

How do elevated CO₂ and O₃ affect the interception and utilization of radiation by a soybean canopy?

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Abstract

Net productivity of vegetation is determined by the product of the efficiencies with which it intercepts light (ϵ_i) and converts that intercepted energy into biomass (ϵ_c). Elevated carbon dioxide (CO₂) increases photosynthesis and leaf area index (LAI) of soybeans and thus may increase ϵ_i and ϵ_c ; elevated O₃ may have the opposite effect. Knowing if elevated CO₂ and O₃ differentially affect physiological more than structural components of the ecosystem may reveal how these elements of global change will ultimately alter productivity. The effects of elevated CO₂ and O₃ on an intact soybean ecosystem were examined with Soybean Free Air Concentration Enrichment (SoyFACE) technology where large field plots (20-m diameter) were exposed to elevated CO₂ (~550 $\mu\text{mol mol}^{-1}$) and elevated O₃ (1.2 \times ambient) in a factorial design. Aboveground biomass, LAI and light interception were measured during the growing seasons of 2002, 2003 and 2004 to calculate ϵ_i and ϵ_c . A 15% increase in yield (averaged over 3 years) under elevated CO₂ was caused primarily by a 12% stimulation in ϵ_c , as ϵ_i increased by only 3%. Though accelerated canopy senescence under elevated O₃ caused a 3% decrease in ϵ_i , the primary effect of O₃ on biomass was through an 11% reduction in ϵ_c . When CO₂ and O₃ were elevated in combination, CO₂ partially reduced the negative effects of elevated O₃. Knowing that changes in productivity in elevated CO₂ and O₃ were influenced strongly by the efficiency of conversion of light energy into energy in plant biomass will aid in optimizing soybean yields in the future. Future modeling efforts that rely on ϵ_c for calculating regional and global plant productivity will need to accommodate the effects of global change on this important ecosystem attribute.

Keywords: crop, leaf area index, light, photosynthesis, production, SoyFACE

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Introduction

The accumulation of energy in plant biomass (W_h) is determined by the efficiency that intercepted radiation is converted to biomass energy (ϵ_c), the efficiency of light interception by the canopy (ϵ_i), and total incident solar radiation (S_t ; $W_h = \epsilon_c \times \epsilon_i \times S_t$; Monteith, 1972, 1977). Because ϵ_c and ϵ_i integrate physiological, structural, and environmental processes in plant canopies, knowing how these parameters respond to predicted

increases in the concentration of carbon dioxide (CO₂) (Prentice *et al.*, 2001) and O₃ (Prather *et al.*, 2001) in the atmosphere will be particularly important for estimating ecosystem productivity over large spatial scales (Sinclair & Muchow, 1999; Turner *et al.*, 2002; Ahl *et al.*, 2004; Ewert, 2004), and for understanding whether changes in productivity are driven by canopy structure or by the efficiency of light use, determined by photosynthesis and respiration.

While elevated CO₂ generally stimulates productivity (Drake *et al.*, 1997; Ainsworth *et al.*, 2002; Long *et al.*, 2004), elevated O₃ often has the opposite effect (Fuhrer, 2003; Morgan *et al.*, 2003). Whether these responses are driven primarily by physiological (ϵ_c) or structural changes (ϵ_i) within the canopy remains largely

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unknown. Of the experiments that have examined the response of ϵ_c to elevated CO₂ or O₃ (Weerakoon *et al.*, 2000; Hui *et al.*, 2001; DeLucia *et al.*, 2002; Ewert *et al.*, 2002; Manderscheid *et al.*, 2003), only two have been conducted under realistic field conditions free of potential experimental artifacts (DeLucia *et al.*, 2002; Ewert *et al.*, 2002). Because of the paucity of data, it is not yet possible to draw a firm conclusion about how elevated CO₂ and O₃ will affect ϵ_c of intact ecosystems.

Elevated CO₂ may increase crop yields by stimulating photosynthesis and thus the rate of biomass accumulation, or by changing structural elements in the plant canopy that control light absorption. Elevated atmospheric CO₂ increases photosynthesis for individual leaves in soybean (Drake *et al.*, 1997; Ainsworth *et al.*, 2002; Anten *et al.*, 2003; Rogers *et al.*, 2004); if this stimulation extends to the entire canopy, the numerator (cumulative biomass) of ϵ_c also will increase (Ainsworth *et al.*, 2002). Although not universal (Drake *et al.*, 1997; Cowling & Field, 2003), elevated CO₂ also may increase the leaf area index (LAI) of crops (leaf area per unit ground area), including soybean (Dermody *et al.*, 2006). Leaf area and orientation control the interception and absorption of photosynthetically active radiation (IPAR and APAR) and thus determine ϵ_i .

Ozone is highly reactive and at moderate concentrations inhibits photosynthesis and reduces the rate of biomass accumulation, particularly after leaf maturation (Sandermann *et al.*, 1998; Ewert & Pleijel, 1999; Isebrands *et al.*, 2001; Morgan *et al.*, 2003). Using a Free Air Concentration Enrichment (FACE) system, Morgan *et al.* (2006) confirmed that ozone damage to photosynthesis occurred primarily late in the growing season, but this damage was less than reported by those using opentop chambers or other enclosures to administer the ozone treatment. At higher O₃ levels, leaf senescence often is accelerated and there is a concomitant reduction in LAI (Isebrands *et al.*, 2001; Morgan *et al.*, 2003). At the Soybean Free Air Concentration Enrichment (SoyFACE) experiment, O₃ significantly decreased LAI (Dermody *et al.*, 2006); however, even large decreases may have only a small effect on light interception and productivity in soybean canopies where LAI can be >6.

Elevated CO₂ may compensate for the negative effects of low background levels of O₃ on productivity (Cardoso-Vilhena *et al.*, 2004; Booker & Fiscus, 2005). The reduction in stomatal conductance for plants grown in elevated CO₂ reduces diffusion of O₃ into leaves and lowers its effective dose (Fiscus *et al.*, 1997; Reid & Fiscus, 1998). Increased activity of anti-oxidant enzymes in elevated CO₂ also may reduce the deleterious effect of O₃ (Rao *et al.*, 1995). Elevated CO₂ reduced the negative effects of O₃ on biomass and LAI of potato, poplar and wheat (McKee *et al.*, 2000; Donnelly *et al.*,

2001; Isebrands *et al.*, 2001; Heagle *et al.*, 2003) and mitigated its effect on ϵ_c in wheat (Rudorff *et al.*, 1996).

Most studies that examined the response of ϵ_c to elevated CO₂ and O₃ relied on different types of enclosures to control the composition of the local atmosphere (Rudorff *et al.*, 1996; Manderscheid *et al.*, 1997, 2003), and may overestimate the effects of these gases, possibly because of edge effects associated with small plot size and microclimatic effects of the chamber (Long *et al.*, 2004, 2006). By increasing humidity around the leaf, growth in an enclosure may increase stomatal opening and O₃ uptake. Furthermore, the forced circulation of air within chambers may increase exposure of lower canopy leaves to the bulk atmosphere, also increasing O₃ uptake by shaded foliage. Most importantly, the small size of open top chambers and their alteration of the light environment preclude accurate measurement of canopy light interception. The SoyFACE experiment avoids these problems by growing soybeans in an intact ecosystem under fully open-air CO₂ and O₃ fumigation.

The objective of this research was to quantify the effects of elevated CO₂ and O₃ on ϵ_c and ϵ_i and how these variables contribute to changes in productivity of a soybean crop. Large plots (20-m diameter) in a soybean field were exposed to elevated levels of CO₂ and O₃, singly and in combination, with FACE technology. Estimates of ϵ_c incorporate changes in energy content and this was calculated at intervals through the entire growing season. We also calculated ϵ_b , defined as accumulated biomass per unit PAR. Because of differences in the energy content of vegetative tissue and seed, ϵ_b was estimated up to the time of maximum LAI. The calculations of ϵ_c and ϵ_b were performed with both IPAR and APAR. We hypothesized that improved photosynthetic efficiency, reflected in increases in ϵ_c and ϵ_b , would account for most of the increase in production in elevated CO₂, rather than increased LAI and altered canopy structure, captured by changes in ϵ_i . Similarly, for O₃ we hypothesized that reductions in productivity would largely be caused by lower ϵ_c and ϵ_b rather than decreased ϵ_i . Finally, we hypothesized, that elevated CO₂ would partially compensate for the effects of O₃ on ϵ_c and ϵ_i when the two gases were elevated in combination.

Materials and methods

Site description

This study was conducted at the SoyFACE facility at the University of Illinois, Urbana-Champaign (40°02'N, 88°14'W, 228 m above sea level; www.soyface.uiuc.edu). Each experimental plot was surrounded by pipes that injected CO₂ or O₃ at supersonic velocity from 300 μ m

pores above the canopy (Miglietta *et al.*, 2001). The rate and position of gas release was automatically altered with wind speed and direction to maintain the desired gas concentrations within the plot. Plots were fumigated during day light hours from planting until harvest. The target concentrations for CO₂ (550 µmol mol⁻¹) and O₃ (1.2 × ambient) represent the predicted atmospheric levels by 2050 (Prather *et al.*, 2001; Prentice *et al.*, 2001). The O₃ fumigation system was turned off during periods of low wind speed and dew. The actual average CO₂ concentrations for each year from 2002 to 2004 were 552, 552 and 550 µmol mol⁻¹, respectively, while the ambient plots were ~370 µmol mol⁻¹ CO₂.

The elevated O₃ treatment was initiated in 2002. The average ambient O₃ concentrations between 10:00 and 18:00 hours in 2002, 2003 and 2004 were 62, 50 and 44 nmol mol⁻¹, respectively. In 2002, 70% of values were within 10% of the set-point; in 2003, 84% of values were within 10% of the set-point; and in 2004, 79% of values were within 10% of the set-point. The full factorial experiment was completed in 2003 and 2004 with the addition of plots exposed to elevated CO₂ and O₃ in combination. Cross-contamination of CO₂ and O₃ was prevented by separating the experimental plots by at least 100 m (Nagy *et al.*, 1994). A more detailed description of the SoyFACE facility can be found in Rogers *et al.* (2004) and Dermody *et al.* (2006).

The experiment consisted of four randomized blocks, each containing 20-m diameter octagonal plots (total area 314 m²). Soybean (cv. 93B15, Pioneer Hi-Bred, Johnston, IA, USA) was planted at 0.38-m row spacing in May 2002. This variety is resistant to soybean cyst nematode and is typical of varieties commonly grown in this region. The soil was a deep and fertile Flanagan (fine, montmorillonitic, mesic aquic Argiudoll) with some low-lying blocks of Drummer [typic Haplaquoll; (Rogers *et al.*, 2004)]. According to standard agronomic practice in this region plots were fertilized with P and K as needed but were not inoculated with *Bradyrhizobium*, which is ubiquitous.

LAI and biomass harvests

LAI was measured weekly with a plant canopy analyzer (LAI-2000, LI-COR, Lincoln, NE, USA) in the growing seasons of 2002, 2003 and 2004 according to the methods in Dermody *et al.* (2006). The efficiency of light interception by the canopy (ϵ_i) was calculated as (1 – transmittance). Soybeans (aboveground tissues) were harvested from two subplots (0.23 m²) in each of the 16 plots every 2 weeks during the growing season as in Morgan *et al.* (2005).

To be comparable with most previous studies (e.g. Sinclair & Muchow, 1999; Manderscheid *et al.*, 2003;

Kiniry *et al.*, 2005; Lindquist *et al.*, 2005) estimates of radiation interception and conversion efficiencies were based on aboveground biomass only. Additionally, measurements of root biomass at SoyFACE were infrequent. The root/shoot ratio of soybean in the SoyFACE experiment (0.15–0.22) was not affected by the treatments (Rodriguez, 2003), so it is unlikely that exclusion of root biomass affected the magnitude of the treatment effect on ϵ_c . The energy contents of vegetative (18 MJ kg⁻¹) and seed (23 MJ kg⁻¹) biomass for the calculation of ϵ_c were from (Amthor *et al.*, 2004). Exposure to elevated CO₂ has been shown to have no effect on the energy content of soybean tissues (Amthor *et al.*, 1994).

Radiation use efficiency

The conversion efficiency of radiation to biomass (ϵ_c) was calculated for each of three growing seasons (2002–2004) as the slope of cumulative energy in aboveground biomass vs. the cumulative energy intercepted ($\epsilon_{c,IPAR}$) or absorbed ($\epsilon_{c,APAR}$) by the canopy (Monteith, 1972). Additionally, ϵ_c was calculated at each measurement date from the slope of pairs of adjacent points. The slope of cumulative biomass vs. cumulative IPAR or APAR up to the time of maximum LAI, was used to calculate $\epsilon_{b,IPAR}$ and $\epsilon_{b,APAR}$. Incident PAR was measured at 10-min intervals for the entire growing season with a quantum sensor (ΔT BF2, ΔT Devices Ltd, Cambridge, UK). Intercepted PAR was calculated as, $IPAR = (\varphi_a) (1 - \exp(-k \times LAI))$; where k is the canopy extinction coefficient and φ_a is incident irradiance (Daughtry *et al.*, 1992; Sinclair & Muchow, 1999; Turner *et al.*, 2002). It was assumed that 1 W m⁻² of sunlight contains 4.6 µmol (photons) m⁻² s⁻¹. The canopy extinction coefficient (k) was obtained from $d = \cos^{-1}(k)$; where d was the foliage inclination angle (Forseth & Norman, 1993). If foliage is randomly distributed, d represents the mean tip angle (MTA; Campbell & Norman, 1989), which was calculated from the angular distribution of canopy gap fraction by the plant canopy analyzer. To calculate cumulative IPAR over the season, weekly values of LAI and k were interpolated using a linear fit between adjacent measurement dates. Diurnal changes in k were not taken into account in the calculation of cumulative IPAR. The integral of incident solar radiation (S_i) was calculated by integrating incident PAR data over all days before each harvest date.

Radiation use efficiency also was calculated based on absorbed photosynthetically active radiation: $APAR = (\varphi_a - \varphi_{cr}) [1 - \exp(-k \times LAI)]$; where φ_{cr} represents canopy reflectance measured with a narrow band spectrometer (Unispec Spectral Analysis System, PP Systems Inc., Haverhill, MA, USA). Measurements of

canopy reflectance were made at six points in each experimental plot between 1200 and 1400 CST under a clear sky. Reflectance did not vary among treatments and the average value was $\sim 7\%$.

Statistical analysis

Repeated measures analysis of variance (PROC MIXED; SAS, The SAS Institute; Version 8.1, Cary, NC, USA.) was used to test for treatment effects on LAI and ϵ_i . All analyses were performed on the plot means and blocks were included as a random component. *Post-hoc* linear contrasts were performed to elucidate treatment effects within interaction terms. Biomass data were analyzed as in Morgan *et al.* (2005). Whole season ϵ_c and ϵ_b values were calculated on a plot basis by linear regression of cumulative plot biomass or energy in biomass vs. cumulative IPAR or APAR (SAS, PROC MIXED). To determine if elevated CO₂ and O₃ affected ϵ_c and ϵ_i , the slopes of the relationships between cumulative biomass and energy in biomass vs. cumulative IPAR or APAR were compared with analysis of covariance (ANCOVA). The least-squared means are presented in the figures and the associated variances are the standard errors from mixed model ANOVAS. To avoid type II

errors, differences were considered significant at $P \leq 0.1$.

Results

The response of LAI to elevated CO₂ and elevated O₃ in 2003 and 2004 was similar to the responses in 2001 and 2002 reported by Dermody *et al.* (2006). Exposure to elevated CO₂ increased maximum LAI by $\sim 9\text{--}25\%$ and this difference persisted as LAI declined, such that elevated CO₂ delayed maturity of the canopy (data not shown). By accelerating canopy senescence, elevated O₃ reduced LAI late in the season; on day 253 in 2003 LAI was 59% lower in elevated O₃ than in ambient air ($F = 4.7$, $P \leq 0.05$, $n = 4$). A hailstorm on July 11, 2003 reduced LAI by 60%, after which it recovered rapidly and attained its maximum value on day 230 (August 19). The exception to this pattern occurred in elevated O₃ plots where a significant reduction in LAI persisted throughout the season (e.g. at maximum LAI, ambient: 4.9; elevated O₃: 4.0; $F = 6.2$, $P \leq 0.01$, $n = 4$). When combined, elevated CO₂ tended to offset the negative effects of elevated O₃; in 2004, elevated CO₂ \times O₃ reduced senescence relative to am-

Table 1 Average interception efficiency (ϵ_i) across the growing season, the conversion efficiency-based on energy content (ϵ_c) for the entire growing season, and the conversion efficiency based cumulative biomass (ϵ_b) at maximum LAI (max LAI, gMJ⁻¹), for soybeans grown in ambient air (control), 550 $\mu\text{mol mol}^{-1}$ CO₂ (CO₂), 1.2 \times ambient O₃ (O₃) or 550 $\mu\text{mol mol}^{-1}$ CO₂ plus 1.2 \times ambient O₃ (CO₂ \times O₃)

Year	Treat	ϵ_i (average)	$\epsilon_{c, \text{IPAR}}$ (whole season)	$\epsilon_{b, \text{IPAR}}$ (max LAI)	$\epsilon_{c, \text{APAR}}$ (whole season)	$\epsilon_{b, \text{APAR}}$ (max LAI)
2002	Control	0.89 (0.01)	0.031 (0.001)	1.4 (0.06)	0.032 (0.001)	1.5 (0.06)
	CO ₂	0.89 (0.01)	0.035 (0.002) ^(*)	1.7 (0.20)*	0.036 (0.002)*	1.8 (0.20)*
	O ₃	0.88 (0.01)*	0.026 (0.002)*	1.2 (0.10)*	0.027 (0.002)*	1.2 (0.11)*
2003	Control	0.75 (0.02)	0.018 (0.002)	0.9 (0.09)	0.019 (0.002)	1.0 (0.09)
	CO ₂	0.80 (0.02)*	0.019 (0.001)	0.9 (0.06)	0.019 (0.001)	1.0 (0.06)
	O ₃	0.69 (0.02)*	0.015 (0.001)*	0.8 (0.06) ^(*)	0.017 (0.001)*	0.8 (0.07) ^(*)
	CO ₂ \times O ₃	0.79 (0.02)*	0.022 (0.001)*	1.1 (0.08)*	0.022 (0.001)*	1.2 (0.08)*
2004	Control	0.78 (0.03)	0.026 (0.001)	1.3 (0.06)	0.027 (0.001)	1.4 (0.06)
	CO ₂	0.79 (0.03)	0.029 (0.002) ^(*)	1.6 (0.06)*	0.031 (0.002) ^(*)	1.7 (0.07)*
	O ₃	0.78 (0.03)	0.024 (0.001)	1.3 (0.01)	0.026 (0.001)	1.4 (0.02)
	CO ₂ \times O ₃	0.81 (0.03)*	0.027 (0.001)	1.5 (0.04) ^(*)	0.029 (0.001)	1.6 (0.04) ^(*)

*Significant differences ($P \leq 0.05$) between elevated CO₂ or O₃ and ambient air.

^(*)Indicates differences significant at $P \leq 0.1$.

Efficiencies were calculated using both intercepted photosynthetically active radiation (IPAR) and absorbed photosynthetically active radiation (APAR). Interception efficiency (ϵ_i) is the fraction of light intercepted by the canopy and was measured with a plant canopy analyzer. The values of $\epsilon_{c, \text{IPAR}}$ were obtained from the slope of the regression between season long measurements of accumulated biomass and IPAR. The values of $\epsilon_{b, \text{IPAR}}$ at the time of maximum LAI were obtained from the slope of the regression between bi-weekly measurements of biomass and IPAR. Absorbed photosynthetically active radiation (APAR; MJ m⁻²) was calculated from PAR and used in a regression of bi-weekly measurements of biomass and APAR to determine $\epsilon_{c, \text{APAR}}$ and $\epsilon_{b, \text{APAR}}$. The least squared mean of four experimental plots are presented with standard error of the mean in parentheses.

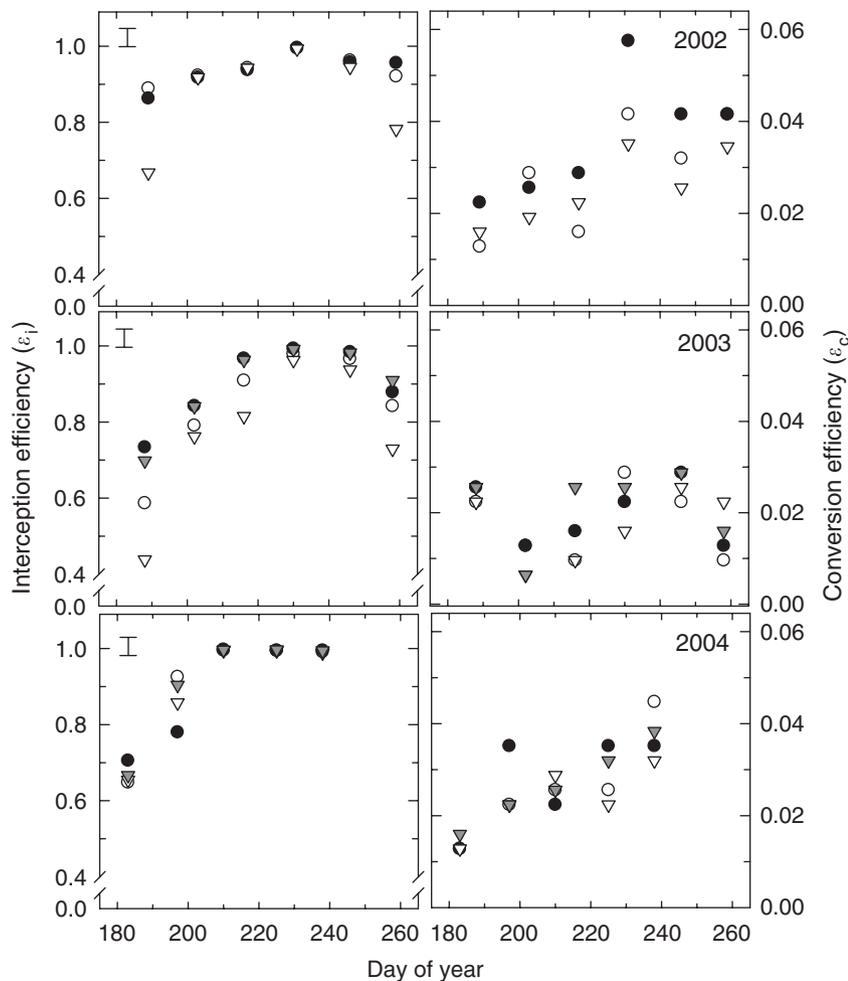


Fig. 1 Interception efficiency (ϵ_i) and conversion (ϵ_c) for each harvest date during the 2002–2004 growing seasons. Interception efficiency (ϵ_i) is the fraction of light intercepted by the canopy and was measured with a plant canopy analyzer. On each date ϵ_c was calculated as the quotient of cumulative total energy content (MJ m^{-2}) of aboveground biomass and cumulative interception and absorption of photosynthetically active radiation (MJ m^{-2}) on that and the preceding date. Soybeans were grown in ambient air (open circles, ○), $550 \mu\text{mol mol}^{-1}$ CO_2 (black circles, ●), $1.2 \times$ ambient O_3 (open triangles, ▽), and $550 \mu\text{mol mol}^{-1}$ CO_2 plus $1.2 \times$ ambient O_3 (gray triangles, ▽). In 2002, only the ambient, elevated CO_2 and elevated O_3 treatments were present; the elevated $\text{CO}_2 \times \text{O}_3$ treatment was added in 2003. Each point represents the least squared mean ($n = 4$); the error bar represents the standard error of the mean. The 15th day of June, July, August, and September correspond to days 167, 197, 228, and 259, respectively.

ambient air and elevated O_3 alone (e.g. day 243, $F = 3.7$, $P \leq 0.05$, $n = 4$).

Although LAI responded to elevated CO_2 and elevated O_3 , the subsequent effects on ϵ_i and cumulative IPAR or APAR were generally small (Table 1, Fig. 1). Even after the hailstorm in 2003, elevated CO_2 increased ϵ_i but only by 6%. A slow recovery of LAI in elevated O_3 reduced IPAR and APAR for the remainder of the season (e.g. 2003, day 230, $F = 1.6$, $P \leq 0.12$, $n = 4$; day 246, $F = 1.8$, $P \leq 0.08$, $n = 4$).

Changes in atmospheric composition had a more pronounced effect on ϵ_c than ϵ_i (Fig. 1). Elevated CO_2

consistently increased whole-season ϵ_c , with the largest increase relative to ambient air (14%) occurring in 2004 (Table 1, Fig. 1). Elevated O_3 also affected ϵ_c , reducing it in 2002 and 2003 by 15% (Table 1, Fig. 1). Whenever CO_2 and O_3 were combined, the effect of CO_2 partially outweighed that of O_3 ; in 2003 this effect was particularly strong and ϵ_c was significantly greater than in ambient air (Table 1, e.g. 2003, $F = 3.5$, $P \leq 0.08$, $n = 4$). In 2004, the magnitude of this effect declined and ϵ_c in $\text{CO}_2 \times \text{O}_3$ was not significantly different from ambient air. The response of ϵ_b to the treatments was similar to ϵ_c . The hailstorm in 2003 reduced the values measured

for ϵ_c and ϵ_b relative to 2002 and 2004 ($F = 23.5$, $P \leq 0.01$). The values of ϵ_c and ϵ_b we calculated (0.01–0.04 and 0.8–1.7, respectively) were within the range for soybeans and other well tended C₃ crops (e.g. ϵ_b 0.7–2.04; Muchow *et al.*, 1993; Sinclair & Muchow, 1999).

Discussion

That the effects of elevated CO₂ and O₃ on ϵ_c were more pronounced than those on ϵ_i , suggests that physiological rather than structural processes drive the response of crop productivity to altered atmospheric chemistry. We measured a 12% stimulation of ϵ_c in soybean exposed to elevated CO₂, and this likely drove the increase of 15–16% in yield measured by Morgan *et al.* (2005). The increase in efficiency of radiation interception (ϵ_i) was small (3%) and was a minor contribution to the increase in biomass under elevated CO₂. By accelerating senescence and lowering LAI, elevated O₃ reduced ANPP by approximately 17% (Dermody *et al.*, 2006; Morgan *et al.*, 2006). However, these changes were driven primarily by ϵ_c , as again it responded more strongly than ϵ_i to altered atmospheric chemistry. When administered together, elevated CO₂ partially ameliorated the negative effects of O₃ on ϵ_c . Under all treatment combinations soybean attained an average interception efficiency of approximately 99% at maximum LAI, but ϵ_c varied considerably among treatments (Fig. 1). The large stimulation in ϵ_c compared with ϵ_i indicates that changes in photosynthesis or respiration, rather than changes in LAI altered production when soybeans were grown in elevated CO₂. Similarly, the proportionately greater reduction of ϵ_c compared with ϵ_i in elevated O₃ indicates that the primary deleterious effects of O₃ operate through changes in photosynthesis rather than canopy structure. Knowing that the processes controlling the conversion of light energy into biomass are impacted more strongly by changes in atmospheric composition than those driving interception, will aid in optimizing crop yields in the future.

Elevated CO₂ caused a relatively small but consistent increase in LAI up to its maximum, but this increase did not translate into a significant increase in ϵ_i or IPAR. Because light attenuates quasi-exponentially through plant canopies, ϵ_i and IPAR are relatively insensitive to changes in LAI, particularly at high values. Assuming an extinction coefficient of 0.5 and applying a Beer's law approximation for light attenuation, a ~17% increase in LAI from six to seven would cause a corresponding increase in IPAR of only 2%. Thus, at the high values of LAI attained by soybean, large treatment effects on LAI would be necessary to affect ϵ_i or IPAR (Daughtry *et al.*, 1992). Elevated CO₂ increased max-

imum LAI on average by 14% (Dermody *et al.*, 2006) which was not sufficient to substantially increase IPAR, and contributed to an average increase of only 3% in ϵ_i at maximum LAI. In a loblolly pine plantation, DeLucia *et al.* (2002) also found no effect of elevated CO₂ on APAR.

An increase in ϵ_c rather than ϵ_i , contributed to the stimulation in aboveground biomass for soybeans grown in elevated CO₂. Greater biomass in the elevated CO₂ plots resulted primarily from higher rates of photosynthesis not increased LAI (Rogers *et al.*, 2004; Bernacchi *et al.*, 2005; Morgan *et al.*, 2005; Dermody *et al.*, 2006). Under strong limitation by soil nutrients, higher rates of photosynthesis under elevated CO₂ may not always contribute to an increase in biomass, partly because of limitations on the formation of new sinks (Rogers *et al.*, 1998; Stitt & Krapp, 1999). However, nitrogen fixation in soybean and N fertilization of corn the previous year reduced nutrient limitations, and the nodules themselves may act as sinks for additional photosynthate (Stitt & Krapp, 1999; Rogers *et al.*, 2004). At SoyFACE the 25% increase in leaf level photosynthesis in elevated CO₂ contributed to an average increase of 12% in ϵ_c and a subsequent increase of 15% in aboveground biomass across three growing seasons (Morgan *et al.*, 2005). That the increase in photosynthesis contributed more than greater light interception to enhanced biomass production is reflected in the relatively small increase in ϵ_i under elevated CO₂ over the same time period.

Consistent with observed reductions in photosynthesis per unit leaf area (Sandermann *et al.*, 1998; Ewert & Pleijel, 1999; Isebrands *et al.*, 2001; Morgan *et al.*, 2003), lower biomass accumulation in elevated O₃ was associated with reduced ϵ_c . The diversion of assimilates to repair and detoxification processes may have reduced ϵ_c throughout the season. It also is possible that later in the season, accelerated senescence in O₃ was sufficient to reduce canopy photosynthesis (Long & Drake, 1991). Exposure to elevated O₃ also reduced ϵ_i ; however, reductions in ϵ_i were detected only toward the end of the growing season and were much smaller than the change in ϵ_c . Elevated O₃ may also reduce the capacity of plants to recover from stress (Miller & McBride, 1999; Eichelmann *et al.*, 2004; Ashmore, 2005). After the hailstorm in 2003, exposure to elevated O₃ reduced LAI and ϵ_c by approximately 44% relative to ambient air, and the subsequent yield was 25% less than in ambient air compared with a reduction of only 15% in the previous year (Morgan *et al.*, 2005).

At least for the doses administered in this experiment, which were below the levels of O₃ predicted for 2050, the detrimental effects of O₃ on soybean ϵ_c were partially counteracted by elevated CO₂ (Table 1). By increasing leaf level photosynthesis, elevated CO₂ may

increase the availability of assimilates for repair of O₃ damage (Allen, 1990; McKee *et al.*, 1997; Booker & Fiscus, 2005). Additionally, by reducing stomatal conductance, elevated CO₂ may lower the effective dose of O₃ reaching the leaf mesophyll (Cardoso-Vilhena *et al.*, 2004; Booker & Fiscus, 2005). However, elevated CO₂ may not mitigate the negative effects of O₃ at levels closer to those predicted for 2050, and the interactive effects of these gases will be modulated by other stress factors (Rudorff *et al.*, 1996; Fuhrer, 2003).

Because of the difficulties associated with measuring belowground biomass much of the research on ϵ_c is limited to aboveground processes (e.g. Muchow *et al.*, 1993; Kiniry *et al.*, 1998; Sinclair & Muchow, 1999; DeLucia *et al.*, 2002; Manderscheid *et al.*, 2003; Ahl *et al.*, 2004; Lindquist *et al.*, 2005). To enable comparison with these studies, we also focus on aboveground processes. Additionally, root biomass data for SoyFACE was not available in all years between 2002 and 2004 or at the same frequency as aboveground biomass data. Based on data previously collected at SoyFACE by Rodriguez (2003), we assumed that elevated CO₂ and O₃ had minimal effects on root-to-shoot ratios. Two meta-analyses that examined soybean responses to elevated CO₂ and O₃ by Ainsworth *et al.* (2002) and Morgan *et al.* (2003) also showed no significant effects of these gases on root-to-shoot ratios.

Despite a range of growing conditions, from optimal in 2004 (Changnon & Changnon, 2005) to stressful in 2003, we detected consistent effects of elevated CO₂ and elevated O₃ on ϵ_c . Growth in elevated CO₂ increased biomass accumulation in soybean by stimulating photosynthesis and ϵ_c , and not by affecting the interception of solar radiation (ϵ_i). Similarly, the primary effect of elevated O₃ on biomass accumulation was a reduction in ϵ_c across the growing season. Elevated O₃ reduced the accumulation of aboveground biomass and although elevated O₃ increased the rate of senescence, this occurred deep in the canopy and had minimal effect on ϵ_i . Radiation use efficiency is widely used in empirical models that predict productivity (Bartelink *et al.*, 1997; Nouvellon *et al.*, 2000; Medlyn *et al.*, 2003; Berry & Roderick, 2004; Chen & Coughenour, 2004; Richter & Semenov, 2005). However, only a few studies have examined the effects of CO₂ or O₃ on ϵ_c (Rudorff *et al.*, 1996; Manderscheid *et al.*, 1997, 2003; DeLucia *et al.*, 2002; Van Oijen *et al.*, 2004) and all but one of these studies have been in enclosed systems. The soybean agro-ecosystem occupies approximately 30 million hectares in the United States and has an approximate value of \$19 billion (<http://www.ers.usda.gov/News/soybeancoverage.htm>). Current yield losses to O₃ are estimated at \$2 billion annually (Murphy *et al.*, 1999). Knowing how ϵ_c and ϵ_i respond to elevated CO₂ and O₃

will thus be crucial to efforts that seek to optimize productivity of soybean in the future.

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