $\times$ CV | $0.3716^{n.s.}$ | |
| | $O_3\times$ Salinity $\times$ CV | $0.5987^{n.s.}$ | |

CF, Charcoal-filtered air.
Each value is the mean of 3 chamber replicates, and the standard deviation is shown in parenthesis.
Result of three-way ANOVA indicates $p$-value and level of significance; $^{***}p<0.001$; n.s. = not significant.

vars. However, soil EC did not vary depending on the other factors or their interactions. For both cultivars, the mean residual EC of the potting soil after final harvest was 0.79, 3.64, and 5.77 dS $m^{-1}$ in the 0, 4, and 8 dS $m^{-1}$ treatments, respectively.

## 3. 3 Plant Biomass

Table 4 shows the effects of $O_3$ and soil salinity, singly and in combination, on the dry mass of BAW1059 and Shatabdi at final harvest. The three-way ANOVA revealed that the whole-plant dry mass varied significantly due to all the individual factors and the interaction between salinity and cultivar. In both wheat cultivars, whole-plant dry mass was significantly reduced by exposure to $O_3$. Averaged across the both cultivars, the $O_3$-induced reduction in whole-plant dry mass was 1.1% in the $1.0\times O_3$ treatment and 9.4% in the $1.5\times O_3$ treatment, as compared with the CF treatment. The extents of the salinity-induced reduction in whole-plant dry mass differed significantly between the two cultivars. In BAW1059 and Shatabdi, the salinity-induced reductions in whole-plant dry mass were 3.8% and 22.3%, respectively, in the 8 dS $m^{-1}$ treatment, as compared with the 0 dS $m^{-1}$ treatment. The result of three-way ANOVA indicates that leaf dry mass was varied significantly due to cultivar or salinity. Averaged across the both cultivars and the three gas treatments, salinity significantly reduced the leaf dry mass by 13.7% in the 8 dS $m^{-1}$ treatment as compared with the 0 dS $m^{-1}$ treatment. According to the results of three-way ANOVA, stem and root dry masses were varied significantly due to salinity, cultivar and the interaction between salinity and cultivar. In BAW1059 and Shatabdi,

**Table 4.** Effects of $O_3$, salinity and/or cultivar on the dry mass of two Bangladeshi wheat cultivars (BAW1059 and Shatabdi).

| Cultivar | Treatment | | Dry mass (g) | | | | Whole-plant dry mass (g) |
|---|---|---|---|---|---|---|---|
| | Salinity | Gas | Leaf | Stem | Root | Panicle | |
| BAW1059 | 0 dS $m^{-1}$ | CF | 0.77 (0.15) | 2.49 (0.21) | 0.48 (0.07) | 4.77 (0.39) | 8.51 (0.68) |
| | | $1.0 \times O_3$ | 0.80 (0.10) | 2.21 (0.22) | 0.48 (0.04) | 4.06 (0.49) | 7.56 (0.81) |
| | | $1.5 \times O_3$ | 0.66 (0.09) | 1.87 (0.22) | 0.36 (0.01) | 3.24 (0.47) | 6.13 (0.65) |
| | 4 dS $m^{-1}$ | CF | 0.76 (0.07) | 2.18 (0.24) | 0.56 (0.02) | 4.28 (0.54) | 7.79 (0.87) |
| | | $1.0 \times O_3$ | 0.79 (0.11) | 2.12 (0.08) | 0.64 (0.07) | 4.16 (0.10) | 7.70 (0.36) |
| | | $1.5 \times O_3$ | 0.70 (0.09) | 1.98 (0.28) | 0.56 (0.05) | 3.67 (0.47) | 6.91 (0.85) |
| | 8 dS $m^{-1}$ | CF | 0.72 (0.06) | 1.90 (0.19) | 0.60 (0.08) | 3.86 (0.33) | 7.08 (0.57) |
| | | $1.0 \times O_3$ | 0.70 (0.05) | 1.92 (0.04) | 0.65 (0.03) | 3.88 (0.12) | 7.15 (0.19) |
| | | $1.5 \times O_3$ | 0.73 (0.11) | 2.03 (0.37) | 0.64 (0.08) | 3.74 (0.72) | 7.13 (1.27) |
| Shatabdi | 0 dS $m^{-1}$ | CF | 1.13 (0.15) | 3.30 (0.15) | 0.70 (0.09) | 5.64 (0.54) | 10.78 (0.74) |
| | | $1.0 \times O_3$ | 1.06 (0.11) | 3.25 (0.28) | 0.68 (0.07) | 5.65 (0.37) | 10.65 (0.74) |
| | | $1.5 \times O_3$ | 0.91 (0.16) | 2.84 (0.40) | 0.54 (0.10) | 5.27 (1.23) | 9.56 (1.82) |
| | 4 dS $m^{-1}$ | CF | 0.88 (0.06) | 2.58 (0.14) | 0.64 (0.04) | 4.91 (0.47) | 9.00 (0.71) |
| | | $1.0 \times O_3$ | 1.00 (0.15) | 2.64 (0.31) | 0.63 (0.12) | 4.83 (0.71) | 9.11 (1.25) |
| | | $1.5 \times O_3$ | 0.79 (0.14) | 2.55 (0.10) | 0.71 (0.08) | 4.43 (0.25) | 8.48 (0.39) |
| | 8 dS $m^{-1}$ | CF | 0.77 (0.08) | 2.29 (0.19) | 0.62 (0.08) | 4.16 (0.32) | 7.83 (0.66) |
| | | $1.0 \times O_3$ | 0.86 (0.27) | 2.57 (0.61) | 0.74 (0.14) | 4.09 (0.62) | 8.26 (1.51) |
| | | $1.5 \times O_3$ | 0.82 (0.03) | 2.39 (0.15) | 0.65 (0.13) | 4.12 (0.70) | 7.99 (0.93) |
| ANOVA | $O_3$ | | $0.0692^{n.s.}$ | $0.0775^{n.s.}$ | $0.1519^{n.s.}$ | $0.0077^{**}$ | $0.0065^{**}$ |
| | Salinity | | $0.0299^{*}$ | $0.0000^{***}$ | $0.0031^{**}$ | $0.0001^{***}$ | $0.0009^{***}$ |
| | $O_3 \times$ Salinity | | $0.3800^{n.s.}$ | $0.0653^{n.s.}$ | $0.1019^{n.s.}$ | $0.2728^{n.s.}$ | $0.1726^{n.s.}$ |
| | Cultivar (CV) | | $0.0000^{***}$ | $0.0000^{***}$ | $0.0000^{***}$ | $0.0000^{***}$ | $0.0000^{***}$ |
| | $O_3 \times$ CV | | $0.7170^{n.s.}$ | $0.4939^{n.s.}$ | $0.1017^{n.s.}$ | $0.3526^{n.s.}$ | $0.7881^{n.s.}$ |
| | Salinity $\times$ CV | | $0.0811^{n.s.}$ | $0.0176^{*}$ | $0.0331^{*}$ | $0.0025^{**}$ | $0.0044^{**}$ |
| | $O_3 \times$ Salinity $\times$ CV | | $0.8178^{n.s.}$ | $0.9484^{n.s.}$ | $0.5617^{n.s.}$ | $0.6186^{n.s.}$ | $0.8480^{n.s.}$ |

CF, Charcoal-filtered air.
Each value is the mean of 3 chamber replicates, and the standard deviation is shown in parenthesis.
Result of three-way ANOVA indicates $p$-value and level of significance; $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$; n.s. = not significant.

**Table 5.** The result of three-way ANOVA of the effects of $O_3$, salinity and/or cultivar (CV) on yield per plant of two Bangladeshi wheat cultivars (BAW1059 and Shatabdi).

| Parameter | $O_3$ | Salinity | $O_3 \times$ Salinity | CV | $O_3 \times$ CV | Salinity $\times$ CV | $O_3 \times$ Salinity $\times$ CV |
|---|---|---|---|---|---|---|---|
| Yield per plant | $0.0058^{**}$ | $0.0023^{**}$ | $0.0914^{n.s.}$ | $0.0000^{***}$ | $0.4984^{n.s.}$ | $0.0024^{**}$ | $0.8251^{n.s.}$ |

Result of three-way ANOVA indicates $p$-value and level of significance; $^{**}p<0.01$, $^{***}p<0.001$, n.s. = not significant.

stem dry mass was lower by 11.0% and 22.8%, while root dry mass was higher by 43.2% and 4.8% in the 8 dS $m^{-1}$ treatment as compared with those in the 0 dS $m^{-1}$ treatment, respectively. Three-way ANOVA revealed that panicle dry mass was significantly varied by all individual factors and the interaction between salinity and cultivar. Averaged across the both cultivars, $O_3$-induced reduction in panicle dry mass was 11.4% in the $1.5 \times O_3$ treatment as compared with the CF treatment. The salinity-induced reductions in panicle dry mass in BAW1059 and Shatabdi were 4.9% and 25.3% in the 8 dS $m^{-1}$ treatment as compared with the 0 dS $m^{-1}$ treatment, respectively.

## 3. 4 Yield and Yield Components

Fig. 1 shows the effects of $O_3$ and soil salinity on the yield per plant of BAW1059 and Shatabdi. The results of the three-way ANOVA revealed that the yield per plant varied significantly due to all of the individual factors and the interaction between salinity and cultivar (Table 5). In both cultivars, the yield per plant was significantly reduced by exposure to $O_3$. Averaged across the both cultivars, the reduction in yield per plant was 4.7% in the $1.0 \times O_3$ treatment and 11.6% in the $1.5 \times O_3$ treatment, as compared with the CF treatment. In BAW1059, there was no significant reduction in yield per plant in the 8 dS $m^{-1}$ treatment as compared with the 0 dS $m^{-1}$ treatment. In Shatabdi, however, the yield per plant was 23.6% lower in the 8 dS $m^{-1}$ treatment than in the 0 dS $m^{-1}$ treatment.

Table 6 summarizes the effects of $O_3$ and soil salinity, singly and in combination, on the yield components of BAW1059 and Shatabdi. According to the results of the three-way ANOVA, spike and floret number per plant and floret number per spike varied significantly due to all of the individual factors and the interaction between salinity and cultivar. In both cultivars, the number of spikes per plant was 3.7% lower in the $1.5 \times O_3$ treatment than in the CF treatment. In BAW1059 and Shatabdi, the number of spikes per plant in the 8 dS $m^{-1}$ treatment was 7.6% and 24.8% lower, respectively, than that in the 0 dS $m^{-1}$ treatment. Averaged across the both cultivars, the number of florets per plant and per spike were 7.0% and 8.8% lower, respectively, in the $1.5 \times O_3$ treatment than in the CF treatment. In the salt treatments, the number of florets per plant and per spike in BAW1059 were 5.1% and 0.5% lower, respectively, in the 8 dS $m^{-1}$ treatment than in the 0 dS $m^{-1}$ treatment. In Shatabdi, the number of florets per plant and per spike were 22.6% and 4.8% lower, respectively, in the 8 dS $m^{-1}$ treatment than in the 0 dS $m^{-1}$ treatment.

The three-way ANOVA indicated that the number of filled grains and the ratio of filled grains to total grains varied significantly due to the cultivar and the interaction between salinity and cultivar (Table 6). The number of filled grains in BAW1059 and Shatabdi was 4.7% and 20.2% lower, respectively, in the 8 dS $m^{-1}$ treatment than in the 0 dS $m^{-1}$ treatment. In the 8 dS $m^{-1}$ treatment, the ratio of filled grain number to total grain number was unchanged in BAW1059, but decreased by 4.8% in Shatabdi. The three-way ANOVA indicated that the number of unfilled grains was significantly affected only by salinity. Averaged across both cultivars, the salinity-induced reduction in the number of unfilled grains was 9.2% in the 8 dS $m^{-1}$ treatment.

The three-way ANOVA showed that the 1000-seeds weight varied significantly due to all of the individual factors and salinity × cultivar and $O_3$ × cultivar interactions (Table 6). In BAW1059 and Shatabdi, the 1000-seeds weight was 7.0% and 4.1% lower, respectively, in the $1.5 \times O_3$ treatment than in the CF treatment. As compared with that in the 0 dS $m^{-1}$ treatment, the 1000-seeds weight were 1.6% and 8.0% lower in BAW1059 and 4.1% and 8.0% lower in Shatabdi in the 4 and 8 dS $m^{-1}$ treatments, respectively.

The three-way ANOVA indicated that harvest index (HI) was significantly affected by $O_3$ treatment and cultivar, but not by salinity or interactions between factors (Table 6). Averaged across both cultivars, the HI was 2.3% lower in the $1.5 \times O_3$ treatment than in the CF treatment.

### 3. 5 Leaf Gas Exchange Rates

Table 7 shows the effects of $O_3$ and soil salinity, singly and in combination, on $A$, $G_s$, and $C_i$ in the flag leaves of BAW1059 and Shatabdi. According to the three-way ANOVA, $A$ varied significantly due to all the individual factors and the interaction between salinity and cultivar. Averaged across both cultivars, the $O_3$-induced reduction in $A$ was 7.1% in the $1.0 \times O_3$ treatment and 11.7% in the $1.5 \times O_3$ treatment. In BAW1059 and Shatabdi, $A$ was 1.1% and 22.1% lower, respectively, in the 8 dS $m^{-1}$ treatment than in the 0 dS $m^{-1}$ treatment. Both $O_3$ and salinity significantly affected $G_s$. Averaged across both cultivars, $G_s$ was 17.7% lower in the $1.5 \times O_3$ treatment than in the CF treatment, and 17.1% lower in the 8 dS $m^{-1}$ treatment than in the 0 dS $m^{-1}$ treatment. The three-way ANOVA revealed that $C_i$ was significantly affected by salinity, cultivar, and the interaction between $O_3$ and cultivar. Because there was significant interaction between $O_3$ and cultivar on $C_i$, percentage changes in $C_i$ due to $O_3$ were calculated for each cultivar, although there was no significant main effect of $O_3$ on $C_i$. The $C_i$ was significantly increased by 2.9% and 0.6% in BAW1059 and Shatabdi, respectively, in the $1.5 \times O_3$ treatment, as compared with the CF treatment. Averaged across both cultivars, $C_i$ was 1.6% lower in the 8 dS $m^{-1}$ treatment than in the 0 dS $m^{-1}$ treatment.

## 4. DISCUSSION

In the present study, exposure to $O_3$ significantly decreased the whole-plant dry mass and grain yield per plant of two Bangladeshi wheat cultivars (Tables 4 and 5, and Fig. 1). There were no significant differences between the two Bangladeshi wheat cultivars in terms of the $O_3$-sensitivity of whole-plant dry mass and grain yield per plant (Tables 4 and 5, and Fig. 1). On average, the $O_3$-induced reduction in whole-plant dry mass and grain yield per plant in the two Bangladeshi wheat cultivars were 1.1% and 4.7%, respectively, in the $1.0 \times O_3$ treatment, and 9.4% and 11.6%, respectively, in the $1.5 \times O_3$ treatment, as compared with the CF treatment. Several studies carried out in North America, Europe, and elsewhere have reported $O_3$-

**Table 6.** Effects of $O_3$, salinity and/or cultivar on yield components of two Bangladeshi wheat cultivars (BAW1059 and Shatabdi).

| Cultivar | Treatment | | Number per plant | | | | % of filled grain | Floret no. / spike | 1000-seed weight (g) | Harvest index (%) |
|---|---|---|---|---|---|---|---|---|---|---|
| | Salinity | Gas | Spike | Floret | Filled grain | Unfilled grain | | | | |
| BAW1059 | 0 dS $m^{-1}$ | CF | 3.2 (0.5) | 123.3 (12.1) | 75.2 (10.8) | 48.2 (5.2) | 61.0 (1.1) | 38.3 (3.0) | 47.6 (1.6) | 42.0 (3.5) |
| | | $1.0 \times O_3$ | 3.2 (0.3) | 118.4 (11.2) | 69.9 (9.3) | 48.1 (3.2) | 59.1 (2.0) | 36.8 (1.2) | 46.0 (1.9) | 41.3 (1.3) |
| | | $1.5 \times O_3$ | 3.0 (0.4) | 101.5 (11.7) | 59.0 (9.2) | 42.5 (4.2) | 59.0 (2.8) | 33.6 (1.8) | 42.5 (2.1) | 40.0 (0.9) |
| | 4 dS $m^{-1}$ | CF | 3.3 (0.5) | 123.1 (14.6) | 75.2 (7.9) | 47.9 (7.4) | 61.4 (2.6) | 37.4 (1.8) | 45.1 (1.2) | 43.3 (1.3) |
| | | $1.0 \times O_3$ | 3.2 (0.2) | 120.5 (7.7) | 73.0 (2.2) | 47.5 (5.7) | 60.6 (2.5) | 37.4 (0.5) | 45.9 (0.9) | 43.2 (1.3) |
| | | $1.5 \times O_3$ | 3.1 (0.3) | 107.8 (7.7) | 67.3 (6.0) | 40.4 (1.8) | 62.6 (2.2) | 35.0 (1.6) | 43.1 (2.9) | 42.1 (1.2) |
| | 8 dS $m^{-1}$ | CF | 2.7 (0.2) | 106.6 (8.9) | 63.9 (8.4) | 42.7 (3.5) | 59.9 (1.7) | 39.3 (3.0) | 42.3 (2.9) | 43.5 (2.5) |
| | | $1.0 \times O_3$ | 3.0 (0.2) | 108.2 (1.7) | 63.4 (0.5) | 45.2 (6.8) | 58.6 (4.3) | 35.6 (2.1) | 43.0 (0.9) | 43.1 (0.4) |
| | | $1.5 \times O_3$ | 3.0 (0.4) | 110.7 (14.8) | 67.1 (14.1) | 43.6 (1.5) | 60.6 (4.7) | 37.4 (5.8) | 40.0 (0.9) | 41.9 (1.0) |
| Shatabdi | 0 dS $m^{-1}$ | CF | 5.2 (0.6) | 158.2 (5.4) | 96.6 (4.8) | 55.9 (3.0) | 66.0 (2.3) | 36.6 (2.5) | 45.3 (1.2) | 39.8 (2.4) |
| | | $1.0 \times O_3$ | 5.0 (0.7) | 142.9 (13.6) | 90.8 (4.5) | 52.1 (7.8) | 65.7 (10.3) | 33.0 (7.4) | 44.9 (0.7) | 38.3 (1.8) |
| | | $1.5 \times O_3$ | 4.4 (0.5) | 139.6 (6.8) | 90.8 (10.2) | 48.8 (3.5) | 64.8 (4.6) | 32.3 (2.4) | 41.8 (2.4) | 40.1 (2.4) |
| | 4 dS $m^{-1}$ | CF | 3.7 (0.2) | 134.1 (10.1) | 85.6 (6.8) | 48.5 (4.1) | 64.3 (1.8) | 33.4 (1.3) | 42.8 (1.6) | 41.9 (1.2) |
| | | $1.0 \times O_3$ | 4.1 (0.3) | 122.3 (20.4) | 83.9 (12.5) | 42.8 (11.3) | 65.7 (0.5) | 29.7 (5.1) | 42.2 (1.3) | 40.5 (1.1) |
| | | $1.5 \times O_3$ | 3.6 (0.2) | 116.8 (9.4) | 67.5 (18.7) | 40.6 (4.4) | 61.4 (4.1) | 28.7 (6.8) | 41.5 (1.6) | 38.9 (3.4) |
| | 8 dS $m^{-1}$ | CF | 3.5 (0.1) | 105.1 (12.1) | 77.4 (8.6) | 43.7 (8.4) | 64.1 (6.1) | 33.4 (1.9) | 40.7 (2.7) | 38.4 (1.4) |
| | | $1.0 \times O_3$ | 3.7 (0.9) | 114.4 (15.1) | 68.5 (11.9) | 45.9 (7.9) | 60.0 (5.2) | 31.2 (4.9) | 40.6 (4.2) | 37.7 (3.9) |
| | | $1.5 \times O_3$ | 3.8 (0.3) | 121.6 (15.3) | 76.2 (5.1) | 47.3 (12.5) | 63.0 (4.5) | 32.3 (2.1) | 40.2 (3.1) | 40.1 (1.9) |
| ANOVA | $O_3$ | | $0.0406^{*}$ | $0.0329^{*}$ | $0.0536^{n.s.}$ | $0.1613^{n.s.}$ | $0.9487^{n.s.}$ | $0.0433^{*}$ | $0.0021^{**}$ | $0.0195^{*}$ |
| | Salinity | | $0.0000^{***}$ | $0.0023^{**}$ | $0.0539^{n.s.}$ | $0.0035^{**}$ | $0.0502^{n.s.}$ | $0.0010^{**}$ | $0.0000^{***}$ | $0.0511^{n.s.}$ |
| | $O_3 \times$ Salinity | | $0.1511^{n.s.}$ | $0.1386^{n.s.}$ | $0.1482^{n.s.}$ | $0.4111^{n.s.}$ | $0.5347^{n.s.}$ | $0.1534^{n.s.}$ | $0.2804^{n.s.}$ | $0.4222^{n.s.}$ |
| | Cultivar (CV) | | $0.0000^{***}$ | $0.0000^{***}$ | $0.0000^{***}$ | $0.1393^{n.s.}$ | $0.0477^{*}$ | $0.0000^{***}$ | $0.0004^{***}$ | $0.0000^{***}$ |
| | $O_3 \times$ CV | | $0.3845^{n.s.}$ | $0.6847^{n.s.}$ | $0.8849^{n.s.}$ | $0.6015^{n.s.}$ | $0.6412^{n.s.}$ | $0.7854^{n.s.}$ | $0.0085^{**}$ | $0.2414^{n.s.}$ |
| | Salinity $\times$ CV | | $0.0000^{***}$ | $0.0084^{**}$ | $0.0012^{**}$ | $0.1265^{n.s.}$ | $0.0111^{*}$ | $0.0052^{**}$ | $0.0457^{*}$ | $0.5926^{n.s.}$ |
| | $O_3 \times$ Salinity $\times$ CV | | $0.5020^{n.s.}$ | $0.9111^{n.s.}$ | $0.4723^{n.s.}$ | $0.7262^{n.s.}$ | $0.1715^{n.s.}$ | $0.8134^{n.s.}$ | $0.4080^{n.s.}$ | $0.2910^{n.s.}$ |

CF, Charcoal-filtered air.
Each value is the mean of 3 chamber replicates, and the standard deviation is shown in parenthesis.
Result of three-way ANOVA indicates $p$-value and level of significance; $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$; n.s. = not significant.

**Table 7.** Effects of $O_3$ salinity and/or cultivar on net photosynthesis rate ($A$), stomatal diffusive conductance to $H_2O$ ($G_s$) and intercellular $CO_2$ concentration ($C_i$) of flag leaf of two Bangladeshi wheat cultivars on 36-40 days after treatment (DAT) (BAW1059) and 42-46 DAT (Shatabdi).

| Cultivar | Treatment | | $A$ ($\mu$mol m$^{-2}$ s$^{-1}$) | $G_s$ (mol m$^{-2}$ s$^{-1}$) | $C_i$ ($\mu$mol mol$^{-1}$) |
|---|---|---|---|---|---|
| | Salinity | Gas | | | |
| BAW1059 | 0 dS m$^{-1}$ | CF | 24.4 (1.5) | 0.476 (0.015) | 286.8 (3.6) |
| | | $1.0\times O_3$ | 22.1 (1.6) | 0.423 (0.059) | 297.7 (7.3) |
| | | $1.5\times O_3$ | 17.7 (1.7) | 0.311 (0.055) | 297.2 (9.4) |
| | 4 dS m$^{-1}$ | CF | 22.1 (0.8) | 0.416 (0.016) | 286.7 (4.5) |
| | | $1.0\times O_3$ | 22.1 (0.5) | 0.407 (0.008) | 286.3 (0.9) |
| | | $1.5\times O_3$ | 20.7 (1.1) | 0.383 (0.041) | 296.9 (12.0) |
| | 8 dS m$^{-1}$ | CF | 22.9 (1.2) | 0.383 (0.036) | 284.8 (3.9) |
| | | $1.0\times O_3$ | 21.4 (0.7) | 0.386 (0.016) | 285.1 (4.2) |
| | | $1.5\times O_3$ | 19.2 (1.8) | 0.323 (0.023) | 289.2 (8.0) |
| Shatabdi | 0 dS m$^{-1}$ | CF | 23.5 (1.9) | 0.459 (0.068) | 289.4 (11.6) |
| | | $1.0\times O_3$ | 22.2 (1.6) | 0.413 (0.016) | 286.9 (5.9) |
| | | $1.5\times O_3$ | 22.2 (0.9) | 0.381 (0.054) | 297.5 (4.8) |
| | 4 dS m$^{-1}$ | CF | 21.9 (1.4) | 0.418 (0.029) | 290.0 (2.8) |
| | | $1.0\times O_3$ | 19.8 (1.8) | 0.345 (0.058) | 280.5 (7.8) |
| | | $1.5\times O_3$ | 18.5 (2.2) | 0.337 (0.052) | 289.2 (7.9) |
| | 8 dS m$^{-1}$ | CF | 18.0 (0.4) | 0.356 (0.028) | 292.8 (9.6) |
| | | $1.0\times O_3$ | 15.9 (0.9) | 0.266 (0.058) | 285.2 (18.7) |
| | | $1.5\times O_3$ | 19.0 (4.7) | 0.328 (0.103) | 290.7 (7.7) |
| ANOVA | $O_3$ | | 0.0003$^{***}$ | 0.0002$^{***}$ | 0.2416$^{n.s.}$ |
| | Salinity | | 0.0020$^{**}$ | 0.0004$^{***}$ | 0.0467$^{*}$ |
| | $O_3\times$ Salinity | | 0.1160$^{n.s.}$ | 0.2062$^{n.s.}$ | 0.2522$^{n.s.}$ |
| | Cultivar (CV) | | 0.0036$^{**}$ | 0.0663$^{n.s.}$ | 0.0211$^{*}$ |
| | $O_3\times$ CV | | 0.0508$^{n.s.}$ | 0.0531$^{n.s.}$ | 0.0081$^{**}$ |
| | Salinity $\times$ CV | | 0.0054$^{**}$ | 0.0511$^{n.s.}$ | 0.8580$^{n.s.}$ |
| | $O_3\times$ Salinity $\times$ CV | | 0.1672$^{n.s.}$ | 0.3188$^{n.s.}$ | 0.9191$^{n.s.}$ |

CF, Charcoal-filtered air.
Each value is the mean of 3 chamber replicates, and the standard deviation is shown in parenthesis.
Result of three-way ANOVA indicates $p$-value and level of significance; $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$; n.s. = not significant.
Measurement condition: atmospheric $CO_2$ concentration, 390 $\mu$mol mol$^{-1}$; air temperature, 25.0 ± 1.0°C; relative air humidity, 70 ± 5%; photosynthetic photon flux density (PPFD), 1500 $\mu$mol m$^{-2}$ s$^{-1}$.

induced reductions in wheat grain yield (Gerosa *et al.*, 2014; Pleijel and Uddling, 2012; Mills *et al.*, 2010; Emberson *et al.*, 2009; Piikki *et al.*, 2008; Fuhrer *et al.*, 1997). In Table 8, the sensitivity to $O_3$ of grain yield per plant is compared among the two Bangladeshi wheat cultivars (BAW1059 and Shatabdi) and European and American wheat cultivars, based on the relationship between relative yield and daylight AOT40 of $O_3$ or 7-h (9:00-16:00) mean $O_3$ concentration (Mills *et al.*, 2010; Emberson *et al.*, 2009). This comparison reveals that the sensitivity to $O_3$ of two Bangladeshi wheat cultivars is greater than that of American winter and spring wheat cultivars and is similar to that of European spring wheat cultivars.

Although BAW1059 showed a larger $O_3$-induced reduction in seed weight than did Shatabdi, both cultivars showed a significant decrease in the number of spikes per plant and number of florets per spike in response to $O_3$ (Table 6). Therefore, the main cause of the $O_3$-induced reduction in grain yield per plant is considered to be due to the decreased number of spikes per plant, number of florets per spike, and 1000-seeds weight (Table 6). Our results are consistent with earlier observations, where elevated $O_3$ strongly affected grain weight (Pleijel and Uddling, 2012; Piikki *et al.*, 2008). The $O_3$-induced yield loss may be attributed to reduced photosynthetic activity and a decreased supply of assimilates to the reproductive parts responsible for seed

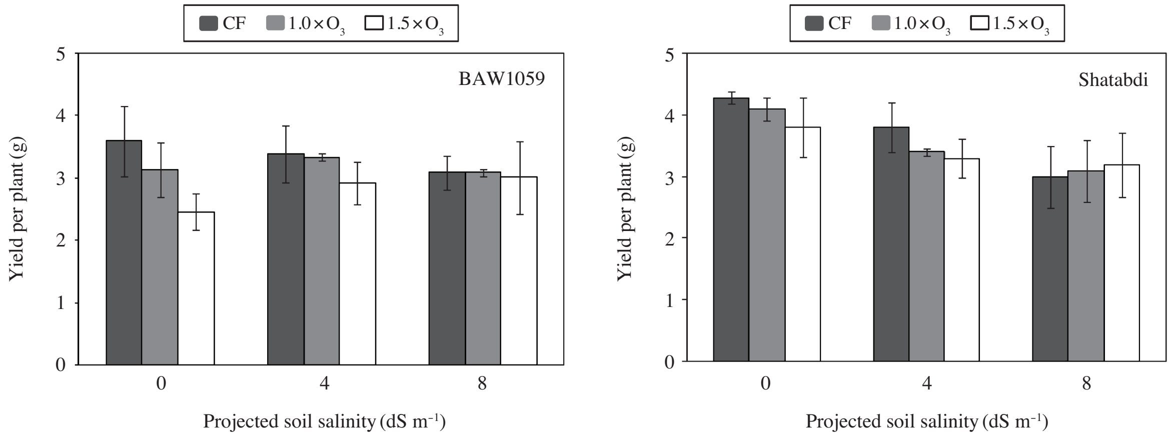


**Fig. 1.** Effects of $O_3$ and soil salinity on yield per plant of two Bangladeshi wheat cultivars (BAW1059 and Shatabdi). Each value shows the mean of 3 chamber replicates, and the standard deviation is given by vertical bar. Result of three-way ANOVA indicating *p*-value and level of significance for yield per plant is shown in Table 5.

**Table 8.** Comparison of $O_3$-induced yield loss among Bangladeshi, European and American wheat cultivars.

| AOT40 of $O_3$ ($\mu L\ L^{-1}$ h) | 7-h mean $O_3$ concentration ($nL\ L^{-1}$)[a] | Observed yield loss in Bangladeshi wheat cultivars (%) | Predicted yield loss (%) | | |
|---|---|---|---|---|---|
| | | | European spring[b] wheat cultivars | American spring[c] wheat cultivars | American winter[d] wheat cultivars |
| 2.9 | 28.4 | 4.7 | 5.0 | 0.1 | 0.9 |
| 8.9 | 50.1 | 11.6 | 15.2 | 1.4 | 6.6 |

[a]7-h: 9:00-16:00.
[b]Calculated according to Fuhrer *et al.* (1997).
[c]Calculated according to Adams *et al.* (1989).
[d]Calculated according to Lesser *et al.* (1990).

growth (Fiscus *et al.*, 2005). Gelang *et al.* (2001) reported that in cereal crops, grain filling depends on the production of carbohydrates and their translocation from the source organs to the sink (grains). Carbohydrate production can be affected by $O_3$-induced changes in net photosynthetic rate and photosynthetic activity (Meyer *et al.*, 2000). An $O_3$-induced reduction in biomass production has been reported for a wide range of crop species (Akhtar *et al.*, 2010a, b; Morgan *et al.*, 2006; Grantz, 2003). Such effects may be the result of $O_3$-induced reductions in net photosynthesis and/or leaf area, or $O_3$-induced changes in phloem loading and assimilate partitioning to plant organs (Crous *et al.*, 2006; Dermody *et al.*, 2006; Hassan, 2004; Morgan *et al.*, 2004). In the present study, $O_3$ significantly reduced the net photosynthetic rate of the flag leaf in both wheat cultivars (Table 7). We propose that the $O_3$-induced reduction in net photosynthetic rate resulted in lower assimilates, leading to a decrease in whole-plant dry mass and yield per plant in both cultivars (Tables 4 and 5, and Fig. 1).

In the present study, the two wheat cultivars showed greater differences in salinity sensitivity than in $O_3$-sensitivity, in terms of biomass production and grain yield. In the 8 dS $m^{-1}$ treatment, the grain yield per plant and the whole-plant dry mass were only slightly affected or not affected in BAW1059, but were decreased by 23.6% and 22.3%, respectively, in Shatabdi (Tables 4 and 5 and Fig. 1). Thus, BAW1059 is relatively more salt-tolerant than is Shatabdi. Our findings are consistent with the salinity-induced reductions in growth and yield reported for Asian, Mediterranean, European, and African wheat cultivars (Ghogdi *et al.*, 2012; Turki *et al.*, 2012; Sadat Noori *et al.*, 2010). In Shatabdi, the negative effects of soil salinity on grain yield per plant might be caused by the salt-induced decreases in the number of spikes per plant, number of florets per spike, and percentage of filled grains, as well as the 1000-seeds weight (Table 6). Also, the salinity-induced reduction in grain yield per plant in Shatabdi might be caused by a salt-induced decrease in photosynthetic capacity (Table 7), leading to less starch synthesis and accumulation in the grain. BAW1059 maintained a higher photosynthetic capacity than did

Shatabdi under salt stress (Table 7). Our results are consistent with those of Zheng *et al.* (2009) and Turki *et al.* (2012), who reported that there was a larger salt-induced decrease in photosynthetic capacity in salt-sensitive than in salt-tolerant wheat cultivars. Thus, although the 1000-seeds weight of BAW1059 was lower in the highest salinity treatment, the yield per plant remained almost unchanged. This result was closely related to the salinity-induced decrease in the number of unfilled grains and increase in the ratio of the number of filled grains to total grains in BAW1059, which reflected the greater induction of reproductive efficiency by salt-stress (Gerosa *et al.*, 2014). In the present study, soil salinity reduced $G_s$ and $C_i$ in the flag leaves of BAW1059 and Shatabdi (Table 7). A salinity-induced reduction of $G_s$ has also been reported for durum wheat (Katerji *et al.*, 2003) and winter wheat (Huang *et al.*, 1994). In salt-sensitive cultivars, the inhibition of photosynthetic capacity under salinity might be due to stomatal closure, which reduces the availability of internal $CO_2$ (Hernandez *et al.*, 1999).

There was no significant interaction between $O_3$ and soil salinity for growth, yield, and leaf gas exchange rates in the two Bangladeshi wheat cultivars (Fig. 1, Tables 4 and 7). This result indicated that the effects of $O_3$ on growth, yield, and gas exchange rates of the two Bangladeshi wheat cultivars were not ameliorated by soil salinity. Our results are consistent with the findings of Gerosa *et al.* (2014) for two durum wheat cultivars grown under Mediterranean conditions with elevated salinity and $O_3$ concentrations. Greater sensitivity to $O_3$ has been attributed to various physiological traits, including higher $G_s$ leading to higher $O_3$ flux into the leaves (Gerosa *et al.*, 2014; Zheng *et al.,* 2014; Saitanis *et al.*, 2014; Emberson *et al.*, 2009). In the present study, both Bangladeshi wheat cultivars exposed to elevated $O_3$ showed a significant decrease in $G_s$, but there was no significant difference in $G_s$ between the two cultivars (Table 7). In both cultivars, soil salinity significantly decreased $G_s$, suggesting that soil salinity reduced stomatal $O_3$ flux. However, soil salinity did not significantly affect the $O_3$-sensitivity of the two Bangladeshi wheat cultivars. Therefore, stomatal $O_3$ flux may also have been similar in the two Bangladeshi wheat cultivars with similar-sensitivity to $O_3$. This might be because increased salinity decreased the antioxidant capacity in the leaves, as reported in other studies (Bai *et al.*, 2013; Ozturk *et al.*, 2012; Burcu *et al.*, 2009; Hameed *et al.*, 2008; Shim *et al.*, 2003). Therefore, the interactions among $O_3$, salinity, and cultivar on the growth, yield, and leaf gas exchange rates of wheat are considered to be closely related to the ability of the plants to detoxify active oxygen radicals produced in the leaves in response to $O_3$ and salinity.

## 5. CONCLUSIONS

Two Bangladeshi wheat cultivars, BAW1059 and Shatabdi, are relatively sensitive to $O_3$ as compared with American winter and spring wheat cultivars. Shatabdi is more sensitive than BAW1059 to soil salinity. There were no significant interactions between $O_3$ and salinity for growth, yield, yield components, and gas exchange parameters, indicating that the effects of $O_3$ were not ameliorated by soil salinity in these two Bangladeshi wheat cultivars, regardless of their salinity tolerance. To mitigate food security challenges in the future, therefore, wheat cultivars with higher tolerance to salinity and $O_3$ should be bred.

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