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EFFECTS OF ENHANCED O_3 AND CO_2 ENRICHMENT ON PLANT CHARACTERISTICS IN WHEAT AND CORN*

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Abstract

*The effects of CO_2 enrichment and O_3 induced stress on wheat (*Triticum aestivum *L.) and corn (*Zea mays *L.) were studied in field experiments using open-top chambers to simulate the atmospheric concentrations of these two gases that are predicted to occur during the coming century. The experiments were conducted at Beltsville, MD, during 1991 (wheat and corn) and 1992 (wheat). Crops were grown under charcoal filtered (CF) air or ambient air +40 nl liter^{-1} O_3 (7 h per day, 5 days per week) having ambient CO_2 concentration (350 μl liter^{-1} CO_2) or +150 μl liter^{-1} CO_2 (12 h per day). Averaged over O_3 treatments, the CO_2-enriched environment had a positive effect on wheat grain yield (26% in 1991 and 15% in 1992) and dry biomass (15% in 1991 and 9% in 1992). Averaged over CO_2 treatments, high O_3 exposure had a negative impact on wheat grain yield (−15% in 1991 and −11% in 1992) and dry biomass (−11% in 1991 and −9% in 1992). Averaged over CO_2 treatments, high O_3 exposure decreased corn grain yield by 9%. No significant interactive effects were observed for either crop. The results indicated that CO_2 enrichment had a beneficial effect in wheat (C_3 crop) but not in corn (C_4 crop). It is likely that the O_3-induced stress will be diminished under increased atmospheric CO_2 concentrations; however, maximal benefits in crop production in wheat in response to CO_2 enrichment will not be materialized under concomitant increases in tropospheric O_3 concentration. Copyright © 1996 Elsevier Science Ltd*

INTRODUCTION

Carbon dioxide (CO_2) and ozone (O_3) concentrations in the troposphere have increased concurrently during the past century (Krupa & Kickert, 1989; Allen, 1990). Further increases in these gases are expected to have an increasingly significant impact on crop production (Krupa & Kickert, 1989). Deleterious effects of O_3 on crops have been well documented (Heagle *et al.*, 1972, 1979*a*,*b*, 1991; Heck *et al.*, 1983; Kress & Miller, 1983, 1984; Unsworth *et al.*, 1984; Endress & Grunwald, 1985; Kress *et al.*, 1985; Mulchi *et al.*, 1986, 1988, 1992; Amundson *et al.*, 1987; Lehnherr *et al.*, 1987; Slaughter, 1987; Heggestad *et al.*, 1988; Miller, 1988; Fuhrer *et al.*, 1989; Heagle, 1989; Slaughter *et al.*, 1989, 1993; Heck, 1990; Pleijel *et al.*, 1991; Sanders *et al.*, 1992; Krupa *et al.*, 1994). Atmospheric CO_2 enrichment, however, may have positive physiological effects on C_3 type plants (Fischer & Aguilar, 1976; Gifford, 1977; Kramer, 1981; Sionit *et al.*, 1981; Kimball & Idso, 1983; Lemon, 1983; Havelka *et al.*, 1984; Strain & Cure, 1985; Chaudhuri *et al.*, 1986, 1987, 1990; Cure & Acock, 1986; Schönfeld *et al.*, 1989; Mott, 1990; Hocking & Meyer, 1991). Insufficient attention has been given to the interaction of these gases on vegetation (Krupa & Kickert, 1989), although several review articles have emphasized the need for studies into their combined effects on plant growth and development (Kimball, 1986; Krupa & Kickert, 1989; Allen, 1990; Ashmore & Bell, 1991).

Recent studies concerned with the interactive effects of long-term exposure to CO_2 and O_3 on vegetation and crop production (Kramer *et al.*, 1991; Barnes & Pfirrmann, 1992; Mulchi *et al.*, 1992; Noble *et al.*, 1992; Polle *et al.*, 1993) indicate that CO_2 may have a protective role against O_3 damage. Conversely, O_3 may reduce the beneficial effect of CO_2 enrichment on plant growth. The ability of CO_2 to decrease the O_3-induced stress depends on the sensitivities of the crop to each gas. For example, C_4 crops are less responsive to CO_2 enrichment than C_3 crops (Cure & Acock, 1986). Corn, a C_4 plant, is less sensitive to O_3 than wheat, a C_3 plant (Heagle *et al.*, 1988).

In order to better understand the potential impact of global change on agricultural production, it is important to concentrate research efforts in areas where uncertainties can be reduced (Schneider, 1989). This requires close co-operation and communication among scientists from multiple disciplines (Krupa & Kickert, 1989).

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Model projections of the impact of future atmospheric changes on agriculture (e.g. Adams *et al.*, 1990; Stockle *et al.*, 1992) would appear to be over-estimated, since they only account for the beneficial physiological effect of atmospheric CO_2 enrichment on plant growth under experimental conditions without considering other air quality factors such as O_3 (Barnes & Pfirrmann, 1992). Refinement of crop growth models for predictive purposes should consider interactive effects of elevated CO_2, as well as other important environmental factors such as water availability, temperature and air quality (Allen, 1990; Barnes & Pfirrmann, 1992).

Tropospheric O_3 concentrations are expected to be 50% higher by the year 2020 (Hough & Derwent, 1990). If elevated CO_2 concentrations expected at that time are able to partially counteract the deleterious effects of increased O_3 levels on crop production (Mulchi *et al.*, 1992), it may be inferred that the predicted CO_2 concentrations will have less impact on crop production than those reported based on studies involving CO_2 alone. Future crop losses due to increases in tropospheric O_3 may also be less than predicted. Interactive effects on crop production need to be tested to obtain a better assessment of the joint effects of CO_2 enrichment and O_3-induced stress on crop production (Krupa & Kickert, 1989).

The objective of this study was to investigate the combined effects of long-term exposure to enhanced O_3 and CO_2 concentrations on grain yield, dry biomass, straw, harvest index, and weight per 1000 seeds in two distinctive crop species: winter wheat (i.e. C_3 crop) and corn (i.e. C_4 crop).

MATERIALS AND METHODS

Experimental site and cultural practices

Experiments were carried out at the USDA Beltsville Agricultural Research Center (BARC) at Beltsville, MD. Soft red winter wheat (*Triticum aestivum*) cultivars Massey and Saluda were sown in October 1990 and 1991, respectively, in rows spaced 0.17 m apart at a predicted rate of 600 seeds m^{-2}. In early March 1991 and mid-March of 1992, prior to the beginning of spring growth, 46 kg ha^{-1} of nitrogen (N) in the form of ammonium nitrate was applied. Irrigation was not necessary for the wheat experiments due to normal rainfall amounts and distribution. Two applications of Bayleton® (Mobey Chemical Corporation, Kansas City) at a rate of 0.14 kg ha^{-1} of active material were performed to control powdery mildew (*Erysiphe graminis*) on 12 May (beginning of heading) and 12 June (ripening) in the 1992 wheat study.

A short-statue commercial hybrid of field corn (*Zea mays* cv. Pioneer 3714) was sown on 14 May 1991 in rows spaced 0.50 m apart. Two weeks after emergence, plants were thinned to approximately 30 cm apart within rows, which resulted in a population of 60 000 plants ha^{-1}. Prior to planting, the site was broadcast fertilized with 0–20–30 (NPK) analysis fertilizer at a rate of 504 kg ha^{-1} plus 56 kg ha^{-1} of ammonium nitrate. Pre-emergence herbicide Atrazine 4L® (Dupont De Nemours, Wilmington, DE) was surface-applied to control annual weeds. Artificial irrigation was applied several times during the corn growing season to complement seasonal rainfall.

CO_2 and O_3 treatments

A concentration of about 500 μl $liter^{-1}$ CO_2 was used to assess the effects of CO_2 enrichment on wheat and corn productivity. CO_2 was supplied from cylinder CO_2 and injected into the blowers of the open-top chambers (OTCs) system (Heagle *et al.*, 1973) 12 h per day (0700–1900 h EST) at rates necessary to raise the ambient CO_2 levels by 150 μl $liter^{-1}$ CO_2. The blowers supplied 27 m^3 min^{-1} of air to each chamber. The inflow of CO_2 to each OTC, metered through flow meters, was adjusted at the beginning of each day (0700 h EST) to correct for small CO_2 flow variations. The CO_2 concentration in the inlet air stream was monitored on a biweekly basis inside the plastic duct supplying air to the chambers using an infrared gas analyzer (Beckman Model 315B), which was calibrated with a certified CO_2 standard (600 μl $liter^{-1}$ CO_2) in N_2 gas. Due to the high air flow to the chamber (27 m^3 min^{-1}), it was presumed that the CO_2 concentrations inside the chambers were similar to the CO_2 concentrations inside the plastic duct. However, it is not possible to achieve a perfectly uniform CO_2 concentration, due to the influence of outside environmental conditions on the inside of the OTC.

During the wheat and corn studies in 1991, all OTCs were equipped with charcoal filters, while during the wheat study in 1992, only OTCs assigned to low O_3 treatments were equipped with charcoal filters, due to a limited amount of available charcoal filters in 1992. It was presumed that there was no need to remove other pollutants for the high-O_3 treatments during 1992, since O_3 is by far the most phytotoxic air pollutant in the area. The high-O_3 treatments were attained by injecting O_3 into the blowers of the OTCs for each high-O_3 treatment at rates to provide current ambient O_3 concentrations (which were constantly being monitored at a distance of ~10 m from the experimental site at a height of 1.5 m above the ground) plus an average of 40 nl $liter^{-1}$ O_3, 7 h per day (0900–1600 h EST) from Monday to Friday according to the following protocol: 20, 30, 40, 50, and 60 nl $liter^{-1}$ O_3 were added on Monday, Tuesday, Wednesday, Thursday, and Friday, respectively. No O_3 was supplied during weekends and rain events. This method of O_3 addition differed from that widely followed during the National Crop Loss Assessment Network (NCLAN) program (Heagle *et al.*, 1988) and was an attempt to closer simulate the natural fluctuation of O_3 concentrations in the lower troposphere as shown in Fig. 1. Also, O_3 additions were halted when treatment levels exceeded the current US air quality standard for O_3 (i.e. 120 nl $liter^{-1}$ O_3 h^{-1}) in order that the treatments remain within the maximum allowable exposure of crops to O_3 under current air

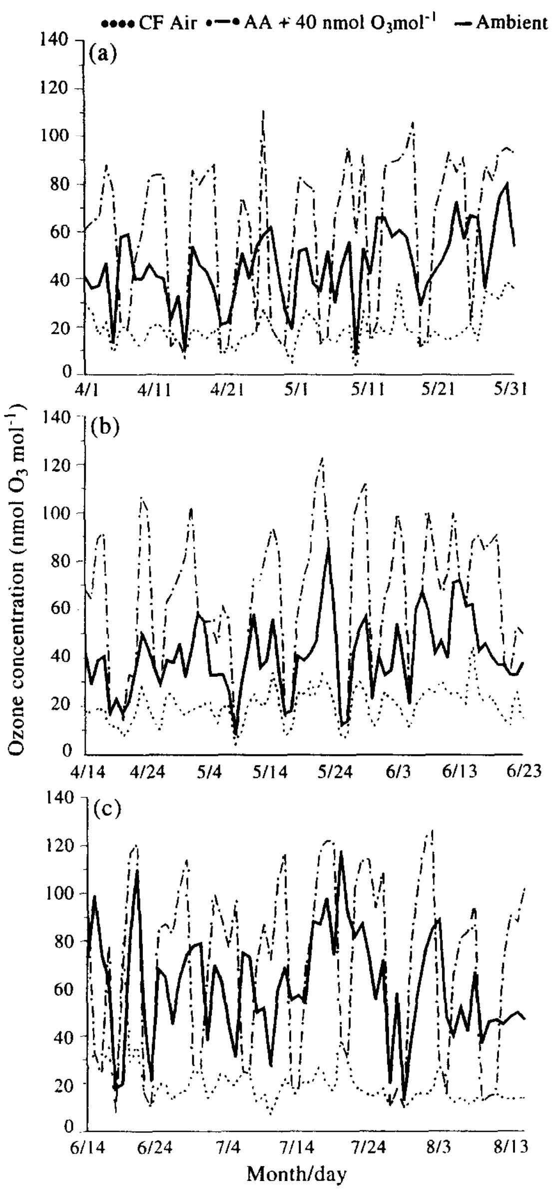

Fig. 1. Mean daily 7-h (0900–1600 h EST) O_3 concentrations for ambient air (AA), charcoal filtered (CF) air and enhanced O_3 (AA + 40 nl liter^{-1} O_3) for wheat in (a) 1991, (b) 1992 and (c) corn in 1991.

quality regulations. For example, on a Thursday, 50 nl liter^{-1} O_3 was supposed to be added on the top of the ambient O_3 concentration, but if this concentration was above 70 nl liter^{-1} O_3 then only less than 50 nl liter^{-1} O_3 was added to stay within the limit of 120 nl liter^{-1} O_3. During the gas dispersion period, air samples from within the chambers were continually drawn from regions about 10 cm above the crop canopy using Teflon® tubing (6.4 mm o.d.) attached to a central vacuum system. The vacuum system was also connected to a solenoid-valve switching device used to serially monitor the O_3 concentrations in each chamber for approximately 4 min each hour. Ambient air O_3 concentrations were monitored 24 h per day throughout the growing season. Treatment O_3 levels during the O_3 fumigation period (0900–1600 h EST) were manually adjusted at the beginning of each hour to equal ambient plus the amounts noted in the dispersing protocol. The mean 7-h O_3 dose during the period of treatment imposition was calculated using the daily means of O_3 concentration, including the periods when no O_3 fumigation was performed (weekends and rain events).

Treatments were arranged in a 2×2 factorial randomized complete block design: (1) charcoal-filtered (CF) air at 350 μl liter^{-1} CO_2 (i.e. control); (2) CF air at 500 μl liter^{-1} CO_2; (3) ambient O_3 + 40 nl liter^{-1} O_3 at 350 μl liter^{-1} CO_2; (4) ambient O_3 + 40 nl liter^{-1} O_3 at 500 μl liter^{-1} CO_2. Winter wheat and corn studies had four and three replicates, respectively. Wheat plants were grown under ambient conditions until 25 March in 1991 and 02 April in 1992. The chambers were then placed on the sites and treatments were initiated. Treatments were terminated at physiological maturity in June for the wheat studies. Corn plants were chambered from 3 weeks after emergence (12 June) until physiological maturity (19 August).

Plant characteristics

At maturity, wheat plants were harvested by being cut at the base. In 1991, three (0.68 m^2) area subsamples per chamber were collected at the centermost region for grain yield and dry biomass determinations. In 1992, due to problems with partial wheat lodging in five chambers, the subsample size was reduced to 0.54 m^2, and two rather than three subsamples were collected per chamber. In both years the subsamples were averaged to obtain a mean value for grain yield and dry biomass per OTC. The warm, dry weather in the late spring of 1991 allowed plants to dry earlier in the field prior to harvest; however, the lower than normal temperatures in 1992 delayed plant drying. Harvest was made soon after physiological maturity to avoid bird damage. Wheat subsamples from both years were dried to constant weight in a greenhouse prior to threshing. Threshing was conducted using a small plot combiner set for wheat. The following characteristics were measured: total dry biomass weight, total grain weight, and 1000-grain weight.

Corn plants were harvested from the center of each chamber (2.0 m×1.8 m area). Ears were covered with paper bags at physiological maturity to avoid bird damage and harvested 4 weeks later. Plants were air-dried in greenhouse to constant weight. Total dry biomass, total grain weight, and 1000-grain weight were determined.

Statistical analysis

Data sets were analyzed with analysis of variance (ANOVA) procedures appropriate for a factorial randomized complete block design using the SAS Statistical Software Package (SAS, 1985). Significances of the CO_2 and O_3 main effects and the CO_2 versus O_3 interactions were identified using F-tests ($p < 0.05$). Data from the two wheat experiments were not combined over years due to cultivar differences between years and also due to the use of charcoal filters in 1991 but not in 1992 for the enhanced O_3 treatments, as explained in the 'CO_2 and O_3 treatments' section.

RESULTS AND DISCUSSIONS

Air quality and seasonal environmental conditions

The seasonal daily 7-h mean (0900–1600 h EST) and the 1-h mean peak O_3 concentration for ambient air (AA), charcoal filtered (CF) air, and AA plus an average of 40 nl liter^{-1} O_3 (5 days per week) for the three crop growing seasons are shown in Table 1. Mean 7-h ambient O_3 concentrations were about 12% higher in the spring of 1991 (45.5 nl liter^{-1} O_3) than in the spring of 1992 (40.7 nl liter^{-1} O_3; Table 1). The 1991 and 1992 wheat seasons had remarkable weather differences, with 1991 being characterized by warm, sunny weather, while 1992 was unseasonably cold with lower solar radiation (Table 2). For instance, during the month of May when heading, flowering, and grain fill occurred for the wheat crop, a difference of more than 5°C in the mean temperature between the two years was registered. The higher ambient O_3 concentrations observed in 1991 are likely to be the result of higher photochemical activity in response to higher solar radiation and air temperatures in 1991. Ambient O_3 levels during the summer months were considerably higher than levels recorded during the early spring, again due to higher solar radiation levels and air temperatures during the summer.

Weekends and a few rainy days accounted for approximately 30% of the days in which O_3 was not fumigated. In spite of the higher ambient O_3 concentrations that occurred in 1991, the high O_3 treatments during the 1992 wheat season had slightly higher O_3 exposure levels (7%; Table 1). This is likely the result of the use of charcoal filters for the high-O_3 treatments in 1991 but not in 1992. It is difficult to evaluate what effects were caused by not using charcoal filters for the high-O_3 treatments in 1992; however, such effects, if any, should be minor since ambient O_3 levels in 1992 were typically below those in 1991 (Table 1 and Fig. 1). High variability in O_3 concentration for the high-O_3 level was experienced in all three crop seasons (Fig. 1) to simulate the natural variability of O_3 concentrations in the troposphere over relative short periods (i.e. days or weeks). The daily 7-h mean O_3 concentrations were, in most cases, not allowed to exceed the 120 nl liter^{-1} O_3 standard (Fig. 1). In all cases, the levels of O_3 in the CF treatments remained below 40 nl liter^{-1} O_3 threshold levels, which causes significant adverse impact on productivity (Heagle *et al.*, 1988; Krupa & Kickert, 1989) for sensitive crops.

Winter wheat productivity

Analysis of variance for the main effects of CO_2 and O_3 on grain yield, above ground dry biomass, harvest index, straw, weight of 1000 seeds, and seeds dm^{-2} for the wheat studies in 1991 and 1992 are illustrated in Tables 3 and 4, respectively. The CO_2-enriched environment had a more pronounced impact on plant characteristics in 1991 than in 1992. Grain yield was increased by 26% in 1991 ($p < 0.01$; Table 3) and by only 15% in 1992 ($p < 0.05$; Table 4). The harvest index (which is the percent of dry biomass converted into harvestable yield) was increased by 9% in 1991 ($p < 0.01$; Table 3), with no change in 1992. This indicates that in 1991 plants were more efficient in converting carbohydrates into harvestable yield under the CO_2-enriched environment.

Table 1. Mean 7 h daytime (0900–1600 h EST) and mean 1 h peak O_3 concentrations for ambient air (AA), charcoal filtered (CF) air and enhanced O_3 air (AA + 40 nl liter^{-1} O_3) for wheat in 1991 and 1992 and corn in 1991

Crop season	Period	Statistic[a]	Air quality: Ambient air 7 h Mean	1 h Peak	CF air 7 h Mean	1 h Peak	AA + 40 nl liter^{-1} C_3 7 h Mean	1 h Peak
Wheat	01 Apr. to 31 May	Mean	45.5	55.6	18.6	21.9	60.7	67.7
(1991)		SD	15.6	18.8	7.8	9.6	31.2	37.6
Wheat	14 Apr. to 23 June	Mean	40.7	51.0	20.2	24.1	64.8	77.1
(1992)		SD	15.2	19.7	7.4	9.7	29.0	33.1
Corn	14 June to 15 Aug.	Mean	60.8	80.6	19.8	22.8	70.2	81.5
(1992)		SD	22.6	28.6	10.4	8.4	38.5	44.7

[a]Estimated using daily means. Ozone concentrations for weekends and rain event were also used to obtain the mean O_3 concentrations.

Table 2. Summary of monthly precipitation, mean temperature, and mean daily solar radiation from March to August 1991 and 1992

	Precipitation (mm)			Mean temperature (°C)[a]			Mean daily solar radiation (MJ m^{-2})	
	1991	1992	Long term average	1991	1992	Long term average	1991	1992
March	77	0	89	7.8	5.6	5.5	11.8	11.6
April	28	1	86	13.1	11.4	13.2	15.3	14.3
May	17	195	97	20.9	15.5	16.6	21.5	17.2
June	41	42	99	22.8	20.7	21.3	20.7	20.2
July	38	251	105	25.2	24.3	24.0	18.3	17.3
August	26	50	120	24.4	21.5	23.3	18.5	16.9

[a](Max. temp + min. temp)/2.

Rudorff *et al.* (1996) showed that net leaf photosynthesis rates were consistently higher in 1991 compared with 1992. The low temperatures in 1992, particularly in May (Table 2), reduced growth and might have contributed significantly to the lower CO_2 response in 1992. Weight per 1000 seeds was increased by 9% in both years, although the increase in 1991 was of borderline significance ($p = 0.06$; Table 3). This might indicate that CO_2 enrichment increased carbohydrate translocation from source (leaves and stems) to sink (grain). Seeds dm^{-2} was increased by 17% ($p < 0.05$) under the CO_2-enriched environment in 1991 (Table 3), but no change was observed in 1992 (Table 4). Number of seeds per spike was not changed significantly by the CO_2 factor in either year (data not shown; Rudorff, 1993).

It is interesting to note that in 1991 chronic O_3 exposure also had a greater impact on wheat plant characteristics. Grain yield was decreased by 15% in 1991 ($p < 0.01$; Table 3) and by 11% in 1992 ($p < 0.05$; Table 4). The impact of chronic O_3 exposure on leaf photosynthesis and stomatal conductance (Rudorff *et al.*, 1996) was not as remarkable as it was on plant characteristics in either year. Decrease in harvest index was of borderline significance in 1991 (6%; $p < 0.10$; Table 3) and was not changed in 1992 (Table 4). Seed weight was decreased by 11% in 1991 ($p < 0.05$; Table 3) and by 6% in 1992, although this decrease was of borderline significance ($p = 0.07$; Table 4). It is possible, but not proven, that plants under chronic O_3 exposure are somewhat limited in translocating the products of photosynthesis to harvestable yield.

No significant interaction of CO_2 versus O_3 were noted in wheat plant characteristics except for grain yield in 1991, although the interaction was of borderline significance ($p = 0.08$). This might indicate that the negative impact of chronic O_3 exposure was more than counteracted by the beneficial effect of CO_2 enrichment. Visual O_3 symptoms were considerably less for wheat plants grown under enriched CO_2, and it is likely that the less O_3-injured plants from the enriched CO_2 environment were more efficient in translocating carbohydrates from source (leaves and stems) to sink (grains); consequently, grain yields were less affected by O_3 when plants were growing under enriched CO_2 atmosphere. As previously shown, seeds dm^{-2} was increased by 17% under the CO_2-enriched environment in 1991 (Table 3), which is likely due to an increase in secondary productive tillers. This, perhaps, is the major contributor to the

Table 3. Summary of the main effects of CO_2 enrichment and O_3 exposure stress on plant characteristics for wheat in 1991

Factors: CO_2	Factors: O_3	Grain yield ($g\ m^{-2}$)	Dry biomass ($g\ m^{-2}$)	Straw ($g\ m^{-2}$)	Harvest index (%)	Weight per 1000 seeds (g)	Number of seeds (dm^{-2})
Ambient	—	476	1392	916	34.2	30.4	156
+ 150 μl liter^{-1} CO_2	—	600	1606	1006	37.3	33.2	182
RC (%)[a]		26	15	10	9	9	17
—	CF	582	1583	1001	36.8	33.7	173
—	+40 nl liter^{-1} O_3	494	1416	922	34.7	29.9	165
RC (%)		−15	−11	−8	−6	−11	−5
Analysis of variance, F-*values*							
CO_2		47.6**	19.2**	5.3*	11.9**	4.8 NS	7.2*
O_3		24.1**	11.7**	4.2 NS	4.8 NS	8.9*	0.6 NS
CO_2 versus O_3		3.9 NS	2.2 NS	0.9 NS	1.1 NS	0.3 NS	1.0 NS
CV (%)		6.7	6.5	8.0	5.4	8.01	1.2

*, ** Significant at the 0.05 and 0.01 levels, respectively; NS, not significant at $p \leq 0.05$.
[a]RC, relative change for CO_2 factor (enriched CO_2 over ambient CO_2) and O_3 factor (enhanced O_3 over CF air).

Table 4. Summary of the main effects of CO_2 enrichment and O_3 exposure stress on plant characteristics for wheat in 1992

Factors: CO_2	Factors: O_3	Grain yield ($g\ m^{-2}$)	Dry biomass ($g\ m^{-2}$)	Straw ($g\ m^{-2}$)	Harvest index (%)	Weight per 1000 seeds (g)	Number of seeds (dm^{-2})
Ambient	—	477	1406	929	33.9	31.5	151
+ 150 μl liter^{-1} CO_2	—	547	1533	986	35.7	34.2	160
RC (%)[a]		15	9	6	5	9	6
—	CF	541	1541	1000	35.1	33.9	160
—	+40 nl liter^{-1} O_3	483	1399	916	34.5	31.8	151
RC (%)		−11	−9	−8	−2	−6	−6
Analysis of variance, F-*values*							
CO_2		9.9*	3.9 NS	1.2 NS	1.9 NS	6.8*	1.6 NS
O_3		6.8*	4.9 NS	2.6 NS	0.5 NS	4.2 NS	1.5 NS
CO_2 versus O_3		1.7 NS	0.8 NS	0.3 NS	0.4 NS	0.0 NS	1.9 NS
CV (%)		8.7	8.8	10.8	7.0	6.3	8.7

*, ** Significant at the 0.05 and 0.01 levels, respectively; NS, not significant at $p \leq 0.05$.
[a]RC, relative change for CO_2 factor (enriched CO_2 over ambient CO_2) and O_3 factor (enhanced O_3 over CF air).

borderline significant interactive effect of CO_2 versus O_3 on wheat grain yields in 1991. Studies in which only the CO_2 enrichment factor was considered also reported an increase in productive tillers (Gifford, 1977; Sionit *et al.*, 1981; Havelka *et al.*, 1984; Chaudhuri *et al.*, 1986, 1987; Hocking & Meyer, 1991), while in studies in which only the O_3 factor was considered a decrease in productive tillers was noted (Heagle *et al.*, 1979*b*; Kress *et al.*, 1985). Proportionally greater decreases in grain yield than in straw or dry biomass were also observed by Lehnherr *et al.* (1987) and Mulchi *et al.* (1986), indicating that O_3 had a greater impact on reproductive than vegetative components of the plant. The patterns for increased number of productive tillers with increased atmospheric CO_2 were likely the result of increased photosynthetic rates under both O_3 exposure regimes (Rudorff *et al.*, 1996). The amounts of photosynthate supplied by the source appear insufficient to meet sink demands during grain fill, especially during high levels of O_3 exposure. The increase in grain yield under the increased CO_2 level is most likely reflecting the combined effect of increased weight of seeds and number of productive tillers per unit area.

From the discussion above and based on data presented in Tables 3 and 4, it is observed that the beneficial effect of CO_2 enrichment typically offsets the negative impact of chronic O_3 exposure with no significant interaction of CO_2 versus O_3. Similar results were also observed for soybeans (Mulchi *et al.*, 1992) and radish (Barnes & Pfirrmann, 1992).

Table 2 shows that below normal rainfall amounts occurred in April–June 1991 and March, April, and June 1992. However, no visual symptoms of moisture stress were apparent in either study. Therefore, the amounts of available water in the Cordorus silt form soil in the experimental site in BARC (Lee *et al.*, 1982) were sufficient to maintain adequate plant moisture levels for prolongated periods during each spring. Even though distinct wheat cultivars were used in each wheat study and considerable differences in mean ambient temperatures were observed during the two growing seasons, plant biomass and grain yields were similar in the two studies (Tables 3 and 4).

Corn productivity

The effects of CO_2 enrichment and O_3 stress on grain yield, above ground dry biomass, harvest index, straw and 1000-seed weight for corn are illustrated in Table 5. CO_2 enrichment caused no change in corn plant characteristics, except for seed weight, which was slightly decreased (2%), although the difference was of borderline significance ($p=0.11$).

Decreases of borderline significance in grain yield (9%; $p<0.10$; Table 5) and dry biomass (6%; $p=0.11$; Table 5) were observed in response to chronic O_3 exposure. Harvest index was decreased by 3% ($p<0.05$) in response to O_3 exposure. It was also noted that plants grown under chronic O_3 exposure produced fewer kernels per cob (data not shown). However, the grain yield loss due to decreased pollination under O_3 exposure stress was partially compensated by an increase of 3% in seed weight ($p<0.05$; Table 5). Fewer kernels per cob under chronic O_3 exposure at ambient CO_2 was noted by Heagle *et al.* (1972) and Kress and Miller (1984). It is likely that the major impact of O_3 exposure in corn occurred during the flowering process. Mumford *et al.* (1972) reported that pollen germination was decreased by O_3 stress.

The CO_2 versus O_3 interaction was not significant for any plant characteristic in corn (Table 5). Based on several studies on CO_2 enrichment in corn under low O_3, Cure and Acock (1986) reported grain yield and dry biomass increases of 29 and 9%, under a doubling of ambient CO_2 concentration (680 μl liter^{-1} CO_2), respectively. Rogers *et al.* (1983) reported an increase in dry biomass of almost 50% under CO_2-doubling. However, a study from Hocking and Meyer (1991) reported that corn was not sensitive to CO_2 enrichment. Similar results were also noted by Surano and Shinn (1984) for corn grown in the field in OTC. In the present study, some inconsistencies may be associated with exposure conditions in the open-top chambers. Since treatment gases enter the chambers through the lower half, they would be expected to have their maximal effect during the early vegetative growth stages. Grain yield in corn is mainly associated with photosynthetic activities in the

Table 5. Summary of the main effects of CO_2 enrichment and O_3 exposure stress on plant characteristics for corn in 1991

Factors: CO_2	Factors: O_3	Grain yield (g m^{-2})	Dry biomass (g m^{-2})	Straw (g m^{-2})	Harvest index (%)	Weight per 1000 seeds (g)
Ambient	—	1167	2005	838	58.2	333
+150 µl liter^{-1} CO_2	—	1210	2079	869	58.2	327
RC (%)[a]		4	4	4	0	−2
—	CF	1244	2103	859	59.2	325
—	+40 nl liter^{-1} O_3	1133	1981	848	57.2	335
RC (%)[a]		−9	−6	−1	−3	3
Analysis of variance, F-*values*						
CO_2		0.8 NS	1.3 NS	2.8 NS	0.0 NS	3.7 NS
O_3		5.0 NS	3.5 NS	0.3 NS	7.4*	10.6*
CO_2 versus O_3		0.3 NS	1.1 NS	4.5 NS	0.5 NS	0.4 NS
CV (%)		7.2	5.5	3.8	2.1	1.6

*, ** Significant at the 0.05 and 0.01 levels, respectively; NS, not significant at $p \leq 0.05$.
[a]RC, relative change for CO_2 factor (enriched CO_2 over ambient CO_2) and O_3 factor (enhanced O_3 over CF air).

leaves in the canopy which receive the highest light levels. The uppermost leaves were near the top of the chamber, where the CO_2-enriched air may have been diluted by the lower ambient CO_2 concentrations, especially during windy conditions. Therefore, corn may not have received the maximal benefit of the CO_2 enrichment during grain fill. Conversely, ambient O_3 concentrations may have enhanced the O_3 effect in the upper part of the canopy, especially on weekends when no O_3 was added. The use of very short-statue corn or taller OTCs should be considered in future research with corn.

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