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Review

How do aphids respond to elevated CO_2?

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ABSTRACT

The performance of herbivore insects is determined directly by the quality of host plants. Elevated CO_2 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 CO_2 and were the only feeding guild to respond positively to elevated CO_2. Although many studies attempt to illuminate the interaction between aphids and plants under elevated CO_2, few studies can explain why some aphids are more successful than other chewing insects in elevated CO_2. Elevated CO_2 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 CO_2 using a single plant component. Instead, it is more likely that aphids are able to overcome the disadvantages of the indirect effects of elevated CO_2 by reducing developmental times and increasing fecundity under elevated CO_2 conditions. Our results provide several clues to why some aphids are successful in elevated CO_2 conditions. We review recent studies of the effects of elevated CO_2 on aphids and discuss the effects of elevated CO_2 on aphid performance on crops using cotton and cereal aphids as examples.

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Introduction

Owing to human activity and to the increased use of fossil fuels, global atmospheric CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 treatment used in global change biology experiments was one and a half or two times the ambient CO_2

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concentration (~600–750 ppm). Compared with weak direct effects, the impact of elevated CO_2 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 CO_2 conditions (Chen et al., 2005b; Wu et al., 2006). In contrast, phloem sap-suckers (e.g., aphids) have a more complex response to elevated CO_2 (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 CO_2 (Pritchard et al., 2007). Thus, comprehensive understanding of aphid from ecological and physiological view may explain how elevated CO_2 modifies the interaction between plant and aphid.

Growth and development

Aphid responses to elevated CO_2 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 CO_2 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 CO_2 on different host plants. For example, Awmack et al. (1996) found that elevated CO_2 increased the fecundity of cereal aphid *Sitobion avenae* when reared on winter wheat. Diaz et al. (1998), however, reported that elevated CO_2 did not change fecundity of cereal aphid when reared on four *Poacea* species. The effects of elevated CO_2 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 CO_2 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 CO_2 conditions, the outcome could be modified by nutrient availability and sensitivity of the plant to elevated CO_2.

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 CO_2 increases the C:N ratio and reduces amino acids in plants, there is no evidence that elevated CO_2 induces the winged morph of aphid.

Elevated CO_2 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 CO_2 treatment (Chen et al., 2004). Additionally, aphids preferred ovipositing on elevated CO_2-grown plants. However, the cause of these changes is unknown. Although several studies have shown that elevated CO_2 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 CO_2 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 CO_2 levels, but the pink genotype was not. These two genotypes also displayed marked differences in phenotypic frequencies. 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 CO_2 increases sucrose in plant tissues, which may explain why cereal aphids prefer wheat plants grown in elevated CO_2 (Awmack et al., 1996).

Aphids face many structural barriers before they can feed successfully from a sieve element elevated CO_2 may affect these structures and modify the feeding behavior of aphids. Elevated CO_2 generally increased the C:N ratio of plant tissues and “excess” carbon was possibly allocated to cell wall (Pritchard et al., 1999). Elevated CO_2 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 CO_2. 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 CO_2 delayed the first shown time of E1 wave which presents the attempting to probe the phloem sieve and excreting watery saliva. Besides, elevated CO_2 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 CO_2 conditions would spend more time to probe and ingest from host plants than aphids reared under ambient CO_2 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 CO_2 environments. Amino acid concentrations were lower in phloem of cotton plants grown under elevated CO_2 conditions than those grown under ambient CO_2 conditions. Higher amounts of free amino acids were found in cotton aphids fed on cotton grown in elevated CO_2 conditions but the contents of amino acids in honeydew were not significantly affected by elevated CO_2. More honeydew was produced by cotton aphids reared under elevated CO_2 conditions than those reared under ambient CO_2 conditions, which indicates that cotton aphids ingest more cotton phloem owing to the higher C:N ratio of cotton phloem in elevated CO_2 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 CO_2 (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 CO_2 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 CO_2 conditions. Furthermore, compensatory feeding may act to satisfy aphid growth requirements (Awmack et al., 1997). For example, the growth of *Acyrthosiphon 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 CO_2 is likely to change these interactions (Inbar et al., 1995; Gonzáles et al., 2002). Aphid species often respond differently to the same host plants grown under elevated vs. ambient CO_2, 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 CO_2 vs. ambient CO_2. 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 CO_2 (Denno and Kaplan, 2007). Sun et al. (2009a) examined effects of elevated CO_2 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 CO_2 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 CO_2 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 CO_2 environments. Microarrays were used to examine *Arabidopsis* responding to elevated CO_2. It was concluded that elevated CO_2 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 CO_2 may modify induced defenses of plants when damaged by insect herbivores (Stiling and Cornelissen, 2007; Li et al., 2008). 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 jasmonic acid (JA) pathway (Zavala et al., 2008, 2009). Thus, the evidence that elevated CO_2 can change induced defenses was found only in chewing insect-damaged plants. It is still unclear whether elevated CO_2 changes phloem sucker-induced defenses (i.e. salicylic acid signaling pathway). Further study should determine whether elevated CO_2 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 CO_2, 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 CO_2 conditions than under ambient CO_2 conditions. Mondor et al. (2004) found that the aphid *Chaitophorus stevensis* on trembling aspen trees exhibited diminished escape responses under elevated CO_2 conditions. Sun et al. (2010c) also found that elevated CO_2 reduces the response of *S. avenae* to alarm pheromone. This phenomenon can be explained by elevated CO_2-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 CO_2 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 CO_2 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 CO_2 is currently impossible. Contrary to other insect guilds, some aphid species exhibit higher fitness under elevated CO_2 conditions. Understanding the unique pattern of how aphids interact with their host plant can elucidate the species-specific responses of aphids to elevated CO_2. Newman (2003) constructed a mathematic model and concluded that aphid populations tend to be larger under elevated CO_2 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 CO_2 environments. Thus, further work examining the plant–aphid interactions in elevated CO_2 conditions using micro-array technology is suggested to drive the current knowledge from descriptive to mechanistic.

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