# Correlative Reductions in Whole-Plant Photosynthesis and Yield of Winter Wheat Caused by Ozone

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## ABSTRACT

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Winter wheat (cultivar Vona) was exposed to four levels of $O_3$ (7-hr exposure period averages of 0.027, 0.054, 0.076, and 0.096 ppm) and four levels of $SO_2$ (4-hr exposure period averages of 0, 0.039, 0.166, and 0.363 ppm) and all combinations of the two pollutants from anthesis until harvest. Sulfur dioxide did not affect net photosynthesis or yield but temporarily reduced stomatal conductances of flag leaves. No interactions between $SO_2$ and $O_3$ were found for any variables measured. Ozone accelerated the senescence of flag leaves, stalks, and heads and also accelerated the loss of moisture from the heads. Ozone significantly reduced stomatal conductances of flag leaves, net photosynthesis of whole plants and individual heads, and seed dry weights per head as a result of reduced seed size but not seed number. Reductions in seed weights caused by ozone were highly correlated with measured reductions in whole-plant and individual head photosynthesis. Exposure of Vona winter wheat to ambient and higher $O_3$ concentrations from anthesis until harvest resulted in yield losses caused by reductions in net photosynthesis.

*Additional key words*: growth, *Triticum aestivum*.

During the growing season, most of the agricultural regions of the United States are exposed frequently if not daily to elevated ozone ($O_3$) concentrations that are mainly of anthropogenic origin. Results of several field studies have shown that ambient $O_3$ concentrations reduce the yields of many crops (13,14). Although $O_3$ has been shown to reduce rates of photosynthesis (15), few studies have used realistically low concentrations and attempted to relate $O_3$-mediated changes in photosynthesis to changes in growth or yield (1,24,25).

In contrast to the chronic exposures to $O_3$, many agricultural regions of the United States are also exposed intermittently to elevated concentrations of sulfur dioxide ($SO_2$). Even though exposures to $SO_2$ are less frequent than exposures to $O_3$, the effects of repeated exposures to $SO_2$ in combination with elevated ambient concentrations of $O_3$ may be important over much wider areas because the two pollutants have been shown to interact (26). However, the nature of the effects of $SO_2$ in combination with $O_3$ on plant injury and growth are variable (11,16,26,27); thus, the potential exists for either positive or negative interactions between these two pollutants and net photosynthesis, growth, and yield.

Because of the paucity of information on the relationships among rates of photosynthesis, growth, and yield, extrapolation of data from studies of the effects of these two pollutants on relatively short-term variables (stomatal conductance, foliar injury, and rates of growth) to predict yield is not advisable. Therefore, studies that measure the effects of realistic concentrations of pollutants on several levels of plant processes are needed to produce a better understanding of the relationships between short-term responses to pollutant exposure and long-term effects on growth and yield. We are not aware of any such studies to date.

Before the late 1970s, a few studies showed a positive correlation between photosynthetic rates and plant growth or yield (2,18,22). Most similar studies indicated that these two obviously related processes were not correlated or were negatively correlated (4). Since then (4), others have reported a strong relationship between net photosynthetic rates (measured for extended periods of time) and growth or yield of corn (28), tobacco (21), and soybean (3,25). Zelitch (29) suggested that the lack of adequate characterization of the photosynthetic rates for the whole population of leaves on the plants and for the range of environmental conditions encountered by the plant could account for the lack of a positive correlation between photosynthetic rates and growth or yield. Other factors that have not been considered in such studies are the influences of elevated concentrations of air pollutants on the relationships between photosynthesis and growth and yield. The present study was conducted to determine whether $O_3$ and $SO_2$ interact to reduce net photosynthesis, growth, and yield of a widely grown cultivar of winter wheat (*Triticum aestivum* cv. Vona) and to determine whether reductions in growth and yield were correlated with reductions in net photosynthesis.

## MATERIALS AND METHODS

**Cultural practices.** Winter wheat (*T. aestivum* cv. Vona) was planted with a drill on 12 October 1982 at a rate of 100 kg of seed per hectare in rows 17.5 cm apart and banded with 10-20-20 (NPK) fertilizer at a rate of about 280 $kg \cdot ha^{-1}$. Soils in the experimental plot are in the Collamer and Niagara series, both of which are Hapludalfs. The soils are described as silt loams. In May 1983, the field was top-dressed with ammonium nitrate fertilizer at about 120 $kg \cdot ha^{-1}$. Stand density during the study was about 120–140 tillers per meter. Plants were sprayed with dinocap (Karathane) on 17 May to control powdery mildew (*Erysiphe graminis*). Soil moisture at a depth of 25 cm was monitored with tensiometers to indicate the need for irrigation. No irrigation was applied during the study.

**Pollutant treatments and monitoring.** There were four $O_3$ treatments in the open-top chambers (10): charcoal-filtered air (CF), nonfiltered air (NF), and NF in which the $O_3$ levels were maintained at 1.4× and 1.8× ambient by $O_3$ additions. Daily $O_3$ additions lasted 7 hr (1000–1700 hours EDT) except when precluded by rain or technical difficulty.

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There were four $SO_2$ treatments in the open-top chambers: NF, and NF to which $SO_2$ was added to produce three additional treatment levels. Exposures lasted 4 hr and were conducted three times each week with minor variations in exposure duration and frequency because of rain and equipment maintenance. The $O_3$ and $SO_2$ generation, distribution, and monitoring systems used in this study are described in detail in a companion paper (19).

The 4 × 4 factorial experiment was conducted in two randomized complete blocks and thus required 32 open-top chambers. Eight additional chambers were divided equally between the NF and 1.8× treatments, thus 40 chambers were used. Ambient plots not enclosed by chambers constituted another treatment.

All chambers were positioned in the field and started between 1 and 4 June. Ozone exposures were initiated on 12 June and terminated on 17 July. At the time exposures began, the wheat heads were three-quarters emerged and flowering had not started. The $SO_2$ exposures were initiated on 22 June and terminated on 15 July. Flowering was completed and the kernels watery when the $SO_2$ exposures began. The kernels were fully ripe when the exposures were terminated and all chambers and plots were harvested for yield on 18 and 19 July. The period for all pollutant exposure calculations in the study was 12 June through 17 July, a 36-day interval.

**Growth and senescence evaluation.** Destructive measures of plant growth were made at about 1-wk intervals from 6 June until final harvest. All plants in a 25-cm section of row were clipped at ground level, and the culms (headbearing stems), tillers (non-headbearing stems), and emerged heads were counted. Dry weights of tillers, culms less the emerged heads, and heads were measured after drying at 75 C for 48 hr.

The degree of yellowing of the flag leaves was rated visually on 23 June. Plots were rated on a scale of 1–5 in increments of 0.5, where 1 = all yellow to dry, 2 = >75% yellow, 3 = 50–75% yellow, 4 = 25–50% yellow, and 5 = <25% yellow-green. On 13 July, five heads were cut from each of the rows bordering the center two rows in each chamber to determine percent moisture content of the heads. A fresh weight of each five-head sample was determined, and after drying at 70 C for 48 hr, dry weights were measured.

**Stomatal conductance and net photosynthesis.** Measurements of stomatal conductance of the flag leaves were made with a steady state porometer (LICOR, Model 1600, Lincoln, NB) beginning on 8 June and ending on 28 June. Measurements were made during midday (1100–1500 hours EDT) at least 2 days per week. Four locally fabricated cylinders (cuvettes) were used to enclose about 25 cm of wheat row for measurement of whole-plant net photosynthetic rates. The cylinder frame was made of clear Plexiglas and was covered with transparent Teflon (Type FEP, 1 mil). The air within the cuvettes was mixed by an impeller attached to a miniature electric motor. The top of the cylinder was perforated to allow entry of ambient air, which was drawn by a pump (Reciprotor, Terracon Corp., Waltham, MA) out the bottom of the cylinder through polypropylene tubing (1.27 cm i.d.) to the $CO_2$ analyzer (Model 600AR, Anarad, Santa Barbara, CA). Flow rates were monitored with a mass flow meter (Model 525, Kurz, Carmel Valley, CA) and maintained at 35–45 L $min^{-1}$ to reduce heating or excessive reduction of $CO_2$ concentrations within the cuvettes. The highest temperature differential monitored between cuvette and ambient air was 2 C, and the highest $CO_2$ depletion allowed was about 40 ppm. Two pieces of plastic film were butted against the wheat stalks parallel to the row and were covered with sand to a depth of about 3 cm to eliminate water and $CO_2$ input from the soil. In addition, the sand helped to physically stabilize the cuvettes and provide a seal at the base. Measurements of whole-plant net photosynthesis were begun on 9 June and terminated on 7 July.

Two thermoelectrically cooled cuvettes (Portable Environment Cuvette, Kananaskis Centre for Environmental Research, Calgary, Alberta) were used to measure the net photosynthetic rates of individual heads of wheat; these measurements were started on 18 June and ended on 11 July. An infrared gas analyzer (Model AR500R, Anarad Inc., Santa Barabara, CA) was used to monitor changes in $CO_2$ concentrations for determination of individual head net photosynthesis.

**Final harvest.** On 18 and 19 July, all plants were harvested from two 1-m rows in the center of each chamber. The plants were cut near the ground and the heads clipped from the straw and counted. Dry weights of the heads and straw were determined after they were oven-dried at 75 C for 48 hr. Twenty heads from each chamber were individually threshed and the seeds weighed and counted.

**Data analysis.** Whole-plant photosynthesis data were calculated on a dry weight basis (mg $CO_2$ $g^{-1}$ $hr^{-1}$) using the total aboveground dry weight minus the respective seed dry weight. For statistical analyses, only photosynthetic rates monitored at near full sunlight intensities (>1,500 $\mu$E $m^{-2}$ $s^{-1}$) and between 1200 and 1500 hours were used. Because the sampling period coincided with the interval between anthesis and senescence, the photosynthetic rates of the plants declined dramatically with time. Therefore, the rates of photosynthesis were analyzed by analysis of covariance with date as a covariant. The same adjustment for date was made for the photosynthetic rates of the individual heads. Analysis of variance and regression analysis were used to assess the final seed dry weights per head.

## RESULTS

**Pollutant monitoring.** For $O_3$, the seasonal 7-hr averages for the treatments during the exposure period (12 June to 17 July) were: CF, 0.027 ppm; NF, 0.054 ppm; 1.4×, 0.076 ppm; 1.8×, 0.096 ppm; and ambient, 0.057 ppm. Ozone additions were made on 34 of the 36 days of the study period. Sulfur dioxide exposures were conducted on 12 days during the study, with 10 exposure periods lasting 4 hr, one lasting 5 hr, and one lasting 3 hr for a total of 48 hr. The following average $SO_2$ concentrations were monitored for the exposure periods: ambient, 0; NF without $SO_2$ addition, 0; and $SO_2$-added treatments, 0.039, 0.166, and 0.363 ppm. Ambient $SO_2$ was low, with detectable levels (>0.005 ppm) occurring in 50 hr of the 864 hr during the study period. Additional data on the pollutant exposure regimes are presented by Kohut et al (19).

**Growth.** Because the pollutant exposures were initiated at head emergence, no effects of the pollutants were found on head number per 25 cm of row. In addition, at the start of the exposures, most of the vegetative portion of the plants had developed; therefore, no effects of treatments were found on total aboveground plant dry weight. The effect of $O_3$ on average dry weights of heads is shown in Figure 1. Exposure to $O_3$ reduced average head weight, with the highest (1.8×) $O_3$ treatment about 40% lower than the CF treatments (Fig. 1). In contrast, exposure to $SO_2$ had no effect on head weight.

**Senescence.** There were dramatic differences in the degree of senescence of flag leaves caused by exposure to the increasing

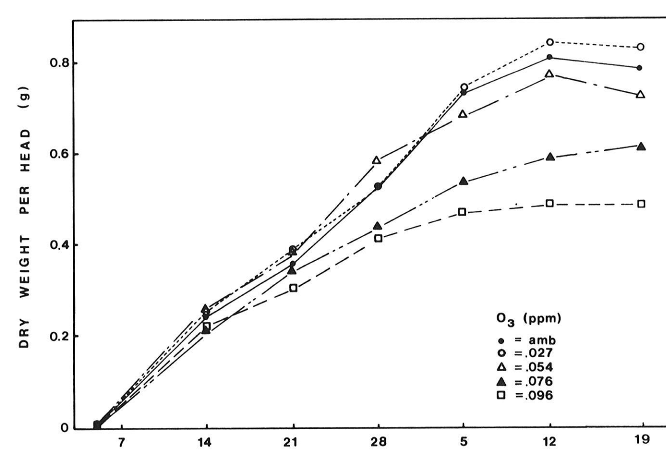


**Fig. 1.** Average dry weights of heads of Vona winter wheat exposed to five $O_3$ treatments from 12 June until final harvest on 17 July.

concentrations of $O_3$ (Table 1). For example, on 23 June, 11 days after the start of the $O_3$ exposures, flag leaves on plants exposed to the CF treatments were less than 25% yellow, in contrast to almost complete yellowing of those exposed to the highest $O_3$ concentrations. Because the $SO_2$ exposures were initiated on 22 June and no $SO_2$ injury was noted after the first day of exposure, only the respective $O_3$ treatments were evaluated on 23 June.

Percent moisture content of the heads was determined on 13 July. There was a dramatic decline in the percent moisture content of the heads due to $O_3$ (Table 2); plants exposed to the CF treatments had on average a 39% moisture content, whereas plants exposed to the 1.8× treatment had a 14% moisture content. There was little change in percent moisture content of the heads with exposure to increasing concentration of $SO_2$. No interactions were found between $O_3$ and $SO_2$ affecting percent moisture content.

**Stomatal conductance.** Stomatal conductances of flag leaves were measured before the starting date of the $O_3$ treatments and continued until the leaves were chlorotic. In general, stomatal conductances increased and then declined with increasing age of the leaf and were higher for adaxial than abaxial surfaces (Figs. 2 and 3, respectively). The highest $O_3$ treatment reduced both adaxial surface (Fig. 2) and abaxial surface (Fig. 3) stomatal conductances of the flag leaves after only 1 day of exposure. The differences in stomatal conductances between the $O_3$ treatments remained essentially the same from the start of the treatments until the end of the measurement period. By 24 June, most leaves in the highest $O_3$ treatment were senescent. Because only nonsenescent leaves were used for conductance measurements, the values shown in Figures 2 and 3 for that period are unrepresentatively high for the 1.8× treatment.

Exposure to $SO_2$ reduced stomatal conductances of both leaf surfaces in all $O_3$ treatments (Fig. 4). The reductions ranged from 15 to 30%, with no apparent interaction between $SO_2$ and $O_3$. On days without $SO_2$ or in the hours preceding $SO_2$ exposures, stomatal conductances of plants exposed to $SO_2$ were similar to those of plants exposed to the same concentrations of $O_3$ but without $SO_2$.

**Net photosynthesis and yield.** Net photosynthetic rates of whole plants were reduced by exposure to increasing concentrations of $O_3$ (Fig. 5). The average net photosynthetic rates of plants exposed to the 1.8× ambient $O_3$ treatments were about 50% of the rates of

TABLE 1. Effect of $O_3$ on the degree of yellowing[a] of flag leaves 11 days after initiation of $O_3$ treatments (10 days after anthesis)

| | Degree of flag leaf yellowing | |
|---|---|---|
| $O_3$ treatment[b] | No.[c] | Rating |
| CF | 8 | 4.9 ± 0.35 |
| NF | 12 | 4.0 ± 0.69 |
| Ambient | 8 | 3.4 ± 0.50 |
| 1.4× | 8 | 1.8 ± 0.60 |
| 1.8× | 12 | 1.1 ± 0.19 |

[a] Plots were rated on a scale of 1–5 in increments of 0.5, where 1 = all yellow to dry, 2 = >75% yellow, 3 = 50–75% yellow, 4 = 25–50% yellow, and 5 = <25% yellow-green.
[b] CF = charcoal-filtered air, NF = nonfiltered air, ambient = chamberless plots, and 1.4× and 1.8× = multiples of ambient $O_3$ concentration during exposure periods.
[c] Number of chambers or plots per treatment.

TABLE 2. Effects of $SO_2$ and $O_3$ on percent moisture[a] content of the wheat heads on 13 July

| | Moisture content (%) | | | | |
|---|---|---|---|---|---|
| | $SO_2$ treatment[c] | | | | Averaged over $SO_2$ |
| $O_3$ treatment[b] | NF | NF+0.04 | NF+0.17 | NF+0.36 | treatments |
| CF | 39 | 39 | 39 | 38 | 39 |
| NF | 37 | 35 | 34 | 37 | 36 |
| Ambient | 36.9 ± 4.6[d] | | | | |
| 1.4× | 32 | 30 | 29 | 27 | 30 |
| 1.8× | 14 | 14 | 14 | 15 | 14 |
| Averaged over $O_3$ treatments | 30 | 30 | 29 | 29 | |

[a] Percent moisture content = (1 − dry wt/fr wt) × 100.
[b] CF = charcoal-filtered air, NF = nonfiltered air, ambient = chamberless plots, and 1.4× and 1.8× = multiples of ambient $O_3$ concentrations during exposure periods.
[c] NF +0.04, +0.17, or +0.36 = NF to which 0.04, 0.17, or 0.36 ppm $SO_2$ (average) was added during the $SO_2$ exposure periods.
[d] There were eight ambient plots, whereas most treatments only had two values.

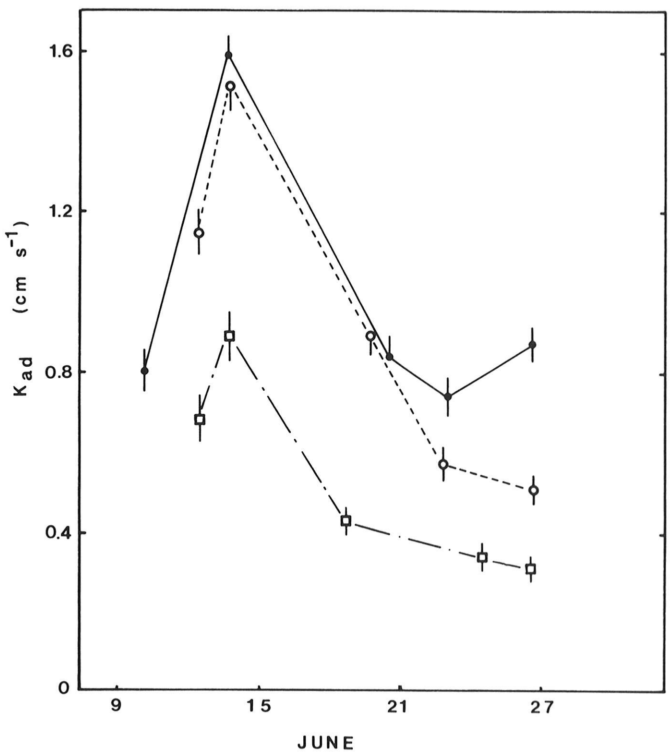

**Fig. 2.** Changes in adaxial stomatal conductance ($K_{ad}$) of the flag leaves of Vona winter wheat exposed to three $O_3$ treatments (CF = •——•, NF = o---o, 1.8× = □–·–□) from 12 June to 17 July. Units are centimeters per second, with ± SE indicated by the vertical bars.

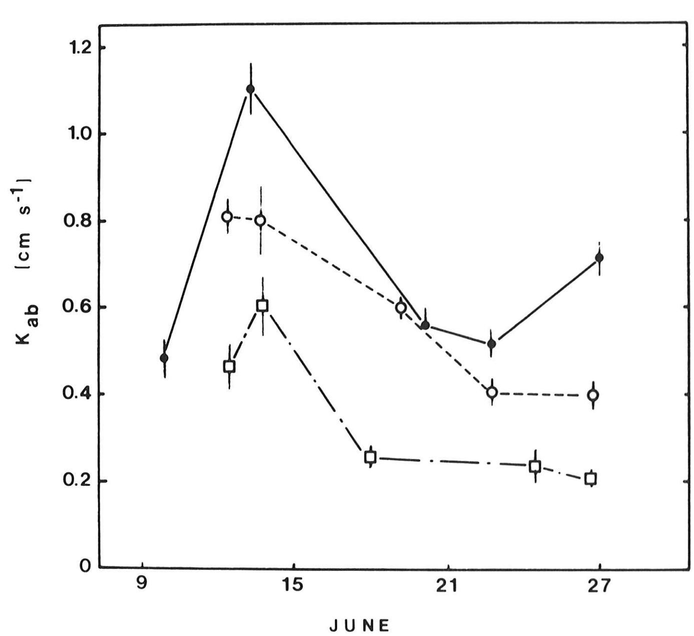

**Fig. 3.** Changes in abaxial stomatal conductance ($K_{ab}$) of the flag leaves of Vona winter wheat exposed to three $O_3$ treatments (CF = •——•, NF = o---o, 1.8× = □–·–□) from 12 June to 17 July. Units are centimeters per second, with ± SE indicated by the vertical bars.

plants exposed to the CF treatments (Fig. 5). The average dry weight of grain per head was also reduced by about 50% in the 1.8× ambient $O_3$ treatment compared with the CF treatment (Fig. 5).

Net photosynthesis of individual heads of wheat was also monitored from 18 June until 6 July. The average net photosynthetic rates of heads exposed to the 1.8× ambient $O_3$ treatment was reduced by about 50% compared with the average rate of heads exposed to the CF treatment (Fig. 6). In addition, the reduction in weight of grain per head was essentially the same as the reduction in net photosynthesis per head (Fig. 6). Net photosynthetic rates of whole plants and individual heads of wheat exposed to $SO_2$ with $O_3$ were not significantly different from the rates of whole plants or heads exposed to comparable $O_3$ concentrations without $SO_2$.

Analysis of variance indicated that only $O_3$ had a significant effect on yield; the effects of $SO_2$ and $O_3 \times SO_2$ were not significant. The regression equation for effect of $O_3$ on 100-seed weight was: 100-seed weight = 2.589 − 13.522 ($O_3$), where 100-seed weight is in grams and $O_3$ is the seasonal 7-hr average in parts per million. The effect of $O_3$ on yield was the result of reduced seed weight and not seed numbers per head. For more information on yields of these plants, see Kohut et al (19).

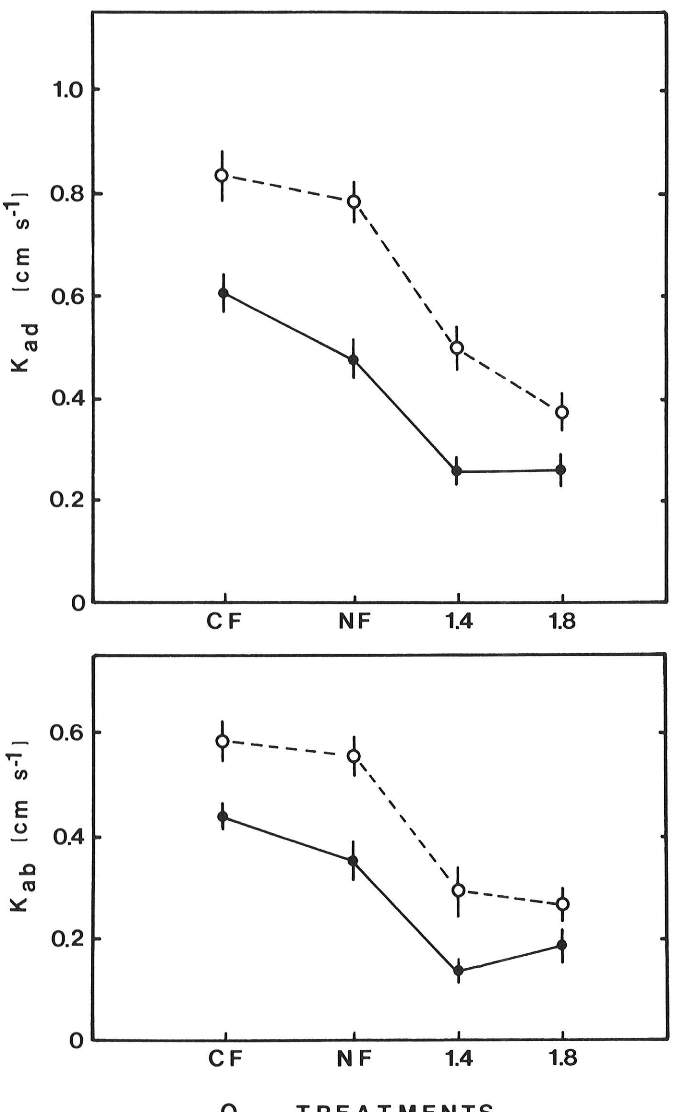


**Fig. 4.** Effect of $O_3$ alone (o---o) or in combination with $SO_2$ (•——•) on stomatal conductances of the adaxial ($K_{ad}$) and abaxial ($K_{ab}$) leaf surfaces of the flag leaves of Vona winter wheat. Values are averages for respective treatments during the $SO_2$ exposure period from 22 June until 15 July. Values for the $SO_2$ + $O_3$ treatments were determined only during the periods of $SO_2$ exposure and were averaged over all three $SO_2$ treatments. Units are centimeters per second, with ± SE indicated by vertical bars.

## DISCUSSION

The significant decline in yield of winter wheat caused by $O_3$ is in agreement with other field studies on winter wheat (12,20). Differences in the magnitude of effect of ambient concentrations of $O_3$ in the different cultivars or years are discussed in detail by Kohut et al (19).

The timing of the start of the $O_3$ treatments helps explain why the effects of $O_3$ were on seed size but not seed number. Fischer (6) and Evans (5) showed that low light conditions during the 10- to 20-day period before pollination can severely reduce the number of seeds per head, presumably because of reduced photosynthesis. Conversely, $CO_2$ enrichment during the same period greatly increased the number of seeds per head (7), and Havelka et al (9) showed that the $CO_2$-mediated increase in yield was associated with increased photosynthesis of the flag leaf. Gifford et al (8) reviewed the literature on the relationship between photoassimilate partitioning and productivity and noted that for cereals, once seed number has been set, the yield has essentially been set except in cases of adverse environmental conditions. In the experiment reported here, elevated $O_3$ concentrations were imposed after seed number had been set, and as would be predicted for a stress imposed at anthesis, yields were reduced as a result of reduced seed size.

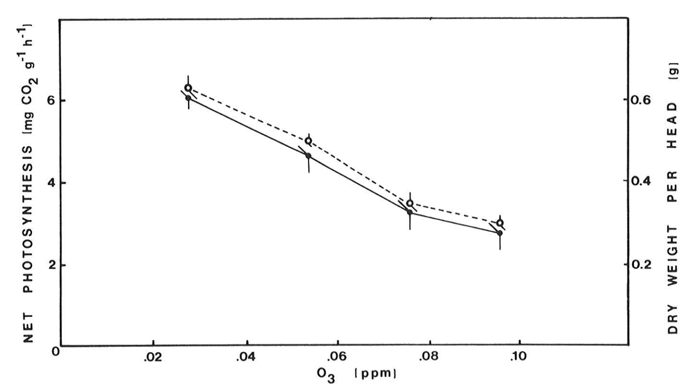


**Fig. 5.** Effects of $O_3$ on whole-plant net photosynthesis (•——•) and average seed weight per head (o---o) in Vona winter wheat. Photosynthetic rates are presented on a total aboveground dry weight minus seed dry weight basis. The measurements presented were made from 12 June until 28 June. Because of the decline in photosynthetic rates over this sampling period, time was used as a covariate for calculating means and standard errors. Dry weight per head was determined at the final harvest. Vertical bars indicate ± SE.

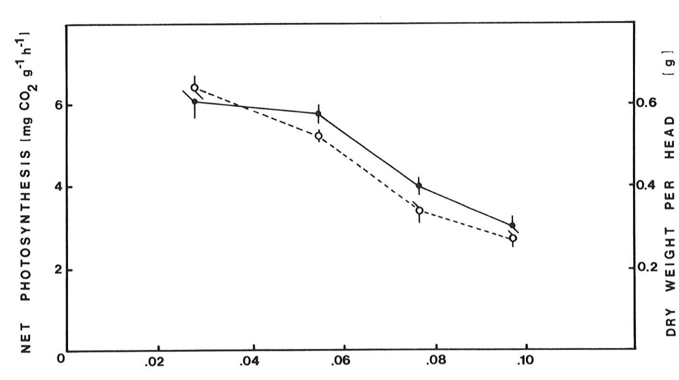


**Fig. 6.** Effects of $O_3$ on individual wheat head photosynthesis (•——•) and average seed weight per head (o---o) in Vona winter wheat. Photosynthetic rates are presented on a total head dry weight minus seed dry weight basis. The measurements were made from 18 June until 11 July. Because of the decline in photosynthetic rates over this sampling period, time was used as a covariate for calculating means and standard errors. Dry weight per head was determined at the final harvest. Vertical bars indicate ± SE.

Rates of net photosynthesis of whole plants declined with time from about 1 wk before anthesis until senescence, and the decline was similar to that found by Puckeridge (22) and Johnson et al (17) for other winter wheat cultivars. The linear reduction in net photosynthesis produced by increasing concentrations of $O_3$ is in agreement with the results of studies on soybean (25) and hybrid poplar (23). Most significantly, the percent reductions in net photosynthesis of both whole plants and individual heads produced by $O_3$ corresponded to the percent reductions in seed dry weights per head produced by $O_3$.

Our findings that exposure to elevated concentrations of $O_3$ from anthesis to harvest reduced net photosynthesis of whole plants and that the reductions in whole-plant photosynthesis were highly correlated with the respective reductions in seed size indicate that yield in this cultivar of winter wheat is intimately associated with photosynthetic rates during this period. The effects of $O_3$ on photosynthesis were also associated with accelerated senescence as indicated by degree of yellowing of the flag leaves and percent moisture content of the wheat heads. The loss in moisture content of the heads was most likely the result of accelerated senescence and not water stress induced by $O_3$, because $O_3$ acted to significantly reduce leaf stomatal conductances and thus should have improved plant moisture status. In a previous study (25) on the effects of $O_3$ on photosynthesis of soybean, $O_3$ reduced both the photosynthetic efficiency and duration of photosynthesis of individual leaves. In this study, the $O_3$ treatments were started at anthesis, when photosynthetic rates naturally decline (17,22), and thus, the relative contributions of the loss of photosynthetic efficiency and the reduced duration of photosynthesis (senescence) to the reductions in whole plant photosynthesis could not be determined.

**Conclusions.** Exposure of Vona winter wheat to four treatment levels of $O_3$ from anthesis until harvest resulted in a significant linear reduction in seed weights. Seed numbers were not affected, but the reduced seed weights resulted in a similar linear reduction in total yield. Ozone acted to accelerate senescence of flag leaves and heads. Rates of net photosynthesis of whole plants and heads were also significantly reduced by $O_3$, and the reductions in net photosynthesis were highly correlated with the $O_3$-induced reductions in yield. We conclude that exposure of Vona winter wheat to elevated concentrations of $O_3$ is likely to cause yield reductions in proportion to the increases in $O_3$ and that the yield reductions will be the result of accelerated senescence and reduced rates of net photosynthesis.

Sulfur dioxide did not produce reductions in yield, even at a fairly substantial exposure concentration. No interactions were found between $SO_2$ and $O_3$ for stomatal conductance, rates of net photosynthesis, percent moisture content of heads, or yield. We conclude that $SO_2$ acts independently of $O_3$ in terms of plant physiological response over the range of exposures used and that either higher concentrations or dosages of $SO_2$ would be needed to reduce the yield of Vona winter wheat.

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