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Response of Cotton to Early-Season Square Abscission under Elevated CO_2

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ABSTRACT

A field study was performed to quantify the compensation capacity of cotton (*Gossypium hirsutum* L.) for simulated damage of square buds loss by manual removal method during early growing season in 2004 and 2005 in combination with elevated CO_2 relative to ambient CO_2. Square buds of cotton plants were wholly removed manually for 1 wk (SR1 treatment) and two consecutive weeks (SR2 treatment) in contrast to no square bud removal (SR0 treatment) after squaring stage, and their compensation ability is quantified by measuring plant growth and production. Two levels of CO_2 (ambient and double-ambient) and three types of manual removal of square buds (SR1 and SR2 vs. SR0) were deployed in a completely randomized design with six treatment combinations. Cotton plants grown in elevated CO_2 had significantly higher leaf area per plant on each sampling date for SR1 treatment compared with SR0 treatment in 2004 and 2005. Significantly higher seedcotton yield, maturity, and harvested biomass were also observed for SR0, SR1, and SR2 treatments under elevated CO_2 relative to ambient CO_2 in 2004 and 2005. Moreover, there were significant interactions between CO_2 level × square removal treatment on seedcotton yield and boll maturity, and significance between square removal treatment × investigation year on plant harvested biomass. Results from these studies provide a profile for developing strategies for future management of cotton ecosystems in Northern China.

The global atmospheric CO_2 level is acutely rising and anticipated to double by the end of the 21st century (Lin and Wang, 2002). The direct fertilizing effects of enriched atmospheric CO_2 on plant physiology and community structure have been well documented (e.g., Curtis and Wang, 1998; Luo et al., 1999). Many investigators report that elevated CO_2 increases plant photosynthesis, growth, aboveground biomass, leaf area, and yield (Cure, 1985; Oechel and Strain, 1985; Cure and Aycock, 1986; Bazzaz, 1990; Pritchard et al., 1999; Oijen et al., 1999; Kimball et al., 2002; Reddy et al., 2000). A CO_2 increase results in increases in photosynthetic rate, plant growth, water use efficiency, C/N ratio, and usage efficiency of N (Masle, 2000; Lin and Wang, 2002; Wu et al., 2006). Paul et al. (2002) reported that elevated CO_2 significantly increased aboveground biomass, but had no effect on shoot density. Heagle et al. (2002) confirmed that clover (*Trifolium repens* L.) leaf growth and area, and leaf laminae and petiole weight all generally increased with increased CO_2.

Cotton, as a C_3 plant, appears to be especially responsive to elevated CO_2. Wu et al. (2007) reported that significantly higher plant height and leaf area per cotton were observed after cotton plants grown in elevated CO_2 compared with ambient CO_2 for 1, 2, and 3 mo in both years' investigation. Chen et al. (2005c) indicated that cotton had lower N and higher harvested biomass under elevated CO_2. Kimball (1986) reported that an elevation of CO_2 levels from 330 to 660 $\mu L\ L^{-1}$ led to a 95% yield increase in cotton. However, yields of C_3 agricultural crops are estimated to only increase by about 30% if CO_2 concentration doubles (Kimball, 1983).

Cotton plants subjected to the loss of squares by insect pests during the early growing season subsequently abscised fewer squares and thus retained more fruit later in the growing season (Wilson, 1986; Stewart and Sterling, 1989). Many factors influence the ability of cottons to compensate for fruit loss by square removal (Stewart et al., 2001), such as soil fertilization (Guo et al., 1985; Sheng and Ma, 1986), fruit age, injury time and severity, and weather conditions (Hearn and Rosa, 1984; Cox et al., 1990; Sadras, 1995). Cotton cultivars (Mulrooney et al., 1992; Brook et al., 1992a, 1992b; Mann et al., 1997), planting density, and number of fruiting branches (Bi et al., 1991) are other key factors affecting the compensation capacity of cotton. However, adverse factors associated with compensation are delayed crop maturity, late season pest problems, and weather-related yield loss (Stewart and Sterling, 1989). Moreover, Bednarz and Roberts (2001) confirmed that spatial yield distribution or yield components may be different for cotton crops in response to fruit loss by manual removal of floral buds during the early growing season. To date, studies of the compensatory growth of cotton plants after loss of reproductive organs were performed at ambient CO_2 (Sadras, 1995), despite the potentially significant consequences of elevated CO_2 for plant growth and physiology, such as reviewed by Curtis and Wang (1998) and Luo et al. (1999). Quantification of the effect of elevated CO_2 on compensation ability of cotton plants for fruit loss is needed to develop integrated pest management strategies (Bazzaz, 1990; Klironomos et al., 2005). Kimball et al. (2002) and Reddy et al. (2000) reported the growth and biomass of cotton responses to elevated CO_2. However, little is known regarding the interaction effects between CO_2 concentration and square removal on the yield and maturity of cotton.

The objective of this study was to address (i) the plant leaf area and harvested biomass compensation ability of cotton to early-season injury under elevated CO_2; and (ii) the effects of interaction between CO_2 atmosphere and square removal treatment on seedcotton yield and maturity.

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Abbreviations: OTC, open-top chamber.

MATERIALS AND METHODS

Open-Top Chambers and Setup of CO_2 levels

This experiment was performed in six 4.2-m diameter open-top chambers (OTCs) in Sanhe County, Hebei Province, China (35°57′ N, 116°47′ E). Two levels of atmospheric CO_2 concentration were continuously applied: current ambient level (about 370 μL L^{-1}) and double-ambient level (750 μL L^{-1}) representing the predicted level in about 100 yr (Houghton et al., 1996). Three OTCs were used for each CO_2 level. During the period from seedling emergence to harvesting of cotton, CO_2 concentrations were monitored 24 h d^{-1} and adjusted with an infrared CO_2 analyzer (Ventostat 8102, Telaire Company, Goleta, CA). Details of the automatic-control system of CO_2 and the OTCs are provided in Chen and Ge (2004) and Chen et al. (2005a, 2005b).

Cultural Practice

Cotton cultivar Simian-3 was used in this study and cotton seeds were potted (35-cm diam., 45-cm height) on 3 May and harvested on 20 Sept. 2004 and 2005. These white plastic pots were filled with 8:3:1 (by volume) loam, cow dung, and earthworm frass. Thirty pots with the density of one plant per pot were randomly placed on 3 May in each OTC and rerandomized daily to minimize position effects. From seedling emergence to harvest, pure CO_2 mixed with ambient air was supplied to each OTC of the elevated CO_2 treatment, in contrast to ambient air to OTCs of the ambient CO_2 treatment. The mixture soil was sampled and triturated to analyze its chemical composition (Institute of Soil Science, Chinese Academy of Science, 1978). Soil pH was 7.2; organic matter, 141 g Kg^{-1}; available N, 403.7 mg Kg^{-1} (hydraulic N, 1 *M* NaOH hydrolysis); available P 276.0 mg Kg^{-1} (0.5 *M* $NaHCO_3$ extraction), available K 267.1 mg Kg^{-1} (1 *M* CH_3COONH_4 extraction). No chemical fertilizers or insecticides were used, and open tops of these OTCs were all covered with netting to prevent insect movement through this experiment.

Cotton Square Removal Treatment

Hand removal of floral buds (diam. ≥ 3mm) began on 2 July 2004 and 2005, when the second week after cotton squaring began. Floral buds that met the size criteria were grasped with index finger and thumb, and twisted until the peduncle snapped and disjoined (Bednarz and Roberts, 2001). Two types of manual removal of cotton square buds were performed as follows: (i) One date of 100% floral bud removal (i.e., SR1 treatment) on 2 July 2004 and 2005; (ii) Two dates of 100% floral bud removal (i.e., SR2 treatment) on 2 and 9 July 2004 and 2005. All floral buds on a sympodial branch that met the size criteria, regardless of position, were wholly removed (Bednarz and Roberts, 2001). No floral buds were manually removed from the control (i.e., SR0 treatment).

Experimental Treatment Setup

Two CO_2 levels (ambient and double-ambient) and three types of manual removal of square buds (SR1 and SR2 vs. SR0) were deployed in a completely randomized design with six treatment combinations: (i) Square buds of cotton plants were wholly removed manually for 1 wk in elevated CO_2; (ii) Square buds of cotton plants were wholly removed manually for 1 wk in ambient CO_2; (iii) Square buds of cotton plants were wholly removed manually for two consecutive weeks in elevated CO_2; (iv) Square buds of cotton plants were wholly removed manually for two consecutive weeks in ambient CO_2; (v) No floral bud removal in elevated CO_2; (vi) No floral bud removal in ambient CO_2. Sampling size was 10 pots per OTC and 30 pots (i.e., 30 plants) of three OTCs for each CO_2 level × manual removal type treatment.

Data Collection

From 9 July to harvest date in 2004 and 2005, leaf area per plant was measured once every 15 d. To avoid destroying cotton leaves, rubbings of all leaves per plant were marked on white papers using pencil, at each sampling of leaf area per plant. The marked rubbings of cotton leaves were cut out using shears, and then leaf (i.e., the cutting rubbings) areas were scanned using a digital area meter (model CI-202 CID Inc., Camas, WA), according to the manufacturer instructions. At harvest (20 Sept. 2004 and 2005), the aboveground tissues (i.e., cotton root, stem, leaves, hull, seedcotton) and the shatters (i.e., the leaves, flowers, buds and bolls withered and dropped from cotton plants) were separately collected for each cotton plant. After these aboveground tissues were harvested, the root ball was soaked in tap water until cotton plant roots were wholly isolated from plastered soil before drying. Each tissue sample was separately oven dried at 80°C for 48 h to constant weight (Pettigrew et al., 1992), measured with the Cahn 20 automatic electrobalance (Cahn, St. Louis, MO). The open bolls per plant were collected to estimate cotton maturity (Gore et al., 2000).

Statistical Analyses

All data were analyzed using the General Linear Models Procedure (SAS Institute, 1996, Cary, NC). Three-way ANOVA was used to analyze the effects of CO_2 level (elevated vs. ambient), square removal type (SR1 and SR2 vs. SR0) and investigation year (2004 or 2005) on each of those measured parameters of cotton plant root, stem, leaf, seedcotton dry weight and harvested biomass per plant. Moreover, sampling dates (24 July, 9 and 24 August, and 10 October) were also considered as another factor in the ANOVA (i.e., four-factor ANOVA) to analyze the impacts of CO_2 level, square removal type, sampling date, and investigation year on the parameter of leaf area per plant. Differences among means were determined using a LSD test at $P < 0.05$.

RESULTS AND DISCUSSION

Leaf Area

In Table 1, the CO_2 level, square removal treatment, sampling date, and investigation year all significantly affected plant leaf area ($P < 0.001$). The interaction between CO_2 level × sampling date and sampling date × investigation year had a significant effect on plant leaf area ($P < 0.001$). Furthermore, the interaction between CO_2 level × investigation year, removal treatment × investigation year, and CO_2 level × removal treatment × investigation year all significantly influenced plant leaf area ($P < 0.05$).

From Table 2, on 24 July, significant differences were observed among three removal treatments under elevated CO_2 ($P < 0.01$) in 2004 and two levels of atmospheric CO_2 concentrations ($P < 0.05$) in 2005. On 9 August, significant differences occurred among three removal treatments in both CO_2 treatments ($P < 0.05$) in 2004 and elevated CO_2 ($P < 0.05$) in 2005. On 24 August, significant differences were found ($P < 0.05$)

Table 1. Significances from ANOVA on the effects of CO_2 level, square removal type, sampling date, investigation year, and the interactions among these four factors on the parameter of plant leaf area.

Influence factors	ANOVAs *F* value	*P* value
CO_2†	321.64	<0.001***
Removal‡	60.79	<0.001***
Date¶	10270.8	<0.001***
Year§	361.18	<0.001***
CO_2 × Removal	1.63	0.2010
CO_2 × Date	6.10	0.0008
CO_2 × Year	4.94	0.0286
Removal × Date	2.19	0.0508
Removal × Year	3.99	0.0217
Date × Year	114.94	<0.001***
CO_2 × Removal × Date	1.50	0.1860
CO_2 × Removal × Year	4.00	0.0214
Removal × Date × Year	1.93	0.0832
CO_2 × Removal × Date × Year	0.94	0.4942

*** $P < 0.001$.
† CO_2 levels (ambient and double-ambient).
‡ Square removal treatments (SR0, SR1, and SR2).
¶ Sampling date.
§ Investigation years (2004 and 2005).

among three removal treatments under elevated CO_2 in 2004. On 10 September, significant differences were observed ($P < 0.05$) among three removal treatments under elevated CO_2 in 2005.

In general, an CO_2 increase results in increased plant photosynthetic rate, growth, and leaf area (Masle, 2000; Wu et al., 2007). Stacey and Fellowes (2002) reported that Brussels sprout plants (*Brassica oleracea* var. *gemmifera* Zenker) grown in elevated CO_2 had more leaves per plant and larger leaf area than plants grown in ambient CO_2. Elevated CO_2 also results in increased leaf-area index (Dermody et al., 2006) and increased rates of growth (Saxe et al., 1998). Chen et al. (2005c) reported that cotton had lower leaf area under elevated CO_2. From this experiment, leaf area per plant increased with the enhancement of atmospheric CO_2 levels in two successive years. And, significantly higher plant leaf area was observed in the 100% square removal for 1- and 2-wk treatments, compared with no square removal treatment on every sampling date in successive years under elevated CO_2, which indicates the compensatory capacity of plant leaf area may depend on the square bud removal time under elevated CO_2.

Plant Bolls Maturity

In Table 3, CO_2 concentration ($P < 0.001$) and square removal treatment ($P < 0.001$) significantly affect plant boll maturity. Moreover, the interaction between CO_2 concentration × square removal treatment has the significant effect on plant boll maturity ($P < 0.05$).

From Table 4, significant differences in plant boll maturity among three removal treatments were found under ambient CO_2 ($P < 0.01$) and elevated CO_2 treatments ($P < 0.05$) in 2004 and under both CO_2 concentrations ($P < 0.01$) in 2005. However, the plant boll maturity was not observed to be significantly different between the same removal treatment in both years.

Crop maturity is an important factor to consider when making management decisions. Sloane et al. (1974) observed delays in cotton maturity when all squares were removed during the first 5-wk of squaring under ambient CO_2. In similar studies that involved early-season removal of squares and flowers, crop maturity was also delayed (Pettigrew et al., 1992; Terry, 1992; Johns et al., 1996). In contrast, in our studies, significantly lower plant boll maturity was found in square removal treatment (SR2) compared with no floral bud removal treatment (SR0) under two CO_2 levels, and significantly higher plant boll maturity was observed under elevated CO_2 compared with ambient CO_2 in the 2 yr of investigations. The interaction between cotton square removal treatments (SR0, SR1, and SR2) and CO_2 levels can significantly affect plant boll maturity, and a significant interaction between cotton square removal treatments (SR0 and SR2) and CO_2 levels was observed in plant boll maturity in both years. However, the interaction between cotton square removal treatments (SR0 and SR1) and CO_2 levels had no significant effect on plant boll maturity, which indicates that medium or later time-dependent square removal (100% square removal for 2-wk treatment) can significantly decrease plant boll maturity compared with the early time-dependent square removal (100% square removal for 1-wk treatment) under elevated CO_2. It is anticipated that later time-dependent square removal treatment beyond 100% square removal for the 2-wk treatment can severely decrease the plant boll maturity under elevated CO_2, and significantly higher plant

Table 2. Leaf area per plant (mean ± SE) of cotton sampled by different days after planting (DAP) under ambient CO_2 and elevated CO_2 in 2004 and 2005.†

Date (DAP)	Ambient CO_2 SR0	Ambient CO_2 SR1	Ambient CO_2 SR2	Elevated CO_2 SR0	Elevated CO_2 SR1	Elevated CO_2 SR2
	cm^2 pot^{-1}					
24 July 2004 (82)	63.4 ± 1.0 b, A	65.5 ± 0.5 ab, B	66.0 ± 1.0 a, B	65.2 ± 0.3 c, A	70.2 ± 0.4 a, A	68.8 ± 0.2 b, A
9 Aug. 2004 (98)	101 ± 0 b, A	103 ± 1 a, B	103 ± 0 a, B	102 ± 1 b, A	106 ± 0 a, A	105 ± 1 a, A
24 Aug. 2004 (113)	92.2 ± 0.9 ab, A	93.6 ± 0.8 a, B	90.6 ± 0.8 b, B	94.3 ± 0.3 b, A	96.2 ± 0.3 a, A	95.5 ± 0.4 a, A
10 Sept. 2004 (130)	73.9 ± 0.4 b, A	75.7 ± 0.5 a, B	75.7 ± 0.6 a, A	74.7 ± 0.4 b, A	77.2 ± 0.2 a, A	77.0 ± 1.0 a, A
24 July 2005 (82)	58.1 ± 0.2 b, B	59.7 ± 0.4 a, B	60.1 ± 0.4 a, B	61.4 ± 0.3 b, A	62.4 ± 0.4 ab, A	63.4 ± 0.4 a, A
9 Aug. 2005 (98)	95.3 ± 0.6 a, B	96.5 ± 0.8 a, B	97.0 ± 0.7 a, B	98.9 ± 0.9 b, A	102 ± 0 a, A	99.8 ± 0.3 ab, A
24 Aug. 2005 (113)	86.7 ± 0.9 a, B	89.1 ± 0.6 a, B	88.5 ± 1.0a, B	91.3 ± 0.6 a, A	92.0 ± 0.7 a, A	92.4 ± 0.8 a, A
10 Sept. 2005 (130)	75.7 ± 0.6 a, B	77.1 ± 0.2 a, B	76.9 ± 0.3 a, B	78.0 ± 0.2 b, B	79.0 ± 0.4 a, B	79.4 ± 0.2 a, B

† SR0, no floral bud removal treatment; SR1, 100% floral bud removal for 1 wk treatment; SR2, 100% floral bud removal for 2 wk treatment. Within a row, means indicated by different lowercase letters are significantly different at same CO_2 level (LSD test, $P < 0.05$, df = 2, 6); means indicated by different uppercase letters are significantly different in double-ambient CO_2 compared with ambient CO_2 (LSD test, $P < 0.05$, df = 1, 4).

Table 3. Significance from ANOVA on the effects of CO_2 level, square removal treatment, investigation year and their interaction among CO_2 level, square removal treatment, and investigation year on harvested biomass of cotton plant root, stem, leaf, shatter, seedcotton yield, harvest biomass dry weight, and boll maturity at harvest (*P* value).

Measured indexes	CO_2†	Removal‡	Year§	CO_2 × Removal	CO_2 × Year	Removal × Year	CO_2 × Removal × Year
Boll maturity	<0.001***	<0.001***	0.21	0.040*	0.55	0.94	0.42
Root	0.27	0.0029**	0.24	1.00	0.90	0.98	0.93
Stem	<0.001***	<0.001***	0.91	0.11	0.13	0.29	0.88
Leaf	0.0005**	<0.001***	<0.001***	0.19	0.21	0.14	0.92
Shatter	<0.001***	0.0052**	<0.001***	0.62	0.13	0.26	0.57
Seedcotton	<0.001***	<0.001***	<0.001***	0.013*	0.0065**	0.11	0.53
Harvested biomass	<0.001***	<0.001***	<0.001***	0.21	0.0046**	0.012*	0.91

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
† CO_2 levels (ambient and double-ambient).
‡ Square removal treatments (SR0, SR1, and SR2).
§ Investigation years (2004 and 2005).

boll maturity will be found with a rising atmospheric CO_2 concentration.

Plant Yield and Biomass

In Table 3, the effects of CO_2 concentration significantly influenced every item investigated ($P < 0.001$) except for plant root dry weight. Significant effects of plant square removal treatment were observed in plant root ($P < 0.01$) and shatter ($P < 0.01$) dry weight and other investigation items ($P < 0.001$). The effects of investigation year were significantly influenced ($P < 0.001$) in plant leaf, shatter, seedcotton yield, and harvested biomass. And the interaction between CO_2 concentration × investigation year had a significant effect on seedcotton yield ($P < 0.01$) and harvested biomass ($P < 0.01$). The interaction between CO_2 concentration × square removal treatment had a significant effect on seedcotton yield ($P < 0.01$). However, significant effects were only observed between interactions of square removal treatment × investigation year ($P < 0.05$) on plant harvested biomass.

From Table 4, significant differences ($P < 0.01$) were observed among three treatments in plant root dry weight under double-ambient CO_2 in 2005. Significant differences ($P < 0.01$) in plant stem dry weight were also found among three removal treatments under elevated CO_2 in both years. The plant leaf dry weights were significantly higher ($P < 0.01$) among three treatments under elevated CO_2 in both years. The shatter dry weight were significantly higher ($P < 0.01$) among three removal treatments under elevated CO_2 in both years. Significant differences in seedcotton yield were observed under elevated CO_2 ($P < 0.05$) and ambient CO_2 ($P < 0.01$) in 2005 and both CO_2 treatments ($P < 0.01$) in 2004. Significant differences in plant harvested biomass were observed under ambient CO_2 ($P < 0.05$) and elevated CO_2 ($P < 0.01$) in 2004 and elevated CO_2 ($P < 0.01$) in 2005.

From the experiment, seedcotton yield per plant increased in 100% square removal for the 1-wk treatment (SR1) compared with the no floral bud removal treatment (SR0) by 6.8% in 2004 and 3.0% in 2005 under elevated CO_2, showing that cotton can compensate for the early-season square removal under elevated CO_2. However, with the removal time of early-season floral buds extension, the seedcotton yield decreased with 100% square removal for the 2-wk treatment (SR2) compared with 100% square removal for SR1 by 6.9% in 2004 and 2.8% in 2005 under elevated CO_2, indicating that the compensatory capacity of cotton may depend on time-dependent compensation under elevated CO_2.

Table 4. Plant root, stem, leaf, shatter, seedcotton, harvested biomass dry weight, and boll maturity (Mean ± SE) of cotton treated by manual removal of square buds in ambient and elevated CO_2 in 2004 and 2005.†

		Ambient CO_2			Elevated CO_2		
Year	Measured indexes	SR0	SR1	SR2	SR0	SR1	SR2
2004	Boll maturity, %	84.3 ± 1.2 a, B	80.7 ± 1.4 a, B	75.5 ± 1.1 b, B	89.1 ± 0.4 a, A	88.2 ± 0.8 a, A	85.2 ± 0.8 b, A
	Root, g	15.7 ± 0.9 a, A	17.5 ± 0.3 a, A	17.4 ± 1.5 a, A	16.4 ± 0.7 a, A	17.8 ± 0.2 a, A	17.8 ± 0.5 a, A
	Stem, g	45.7 ± 0.9 a, A	47.6 ± 0.6 a, B	48.0 ± 0.5 a, B	47.5 ± 0.3 b, A	51.2 ± 0.9 a, A	51.5 ± 0.3 a, A
	Leaf, g	10.2 ± 0.4 a, A	10.3 ± 0.2 a, B	11.1 ± 0.2 a, B	10.8 ± 0.2 b, A	11.5 ± 0.2 a, A	12.1 ± 0.2 a, A
	Shatter, g	8.45 ± 0.33 a, A	8.95 ± 0.06 a, B	8.59 ± 0.19 a, B	9.22 ± 0.07 b, A	9.68 ± 0.13 a, A	9.36 ± 0.03 b, A
	Seedcotton, g	30.5 ± 0.2 b, B	33.8 ± 0.1 a, B	30.8 ± 0.3 b, B	33.6 ± 0.2 b, A	35.8 ± 0.3 a, A	33.5 ± 0.4 b, A
	Harvested biomass, g	125 ± 0 b, B	133 ± 1 a, B	130 ± 2 a, B	133 ± 1 b, A	141 ± 1 a, A	139 ± 1 a, A
2005	Boll maturity, %	83.5 ± 1.7 a, B	81.1 ± 1.8 a, B	75.5 ± 1.7 b, B	89.0 ± 1.7 a, A	87.0 ± 1.7 a, A	83.6 ± 1.7 b, A
	Root, g	15.5 ± 1.0 a, A	17.0 ± 0.2 a, A	16.8 ± 0.3 a, A	15.7 ± 0.4 b, A	17.5 ± 0.2 a, A	17.1 ± 0.1 a, A
	Stem, g	47.3 ± 0.5 a, B	48.6 ± 0.1 a, B	48.0 ± 0.5 a, B	51.1 ± 0.2 b, A	52.2 ± 0.4 a, A	51.2 ± 0.2 b, A
	Leaf, g	10.9 ± 0.2 a, A	11.7 ± 0.3 a, B	12.0 ± 0.6 a, A	11.2 ± 0.1 b, A	12.8 ± 0.2 a, A	12.4 ± 0.3 a, A
	Shatter, g	9.8 ± 0.6 a, A	10.4 ± 0.3 a, B	10.7 ± 0.1 a, B	11.0 ± 0.1 b, A	11.9 ± 0.1 a, A	11.5 ± 0.1 a, A
	Seedcotton, g	31.2 ± 0.2 b, B	34.1 ± 0.6 a, B	31.4 ± 0.2 b, B	35.5 ± 0.2 b, A	36.6 ± 0.2 a, A	35.6 ± 0.3 b, A
	Harvested biomass, g	132 ± 1 b, B	135 ± 0 a, B	133 ± 1 ab, B	142 ± 1 b, A	146 ± 1 a, A	146 ± 0 a, A

† SR0, no floral bud removal treatment; SR1, 100% floral bud removal for 1 wk treatment; SR2, 100% floral bud removal for 2 wk treatment. Within a row, means indicated by different lowercase letters are significantly different at same CO_2 level (LSD test, $P < 0.05$, df = 2, 6); means indicated by different uppercase letters are significantly different in double-ambient CO_2 compared with ambient CO_2 (LSD test, $P < 0.05$, df = 1, 4).

Klatter and Wallach (1982) placed causal mechanisms of compensation for early-season losses into two categories, abiotic (e.g., moisture and nutrient deficiency, temperature) and biotic (arthropods and pathogens) stresses. Both could result in physiological shedding, simultaneously result in additional numbers of bolls and increase boll weight owing to the compensation physiology of cotton plants (Kennedy et al., 1986; Terry, 1992; Brook et al., 1992a, 1992b). Sadras (1995) hypothesized that over- and undercompensation would be more likely to occur in low- and high-yielding situations, respectively. Presumably, the cotton plant can more easily compensate for the early loss of squares than for loss at a later time, as the plant has invested less time or energy into production of the former under elevated CO_2. Moreover, later square removal represents a much larger loss of investment for the plant and, in many cotton-producing environments, leaves little time for the plant to compensate for this injury under elevated CO_2. The cotton growth and production parameters following early-season square bud removal in these three removal treatments were significantly higher under elevated CO_2 than those under ambient CO_2, considering that the plant has the active compensatory capacity under elevated CO_2.

Also, from the present study, seedcotton yield per plant was significantly higher in the 100% square removal for the 1-wk treatment (SR1) than in the no floral bud removal treatment (SR0) regardless of CO_2 levels, and a significant interaction between cotton square removal treatments (SR0 and SR1) and CO_2 levels (ambient and elevated) was simultaneously observed. However, there was no interaction between cotton square removal treatments (SR0 and SR2) and CO_2 levels (ambient and elevated). This indicates that early time-dependent square removal (100% square removal for the 1-wk treatment) has the most significant effect on plant compensation for fruit loss and results in increased seedcotton yield under two CO_2 levels. Nevertheless, medium or later time-dependent floral bud injury (100% square removal for 2-wk treatment) has insufficient compensatory capacity to increase seedcotton yield under two CO_2 levels. Although the interaction between cotton square removal treatments (SR0, SR1, and SR2) and CO_2 levels can significantly affect the seedcotton yield per plant, the compensatory capacity of cotton yield may depend on the square bud removal time under elevated CO_2. It is suspected that the compensatory capacity of seedcotton yield may decrease along with the square bud removal time beyond 100% square removal for the 2-wk treatment under elevated CO_2.

CONCLUSIONS

In this study, cotton harvested biomass per plant increased in 100% square removal for the 1-wk treatment (SR1) compared with no floral bud removal treatment (SR0) in 2004 and 2005 under elevated CO_2, showing that cotton can compensate for the early-season square removal under elevated CO_2. However, with the removal time of early-season floral bud extension, cotton harvested biomass decreased with 100% square removal for the 2-wk treatment (SR2) compared with 100% square removal for SR1 in 2004 and 2005 under elevated CO_2, which indicates the harvested biomass compensatory capacity of cotton may rely on time-dependent compensation under elevated CO_2.

Our results showed cotton can tolerate modest levels of early-season floral bud injury without seedcotton yield reduction under elevated CO_2, which should be considered to reflect cotton bollworm damage or behavior of pest populations. Cotton has the ability to compensate for early-season floral bud removal losses by cotton bollworm damage under elevated CO_2, which is an optimal point of early-season pest management that allows some flexibility in early-season insect management without increasing risk to producers under elevated CO_2 atmosphere. Results from these studies provide a profile for developing strategies for future management of cotton ecosystems. Establishing pest management approaches based on early-season floral bud removal treatments under elevated CO_2 atmosphere could reduce cotton bollworm resistance, insecticide costs, and environmental contamination in Northern China.

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