



Assessing the impact of increasing carbon dioxide and temperature on crop-weed interactions for tomato and a C₃ and C₄ weed species



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ABSTRACT

Based on the carboxylation kinetics of the C₃ and C₄ photosynthetic pathway, it is anticipated that C₃ crops may be favored over C₄ weeds as atmospheric CO₂ increases. In the current study, tomato (*Lycopersicon esculentum*), a C₃ crop species, was grown at ambient (400 μmol mol⁻¹) and enhanced carbon dioxide (800 μmol mol⁻¹) with and without two common weeds, lambsquarters (*Chenopodium album*), a C₃ weed, and redroot pigweed (*Amaranthus retroflexus*), a C₄ weed, from seedling emergence until mutual shading of crop-weed leaves. Because growth temperature is also likely to change in concert with rising CO₂, the experiment was repeated at day/night temperatures of 21/12 and 26/18 °C. For both day/night temperatures, elevated CO₂ exacerbated weed competition from both the C₃ and C₄ weed species. A model based on relative leaf area following emergence was used to calculate potential crop losses from weeds. This analysis indicated that potential crop losses increased from 33 to 55% and from 32 to 61% at the 21/12 and 26/18 °C day/night temperatures, for ambient and elevated CO₂, respectively. For the current study, reductions in biomass and projected yield of tomato appeared independent of the photosynthetic pathway of the competing weed species. This may be due to inherent variation and overlap in the growth response of C₃ and C₄ species, whether weeds or crops, to increasing CO₂ concentration. Overall, these results suggest that as atmospheric CO₂ and/or temperature increases, other biological interactions, in addition to photosynthetic pathway, deserve additional consideration in predicting competitive outcomes between weeds and crops.

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1. Introduction

Although the physical or abiotic nature of climate change impacts on plant function is often emphasized (e.g., drought, temperature), differential responses to those impacts, and changes in competitive outcomes are also likely. For example, numerous reviews and meta-analyses indicate that recent and projected increases in atmospheric carbon dioxide (CO₂), one of the most predictable anthropogenic changes, are likely to stimulate photosynthesis, growth and reproduction for a wide range of plant species. However, it is unlikely that the degree of stimulation will be the same for each plant species. This has obvious consequences for agriculture, as any differential response between a

crop and associated weeds to increasing CO₂ will alter weed-crop interactions and potential crop production losses.

Because of differing carboxylation kinetics related to the degree of carbon loss through photorespiration, plants with the C₃ photosynthetic pathway, about 94% of all plant species, are expected to respond to a greater extent than plants possessing the C₄ photosynthetic pathway, about 1–2% of all plant species. This has been shown in literally hundreds of studies that have examined the relative response of C₃ and C₄ plant species (see Barnaby and Ziska, 2012 for a review).

That C₃ and C₄ plant species can, and do, respond differently to rising CO₂ levels has important consequences for crop-weed interactions. Many weeds possess the C₄ photosynthetic pathway, while a number of major crops are C₃ plants (Holm et al., 1977; Patterson, 1995; Wand et al., 1999; Bunce and Ziska, 2000). As a consequence, weed research has focused on how increasing atmospheric CO₂ could alter the competitive ability of C₃ crops relative to C₄ weeds (Ziska, 2010). Overall, these published results were consistent with the known carboxylation kinetics of the different photosynthetic pathways, i.e., C₃ crops became more competitive with C₄ weeds (Bunce and Ziska, 2000; Patterson and Flint, 1980; Patterson et al., 1984; Patterson, 1986; Rosenzweig and Hillel, 1998).

Abbreviations: LAI, leaf area index; Lambsquarters, *Chenopodium album* L., CHEAL; Red-root pigweed, *Amaranthus retroflexus*; AMARE, tomato (*Lycopersicon esculentum*); YL, yield loss.

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However, there is considerable variation in the published growth and yield responses of C₃ and C₄ plant species to a doubling of current CO₂ levels (Patterson et al., 1999; Ziska and Bunce, 1997). Such variation in CO₂ response would suggest that, potentially, rising CO₂ could still result in a greater enhancement of a C₄ plant relative to a C₃ plant. In addition, it seems likely that increased surface temperatures will accompany rising CO₂ levels (IPCC, 2007) and that temperature could also be a significant factor in the determination of C₃ crop, C₄ weed responses to elevated CO₂ (Alberto et al., 1996).

A critical time for crop-weed competitive interactions in agricultural systems occurs at the seedling stage during leaf initiation when light competition (i.e., shading) between and within species is a primary growth constraint (see Zimdahl, 2004). That is, shading of crop by weed (or vice versa) at this stage can be a good indicator of competitive outcomes. In fact, it has been shown that there is a close relationship between yield loss and relative leaf area of weeds and crop when determined shortly after crop emergence (Kropff, 1988; Kropff et al., 1995). Based on these findings, a simple descriptive regression model for early prediction of crop losses by weed competition was developed by Kropff and Spitters (1991). Such a model is useful as an integrator of eco-physiological effects on crop-weed interactions and subsequent weed-induced crop losses (Zimdahl, 2004).

Because most work examining the impact of rising CO₂ on crop-weed interactions has focused on the interaction between C₃ crops and C₄ weeds, we wanted to assess the relative impact of both a C₃ and/or C₄ weed on the vegetative parameters of a C₃ crop using IPCC projected increases in atmospheric CO₂ at different temperatures (IPCC, 2007). This objective was evaluated using tomato, a C₃ crop, with two commonly associated weeds *in situ*, lambsquarters (CHEAL, C₃), and red-root pigweed (AMARE, C₄) following mutual leaf shading. To determine projected yield outcomes, we used the guidelines suggested by the Kropff–Spitters model for climatic conditions in southern Italy, a recognized tomato production region.

2. Materials and methods

The study was conducted using four controlled environment chambers at Beltsville, Maryland, U.S.A. with a given chamber set at CO₂ concentrations of either 400 or 800 μmol mol⁻¹ for 24 h d⁻¹. These concentrations approximate current atmospheric CO₂ concentration and the concentration projected by 2080 (AIF1 scenario, IPCC, 2007), respectively. The CO₂ concentration of the air within each chamber was controlled by adding either CO₂ or CO₂-free air to maintain the set-point concentration. Actual average 24 h CO₂ values (±SD) were 394 ± 11 and 789 ± 21 μmol mol⁻¹ over the course of the study. Injection of CO₂ or CO₂-free air was controlled by a TC-2 controller at 1 minute intervals using input from an infrared gas analyzer operating in absolute mode. Day/night (13/11 h) temperatures were set at either 21.2/12.2 °C or 26.4/18.1 °C, consistent with current average day/night temperatures for the month of April and that projected for April in 2080 for southern Italy (IPCC, 2007). Set temperatures did not vary by more than ±0.2 °C during the study. Photosynthetically active radiation (PAR) was between 700–800 μmol m⁻² s⁻¹. Daily PAR was supplied by a mixture of high pressure sodium and metal halide lamps.

Seeds of tomato (cv. “San Marzano”, C₃ crop), an Italian processing variety, and lambsquarters (*Chenopodium album*, CHEAL, a C₃ weed) and redroot pigweed (*Amaranthus retroflexus*, AMARE, a C₄ weed) were sown in tubs [960 cm², 6.0 L in volume (24 × 40 × 6 cm), 1:1:1 mixture of silt loam, perlite and metro mix] in the following combinations: tomato (no weeds), tomato with CHEAL, tomato with AMARE, or tomato with CHEAL and AMARE. CHEAL and AMARE were chosen as they are common weeds of

tomato in Italy, and similar in terms of growth habit and leaf architecture. Tomato was sown in the center line of the tub, and thinned to four plants following emergence. Weed seed was sown on either side of the tomato and thinned to either 8 plants per tub (CHEAL and AMARE) or 4 plants each (CHEAL and AMARE), so that the density of weed to crop was always 2:1. Equal numbers of weed plants were on either side of the tomato row, with variable spacing between the weed and crop. All tubs were watered daily to the drip point with a complete nutrient solution (Robinson, 1984).

Harvest was determined visually approximately one week after mutual shading occurred between the weed and crop; when each of the four tomato seedlings was either shading, or was shaded by, the associated weed. The time to mutual shading as determined by days after sowing (DAS) did not differ with weed treatment, or CO₂ concentration. However, temperature accelerated the time to mutual shading by 10 days for the 26/18 °C relative to the 21/12 °C treatment. At harvest, plant height was determined and then all plants were cut at ground level and separated into leaf laminae and stems. Leaf area was determined photometrically using a leaf area meter. Above ground dry weights were obtained separately for all plant parts following drying at 55 °C in a forced air oven for a minimum of 72 h or until a constant dry weight was observed. Although roots were not separated between species, visual inspection of roots indicated that plants were not root-bound.

To express potential yield loss of the crop as a function of weed competition, we used harvest data and the Kropff–Spitters model of relative leaf area (Kropff and Spitters, 1991, Kropff and van Laar, 1993), derived from a well-tested hyperbolic yield loss-weed density model. The model relates reproductive or yield loss (YL) to relative weed leaf area shortly after crop emergence:

$$YL = qL_w/1 + (q - 1)L_w \text{ or, with multiple weed species,}$$

$$YL = \sum q_i L_{w,i} / 1 + \sum (q_i - 1) L_{w,i}$$

where L_w is the leaf area index of the weed (LAI_w) divided by the sum of the LAI of weed (w) and crop (c), or:

$$L_w = LAI_w / LAI_w + LAI_c$$

and LAI is the product of the leaf area per plant (LA) and the plant density:

$$LAI = N \times LA$$

where LA_c and LA_w are the average leaf area per plant of the crop and the weed at the moment of observation and N is plants m⁻². The value of q , the relative damage coefficient, was taken from Kropff and Lotz (1992) for direct seeded tomato, consistent with the current study.

A randomized complete block design was utilized with runs over time as replications (blocks). That is, each chamber was assigned one of the two CO₂ treatments at a given day/night temperature for a given run, with CO₂ temperature treatments reassigned and the entire experiment repeated at the end of each run (three runs total). All tubs (4) within a given chamber were rotated weekly until approximately 7–8 days following mutual shading of crop and weed for each run during the experiment. PAR, humidity and temperature were quantified prior to, and at the end of each run in order to determine variability within and among chambers. Values for temperature, PAR and humidity were consistent among chambers and between runs. However, because temperature accelerated the time to mutual shading for the higher temperature treatment by 10 days, there was no common harvest date for comparison of a temperature by CO₂ interaction. Hence, CO₂ concentration was evaluated for tomato growth parameters independently for each day/night temperature using a 2-way ANOVA, with weed species and competition as fixed effects. Unless otherwise stated, differences

Table 1
Average tomato seedling vegetative characteristics (per plant) grown with and without weedy species at a day/night temperature of 21/12 °C at two different atmospheric CO₂ concentrations ($\mu\text{mol mol}^{-1}$). Weed to Crop Ratio was maintained at 2:1. Different letters indicate significant differences for a given CO₂ concentration as a function of weed competition (Fishers Protected Isd).

CO ₂	Weed	Height (cm)	Leaf area (cm ²)	Leaf wt. (g)	Stem wt. (g)	Total wt. (g)
400	None	8.53	188.6a	0.767a	0.219a	0.986a
	AMARE	8.38	172.6a	0.742a	0.198a	0.940a
	CHEAL	8.02	127.3b	0.509b	0.144b	0.654b
	AMARE + CHEAL	7.84	132.7b	0.545ab	0.155b	0.699ab
800	None	9.79a	200.4a	1.045a	0.259a	1.304a
	AMARE	6.91b	118.2b	0.557b	0.148b	0.706b
	CHEAL	7.17b	94.9b	0.492b	0.141b	0.633b
	AMARE + CHEAL	7.11b	119.2b	0.586b	0.146b	0.732b

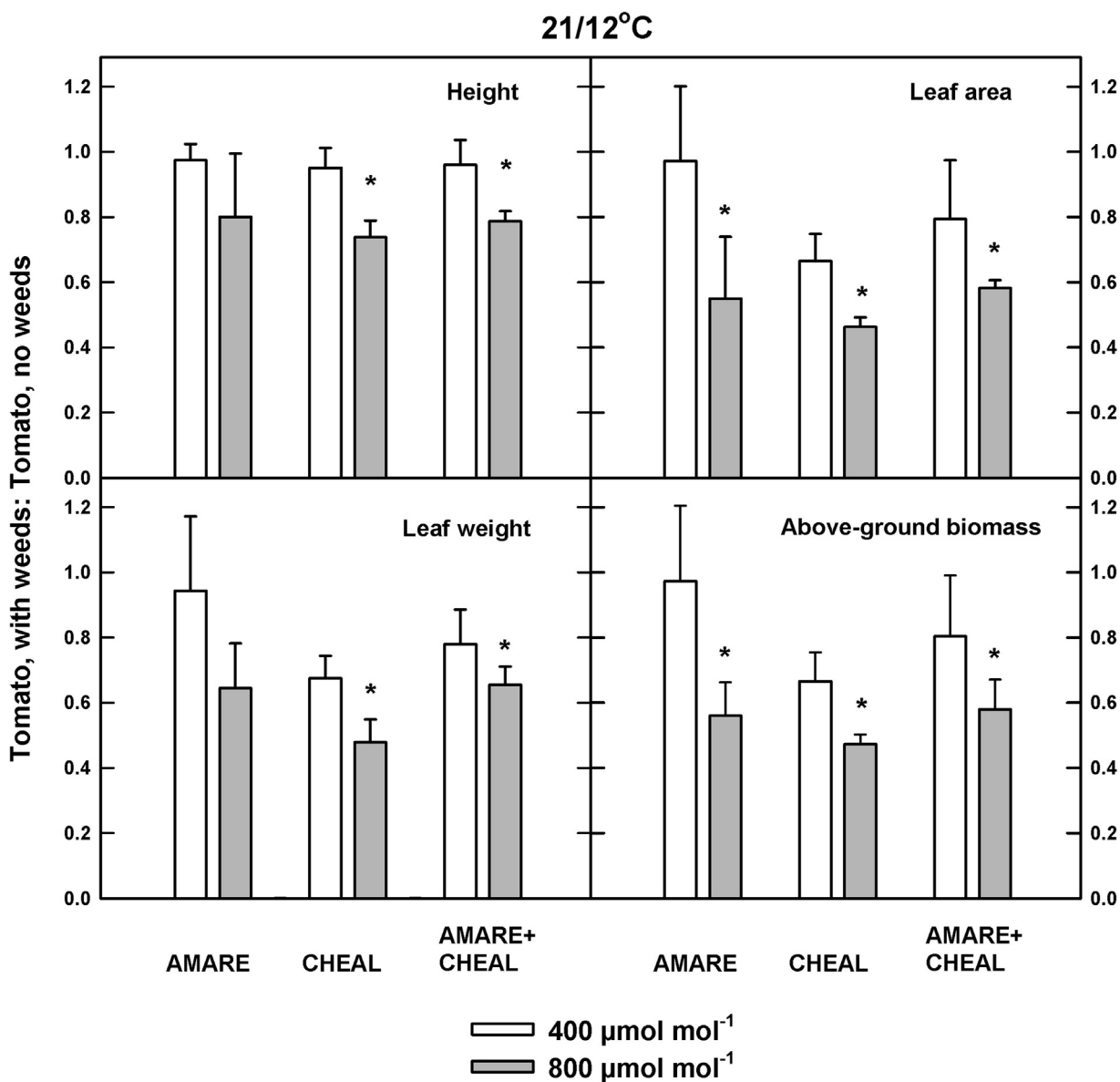


Fig. 1. The ratio of a given measured parameter for tomato (e.g. height) at ca 22 DAS for tomato with and without weeds (i.e., a value of 1 indicates no effect of weedy competition) at either ambient or elevated CO₂ concentration (400 and 800 $\mu\text{mol mol}^{-1}$, clear and shaded bars). Tomato was grown with either AMARE or CHEAL in monoculture or with AMARE and CHEAL in combination. Ratio of weed to crop density was 2:1. Day night temperature was 21/12 °C. Bars are \pm SE. * indicates a significant difference in the weed to weed free ratio as a function of CO₂ concentration. See Section 2 for additional details.

for any parameter were deemed significant at the $P < 0.05$ level using Fisher Protected Lsd.

3. Results

At current April temperatures and CO_2 levels for southern Italy, reductions were observed for leaf area, leaf weight and stem weight of tomato when grown in competition with *C. album* and in the leaf area and stem biomass of tomato with *C. album* and *A. retroflexus* in combination (Table 1). No significant effects of *A. retroflexus* were noted relative to the weed free condition in tomato (Table 1). However, at the higher CO_2 concentration, reductions in tomato biomass and leaf area were noted for all weed combinations relative to the weed free control. The ratio of tomato seedlings with weedy competition to tomato in a weed free condition declined at the higher CO_2 concentration for leaf area and above-ground weight for all weed combinations at both growth temperatures (Figs. 1 and 2) suggesting a greater effect of rising CO_2 on weed

induced reductions in tomato biomass that was not weed species specific.

At warmer temperatures ($26/18^\circ\text{C}$), reductions in vegetative characteristics of tomato (relative to the weed-free condition) were observed for leaf area and biomass at $400 \mu\text{mol mol}^{-1} \text{CO}_2$ for competition with *C. album* and *A. retroflexus* separately, but not in combination (Table 2). At the $800 \mu\text{mol mol}^{-1} \text{CO}_2$ concentration, reductions were observed in leaf area, leaf and total above ground biomass of tomato for all weed combinations relative to the weed-free treatment (Tables 1 and 2).

Calculations of potential yield losses using the Kropff-Spitters model indicated that the higher CO_2 concentration would have resulted in greater yield losses in tomato for *A. retroflexus* and *C. album*, but not for a mixture of these weeds at current temperatures (Fig. 3). At the higher growth temperature however, an increase in yield loss from weedy competition was observed for both weed species, singly and in combination, at 800 relative to $400 \mu\text{mol mol}^{-1} \text{CO}_2$ (Fig. 3).

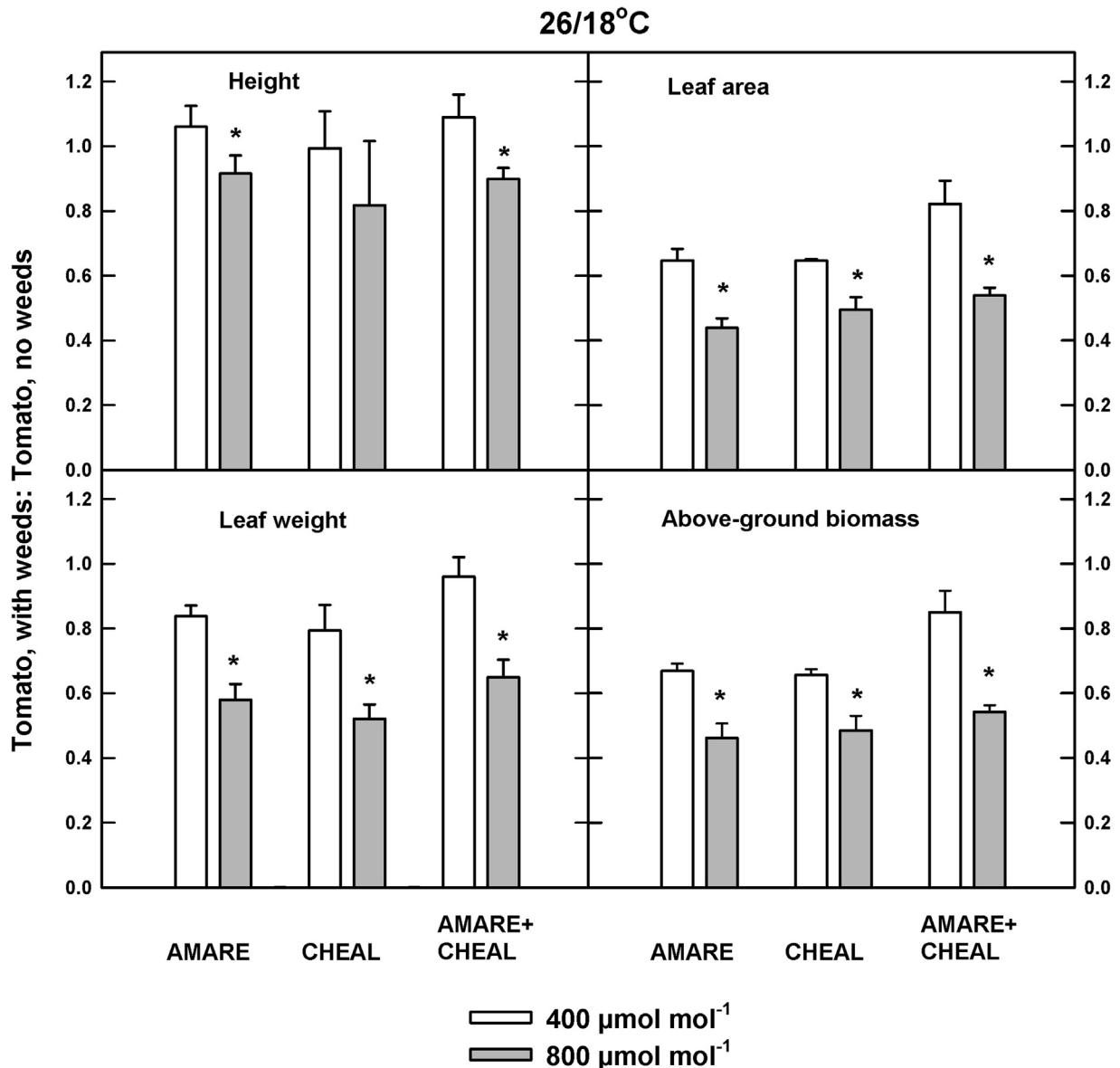


Fig. 2. The ratio of a given measured parameter for tomato (e.g. height) at ca 22 DAS for tomato with and without weeds (i.e., a value of 1 indicates no effect of weedy competition) at either ambient or elevated CO_2 concentration (400 and $800 \mu\text{mol mol}^{-1}$). Tomato was grown with either AMARE or CHEAL in monoculture or with AMARE and CHEAL in combination. Ratio of weed to crop density was 2:1. Day night temperature was $26/18^\circ\text{C}$. Bars are $\pm\text{SE}$. * indicates a significant difference in the weed to weed free ratio as a function of CO_2 concentration. See Section 2 for additional details.

Table 2
Average tomato seedling vegetative characteristics (per plant) grown with and without weedy species at a day/night temperature of 26/18 °C at two different atmospheric CO₂ concentrations ($\mu\text{mol mol}^{-1}$). Weed to Crop Ratio was maintained at 2:1. Different letters indicate significant differences for a given CO₂ concentration as a function of weed competition (Fishers Protected Isd).

CO ₂	Weed	Height (cm)	Leaf area (cm ²)	Leaf wt. (g)	Stem wt. (g)	Total wt. (g)
400	None	10.48	214.3a	0.754a	0.244a	0.998a
	AMARE	10.76	165.7b	0.473b	0.172b	0.645b
	CHEAL	10.28	168.4b	0.488b	0.167b	0.654b
	AMARE + CHEAL	10.59	190.7ab	0.543ab	0.198ab	0.741ab
	None	10.76a	210.7a	0.801a	0.238a	1.039a
800	None	10.76a	210.7a	0.801a	0.238a	1.039a
	AMARE	8.49b	89.2b	0.318b	0.107b	0.425b
	CHEAL	8.36b	103.6b	0.394b	0.108b	0.502b
	AMARE + CHEAL	9.27ab	131.0b	0.470b	0.137b	0.607b
	None	10.76a	210.7a	0.801a	0.238a	1.039a

4. Discussion

Plants with the C₃ pathway should be at a competitive advantage relative to C₄ plants as atmospheric CO₂ increases because they do not have to bear the metabolic costs of concentrating CO₂ at the site of carboxylation. Thus, as CO₂ concentrations increase, crops with the C₃ pathway should, *a priori*, be more competitive with C₄ weeds (Patterson and Flint, 1980).

However, this was not observed in the current study. That is, negative effects on tomato seedling leaf area and biomass were noted at elevated, relative to ambient CO₂ concentrations for both

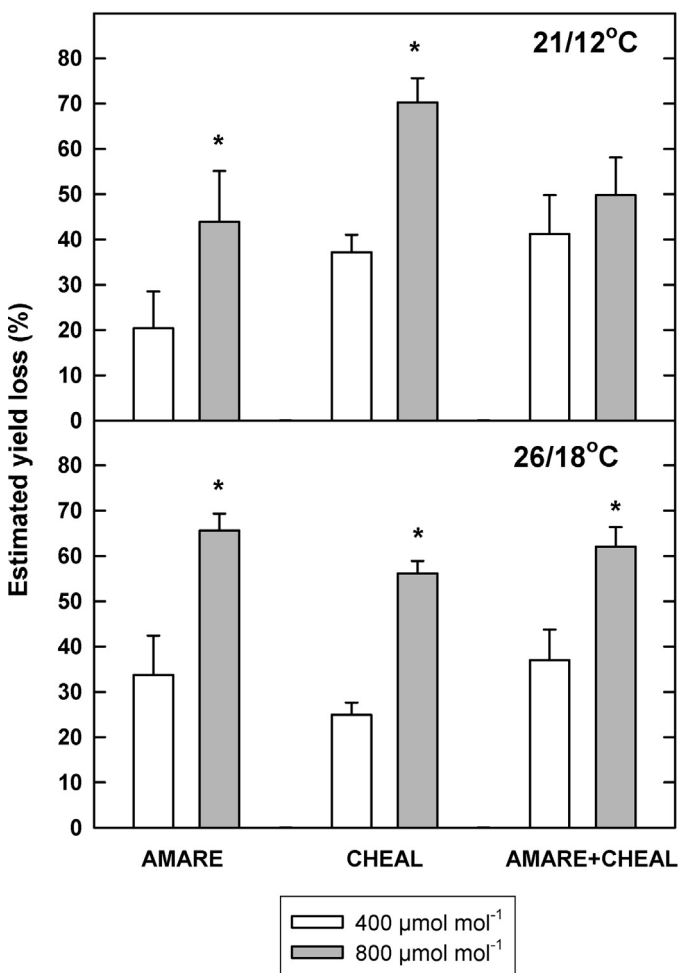


Fig. 3. Estimated yield loss (\pm SE) in tomato using a relative leaf area approach (i.e. Kropff–Spitters model estimate) as a function of different day/night temperatures and CO₂ concentrations for AMARE or CHEAL in monoculture or with AMARE and CHEAL in combination. *Indicates a significant effect of CO₂ concentration for a given day/night temperature and tomato: weed arrangement.

sets of day/night temperatures when tomato was grown with a C₃ weed, (*C. album*), as well as a C₄ weed, (*A. retroflexus*) following mutual shading.

Estimates of crop yield loss using the Kropff and Spitters (1991) model indicated that elevated CO₂ enhanced yield loss in tomato from a C₃ as well as the C₄ weed, for both sets of temperatures, with no significant interaction of weed species with competition with respect to a given tomato parameter or induced yield loss. Although an analysis of CO₂ by temperature interactions was not possible, it is worth emphasizing that mutual shading began ca 10 days earlier with the higher day/night temperature, and as a result, the overall degree of competition is likely to have been enhanced at the higher temperature per se.

It has been previously noted in the Kropff–Spitters model that the *q* value, or relative damage coefficient, can vary between years and is dependent on when the relative leaf estimate was determined (Zimdahl, 2004). For the current study, it is also worth noting that while a single *q* value was utilized in projecting crop yield losses based on previously published studies on tomato and weed competition (Kropff and Lotz, 1992, 1993), it seems probable that *q* would change in response to concurrent increases in temperature and CO₂ concentration. Therefore, while weedy competition was enhanced in the early vegetative stage with elevated CO₂, and relative greater crop losses would be anticipated, the absolute yield losses estimated by the Kropff–Spitters model in this study are likely to be subjective for future CO₂ conditions and should be tested against these model projections in situ.

To date, there have been only a few studies that have examined the impact of rising CO₂ on crop: weed interactions and/or yield loss when the photosynthetic pathways of the weed and the crop differed. For sorghum (*Sorghum bicolor*), a C₄ crop, competition from two C₃ weeds, cocklebur (*Xanthium strumarium*) and velvetleaf (*Abutilon theophrasti*) was enhanced in response to elevated CO₂ (Ziska, 2001, 2003); conversely, for C₃ crops soybean and rice, competition from C₄ weeds was reduced in response to elevated CO₂ (Alberto et al., 1996; Patterson et al., 1984; Ziska, 2000). Overall, these competition studies are consistent with the known characteristics of the C₃ and C₄ photosynthetic pathways.

However, the range of growth responses to increasing CO₂ (relative to ambient CO₂ levels of 370 $\mu\text{mol mol}^{-1}$) has been reported as highly variable not only for C₃ species, but for C₄ species as well (Patterson, 1995; Wand et al., 1999; Ziska and Bunce, 1997). For example, published values for C₃ and C₄ crops show a range of responses from 1.10 to 2.43 and 0.98 to 1.24 times ambient concentrations, whereas C₃ and C₄ weeds show a range of responses from 0.95 to 2.72 and 0.6 to 1.61 times ambient, respectively, with a projected doubling of atmospheric CO₂ (Patterson and Flint, 1990; Patterson, 1995; Patterson et al., 1999). Although the limited number of weed: crop competition studies at elevated CO₂ has, to date, been consistent with the kinetics of the C₃ and C₄ pathway, sufficient species overlap exists so that, theoretically, a C₄ weed could respond more than a C₃ crop as CO₂ increases.

Previously published responses of biomass for individual *A. retroflexus* plants (a C_4 weedy species) to elevated ($2\times$ ambient) CO_2 under well-watered conditions can be substantial, up to 40% greater than the ambient CO_2 condition (Patterson, 1995; Ziska and Bunce, 1997); and can exceed the CO_2 induced biomass response of tomato (see Table 4.8, Acock and Allen, 1985). In that regard, the current study is consistent with previous responses of individual *A. retroflexus* plants to elevated CO_2 but is the first to demonstrate that elevated CO_2 could, potentially, enhance the degree of weed damage from a C_4 weed, relative to a C_3 crop (tomato) in competitive mixtures, even at ambient temperatures.

Considerable variation among C_4 crops and weeds to rising CO_2 has been noted previously (e.g. Ziska and Bunce, 1997), however the physiological basis for the variability is unclear. Additional information is needed to elucidate how abiotic parameters and genetic factors could influence the carboxylation kinetics and potential photosynthetic response among C_4 species (weeds and crops) as atmospheric CO_2 continues to increase.

Overall, as observed here, and consistent with previous publications regarding the range of responses of individual C_3 and C_4 species to CO_2 (e.g. Patterson, 1995; Patterson et al., 1999), sufficient variation exists so that a C_4 weed can, in fact, respond more to a CO_2 increase than a C_3 crop with subsequent increases in weed-induced vegetative and/or reproductive losses relative to ambient CO_2 conditions. The current data, while preliminary, suggest that in addition to photosynthetic pathway per se, other phenological and developmental aspects will deserve additional scrutiny in the context of understanding and predicting the impact of increasing atmospheric carbon dioxide on crop-weed interactions.

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