

CROP PHYSIOLOGY & METABOLISM

Sensitivity of Wheat and Rice to Low Levels of Atmospheric Ethylene

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ABSTRACT

Ethylene (C_2H_4) gas is produced throughout the life cycle of plants and can accumulate in closed growth chambers to levels 100 times higher than in outside environments. Elevated atmospheric C_2H_4 can cause a variety of abnormal responses, but the sensitivity to elevated C_2H_4 is not well characterized. We evaluated the C_2H_4 sensitivity of wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) in five studies. The first three studies compared the effects of continuous C_2H_4 levels ranging from 0 to 1000 $nmol\ mol^{-1}$ (ppb) in a growth chamber throughout the life cycle of the plants. A short-term 1000 $nmol\ mol^{-1}$ treatment was included in which exposure was stopped at anthesis. Yield was reduced by 36% in wheat and 63% in rice at 50 $nmol\ mol^{-1}$ and both species were virtually sterile when continuously exposed to 1000 $nmol\ mol^{-1}$. However, the yield reductions were much less with exposure that stopped at anthesis, suggesting the detrimental effect of C_2H_4 on yield was greatest around the time of seed set. Two additional studies evaluated the differential sensitivity of two wheat cultivars (Super Dwarf and USU-Apogee) to 50 $nmol\ mol^{-1}$ C_2H_4 at three CO_2 levels [350, 1200, 5000 $\mu mol\ mol^{-1}$ (ppm)] in a greenhouse. Yield of USU-Apogee was not significantly reduced by C_2H_4 but the yield of Super Dwarf was reduced by 60%. Elevated CO_2 did not influence the sensitivity to C_2H_4 . A difference in the C_2H_4 sensitivity of USU-Apogee between greenhouse and growth chamber trials suggests that C_2H_4 sensitivity is dependent on the environment. Collectively, the data suggest that relatively low levels of C_2H_4 could induce anomalous plant responses by accumulation in greenhouses and growth chambers with inadequate ventilation. The data also suggest that C_2H_4 sensitivity can be reduced by both genetic and environmental manipulations.

PLANTS CONTINUOUSLY SYNTHESIZE C_2H_4 throughout their life cycles and it mediates a broad range of physiological responses (Abeles et al., 1992). Several papers have described patterns of C_2H_4 synthesis and efflux in wheat (Beltrano et al., 1994; Labrana et al., 1991; Petruzzeli et al., 1994). Ethylene efflux appears to be correlated with growth rate and may peak during anthesis in grain crops. Wheeler et al. (1996) found that C_2H_4 production from a wheat canopy was several times higher during vegetative growth than during grain fill. Rates of 0.1 to 0.2 $nmol\ C_2H_4\ kg^{-1}\ DW\ s^{-1}$ have been measured in wheat, lettuce (*Lactuca sativa* L.), and cotton (*Gossypium* spp.) during vegetative growth (Wheeler et al., 1996; Morgan et al., 1990). We have measured C_2H_4 production rates five times higher than

this (1.0 $nmol\ C_2H_4\ kg^{-1}\ DW\ s^{-1}$) in the heads of wheat at anthesis (unpublished data).

Terrestrial atmospheric C_2H_4 levels rarely exceed 10 $nmol\ mol^{-1}$ (Abeles et al., 1992). Levels from 50 to 100 $nmol\ mol^{-1}$ are common in greenhouses with heating or ventilation problems and have resulted in a broad range of crop damage in the horticulture industry (Blankenship and Kemble, 1996; Gibson et al., 2000; Mortensen, 1989). North Carolina State University provides helpful information on how to prevent C_2H_4 problems in greenhouses and a service for checking air samples posted on the web at http://www.ces.ncsu.edu/depts/hort/greenhouse_veg; verified 28 Nov. 2001. Levels as high as 1000 $nmol\ mol^{-1}$ have been measured in controlled environments in both ground and space studies (Abeles et al., 1992; Bingham et al., 2000; Campbell et al., 2001; Salisbury, 1997). Elevated C_2H_4 levels can cause a variety of abnormal responses including shortened height, epinasty, leaf rolling, premature leaf senescence, and sterility (Abeles et al., 1992; Bennet and Hughes, 1972; Morison and Gifford, 1984).

Elevated C_2H_4 levels may cause anomalous results in greenhouses and growth chambers, but the threshold for C_2H_4 sensitivity is poorly characterized. Elevated C_2H_4 levels are of particular concern in tightly sealed bioregenerative life support systems, which are being developed for space by the National Aeronautics and Space Administration (NASA). The objectives of a bioregenerative life support system are to provide food, O_2 , CO_2 removal, and water purification for long-term space exploration. NASA has recognized that atmospheric C_2H_4 may need to be scrubbed to prevent abnormal plant growth in space. Recent advances in catalytic scrubbing technology have improved significantly our ability to remove C_2H_4 from air (Tibbitts et al., 1998). However, it is difficult to remove C_2H_4 below 50 $nmol\ mol^{-1}$ in closed plant growth chambers and this is still 10 to 50 times higher than levels in the field.

There is considerable genetic variability in C_2H_4 sensitivity. Variation in post harvest flower longevity among carnations has been attributed to genetic variation in both C_2H_4 synthesis and perception (Wu et al., 1991; Brandt and Woodson, 1992). Recent advances in the identification of genes associated with C_2H_4 perception facilitate breeding C_2H_4 tolerant genotypes (Barry et al., 2000; Bleeker and Kende, 2000; Bleeker and Schaller, 1996; Gubrium et al., 2000; Lindstrom et al., 1999). Ethylene insensitive transgenic tomatoes, petunias, and tobacco have been developed by transforma-

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Abbreviations: DW, dry weight; HI, harvest index; PPF, photosynthetic photon flux.

tion with the *Arabidopsis* *etr1-1* gene (Wilkinson et al., 1997). However, C_2H_4 insensitive *Arabidopsis* mutants and transgenic plants can have abnormal developmental processes that affect seed germination, flower initiation, flower longevity, and fruit set (Bleeker et al., 1988; Gubrium et al., 2000).

In addition to genetics, environmental factors including light, temperature, O_2 , and CO_2 influence C_2H_4 production (Abeles et al., 1992; Finlayson and Reid, 1996; Grodzinski and Woodrow, 1989; Preger and Gepstein, 1984; Sanders et al., 1990; Sisler and Wood, 1988). How these factors influence C_2H_4 perception is not well understood. Gubrium et al. (2000) observed significant differences between the temperature responses of insensitive transgenic petunias (*Petunia* × *hybrida* Vilm.) and wild-type plants, suggesting a possible interaction between temperature and C_2H_4 perception. Burg and Burg (1967) classified hypoxia (<5% O_2) as an inhibitor of C_2H_4 responses, but later studies found no effect of hypoxia on C_2H_4 binding activities in plants (Sanders et al., 1990).

CO_2 is of particular interest since it is normally high in space environments and is commercially used in fruit storage to inhibit the ripening action of C_2H_4 (Yang, 1985). Burg and Burg (1967) reported that CO_2 competitively inhibits C_2H_4 action, but only at very high levels (10%). Later studies suggested the inhibitory effects of CO_2 are noncompetitive (Sisler, 1979; Sanders et al., 1990). We know that exposure to elevated CO_2 (>0.2%) at the time of anthesis decreases seed set in wheat (Grotenhuis and Bugbee, 1997). Similarly, we know that exposure to C_2H_4 at anthesis also inhibits seed set in wheat (Klassen et al., 1999). The effect of elevated CO_2 on C_2H_4 sensitivity at levels much lower than required to inhibit C_2H_4 action needs to be examined.

Our previous studies found that 250 $nmol\ mol^{-1}$ C_2H_4 caused a 60% yield reduction in wheat and 500 $nmol\ mol^{-1}$ completely inhibited seed production (Klassen et al., 1999). Microscopic examination of developing heads indicated that failed seed production was caused by an inhibition of anther dehiscence. Exposure to 1000 $nmol\ mol^{-1}$ prior to anthesis did not reduce yields, suggesting wheat is most susceptible to C_2H_4 induced sterility

around the time of anthesis. Our results implicated C_2H_4 as the cause of failed seed production in wheat grown on the Russian Space Station MIR in 1996 (Bingham et al., 2000; Campbell et al., 2001; Salisbury, 1997).

The objective of these studies was to evaluate further the effects of low C_2H_4 levels on wheat and rice. Specifically, we sought to determine (i) the threshold level at which yield is not reduced, (ii) the differential sensitivity of similar species and cultivars, and (iii) if sensitivity to low C_2H_4 levels (50 $nmol\ mol^{-1}$ C_2H_4) is influenced by elevated CO_2 levels typical of space environments (1200–5000 $\mu mol\ mol^{-1}$ CO_2).

MATERIALS AND METHODS

Growth Chamber Studies

Three trials were conducted in six cylindrical acrylic plastic (Lucite, ICI Acrylics, Wilmington, DE) chambers within a growth chamber (Fig. 1). Light was supplied with cool white fluorescent lamps providing a photosynthetic photon flux (PPF) of 21.6 and 48.5 $mol\ m^{-2}\ d^{-1}$ in the two wheat trials and 21.6 $mol\ m^{-2}\ d^{-1}$ in the rice trial (Table 1). CO_2 was enriched to 1200 $\mu mol\ mol^{-1}$ in all three trials. CO_2 levels remained constant in the wheat trials (24-h photoperiod) and nighttime levels in the rice were less than 50 $\mu mol\ mol^{-1}$ higher than daytime values. The six chambers shared a common recirculating nutrient solution. Hydroponics methodology was previously described in detail (Bugbee and Salisbury, 1988). Airflow through each cylinder was maintained at $3.3 \times 10^{-4}\ m^3\ s^{-1}$ (20 L min^{-1}) to provide a rapid rate of air turnover, and thus maintain a constant gas composition in each chamber. Pure C_2H_4 from a compressed gas cylinder was diluted with air and introduced to the chambers at flows necessary to maintain steady-state C_2H_4 levels in each treatment. Chamber CO_2 levels were monitored every 60 min with an automated infrared gas analyzer. Chamber C_2H_4 concentrations were monitored every 30 min by automated gas chromatography (Shimadzu GC17-A, Columbia, MD). The C_2H_4 concentration of ambient air used for the clean air control remained below the detection limit of 5 $nmol\ mol^{-1}$ for the duration of these studies and the levels of all other treatments remained within 10% of set point.

USU-Apogee wheat (Trials 1 and 2) and Super Dwarf rice (Trial 3) were direct-seeded (500 plants per m^{-2}) into 10-

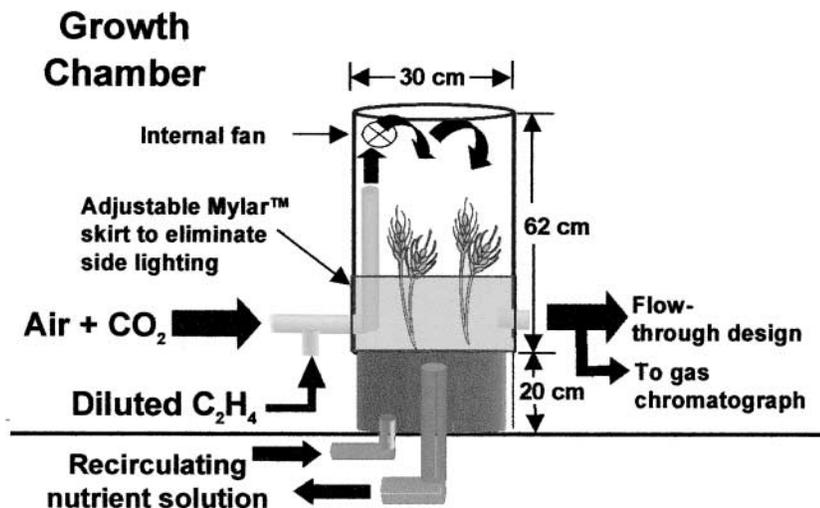


Fig. 1. Diagram of one of six cylindrical chambers in the growth chamber system.

Table 1. Environmental parameters for the five studies.

Trial	1	2	3	4 and 5
System	Chamber	Chamber	Chamber	Greenhouse
Root zone medium	Hydroponics	Hydroponics	Hydroponics	Peat/Perlite
Crop	Wheat	Wheat	Rice	Wheat
Temperature (°C)	24	22/17†	32 day/26 night	22/17†
Photoperiod (h)	24	24	12	24
PPF (mol m ⁻² d ⁻¹)	21.6	47.5	21.6	51
CO ₂ (μmol mol ⁻¹)	1200	1200	1200	350, 1200, 5000

† The temperature was reduced from 22 to 17°C following anthesis in Trials 2, 4, and 5.

Table 2. Treatment parameters for the five trials.

Trial	C ₂ H ₄	CO ₂	Crop	Cultivar
	nmol mol ⁻¹	μmol mol ⁻¹		
1	0, 250, 500, 750, 1000, pre-anthesis†	1200	Wheat	USU-Apogee
2	0, 50, 100, 300, 1000, pre-anthesis†	1200	Wheat	USU-Apogee
3	0, 50, 100, 300, 1000, pre-anthesis†	1200	Rice	Super Dwarf
4 and 5	0, 50	350, 1200, 5000	Wheat	USU-Apogee, Super Dwarf

† Short-term C₂H₄ exposure, 1000 nmol mol⁻¹ until boot stage followed by 0 nmol mol⁻¹.

mm-deep hydroponic trays filled with extruded diatomaceous earth (Isolite, size CG-2, Sundine Enterprises, Arvada, CO) and placed over recirculating nutrient solution. Each study included five C₂H₄ treatments and a single control chamber without C₂H₄ (Table 2). Ethylene treatments began 7 d after emergence and were maintained at constant levels until harvest except for the preanthesis treatment. The preanthesis treatment was maintained at 1000 nmol mol⁻¹ until the boot stage (20, 25, and 49 d after emergence in Trials 1 to 3, respectively) as determined by the presence of the emerging head in the stem of the plant, after which C₂H₄ addition was ceased. Plants were harvested at physiological maturity (66, 81–110, and 75–96 d after emergence in Trials 1–3, respectively) as determined by a loss of green color from the seeds. Ethylene addition at the 1000 nmol mol⁻¹ level significantly delayed maturation in rice (Trial 3), so these treatments were harvested prematurely on Day 96. Plants were harvested by hand. Wheat was thrashed with a small plot thrasher and the rice was thrashed by hand. A head with at least one seed was considered fertile. Plant height was measured with a meter stick. Seed

was air dried for 72 h and vegetative tissues were oven dried at 80°C for 48 h prior to weighing.

Yield data are presented as yield per day since this more precisely describes yield in controlled environments. Differences in the length of the life cycle among studies result in differences in yield. Factoring out time to harvest allows for better comparisons among studies.

Greenhouse Studies

Two replicate studies were conducted in a greenhouse in 12 acrylic (Lucite) chambers. Supplemental high pressure sodium (HPS) lighting was used overnight to provide a 24-h photoperiod and to ensure that both studies had a similar average PPF of 51 mol m⁻² d⁻¹ (Table 1). In one study, the lights were on for 16 h per day providing 45 mol m⁻² d⁻¹ and natural light provided 6 mol m⁻² d⁻¹. In the replicate study, lights were on for 12 h per day providing 34 mol m⁻² d⁻¹ and natural light provided 17 mol m⁻² d⁻¹. Each cultivar was planted (500 plants per m⁻²) in adjacent plots (0.45 by 3.60 m) lengthwise

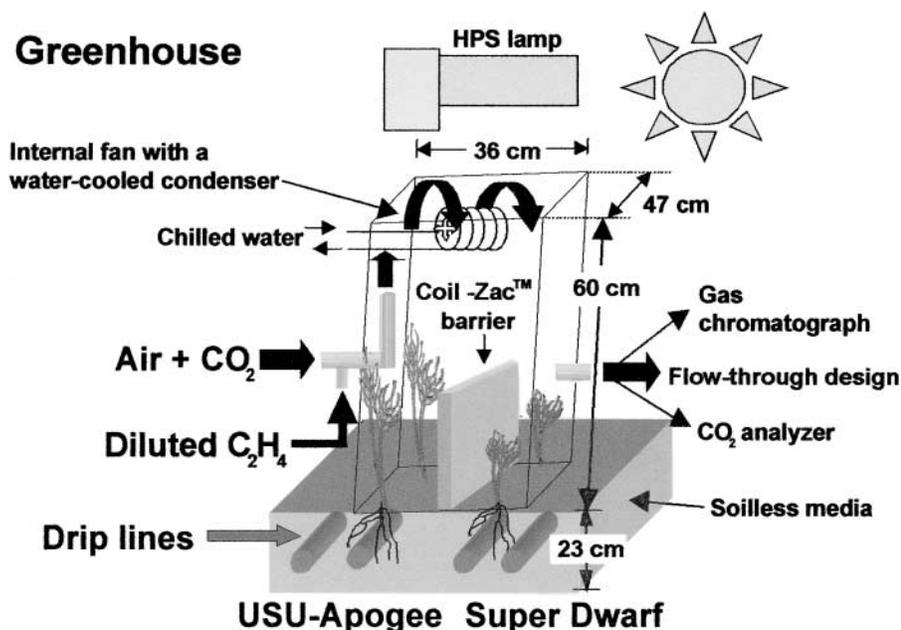


Fig. 2. Diagram of one of 12 rectangular chambers in the greenhouse system. Two cultivars were grown within each chamber.

along each of two replicate benches filled with soilless media (1:1; peat:Perlite) 23 cm deep (Fig. 2, 3). Following emergence, the 12 chambers were placed so that equal areas (23.5 by 36.0 cm) of each cultivar were included in each chamber (Fig. 2, 3). A 30-cm-tall reflective metal barrier (Coil-Zac, Environmental Growth Chambers, Chagrin Falls, OH) was placed between the two cultivars to prevent shading of the shorter cultivar. Each chamber had a water-cooled condenser for temperature control and air sampling lines for automated CO_2 and C_2H_4 analysis. Airflow into each chamber was maintained at $6.6 \times 10^{-4} \text{ m}^3 \text{ s}^{-1}$ (40 L min^{-1}) to provide a rapid rate of air turnover. Air, CO_2 , and C_2H_4 were supplied as in the growth chamber trials. Drip irrigation lines buried in the media supplied nutrient solution three times a day as previously described (Reuveni and Bugbee, 1997). Plants in each chamber were exposed to one of three CO_2 levels (350, 1200, and 5000 $\mu\text{mol mol}^{-1}$) and one of two C_2H_4 levels (0 and 50 nmol mol^{-1}). Plants growing between chambers provided guard rows to minimize the effects of side lighting. Plants were harvested and processed following the same procedures as in the growth chamber studies. Data were analyzed as a randomized split block design including two cultivars, two C_2H_4 levels,

three CO_2 levels, and two replicate treatment chambers per study by a standard ANOVA procedure (Tables 2, 3).

RESULTS AND DISCUSSION

Growth Chamber Trials: USU-Apogee Wheat

Plants grew well in all treatments and headed at the same time as the control. Although the C_2H_4 levels were lower than in our previous studies, typical indicators of C_2H_4 exposure in wheat including shortened and rolled flag leaves and shortened awns were observed in all C_2H_4 treatments. Wheeler et al. (1996) noted cone shaped longitudinally rolled leaves in wheat (cv. Yecora Rojo) at 100 $\text{nmol mol}^{-1} \text{ C}_2\text{H}_4$. This study confirms that leaf rolling is a good indicator of C_2H_4 exposure in wheat. Ethylene reduced plant height in all continuous treatments ranging from a 17% reduction in the 50 nmol mol^{-1} treatment and 37% in the 1000 nmol mol^{-1} treatment as compared to the control (data not given). How-

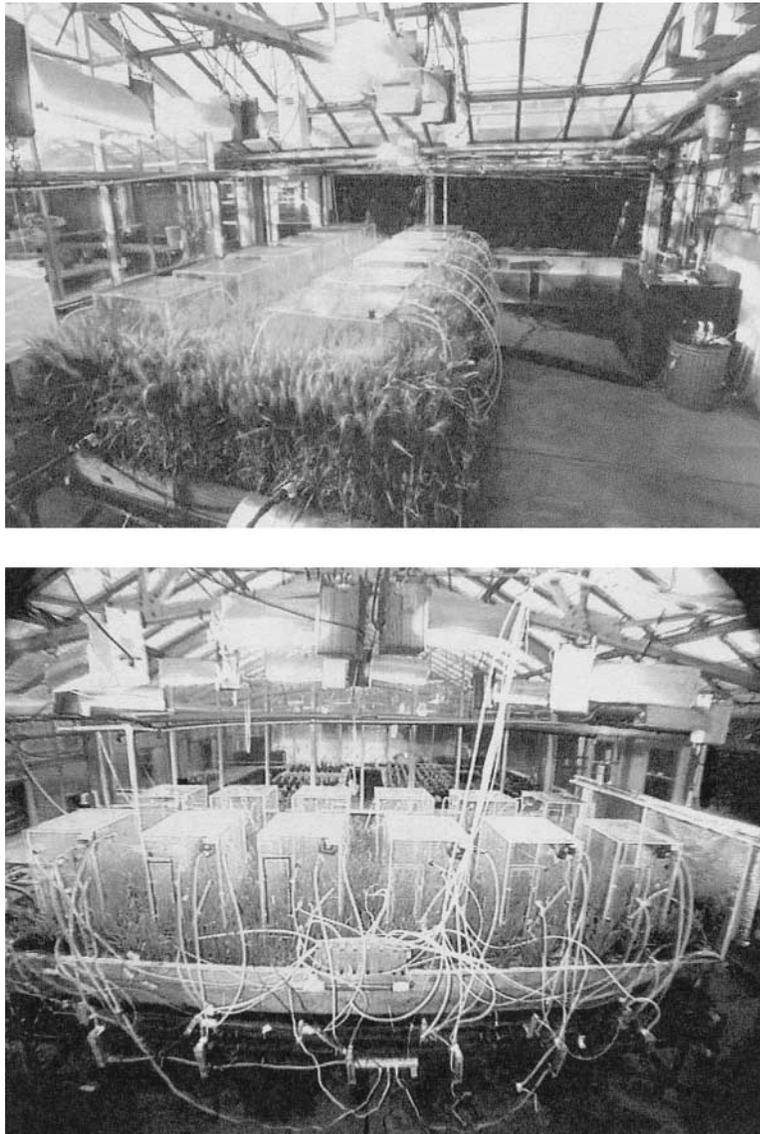


Fig. 3. Picture of the 12-chamber greenhouse system.

Table 3. Statistical results for yield (g) in Trials 4 and 5.

Source	DF	SS	MS	F	P > F
Model	13	56 073	4 313	17.8	<0.0001
Error	34	8 262.8	243.0		
Corrected Total	47	64 335			
	<i>R</i> ²	CV	Root MSE	Mean	
	0.872	23.67	15.589	65.86	
Source	DF	SS	MS	F	P > F
Trial (4 and 5)	1	397.2	397.2	1.63	0.2097
Block (Bench 1 and 2)	1	66.13	66.13	0.27	0.6053
C ₂ H ₄ (0 and 50 nmol mol ⁻¹)	1	3 724	3 724	15.3	0.0004
CO ₂ (350, 1200, 5000 μmol mol ⁻¹)	2	4 406	2 203	9.07	0.0007
C ₂ H ₄ × CO ₂	2	594.3	297.1	1.22	0.3071
cv. (Apogee and SD)	1	43 406	43 406	178	<0.0001
C ₂ H ₄ × cv.	1	3 168	3 168	13.0	0.0010
CO ₂ × cv.	2	233.4	116.7	0.48	0.6228
C ₂ H ₄ × CO ₂ × cv.	2	75.38	37.69	0.16	0.8569

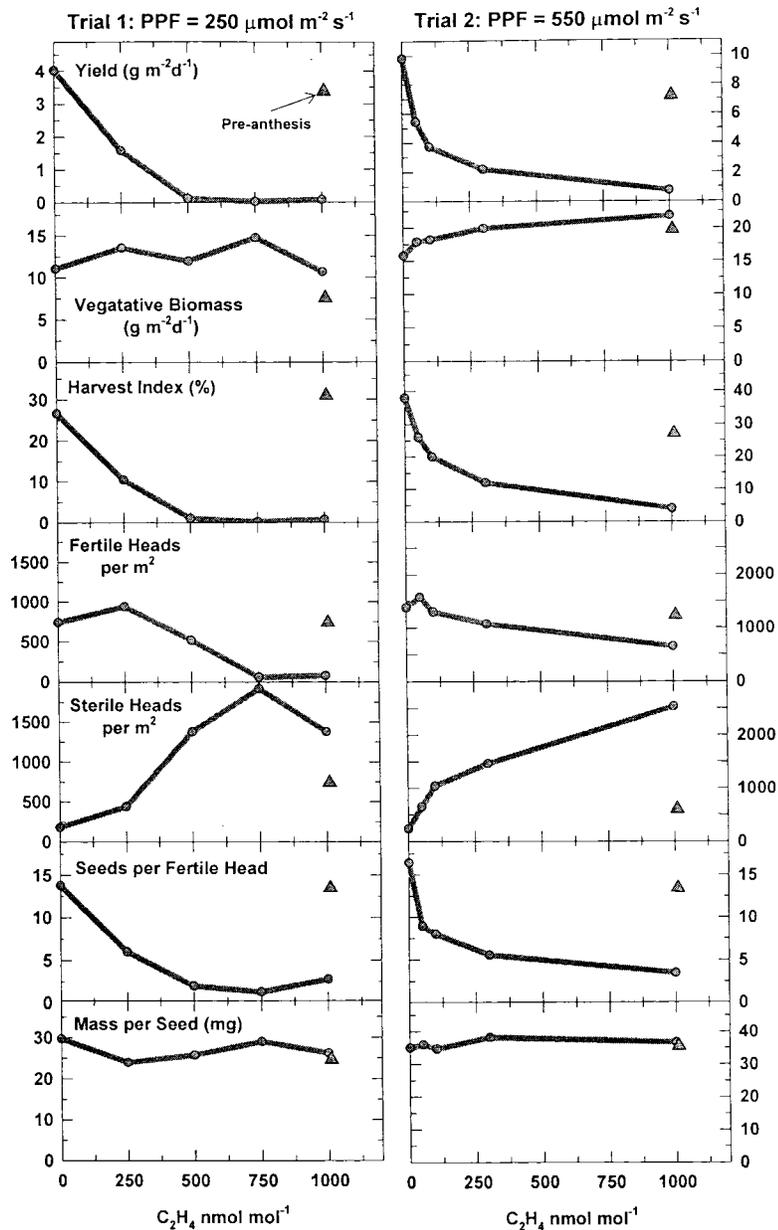


Fig. 4. Ethylene response curves for yield components of USU-Apogee wheat grown at different photosynthetic photon fluxes (PPF). The short-term exposure pre-anthesis treatment is represented by a triangle.

ever, plant height was not affected by C_2H_4 in the 1000 $nmol\ mol^{-1}$ pre-anthesis treatment.

Seed yield was reduced by 37% in the 50 $nmol\ mol^{-1}$ C_2H_4 treatment and plants in the 1000 $nmol\ mol^{-1}$ treatment were almost completely sterile (Fig. 4). A similar trend was observed in harvest index (HI). Although C_2H_4 increased tillering as indicated by an increased number of total heads (sterile + fertile), seed set per head was significantly reduced. Seed mass was not significantly different among treatments. Yield and HI were only slightly reduced in the preanthesis treatment verifying our previous finding that C_2H_4 induced male sterility is most significant around the time of anthesis (Klassen et al., 1999).

The root:shoot ratio increased with increasing C_2H_4 levels. The ratio of root biomass to total biomass increased by 8 and 15% in the 50 and 1000 $nmol\ mol^{-1}$ treatments, respectively, as compared to the control (data not given). Grodzinski and Woodrow (1989) reported a similar shift in the root:shoot ratio of ethephon (C_2H_4 source) treated tomatoes and suggested this shift in carbon partitioning may be caused by a reduction in the dominant carbon sinks.

Growth Chamber Trial: Super Dwarf Rice

The effects of C_2H_4 on rice were unique. Rice plants did not exhibit rolled leaves, shortened leaf length, or shortened plant height, but did exhibit chlorosis, premature leaf senescence, and delayed heading in all C_2H_4 treatments.

Similar to wheat, a C_2H_4 level of 50 $nmol\ mol^{-1}$ significantly reduced yield (Fig. 5). Seed yield and HI were reduced by more than 50% in the 50 $nmol\ mol^{-1}$ treatment and plants exposed to 300 and 1000 $nmol\ mol^{-1}$ were almost completely sterile. The yield of the 1000 $nmol\ mol^{-1}$ preanthesis treatment was not determined because of the long delay in heading (38 d > control). Similar to wheat, yield reductions were associated with poor seed set. Seeds per head were reduced in the 50 and 100 $nmol\ mol^{-1}$ treatments but the number of heads was not affected. Both seeds per head and head number were reduced in the 300 $nmol\ mol^{-1}$ treatment, and there were no heads in the 1000 $nmol\ mol^{-1}$ treatment.

Similar to wheat, the root:shoot ratio of rice increased in all C_2H_4 treatments (data not given).

Greenhouse Trials: Wheat Cultivar \times CO_2 Interactions

USU-Apogee was more tolerant of elevated C_2H_4 levels than Super Dwarf. Yield was not affected by 50 $nmol\ mol^{-1}$ C_2H_4 for USU-Apogee, but was reduced by 60% in Super Dwarf (Fig. 6). The insensitivity of USU-Apogee to 50 $nmol\ mol^{-1}$ C_2H_4 was surprising since this C_2H_4 level reduced the yield of USU-Apogee by 35% in the growth chamber (Trial 2). This difference suggests an interaction between C_2H_4 and environmental factors that were different between the greenhouse and growth chamber trials.

As expected, elevated CO_2 increased the yield of both cultivars at 1200 $\mu mol\ mol^{-1}$ CO_2 , but had a deleterious

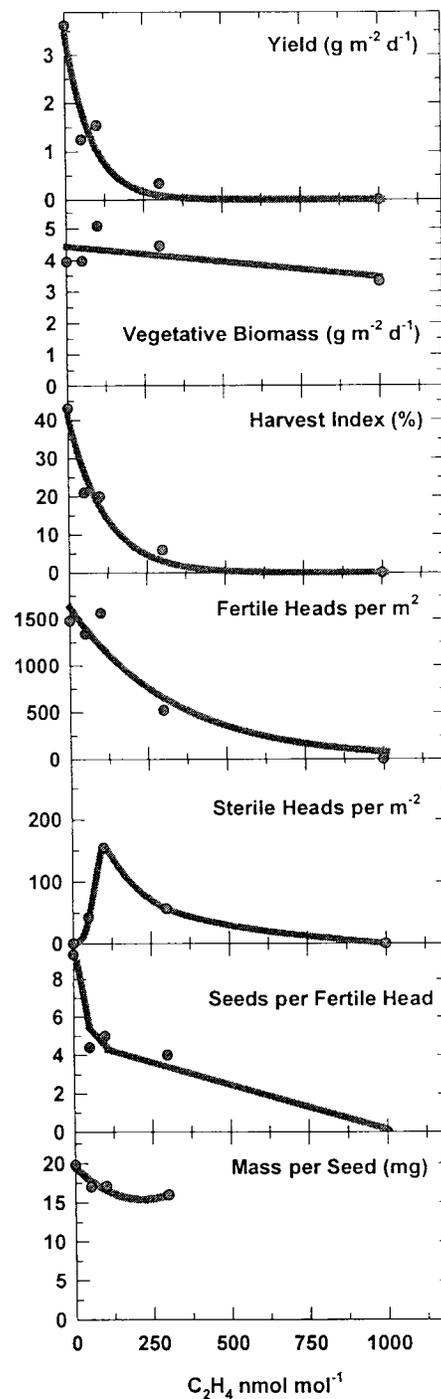


Fig. 5. Ethylene response curves for yield components of Super Dwarf rice. Data for the short-term exposure, pre-anthesis treatment is not included since this treatment failed to reach maturity.

effect at 5000 $\mu mol\ mol^{-1}$ CO_2 (Fig. 6). The reduced yield at 5000 $\mu mol\ mol^{-1}$ CO_2 is consistent with yield reductions in other studies (Reuveni and Bugbee, 1997; Grotenhuis and Bugbee, 1997). No statistically significant interaction between C_2H_4 and CO_2 was observed for either cultivar ($F = 1.22$, $P > 0.3$, Table 3).

Environmental differences between the growth chamber and greenhouse trials that may have contributed to the observed difference in the C_2H_4 response of wheat

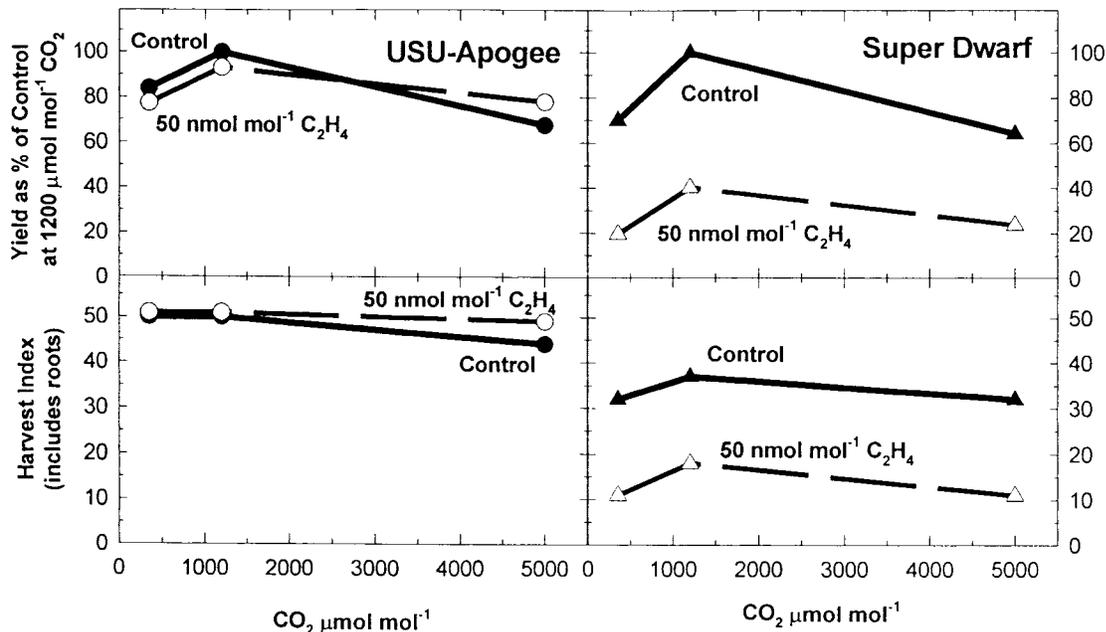


Fig. 6. Mean yield and harvest index (HI) of USU-Apogee and Super Dwarf wheat with and without $50 \text{ nmol mol}^{-1} \text{ C}_2\text{H}_4$ at three levels of CO_2 . Yields are normalized to percent of the control at $1200 \mu\text{mol mol}^{-1} \text{ CO}_2$ for ease of comparison. HI was calculated assuming the root mass to be 10% of the total above ground biomass.

include temperature, light, and rooting medium. Although the temperature set points were the same for both the greenhouse and growth chamber studies, it was not possible to maintain constant temperatures in the greenhouse. Temperatures in the greenhouse followed a diurnal pattern with cool mornings and gradual warming until reaching a maximum at midday. Thus, when the daily average temperature of the greenhouse was maintained to be 22°C , instantaneous values typically ranged from 16 to 28°C . In contrast, temperatures in the growth chamber were stable ($\pm 1^\circ\text{C}$ from set point) throughout the trial.

We hypothesize that temperature may interact with C_2H_4 sensitivity in wheat and rice. We know that high temperature inhibits fertilization in both wheat and rice and that fertilization is most sensitive to high temperature around the time of anthesis (Evans et al., 1975; Gusta and Chen, 1987; Mackill et al., 1982). Satake and Yoshida (1978) found that high temperature interferes with anther dehiscence and causes poor pollination in rice. We previously determined that C_2H_4 inhibits anther dehiscence, causing failed seed production in wheat (Klassen et al., 1999). Thus, high temperature affects yield in both wheat and rice in ways similar to that of C_2H_4 . We are now preparing to examine the effects of temperature on C_2H_4 sensitivity.

Like temperature, light levels were more variable in the greenhouse than in the growth chamber. While the average light intensity was similar in the second growth chamber study and the greenhouse studies (47.5 vs. $50 \text{ mol m}^{-2} \text{ d}^{-1}$), instantaneous levels in the greenhouse typically ranged from 400 to $800 \text{ mol m}^{-2} \text{ s}^{-1}$. Mortensen (1989) studied interactions between light (50 , 100 , $150 \text{ mol}^{-2} \text{ s}^{-1}$) and C_2H_4 (55 and $112 \text{ nmol mol}^{-1}$) on lettuce growth. His data indicated that the effect of C_2H_4 was minimized at the highest light level examined. The effect

of light intensity on C_2H_4 sensitivity warrants further investigation since high light intensity has also been shown to promote seed set in wheat (Wardlaw, 1970).

Finally, although the greenhouse and growth chamber rooting media were different (peat:Perlite media vs. hydroponics), the root zone environments were similar since the soilless media was watered three times a day with a nutrient solution. Both systems thus provided ample water, oxygen, and nutrients. Growth rates and yields of plants grown hydroponically and in soilless media have been comparable in several previous studies (Bugbee et al., 1994; Reuveni and Bugbee, 1997).

CONCLUSIONS

A C_2H_4 level of 50 nmol mol^{-1} significantly reduced yields in both wheat and rice. Although this level is higher than typical field levels, it is sufficiently low to be of concern in poorly ventilated greenhouses and growth chambers, and in urban areas where atmospheric levels may exceed 50 nmol mol^{-1} . Significant variability in C_2H_4 sensitivity was observed between species and cultivars. USU-Apogee is less sensitive to C_2H_4 than either Super Dwarf wheat or Super Dwarf rice. Although C_2H_4 sensitivity varied with environment, elevated CO_2 (up to $5000 \mu\text{mol mol}^{-1}$) did not affect C_2H_4 sensitivity in wheat.

Our results suggest yield reductions associated with elevated C_2H_4 can be minimized through a combination of screening for C_2H_4 tolerant genotypes and the identification and control of environmental factors affecting C_2H_4 sensitivity.

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