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The impact of elevated CO_2 on yield loss from a C_3 and C_4 weed in field-grown soybean

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Abstract

Soybean (*Glycine max*) was grown at ambient and enhanced carbon dioxide (CO_2, + 250 $\mu L\ L^{-1}$ above ambient) with and without the presence of a C3 weed (lambsquarters, *Chenopodium album* L.) and a C4 weed (redroot pigweed, *Amaranthus retroflexus* L.), in order to evaluate the impact of rising atmospheric carbon dioxide concentration [CO_2] on crop production losses due to weeds. Weeds of a given species were sown at a density of two per metre of row. A significant reduction in soybean seed yield was observed with either weed species relative to the weed-free control at either [CO_2]. However, for lambsquarters the reduction in soybean seed yield relative to the weed-free condition increased from 28 to 39% as CO_2 increased, with a 65% increase in the average dry weight of lambsquarters at enhanced [CO_2]. Conversely, for pigweed, soybean seed yield losses diminished with increasing [CO_2] from 45 to 30%, with no change in the average dry weight of pigweed. In a weed-free environment, elevated [CO_2] resulted in a significant increase in vegetative dry weight and seed yield at maturity for soybean (33 and 24%, respectively) compared to the ambient CO_2 condition. Interestingly, the presence of either weed negated the ability of soybean to respond either vegetatively or reproductively to enhanced [CO_2]. Results from this experiment suggest: (i) that rising [CO_2] could alter current yield losses associated with competition from weeds; and (ii) that weed control will be crucial in realizing any potential increase in economic yield of agronomic crops such as soybean as atmospheric [CO_2] increases.

Keywords: carbon dioxide, climate change, competition, lambsquarters, pigweed, yield

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Introduction

The ongoing increase in atmospheric carbon dioxide concentration [CO_2] stimulates net photosynthesis (and subsequent growth) in plants with the C3 photosynthetic pathway by increasing the CO_2 concentration gradient from the air to the leaf interior and by decreasing the loss of CO_2 via photorespiration. Alternatively, plants with the C4 photosynthetic pathway already have an internal biochemical pump for concentrating CO_2 at the site of C3 pathway carboxylation and have a smaller response to rising atmospheric [CO_2] (for reviews see Bowes 1996; Ghannoum *et al*. 2000).

The ways in which different photosynthetic pathways respond to enhanced [CO_2] is particularly relevant to crop/weed interactions in agricultural systems. This is because many of the most 'troublesome' weedy species (i.e. those which are inadequately controlled) are C4 plants, while most major crops are C3 plants (see Patterson 1995b). For example, among the 18 most troublesome weeds in the world (Holm *et al*. 1977), 14 are C4, whereas of the 86 plant species which supply most of the world's food, only five are C4 species (Patterson 1995a). Because of this variable distribution of the C4 and C3 pathway between weed and crop species, many experiments and most reviews concerned with weeds and rising [CO_2] have focused on C3 crop/C4 weed interactions (e.g. Patterson *et al*. 1984; Patterson 1986, 1993; Patterson & Flint 1990; 1995a; Alberto *et al*. 1996; Froud-Williams 1996). Data obtained from these greenhouse and growth chamber experiments are con-

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sistent with the photosynthetic pathways, i.e. that higher [CO_2] favours the vegetative growth of C3 over C4 species.

However, the generalization that crops are C3 and weeds are C4 and that weed competition will consequently decrease with increasing atmospheric [CO_2], should not be viewed as universal. Clearly there are major C4 crops of economic importance (e.g. maize, sorghum, millet and sugarcane), and many important C3 weeds (e.g. *Chenopodium album*, *Avena fatua*). In addition, it should be noted that crop/weed interactions vary substantially by geographical region; within a given region, depending on temperature, precipitation, etc. C3 and C4 crops may interact with both C3 and C4 weeds. For example, for soybean in the temperate U.S., four of the five most troublesome weeds are C3 (Bridges 1992), whereas on a global basis the predominant troublesome weeds for soybean in tropical locations are C4 (Holm *et al*. 1977).

Although interactions between C3 crops and C4 weeds have been well documented, fewer studies have examined weed/crop interactions for the same photosynthetic pathway at elevated [CO_2]. For the few studies which exist, the vegetative growth of the C3 weed was consistently favoured over that of the C3 'crop' (either pasture grass or alfalfa) as [CO_2] increased (Bunce 1995; Newton *et al*. 1996; Potvin & Vasseur 1997). In a study utilizing lambsquarters and sugarbeet, the competitive advantage of sugarbeet was attributed to the late emergence of lambsquarters in the experiment (Houghton & Thomas 1996).

Clearly, the ongoing increase in atmospheric [CO_2] may have important consequences for weed/crop competition and subsequent economic losses. Available data indicate that vegetative growth of C3 crops is favoured relative to C4 weeds with rising [CO_2], while preliminary results suggest that C3 weeds may be favoured over C3 crops as [CO_2] increases. However, no data have quantified the impact of [CO_2] on reproductive losses resulting from weeds under field conditions and, hence, it is premature to conclude the magnitude or direction of changes in the interactions. Clearly, field-based information on crop/weed interactions is essential to achieve a better understanding and predictive capacity of how changes in atmospheric [CO_2] may alter weed growth and potential yield losses.

In the current experiment, the principle objective was to test whether increased atmospheric [CO_2] would alter current production losses due to competition with C3 and C4 weeds using soybean as a test case. CO_2-induced changes in weed growth could alter the vegetative and reproductive response of crop plants to rising atmospheric [CO_2] significantly.

Materials and methods

Soybean (*Glycine max* L. Merr. cv. 'Ascro' (Ag3002, 'Round-up Ready', Maturity Group II, determinate) was grown in 12 open top chambers (OTCs) located in a field plot at Beltsville Maryland. 'Round-up Ready' is a genetically modified soybean line which allows indiscriminate application of glyphosate (Round-up, a post-emergent herbicide) for weed control. The field soil is classified as a Codurus silt-loam with pH 5.5 and high availability of potash, phosphate and nitrate (Codurus hatboro). New experimental chambers consisting of a cylindrical aluminium frame (3 m in diameter $\times$ 2.24 m in height) which covered an area of 7.2 m^2 were constructed prior to the experiment. After initial testing, a modified frustum (2.5 m in diameter) was suspended from the top of the chamber frame to prevent wind intrusion and to maintain a stable CO_2 concentration. Each chamber was assigned one of two [CO_2] treatments (ambient or ambient +250 $\mu L\ L^{-1}$). Fixed levels of elevated [CO_2] were not used because ambient CO_2 often increased substantially during the night. CO_2 treatments were maintained 24-h per day from germination until maturity. Air was supplied through perforations in the inner wall of the lower half of the chamber. Air was adjusted to the proper [CO_2] with pure CO_2 supplied from a CO_2 tank. Mixing occurred in a fan-driven plenum box where the air and CO_2 were brought together. Gas samples from a given chamber were drawn at 3 minute intervals at 10 cm above the canopy and adjustments to [CO_2] for the elevated chambers were made daily. [CO_2] values were checked periodically with an absolute CO_2 analyser (Li-C0R 6252, Li-Cor Corporation, Lincoln, NE USA). Seasonal values indicated an average daytime (06.00–18.00 hours) [CO_2] of 378 ± 28.3 and $613 \pm 55\ \mu L\ L^{-1}$ and an average night-time [CO_2] value of 460 ± 61 and $729 \pm 73\ \mu L\ L^{-1}$ for the ambient and elevated [CO_2] treatments, respectively. Micro-meteorological comparisons of photosynthetic photon flux and air temperature indicated that the chamber transmitted ~90% of all incoming light, with an average daytime temperature increase of 1.8 °C relative to the outside condition.

Soil was tilled on 31 May and soybean planted within the chambers and in border rows surrounding the chambers on 4 June. Row widths were ~30 cm with all plants thinned to 1 plant per 10 cm of row following emergence. Seeds of lambsquarters (*Chenopodium album* L, C3 photosynthetic pathway) and redroot pigweed (*Amaranthus retroflexus* L., C4 photosynthetic pathway) were obtained from local populations. Weed seeds were sown in flats on 4 June in climate-controlled greenhouses at either ambient (370 $\mu L\ L^{-1}$) or elevated (700 $\mu L\ L^{-1}$) [CO_2]. Weed seedlings were transplanted to the field on 17 June (immediately after soybean emergence) at a spacing of two weeds per metre of row. Weed seedlings were marked with plastic stakes and all other weeds that emerged during the experiment were removed by hand at weekly intervals from all experimental plots. There were three replications of [CO_2] and weed/crop interaction arranged in a complete randomized block at the field site with chambers split in a north/south direction. Soybean and weeds were arranged in four pairs (soybean with lambsquarters, soybean without lambsquarters, soybean with pigweed, soybean without pigweed) among the 24 plots (i.e. 4 pairs $\times$ 3 replications $\times$ 2 [CO_2]). No differences in vegetative biomass and seed yield were observed between the weed-free controls for a given [CO_2]. Chambers were watered weekly to match precipitation.

Flowering began in the week commencing 5 July, with no observable differences in time to flowering between treatments. Plants were considered mature when >95% of the leaves had senesced and dropped and pods were noticeably brown. Maturity occurred by 10 September in all ambient plots, but was not observed until 17 September in the elevated [CO_2] treatment (i.e. leaves stayed greener longer). At maturity, one metre of soybean row from each of the two centre rows (i.e. excluding border rows) within the split plot was cut at the base of the plant and harvested. At harvest individual pods were counted and separated by treatment. Pods were air-dried and aboveground shoot dry matter (i.e. stems, petioles, peduncles) was oven-dried at 65 °C for 72 h. Pods were threshed with seed collected and weighed. Weeds (either pigweed or lambsquarters) were cut at ground level, dried at 65 °C for 5 days (or until dry weight was constant) and then weighed. Because of leaf senescence and drop in soybean, harvest index was calculated as the ratio of seed to stem, petiole, peduncle and pod biomass. This parameter has been called apparent harvest index (AHI) and correlates highly with the traditional harvest index (Schapaugh & Wilcox 1980).

Aboveground biomass at maturity for soybean and weeds, seed yield and yield parameters of soybean were analysed using a two-way anova (Super anova, Berkeley, CA) for [CO_2] and weed–crop interactions. Analysis of covariance was used to test for differences in the slope of regression lines between weed biomass and soybean seed yield. Unless otherwise stated, all differences were compared to the ambient [CO_2] or elevated [CO_2] weed-free condition at the 0.05 level of significance.

Results

Increasing the [CO_2] by 250 $\mu L\,L^{-1}$ significantly increased soybean total aboveground biomass at maturity by 32% under a weed-free condition (Fig. 1). At the ambient

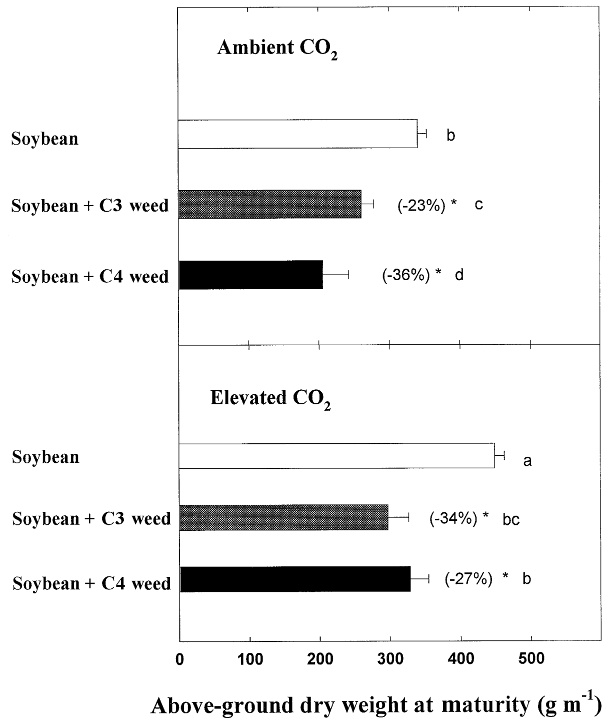

Fig. 1 Total aboveground biomass at maturity (pods, stems, petioles) for soybean (g m^{-1}) at ambient and elevated (ambient + 250 $\mu L\,L^{-1}$) carbon dioxide when grown with and without the presence of either the C3 weed, lambsquarters, or the C4 weed, redroot pigweed. Bars are ± SE. * indicates a significant difference (and the percentage change) relative to the weed-free condition within a given [CO_2] treatment. Different letters indicate significant differences relative to the weed-free ambient [CO_2] condition (least significant difference, 2-way ANOVA).

[CO_2] condition, pigweed resulted in a greater reduction in maturity biomass of soybean than lambsquarters, with no difference between weeds at the elevated [CO_2] condition. Both pigweed and lambsquarters significantly reduced soybean biomass at elevated [CO_2] (Fig. 1). Relative to the ambient [CO_2] treatment, however, the presence of either weed negated any stimulation in aboveground dry weight at maturity for soybean at elevated [CO_2] (Fig. 1).

The stimulation of seed-yield at elevated [CO_2] was less than that of biomass stimulation (23%) but still significant relative to the ambient [CO_2] condition. As observed for overall biomass, the presence of pigweed reduced seed yield to a greater extent than lambsquarters at ambient [CO_2] (45 vs. 28%, Fig. 2). At elevated [CO_2] significant reductions in seed yield were observed for both weed species, with the reduction in yield slightly, but not significantly, greater for lambsquarters than pigweed (39 vs. 30%). Relative to the weed-free ambient [CO_2] condition, lambsquarters still significantly reduced seed yield at elevated [CO_2] (28%), while the effect of

Table 1 (a) Dry weight of harvested plant components and reproductive growth parameters of soybean grown with and without weedy competition at ambient and elevated carbon dioxide concentrations. The C3 and C4 weeds were lambsquarters and redroot pigweed, respectively. Data are given per metre of row (30 cm row widths). Shoot weight represents stems, petioles and peduncles. AHI, apparent harvest index. Seed:pod, ratio of seed to seed + pod weight (i.e. what percentage of the pod is seed). Different letters indicate significant differences relative to the ambient [CO_2] weed-free control. (b) *P*-values for sources of error are given for each soybean/weed interaction

Weed	[CO_2]	Shoot wt. (g)	Pod wt. (g)	50 seed wt. (g)	Pod no.	Seeds pod^{-1}	Seed: Pod	AHI
(a)								
None	Amb.	85.9^{b}	255^{b}	7.19^{a}	571^{b}	2.28^{a}	0.73^{a}	0.55^{a}
C3	Amb.	68.2^{c}	192^{c}	6.20^{c}	501^{c}	2.20^{a}	0.70^{ab}	0.52^{b}
C4	Amb.	57.8^{c}	148^{d}	6.18^{c}	388^{d}	2.11^{a}	0.69^{ab}	0.50^{b}
None	Elev.	121.5^{a}	327^{a}	7.02^{ab}	722^{a}	2.26^{a}	0.70^{ab}	0.51^{b}
C3	Elev.	82.2^{b}	211^{bc}	6.49^{bc}	519^{c}	2.10^{a}	0.66^{b}	0.47^{c}
C4	Elev.	84.3^{b}	224^{bc}	6.63^{b}	545^{b}	2.18^{a}	0.65^{b}	0.48^{c}
(b) Source of error		*P*						
CO_2		0.015	0.048	0.410	0.039	0.064	0.004	0.013
C3 weed		0.005	0.001	0.025	0.001	0.405	0.007	0.010
$CO_2 \times$ C3 weed		0.417	0.166	0.905	0.104	0.422	0.266	0.256
CO_2		0.001	0.001	0.862	0.001	0.333	0.001	0.037
C4 weed		0.001	0.001	0.030	0.001	0.078	0.001	0.024
$CO_2 \times$ C4 weed		0.149	0.624	0.123	0.857	0.904	0.990	0.216

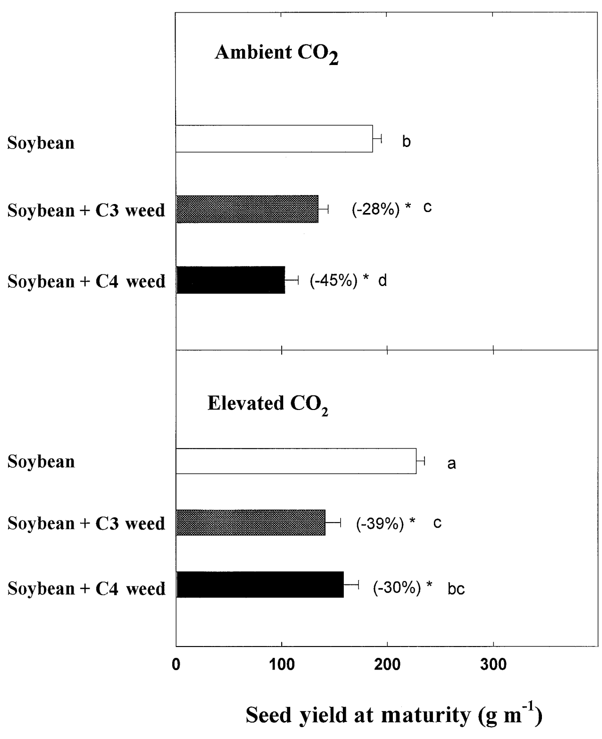

Fig. 2 Same as Fig. 1, but for seed yield of soybean.

pigweed on soybean seed yield was not significant (–15%, $P = 0.063$). As with vegetative biomass, no stimulation in seed yield with elevated [CO_2] occurred if either weed species was also present at elevated [CO_2].

Among growth and reproductive parameters, significant increases were observed in shoot (stem, petioles and peduncles) dry weight, pod weight and pod number at the elevated [CO_2] condition (Table 1). If weeds were present at a given [CO_2] treatment, significant reductions in shoot weight, average seed weight and pod weight and number were evident. In addition, weeds significantly reduced the seed:pod ratio (i.e. pods had proportionally less seed weight). Both increasing [CO_2] and weeds reduced the AHI. No significant [CO_2]–weed interactions were observed for any parameter. No significant change in seeds per pod was observed for any treatment variable.

In order to determine the effectiveness of weeds in reducing crop yield as a function of [CO_2], soybean seed yield was regressed against weed biomass for each weed species (Fig. 3). No difference in the slopes was observed between these two weed species at a given [CO_2]. Although the slope of the line for lambsquarters appears steeper at elevated than ambient [CO_2], the difference was not significant. These data indicate that approximate weed biomasses of ≈ 120 and 160 g per meter of row would eliminate any increase in seed yield with elevated [CO_2] for lambsquarters and pigweed, respectively, relative to the weed-free ambient [CO_2] condition (Fig. 3).

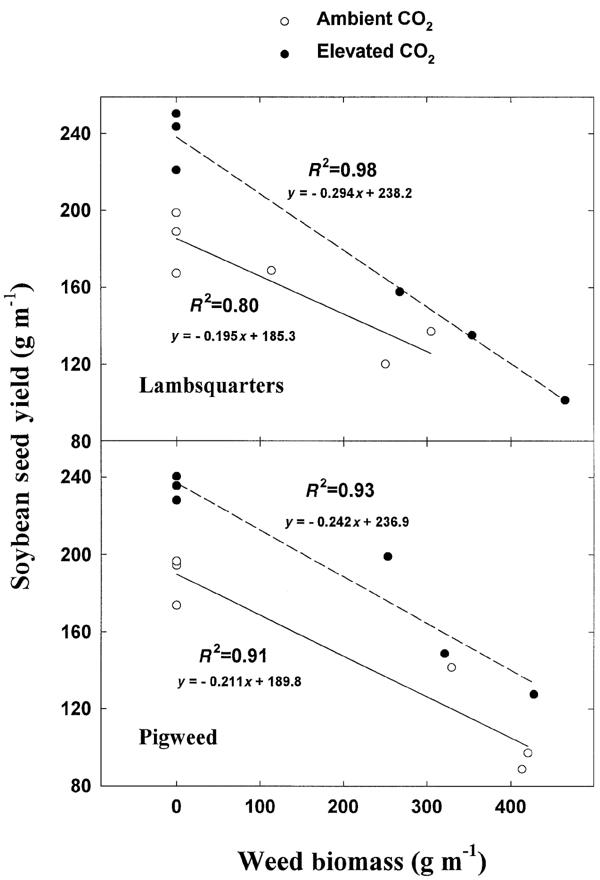

Fig. 3 Soybean seed yield (g m^{-1} of row) as a function of increasing weed biomass (g m^{-1} of row) when grown in 30-cm-wide rows at either ambient or elevated (ambient + 250 μL L^{-1}) carbon dioxide. No differences in the slope of the regression were observed (ANCOVA).

Discussion

In a weed-free environment, increasing [CO_2] by 250 μL L^{-1} resulted in a significant increase in both biomass at maturity and seed yield. However, increasing [CO_2] also resulted in a significant reduction in AHI, suggesting that vegetative growth may be a greater sink for additional carbon than reproductive growth. Previous work with soybean under controlled environment field conditions, or in glasshouses has demonstrated similar relative increases in biomass and seed yield with corresponding reductions in AHI over a range of growth temperatures (Baker *et al.* 1989) or modern genotypes (Ziska *et al.* 1998). Progress in increasing agronomic productivity in recent decades has been made primarily by increasing harvest index (see Gifford 1986). Data obtained from the current soybean cultivar and that of other experiments (e.g. Baker *et al.* 1989) demonstrate that modern soybean cultivars may not be as well adapted as they could be to elevated [CO_2] environments. Overall, however, the response of soybean observed here is consistent with the response of a large number of C3 crop species to elevated [CO_2] (e.g. Kimball 1983; Kimball *et al.* 1993).

Nevertheless, it is important to emphasize that observed stimulations in yield with enhanced [CO_2] have been obtained almost exclusively from single plants or plants grown in monoculture. They do not necessarily reflect *in situ* agronomic conditions in which a crop species must compete with weedy species for light, nutrients, water, etc. In the present experiment weedy competition reduced seed size, the proportion of seed within the pod and subsequent AHI. The greater height of the weeds relative to the soybean (data not shown) suggests that shading or light availability may have been one factor in soybean/weed competition. However, weeds can compete with crops for nutrients, water and light. Consequently, separation and quantification of specific yield limitations due to above- or belowground competition in a field situation is extremely difficult (See Patterson & Flint 1990).

But is weed/crop competition even likely if weeds are controlled chemically? Initial use of a genetically modified organism such as a 'Round-up Ready' soybean should prevent any increase in weed/crop competition by allowing nonselective application of herbicides such as glyphosate. However, recent research indicates that the effectiveness of glyphosate is diminished when C3 weeds such as lambsquarters or quackgrass are grown in an elevated [CO_2] environment (Ziska *et al.* 1999; Ziska & Teasdale 2000). This would suggest an increased presence of certain weeds in agricultural systems with increasing [CO_2] and continued weed/crop competition.

If the responses of both weeds and crops to elevated [CO_2] are to be considered within a realistic agricultural system, what are the probable impacts on seed yield and crop productivity? At current CO_2 levels, pigweed shows a larger biomass at maturity relative to lambsquarters (387 vs. 223 g m^{-1} of row), with a corresponding greater reduction in soybean seed yield. However, a significant increase in the average lambsquarter biomass (362 g m^{-1} row) and no change in pigweed biomass (343 g m^{-1} row) was observed at elevated [CO_2] with an analogous increase in seed yield loss of soybean when grown with lambsquarters at elevated [CO_2].

Increasing [CO_2] *per se* does not appear to increase or decrease the overall effectiveness of lambsquarters or pigweed in reducing productivity, because the decrease in seed yield per increase in weed biomass is constant (i.e. Fig. 3). Rather, elevated [CO_2] stimulates differentially the amount of weed biomass present relative to that of soybean either within a C3 weed/C3 crop or C4 weed/C3 crop situation.

The data obtained here for the C4 weed/C3 crop interaction are similar to those obtained in earlier single plant competition studies in environmental chambers (e.g. johnson grass and soybean; Patterson *et al*. 1984), that demonstrate a relative enhancement of vegetative biomass for the C3 crop. These data reinforce the idea that the presence of C4 weeds would result in less yield loss for soybean with increasing [CO_2]. However, as evidenced by the present data, the reductions in seed yield with pigweed while less, are still significant (e.g. –45 vs. –30% for each [CO_2]), and the presence of such weeds, even at two weeds per metre of row, prevented any response of soybean seed yield to enhanced [CO_2].

In contrast, data from the C3 weed/C3 crop interaction indicate a greater overall response of the C3 weed relative to the C3 crop with a further reduction in seed yield for soybean when grown at elevated [CO_2]. Even relative to the weed-free ambient [CO_2] condition, there is still a significant reduction in seed yield when soybean is grown with lambsquarters at elevated [CO_2]. The response of soybean and lambsquarters to elevated [CO_2] is consistent with the suggestion of Treharne (1989) that the physiological plasticity of weed species, and their greater genetic diversity within species relative to that of modern bred crops, could provide a greater competitive advantage as atmospheric [CO_2] increases.

Critics of atmospheric [CO_2]'s role in climate change correctly point out that rising [CO_2] should result in greater crop growth and productivity (e.g. Idso 1995). However, it should also be emphasized that the projected increase in atmospheric [CO_2] is indiscriminate, stimulating both beneficial and noxious plant species. The argument that rising [CO_2] will reduce weedy competition because the C4 photosynthetic pathway is over-represented among weedy species is not applicable to all weed/crop interactions. There are, in fact, few agronomic situations where a given C3 crop competes exclusively with C4 weeds. Rather, crops compete against an assemblage of both C3 and C4 weeds whose makeup is subject to environmental and anthropogenic change. Consequently, field data on multiple crop/weed comparisons over a range of [CO_2]s are critical in assessing more accurately weed/crop competition, weed seed bank dynamics, weed induced yield losses and agricultural productivity. The data presented here suggest that current projections of weed-induced yield loss may be altered, and stimulation of yield in some C3 crops overestimated, as atmospheric carbon dioxide increases.

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