Growth, Radiation Use Efficiency, and Canopy Reflectance of Wheat and Corn Grown under Elevated Ozone and Carbon Dioxide Atmospheres

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*Estimates of increases in future agricultural production in response to increases in carbon dioxide (CO_2) concentrations in the atmosphere are often based on the beneficial physiological effect of CO_2 enrichment on plant growth, especially in C_3 plants. However, these estimates fail to consider the negative impact of ozone (O_3) air pollution on crop production. Increases in tropospheric concentrations of both gases, CO_2 and O_3, have been observed over the past century, and both are predicted to continue to increase at even higher rates in the near future to levels when they may have a significant impact on agricultural production. Field studies with wheat (*Triticum aestivum *L.) in 1991 and 1992, and corn (*Zea mays *L.) in 1991 were conducted using open-top chambers to mimic atmospheric concentrations of CO_2 ($\sim 500\ \mu L^{-1}$ CO_2) and O_3 (~ 40 nL L^{-1} O_3 above ambient air [O_3] during 7 h day^{-1}, 5 days $week^{-1}$) that are predicted to occur at the Earth's surface during the first half of the 21st century. Wheat and corn (C_3 vs. C_4) produced clearly different responses to CO_2 enrichment, but similar responses to O_3 exposure. In wheat, O_3 exposure led to reduced grain yield, biomass, and radiation use efficiency (RUE, phytomass production per unit of energy received); in both years; but reduction in accumulated absorbed photosynthetically active radiation (AAPAR) was observed only in 1991. Conversely, CO_2 enrichment produced greater grain yield, dry biomass, and RUE. With CO_2 enrichment, the O_3-induced stress to wheat plants was apparently ameliorated since responses were equivalent to the control group (low O_3 and ambient CO_2) for all variables. In contrast, corn demonstrated no benefit to CO_2 enrichment for measured variables, and corn grain yield was the only parameter negatively influenced by O_3 exposure that is attributed to O_3-induced damage during the flowering process. Additionally, no treatment differences were observed for leaf area index (LAI) as determined nondestructively using the LICOR LAI-2000 Plant Canopy Analyzer. Also, treatment differences for normalized difference vegetation index (ND) were only observed for wheat plants from the high-O_3 and ambient-CO_2 treatment, at some growing stages. Otherwise, ND data were not helpful for identifying damage due to O_3 fumigation or benefits due to CO_2 enrichment. Significant interactive effects of CO_2 vs. O_3 were observed only for wheat grain yield in 1991 (*$p < 0.10$*), indicated that the detrimental effect of O_3 air pollution was more than overcome under the CO_2-enriched environment.*

INTRODUCTION

It is widely accepted that both CO_2 and O_3 have concurrently increased in concentration in the troposphere over the past century and are expected to continue to increase at even higher rates to levels where they may have a significant impact on crop production (Krupa and Kickert, 1989). Much attention has been given to separate effects of CO_2 and O_3 with respect to plant

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characteristics, as was recently reviewed by Rudorff (1993). However, insufficient attention has been given to the joint effects of these gases on vegetation (Krupa and Kickert, 1989; Ashmore and Bell, 1991; Allen, 1990; Kimball, 1986). Only a few studies available in the literature are concerned with the interactive effects of long-term exposure to CO_2 and O_3 on vegetation (Barnes and Pfirrmann, 1992; Polle et al., 1993; Noble et al., 1992), and even fewer address crop production (Mulchi et al., 1992). Mulchi et al. (1992) showed that the combined effects of enhanced CO_2 and O_3 on soybean grain yield were largely additive (i.e., independent), which means that the CO_2 enriched environment was able to counteract the negative impact of O_3 on growth and yields. Similar conclusions were also drawn by Barnes and Pfirrmann (1992) for the dry weight of radish plants. From these studies, it seems that CO_2 has a protective role against O_3 damage while, conversely, O_3 reduces the beneficial effect of CO_2 enrichment on plant growth. The ability of CO_2 to counteract O_3-induced stress on plants will be determined not only by the CO_2 concentration and the plant response to CO_2 enrichment but also by the magnitude of the O_3-induced stress (Cure and Acock, 1986; Heagle et al., 1988).

To better understand the impact of global change on agricultural production, it is important to concentrate research efforts in areas where uncertainties can be reduced (Schneider, 1989), and this will require close cooperation and communication among scientists from multiple disciplines (Krupa and Kickert, 1989). Projections of global impacts often account for the beneficial physiological effect of atmospheric CO_2 enrichment on plant growth without considering the air quality factor (Mulchi et al., 1992; Barnes and Pfirrmann, 1992). These projections are also based on results from plants grown under experimental conditions. Refinement of crop growth models for predictive purposes cannot be made before interactive studies of elevated CO_2 and other important environmental factors such as water availability, temperature, and air quality are better understood (Allen, 1990; Barnes and Pfirrmann, 1992). Therefore, published projections of global climate change impact on agriculture (e.g., Adams et al., 1990; Stockle et al., 1992) may be overestimated.

Remote sensing techniques have potential value for estimating important crop parameters, over large areas, related to growth and yield that are manifested in the multispectral crop canopy reflectance (Bauer, 1985). Daughtry et al. (1992) demonstrated that the fraction of absorbed photosynthetically active radiation (f_A) can be estimated with canopy reflectance measurement. Unsworth et al. (1984) and Leadley et al. (1990) observed a significant decrease in the radiation use efficiency (RUE; phytomass production per unit of energy received) in soybean plants exposed to enhanced O_3 concentration (~ 100 nL L^{-1} O_3). Their studies were based on measured fraction of intercepted radiation (f_I); however, fraction of absorbed solar radiation used in photosynthesis ("biologically effective" f_A) rather than intercepted energy by the crop canopy is likely to yield better results due to the nature of O_3 exposure stress on vegetation (decreased chlorophyll content and visual leaf injury). In general, differences between the fraction of intercepted energy f_I and f_A for healthy crops are less than 4% when measured by traditional approaches (Daughtry et al., 1992). Multispectral vegetation indices respond to the photosynthetically active portion of the canopy; therefore, they offer a superior method for evaluating the biologically effective f_A (Daughtry et al., 1992; Pinter, 1993). Reduced chlorophyll content and early senescence caused by O_3 exposure are likely to reduce the seasonally accumulated absorbed PAR, which should be related to reduced biomass production. However, the efficiency with which the absorbed radiation is converted to dry matter production should be approached with caution (Demetriades-Shah et al., 1992). Light absorption is only one of many variables related to the production of biomass. For example, both O_3 and CO_2 have important roles in many physiological and biochemical processes not related to the light absorption process, which may impose limitations on the use of remote sensing techniques to detect effects of O_3 and CO_2 on crop growth and yield. Therefore, remote sensing data should be used in combination with weather and other ancillary data to increase the capability to identify specific types of stress and how they relate to biomass and yield production (Bauer, 1985).

The objectives of this study were to investigate the combined (i.e., interactive) effects of long-term exposure to O_3 air pollution and CO_2 enrichment on two distinctive crop species: winter wheat (C_3 crop) and corn (C_4 crop) grown in open-top field chambers. Information of interest include: leaf area index and canopy reflectance during the crop growing season; radiation use efficiency over the crop growing season; and above-ground dry biomass and grain yields at harvest.

MATERIALS AND METHODS

Experimental Site and Atmospheric Treatments

Experiments were carried out at the United States Department of Agriculture (USDA) / Beltsville Agriculture Research Center (BARC) at Beltsville, Maryland. Soft red winter wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.) were chosen as models for their major relevance to world agricultural production. Winter wheat was sown in October of 1990 (cv. Massey) and 1991 (cv. Saluda) in rows spaced 0.17 m apart with a seed rate of 3.3 g m^{-1} of row. Wheat row direction was north–south in 1990/91 and east–west in 1991/92. A short-statue hybrid of field corn (cv. Pioneer 3714) was

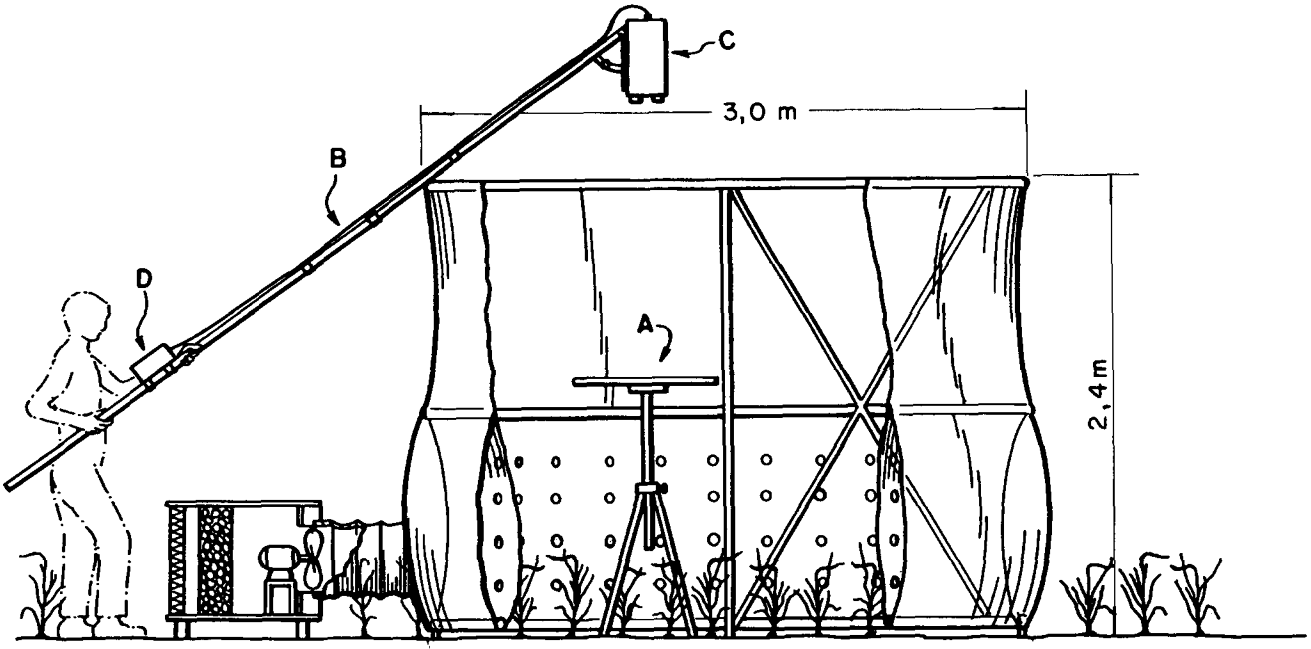

Figure 1. Arrangement for spectral measurements within open-top chambers: A) reference panel supported by a camera tripod; B) boom; C) spectroradiometer; D) data logger.

sown on 14 May 1991 in rows spaced 0.5 m apart. Plants within rows were 30 cm apart which resulted in a population of 60,000 plants ha^{-1}. Row direction for the corn study was north–south. Irrigation water was applied several times during the corn growing season to supplement seasonal rainfall.

Plants were grown in open-top chambers (OTCs; Fig. 1; Heagle et al., 1973) in the field under controlled atmospheric environments predicted to occur during the first half of the coming century in terms of O_3 (Hough and Derwent, 1990) and CO_2 (Schneider, 1989). Fumigation with gases was performed to simulate realistic environmental conditions (Rudorff, 1993). Two levels of O_3 and two levels of CO_2 were arranged in a 2×2 factorial randomized complete block design. Low levels of O_3 were achieved by filtering the air through charcoal filters. High levels of O_3 were achieved by adding a mean concentration of ~ 40 nL L^{-1} O_3 on the top of the existing ambient air O_3 concentrations during 7 h day^{-1}, 5 days $week^{-1}$, from early growth until physiological maturity. To mimic the natural O_3 concentration dynamic in the ambient air, O_3 was dispersed to the OTCs from Monday through Friday during 7 H (09:00–16:00 h EST) according to the following protocol: 20 nL L^{-1} O_3, 30 nL L^{-1} O_3, 40 nL L^{-1} O_3, 50 nL L^{-1} O_3, and 60 nL L^{-1} O_3 were added on Monday, Tuesday, Wednesday, Thursday, and Friday, respectively (Rudorff, 1993). Fumigation with O_3 was not performed on rainy days. Also, O_3 fumigation was not allowed to exceed the National Ambient Air Quality Standard (120 nL L^{-1} O_3). Charcoal filters were used in all OTCs during the wheat and corn studies of 1991 while during the wheat study of 1992 the ambient air was filtered only for treatments with low-O_3 level. Therefore, wheat and corn plants from high-O_3 treatments were exposed to charcoal filtered air (CF) during the weekends and whenever O_3 fumigation was not performed in 1991, while in the wheat study of 1992 plants were exposed to ambient air during the weekends and outside the time frame of O_3 fumigation (16:00–09:00 EST) when ambient O_3 concentrations are in general below the threshold for O_3 damage to wheat (30 nL L^{-1} CO_3; Adams et al., 1988; Fig. 3). The CO_2 levels consisted of ambient CO_2 (~350 μL L^{-1} CO_2) and enriched CO_2 (~500 μL L^{-1} CO_2). Carbon dioxide enrichment was performed during 12 h day^{-1} (07:00–19:00 h EST). Treatments were as follows; 1) low-O_3 and ambient-CO_2 (i.e., control); 2) high-O_3 and ambient-CO_2; 3) low-O_3 and enriched-CO_2; 4) high-O_3 and enriched-CO_2. See Table 1 for actual 7-h mean (09:00–16:00 EST) and 1-h mean peak O_3 concentrations during the crop growing seasons. The winter wheat and corn studies had four and three block replicates, respectively. Wheat plants were enclosed in the chambers shortly after spring growth began and corn plants were enclosed in the chambers 3 weeks after emergence, when treatments were initiated. The fumigation treatments were terminated at physiological maturity of the wheat and corn plants.

Leaf Area Index

Nondestructive leaf area index (LAI) measurements were taken under overcast sky conditions with the Plant

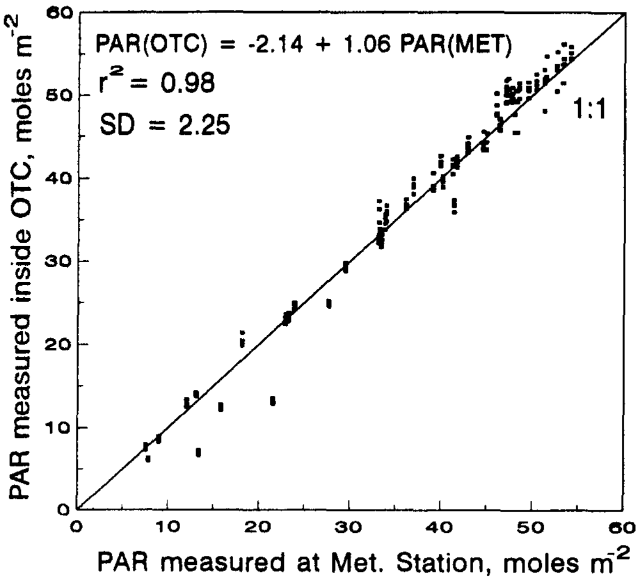

Figure 2. Relationship between incident PAR (I_0) measured inside four open top chambers (OTCs) and I_0 measured at a meteorological station close to the experimental site.

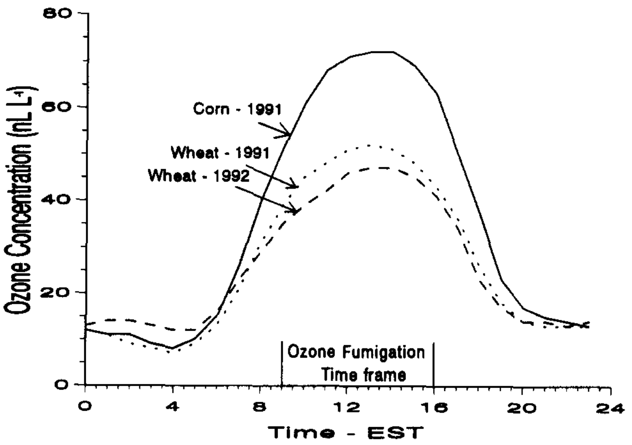

Figure 3. Diurnal pattern of the mean hourly ambient O_3 concentrations for wheat and corn studies. Values were averaged over the respective crop-year periods presented in Table 1.

Canopy Analyzer[1] (Model LAI-2000, LI-COR, Lincoln, Nebraska). The instrument estimates LAI as a function of incoming diffuse solar radiation at the top and at the bottom of the canopy. Pinter (personal communication, 1995) observed that the LAI-2000 underestimated absolute wheat LAI by 25–30% but provided good comparative LAI data in their free air CO_2 enrichment (FACE) experiment. The instrument is sensitive to both green and brown elements in the canopy, and it is likely to provide a relative overestimate of green LAI for plants with leaf injury caused by high-O_3 exposure. Due to the small amount of plant material within each OTC, it was not possible to compare the LAI-2000 measurements with absolute LAI.

During the wheat studies the LAI-2000 measurements were performed on a weekly basis at fixed positions within the individual chambers (three samples per OTC) from early growth until maximum LAI was reached at the beginning of heading (stage 10.1). Leaf area index measurements for the corn experiment were also performed on a weekly basis from growth stage 1.5 (sixth leaf fully emerged) until shortly after maximum LAI was reached at growth stage 6.0 (12 days after silking). These weekly LAI data were linearly interpolated to estimate LAI on days coincident with spectral canopy reflectance measurements described below.

Canopy Reflectance

Spectral reflectance measurements of the canopy were made on 11 dates for wheat and nine dates for corn at approximately weekly intervals, weather permitting, from early vegetative stages until maturation. An Exotech radiometer (Model 100 BX, Exotech Inc., Bethesda, Maryland) with a 15° field of view was used to obtain canopy reflected radiance values in four spectral bands similar to the Landsat TM bands (i.e., 450–520 nm, 520–600 nm, 630–690 nm, and 760–900 nm). The radiometer was mounted on the upper end of a hand-held boom, elevated approximately 3.0–3.6 m above the soil, and leveled for a nadir view as illustrated in Figure 1. The field of view was a circular area of about 0.7 m in diameter at the beginning of the growing season, but decreased as the plants grew. Four readings per OTC, around the center of the chamber, were acquired to minimize sampling errors due to the small field of view (Daughtry et al., 1982) and also to minimize specular reflection from the chamber plastic. Measurements were taken under clear skies (i.e., no clouds near solar disc) around solar noon to avoid shade projections from the chamber walls on the center part of the canopy. During the experiments of 1991 spectral reflectance measurements were also obtained in four wheat and three corn chambers without the bottom plastic walls of the OTCs (ambient-CO_2 and -O_3 concentrations) that could mostly influence the reflectance measurements due to specular reflectance of the inflated bottom chamber walls. These measurements were performed to estimate the influence of the specular reflection on the canopy reflectance measurements and to demonstrate the feasibility of using remote sensing techniques for plants grown in OTCs.

Canopy reflectance factor (RF) was calculated as the ratio of the reflected radiance from vegetation to that reflected from a reference panel. The reference panel was barium sulfate and maintained in a horizontal position above the canopy within one of the OTC (Fig. 1). Measurements over the reference panel were repeated at intervals of approximately 5–10 min. Reflec-

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[1] Company and trade names are given for the benefit of the reader and do not imply any endorsement of the product or the company.

Table 1. 7-h Mean (9:00 to 16:00 EST) and 1-h Mean Peak O_3 *Contentrations* ($nL\ L^{-1}$) *for Ambient Air (AA), Low* O_3 *(Charcoal-Filtered Air) and High-*O_3 *(AA* + *40* $nL\ L^{-1}$ O_3 *during 7 h* day^{-1}, *5 days* $week^{-1}$) *for the Wheat and Corn Experiments*

			Air Quality						
			Ambient		*Low-*O_3		*High-*O_3		$\Delta[O_3]$ *High-*O_3*–AA*
Crop-Year	*Period*	*Statistic*[a]	*7-h Mean*	*1-h Peak*	*7-h Mean*	*1-h Peak*	*7-h Mean*	*1-h Peak*	*7-h Mean*
Wheat-1991	1 Apr–31 May	Mean	45.5	55.6	18.6	21.9	60.7	67.7	15.2
		SD	15.6	18.8	7.8	9.6	31.2	37.6	
Wheat-1992	14 Apr–23 Jun	Mean	40.7	51.0	20.2	24.1	64.8	77.1	24.1
		SD	15.2	19.7	7.4	9.7	29.0	33.1	
Corn-1991	14 Jun–15 Aug	Mean	60.8	80.6	19.8	22.8	70.2	81.5	9.4
		SD	22.6	28.6	10.4	8.4	38.5	44.7	

[a] SD = standard deviation.

tance factor values acquired on 11 dates throughout the 1991 and 1992 growing season were converted to the normalized difference vegetation index (ND; Tucker, 1979).

Radiation Use Efficiency

Radiation use efficiency in this study was used to relate dry biomass production to energy received by the crop and has units g MJ^{-1}. To assess the accumulated absorbed PAR over the crop growing seasons, we first used the canopy reflectance data (transformed to ND) to estimate the fraction of absorbed PAR (f_A) based on a linear empirical relationship between ND and f_A) developed for corn and soybeans by Daughtry et al. (1992):

$$f_A = -0.205 + 1.254\ \mathrm{ND}. \qquad (1)$$

The authors suggested that the relationship could also be used to estimate f_A for other crops and that variances observed in the ralationship appears to originate in the ND of bare soil. Since the present study was performed on the same soil type as for one of the experiments carried out by Daughtry et al. (1992), we used the relationship shown in Eq (1) not only to estimate f_A for the corn experiment but also for the wheat experiments. Further, Eq. (1) is quite similar to the equation obtained by Asrar et al. (1984) for wheat ($f_A = -0.109 + 1.253$ ND).

Incident PAR (I_0) measurements from a meteorological station close to the experimental site were related to I_0 measurements inside four OTCs during the wheat study of 1992 over a period of 47 days (day of year 128 to 176; Fig. 2). The close 1:1 relationship suggested that the I_0 measurements from the meteorological station were a good estimate of the I_0 inside the OTCs. Therefore, I_0 measurements from the meteorological station were used in both years (1991 and 1992) without performing any correction due to radiation attenuation by the plastic wall of the OTC.

Using f_A from Eq. (1) and the I_0 from the meteorological station, absorbed PAR (APAR) could then be estimated as

$$\mathrm{APAR} = f_A I_0, \qquad (2)$$

according to the methods presented by Daughtry et al. (1992).

Daily APAR was obtained through linear interpolation since canopy reflectance readings were obtained only on a weekly basis. Also, bare soil reflectance data were included in the analysis to interpolate data between emergence and first canopy reflectance measurements. This allowed us to obtain APAR values from emergence to physiological maturity which were integrated to estimate the seasonal accumulated APAR. Finally, the RUE could be assessed:

$$\mathrm{RUE} = \frac{\text{above ground dry biomass}}{\text{accumulated APAR}} \quad (\mathrm{g\,MJ^{-1}}). \qquad (3)$$

Plant Characteristics and Statistical Procedure

Whole wheat and corn plants were harvested at maturity. Total above ground dry biomass and grain weight were measured. Data were analyzed using analysis of variance (ANOVA) procedures appropriate for randomized complete block design with two factors. Mean differences among the four treatments were evaluated by the least significant difference (LSD) method. All statistical analysis were performed using the software developed by Statistical Analysis System (SAS; SAS Institute, Cary, North Carolina.

RESULTS AND DISCUSSION

Air Quality and Environmental Conditions

The 7-h mean (09:00–16:00 EST) and the 1-h mean peak O_3 concentration for both ambient air (AA) and chamber air quality (low- and high-O_3 levels) for the wheat and corn studies are contained in Table 1. During the wheat growing seasons of 1991 and 1992 the 7-hour mean O_3 concentration for the high-O_3 level was 15.2 $nL\ L^{-1}$ O_3 (33%) and 24.1 $nL\ L^{-1}$ O_3 (59%) above ambient air (AA) O_3 concentration, respectively (Table 1). This remarkable difference between the two wheat growing seasons is mainly due to the use of charcoal

Table 2. Summary of Meteorological Conditions for the Wheat and Corn Experimental Periods

Crop-Year	*Period*	*Air Temperature (°C)* *Min*	*Max*	*Mean*	*Radiation ($MJ\ m^{-2}$)*	*Rainfall (mm)*
Wheat-1991	1 Apr–31 May	11.0	22.8	17.1	18.5 day^{-1}	46
Wheat-1992	14 Apr–23 Jun	11.0	21.6	16.4	16.8 day^{-1}	232
Corn-1991	14 Jun–15 Aug	19.3	29.8	24.6	18.7 day^{-1}	94

filters (CF) in all OTCs in 1991 while in 1992 the incoming air was only filtered in OTCs subjected to low-O_3 treatments. Therefore, during the weekends, when O_3 fumigation was not performed, wheat plants from the high-O_3 treatments were exposed to CF air in 1991 and to AA in 1992. The influence of the use of charcoal filters on plants treated with high-O_3 air is expected to be minor since it affected only lower levels of O_3 (Rudorff, 1993). The 7-h mean O_3 concentration for the high-O_3 level during the corn study was only 9.4 nL L^{-1} O_3 (15%) above AA (Table 1), which is the result of frequent halted O_3 fumigation in order to stay within the limits of the air quality standard (120 nL L^{-1} O_3). The charcoal filters effectively reduced the seasonal 7-h mean ambient O_3 concentrations in all seasons (Table 1) to levels below the threshold for O_3 damage to wheat and corn (Adams et al., 1988).

The diurnal pattern of the mean hourly ambient O_3 concentration for the wheat and corn studies are illustrated in Figure 3. Hourly O_3 concentrations for ambient air, over the time frame from 9:00 to 16:00 EST, during the corn season were considerably higher than levels recorded during the spring (Fig. 3). due to the higher solar radiation levels during the summer months (Table 2). The two wheat growing seasons had substantial weather differences with 1991 being characterized by warm and sunny weather while 1992 was unseasonably cool with lower solar radiation (Table 2). The wheat crop appeared to develop approximate 2–3 weeks faster in 1991 than in 1992 (Table 3).

Winter Wheat

No treatment effect was observed for LAI during any measurement date in either 1991 or 1992, where mean maximum LAI were 5.6 and 4.6, respectively (Fig. 4). The difference in LAI between years is likely due to the combined effects of interyear weather differences and/or the use of different cultivars in each study. Reduction in green leaf area in response to visually noticeable O_3 symptoms in the high-O_3 treatments was not detected with the LI-2000 canopy analyzer, since no distinction between green and senesced leaf material is possible with this instrument.

Canopy reflectance data transformed to the normalized difference vegetation index (ND) showed significantly lower values for plants grown under the high-O_3 level. Reduced ND values were coincident with the appearance of visual O_3 symptoms on wheat leaves in both years; however, plants were more sensitive to O_3 fumigation in 1991 than in 1992, where first O_3 symptoms appeared 30 days later than in the previous year (Fig. 5). This might be attributed to differences in cultivar sensitivity to O_3 exposure. Late in the season, after physiologic maturity, ND values were not influenced by O_3 exposure. The canopy spectral ratio was not sensitive enough to detect the increased biomass observed in plants from the CO_2-enriched treatments, possibly because ND values tended to reach their maximum values at LAI around 3.5, which was considerably below the maximum LAI for wheat. Figure 5a (wheat 1991) also presents mean ND values for the chambers without the bottom inflated plastic wall (ambient-CO_2 and -O_3), and results indicate that ND values were not significantly influenced by the OTCs system and that the use of remote sensing techniques for crops growing within OTCs are feasible.

Table 4 presents the ANOVA results in two years (1991 and 1992) for the main and simple effects of CO_2 and O_3 on four variables: grain yield, above ground dry biomass, accumulated APAR (AAPAR), and radiation use efficiency (RUE). The O_3 factor reduced grain yield by 15.1% in 1991 ($p<0.01$) and 10.7% in 1992 ($p<0.05$). Dry biomass production was reduced by 10.5% in 1991 ($p<0.01$) and 9.2 in 1992 ($p<0.10$). Accumulated AAPAR was reduced by 2.5% only in 1991 ($p<0.05$) in response to O_3 exposure. Reduced RUE values in response to O_3 exposure in 1991 (8.4%; $p<0.01$) and in 1992 (8.5%; $p<0.05$) indicate that wheat growth was essentially limited by factors other than the amount of AAPAR. The overall negative impacts of O_3 exposure were largely associated with high-O_3 level at ambient-CO_2 concentration. Ozone acted to reduce the amount of photosynthesizing tissue (i.e., senesced leaf spots) and also reduced the capacity of plants to convert absorbed PAR into carbohydrates by reducing the rate of photosynthesis (Rudorff, 1993).

Conversely, the CO_2 factor increased grain yield by 26.0% in 1991 ($p<0.01$) and 14.7% in 1992 ($p<0.05$). Dry biomass was increased by 15.4 in 1991 ($p<0.01$) and 9.0% in 1992 ($p<0.10$). Carbon dioxide had no

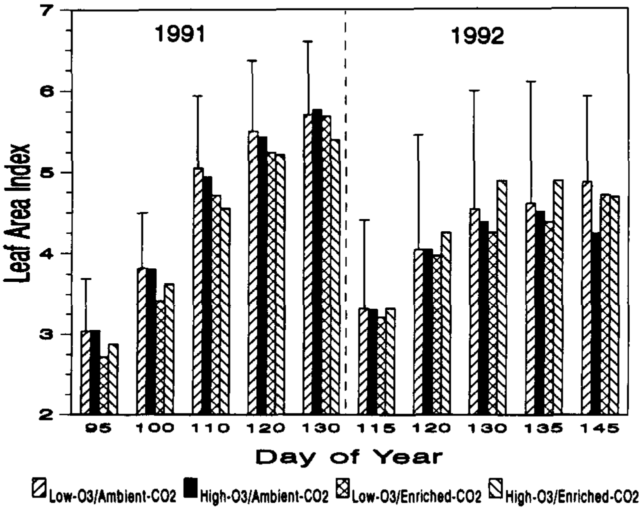
Table 3. Day of Year (DOY) and Key Growth Stages (Feekes-Large Scale) in Wheat Studies of 1991 and 1992

	5 Leaf Erected	*6 First Node Visible*	*7 Second Node Visible*	*8 Last Leaf Visible*	*9 Ligule Visible*	*10 In "Boot"*	*10.1 First Ears Visible*	*10.5 Ears out of Sheath*	*11 Milky-Ripe*	*11.2 Mealy-Ripe*
DOY 1991	83	90	94	102	110	118	120	125	135	150
DOY 1992	105	110	114	120	126	132	135	140	135	175

effect on AAPAR in either year. It is likely that the CO_2 effect on AAPAR was missed in the present study because measurements did not start until the canopies were substantially developed. Pinter et al. (1994) observed that CO_2 enrichment stimulates early season development of f_A and that by mid- to late season the f_A advantage disappears. The increases observed in RUE (~15% in 1991 and ~ 8% in 1992) in response to CO_2 enrichment is likely to be the combined result of both overall increased photosynthetic rates and increase in productive tillers determined early in the spring growth (Rudorff, 1993). The greater impact of CO_2 enrichment in 1991 compared with 1992 may be attributed to higher temperatures observed in 1991 (Table 2). Significant interactive effects of CO_2 vs. O_3 were observed only for grain yield in 1991 ($p < 0.10$), indicating that the detrimental effect of O_3 air pollution was more than overcome under the CO_2 enriched environment.

The simple effect analysis is also illustrated in Table 4. Interesting to note is that the differences between the control (low-O_3 / ambient-CO_2) and the high-O_3 / enriched-CO_2 treatments are not significant ($p < 0.05$) for any of the variables presented in Table 4. Again, this indicates that the CO_2-enriched environment had a counteractive effect against O_3-induced stress. The visual O_3 symptoms were considerably less for plants grown under enriched-CO_2 than for those grown under ambient-CO_2. Mean RUE in response to O_3 and CO_2 treatments are also presented in Figure 6. RUE values are likely overestimated since the control treatment (low-O_3 / ambient-CO_2) had considerably higher RUE values than those reported by Kiniry et al. (1989) for wheat prior to grain filling (2.8 g MJ^{-1}). However, the time frame over which the radiation data are integrated is crucial in determining RUE, and it is difficult to compare results from different studies.

Figure 4. Mean leaf area index (LAI) from early growth (growth stage 7) until maximum LAI (growth stage 10.5.2) in response to O_3 and CO_2 treatments for wheat in 1991 and 1992. Bars indicate LSD values with $p < 0.05$.



Corn

Plants grown under enriched CO_2 environment had trends for higher LAI values (not significant) at growth

Figure 5. Mean normalized difference vegetation index (ND) from early growth (growth stage 6 in 1991 and growth stage 7 in 1992) until maturity (growth stage 11.2) in response to O_3 and CO_2 treatments for wheat in 1991 and 1992. Bars indicate LSD values with $p < 0.05$.

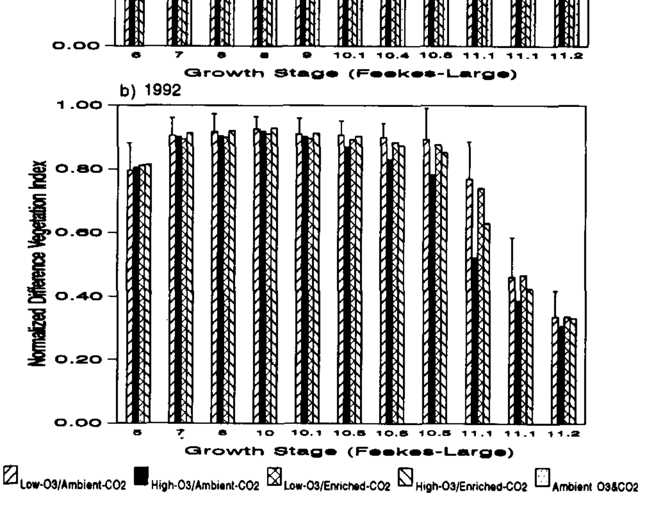


Table 4. Main and Simple Effects of CO_2 and O_3 on Grain Yield (g m^{-2}), Dry Biomass (g m^{-2}), Accumulated Absorbed PAR (AAPAR; MJ m^{-2}), and Radiation Use Efficiency (RUE; g MJ^{-1}) in Wheat in 1991 and 1992[a]

Chamber Treatments O_3 CO_2	*Grain Yield* (*g* m^{-2}) 1991	*Dry Biomass* (*g* m^{-2}) 1991	*AAPAR* (*MJ* m^{-2}) 1991	*RUE* (*g* MJ^{-1}) 1991	*Grain Yield* (*g* m^{-2}) 1992	*Dry Biomass* (*g* m^{-2}) 1992	*AAPAR* (*MJ* m^{-2}) 1992	*RUE* (*g* MJ^{-1}) 1992
CO_2 treatment means								
Ambient-CO_2	476	1392	353	3.94	477	1406	392	3.58
Enriched-CO_2	600	1606	356	4.52	547	1533	396	3.87
Percent change	+ 26.0	+ 15.4	+ 0.8	+ 14.7	+ 14.7	+ 9.0	+ 1.0	+ 8.1
Statistical significance	**	**	NS	**	*	†	NS	†
O_3 treatment means								
Low-O_3	582	1583	359	4.41	541	1541	396	3.89
High-O_3	494	1416	350	4.04	483	1399	392	3.56
Percent change	- 15.1	- 10.5	- 2.5	- 8.4	- 10.7	- 9.2	- 1.0	- 8.5
Statistical significance	**	**	*	**	*	†	NS	*
O_3 and CO_2 treatments								
Low-O_3 and ambient-CO_2	538b	1513b	359b	4.22b	520b	1506ab	397	3.78ab
High-O_3 and ambient-CO_2	414a	1272a	347a	3.66a	434a	1307a	387	3.38a
Low-O_3 and enriched-CO_2	627c	1653b	359b	4.61c	561b	1577b	394	4.00b
High-O_3 and enriched-CO_2	574bc	1559b	352ab	4.42bc	532b	1490ab	398	3.75ab
LSD ($p < 0.05$)	58	156	11	0.36	71	206	32	0.43

[a] Significance of main effects: ** $p < 0.01$; * $p < 0.05$; † $p < 0.10$; NS, not significant. Means followed by the same letters are NS different at 5% by LSD.

stages 2.0 and 2.5. As the season progressed, plants from all treatments had similar LAI (Fig. 7).

Normalized difference vegetation index values were not sensitive to any effect caused by either CO_2 or O_3 enhancement. The lack of visual leaf O_3 symptoms and the minor impact of CO_2 enrichment on corn were likely the major reasons for the general absence of treatment effects on ND values (Fig. 8). The OTC also had no significant impact on corn ND values (Fig. 8: ambient-O_3 and -CO_2) as was also demonstrated in the previous section for the wheat study.

Table 5 illustrates the ANOVA for the main and simple effects of CO_2 and O_3 treatments on grain yield, above-ground dry biomass, accumulated APAR (AAPAR), and radiation use efficiency (RUE) for corn. Decreases in grain yield (9%; $p < 0.10$) and dry biomass (5.8%; $p = 0.11$) resulting from O_3 exposure were marginally significant. It is likely that reduced grain production in the enhanced O_3 environment was caused by O_3 damage during the flowering process. Increased grain yield and dry biomass (~4%) resulting from CO_2 enrichment were not statistically significant. Apparently, AAPAR (Table 5) and RUE (Table 5 and Fig. 6) were not influenced by either CO_2 or O_3 in corn. Seasonal RUE value for the control treatment (4.21 g MJ^{-1} for 6 plants m^{-2}; low-O_3 / ambient-CO_2) was similar to that reported by Gallo et al. (1993) for corn (3.71 g MJ^{-1} and 4.38 g

Figure 6. Mean radiation use efficiency in response to O_3 and CO_2 treatments for wheat in 1991 and 1992 and corn in 1991.

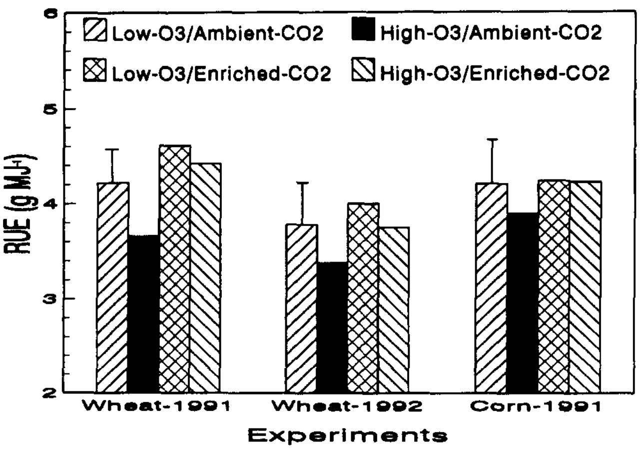


Figure 7. Mean leaf area index (LAI) in response to O_3 and CO_2 treatments for corn in 1991. Bars indicate LSD values with $p < 0.05$.

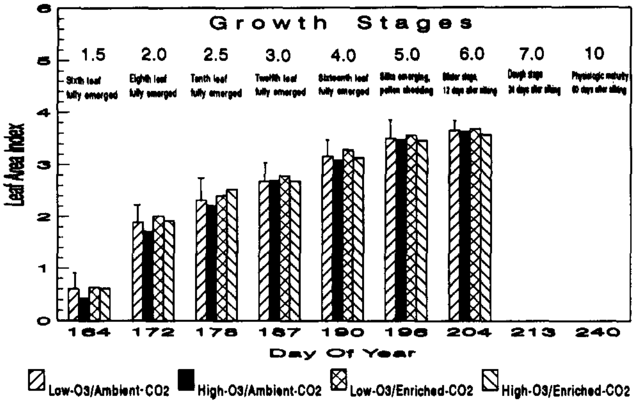


Table 5. Main and Simple Effects of CO_2 and O_3 on Grain Yield (g m^{-2}), Dry Biomass (g m^{-2}), Accumulated Absorbed PAR (AAPAR; MJ m^{-2}), and Radiation Use Efficiency (RUE; g MJ^{-1}) in Corn in 1991[a]

Chamber Treatments *O_3 CO_2*	*Grain Yield (g m^{-2})*	*Dry Biomass (g m^{-2})*	*AAPAR (MJ m^{-2})*	*RUE (g MJ^{-1})*
CO_2 treatment means				
Ambient-CO_2	1167	2005	494	4.05
Enriched-CO_2	1210	2079	491	4.23
Percent change	+ 3.7	+ 3.7	− 0.6	− 4.4
Statistical significance	NS	NS	NS	NS
O_3 treatment means				
Low-O_3	1244	2103	498	4.23
High-O_3	1133	1981	489	4.06
Percent change	− 8.9	− 5.8	− 1.8	− 4.0
Statistical significance	†	$p = 0.11$	NS	NS
O_3 and CO_2 treatments				
Low-O_3 and ambient-CO_2	1236	2100	499	4.21
High-O_3 and ambient-CO_2	1097	1910	490	3.90
Low-O_3 and enriched-CO_2	1251	2106	496	4.24
High-O_3 and enriched-CO_2	1168	2052	486	4.23
LSD ($p < 0.05$)	172	223	26	0.45

[a] Significance of main effects: † $p < 0.10$; NS, not significant.

MJ^{-1} for 5 plants m^{-2} and 10 plants m^{-2}, respectively) using APAR data estimated from ND values.

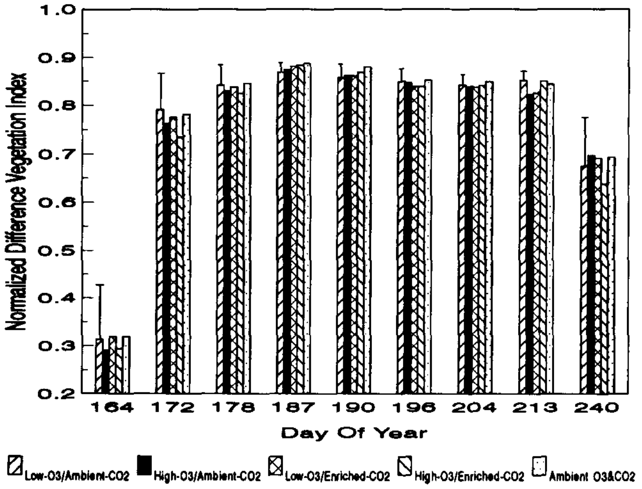
Reductions in both grain yield and dry biomass in response to O_3 exposure were much smaller when plants were grown under enriched-CO_2 environment, indicating that CO_2 enrichment partially counteracted the damaging effect of O_3 exposure (Table 5). The counteracting effect of CO_2 enrichment against O_3-induced stress was also observed in wheat (see previous section), soybeans (Mulchi et al., 1992) and radish (Barnes and Pfirrmann, 1992). The CO_2 vs. O_3 interaction was not significant for any plant characteristic in corn.

Carbon dioxide enrichment under low-O_3 level typically caused no impact on plant characteristics (Table 5). This agrees with a recent study from Hocking and Meyer (1991) reporting that corn was not sensitive to CO_2 enrichment. Similar results were also noted by Surano and Shinn (1984) for corn grown in OTCs under enriched CO_2 environment. However, large discrepancies were observed by Rogers et al. (1983), who reported an increase in dry biomass of almost 50% under a CO_2-doubling atmosphere. Based on several studies on CO_2 enrichment in corn, Cure and Acock (1986) reported grain yield and dry biomass increases of 29% and 9%, under a doubling of current ambient CO_2 concentration, respectively. Due to such inconsistent results for CO_2 enrichment studies in corn, future research should be more tightly controlled.

SUMMARY

Concentrations of both carbon dioxide (CO_2) and ozone (O_3) in the troposphere are expected to increase to levels where they may have a significant impact on crop production. We conducted field studies with wheat and corn using open-top chambers to mimic atmospheric concentrations expected during the first half of the 21st century. Wheat and corn plant characteristics produced clearly different responses to CO_2 enrichment, but similar responses to O_3 exposure. In both crops, O_3 exposure reduced grain yields. In wheat, CO_2 enrichment produced greater grain yield, dry biomass, and radiation use efficiency and apparently ameliorated the O_3 damage. In contrast, corn demonstrated no benefit to CO_2 enrich-

Figure 8. Mean normalized difference vegetation index (ND) from early growth (growth stage 1.5) until physiologic maturity (growth stage 10) in response to O_3 and CO_2 treatments for corn in 1991. Bars indicate LSD values with $p < 0.05$. See Figure 7 to reference for growth stages.



ment. Ozone exposure reduced corn grain yield in response to O_3 damage during the flowering process. Visible and near-infrared reflectance data were not helpful for identifying damage due to O_3 fumigation in combination with CO_2 enrichment. Thus remotely sensed data may have limited value in monitoring subtle changes in reflectance percentage due to chronic exposure to elevated levels of O_3 under CO_2-enriched environment. Also, these gases had a major impact on physiological processes that are independent on PAR absorption. Therefore, radiation use efficiency (RUE) in response to gases treatments, in wheat, was significantly increased in response to CO_2 enrichment and significantly reduced in response to O_3-induced stress. Similar results were observed for the control treatment and the high-O_3 / enriched-CO_2 treatment, indicating that the damaging effect of O_3 air pollution was counteracted by the beneficial effect of CO_2 enrichment without any interactive effects between the two gases for the measured variables except for grain yield, during the first wheat experiment, where the CO_2-enriched environment more than overcame the O_3-induced stress.

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