



Review

How do aphids respond to elevated CO₂?

Yucheng Sun, Feng Ge*

State Key Laboratory of Integrated Management of Pest and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

ARTICLE INFO

Article history:

Received 8 April 2010

Revised 21 July 2010

Accepted 3 August 2010

Available online 10 August 2010

Keywords:

Aphid

Elevated CO₂

Fitness

Interspecific interaction

Nutrient effect

ABSTRACT

The performance of herbivore insects is determined directly by the quality of host plants. Elevated CO₂ induced a decline in foliar nitrogen, which reduced the growth of chewing insects. Phloem-sucking insects (i.e. aphid), however, had species-specific responses to elevated CO₂ and were the only feeding guild to respond positively to elevated CO₂. Although many studies attempt to illuminate the interaction between aphids and plants under elevated CO₂, few studies can explain why some aphids are more successful than other chewing insects in elevated CO₂. Elevated CO₂ leads to a re-allocation of the carbon and nitrogen resources in plant tissue, which increases the thickness of the microscopic structures of leaves, reduces amino acids content of leaf phloem sap and increases the secondary metabolites. Considering the complexity of aphid–plant interactions, it is difficult and unreasonable to predict the general response of aphids to elevated CO₂ using a single plant component. Instead, it is more likely that aphids are able to overcome the disadvantages of the indirect effects of elevated CO₂ by reducing developmental times and increasing fecundity under elevated CO₂ conditions. Our results provide several clues to why some aphids are successful in elevated CO₂ conditions. We review recent studies of the effects of elevated CO₂ on aphids and discuss the effects of elevated CO₂ on aphid performance on crops using cotton and cereal aphids as examples.

© Korean Society of Applied Entomology, Taiwan Entomological Society and Malaysian Plant Protection Society, 2010. Published by Elsevier B.V. All rights reserved.

Contents

Introduction	217
Growth and development	218
Phenotype and reproduction	218
Feeding behavior	218
Nutrient effects	218
Interspecific interaction	219
Response to plant defenses	219
Chemical signals	219
Conclusions	219
Acknowledgments	219
References	220

Introduction

Owing to human activity and to the increased use of fossil fuels, global atmospheric CO₂ concentration has increased from 280 ppm in pre-industrial times to 379 ppm in 2010, and is predicted to at least double by the end of this century (IPCC, 2007). Increases in atmospheric CO₂ accelerates photosynthetic rate, stimulates plant

growth, and increases the carbon:nitrogen ratio of most plant species (Barbehenn et al., 2004; Reich et al., 2006). In addition, elevated CO₂ can affect plant quality by inducing changes in allocation of carbon and nitrogen to primary and secondary metabolites, which affects tritrophic interactions (Hartley et al., 2000; Sun et al., 2010b). There is widespread evidence that elevated CO₂ can promote plant growth, with consequent reallocation of resources and dilution of foliar nitrogen, which modify both consumption rates and fitness of herbivores (Yin et al., 2009; Sun et al., 2010a).

Generally, the elevated CO₂ treatment used in global change biology experiments was one and a half or two times the ambient CO₂

* Corresponding author. Fax: +86 0 10 6480 7099.

E-mail addresses: sunyc@ioz.ac.cn (Y. Sun), gef@ioz.ac.cn (F. Ge).

concentration (~600–750 ppm). Compared with weak direct effects, the impact of elevated CO₂ on herbivores acts mainly through altering host plant composition, and are called “indirect effects” (Coviella and Trumble, 1999; Hunter, 2001). Typically, chewing insects develop more slowly, suffer greater mortality and have higher consumption rates when fed foliage grown under elevated CO₂ conditions (Chen et al., 2005b; Wu et al., 2006). In contrast, phloem sap-suckers (e.g., aphids) have a more complex response to elevated CO₂ (Newman, 2003). Like many homopteran insects, aphids feed exclusively on the phloem sap and are very sensitive to changes in quantity/quality of plants resulting from elevated CO₂ (Pritchard et al., 2007). Thus, comprehensive understanding of aphid from ecological and physiological view may explain how elevated CO₂ modifies the interaction between plant and aphid.

Growth and development

Aphid responses to elevated CO₂ are frequently “species-specific” and can be negative, positive or neutral (Bezemer and Jones, 1998; Hughes et al., 2001). Bezemer et al. (1999) proposed several reasons for variability in aphid species responses to elevated CO₂ and suggested that differential feeding behavior between generalist and specialist aphid species may result in variation in responses. Additionally, the same aphid species exhibits various responses to elevated CO₂ on different host plants. For example, Awmack et al. (1996) found that elevated CO₂ increased the fecundity of cereal aphid *Sitobion avenae* when reared on winter wheat. Diaz et al. (1998), however, reported that elevated CO₂ did not change fecundity of cereal aphid when reared on four *Poacea* species. The effects of elevated CO₂ on fecundity or nymph size are not always reflected in the final population sizes of aphids (Docherty et al., 1997). Chen et al. (2004) found that elevated CO₂ increased population abundance and mean rate growth rate (MRGR) of cereal aphid reared on spring wheat while having no effect on fecundity and longevity. Thus, although cereal aphid populations tend to increase under elevated CO₂ conditions, the outcome could be modified by nutrient availability and sensitivity of the plant to elevated CO₂.

Phenotype and reproduction

Aphids can switch between apterous and alate morphs with environmental change to increase fitness. Alate morphs developed slower and produced significantly fewer nymphs than apterous morphs (Liu and Yue, 2001). Alate aphids (*Aphis fabae*) may also reduce their weight by fasting before take-off, which results in aerodynamic benefits (Powell and Hardie, 2002). Zou et al. (1997) indicated that the apterous:alate ratios of aphids are related to the content of some amino acids, foliar nitrogen, and some other measures of host plants. Although elevated CO₂ increases the C:N ratio and reduces amino acids in plants, there is no evidence that elevated CO₂ induces the winged morph of aphid.

Elevated CO₂ reduces the fecundity of chewing insects (e.g. cotton bollworm) but may increase the number of offspring of aphids (Peltonen et al., 2006). For example, the total number of offspring produced by alate cereal aphids increased by 18.6% in the elevated CO₂ treatment (Chen et al., 2004). Additionally, aphids preferred ovipositing on elevated CO₂-grown plants. However, the cause of these changes is unknown. Although several studies have shown that elevated CO₂ affects some phenolic compounds in plant, there is no evidence that these changes correlate with the observed changes in aphid oviposition (Peltonen et al., 2006).

Elevated CO₂ not only affects the population abundance of aphids, but also the genotypic and phenotypic frequencies (Mondor et al., 2005). The green genotype of pea aphid was positively influenced by elevated CO₂ levels, but the pink genotype was not. These two genotypes also displayed marked differences in phenotypic frequen-

cies. The pink genotype exhibited higher levels of wing induction under all atmospheric treatments.

Feeding behavior

Once aphids arrive at a new plant, they probe the plant to determine if it is acceptable. Sucrose is an attractant and an important cue in sieve element location. Elevated CO₂ increases sucrose in plant tissues, which may explain why cereal aphids prefer wheat plants grown in elevated CO₂ (Awmack et al., 1996).

Aphids face many structural barriers before they can feed successfully from a sieve element elevated CO₂ may affect these structures and modify the feeding behavior of aphids. Elevated CO₂ generally increased the C:N ratio of plant tissues and “excess” carbon was possibly allocated to cell wall (Pritchard et al., 1999). Elevated CO₂ increased the thickness of epidermis cells, spongy tissue, palisade cells and whole leaves of the cotton plant (Chen unpublished data). Leaves may be tougher to penetrate under elevated CO₂. Zhang et al. (2009) used the electronic penetration graph (EPG) technique to measure the feeding behavior of aphids on host plants. They found that elevated CO₂ delayed the first shown time of E1 wave which presents the attempting to probe the phloem sieve and excreting watery saliva. Besides, elevated CO₂ also deferred the first shown time of E2 (passive ingestion) wave and elongated the lasting time of E2 wave when *S. avenae* was reared on wheat plants. It was concluded that aphids reared under elevated CO₂ conditions would spend more time to probe and ingest from host plants than aphids reared under ambient CO₂ conditions.

Nutrient effects

The nutritional quality of phloem sap may be an important limiting resource for the growth, development and performance of aphid populations (Bezemer and Jones, 1998). Aphids, however, feed on different plants and appear to have species-specific requirements for amino acids (Wilkinson and Douglas, 2003). Generally, only around 20% (mol%) relative concentration of the essential amino acids compared to concentration of all amino acids were found in phloem sap, with a range from 15% to 48%, while aphid body proteins and optimal diets for herbivorous insects were approximately 50% (Sandström and Moran, 1999). Thus, these imbalanced diets did not match the aphids' needs. Free amino acids, more specifically, are needed to be transformed into other proteins (e.g., tyrosine for sclerotization in the cuticle after insect moulting), and they are utilized as an energy resource, as major respiratory substrates, and in reproduction (Rhodes et al., 1996). Therefore, the amino acid content of aphids may be responsible for its performance and honeydew excretion.

Sun et al. (2009b) examined the ingestion/excretion balance of cotton aphid amino acids in both ambient and elevated CO₂ environments. Amino acid concentrations were lower in phloem of cotton plants grown under elevated CO₂ conditions than those grown under ambient CO₂ conditions. Higher amounts of free amino acids were found in cotton aphids fed on cotton grown in elevated CO₂ conditions but the contents of amino acids in honeydew were not significantly affected by elevated CO₂. More honeydew was produced by cotton aphids reared under elevated CO₂ conditions than those reared under ambient CO₂ conditions, which indicates that cotton aphids ingest more cotton phloem owing to the higher C:N ratio of cotton phloem in elevated CO₂ conditions. It is tempting to speculate that more phloem sap will be ingested by cotton aphids to satisfy their nutrition requirements and to balance the break-even point of amino acids in elevated CO₂ (Sun et al., 2009b). Likewise, this nutrient imbalance suggests that, in order to match their needs, aphids may modify their feeding and metabolism. Dixon et al. (1993) found that the feeding rates and ingestion efficiency of aphids increased as the

amino acids concentration of their host plants decreased. Based on these results, one could predict that the future elevated atmospheric CO₂ will enhance aphid feeding activities and result in heavier ingestion on host plants. These results support the hypothesis proposed by Awmack et al. (1997), who speculated that this feeding guild might display compensatory feeding responses when feeding on plants grown under elevated CO₂ conditions. Furthermore, compensatory feeding may act to satisfy aphid growth requirements (Awmack et al., 1997). For example, the growth of *Acyrtosiphon pisum* was compensated by changing feeding location, metabolism and ingestion rates (Abisgold et al., 1994). Increases in phloem-sap pressure and flow rates, leaf toughness and stylet penetration frequency also contributes to aphid compensatory feeding (Watling et al., 2000).

Interspecific interaction

Because changes in plant quantity/quality can alter the interspecific interactions among insect herbivores, elevated CO₂ is likely to change these interactions (Inbar et al., 1995; Gonz  les et al., 2002). Aphid species often respond differently to the same host plants grown under elevated vs. ambient CO₂, and this may change the outcome of interspecific competition (Harrington et al., 1999). For example, Stacey and Fellowes (2002) found a significantly lower ratio of *Myzus persicae* : *Brevicoryne brassicae* on plants grown under elevated CO₂ vs. ambient CO₂. Moreover, interspecific competition mainly affects the aphids mediated by plant, i.e., resulted from the interaction of each species with the vascular system of the host plant, and this interaction may be modified by elevated CO₂ (Denno and Kaplan, 2007). Sun et al. (2009a) examined effects of elevated CO₂ on the interspecific competition among three species of wheat aphids (*Sitobion avenae*, *Rhopalosiphum padi*, and *Schizaphis graminum*) as well as on wheat–aphid interactions, and the results suggested that increases in atmospheric CO₂ would alter the spatial distribution of three cereal aphids on wheat plant and in turn alleviate interspecific competition among them. The different response of aphid species must be due to differences in the way they respond to the range of chemical cues presented by the plant, or species specific differences in their physiology that facilitate feeding at different sites on the plant.

Response to plant defenses

As predicted by the Carbon Nutrient Balance (CNB) hypothesis, excess carbon accumulating in plant tissues due to elevated CO₂ is probably allocated to more carbon-based secondary metabolites, such as phenolics, condensed tannins, and terpenoids (Sun et al., 2009a). Although these responses are species-specific in plants, aphids may enhance the activities of superoxide dismutase and catalase in elevated CO₂ environments. Microarrays were used to examine *Arabidopsis* responding to elevated CO₂. It was concluded that elevated CO₂ up-regulated the genes of secondary metabolism, the heat shock protein family and antioxidant enzymes, but it remains unclear how these changes affect aphid performance (Li et al., 2008).

Elevated CO₂ may modify induced defenses of plants when damaged by insect herbivores (Stiling and Cornelissen, 2007; Li et al., 2008). For example, elevated CO₂ increased the susceptibility of soybean to Japanese beetle and western corn rootworm by down-regulating the expression of genes related to the jasmonic acid (JA) pathway (Zavala et al., 2008, 2009). Thus, the evidence that elevated CO₂ can change induced defenses was found only in chewing insect-damaged plants. It is still unclear whether elevated CO₂ changes phloem sucker-induced defenses (i.e. salicylic acid signaling pathway). Further study should determine whether elevated CO₂ impairs induced defenses against aphids by using defense pathway mutants.

Chemical signals

The aphid alarm pheromones warn aphids of attack by natural enemies (Nault et al., 1973). Aphids perceiving the alarm pheromone increase production of alate offspring and reduce their foraging rate, which increase their ability to disperse into enemy-free space thereby reducing exposure to predators (Montgomery and Nault, 1977; Kunert et al., 2005). Previous studies suggest that, under elevated CO₂, parasitoids and predators are more abundant or effective (Percy et al., 2002; Chen et al., 2005a) and that aphids are less sensitive to alarm pheromones. Awmack et al. (1997) reported that the potato aphid *Aulacorthum solani* was less sensitive to disturbance under elevated CO₂ conditions than under ambient CO₂ conditions. Mondor et al. (2004) found that the aphid *Chaitophorus stewartensis* on trembling aspen trees exhibited diminished escape responses under elevated CO₂ conditions. Sun et al. (2010c) also found that elevated CO₂ reduces the response of *S. avenae* to alarm pheromone. This phenomenon can be explained by elevated CO₂-induced plant changes and the pseudo-crowding hypothesis (Kunert et al., 2005). The perception of alarm pheromone increases walking behavior in aphids, which increases the number of physical contacts between individuals, as happens when aphids are crowded. Plants grown under elevated CO₂ conditions can grow larger which might reduce the physical contacts between aphids, which may decrease the perception of alarm pheromone and alarm pheromone-mediated walking behavior.

Some aphid species switch between woody and crop host according to the environments (Dixon, 1971, 1998). Methyl salicylate may be a cue by which the aphid discriminates between hosts during migration. In spring, the emission of methyl salicylate, which repels aphids, increased in woody hosts and in turn triggered migration signal of aphids to their summer host. Methyl salicylate, however, does not exist in the volatiles from the summer host. Thus, when the weather gets cold and the levels of nitrogen decrease in the summer host, aphids migrate back to their woody host (Glinwood and Pettersson, 2000a). Aphids must finish mating and oviposition before leaf abscission, which determines the success of overwintering of the clone (Glinwood and Pettersson, 2000b). Additionally, elevated CO₂ may accelerate the senescence and abscission of the leaves of the woody host, thereby influencing oviposition and overwintering of aphids (Stiling et al., 2002).

Conclusions

A general prediction of the response of aphids to elevated CO₂ is currently impossible. Contrary to other insect guilds, some aphid species exhibit higher fitness under elevated CO₂ conditions. Understanding the unique pattern of how aphids interact with their host plant can elucidate the species-specific responses of aphids to elevated CO₂. Newman (2003) constructed a mathematic model and concluded that aphid populations tend to be larger under elevated CO₂ if soil N levels are high, that the nitrogen requirement of aphids is low and that their density-dependent response is weak. Although this model attempts to give us a general prediction and explanation, it still lacks the physiological and molecular evidence to explain why some aphids are more successful in elevated CO₂ environments. Thus, further work examining the plant–aphid interactions in elevated CO₂ conditions using micro-array technology is suggested to drive the current knowledge from descriptive to mechanistic.

Acknowledgments

This project was supported by the “National Basic Research Program of China” (973 Program) (No. 2006CB102006), the National Nature Science Fund of China (No. 30770382, 31000854 and 30621003) and National Key Technology R&D Program (2008BADA5B01-04).

References

- Abisgold, J.D., Simpson, S.J., Douglas, A.E., 1994. Nutrient regulation in the pea aphid, *Acyrtosiphon pisum*: application of a novel geometric framework to sugar and amino acid composition. *Physiol. Entomol.* 19, 95–102.
- Awmack, C.S., Harrington, R., Leather, S.R., Lawton, J.H., 1996. The impacts of elevated CO₂ on aphid–plant interactions. *Aspects Appl. Biol.* 45, 317–322.
- Awmack, C.S., Woodcock, C.M., Harrington, R., 1997. Climate change may increase vulnerability of aphids to natural enemies. *Ecol. Entomol.* 22, 366–368.
- Barbehenn, R.V., Chen, Z., Karowe, D.N., Spickard, A., 2004. C3 grasses have higher nutritional quality than C4 grasses under ambient and elevated atmospheric CO₂. *Global Change Biol.* 10, 1565–1575.
- Bezemer, T.M., Jones, T.H., 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂ quantitative analyses and guild effects. *Oikos* 82, 212–222.
- Bezemer, T.M., Knight, K.J., Newington, J.E., Jones, T.H., 1999. How general are aphid responses to elevated atmospheric CO₂? *Ann. Entomol. Soc. Am.* 92, 724–730.
- Chen, F.J., Wu, G., Ge, F., 2004. Impacts of elevated CO₂ on the population abundance and reproductive activity of aphid *Sitobion avenae* Fabricius feeding on spring wheat. *J. Appl. Entomol.* 128, 723–730.
- Chen, F.J., Ge, F., Parajulee, M.N., 2005a. Impact of elevated CO₂ on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossypii*, and *Leis axyridis*. *Environ. Entomol.* 34, 37–46.
- Chen, F.J., Wu, G., Ge, F., Parajulee, M.N., Shrestha, R.B., 2005b. Effects of elevated CO₂ and transgenic Bt cotton on plant chemistry, performance, and feeding of an insect herbivore, the cotton bollworm. *Entomol. Exp. Appl.* 115, 341–350.
- Coviella, C.E., Trumble, J.T., 1999. Effects of elevated atmospheric carbon dioxide on insect–plant interactions. *Conserv. Biol.* 13, 700–712.
- Denno, R.F., Kaplan, I., 2007. Plant-mediated interactions in herbivorous insects: mechanisms, symmetry, and challenging the paradigms of competition past. In: Ohgushi, T., Craig, T.P., Price, P.W. (Eds.), *Ecological Communities: Plant Mediation in Indirect Interaction Webs*. Cambridge University Press, London, pp. 19–50.
- Diaz, S., Fraser, L.H., Grime, J.P., Falczuk, V., 1998. The impact of elevated CO₂ on plant–herbivore interactions: experimental evidence of moderating effects at the community level. *Oecologia* 117, 177–186.
- Dixon, A.F.G., 1971. The life cycle and host preferences of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.) and their bearing on the theories of host alternation in aphids. *Ann. Appl. Biol.* 68, 135–147.
- Dixon, A.F.G., 1998. *Aphid Ecology*, 2nd edn. Chapman and Hall, London, UK.
- Dixon, A.F.G., Wellings, P.W., Carter, C., Nichols, J.F.A., 1993. The role of food quality and competition in shaping the seasonal cycle in the reproductive activity of the sycamore aphid. *Oecologia* 95, 89–92.
- Docherty, M., Wade, F.A., Hurst, D.K., Whittaker, J.B., Lea, P.J., 1997. Responses of tree sap-feeding herbivores to elevated CO₂. *Global Change Biol.* 3, 51–59.
- Glinwood, R., Pettersson, J., 2000a. Change in response of *Rhopalosiphum padi* spring migrants to the repellent winter host component methyl salicylate. *Entomol. Exp. Appl.* 94, 325–330.
- Glinwood, R., Pettersson, J., 2000b. Movement by mating females of a host alternating aphid: a response to leaf fall. *Oikos* 90, 43–49.
- González, W.L., Fuentes-Contreras, E., Niemeyer, H.M., 2002. Host plant and natural enemy impact on cereal aphid competition in a seasonal environment. *Oikos* 96, 481–491.
- Harrington, R., Woiwood, I., Sparks, T., 1999. Climate change and trophic interactions. *Trends Ecol. Evol.* 14, 146–150.
- Hartley, S.E., Jones, C.G., Couper, G.C., Jones, T., 2000. Biosynthesis of plant phenolic compounds in elevated atmospheric CO₂. *Global Change Biol.* 6, 497–506.
- Hughes, L., Bazzaz, F.A., Lesley, H., Fakhri, A.B., 2001. Effects of elevated CO₂ on five plant–aphid interactions. *Entomol. Exp. Appl.* 99, 87–96.
- Hunter, M.D., 2001. Effects of elevated atmospheric carbon dioxide on insect–plant interactions. *Agric. For. Entomol.* 3, 153–159.
- Inbar, M., Eshel, A., Wool, D., 1995. Interspecific competition among phloem-feeding insects mediated by induced host–plant sinks. *Ecology* 76, 1506–1515.
- Intergovernmental Panel on Climate Change, 2007. *Climate Change 2007: the physical science basis. Summary for policy makers. Report of Working Group I of the Intergovernmental Panel on Climate Change*. <http://www.ipcc.ch/pub/spm18-02.pdf>.
- Kunert, G., Otto, S., Weisser, W.W., Röse, U.S.R., Gershenzon, J., 2005. Alarm pheromone mediates production of winged dispersal morphs in aphids. *Ecol. Lett.* 8, 596–603.
- Li, P., Ainsworth, E.A., Leakey, A.D.B., Ulanov, A., Lozovaya, V., Ort, D.R., Bohnert, H.J., 2008. *Arabidopsis* transcript and metabolite profiles: ecotype-specific responses to open-air elevated [CO₂]. *Plant Cell Environ.* 31, 1673–1687.
- Liu, T.X., Yue, B., 2001. Comparison of some life history parameters between alate and apterous forms of turnip aphid (Homoptera: Aphididae) on cabbage under constant temperatures. *Fla. Entomol.* 84, 239–242.
- Mondor, E.B., Tremblay, M., Awmack, C.S., Lindroth, R.L., 2004. Divergent pheromone-mediated insect behaviour under global atmospheric change. *Global Change Biol.* 10, 1820–1824.
- Mondor, E.B., Tremblay, M.N., Awmack, C.S., Lindroth, R.L., 2005. Altered genotypic and phenotypic frequencies of aphid populations under enriched CO₂ and O₃ atmospheres. *Global Change Biol.* 11, 1990–1996.
- Montgomery, M.E., Nault, L.R., 1977. Comparative response of aphids to the alarm pheromone, (E)-beta-farnesene. *Entomol. Exp. Appl.* 22, 236–242.
- Nault, L.R., Edwards, L.J., Styer, W.E., 1973. Aphid alarm pheromones: secretion and reception. *Environ. Entomol.* 2, 101–105.
- Newman, J.A., 2003. Climate change and cereal aphids: the relative effects of increasing CO₂ and temperature on aphid population dynamics. *Global Change Biol.* 10, 5–15.
- Newman, J.A., Gibson, D.J., Parsons, A.J., Thornley, J.H.M., 2003. How predictable are aphid population responses to elevated CO₂? *J. Anim. Ecol.* 72, 556–566.
- Peltonen, P.A., Julkunen-tiitto, R., Vapaavuori, E., Holopainen, J.K., 2006. Effects of elevated carbon dioxide and ozone on aphid oviposition preference and birch bud exudate phenolics. *Global Change Biol.* 12, 1670–1679.
- Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R., Karnosky, D.F., 2002. Altered performance of forest pests under atmospheres enriched by CO₂ and O₃. *Nature* 420, 403–407.
- Powell, G., Hardie, J., 2002. Xylem ingestion by winged aphids. *Entomol. Exp. Appl.* 104, 103–108.
- Pritchard, S.G., Rogers, H.H., Prior, S.A., Peterson, C.M., 1999. Elevated CO₂ and plant structure: a review. *Global Change Biol.* 5, 807–837.
- Pritchard, J.B., Griffiths, B., Hunt, E.J., 2007. Can the plant-mediated impacts on aphids of elevated CO₂ and drought be predicted? *Global Change Biol.* 13, 1616–1629.
- Reich, P.B., Hungate, B.A., Luo, Y., 2006. Carbon–nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annu. Rev. Ecol. Syst.* 37, 611–636.
- Rhodes, J.D., Croghan, P.C., Dixon, A.F.G., 1996. Uptake, excretion and respiration of sucrose and amino acids by the pea aphid, *Acyrtosiphon pisum*. *J. Exp. Biol.* 199, 1269–1276.
- Sandström, J.P., Moran, N.A., 1999. How nutritionally imbalanced is phloem sap for aphids? *Entomol. Exp. Appl.* 91, 203–210.
- Stacey, D.A., Fellowes, M.E., 2002. Influence of elevated CO₂ on interspecific interactions at higher trophic levels. *Global Change Biol.* 8, 668–678.
- Stiling, P., Cornelissen, T., 2007. How does elevated carbon dioxide (CO₂) affect plant–herbivore interactions? A field experiment and meta-analysis of CO₂-mediated changes on plant chemistry and herbivore performance. *Global Change Biol.* 13, 1823–1842.
- Stiling, P., Cattell, M., Moon, D.C., Rossi, A., Hungate, B.A., Hymus, G., Drakes, B., 2002. Elevated atmospheric CO₂ lowers herbivore abundance, but increase leaf abscission rates. *Global Change Biol.* 8, 658–667.
- Sun, Y., Chen, F.J., Ge, F., 2009a. Elevated CO₂ changes interspecific competition among three species of wheat aphids: *Sitobion avenae*, *Rhopalosiphum padi*, and *Schizaphis graminum*. *Environ. Entomol.* 38, 26–34.
- Sun, Y., Jing, B.B., Ge, F., 2009b. Response of amino acid changes in *Aphis gossypii* (Glover) to elevated CO₂ levels. *J. Appl. Entomol.* 133, 189–197.
- Sun, Y., Cao, H., Yin, J., Kang, L., Ge, F., 2010a. Elevated CO₂ changes the interactions between nematode and tomato genotypes differing in the JA pathway. *Plant Cell Environ.* 33, 729–739.
- Sun, Y., Feng, L., Gao, F., Ge, F., 2010b. Effects of elevated CO₂ and plant genotype on interactions among cotton, aphids, and parasitoids. *Insect Sci.* 00, 1–11. doi:10.1111/j.1744-7917.2010.01328.x.
- Sun, Y., Su, J.W., Ge, F., 2010c. Elevated CO₂ reduces the response of *Sitobion avenae* (Homoptera: Aphididae) to alarm pheromone. *Agric. Ecosyst. Environ.* 135, 140–147.
- Watling, J.R., Press, M.C., Quick, W.P., 2000. Elevated CO₂ induces biochemical and ultrastructural changes in leaves of the cereal sorghum. *Plant Physiol.* 123, 1143–1152.
- Wilkinson, T.L., Douglas, A.E., 2003. Phloem amino acids and the host plant range of the polyphagous aphid, *Aphis fabae*. *Entomol. Exp. Appl.* 106, 103–113.
- Wu, G., Chen, F.J., Ge, F., 2006. Response of multiple generations of cotton bollworm *Helicoverpa armigera* Hübner, feeding on spring wheat, to elevated CO₂. *J. Appl. Entomol.* 130, 2–9.
- Yin, J., Sun, Y., Wu, G., Parajulee, M.N., Ge, F., 2009. No effects of elevated CO₂ on the population relationship between cotton bollworm, *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae), and its parasitoid, *Microplitis mediator* Haliday (Hymenoptera: Braconidae). *Agric. Ecosyst. Environ.* 132, 267–275.
- Zavala, J.A., Casteel, C.L., DeLucia, E.H., Berenbaum, M.R., 2008. Anthropogenic increase in carbon dioxide compromises plant defense against invasive insects. *PNAS* 105, 5129–5133.
- Zavala, J.A., Casteel, C.L., Nabity, P.D., Berenbaum, M.R., DeLucia, E.H., 2009. Role of cysteine proteinase inhibitors in preference of Japanese beetles (*Popillia japonica*) for soybean (*Glycine max*) leaves of different ages and grown under elevated CO₂. *Oecologia* 161, 35–41.
- Zhang, G., Hu, C., Su, J., Ge, F., 2009. Electrical penetration graph (EPG) of feeding behavior of *Sitobion avenae* (Fab.) on resistant and susceptible wheat plants grown under elevated CO₂ concentration. *Acta Ecol. Sin.* 29, 4745–4752 (in Chinese with English abstract).
- Zou, Y.D., Huang, S.X., Di, J.G., Chen, G.C., Meng, Q.L., Ma, F., Wang, G.M., Hu, M.L., Ji, J., 1997. Factorial analysis on alate rate of *Sitobion avenae* and *Schizaphis graminum* adults. *Chin. J. Appl. Ecol.* 8, 189–193.