

Elevated CO₂ lessens predation of *Chrysopa sinica* on *Aphis gossypii*

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Accepted: 11 January 2010

Key words: cotton aphid, development, survival rate, predatory ability, successive generation, Neuroptera, Chrysopidae, Hemiptera, Aphididae

Abstract

Most studies on the effects of elevated atmospheric CO₂ on organisms have focused on the performance of plants or herbivores. Few reports have examined the impact on the ability of predators at the third trophic level. In this experiment, we made use of open-top chambers to quantify the effects of elevated CO₂ on growth, development, and predatory ability of two successive generations of Chinese lacewing, *Chrysopa sinica* (Tjeder) (Neuroptera: Chrysopidae), feeding on cotton aphids, *Aphis gossypii* (Glover) (Hemiptera: Aphididae), which were reared on cotton, *Gossypium hirsutum* L. (Malvaceae), grown under elevated CO₂ (double ambient vs. ambient). Higher atmospheric CO₂ concentrations reduced the duration of larval development and the survival rate of pupae, and caused decreased weight in adult female *C. sinica*, but had no significant effects on survival rate of each larval stage, female adult fecundity, egg hatch rate, or adult life span. The predatory ability of larvae in the third instar and the total larval stage of *C. sinica* that fed on *A. gossypii* were significantly lower in elevated CO₂ environments. The number of aphids consumed by first-generation lacewing population did not change significantly with different CO₂ treatments; however, significantly fewer aphids were consumed by the second generation of the lacewing population with elevated CO₂. We speculate that *A. gossypii* may become a more serious pest under an environment with elevated CO₂ concentrations because of the reduced predatory ability of *C. sinica* on *A. gossypii*.

Introduction

The Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2007) noted that the global atmospheric concentration of carbon dioxide has increased markedly from pre-industrial levels of about 280 to 379 p.p.m. in 2005 as a result of human activities. The annual increase in carbon dioxide concentration was larger during the last 10 years (1995–2005; average: 1.9 p.p.m. year⁻¹) than it had been since the commencement of continuous direct atmospheric measurements (1960–2005; average: 1.4 p.p.m. year⁻¹), although there is year-to-year variability in growth rates (IPCC, 2007).

Profound impacts on individual species and communities in agro-ecosystems are expected in the presence of elevated CO₂ levels, both as a direct result of the ‘fertilizing’

effect of atmospheric CO₂ enrichment on plant growth and, indirectly, from the effect on host plants cascaded to higher trophic levels through food chains (Stiling et al., 2002). As foliar C:N ratios increase, insect herbivores exhibit compensatory increases in the foliar consumption rate, reduced larval growth, and lower populations (Masters et al., 1998). However, insect responses to elevated CO₂ may depend on both host plants and herbivore species (Bezemer & Jones, 1998). Most research on CO₂ concentrated on the performance of plants and herbivorous insects under elevated levels of atmospheric CO₂ (Awmack et al., 1997; Bezemer & Jones, 1998; Stacey & Felowes, 2002). Few studies have explored the impact of elevated levels of atmospheric CO₂ on natural enemies (predators and/or parasitoids) at the third trophic level (e.g., Chen et al., 2005a). Some studies have suggested that the effect of elevated CO₂ on the third trophic level is either weak or non-existent (Salt et al., 1995; Stacey & Felowes, 2002). However, in our previous research we found that elevated CO₂ concentrations significantly prolonged the duration of the total larval stage for the lady beetle, *Propylaea japon-*

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ica (Thunberg), when fed cotton aphids, *Aphis gossypii* (Glover) (Hemiptera: Aphididae), reared under elevated CO₂ (Gao et al., 2008). On the contrary, the duration of the fourth instar, the total larval stage, and the pupal stage of the lady beetle, *Leis axyridis* (Pallas), was significantly shortened when fed *A. gossypii* reared under elevated CO₂ levels (Chen et al., 2005a). Moreover, elevated CO₂ concentrations could enhance consumption of cotton aphids, *A. gossypii*, by *L. axyridis* (Chen et al., 2005a). However, how much the predatory ability of natural enemies changes under conditions of elevated CO₂ is still unclear. Natural enemies are considered one of the most important components of integrated pest management (IPM), so it is clear that the responses of natural enemies to elevated CO₂ need to be examined closely (Chen et al., 2007).

The predatory Chinese green lacewing, *Chrysopa sinica* (Tjeder) (Neuroptera: Chrysopidae), is a major biological control agent of the cotton aphid, *A. gossypii*, in northern China (Ge & Ding, 1996). *Chrysopa sinica* prefers to consume aphids during its larval stage, and then consumes pollen, nectar, and insect eggs during its adult stage (Li, 2000). Su & Gao (2007) reported its growth rate and anticipated longevity when feeding on *A. gossypii*. Hu et al. (1994) observed that third-instar *C. sinica* can consume about 137 aphids day⁻¹ in the field. Gao et al. (2007) found that *C. sinica* was able to consume 627 3-day-old aphids during the larval stage in a laboratory setting. However, no studies have examined the predatory ability of *C. sinica* on cotton aphids under elevated CO₂ levels. Moreover, despite the recognized need for long-term studies (Lindroth et al., 1995), to date, few studies have been published that evaluate the predatory ability of *C. sinica* for more than one generation.

This study was designed to quantify the effect of elevated CO₂ on the predatory efficiency of *C. sinica* at the third trophic level for the first and subsequent potential generations. The specific objectives were: (1) to estimate the effects of elevated CO₂ on development, reproduction, and survivorship of *C. sinica* in different developmental stages through their interactions with other members of the food chain, and (2) to quantify the predatory ability and potential predatory consumption of cotton aphids by *C. sinica* in an elevated CO₂ environment.

Materials and methods

CO₂ levels

This experiment was carried out using eight open-top chambers (OTCs; 1.63 × 4.2 × 2.4 m) in Sanhe County, Hebei Province, China (35°57'N, 116°47'E). Two levels of atmospheric CO₂ concentration were continuously applied, i.e., current ambient level (about 375 μl l⁻¹) and

double-ambient level (750 μl l⁻¹), which represents the predicted level in about 100 years (IPCC, 2007). Four OTCs were used for each CO₂ level. During the period from seedling emergence to cotton harvesting, CO₂ concentrations were monitored 24 h per day and adjusted with an infrared CO₂ analyzer (Ventostat 8102; Telaire Company, Goleta, CA, USA). Details of the automatic-control system of CO₂ and the OTCs are provided by Chen & Ge (2004) and Chen et al. (2005a,b).

Cotton cultivation

The cotton, *Gossypium hirsutum* L. (Malvaceae), cultivar 'Simian-3' (SM-3) was planted in white plastic pots (15 cm diameter, 17 cm high) filled with 8:3:1 (by volume) loam:cow dung:earthworm frass. Forty pots were randomly placed in each chamber and re-randomized once a week to minimize positional effects. Cotton plants were planted on 3 May 2006. No chemical fertilizers or insecticides were used and throughout the experiment the tops of all the OTCs were covered with netting to prevent insect movement.

Insects

Chrysopa sinica, collected from cotton fields in Sanhe County, Hebei Province, China was reared in the laboratory (at L14:D10, 27 ± 1 °C, and 75 ± 2% r.h.) for at least two generations and was supplied with aphids fed on SM-3 cotton. Cotton aphids were collected from the same fields and reared in the laboratory for at least two generations, and then transferred to cotton plants in two separate climatic chambers and maintained for at least four generations.

Experimental observations

Fifteen newly hatched larvae of *C. sinica* were individually reared on *A. gossypii* fed on leaves from cotton plants grown in OTC. These leaves were placed with larvae in glass tubes (4 cm diameter, 8 cm deep) in each OTC with 375 and 750 μl l⁻¹ CO₂ every 12 h. The tubes were covered with nylon netting to insure an equilibrium CO₂ concentration inside and outside the tube as described by Gao et al. (2008). Twenty uniformly sized third-instar aphids (0.223 ± 0.002 mg individual⁻¹) fed on leaves from the cotton plants grown in OTC. They were placed every 12 h onto the fresh leaves to act as prey for first-instar lacewings. Similarly, 100 aphids were supplied daily for second-instar, and 250 aphids for third-instar *C. sinica*.

Dead and uneaten aphids in each tube were removed every 12 h. The number of aphids eaten by lacewing larvae in each tube was recorded every 12 h. The number of molting and dead lacewing larvae in each tube was recorded at 8-h intervals. Cotton leaves were replaced

every day with fresh leaves from cotton plants grown in OTC. *Chrysopa sinica* adults were weighed immediately after pupal eclosion using a Cahn 20 automatic electro balance (Cahn, St. Louis, MO, USA). After the sex of *C. sinica* adults was determined, one male and one female lacewing from the same treatment were placed together in a larger glass container (6 cm in diameter, 8 cm deep) to allow them to mate and lay eggs. The number of eggs laid in each container was recorded every 12 h until the adults died and hatching was completed.

Population predatory ability

The population predatory ability of *C. sinica* reared on *A. gossypii* was estimated using the number of cotton aphids consumed by *C. sinica*:

Number of cotton aphids consumed by the first generation of *C. sinica* = initial number of larval individuals of the first generation × larval survival rate × number of cotton aphids consumed per larva at each stage.

The impact of small changes in several varied metrics of performance may be difficult to intuit, we therefore calculated the 'potential aphids consumed' as a variable that integrates the impacts of these varied metrics into an overarching response as following:

Potential number of cotton aphids consumed by the next (second) generation of *C. sinica* = number of cotton aphid consumed by the first generation × survival of female × eggs laid per female × hatch rate.

Statistical analysis

One-way ANOVAs (SAS 6.12; SAS Institute, Cary, NC, USA) were used to analyze the effect of CO₂ level (ambient vs. elevated) on the number of prey consumed by *C. sinica* and life parameters of *C. sinica* (life span, survival rate of lacewing larval stage, adult weight, eggs laid per female, hatching rate). Values were ln or arcsine transformed where appropriate to normalize variance in the data. Means were compared using the least significant difference (LSD) test at $\alpha = 0.05$.

Results

Developmental time of immature *Chrysopa sinica*

A significantly shorter developmental duration of first-instar *C. sinica* was observed in the elevated compared to the ambient CO₂ environment ($F_{1,6} = 5.35$, $P = 0.01$). The developmental duration of *C. sinica* was significantly longer in the third-instar ($F_{1,6} = 4.43$, $P = 0.032$) and

pupal stage ($F_{1,6} = 16.50$, $P < 0.001$) in elevated compared to ambient CO₂ levels (Figure 1).

Survival rate of immature *Chrysopa sinica*

Significantly lower pupal survival was observed under elevated compared to ambient CO₂ levels ($F_{1,6} = 4.58$, $P = 0.03$). However, no significant effects were found in the survival rates of first, second, or third instars, or total larval plus pupal stages (Figure 2).

Life history parameters of adult *Chrysopa sinica*

Adult females weighed less ($F_{1,6} = 7.89$, $P = 0.006$) and males lived shorter ($F_{1,6} = 5.45$, $P = 0.009$) under elevated levels of CO₂ than on ambient levels of CO₂. CO₂ concentration did not affect life span of adult females, weight of adult males, nor fecundity or egg hatching rate in a significant way (Table 1).

Aphid consumption per larva under elevated and ambient CO₂ levels

The number of aphids consumed per larva by third instars ($F_{1,6} = 9.87$, $P = 0.003$) and by the entire larval stage ($F_{1,6} = 5.06$, $P = 0.012$) was significantly lower under

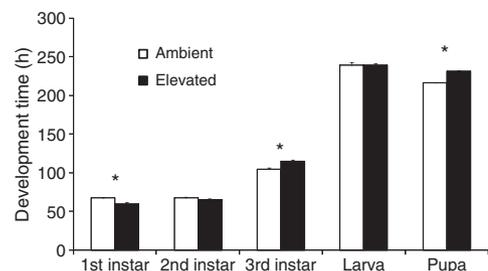


Figure 1 Stage-specific development time (mean + SE) of *Chrysopa sinica* larvae and pupae reared on cotton-fed *Aphis gossypii* in ambient and elevated CO₂. *Indicates a significant difference between CO₂ treatments within a developmental stage (LSD test: $P < 0.05$).

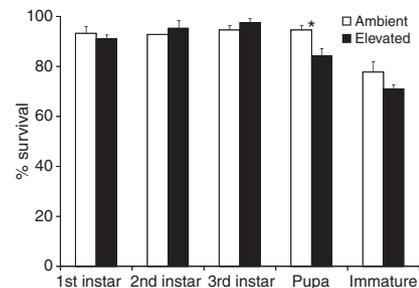


Figure 2 Survival rate (mean + SE) of immature *Chrysopa sinica* reared on *Aphis gossypii* under elevated or ambient CO₂ levels. *Indicates a significant difference between CO₂ treatments within a developmental stage (LSD test: $P < 0.05$).

Table 1 Mean (\pm SE) weight (mg), life span (days), and fecundity of adults, and egg hatching rate of *Chrysopa sinica* supplied with *Aphis gossypii* reared on cotton leaves under ambient and elevated CO₂ levels

Parameters	CO ₂ levels	
	375 p.p.m.	750 p.p.m.
Life span (days)		
Female	47.3 \pm 1.1a	46.8 \pm 0.1a
Male	34.6 \pm 0.7a	31.5 \pm 0.4b
Weight (mg)		
Female	16.7 \pm 0.9a	12.8 \pm 0.8b
Male	10.2 \pm 0.2a	9.6 \pm 0.4a
Fecundity (no. eggs female ⁻¹)	675.4 \pm 20.8a	642.4 \pm 2.1a
Egg hatching (%)	69.9 \pm 1.4a	71.5 \pm 2.3a

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

elevated than under ambient concentrations. However, significantly more aphids were consumed individually by first-instar *C. sinica* under high CO₂ levels than under low CO₂ levels ($F_{1,6} = 4.88$, $P = 0.011$) (Figure 3).

Predatory ability of larval *Chrysopa sinica* on *Aphis gossypii*

When integrating aphid consumption per larva and population abundance, consumption of aphids was significantly higher in the first-instar population of *C. sinica* placed in elevated CO₂ concentrations ($F_{1,6} = 5.13$, $P = 0.02$). However, CO₂ concentrations did not affect population predatory ability in the second or third instars, or in the entire larval stage (Figure 4).

Potential predatory ability of larval *Chrysopa sinica* on *Aphis gossypii* in next generation

No significant effects were shown on potential predatory ability in subsequent generation populations of first and second instars of *C. sinica* (Figure 5). However, the

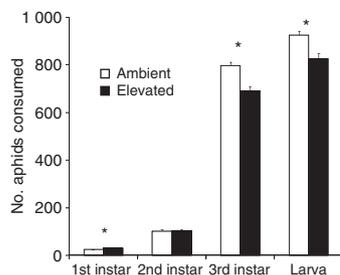


Figure 3 Consumption of cotton aphids (mean number \pm SE) by each instar separately and all instars together for individual *Chrysopa sinica* under ambient and elevated CO₂ levels. *Indicates a significant difference between CO₂ treatments within a developmental stage (LSD test: $P < 0.05$).

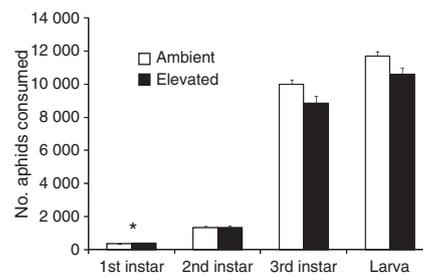


Figure 4 Total number (mean + SE) of aphids consumed by each instar separately and all instars together of the first generation of *Chrysopa sinica* under ambient and elevated CO₂ levels. *Indicates a significant difference between CO₂ treatments within a developmental stage (LSD test: $P < 0.05$).

potential population predatory ability of third instars ($F_{1,6} = 6.33$, $P = 0.004$), and that of the whole larval stage ($F_{1,6} = 15.81$, $P < 0.001$) of *C. sinica* raised on *A. gossypii* was reduced significantly when CO₂ concentrations were doubled compared to ambient.

Discussion

The current data clearly demonstrated that the elevated CO₂ level resulted in prolonged duration at both (third-instar) larval and pupal stage when *C. sinica* were fed *A. gossypii*. These observations are consistent with previous reports (Gao et al., 2008). The duration of the first instar of *C. sinica*, however, was significantly shortened under elevated CO₂. Roth & Lindroth (1995) reported that the effects of *Cotesia melanoscela* (Ratzeburg) on the performance of the gypsy moth, *Lymantria dispar* L., were not significantly affected by changes in the CO₂ level. Salt et al. (1995) also indicated that predators generally were not affected by high CO₂ levels in a free air CO₂ enrichment (FACE) experiment with *Pegomya euphorbiae* (Kieffer). Chen et al. (2005a) reported a significantly shorter

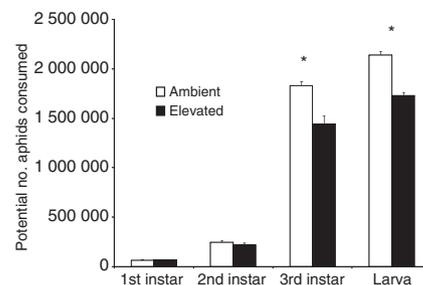


Figure 5 Estimations of potential population predatory ability of the second generation of *Chrysopa sinica* reared on *Aphis gossypii* fed on cotton under ambient and elevated CO₂ levels. *Indicates a significant difference between CO₂ treatments within a developmental stage (LSD test: $P < 0.05$).

duration of total larval and pupal stage for *L. axyridis* fed *A. gossypii* reared under elevated CO₂. Obviously the responses of insectivores to levels of elevated CO₂ are species-specific.

The survival of natural enemies of herbivorous species will be affected by high CO₂ conditions (Coviella & Trumble, 1999). For example, Roth & Lindroth (1995) observed that parasitoid mortality increased under elevated CO₂ conditions, suggesting that natural enemies may kill fewer insects under the high CO₂ levels that are expected in the near future. Gao et al. (2008) found that no significant differences in survival and lifetime fecundity of *P. japonica* maintained under various concentrations of CO₂ occurred. Our results indicated that pupal survival rate was significantly lower at elevated CO₂, but no significant differences were observed in the survival rate of first, second, and third instars, or total immature stage of *C. sinica*. Survival of natural enemies depends on their survival during various stages and the condition of their hosts. Marcel & Andreas (2003) suggested that insect fecundity responses to elevated CO₂ appear to be species-specific. Buse et al. (1998) found that the winter moth, *Operophtera brumata* L., produced more eggs when reared on oak, *Quercus robur* L., leaves grown under elevated CO₂ conditions. However, other studies (Fajer et al., 1989; Brooks & Whittaker, 1998; Marcel & Andreas, 2003) have reported no effects of elevated CO₂ on the fecundity of herbivorous insects.

Our results clearly demonstrated that fecundity of *C. sinica* did not differ significantly when CO₂ concentration was doubled as compared with the ambient condition. Differences in the fatty acid content of aphids, which are influenced by their host plant, may affect survival, growth, and development of aphidophages (Kaplan et al., 1986; Giles et al., 2001; Du et al., 2004; Gao et al., 2008). Scriber (1982) and Masters et al. (1998) suggested that most herbivorous insects exhibit reduced growth, survival, and density, presumably due to an increasing foliar C:N ratio. Although we have not ascertained the biochemistry of aphids and cotton in this experiment, our previous studies indicated that increase in the C:N ratio in foliage and decrease in foliar N of cotton plants, which usually correlate with both N content of phloem sap and aphid performance, resulted in reduction of soluble protein in sap-feeding *A. gossypii* under elevated CO₂ (Chen et al., 2005a,b). Additionally, the percentage free fatty acids in *A. gossypii* decreased as atmospheric CO₂ concentration increased (Gao et al., 2008). We speculate that the nutrient imbalance of cotton aphids reared under elevated CO₂ conditions, i.e., reduced soluble protein and free fatty acids, may have primarily resulted in faster larval development, lower pupal survival, and lighter adult females.

The effect of elevated CO₂ levels on plant-herbivore interactions may further influence the predator's characteristics. Our previous research found that larvae of *H. axyridis* consumed more *A. gossypii* fed elevated CO₂-grown cotton plants and speculated that the lady beetle is thus compensating for the reduced soluble protein in the cotton aphid due to the decrease in foliar N (Chen et al., 2005a). In this study, single generation and subsequent generation analyses have provided a clearer picture of the dynamic predation responses of *C. sinica* to elevated levels of CO₂. Predatory ability per third-instar lacewing and per total larval stage fed *A. gossypii* raised under elevated CO₂ concentrations were significantly reduced compared to those fed *A. gossypii* raised under ambient conditions. Although, predatory consumption of the first lacewing generation was apparently not affected under elevated CO₂, reduced predatory ability per larva, lower pupal survival rate, and lower adult female weight resulted in significant decreases in potential predatory consumption in the subsequent generation of the lacewing population under elevated CO₂. Our previous studies showed that a greater proportion of aphids colonized on cotton plants taken from elevated CO₂ treatments, and the marginal increase in colonization resulted in significantly higher aphid offspring density (Chen & Ge, 2004; Chen et al., 2005a). As the population abundance of *A. gossypii* markedly increased under elevated CO₂ conditions, our results suggest that the predatory ability of *C. sinica* on *A. gossypii* will decrease, and damage caused by *A. gossypii* to cotton plants will increase when CO₂ concentrations are doubled.

As far as we know, this is the first report that quantifies the predatory ability of a natural enemy under elevated CO₂ levels, in this case the first and potential successive generations of *C. sinica*. A more complete picture of the population dynamic consequences of these results could be obtained through the use of mathematical models of this interaction (Hoover & Newman, 2004). In this experiment, however, we just observed the predatory consumption of one lacewing generation. The fate of the predator depends not just on the nutritional value of the prey species, but also on prey population dynamics. It would be useful to measure lacewing development and predation over more than one generation when associated with prey population dynamics.

Acknowledgements

We are grateful to Mrs. Ding Yu Lei, Dean of the Beiai Science and Technology Center of Hebei Province for much help in field OTC experiments. This project was supported by 'National Basic Research Program of

China' (973 Program) (No. 2006CB102006), National Key Technology R&D Program (2006BAD08A07-3-2 and 2008BADA5B01), and National Nature Science Fund of China (Nos. 30770382 and 30621003).

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