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No effects of elevated CO_2 on the population relationship between cotton bollworm, *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae), and its parasitoid, *Microplitis mediator* Haliday (Hymenoptera: Braconidae)

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ABSTRACT

Estimating the population consumption of an insect population under elevated CO_2 is an important step in understanding the effects of elevated CO_2 on herbivore–crop interactions. Two successive generations of cotton bollworm, *Helicoverpa armigera* Hübner, were reared on milky grains of spring wheat (*Triticum aestivum* L.) grown in open-top chambers under increased carbon dioxide (CO_2) concentration. *H. armigera* development, wheat consumption, and parasitism by *Microplitis mediator* Haliday were examined, as were the effects of elevated CO_2 on the wheat itself. We experimentally tested the hypotheses that, by quantifying the population consumption of *H. armigera*, elevated CO_2 enhanced the pest-control ability of *M. mediator* again *H. armigera*. Decreases in protein, total amino acid, and nitrogen (N) content were noted in spring wheat when grown in an elevated-CO_2 environment, as were increases in total non-structure carbohydrates (TNCs) and in the ratio of TNC to N. In the first generation of *H. armigera* reared under elevated CO_2, no significant changes were observed in population generation time (T) or in the intrinsic rate of increase (r_m) between CO_2 treatments. However, in the second treatment generation, longer generation time resulted in a lower r_m value. Elevated-CO_2 levels caused no significant changes in the *H. armigera* population's total wheat consumption. The rates of parasitism, cocooning, and emergence by *M. mediator* were also unaffected, as were its average weight and adult lifespan. As no significant changes in wheat consumption by *H. armigera* or in the parasitic rate of *M. mediator* were revealed, the results indicate that the population relationship between *H. armigera* and *M. mediator* is unlikely to vary due to future elevated atmospheric CO_2 concentrations.

1. Introduction

The global atmospheric concentration of CO_2 has increased from a pre-industrial value of about 280–379 ppm in 2005, with an annual rate of increase of 1.9 ppm for the last 10 years (IPCC, 2007). Levels of atmospheric CO_2 are anticipated to double by the end of the 21st century (Houghton et al., 2001; Veteli et al., 2002).

Elevated-CO_2 levels directly impact plant physiology. Among these effects is an increase in photosynthetic rate which alters growth, aboveground biomass, yield, carbon-to-nitrogen ratio (C:N), and the efficiency of water use in most plant species. Reduced N concentrations impact the production of plant nutrients and secondary metabolites, especially in C_3 plants (Cotrufo et al., 1998; Pritchard et al., 1999; Agrell et al., 2000; Hartley et al., 2000). Decreased foliar N concentration reduces leaf nutritional quality, diminishing the value of foliage as a resource for insect herbivores (Mattson, 1980; Johns and Hugher, 2002).

Most leaf-chewing insects exhibit compensatory increases in food consumption and/or development times (thereby increasing the herbivores' exposure to predators, parasitoids, and pathogens), reduced growth, survival rates, population density and fitness in elevated-CO_2 environments, presumably due to the increased foliar C:N ratios of host plants (Scriber, 1982; Ayres, 1993; Masters et al., 1998; Coviella et al., 2002). The grasshoppers (Johnson and Lincoln, 1990, 1991) and caterpillar larvae (Lindroth et al., 1993, 1995), for example, generally consume more leaf area when they feed upon plants grown in elevated-CO_2 environments. Thus, elevated-CO_2 conditions may amplify the crop damage caused by pests (Lincoln et al., 1984). Most published studies describe plant

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consumption by herbivorous insects "per individual" by developmental rate, by mortality, and by fecundity (Bezemer and Jones, 1998a; Chen et al., 2007). Few experiments (except for Wu et al. (2006)) have been carried out at the population levels, making it difficult to estimate an insect population's potential consumption of a crop growing in an elevated-CO_2 system. Wu et al. (2006) demonstrates that elevated CO_2 adversely affects grain quality, increasing the consumption per individual larva of *H. armigera*. However, in the Wu et al. (2006) study, the potential population consumption of cotton bollworm under elevated CO_2 was reduced in the two latter generations, due to increased mortality and reduced fecundity within the population (Wu et al., 2006). These results suggest that the net damage caused by cotton bollworm on wheat will be reduced under elevated CO_2. However, quantifying consumption at a population levels to assess the impact of elevated CO_2 on future agro-ecosystems is a major task.

Altered plant nutrition under elevated-CO_2 conditions may influence the third trophic levels (host plant – herbivorous insect – insect predator) through "bottom up" effects. Patterns of chemical allocation not only regulate the interactions between herbivorous insects and their host plants, but potentially also those between herbivores and their natural enemies (Ohgushi, 1995; Coley, 1998; Bezemer et al., 1998b; Stiling et al., 1999). Coll and Hughes (2008) suggested that the omnivorous predator *Oechalia schellenbergii* may impose greater pressure on its prey, *H. armigera*, at elevated-CO_2 levels because the prey became more vulnerable to predation under such conditions; possibly due to their consumption of lower-quality foliage during growth in an environment with elevated CO_2. Stacey and Fellows (2002), however, found that neither body size or food consumption or prey choice or prey number of ladybird *Hippodamia convergens* nor body size of parasitoid *Diaeretiella rapae* changed under elevated-CO_2 levels. Because of the complexity involved in discerning the effects of rising CO_2 on the third trophic levels by studying three levels food chains, further studies on these higher trophic levels are needed (Bezemer et al., 1998b; Stacey and Fellows, 2002; Hoover and Newman, 2004). Moreover, as natural enemies are considered to be one of the most efficient methods of pest control, their reactions to elevated environmental CO_2 levels deserve particular scrutiny (Chen et al., 2004).

In this study, we examine the effects of elevated-CO_2 levels on the three levels food chain between spring wheat, *H. armigera* and *M. mediator*. Spring wheat (*Triticum aestivum* L.), a C_3 plant, seems especially sensitive to elevated-CO_2 levels. Elevated CO_2 can increase growth, with the grain yield observed to increase by 35%, when the ambient-CO_2 levels are doubled (Cure and Aycock, 1986; Amthor, 2001; Chen et al., 2004).

One of the common pests affecting spring wheat is cotton bollworm *Helicoverpa armigera* Hübner, a cosmopolitan phytophagous chewing insect (Zalucki et al., 1986; Zalucki and Furlong, 2005). In North China, the first generation of cotton bollworm damages wheat, and alters their host between corn and cotton in their successive generation (Ge et al., 2003). The endoparasitoid larvae of wasps *Microplitis mediator* Haliday parasitize the second instar larvae of *H. armigera* (Wang et al., 1984; Liu et al., 2004). *M. mediator* is widely used as a biocontrol agent against *H. armigera* in the wheat agro-ecosystem (Li, 2005). However, the effects of *H. armigera* on spring wheat in the presence of both *M. mediator* and elevated carbon dioxide levels are currently unclear.

In this study, *H. armigera* were reared using milky grains of spring wheat grown under elevated-CO_2 conditions as a food source. The growth, development, and consumption of two successive generations of *H. armigera* were examined, as well as their parasitism by two successive generations of *M. mediator*. Our specific objectives were to quantify: (1) the parasitism rates of two successive generations of *M. mediator* on an *H. armigera* population reared on a food source grown under elevated CO_2, (2) the development, survival rate, and population parameters of two successive generations of *H. armigera* in an elevated-CO_2 environment when parasitized by *M. mediator*, and when unparasitized, and (3) the population's total consumption of two successive generations of *H. armigera* under the aforementioned conditions.

2. Materials and methods

2.1. CO_2 concentration

2.1.1. Open-top chamber

This experiment was carried out using six octagonal open-top chambers (OTC), each 4.2 m in diameter, located at the Observation Station of the global change biology group, Institute of Zoology, Chinese Academy of Science (CAS) in Xiaotangshan County, Beijing, China (40°11′N, 116°24′E). The atmospheric CO_2 concentration treatments were: (1) current ambient-CO_2 levels (375 μl/L) ("ambient CO_2") and (2) double the current ambient-CO_2 levels (750 μl/L) ("elevated CO_2") (Chen et al., 2004). Three OTCs were used for each CO_2 concentration treatment. During the period from seedling emergence to harvesting for wheat, CO_2 concentrations were monitored continuously and were adjusted using an infrared CO_2 analyzer (Ventostat 8102, Telaire Company, USA) once every 20 min to maintain the assigned CO_2 concentrations. The automatic-control system for adjusting the levels of CO_2 concentration as well as specifications for the open-top chambers is detailed in Chen et al. (2005a, 2005b, 2005c).

2.1.2. Closed-dynamics CO_2 chamber

Insects were reared in a growth chamber (HPG280H; Orient Electronic, Haerbin, China). Growth chamber conditions were maintained at 25 ± 1 °C, 60–70% relative humidity, a photoperiodic ratio of 14:10 (hours of light:hours of dark), and active radiation measuring 9000 lux (supplied by 1260 W fluorescent lamps in each chamber). Two atmospheric CO_2 concentrations consisting of the current ambient-CO_2 levels (375 μl/L) and double the current ambient-CO_2 levels (750 μl/L), were maintained to match the OTCs used for wheat growth. Three chambers were used for each CO_2 treatment. As previously mentioned, CO_2 concentrations were automatically monitored and adjusted with an infrared CO_2 analyzer (Ventostat 8102; Telaire, Goleta, CA, USA). A detailed explanation of the methodology employed by the automatic-control system for maintaining and adjusting the CO_2 concentrations is described in Chen and Ge (2004).

2.2. Wheat variety and growth conditions

Spring wheat (Longfu174379 variety) seeds were sown on 10 March 2007 in plastic pots (height: 35 cm, diameter: 45 cm), in the six open-top chambers previously mentioned with a seeding rate of 150 seeds per pot. 35 pots were placed in each OTC. Pot placement was re-randomized in each OTC weekly.

On 19 April 2007, the crop was thinned to 100 plants per pot. Pure CO_2 was mixed with ambient air and supplied to each chamber throughout wheat development. The crop was irrigated sufficiently every other day using tap water. During the milky-grain stage of spring wheat, ears and grains were harvested from all six OTCs, and then refrigerated at −20 °C until supplied to *H. armigera* as food.

2.3. Insect stocks

2.3.1. H. armigera

Egg masses were obtained from a laboratory colony maintained by the Insect Physiology Laboratory, Institute of Zoology at CAS,

and reared in a growth chamber (HPG280H, Orient Electronic Ltd. Co., Haerbin City, China) using wheat milky grains as a food source. The temperature in each chamber was maintained at 25 ± 1 °C, the relative humidity at 70 ± 10% and the photoperiod/scotoperiod ratio at 14:10 (hours of light:hours of dark).

2.3.2. M. mediator

Specimens were obtained from Chinese Agricultural University, and were reared in a growth chamber (HPG280H, Orient Electronic Ltd. Co., Haerbin City, China) using 15% hydromel (a fermentation of honey) as a food source. Growth chamber conditions were maintained exactly as above.

2.4. Insect feeding

A split-plot design was adopted for this experiment. In both of the two treatments, *H. armigera* was exposed to *M. mediator*. In Treatment #1, the carbon dioxide levels was set to the normal ambient concentration (375 μl/L) whereas in Treatment #2, the carbon dioxide levels was set to double the normal ambient carbon dioxide concentration (750 μl/L). In each treatment, *H. armigera* were reared in growth chambers as described above, and fed wheat grown in the concentration of carbon dioxide corresponding to their treatment levels (ambient or elevated). Feedings occurred daily, with unconsumed wheat grains collected each day and oven dried at 80 °C for 72 h. Individual consumption (measured in grams per larva) was determined at each developmental stage and noted in detail. Three replicates of thirty individuals each yielded a total of 90 insects studied for each treatment.

2.5. Inoculation with M. mediator

Thirty *H. armigera* were entirely reared with milky grains of spring wheat in Petri dishes (diameter: 10 cm, height: 5 cm). At the second instar stage, when 80.5% of *H. armigera* larvae parasitization by *M. mediator* has been reported to occur (Liu et al., 2004), one pair of *M. mediator* (a male and a female, both newly emerged) were introduced into each Petri dish. At the third instar, *H. armigera* were transferred to individual Petri dishes to prevent cannibalism. Measurements including molting and mortality were recorded separately for parasitized and unparasitized larvae.

2.5.1. Parasitized H. armigera

For parasitized *H. armigera*, larval lifespan was calculated as the period from hatching until death. Observations of parasitized larvae in each CO_2 treatment were recorded daily. *M. mediator* were retrieved from parasitized larvae, counted and weighed; adults were sexed upon emergence. The ratios of adult emergence to non-emergence and females to males were noted. Newly emerged wasps were placed in cages, 15% hydromel was provided as a food source. Mated individuals were then housed in pairs (one female, one male) for observation of adult longevity.

2.5.2. Unparasitized H. armigera

For unparasitized *H. armigera*, larval lifespan was calculated as the period from hatching until pupation. The rate of pupation was recorded and adult moths were sexed upon emergence, with the ratios of adult emergence to non-emergence and females to males noted. Newly emerged *H. armigera* moths were placed in cages (length: 30 cm, width: 30 cm, height: 40 cm) for 3 days, then paired, one female with one male. Females were allowed to oviposit in plastic cups (diameter: 9 cm, height: 15 cm) covered with degreased cotton yarn netting. On a daily basis, eggs were counted, cotton yarn covers were replaced, and the number of hatched eggs per female was recorded.

2.5.3. Second generation

Thirty insects (one replicate) were reared in a Petri dish (diameter: 10 cm, height: 5 cm) with three replications per treatment for a total of 90 insects observed for each treatment. Following *H. armigera* first instar exuviation, one pair of first-generation *M. mediator* (one male and one female, both newly emerged) were inoculated in each Petri dish with 30 *H. armigera* larvae in the second instar. *H. armigera* third instars were transferred to individual Petri dishes to prevent cannibalism. The life history parameters, consumption, and parasitism by *M. mediator* were measured for second-generation cotton bollworms as they for the first generation.

2.6. Chemical composition assays of wheat ears

Ears of spring wheat were collected at harvest and transferred to a −20 °C refrigerator for later chemical composition assays. Thirty ears of spring wheat were selected for each of the two CO_2 treatments, on three separate occasions, making a total of 90 ears. Water content as a proportion of fresh weight was calculated after wheat ears had dried at 80 °C for 72 h. Total non-structural carbohydrates (TNCs), protein, and total amino acid were measured according to the reagent protocol (Nanjing Jiancheng Ltd. Co., Nanjing, Jiangsu Province, China). N content was assayed using the Kjeltec N analysis (Foss automated Kjeltec™ instruments, Model 2100).

2.7. Population parameter estimation

Net reproduction (R_0), mean generation time (T), and intrinsic rate of increase (r_m) were analyzed based on the age-stage, two-sex life table model developed by Chi and Liu (1985) and Chi (1988). Means and standard errors of population parameters were estimated using the jackknife method (Sokal and Rohlf, 1995). A computer program, TWOSEX-MSChart (Chi, 2004), was developed for data analysis and jackknife estimation in Visual BASIC for the Windows operating system. This program is available at: http://140.120.197.173/Ecology/prod02.htm (Chung Hsing University) and http://nhsbig.inhs.uiuc.edu/wes/chi.html (Illinois Natural History Survey).

2.8. Data analysis

One-way analysis of variance (ANOVA) tests (SAS 6.12, SAS Institute Inc. USA, 1996) were used to analyze the effects of elevated CO_2 on the chemical compositions of spring wheat ears. The differences between means were compared with the least significant difference (LSD) test.

Population indices (mortality, fecundity, net reproductive rate (R_0), mean generation time (T), intrinsic rate of increase (r_m)), larval lifespan, pupal weight, survival rate, consumption, and the number of eggs laid per female were factors analyzed by ANOVA with CO_2 levels as the main factor and cotton bollworm generation as a sub-factor deployed in a split-plot design. The differences between means were determined using an LSD test. The data for parasitism rate and cocoon rate of *M. mediator*, as well as the emergence rate, weight, and adult-longevity of *M. mediator* were also analyzed following the method above.

3. Results

3.1. Wheat ear quality

N Content, protein, and total amino acids decreased 2.6%, 17.0% and 17.3% respectively, but TNC and TNC:N increased 27.9% and

Table 1
The chemical composition (mean ± SE) of wheat grains grown in ambient and elevated CO_2.

Measured indices	CO_2 levels		*F* value	*P* value
	Ambient	Elevated		
Water content (%)	59.10 ± 1.07 a	58.72 ± 1.23a	2.988	0.168
Nitrogen content (mg/g)	11.97 ± 0.11 a	11.66 ± 0.03b	7.89	0.048
TNCs (mg/g)	132.01 ± 1.48 b	168.89 ± 8.87a	16.79	0.015
Ratio of TNCs:nitrogen	11.03 ± 0.04 b	14.49 ± 0.79 a	19.20	0.012
Protein (g/L)	1.59 ± 0.01 a	1.32 ± 0.04 b	54.98	0.002
Total amino acid (μmol/ml)	400.69 ± 2.13 a	331.18 ± 3.86b	747.72	<0.001

Means within a row indicated by different letters are significantly different (LSD test, $P < 0.05$).

31.4% respectively, in grains of wheat plants grown under elevated CO_2 relative to ones growing under ambient conditions (Table 1).

3.2. Parasitism rate

As seen in Table 2, 24 ± 6% and 22 ± 6% of the first generation of *H. armigera* were parasitized by *M. mediator* in the ambient- and elevated-CO_2 treatments, respectively. In the second generation of *H. armigera*, values of 25 ± 6% and 27 ± 7% were found for the ambient- and elevated-CO_2 treatments, respectively. No significant differences related to the experimental conditions (CO_2 levels) were found in the parasitism rate, cocoon rate, emergence rate, wasp weight, or in the adult lifespan of *M. mediator* ($P > 0.05$, Table 2). However, when results were compared for *M. mediator* parasitizing first-generation *H. armigera* as opposed to second generation, significant increases were observed in cocoon rate (DF = (2, 23), $F = 4.930$, $P = 0.017$), emergence rate (DF = (2, 22), $F = 9.736$, $P = 0.009$).

3.3. Developmental durations

The factors of CO_2 concentration (DF = (1, 241), $F = 66.652$, $P < 0.001$), parasitism (DF = (1, 241), $F = 745.994$, $P < 0.001$) and generations (DF = (1, 241), $F = 5.789$, $P < 0.001$) influenced the larval stage duration of *H. armigera* (Table 3). Longer[0] developmental durations were observed for some larval stages of unparasitized cotton bollworms in both generations under elevated CO_2 (DF = (1, 163), $F = 37.731$, $P < 0.001$). In the first generation, longer developmental durations were observed in all stages except the first instar (DF = (1, 137), $F = 2.845$, $P = 0.094$) and sixth instar (DF = (1, 78), $F = 0.831$, $P = 0.365$). However, in the second generation, only the developmental duration of sixth instar increased 31.5% (Table 4).

In the first generation, after parasitization, the developmental duration of second instar and third instar increased 27.3% and 41.5% respectively, but the developmental duration of fourth instar decreased 16.8% when rearing under elevated-CO_2 levels relative to those rearing under ambient conditions levels (Table 4). Under elevated CO_2, in both generations, longer developmental times for the third instar (DF = (1, 318), $F = 24.75$, $P < 0.001$), fourth instar (DF = (1, 298), $F = 2145.6$, $P < 0.001$) and total larvae stage (DF = (1, 206), $F = 9.39$, $P = 0.003$) were observed in parasitized cotton bollworm larvae than were observed in unparasitized cotton bollworm larvae (Table 4).

3.4. Individual consumption

Among parasitized insects, neither generation showed any significant difference in individual consumption of wheat ears grown in an elevated-CO_2 environment (DF = (1, 16), $F = 1.7$, $P = 0.211$). Unparasitized first-generation larvae also showed no significant difference in individual consumption ($P > 0.05$), with the exception of the third instar (DF = (1, 4), $F = 81.611$, $P = 0.001$) (Table 5). Unparasitized second-generation larvae also showed a significant difference in the third instar (DF = (1, 4), $F = 84.472$, $P = 0.001$), with increased consumption. Regardless of generations and CO_2 levels, being parasitized decreased individual consumption of cotton bollworm larvae (DF = (1, 16), $F = 316.49$, $P < 0.001$).

Table 2
Parasitism rate, cocoon rate, emergency rate, wasp rate, wasp weight and adult lifespan (mean ± SE) of *M. mediator* parasitizing two successive generations of *H. armigera* fed with wheat grains grown in ambient and elevated CO_2.

Gen	Life history parameter	CO_2 levels		*F*	*P*
		Ambient	Elevated		
Generation 1	Parasitism rate (%)	0.24 ± 0.06 a, A	0.22 ± 0.06 a, A	0.06	0.815
	Cocoon rate (%)	0.84 ± 0.12 a, B	0.96 ± 0.01 a, B	0.68	0.446
	Emergency rate (%)	0.65 ± 0.16 a, B	0.72 ± 0.17 a, B	0.09	0.779
	Wasp weight (g)	0.0030 ± 0.0010 a, A	0.0020 ± 0.0005 a, A	1.50	0.228
	Adult lifespan (days)	5.19 ± 0.44 a, A	4.39 ± 0.31 a, A	2.07	0.159
Generation 2	Parasitism rate (%)	0.25 ± 0.06 a, A	0.27 ± 0.07 a, A	0.10	0.757
	Cocoon rate (%)	1.00 ± 0.01 a, A	0.99 ± 0.03 a, A	0.82	0.389
	Emergency rate (%)	0.92 ± 0.05 a, A	0.88 ± 0.06 a, A	0.23	0.642
	Wasp weight (g)	0.0020 ± 0.0009 a, B	0.0020 ± 0.0003 a, A	0.61	0.437
	Adult lifespan (days)	5.36 ± 0.37 a, A	4.76 ± 0.34 a, A	1.41	0.240

Means within a row indicated by different lowercase letters are different; means of each life history parameter across two generations within a column indicated by different uppercase letters are different (LSD test, $P < 0.05$).

Table 3
P value from ANOVAs for the effect of CO_2 level, generation, and parasitism on *H. armigera* and *M. mediator*.

Parameters	CO_2	Gen	Para	CO_2 × Gen	CO_2 × Para	Gen × Para	CO_2 × Gen × Para
Parasitism rate	0.917	0.861	–	0.692	–	–	–
Larval durations	0.000	0.000	0.000	0.070	0.001	0.002	0.026
Mortality	0.255	0.202	–	0.833	–	–	–
Mean generation time (*T*)	0.001	0.404	–	0.007	–	–	–
Net R_0	0.081	0.340		0.472			
Fecundity	0.317	0.365	–	0.800	–	–	–
Intrinsic rate of increase (r_m)	0.020	0.705	–	0.487	–	–	–
Individual consumption of larval stage	0.211	0.002	0.000	0.101	0.118	0.004	0.086

Table 4
Developmental time (in days) (mean ± SE) of two successive generations of *H. armigera* larvae (both parasitized and unparasitized) fed with wheat grains grown in ambient and elevated CO_2 with *M. mediator* present.

Developmental time	Unparasitized larvae (days)		Parasitized larvae (days)	
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2
Generation 1				
First instar	2.27 ± 0.45 a b, B	2.41 ± 0.50 a, B	2.35 ± 0.49 a b, A	2.14 ± 0.36 b, B
Second instar	1.90 ± 0.30 b, B	2.03 ± 0.18 a, B	1.65 ± 0.49 c, B	2.10 ± 0.30 a, B
Third instar	2.13 ± 0.39 c, A	2.66 ± 0.69 b, A	2.29 ± 0.77 c, A	3.24 ± 0.62 a, A
Fourth instar	3.33 ± 0.13 d, A	4.34 ± 1.68 c, A	13.7 ± 2.12 a, A	11.4 ± 3.50 b, B
Fifth instar	3.79 ± 1.26 b, A	5.35 ± 1.58 a, A	–	–
Sixth instar	4.80 ± 1.13 a, B	4.76 ± 0.91 a, B	–	–
Larval stage	18.5 ± 2.44 c, A	20.8 ± 1.92 b, A	22.9 ± 1.85 a, B	21.1 ± 3.37 a b, B
Generation 2				
First instar	2.49 ± 0.50 a, A	2.62 ± 0.49 a, A	2.36 ± 0.49 a, A	2.50 ± 0.51 a, A
Second instar	2.46 ± 0.50 a, A	2.38 ± 0.49 a, A	2.59 ± 0.50 a, A	2.50 ± 0.51 a, A
Third instar	2.21 ± 0.45 a b, A	2.08 ± 0.27 b, B	2.41 ± 0.73 a, A	2.33 ± 0.48 a, B
Fourth instar	2.65 ± 0.67 b, B	2.94 ± 0.97 b, B	13.9 ± 2.14 a, A	15.2 ± 2.43 a, A
Fifth instar	3.37 ± 1.25 a, A	3.54 ± 1.95 a, B	–	–
Sixth instar	5.93 ± 1.37 b, A	7.80 ± 1.01 a, A	–	–
Larval stage	19.2 ± 2.24 c, A	21.2 ± 1.70 b, A	24.3 ± 1.96 a, A	25.5 ± 1.97 a, A

Means within a row indicated by different lowercase letters are different; means of each developmental stage parameter across two generations within a column indicated by different uppercase letters are different with *M. mediator* present (LSD test, $P < 0.05$).

Table 5
Stage-specific individual consumption (in grams per larva) (mean ± SE) of *H. armigera* larvae (both parasitized and parasitized) for two successive generations, fed with wheat grains grown in ambient and elevated CO_2 in the presence of *M. mediator*.

Sampling date	Unparasitized (days)		Parasitized (days)	
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2
Generation 1				
First instar	–	–	–	–
Second instar	–	–	–	–
Third instar	0.036 ± 0.002 a, A	0.017 ± 0.0002 b, B	0.003 ± 0.001 c, A	0.002 ± 0.001 c, A
Fourth instar	0.067 ± 0.005 a, A	0.054 ± 0.002 a, A	0.008 ± 0.008 b, A	0.004 ± 0.002 b, A
Fifth instar	0.211 ± 0.041 a, A	0.159 ± 0.016 a, B	–	–
Sixth instar	0.029 ± 0.015 a, A	0.105 ± 0.009 a, B	–	–
Larval stage	0.308 ± 0.06 a, A	0.296 ± 0.01 a, B	0.011 ± 0.009 b, A	0.006 ± 0.002 b, A
Generation 2				
First instar	–	–	–	–
Second instar	–	–	–	–
Third instar	0.028 ± 0.0002 b, B	0.056 ± 0.003 a, A	0.01 ± 0.005 c, A	0.002 ± 0.001 c, A
Fourth instar	0.061 ± 0.008 a, A	0.071 ± 0.007 a, A	0.007 ± 0.002 b, A	0.006 ± 0.003 b, A
Fifth instar	0.251 ± 0.023 a, A	0.304 ± 0.038 a, A	–	–
Sixth instar	0.111 ± 0.028 a, A	0.233 ± 0.015 a, A	–	–
Larval stage	0.379 ± 0.021 b, A	0.512 ± 0.049 a, A	0.017 ± 0.007 c, A	0.008 ± 0.004 c, A

Means within a row indicated by different lowercase letters are different; means of individual consumption of each developmental stage across two generations within a column indicated by different uppercase letters are different (LSD test, $P < 0.05$).

3.5. Population parameters and population consumption

3.5.1. Population parameters

For both generations of *H. armigera* exposed to *M. mediator*, CO_2 concentration influenced population mean generation time (T) (DF = (1, 274), $F = 20.023$, $P < 0.001$) and intrinsic rate of increase (r_m) (DF = (1, 274), $F = 5.44$, $P = 0.02$) (Table 3). However, exposed to *M. mediator*, no significant differences were observed in larvae mortality (DF = (1, 8), $F = 1.93$, $P = 0.202$), fecundity per female (DF = (1, 39), $F = 0.839$, $P = 0.365$), net R_0 (DF = (1, 38), $F = 0.933$, $P = 0.34$), mean generation time (T) (DF = (1, 274), $F = 0.697$, $P = 0.404$), or intrinsic rate of increase (r_m) (DF = (1, 274), $F = 0.144$, $P = 0.705$) in second generation of *H. armigera*, compared with the first generation. CO_2 concentration had no significant effect on larvae mortality (DF = (1, 8), $F = 1.5$, $P = 0.255$), fecundity per female (DF = (1, 39), $F = 1.03$, $P = 0.317$), or on the net R_0 value (DF = (1, 38), $F = 3.222$, $P = 0.081$) in either generation of *H. armigera* population exposed to *M. mediator*. Generation time (T) increased 13.4% and r_m value decreased 16.7% for the second-generation *H. armigera* population fed wheat grown in elevated CO_2, compared to those fed spring wheat grown in ambient CO_2 (Table 6).

3.5.2. Population consumption

Consumption by the parasitized and unparasitized members of the *H. armigera* population was calculated based upon individual consumption and the number of individuals in each specific developmental stage (Table 7). For the treatment of unparasitized *H. armigera* population members, third instar of population's total consumption of *H. armigera* increased 99.4% for the second generation and sixth instar increased 329% for the first generation and 87% for the second generation under elevated-CO_2 levels, compared with those under ambient levels (Table 7). Higher consumption was observed in the second generation than in the first generation for both CO_2 treatments, specifically in the third instar (DF = (1, 4), $F = 28.36$, $P = 0.008$ [elevated]; DF = (1, 4), $F = 83.57$, $P = 0.001$ [ambient]), fourth instar (DF = (1, 4), $F = 17.98$, $P = 0.013$ [elevated]; DF = (1, 4), $F = 44.92$, $P = 0.003$ [ambient]),

Table 6
Population parameters (mean ± SE) of *H. armigera* fed with wheat grains grown in ambient and elevated CO_2 in the presence of *M. mediator*.

Measured indices	Ambient CO_2	Elevated CO_2	*F*	*P*
Generation 1				
Mortality (%)	0.63 ± 0.11 a, A	0.52 ± 0.03 a, A	0.99	0.376
Fecundity (eggs per female)	427.9 ± 37.56 a, A	370 ± 37.77 a, A	1.10	0.305
Net reproductive rate (R_0)	77.95 ± 20.59 a, A	50.77 ± 16.08 a, A	0.77	0.389
Mean generation time (T) (day^{-1})	36.65 ± 0.56 a, A	37.82 ± 0.69 a, B	1.73	0.190
Intrinsic rate of increase (r_m) (day^{-1})	0.12 ± 0.007 a, A	0.11 ± 0.009 a, A	1.53	0.218
Generation 2				
Mortality (%)	0.51 ± 0.02 a, A	0.43 ± 0.10 a, A	0.54	0.504
Fecundity (eggs per female)	375 ± 57.37 a, A	340 ± 46.84 a, A	0.21	0.653
Net reproductive rate (R_0)	73.06 ± 23.61 a, A	43.57 ± 15.29 a, A	2.34	0.146
Mean generation time (T) (day^{-1})	35.42 ± 0.79 b, A	40.15 ± 0.59 a, A	23.40	0.000
Intrinsic rate of increase (r_m) (day^{-1})	0.12 ± 0.01 a, A	0.10 ± 0.009 b, A	4.04	0.047

Means within a row indicated by different lowercase letters are different; means of each life history parameter across two generations within a column indicated by different uppercase letters are different (LSD test, $P < 0.05$).

Table 7
Stage-specific population consumption (g) (mean ± SE) of *H. armigera* larvae (both parasitized and unparasitized) for two successive generations fed with wheat grains grown in ambient and elevated CO_2 and when exposed to *M. mediator*.

Sampling date	Unparasitized		Parasitized	
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2
Generation 1				
First instar	–	–	–	–
Second instar	–	–	–	–
Third instar	0.329 ± 0.119 a, B	0.333 ± 0.019 a, B	0.014 ± 0.007 b, A	0.002 ± 0.001 b, A
Fourth instar	0.607 ± 0.232 a, B	0.92 ± 0.066 a, B	0.058 ± 0.058 b, A	0.014 ± 0.01 b, A
Fifth instar	1.721 ± 0.849 a, B	2.523 ± 0.37 a, B	–	–
Sixth instar	0.295 ± 0.227 b, B	1.266 ± 0.106 a, B	–	–
Larval stage	2.953 ± 1.415 a, B	5.051 ± 0.47 a, B	0.071 ± 0.063 b, A	0.016 ± 0.01 b, A
Generation 2				
First instar	–	–	–	–
Second instar	–	–	–	–
Third instar	0.689 ± 0.077 b, A	1.374 ± 0.212 a, A	0.064 ± 0.043 c, A	0.014 ± 0.011 c, A
Fourth instar	1.457 ± 0.34 a, A	1.456 ± 0.108 a, A	0.038 ± 0.026 b, A	0.047 ± 0.024 b, A
Fifth instar	5.389 ± 1.133 a, A	6.121 ± 1.776 a, A	–	–
Sixth instar	2.059 ± 0.422 b, A	3.851 ± 0.414 a, A	–	–
Larval stage	9.321 ± 1.491 a, A	12.678 ± 2.454 a, A	0.102 ± 0.069 b, A	0.061 ± 0.033 b, A

Stage-specific population consumption of both parasitized and unparasitized *H. armigera* population was calculated from the individual consumption and the numbers for each specific developmental stage. Means within a row indicated by different lowercase letters are different; means of population consumption of each developmental stage across two generations within a column indicated by different uppercase letters are different (LSD test, $P < 0.05$).

fifth instar (DF = (1, 4), $F = 20.83$, $P = 0.01$ [elevated]; DF = (1, 4), $F = 53.51$, $P = 0.002$ [ambient]), and sixth instar (DF = (1, 4), $F = 36.55$, $P = 0.004$ [elevated]; DF = (1, 4), $F = 13.5$, $P = 0.021$ [ambient]), and in larvae total population consumption (DF = (1, 4), $F = 9.31$, $P = 0.038$ [elevated]; DF = (1, 4), $F = 9.6$, $P = 0.036$ [ambient]) (Table 7).

The total population consumption of *H. armigera* after exposure to *M. mediator*, including both parasitized and unparasitized larvae, was estimated (Fig. 1). CO_2 concentrations had no effect on cotton bollworm larvae consumption in either of two successive generations ($P > 0.05$). The interaction between CO_2 levels and generation number also had no effect on cotton bollworm larvae consumption ($P > 0.05$). However, an effect was found for generation, with higher population consumption in the second generation of *H. armigera* than in the first generation (DF = (1, 4), $F = 19.72$, $P = 0.002$) (Fig. 1).

4. Discussion

Elevated-CO_2 levels alter the chemical composition of plant tissue (Fajer et al., 1989). In response to atmospheric CO_2 enrichment, most plants increase the C:N ratio and decrease the N concentration of their larger foliage in order to sequester carbon, which, in turn, changes the syntheses of nutrients and secondary metabolites in the plants (Osbrink et al., 1987; Lindroth et al., 1995; Rogers et al., 1996; Lawler et al., 1997; Poorter et al., 1997). N is the single most important limiting resource for herbivorous insects (Mattson, 1980), and a decrease in the foliar N of host plants could limit insect growth and development, and decrease the survival rates of phytophagous insects (Brooks and Whittaker, 1999). Common to many reports on spring wheat grown under elevated CO_2 (e.g., Lincoln et al., 1986; Fajer et al., 1989; Lindroth et al., 1993, 1995; Masters et al., 1998; Wu et al., 2006) are observations of lower N, protein, and total amino acid content, as well as higher TNC content and TNC:N. In the past, our research has shown that when *H. armigera* is fed milky grains of spring wheat grown under elevated-CO_2, larval durations increase by approximately 7% in successive generations, with a significant difference between elevated- and ambient-CO_2 populations in the third generation (Wu et al., 2006). In the present study, when *H. armigera* are exposed to *M. mediator*, CO_2 concentration is also seen to influence the larval stage durations of cotton bollworm over two successive generations, with longer developmental durations observed in unparasitized cotton bollworms exposed to *M. mediator* under elevated-CO_2 conditions. In the first generation under elevated CO_2, longer developmental durations were observed in all larval stages of unparasitized cotton bollworm larvae, with the exceptions of the first instar and sixth instar.

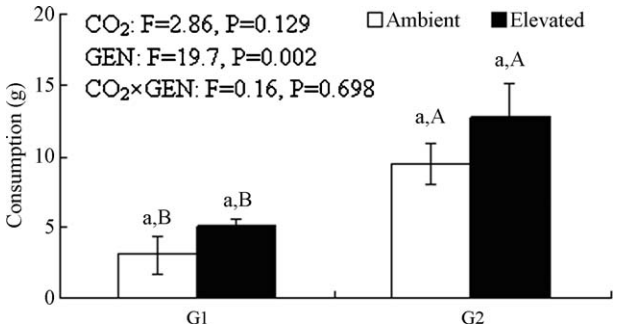

Fig. 1. Total population consumption of *H. armigera* (mean ± SE) (both parasitized and unparasitized larvae) exposed to *M. mediator* for two successive generations fed with wheat grains grown at ambient and at elevated CO_2 at 25 ± 1 °C (G1, the first generation; G2, the second generation; different lowercase letters show significant difference between CO_2 treatments and different uppercase letters indicate significant differences across three generations by LSD test at $P < 0.05$). The total population consumption of *H. armigera* including both parasitized and unparasitized larvae exposed to *M. mediator* were estimated for two treatments in this experiment: (1) *H. armigera* population fed with milky grains from spring wheat grown under ambient-CO_2 level (375 μl/L) with a growth chamber set at ambient-CO_2 level (375 μl/L) and exposed to *M. mediator* and (2) *H. armigera* population fed with milky grains from spring wheat grown under double-ambient-CO_2 level (750 μl/L) with a growth chamber set at double-ambient-CO_2 level (750 μl/L) and exposed to *M. mediator*.

A reduction in N content may be lead to reduced rates of growth and/or survival, and lower insect density (Masters et al., 1998). In this study, in the first generation of *H. armigera* under elevated CO_2 no significant differences were observed in fecundity per female, net R_0 value, mean generation time (T), or in the intrinsic rate of increase (r_m) of unparasitized cotton bollworm larvae. However, in the second generation a longer mean generation time (T) resulting in a lower r_m value was observed, indicating that the *H. armigera* population was not influenced in the first generation exposed to *M. mediator* but was decreased in the second.

Elevated CO_2 may change the performance of natural enemies and/or prey indirectly through the food chain (Bezemer et al., 1998b; Stiling et al., 1999). Because plants grown under elevated CO_2 are deficient in certain nutrients and have lower foliage N concentration, herbivores need to feed for a longer time, and thus prolong their self-exposure to natural enemies, which, in turn, leads to higher parasitism rates (Stiligng et al., 2002). In addition, herbivores may be physically weakened while feeding on poorer-quality plant hosts under elevated-CO_2 conditions, and can thus become more susceptible to their predators and parasitoids as a result (Barbosa et al., 1982). However, several studies found that elevated CO_2 had little effect on natural enemy of herbivores. Bezemer et al. (1998b) observed that parasitism rates remains unchanged under elevated CO_2, when the long-term effects of elevated CO_2 and temperature on populations of the peach photo aphid *Myzus persicae*, which is parasitized by *Aphidium matricariae*. Furthermore, Stacey and Fellows (2002) report that as elevated CO_2 changes plant quality it has a cascade effect on intraspecific interactions between *Myzus persicae* and *Brevicoryne brassicae*. However, this "bottom up" effect did not extend to the natural enemies of the aphids, the number of aphids consumed by ladybird *Hippodamia convergens*, or parasitized by the parasitoid wasp *Diaeretiella rapae* did not change (Stacey and Fellows, 2002). In our experiment, CO_2 treatment and interactions between CO_2 and cotton bollworm generation did not change the parasitism rate, cocoon rate, emergence rate, wasp weight, or adult lifespan of *M. mediator*. Moreover, elevated-CO_2 treatment did not change the status of cotton bollworm as host insect for its parasitoids, nor did it affect the population parameters of *M. mediator*.

As mentioned previously, most leaf-chewing insects exhibit compensatory increases in food consumption under certain conditions (Masters et al., 1998). Insects fed with plant material grown under elevated-CO_2 conditions have been shown to increase their individual consumption (Ayres, 1993; Watt et al., 1995; Coviella et al., 2000). These results are generally explained as a response of herbivorous insects to reduced forage quality, especially the reduction in forage N, of plants grown under elevated-CO_2 conditions (Wu et al., 2006). For example, Lincoln et al. (1984, 1986) found that larvae increased consumption up to 80% on leaves from elevated-CO_2 treatments. Fajer et al. (1989) documented that insect weight increase positively correlates with foliar N concentration, while consumption is negatively correlated with foliar N concentration. In this study, among unparasitized larva fed wheat grown in elevated CO_2, higher consumption per individual was observed in the second generation. In contrast, no significant difference was observed in the parasitized larvae of either generation. However, a decrease in consumption per individual larva of greater magnitude was observed between parasitized and unparasitized cotton bollworm larvae in both generations, for both CO_2 treatments. When *H. armigera* was parasitized by its natural enemy, consumption per individual larva decreased.

Estimating the potential consumption of an insect population under elevated-CO_2 conditions is an important step in understanding the effects of elevated CO_2 on herbivore–crop interactions. Most published studies of the responses of herbivorous insects to rising CO_2 have been short-term experiments measuring consumption rates and development rates at the individual levels (Brooks and Whittaker, 1998). The emergence of a combination of short- and long-term experiments on population consumption will help paint a clearer picture of the response of ecosystems to elevated CO_2 (Brooks and Whittaker, 1998; Wu et al., 2006). Our previous research inferred that under elevated-CO_2 treatments, the potential damage of cotton bollworm to spring wheat would be decreased because higher mortality, lower fecundity per female and decreased population number would counteract the increased individual consumption observed when wheat grown under elevated-CO_2 treatment was given as a food source (Wu et al., 2006). However, in this study we introduce another factor, the presence of parasitoid wasp *M. mediator*, and we observe an increase in the individual consumption by cotton bollworms in the second generation in the elevated-CO_2 treatment, but no changes in mortality, fecundity per female, or population number. Ultimately, the presence of *M. mediator* did not result in any significant difference in consumption by parasitized *H. armigera* of milky grains of wheat. This was observed in each developmental stage across two successive generations in both CO_2 treatments. Furthermore, integrative estimation of the total population consumption of *H. armigera* including both parasitized and unparasitized larvae (all exposed to *M. mediator*), based upon individual consumption and the numbers for each specific developmental stage, indicates that CO_2 treatment has no significant effect on the consumption of milky grains of spring wheat by cotton bollworm larvae in two successive test generations. In the elevated-CO_2 treatments for both generations, results indicate that no significant difference occurred in either the rate of parasitism by *M. mediator* or in the total wheat consumption of the cotton bollworm population exposed to *M. mediator*. The same results clearly suggest that the population relationship, "*H. armigera–M. mediator*," is unlikely to change due to elevated-CO_2 levels in the future.

5. Conclusion

Estimating the population consumption of an insect population under elevated CO_2 is an important and intriguing step in understanding the effects of elevated CO_2 on herbivore–crop

interactions. In this study, the population consumption of two successive generations of *H. armigera* was examined: *H. armigera* larvae were fed milky grains from spring wheat ears grown under elevated-CO_2 conditions, and were then examined after exposure to *M. mediator*. Consistent with some previous studies, elevated-CO_2 concentration ($P < 0.001$), parasitism ($P < 0.001$) and generation ($P < 0.001$) increase the larval stage duration of *H. armigera*. However, parasitism had no effect on larval mortality in the *H. armigera* population over the two successive generations. Longer mean generation time (T) and lower intrinsic rate of increase (r_m) were observed in the second generation of *H. armigera* once exposed to *M. mediator*. These results show a decrease in the second-generation *H. armigera* population which had been fed wheat grown under elevated-CO_2 conditions, and exposed to *M. mediator*. This is the first study focusing on studying the potential effects of elevated CO_2 on the "*H. armigera–M. mediator*" relationship. The results of this experiment clearly indicate that no significant difference occurs in the parasitism rate of *M. mediator* upon *H. armigera* or in the total wheat consumption of the cotton bollworm population when two successive generations are exposed to *M. mediator* under elevated CO_2. This suggests that the population relationship of "*H. armigera–M. mediator*" will not change in the future due to elevated atmospheric CO_2 concentrations.

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