S33-003

Unconsidered environmental stresses may cause overestimates of the CO_2-fertilization effect

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Keywords: CO_2-fertilization, environmental stress, crop productivity, air pollutants, elevated CO_2

Introduction

Both atmospheric CO_2 and background concentrations of tropospheric O_3 are rising, although the latter at a much lower rate. While elevated CO_2 is thought to be beneficial to plant growth, current levels of O_3 are already at highly phytotoxic levels in some areas. O_3 is a natural component of the atmosphere and originates primarily from photochemical reactions of nitrogen oxides (NO_X) and hydrocarbons with O_2. However, background levels are increasing as a result of anthropogenic emissions of these precursors, which may travel for hundreds of miles before reacting to form O_3. Thus, O_3 pollution is not confined to highly polluted source areas. Agricultural soils are thought to contribute significant quantities of O_3 precursors in rural areas as well and so some of the most productive agricultural areas in the United States are subjected to potentially phytotoxic O_3 levels.

Atmospheric CO_2 affects plants and ecosystems because it is a substrate for photosynthesis and elevated CO_2 stimulates photosynthesis, growth and sometimes crop yield. Kimball (1983) has shown that the magnitude of the response to elevated CO_2 is highly variable, not only across but within species and cultivars. Although there appears to be a major genetic component to this variability, much of it may be due to environmental stresses that occurred during plant growth. It is not surprising that there are significant physiological interactions between CO_2 and O_3.The most relevant interaction for present purposes involves the reduction of leaf conductance at elevated levels of atmospheric CO_2 that has the effect of preventing reductions of photosynthesis, growth and yield in many crops grown in the presence of toxic levels of O_3 (Fiscus *et al.*, 1997; Fiscus *et al.*, 2001). Similar interactions are known to occur between water stress and elevated CO_2 with the same effect that the elevated CO_2 reduces photosynthetic, growth and yield losses which might have occurred at ambient CO_2 levels. Conversely, if plants are grown in elevated CO_2 in the presence of any stress that might reduce photosynthesis, growth and yield but is unrecognized or unmonitored, the beneficial effects of the elevated CO_2 (CO_2-fertilization) may appear exaggerated. Using such studies to estimate world food supplies in future atmospheres may result in overly optimistic projections. Analysis of published and unpublished data from our field site at Raleigh, NC, U.S.A. provides a means to analyze this situation. Using phytotoxic levels of ozone as the primary stressor, we can examine the relationship between the magnitude of the CO_2-fertilization effect on photosynthesis, vegetative biomass production and yield and the level of plant stress.

Materials and methods

Plants in all of the experiments discussed here were grown in open-top chambers (Heagle *et al.*, 1973) and subjected to reciprocal CO_2 X O_3 treatments. The CO_2 treatments consisted of current ambient concentrations (A) and a nominally double ambient concentration, designated CO2. O_3 treatments always consisted of at least charcoal-filtered air (CF) and a CF or NF (non-filtered) treatment to which O_3 was added (NF+) to bring the air to a concentration approximately 50% higher than background levels. Occasionally there was an NF treatment as well in which the plants were exposed to existing ambient levels of O_3. Averaged across all experiments the ambient and elevated CO_2 concentrations were 372 $\mu L\ L^{-1}$ and 706 $\mu L\ L^{-1}$ while the CF, NF and NF+ O_3 concentrations averaged 25 $nL\ L^{-1}$, 50 $nL\ L^{-1}$ and 80 $nL\ L^{-1}$, respectively. In all instances discussed here, except for one experiment, plants were grown in 15L or 21 L pots which were fertilized, watered, treated for pests and harvested as reviewed by Fiscus *et al.* (2001). Crop economic yields were obtained in the usual manner but discussions of vegetative biomass in this paper will be confined to the above-ground plant parts exclusive of reproductive structures. Both yield and biomass values were regressed against O_3 concentrations according to $Y = a + b(\ln[O_3])^2$. Over a period of 8 years, 4 species (cotton, rice, soybean and wheat), including 7 different cultivars, were grown under the reciprocal gas treatments as well as with planting density (rice) and soil nitrogen levels (cotton) as variables. The plant data will be discussed in terms of "cultivar years" (CVY), where each CVY represents one cultivar grown for a single season in the complete set of reciprocal gas treatments. Any additional treatments imposed on an entire CO_2 X O_3 block such as soil N or planting densities are counted as additional CVYs. For example, in 1997 and 1998 rice (one cultivar) was grown under the reciprocal gas treatments with five planting densities as subplots. In those particular experiments each density would count as a separate CVY. Thus the experiments discussed here consisted of a total of 31 CVYs.

Results

Typical interactive effects of elevated CO_2 and O_3 on net photosynthetic rates are shown in

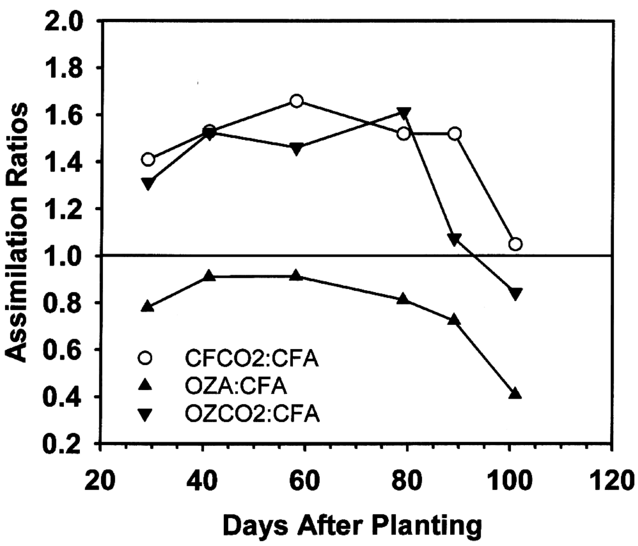

Fig.1. Ratios of net assimilation rates of soybean plants grown in reciprocal mixtures of CO_2 and O_3 during 1994. Drawn from data of Reid and Fiscus (1998).

Figure 1 where it can be seen that elevated CO_2 increases NAR in the presence and absence of damaging O_3. At ambient CO_2, O_3 reduced NAR throughout the season but its effect, relative to clean air (CFA), increased after flowering. In elevated CO_2 this decline was delayed for another 20 days but throughout most of the season NAR was increased by 30% to 60% by elevated CO_2. However, as table 1 illustrates, the increased photosynthetic rates did not always result in increased economic yield either in soybean or the other crops examined in the paper. The first significant point to be derived from Table 1 is the high degree of variability in the CO_2-fertilization effect, ranging in soybean for example from a yield decrease of 11 % to an increase of 39% in clean air (CF). The other crops, cultivars and O_3 treatments exhibited similarly high variability both within seasons and across multiple seasons. Secondly, the magnitude of the CO_2-fertilization effect is highly dependent on the level of O_3 stress present during growth. Again, variability was high but the trends for each crop are clear and characterized by the mean value for all crops which showed a small effect in clean air and larger effects as the level of stress increased.

Table 1. Percentage change in seed yield resulting from a doubled CO_2 concentration in the presence of 3 levels of O_3. Table is condensed and updated from Fiscus *et al.* (2001).

Species and Data Source	Parameter	CF	NF	NF+
Glycine max	Mean	11.8	35.0	57.4
Fiscus *et al.* (1997) 3 CVY	Maximum	39	84	94
Heagle *et al.* (1998) 3 CVY	Minimum	-11	7	9
Booker (Unpublished Data) 5 CVY	Median	8	24.5	58
Gossypium hirsutum	Mean	5.3	36.0	89.7
Heagle *et al.* (1999) 6 CVY	Maximum	23	50	141
	Minimum	-16	11	31
	Median	7.0	47.0	97.0
Oryza sativa	Mean	-5.1		13.9
Reid (Unpublished Data) 10 CVY	Maximum	13		28
	Minimum	-26		-2
	Median	-2.0		14.5
Triticum aestivum	Mean	-0.8	2.0	38.0
Heagle *et al.* (2000) 4 CVY	Maximum	17	39	79
	Minimum	-14	-20	13
	Median	-3.0	-5.0	30.0
Mean for all crops (31 CVY)		2.8	24.3	49.8

Above-ground vegetative biomass also showed large data variability but the mean across all crops in CF air was substantial at a little over 30%. A comparison of vegetative biomass and yield is shown in Figure 2. Like yield, vegetative biomass increased with increasing O_3 stress to a mean value approaching 80% in the presence of relatively high levels of O_3.

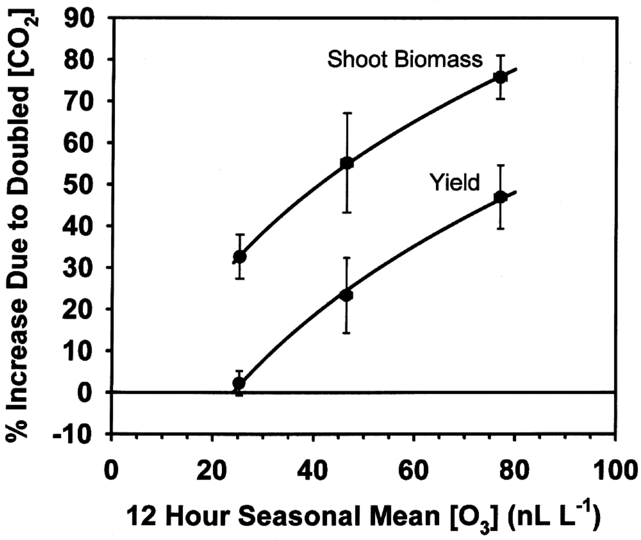

Fig.2. Effect of doubling the CO_2 concentration on vegetative biomass and eventual yield of crops grown in different levels of pollutant O_3. Bars are ± one standard error. For biomass and yield respectively, a = -20.50 and –53.58; b = 5.116 and 5.299.

Nonetheless, the point is clear that even the 30% increase in vegetative biomass in the CFA treatment ultimately resulted, on average, in a yield increase of less than 3%.

Average yield losses due to O_3 and the effect of elevated CO_2 in ameliorating those losses are shown in Table 2. Both biomass and yield are reduced by the same amount at current CO_2 levels but that reduction virtually disappeared at double ambient CO_2 concentrations with only a 4% increase in biomass and less than 1% for yield. In addition, the amelioration ratio indicates that even at high levels of O_3 stress, biomass was still increased about 25% by elevated CO_2 above what it was in CF air at ambient levels. However, yield was only restored to the same level observed in CFA air.

Table 2. Mean (± se) reduction and amelioration of yield and biomass losses due to O_3 stress for all crops.

	% Reduction by O_3 in Ambient CO_2	**% Reduction by O_3 in Doubled CO_2**	**Amelioration Ratio (2A/NF+) : (A/CF)**
Biomass	**26.8 ± 1.8**	**4.1 ± 2.1**	**1.254 ± 0.062**
Yield	**28.0 ± 2.7**	**0.4 ± 1.9**	**1.031 ± 0.026**
n	**31**	**31**	**31**

Discussion

The data examined in this paper clearly illustrate that the relationship between crop yields, biomass production, elevated CO_2 and co-occurring stresses presents a complex picture and may confound efforts to estimate future world food supplies based on changing gaseous environments. The data strongly suggest that plants in which the vegetative portion is consumed could benefit substantially from CO_2 increases but for those which are grown for their reproductive structures the picture is less clear. Even in non-domesticated species there often can occur a similar lack of positive relationship between vegetative and reproductive biomass with elevated CO_2. The increased vegetative biomass is not translated into increased reproductive biomass for *Arabidopsis thaliana* (Ward and Strain, 1997), *Bromus madritensis* (Huxman, *et al.*, 1999), *Casia obtusifolia* (Thomas *et al.*, 1999), *Heterotheca subaxillaris* (Johnson and Lincoln, 2000), *Poa annua* and *Senecio vulgaris* (Leishman *et al.*, 1999) and *Raphanus raphanistrum* (Curtis *et al.*, 1994; Jablonski, 1997). Farnsworth and Bazzaz (1995) suggested that the vegetative response to CO_2 was not a good indicator of reproductive output as they observed different trends among and within genera of 9 annual species representing 3 genera. Similary, several genotypes of *Abutilon theophrasti* showed lower reproduction with elevated CO_2 while others showed no change or a positive enhancement (Thomas *et al.*, 1999). Curtis *et al.* (1994) also reported a range of reproductive responses for *Raphanus raphanistrum*. Changes in the balance between C and N resources within a plant and the inability of some plants to adjust this balance has been suggested to explain the lack of a CO_2 effect on reproduction.

Competition for limiting resources may also play a role in limiting the reproductive response to CO_2. Bazzaz *et al.* (1992) reported decreased reproductive output per unit soil surface area with an increase in planting density of *Abutilon theophrasti* and no productivity enhancement due to elevated CO_2. Thomas *et al.* (1999) found that more genotypes of *Abutilon theophrasti* responded with a decrease in reproductive to vegetative biomass with elevated CO_2 when grown in stand than when grown individually. The decrease in reproductive biomass was larger than the increase in vegetative biomass. Microcosm studies of two grassland species *Pascopyrum smithii* (C_3) and *Bouteloua gracilis* (C_4) grown in pure stands, have shown a 19% increase in total biomass after two years of growth in elevated CO_2 but no CO_2 effect on seed head production for *Bouteloua* and samller reproductive heads for *Pascopyrum* at both CO_2 levels (Hunt *et al.*, 1996). Likewise, for old-field Mediterranean microcosms , Navas *et al.* (1997) reported that total biomass significantly increased in 4 of the 19 species represented while reproductive biomass was decreased by elevated CO_2 in 13 of the 19 species with 4 showing significant changes. Although the majority of these studies were conducted in controlled environment chambers, similar results have been found in field studies. *Avena barbata* grown in open-top field chambers (OTC) at elevated CO_2 showed an increase from ca. 5 to 7 seeds per plant associated with a reduction in seedling density, indicating a reduction in yield per unit ground area (Jackson, *et al.*, 1994). A rare calcareous grassland species, *Gentianella germanica*, significantly increased its total biomass with elevated CO_2 but its seed mass was decreased because of a 79% decrease in seed set (Fischer *et al.*, 1997). These studies suggest that resources become limiting as plants compete with their neighbors and that this competition for resources has a direct effect on reproductive yields at elevated CO_2. These studies are consistent with fertilization studies suggesting that N limits the stimulatory effect of CO_2, e.g., *Hordeum spontaneum* (Gr 2000) and *Bromus mollis* (Larigauderie *et al.*, 1988). In addition, the study on cotton seed production conducted by Heagle *et al.*, (1999) clearly showed that the N fertilization effect dwarfs the effect of doubled CO_2. The N effect taken across CO_2 in CF air averaged 150% and in NF+ air 154% while the CO_2 effect averaged across N was 5% in CF air. The unpublished planting density data of Reid for rice, cited in table 1, is also consistent with the concept that the effect of elevated CO_2 may be limited by availability of resources other than CO_2. Finally, an analysis of historical wheat yield data led Amthor (1998) to conclude that productivity increases due to elevated CO_2 will be small compared to those due to future advances in technology. Thus, the certitude of crop productivity increases due to higher atmospheric CO_2 concentrations is diminishing while the costs and methodologies necessary to take advantage of the situation are still somewhat obscure.

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