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REVIEW

How does atmospheric elevated CO_2 affect crop pests and their natural enemies? Case histories from China

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Abstract Global atmospheric CO_2 concentrations have risen rapidly since the Industrial Revolution and are considered as a primary factor in climate change. The effects of elevated CO_2 on herbivore insects were found to be primarily through the CO_2-induced changes occurring in their host plants, which then possibly affect the intensity and frequency of pest outbreaks on crops. This paper reviews several ongoing research models using primary pests of crops (cotton bollworm, whitefly, aphids) and their natural enemies (ladybeetles, parasitoids) in China to examine insect responses to elevated CO_2. It is generally indicated that elevated CO_2 prolonged the development of cotton bollworm, *Helicoverpa armigera*, a chewing insect, by decreasing the foliar nitrogen of host plants. In contrast, the phloem-sucking aphid and whitefly insects had species-specific responses to elevated CO_2 because of complex interactions that occur in the phloem sieve elements of plants. Some aphid species, such as cotton aphid, *Aphis gossypii* and wheat aphid, *Sitobion avenae*, were considered to represent the only feeding guild to respond positively to elevated CO_2 conditions. Although whitefly, *Bemisia tabaci*, a major vector of *Tomato yellow leaf curl virus*, had neutral response to elevated CO_2, the plants became less vulnerable to the virus infection under elevated CO_2. The predator and parasitoid response to elevated CO_2 were frequently idiosyncratic. These documents from Chinese scientists suggested that elevated CO_2 initially affects the crop plant and then cascades to a higher trophic level through the food chain to encompass herbivores (pests), their natural enemies, pathogens and underground nematodes, which disrupt the natural balance observed previously in agricultural ecosystems.

Key words aphid, cotton bollworm, elevated CO_2, fitness, whitefly

Introduction

The increased use of fossil fuels and deforestation since the Industrial Revolution have been accompanied by an increase in global atmospheric carbon dioxide (CO_2) concentration of 35% from 280 ppm to 379 ppm that is anticipated to double by the end of this century (IPCC, 2007). Elevated CO_2 alters the plant phenotype and affects plant quality by inducing changes in allocation of carbon and nitrogen resources to primary and secondary metabolites in plant tissue (Barbehenn *et al.*, 2004; Reich *et al.*, 2006). Reduced nitrogen in plant tissue impacts the production of plant nutrients and secondary metabolites, which can modify the multi-trophic interactions via cascading effects through the food chain in the agro-ecosystem (Pritchard *et al.*, 1999; Hartley *et al.*, 2000; Percy *et al.*, 2002; Stiling & Cornelissen, 2007). Herbivore insects and their

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natural enemies are important organisms in the agricultural ecosystem and are sensitive to environmental changes. Understanding the effects of elevated CO_2 on major crop pests and their natural enemies is critical to maintaining sustainable agriculture in China.

Cotton bollworm, *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae), is a cosmopolitan phytophagous chewing insect. In northern China, the first generation of cotton bollworm damages wheat, whereas successive generations alternate between maize and cotton. Whitefly *Bemisia tabaci*, is a vector of hemipteran-borne plant viruses, and together with aphids, are important phloem-feeding pests in China. Their population dynamics, damage potential and virus transmission ability under elevated CO_2 have been a recent focus of concern and the subject of research on the response of pest insects and their natural enemies to elevated CO_2 that have been reported from China.

In this paper, we review the advances of recent research in China and discuss the effect of elevated CO_2 on the performance of major crop pests by using cotton bollworm *Helicoverpa armigera*, whitefly *Bemisia tabaci* and aphids as examples. All of these researches used closed-dynamics CO_2 chambers (CDCC) and open-top chambers (OTC) to provide a doubled-ambient CO_2 level (370 ppm *vs*. 750 ppm). The potential effects of elevated CO_2 on pests and their natural enemies, as well as the biological control ability of natural enemies have been summarized in Table 1.

Effects of elevated CO_2 on crop pests

The response of cotton bollworm, an important chewing insect in China to elevated CO_2

Documentation of the direct effects of elevated CO_2 on developmental time and consumption by insect herbivores is rare. Yin *et al.* (2010) found that elevated CO_2 did not directly affect the developmental time, density and consumption by cotton bollworm through three successive generations fed on artificial diet, which suggested that the direct effects of elevated CO_2 were weak or non-existent.

Elevated CO_2 does affect herbivore insects by altering host plant quality (Coviella & Trumble, 1999; Hunter, 2001). Elevated CO_2 enhances photosynthetic efficiency, accelerates plant growth and increases the carbon-to-nitrogen ratio and yield of most C_3 plants (Barbehenn *et al.*, 2004; Reich *et al.*, 2006). Meanwhile, the decreased foliar nitrogen level reduces leaf nutritional quality, diminishing the value of foliage as a resource for insect herbivores (Johns & Hugher, 2002). This indicates that the nitrogen dilution effect of elevated CO_2 increased mortality, reduced fecundity and reduced the density of cotton bollworm larvae through three successive generations when fed on wheat, cotton and maize, respectively (Wu *et al.*, 2006; Chen *et al.*, 2007; Yin *et al.*, 2010). Thus, elevated CO_2 negatively affects cotton bollworm via the host plant.

Cotton bollworm can compensate for decreased leaf nutritional quality with increased individual consumption even if their density is reduced when grown under elevated CO_2 conditions. Thus, it is necessary to assess consumption and density of cotton bollworm to differentiate between these effects. Chen *et al.* (2007) reported that consumption by cotton bollworm under elevated CO_2 is higher than that under an ambient CO_2 condition. On the other hand, elevated CO_2 enhances the compensatory ability of cotton as shown by manually removing squares during the early growing season (Wu *et al.*, 2007a,b). Thus, the economic threshold for biological control of cotton may not be materially affected under elevated CO_2 conditions. Similarly, elevated CO_2 also increased consumption by cotton bollworm on maize, a C_4 crop in China (Yin *et al.*, 2010). In contrast, elevated CO_2 had an adverse effect on grain quality and increased consumption per individual larva of *H. armigera* through three successive generations. However, consumption by cotton bollworm under elevated CO_2 was reduced in the subsequent two generations, due to increased mortality and reduced fecundity within the population of cotton bollworm (Wu *et al.*, 2006). These results suggest that the net damage caused by cotton bollworm on wheat will be reduced under elevated CO_2. Accordingly, elevated CO_2 would exacerbate the feeding damage on cotton and maize but alleviate the damage on wheat plants.

The response of aphids, the severe phloem-feeder pest in China to elevated CO_2

Elevated CO_2 tends to increases the densities of cotton and cereal aphids. Chen *et al.* (2005b) found that elevated CO_2 increases the density of *Aphis gossypii* on transgenic Bt cotton (GK-12) and non-transgenic cotton (Simian-3) simultaneously due to a shorter developmental time and higher fecundity. Additionally, the same aphid species exhibits various responses to elevated CO_2 on different varieties within the same plant species. For example, elevated CO_2 increases the density of *Aphis gossypii* on three cotton varieties respectively, which differed in gossypol contents. When consuming the high gossypol cotton grown under elevated CO_2, aphid fitness declined through three successive generations (Sun *et al.*, 2010b).

Table 1 Potential effect of elevated CO_2 on pests, their natural enemies and the biological control ability of natural enemies in different tri-trophic studies.

System of crop–pest–natural enemy	Type of natural enemy	Pest	Natural enemy	Biolgical control of enemy	Reference
Wheat–*Helicoverpa armigera–Microplitis mediator*	Parasitoid	Decrease	Neutral	Negative	Yin *et al.*, 2009
Cotton–*Aphis gossypii–Propylaea japonica*	Predator	Increase	Negative	Negative	Gao *et al.*, 2008
Cotton–*Aphis gossypii–Harmonia axyridis*	Predator	Increase	Positive	Positive	Chen *et al.*, 2005a
Cotton-*Aphis gossypii–Chrysopa sinica*	Predator	Increase	Positive	Negative	Gao *et al.*, 2010
Cotton–*Aphis gossypii–Lysiphlebia japonica*	Parasitoid	Increase	Positive	Positive	Sun *et al.*, 2010b
Wheat–*Sitobion avenae– Harmonia axyridis*	Predator	Increase	Negative	Positive	Chen, 2004
Wheat–*Sitobion avenae–Aphidius avenae*	Parasitoid	Increase	Positive	Positive	Chen, 2004
Cotton–*Bemisia tabaci–Encarsia formosa*	Parasitoid	No effect	Neutral	Neutral	Wang, 2009

Elevated CO_2 is likely to increased secondary metabolites i.e. condensed tannin and gossypol in cotton plant, which increased the catalase and superoxide dismutase activities and reduced the true choline esterase activity of cotton aphid (Wu *et al.*, 2011). Similarly, elevated CO_2 increased density and body weight of *Sitobion avenae*, the wheat aphid reared on spring wheat, while there was no effect on its fecundity and longevity (Chen *et al.*, 2004). Aphids produced more offspring on elevated CO_2-grown plants and the total number of offspring produced by alate wheat aphids increased by 19% under elevated CO_2.

Aphids ingested more phloem sap to compensate for elevated CO_2-induced reduction of amino acids in phloem sap of plant leaves. Elevated CO_2 reduced amino acid levels in the phloem of cotton plants, but amino acid levels in tissue and in honeydew excreted from the aphid did not decrease. Aphids ingested more photosynthate to maintain their development and growth on their host plants (Sun *et al.*, 2009b). On the other hand, Zhang *et al.* (2009) analyzed the feeding behavior of aphids by using the electronic penetration graph technique. They found that elevated CO_2 prolonged the probing attempts by the aphid and increased the time of aphid passive ingestion, which suggested that aphids were devoting more time to probing and ingestion.

Aphids have different responses to the same host plants when grown under elevated CO_2, and this may alter the original pattern of interspecific competition among aphids (Harrington *et al.*, 1999; Gonzáles *et al.*, 2002). Interspecific competition among aphid species is mainly mediated by the vascular system of the plant, through indirect interactions due to changes in plant defense and nutrients, which may be modified by elevated CO_2 (Inbar *et al.*, 1995; Stacey & Fellowes, 2002; Denno & Kaplan, 2007). Sun *et al.* (2009a) examined effects of elevated CO_2 on interspecific competition among three species of wheat aphids *Sitobion avenae*, *Rhopalosiphum padi* and *Schizaphis graminum*. The results suggested that increases in atmospheric CO_2 would reorder the spatial distribution pattern of these three wheat aphids on winter wheat and in turn alleviate interspecific competition among them. Thus, elevated CO_2 affects aphid density and interspecific interactions. This indicates that elevated CO_2 would accentuate the abundance of and the damage caused by these wheat aphids.

The alarm pheromone of aphids is the most efficient signal used for defense against natural enemies (Edwards *et al.*, 1973; Nault *et al.*, 1973). Densities of *S. avenae* declined with increased frequency of alarm pheromone application under ambient CO_2 but were unaffected by alarm pheromone application under elevated CO_2. This suggests that elevated CO_2, in terms of aphid density, reduced the response of *S. avenae* to the alarm pheromone. Although the underlying mechanism remains unclear, lower activity of acetylcholinesterase in *S. avenae* may be involved in its reduced sensitivity to alarm pheromone under elevated CO_2 (Sun *et al.*, 2010b). Therefore, elevated CO_2 may also modify the interspecific chemical communication of aphids (Awmack *et al.*, 1997; Mondor *et al.*, 2004).

Elevated CO_2 is likely to change the virus transmissal ability of aphids. In the context of tobacco–*Myzus persicae*–plant virus, elevated CO_2 alleviates the damage from potato virus Y and cucumber mosaic virus infection in tobacco plants by artificial inoculation (Fu *et al.*, 2010; Ye *et al.*, 2010). It seems that the plant virus, regardless of aphid vector, would be less severe under elevated CO_2 conditions. However, elevated CO_2 tends to increase the density of *M. persicae* on tobacco plants. The mechanisms whereby elevated CO_2 affects the aphid-transmitted viruses on plants remain unknown and more investigations are needed to elucidate this.

The response of whitefly, a serious invasive species in China to elevated CO_2

Elevated CO_2 has little effect on population density of whitefly. The whitefly, *Bemisia tabaci* biotype B is a very serious invasive pest in China that causes substantial losses in many crops. Elevated CO_2 increased developmental time from egg to adult and reduced mortality of nymphs through three successive generations on cotton with no significant differences in life-span, sex ratio and fecundity of *B. tabaci*: elevated CO_2 did not affect the density of *B. tabaci* (Wang, 2009). Thus, the threat of this invasive insect on crops remains severe under elevated CO_2 environments. However, when cotton aphid and whitefly coexisted, there is interspecific competition between the two ecologically similar feeding guilds, elevated CO_2 tends to increase the population abundances and the proportions of whitefly on cotton plants. It is indicated that elevated CO_2 would be favorable for whitefly to out-compete the cotton aphid under the predicted global climate change (Li *et al.*, 2011). Elevated CO_2 also tends to increase the plant virus transmission ability of whitefly. *Tomato yellow leaf curl virus* (TYLCV) causes heavy losses in yield throughout the tropical and temperate regions of the world, which is more severe than the direct damage inflicted by the whitefly vector (Moffat, 1999; Lapidot *et al*., 2001). Elevated CO_2 reduced TYLCV incidence, severity and coat protein in mechanically inoculated tomatoes. Additionally, elevated CO_2 only increased virus acquisition quantity of whitefly at 1 hour but had no effect on virus acquisition at 8/24/48 hours or virus retention after 1/2/3 weeks of whitefly exposure. Meanwhile, elevated CO_2 dramatically increased the fecundity and the density of whitefly biotype B on virus-infected tomato plants. Thus, the virus transmission quantity of whitefly was enhanced by elevated CO_2 (L.C. Huang, 2010, unpubl. data). The mechanisms governing the direct negative effects of elevated CO_2 on TYLCV remain to be elucidated.

Effects of elevated CO_2 on natural enemies

Elevated CO_2 had little direct effect on natural enemies of insect herbivores but a flow-through effect from the plant to higher consumers (predators and parasitoids) occurred to affect the third trophic level (Roth & Lindroth, 1995; Stiling *et al.*, 1999, 2002). Basically, elevated CO_2 may alter the size and composition of prey insects for predators and/or disrupt developmental synchrony for parasitoids. Thus, the insect preys' inconsistent response to elevated CO_2 determined the complex responses of natural enemies to elevated CO_2. The species-specific response of natural enemies are categorized by insect herbivores as below and summarized in Table 1.

Microplitis mediator (Hymenoptera: Braconidae) is a solitary endoparasitoid, which plays a major role in the biological control against *H. armigera* in agricultural ecosystems in China (Li, 2005). Elevated CO_2 did not significantly affect the rate of parasitism, cocooning, emergence and adult lifespan by *M. mediator* when parasitizing cotton bollworm. The presence of *M. mediator* under elevated CO_2 did not affect the total consumption by cotton bollworm on wheat (Yin *et al.*, 2009). With *M. mediator* absent, elevated CO_2 alleviated the total consumption by cotton bollworm on wheat (Wu *et al.*, 2006). This implies that, in terms of total consumption by cotton bollworm, the biological control ability of *M. mediator* may be decreased by elevated CO_2.

We also reviewed effect of elevated CO_2 on three predators and two parasitoids in biological control against cotton and wheat aphids in China. Two kinds of ladybirds *Propylaea japonica* (Coleoptera: Coccinellidae) and *Harmonia axyridis* (Coleoptera: Coccinellidae) are prominent predators in cotton and wheat fields. They mainly feed on cotton and wheat aphids, spider mites, eggs and young larvae of lepidopteran pests (Du *et al.*, 2004). *Chrysopa sinica* (Neuroptera: Chrysopidae) is a predatory green lacewing. *Lysiphlebia japonica* (Hymenoptera: Aphidiidae) is also a predominant parasitoid of cotton aphids in China and can effectively suppress the population of cotton aphids in early summer (Hou *et al.*, 1997). Elevated CO_2 prolonged the development time of *P. japonica* but reduced larval and pupal durations of *H. axyridis*, *C. sinica* and *L. japonica* when preying on cotton aphids (Chen *et al.*, 2005a; Gao *et al.*, 2008). Moreover, elevated CO_2 increased aphid predation rate by *H. axyridis*, but reduced predation by *C. sinica* (Gao *et al.*, 2010).

There is no difference in parasitism or emergence rates for *L. japonica* under elevated CO_2 (Sun *et al.*, 2011). The biological control of cotton aphids by predators and parasitoids were accordingly evaluated (Table 1). In wheat crops of temperate areas, *Aphidius avenae* (Hymenoptera: Aphidiinae) can parasitize the main aphid pest, the wheat aphid *Sitobion avenae* (van Baaren *et al.*, 2004). Elevated CO_2 increased the developmental time but reduced mean relative growth rates and aphid consumption rates by *H. axyridis* when preying on wheat aphids. In contrast, the density and parasitism rates of *A. avenae* were increased with elevated CO_2 (Chen, 2004).

Encarsia formosa (Hymenoptera: Aphelinidae) is an important parasitoid of *B. tabaci*. *E. formosa* is thelytokous, producing only females and now has a worldwide distribution in conjunction with its host whiteflies. The application of *E. formosa* for controlling greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) is one traditional example of successful biological control (Cahagirone, 1981; van Lenteren, 2000). Elevated CO_2 did not affect the developmental duration, parasitization rate and adult emergence rate of *E. formosa* after parasitizing *B. tabaci* for three successive generations, and the impact of elevated CO_2 on interaction between *B. tabaci* and *E. formosa* were also not significantly affected. The results suggested that the effect of biological control of *E. formosa* on *B. tabaci* will not be changed under elevated CO_2 (Wang, 2009).

Conclusion and perspective

Elevated CO_2 mainly affects herbivores and their natural enemies via indirect effects on the plant and few if any direct effects by the atmosphere. Elevated CO_2 delayed the growth and development of chewing insects by decreasing the food quality of the host plant. Conversely, some aphid species were successful under elevated CO_2 conditions. O'Neill *et al.* (2011) proposed an interesting explanation that elevated CO_2 was likely to decrease the evapotranspiration and stomatal conductance of plant leaves, which increases leaf temperatures (up to 2°C), and in turn increased aphid population density.

The difficulty in forecasting how insect herbivores will respond to elevated CO_2 lies in first understanding how the plant will be affected and then determining how each herbivore will be affected. Plant–insect herbivore–natural enemy interactions are even more complex and it is currently impossible to predict a general response of insects to elevated CO_2 (Pritchard *et al.*, 2007). There is some evidence that the nutritional suitability of the plant to chewing insects is reduced under elevated CO_2. However, species-specific responses of phloem sap feeder insects have so far defied generalization (Bezemer *et al.*, 1999; Hughes *et al.*, 2001). A model proposed by Newman *et al.* (2003) concluded that higher aphid densities under elevated CO_2 critically depended on higher soil nitrogen fertility; given aphid species have a lower nitrogen requirement and a weaker density-dependent response. The inability to determine the exact substrate composition consumed by the phloem feeder remains a barrier to unraveling the mechanisms whereby elevated CO_2 may be affecting such herbivores.

The crop food web and food chain includes underground organisms, crops, pathogens, insect herbivores and natural enemies. Most research on CO_2 effects focuses on aboveground insects; Sun *et al.* (2010a) examined the effect of elevated CO_2 on the interactions between the root-knot nematode *Meloidogyne incognita* and three isogenic tomato genotypes differing in jasmonic acid (JA), including prosystemin over-expression mutant, jasmonate-deficient mutant and wild-type. Elevated CO_2 increased the number of nematode-induced root galls in the JA-defense-dominated genotype but not in the wild-type or defense-recessive genotype. It suggests that elevated CO_2 will attenuate the resistance against the nematodes in genetically modified varieties using the JA pathway. Further studies are needed that combine the under- and aboveground pest complex on a single host plant to examine how plant mediated interactions occur within the herbivore complex and their natural enemies to obtain ecologically relevant conclusions. For example, whitefly reduced their fecundity on tomato mutants that over-expressed JA while their fecundity was increased when root-knot nematodes were inoculated on the same plant (H.F. Cao, 2010, unpubl. data). Elevated CO_2 was expected to modify the resistance of plant by increasing the carbon : nitrogen ratio and re-allocating resources (Hartley *et al.*, 2000), and this may change how plants affect under- and aboveground insects.

Microarray and proteomic technologies were applied to investigate a model plant *Arabidopsis* responding to elevated CO_2; elevated CO_2 up-regulated the genes of secondary metabolism, heat shock protein family and antioxidant enzymes, but caused only small changes of the proteome (Miyazaki *et al.*, 2004; Li *et al.*, 2008). New molecular and analytical technologies should be used in crops (i.e., tomato, cotton) to determine which pathways in the plant maintain relationships among elevated CO_2, herbivores (including underground organisms) and their natural enemies. It is very likely that JA signaling defenses involve the connection of multitrophic levels in different spaces. Moreover, the JA signaling pathway not only induces systematic defenses in plants which mediate the interactions between under- and aboveground pests, but also regulates the volatiles from plants that attract natural enemies. Most importantly, elevated CO_2 tends to impair the JA signaling defense. For example, elevated CO_2 increased the susceptibility of soybean to Japanese beetle and western corn rootworm by down-regulating the expression of genes related to the JA pathway (Zavala *et al.*, 2008, 2009).

In summary, elevated CO_2 has diverse effects on different guilds of herbivorous insects, which disrupts the balance of agricultural ecosystems. In order to predict the intensity of pest outbreaks and make policies for pest control, future work in this area should mainly focus on the large-scale and long-term interactive effects of elevated CO_2 associated with temperature, O_3 and drought on major crop pests and severe invasive insects in agricultural ecosystems.

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