

Potential effects of elevated carbon dioxide on leaf-feeding forest insects

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Abstract The elevated concentration of atmospheric CO₂ may result in a decline of leaf nutritional quality (especially N) and an increase in some kinds of defensive secondary components (such as phenolics). The changes in the phytochemistry of trees, combined with the effect of elevated CO₂ *per se*, have a potential negative influence on insect herbivores. Here, we review the effect of elevated CO₂ on the performance of leaf-feeding forest insects at individual-level and community-level. The elevated CO₂ *per se* have little influence on the metabolism of insects. Over half of the tree-insect experimental systems show that the performance of individual insect become poorer under high-CO₂ grown trees; but the others show that the insects have just little or no response to the treatments. The direction and magnitude of the changes in the performance of insects could be mediated by various factors. The effects of treatment are strongly species-dependent. The magnitude of changes in the phytochemistry, the sensitivity and adaptive capacity of insects to the poorer leaf quality, the differences in plant growth conditions and experimental methods, and the mediated effects of other environmental factors (such as soil nutrient availability, light, temperature, O₃) were all closely related to the final performance of insects. However, the larvae's consumption usually increased under enriched CO₂ treatment, which was widely thought to be a compensatory response to poorer plant quality. The experiments on forest community-level found identically a reduction in herbivory, which was contrary to the results from small-scale experiments. The changes in insect population and the actual response of consumption by leaf-feeding forest insects under CO₂ enrichment remain

unclear, and more field-based experiments need to be conducted.

Keywords elevated CO₂, forest, leaf-feeding insect, phytochemistry, herbivory

1 Introduction

Due to increased fossil-fuel emission and land use changes (especially the loss of tropical rain forests), the atmospheric concentration of CO₂ had increased from 280 μL·L⁻¹ in the pre-industrial times to 368 μL·L⁻¹ in the year 2000, and it is still increasing (IPCC, 2001). The predicted concentration of CO₂ will range from 540 to 970 μL·L⁻¹ in the year 2100 (IPCC, 2001). Exploring the biological significance of atmospheric CO₂ enrichment has been one of the most important subjects of ecological research (Coviella and Trumble, 1999). These studies pay great attention to the responses of plant growth and physiology (Ceulemans and Mousseau, 1994; Curtis and Wang, 1998). Nearly all the life on earth is based on the photosynthesis of green plants. Therefore, atmospheric CO₂ enrichment will also have potential influences on the species at other trophic levels (Hättenschwiler and Schafellner, 1999; Korner, 2003). Many scholars have studied the potential effects of atmospheric CO₂ enrichment on phytophagous insects (Bezemer and Jones, 1998; Coviella and Trumble, 1999), but few researches have been conducted on this subject in China (Zhang et al., 2001; Chen et al., 2004; 2005). A wide range of studies have indicated that elevated atmospheric CO₂ could not only increase photosynthesis, growth and biomass (Hunter, 2001), but also accumulate non-structural carbohydrate, decrease nitrogen concentrations and enhance carbon/nitrogen ratio in plant tissues (Traw et al., 1996; Norby et al., 1999). The higher carbon/nitrogen ratio may in turn

result in the accumulation of carbon-based secondary metabolites (Watt et al., 1995; Veteli et al., 2002). The CO₂-induced changes in the chemical components of green leaves, which have important impacts on phytophagous insects, will both influence the quality and availability of food for insects (Hättenschwiler and Schafellner, 1999; Williams et al., 2003), and further influence the consumption, growth, development and population dynamics of insect herbivores. The changes in these individual and population parameters of insect may feedback to affect plant communities and productivities (Watt et al., 1995; Lindroth, 1996b; Korner, 2003; Hamilton et al., 2004).

Forests cover about one-third of the earth's surface and conduct about two-thirds of global photosynthesis; therefore, they play an extremely important role in the global carbon cycle and balance (Lindroth, 1996a; Liu et al., 1998). The consumption activities of insect herbivores affect the forest primary productivity, species composition, energy flow and nutrient cycle (Lindroth, 1996a). Forest net primary productivity, which is removed by leaf-feeding insects, can be considerable, typically ranging from about 2% to 15%. However, this percentage can exceed 70% during outbreaks of insects (Hamilton et al., 2004). Therefore, investigating the effects of elevated atmospheric CO₂ on the interactions between trees and leaf-feeding insects is of particular importance. Furthermore, the effects of forest insect herbivores, especially the potential influences of insect defoliation on forest productivity should also be considered while assessing the impacts of elevated atmospheric CO₂ on forest ecosystems. The herbivorous insects that cause the greatest damage to forest ecosystems are mainly the leaf-feeders, which have chewing mouthparts and are primarily in the orders of Lepidoptera and Hymenoptera (Lindroth, 1996b); thus, the focus of this article is to review the primary experimental methods and results about these leaf-chewers.

2 CO₂ fumigation systems

At present, the commonly used CO₂ fumigation systems include: (1) The environmental controlled (airtight) facilities, which include the air-controlled growth chamber. These facilities can control the environmental variables accurately and constantly. (2) Open-top chambers (OTCs), which can be used in the field and are inexpensive to build and maintain. (3) Free-Air CO₂ Enrichment (FACE), which is most suitable for investigating the effects of the changes in atmospheric compositions on the interaction of plant-insect population at larger temporal and spatial scales. However, the maintenance cost is extremely expensive (Strain, 1991; Ceulemans and Mousseau, 1994; Liu et al., 1998; Jiang and Qu, 2000).

3 The responses of leaf-chewing forest insects to elevated CO₂ at individual level

3.1 The effect of high CO₂ *per se* on the performance of leaf-chewing insect individuals

Both host plant quality and non-biological environmental factors influence the insect's food choice and recognition behaviors before ingestion and the food consumption during ingestion, and also influence the food utilization rate and insect performance after ingestion (Scriber and Slansky, 1981). Therefore, in theory, both high CO₂ *per se* and CO₂-induced changes in the host-plant physiology will influence the consumption, growth and development of leaf-chewing insects (Willimas et al., 2003).

Rearing insect herbivores with artificial food in different CO₂ concentrations can exclude the indirect effect of the changes in plant physiology and separate the direct effect of high CO₂ *per se* on the performance of insects. Agrell et al. (2000) conducted a similar experiment, but they did not find that the survival, development and body weight of *Orgyia leucostigma*, which fed on standard artificial food, were directly influenced by high CO₂ *per se*.

Nevertheless, some scholars presumed that some insect the host-locating behavior or the frequency of spiracular opening might be affected by elevated CO₂ (Wu and Jin, 1993; Lincoln, 1993; Covilella et al., 1999). Kopper and Lindroth (2003b) showed that the natural colonization rate of leafminer (*Phyllonorycter tremuloidella*) for tree species (*Populus tremuloides*) that grew in FACE (free-air CO₂ enrichment) was reduced by 42% at high CO₂ (about 560 ppm) compared with that at ambient CO₂. Although the extremely high CO₂ can influence the insect physiology, growth and development intensely, or even cause insect death (Wu and Jin, 1993), there is no experimental evidence indicating that the metabolism and performance of leaf-chewing insect individuals are affected by enriched atmospheric CO₂ levels (such as doubled CO₂ level) (Lincoln, 1993; Covilella et al., 1999; Agrell et al., 2000).

3.2 Effect of CO₂-induced changes in phytochemistry on performance of leaf-chewing insect individuals

3.2.1 Phytochemical changes

A wide range of studies show that the foliar chemistry consistently respond to elevated CO₂ with nitrogen concentration reducing and starch content increasing (Table 1 and 2). The response of the secondary metabolites and soluble sugar concentrations are different for different tree species and compounds. It is generally believed that CO₂-induced changes in foliar chemistry

Table 1 Effect of elevated CO₂ on leaf chemistry and insect performance in relative long-term feeding trials (several instars or the whole larval stage)

insect species	host species	insect performance				leaf chemistry			references
		TC	RGR	development time	pupal weight	N	starch	condensed tannin	
<i>Operophtera brumata</i>	<i>Quercus robur</i>	↑	—	ns	ns	↓	—	ns	Buse et al., 1998
<i>Lymantia dispar</i>	<i>Betula allegheniensis</i>	—	♀ ↓ * σns	ns	♀ ↓ 38*** σns	↓	ns	↑***	Traw et al., 1996
	<i>Betula populifolia</i>	—	♀ ↓ *** σ ↓	♀ ↑ ** σ ↑ *	ns	↓	↑***	↑***	Traw et al., 1996
	<i>Quercus petraea</i>	—	↓ 30	—	—	↓	↑ 42	↑	Hättenschwiler and Schafellner, 2004
	<i>Fagus sylvatica</i>	—	ns	—	—	ns	↑ 21	↓	Hättenschwiler and Schafellner, 2004
	<i>Carpinus betulus</i>	—	↑ 29	—	—	↑	↓ 32	ns	Hättenschwiler and Schafellner, 2004
<i>Malacosoma disstria</i>	<i>Acer rubrum</i>	—	—	ns	ns	↓	ns	—	Williams et al., 2003
	<i>Populus tremuloides</i>	↑ * ③	♀ ↓ σ ↓	♀ ↑ 9* σ ↑ 12 ^s	ns	↓ 18 ^s	ns	↑ *	Lindroth et al., 1997
	<i>Populus tremuloides</i>	—	—	—	♀ ↓ ①	—	—	↑ ②	Percy et al., 2002
	<i>Populus tremuloides</i>	—	—	♀ ns; G ₂₁₆ σ ↑	ns	↓ ns	ns	ns	Holton et al., 2003
	<i>Populus tremuloides</i>	G ₂₁₆ ns; G ₂₇₁ ↓ 16 ③	—	G ₂₇₁ ♀ ↑ 11; σ ns	ns	↓ 13	↑ 19	ns	Kopper and Lindroth, 2003a
<i>Phyllonorycter tremuloidella</i>	<i>Populus tremuloides</i>	ns	—	ns	ns	↓ 11	ns	ns	Kopper and Lindroth, 2003b
<i>Orygia leucostigma</i>	<i>Populus tremuloides</i>	—	—	G ₂₇₁ ♀ ↑ *; G _{259,271} σ ↑ *	G ₂₅₉ ♀ ↓ ***; σ ns	↓ 5	ns	G ₂₁₆ ↓ ; G _{259,271} ↑	Lindroth et al., 2002

Note: TC: total consumption; PGR: relative growth rate; Number after arrows represents the increase or decrease percentage in insect performance under elevated CO₂; —: not measured parameters; *, **, *** and **** indicate significant differences at $P < 0.1$, $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively; ns: not significant; Only part of the phytochemistry data are included in this table; ①: More significant under high O₃; ②: Phenolic glycosides concentration; ③: G₂₁₆, G₂₇₁, G₂₅₉ indicate aspen genotype 216, 271, 259, respectively; ④: Total frass production was measured as an index of leaf consumption.

Table 2 Effect of elevated CO₂ on leaf chemistry and insect performance in short-term feeding trials (only one instar)

insect species	host species	consumption				insect performance			food utilization efficiencies				leaf chemistry			references
		RCR		TC	RGR	development time	final weight	AD	ECD	ECI	nitrogen	starch	condensed tannin			
		↑	ns	↓	↑	↓	↑	↓	↓	↓	↑	↑	↑			
<i>Lymantria dispar</i>	<i>Populus tremuloides</i>	↑100***	↑100***	↓35***	↑25**	↓*	↑14*	↓ ^{ns}	↓***	↓***	↑***	↑ ^{ns}	↑ ^{ns}	Lindroth et al., 1993		
	<i>Quercus rubra</i>	ns	ns	↑20 ^s	ns	↑*	↑51*	↓*	ns	ns	↑*	↑ ^{ns}	Lindroth et al., 1993			
	<i>Acer saccharum</i>	ns	ns	ns	ns	ns	↓27 ^s	↑*	ns	↓***	ns	↑*	Lindroth et al., 1993			
	<i>Pinus strobus</i>	↑ ^s ⓪	↑ ^s	ns	↑***	ns	ns	ns	ns	ns	↑ ^{ns}	↑ ^{ns}	Roth and Lindroth, 1994			
	<i>Betula papyrifera</i>	ns	ns	↓*	ns	↓*	ns	ns	↓***	↓ ^s	↑ ^{ns}	↑ ^s	Roth and Lindroth, 1994			
	<i>Populus tremuloides</i>	↑14 ^s	ns	♀↑18♂↓13	ns	—	♀↓23♂↓7	ns	ns	↓18 ^s	ns	↑*	Lindroth et al., 1997			
	<i>Populus tremuloides</i>	—	↑	↓30	↑	↓15	—	↓	—	↓12	↑270	↑44	Lindroth and Kinney, 1998			
	<i>Acer saccharum</i>	—	↑	ns	ns	ns	—	ns	—	↓24	↑	↑59	Lindroth and Kinney, 1998			
	<i>Populus tremuloides</i>	↑86 ^⓪	↑	ns	ns	ns	↑20	↓48	↓43	↓37	↑	↑	Kinney et al., 1997			
	<i>Acer saccharum</i>	↑7 ^⓪	↑	ns	ns	ns	↑6	↓6	↓5	↓43	↑	↑	Kinney et al., 1997			
<i>Malacosoma disstria</i>	<i>Quercus alba</i> L.	ns	—	EI ↓ * LI ns ^⓪	—	—	ns	EI ns	EI ns	↓*	IL ns	—	Williams et al., 1998			
	<i>Acer rubrum</i>	—	ns	AT ↓ 39 ET ↓ 7 ^⓪	—	—	—	LI ↓ ^s	LI ↓ ^s	↓*	ML ↑ ^s ⓪	↑ ^s	Williams et al., 2000			
	<i>Acer saccharum</i>	—	ns	ns	—	—	—	—	—	↓*	↑ ^{ns}	—	Williams et al., 2000			
	<i>Populus tremuloides</i>	↑75*	↑100***	↓20 ^s	ns	ns	ns	ns	↓ ^s	↓***	↑***	↑ ^{ns}	Lindroth et al., 1993			
	<i>Quercus rubra</i>	ns	↑145 ^s	ns	ns	ns	ns	ns	↓*	ns	↑*	↑ ^{ns}	Lindroth et al., 1993			
	<i>Acer saccharum</i>	ns	↓25*	ns	ns	↓*	ns	ns	ns	↓***	ns	↑*	Lindroth et al., 1993			
	<i>Populus tremuloides</i>	ns	—	↓	ns	—	ns	↓	↓	↓	↑	↑	Roth et al., 1994			
	<i>Acer saccharum</i>	↑40	—	↓	ns	—	—	↓	↓	IL ↓ **	↑	ns	Roth et al., 1994			
	<i>Quercus alba</i> L.	ns	—	ns	—	—	ns	ns	ns	ML ↓ *	IL ns	—	Williams et al., 1998			
	<i>Picea abies</i>	↑ ^s	↓*	↓**	—	↓*35	—	—	↓*	ML ↓ *	ML ↑ ***	↑100***	↑15***	Hättenschwiler et al., 1999		
<i>Lymantria monacha</i>	<i>Pinus elliotii</i>	—	—	↓21.9 ^s	—	↓65.1	ns	ns	↓27***	—	—	ns	Saxon et al., 2004			
	<i>Pinus taeda</i> (L.)	↑*	—	ns	—	—	—	↓*	↓28***	↑46	—	—	Williams et al., 1994			
	<i>Salix myrsinifolia</i>	↑ ^s	—	↓14*	—	—	—	—	↓*	—	—	—	Traw et al., 1996			

Note: ⓪ Date indicate consumption rate; ⓪ EI, LI indicate early instar and late instar, respectively; ⓪ IL, ML indicate immature and mature leaves, respectively; ⓪ AT, ET indicate CO₂ enrichment at ambient- and high-temperature condition, respectively. More notation is in Table 1.

play the most important role on the performance of leaf-feeding insects. The changes in both the primary metabolites (nutrient components, such as non-structural carbohydrates and protein) and secondary metabolites (allelochemicals) will markedly influence the performance of insects (Lindroth, 1996a).

Leaf nitrogen concentration is the key factor that affects the consumption, digestion, growth and development and the reproduction of herbivorous insects (Williams et al., 1994; Saxon et al., 2004). Several review articles have shown that the leaf nitrogen contents of trees grown under elevated CO₂ decrease by 21% (McGuire et al., 1995), 16% (Curtis and Wang, 1998), or 13% (Norby et al., 1999) on average. Because starch can facilitate food assimilation, the higher starch concentrations in leaves may be beneficial to leaf-feeding insects (Watt et al., 1995). The carbon-based secondary compounds (e.g. tannin) and structural carbohydrates (e.g. cellulose) can influence insect growth by retarding herbivory and decreasing assimilation rate, and the concentrations of these components will increase under an elevated CO₂ environment according to the carbon-nutrient balance hypothesis (Bryant et al., 1983; Peñuelas and Estiarte, 1998; Coviella et al., 1999). But so far, the results of a large number of studies about these compounds are not consistent. Of these, the concentration of monoterpene was often unaffected or just marginally affected by elevated CO₂ (Williams et al., 1994; Roth and Lindroth, 1994), concomitant with the definite increases in the soluble phenolics and in particular, the condensed tannins (Peñuelas and Estiarte, 1998).

3.2.2 The responses of total consumption and consumption rate of leaf-feeding insect individuals

Most feeding experiments in laboratories are non-choice trials, which usually only examine the response of one insect species to a single host plant. The common method in this kind of trial is rearing caterpillars in a Petri dish or similar containers using detached leaves to examine the effects of CO₂-induced changes in leaf quality (mainly chemical quality) on consumption, growth and food utilization rates of individual leaf-chewers. This kind of trial is usually short-term within only a single instar. Consumption was calculated as the initial leaf dry weight (converted from initial fresh weight with regression analysis) subtracting the remaining leaf dry mass after feeding trials. Because of the significant difference between feeding trials within Petri dishes and the herbivory in a natural environment, some researchers covered the insects and the whole plant (Traw et al., 1996; Buse et al., 1998) or its partial twigs (Hättenschwiler and Schafellner, 1999; Williams et al., 2000; Percy et al., 2002; Kopper and Lindroth, 2003a; Holton et al., 2003; Williams et al., 2003; Hättenschwiler

and Schafellner, 2004) in a nylon mesh bag, with both insects and plants exposed to elevated CO₂ at the same time and allowing the test insects to consume freely in the bags. These feeding trials also prolonged observation time, which allowed researchers to measure larval development time, mortality and pupal weight, etc., over the whole larval stage from egg or early instar to pupa (Traw et al., 1996; Agrell et al., 2000; Lindroth et al., 2002; Percy et al., 2002; Williams et al., 2003; Holton et al., 2003; Kopper and Lindroth, 2003a). To quantify the food consumption of on-tree feeding insects, the initial leaf area should be converted first to initial dry weight by area-mass regression formula (Williams et al., 2000; Kopper and Lindroth, 2003a).

Accumulated studies indicated that the leaf-feeding insects consumed more leaves under elevated CO₂ (Lindroth et al., 1993; Williams 1994; Roth et al., 1998; Buse et al., 1998; Veteli et al., 2002; Saxon et al., 2004). In this article, the responses of the tree-insect experimental systems are summarized in Table 1 and Table 2, and over 60% of which showed that the total consumption or consumption rate increased. The increase in the consumption of leaf-feeding insects under elevated CO₂ was generally attributed to the compensatory feeding to reduced nitrogen concentration in leaves (Lincoln, 1993; Lindroth, 1996b; Bezemer and Jones, 1998; Hunter, 2001). In other words, to accumulate enough nutrients for their development, herbivorous insects might compensate the dilution of nitrogen by eating more or faster (Veteli et al., 2002). In addition, CO₂-induced increase in foliar carbohydrates may act as a stimulus for insect herbivory (Lindroth, 1996b). However, different insect species have different abilities of compensatory feeding. If leaf nitrogen concentrations decline to a greater extent, consumption is unable to compensate completely for the reductions in ingested nitrogen. Moreover, this compensatory feeding behavior of insects under elevated CO₂ may also be associated with the increase in ingested secondary compounds (Lindroth et al., 1993; Lindroth, 1996a, 1996b; Coviella et al., 1999; Saxon et al., 2004), which will reduce the food utilization efficiencies (e.g., approximate digestibility and efficiency of conversion of digested food), and cause the subsequent poor growth and development performances.

3.2.3 The responses of growth and development of leaf-feeding insect individuals

Some non-choice feeding experiments based on single tree species showed that, at elevated CO₂, the altered tissue chemistry and the declined foliar palatability had negative effects on insects at different degrees (Lindroth et al., 1993; Roth and Lindroth, 1994; Traw et al., 1996; Lindroth et al., 1997; Roth et al., 1998; Hättenschwiler and Schafellner, 1999; Percy et al., 2002; Saxon et al., 2004; Hättenschwiler and Schafellner, 2004). With *Pinus*

elliottii and *Neodiprion lecontei* as experimental materials, Saxon et al. (2004) found that at elevated CO₂, the levels of leaf nitrogen declined by 27%, carbon/nitrogen ratio increased, leaf water concentrations declined by 7% and levels of total phenolics increased. At elevated CO₂, the larval weight was reduced by 65.1%; the relative growth rate (RGR) was decreased by 21.9% and the days to pupation prolonged 4.4 days than those of the control at ambient CO₂.

Over half of the tree-insect experimental systems summarized in this article showed that the performance of insect individuals became poorer under high-CO₂ grown trees (Table 1 and 2). In short-term feeding trials within one certain instar, the growth of insects were restrained and the development time prolonged. In relative long-term feeding trials within several instars or the whole larval stage, the development time of insects prolonged or pupal weight reduced. The reduction in female pupal weight may reduce fecundity (Lindroth et al., 2002), and the prolonged development time is likely to expose the insects to high hazards of predation and parasitism (Veteli et al., 2002; Willimas et al., 2003). Therefore, some scholars presumed that the reduced growth rate and prolonged development could turn to influence the survival and reproductive success of insects, which could in turn affect the population density of herbivorous insect. To some extent, however, insects at elevated CO₂ could compensate the reduced growth rate with prolonged development time (Roth and Lindroth, 1994; Lindroth, 1996b), which could keep the final weight or pupal weight approaching their counterparts at ambient CO₂. For example, the study of Lindroth et al. (1997) revealed that the growth rate of the gypsy moth larvae, especially females, reduced when fed high-CO₂ grown foliage, but the final pupal weight or fecundity did not change significantly. Lindroth et al. (1997) believed that the reason was that the insects prolonged their development time by about 3 days.

Some insects increased consumption rate under elevated CO₂, but they still exhibited significant reduction in growth rate and prolonged development time, which can not only be attributed to the incomplete compensation-feeding but also to the poor food processing efficiencies and particularly the poor conversion efficiency of digested food (ECD) (Lindroth et al., 1993; Lindroth, 1996a, 1996b; Agrell et al., 2000) (Table 1). Poor food-processing efficiencies are likely the consequence of decreased nitrogen and/or increased concentrations of allelochemicals (Lindroth, 1996b), but the contrary results that the approximate digestion rate (AD) increased under elevated CO₂ in some studies may be attributed to the accumulation of starch content (Lindroth et al., 1993). According to the correlation analysis between the changes in the phytochemistry and insect responses, researchers detected that the growth of insects (e.g. RGR) were positively related to the nitrogen content and negatively to some secondary metabolites

and starch/nitrogen ratios (Traw et al., 1996; Lindroth et al., 1997; Veteli et al., 2002; Saxon 2004; Hättenschwiler and Schafellner, 2004).

Although several other researchers showed that the palatability of leaves declined under elevated CO₂ compared with that under ambient CO₂, the performance of insect individuals was only marginally affected or not affected (Williams et al., 1994; Kinney et al., 1997; Buse et al., 1998; Williams et al., 2000; Holton 2003; Williams et al., 2003; Kopper and Lindroth, 2003a). For example, Willimas et al. (2003) found that the concentrations of foliar nitrogen and water of *Acer rubrum* L. grown at elevated CO₂ had a significant decrease, whereas mortality, development time to pupation and pupal weight of the gypsy moth larvae did not differ statistically between two CO₂ treatments. In other words, the alteration in foliar chemistry had no negative effect on gypsy moth larvae. In the study of Kopper and Lindroth (2003a), *Populus tremuloides* were grown in a FACE system to receive high CO₂ enrichment, and gypsy moth larvae were allowed to grow on trees within nylon bags. The results showed that elevated CO₂ had just little or no effect on larval development, consumption and pupal weight. Nevertheless, some scholars believed that the cumulation of multiple relatively minor effects might influence the insect population dynamics (Lindroth, 1996b). In addition, extremely few studies found that the growth rate of herbivorous insects increased under elevated CO₂ (Table 2).

It is obvious that although a large number of experimental studies have indicated that the phytochemistry changed and the tissue palatability for insect declined at elevated CO₂, the responses of these leaf-feeders were heterogeneous. On one hand, the differences in the sensitivity to high-CO₂ for different plants resulted in variable magnitudes of change in phytochemistry. Therefore, the response of the same kind of insect species differed when fed on different host plants (Lindroth et al., 1993; McDonal 1999; Williams et al., 2000). For example, Lindroth et al. (1993) showed that elevated CO₂ significantly decreased the foliar nitrogen concentrations and increased condensed tannin contents of quaking aspen (*Populus tremuloides*) and sugar maple (*Acer saccharum*). At elevated CO₂ conditions, the growth rate of forest tent caterpillar larvae feeding on aspen leaves was decreased by 120%, while the growth rate of larvae feeding on maple leaves was not affected. On the other hand, leaf-feeding insects differed in their ability to deal with the CO₂-induced reduction in leaf quality (Williams et al., 2003), thus, there will be a difference in the responses of different insect species feeding on the same host plant. For example, Williams et al. (1998) indicated that the ratio of total nonstructural carbohydrate to nitrogen of *Quercus alba* L. young leaves was significantly increased by elevated CO₂, and the changes in young leaf chemistry markedly reduced the growth rate

of early instar gypsy moth larvae, while the growth rate of early instar larvae of forest tent caterpillar were not affected. Williams et al. (1998) further proved that the differences in responses of the two insects could be attributed to the increase in the nitrogen utilization efficiency (NUE) of early instar forest tent caterpillar larvae, while early instar gypsy moth larval NUE remained unchanged.

In addition, the effects of elevated CO₂ on the insect performance differed in females and males (Traw et al., 1996; Lindroth et al., 1997; Kopper and Lindroth, 2003a). For example, the results of Traw et al. (1996) showed that the relative growth rate of female gypsy moth larvae grown on leaves of *Betula allegheniensis* at elevated CO₂ were significantly lower than their counterparts under ambient CO₂, and the pupal weight of females declined by 38%, while the growth rate and pupal weight of males were not affected by CO₂ enrichment.

The responses of different instar larvae to CO₂-induced changes in phytochemistry may be also different. For example, Lindroth et al. (1997) studied the growth and development of gypsy moth larvae from its third to fifth instar. The results showed that for the first 12 days, the difference in larval weights was little between CO₂ treatments. Then, however, larval weights diverged between treatments, with the larvae which fed on high-CO₂ foliar growing slower. This study also indicated that the alterations of insect performances would tend to be significant under long-term experiments, especially when the magnitude of the changes in phytochemistry was little.

In summary, the magnitude of changes in phytochemistry, the sensitivity and adaptive capacity of insect to the changes in leaf quality are all closely related to the final performance of insect grown under elevated CO₂. In other words, the responses of different species (plant & insect) to CO₂ enrichment are strongly species-dependent (Lindroth, 1996a; Hunter, 2001). Moreover, under elevated CO₂, the other environmental factors, such as soil nitrogen availability (Hättenschwiler and Schafellner, 1999; Saxon et al., 2004), light availability (Agrell et al., 2000) and temperature (Buse et al., 1998; Veteli et al., 2002; Williams et al., 2003) all affect the response magnitude of phytochemistry, which could in turn influence the insect performance. Therefore, the differences in plant growth conditions and experimental methods are another reason which caused the large variability of plant-insect responses in different studies. For the same reason, one should be very cautious to directly compare the data of plant-insect responses in different experimental conditions.

3.3 The limitations of artificial systems of tree-herbivorous insects

A controllable artificial environment is indispensable in the study of the responses of insect individuals to elevated CO₂ and altered plant quality (Hunter, 2001),

and it is necessary to reveal the insect physiological response and compensatory-feeding mechanism. However, the artificial systems of tree-herbivorous insect interactions usually only consist of two or a few species, which often have the following problems: (1) The excised leaves used in feeding trials within Petri dishes may change rapidly in terms of water and nutrient content (Brooks and Whittaker, 1998). (2) The food preference behaviors of the insect herbivores are always restricted, which may influence the preciseness of the insect response. While in nature, herbivorous insects could choose food from a larger range of host plants, or from different phenotypes of the same plant, or from different parts of an individual plant, which could greatly compensate the negative effects of poor tissue quality. (3) The effects of the other species on the third trophic level were not considered. The modified plant quality that is induced by elevated atmospheric CO₂ could affect the feeding of herbivorous insects, but the CO₂-mediated alterations in the “top-to-down” effects of the natural enemies, i.e., predators, parasitoids and pathogen of insect herbivores, could affect the individual and population responses of insects (Hunter, 2001; Veteli et al., 2002; Stiling et al., 2003). (4) The research duration may be too short for certain instar or even the whole larval stage. Some studies showed that the responses of early instar larvae differed from that of later instar larvae (Lindroth et al., 1997; Williams et al., 1998). Moreover, only insect feeding trials conducted for multi-generations could detect notable influences of CO₂-induced poor plant quality on insect herbivores (see Brooks and Whittaker, 1998), yet there are nearly no studies conducted over multi-generations of leaf-feeding forest insects. (5) The artificial environments for plant growth are different from that in nature (Hunter, 2001). For example, the stochastic fluctuations of artificial environments were eliminated; the roots of potted plants were restricted, and the nutrient or light availability was artificially changed, etc. These factors may disturb revealing the actual influence of elevated CO₂ on phytochemistry and insects. Therefore, when dealing with scale conversion, the insect population response and the changes in herbivores damage to trees and forests at elevated CO₂ are difficult to predict with the results of studies based on a few species.

4 Responses of leaf-feeding insects to elevated CO₂ at forest community-level

4.1 Changes in pest damage to forest

The studies at individual insect levels found that the herbivorous forest insect increased foliar consumption at

elevated CO₂. According to this result, some scholars presumed that the insect herbivores are likely to enhance damage to their preferred tree species along with the continuous increase in atmospheric CO₂ concentrations, or even to influence the competitive relationship among plant species in communities (Korner, 2003). Other scholars presumed that the increased consumption would reduce or counteract the productivity increased by “CO₂ fertilizer effect” (Lindroth et al., 1993; Watt et al., 1995). However, as pointed out by Hunter (2001), the increases in the per capita consumption of foliage by insects under elevated CO₂ does not mean that plants will suffer from more damage overall, because the pest damage to forests not only is related to the consumption ability of individual insects, but also affected by insect population density. Moreover, many factors such as non-biological environmental variables, plant chemical and physical defense, predators, parasites and forest structures can all influence the individual insect performance, population size and dispersal, which in turn affect the levels of forest pest defoliation (Schowalter et al., 1986).

To explore the actual effects of elevated CO₂ on the population of insect herbivores and the alteration in the pest damage levels to forest, large-scale studies in the field are needed (Stiling et al., 2003). To date, just extremely few studies were conducted by using unrestricted insects to examine the changes in herbivory and pest damage levels in natural forests under elevated CO₂. In these studies, the CO₂ exposure facilities were directly set up at field plots, which more approached the natural forest environment and comprised the interactions of species from various trophic levels in a community.

Stiling et al. (2002, 2003) built 16 open top chambers directly on a native scrub-oak forest community (two levels of CO₂ and 8 chambers for each treatment). In their research, the levels of damage which was caused by insect herbivores were not measured by the loss of leaf dry weights or leaf areas, but by the percent of damaged leaves to large numbers of marked leaves. The numbers of mines on all marked leaves represented the densities of leaf miners. The areas of each mine represented the leaf consumption of the leaf miner in this mine. Stiling et al. (2002) showed that the foliar damage which was caused by both chewers and leaf miners, was only 19% under elevated CO₂, significantly lower than the controls (30.8%) under ambient CO₂, and the densities of leaf miners were also much lower under elevated CO₂. Furthermore, more leaf miners died of reduced leaf quality (reduced nitrogen or increased defensive compound concentrations) and rates of leaf miners attacked by parasitoids which were also higher under elevated CO₂. Stiling et al. (2002) also indicated that the mine areas of the most common leaf miner in the community were significantly greater at elevated CO₂ than at ambient CO₂, which suggested that these leaf miner individuals increased leaf consumption to compensate the poor foliar quality. This finding was associated with the

results of non-choice feeding trials with single plant species and restricted insects. With the same experimental facility and conditions as Stiling et al. (2002, 2003), Hall et al. (2005) investigated the herbivory damages of six leaf-feeding insects to a scrub-oak community, and the results showed that the damage levels reduced in four of the six insect species.

Hamilton et al. (2004) chose three understory woody species in Duke FACE and randomly collected leaves of each tree species on different sampling dates in the growing season. The collected leaves were photographed with a high-resolution digital camera, and the digital image of each leaf was processed with ScionImage software to quantify the leaf damage classes. The estimate of herbivory levels of plants at elevated and ambient CO₂ was represented by the leaf damage classes. In 1999, the results showed a lower herbivory on winged elm (*Ulmus alata*) at elevated CO₂, while the herbivory on red maple (*Acer rubra*) and sweetgum (*Liquidambar styraciflu*) did not change. In 1999 and 2000, the herbivory at community level declined by 10%–46% under elevated CO₂ plots. However, researchers were not sure about the reasons why herbivory reduced under elevated CO₂ for specific plant species and the whole community. The possible explanations may be the reduced populations of herbivores, decreased leaf consumption by herbivorous individuals, or the combination of both.

4.2 Potential changes in feeding preference behavior of leaf-feeding insects

Agrell et al. (2005) conducted food-choice trials in Petri dishes, and the result indicated that the elevated CO₂ could result in the alterations in larval preferences of forest tent caterpillar for different plants or different genotypes of the same plant. At community levels, the potential changes in feeding behaviors of insects are more complex, and so far, there is no extraordinarily effective method to examine it. Because of the differentiation in the responses of different plant species to elevated CO₂ and the mediated effects of many other environmental factors on the response magnitude in phytochemistry, some scholars presumed that the generalist insect herbivores in natural communities might choose to feed on another nearby plant which does not negatively respond to CO₂ enrichment, and/or choose another genotype of the same host plant species (Lindroth et al., 2002), and/or choose other leaves at different canopy heights (Agrell et al., 2000) or age classes (Williams et al., 1998), and/or choose plant tissues at different soil nutrient availabilities (Saxon et al., 2004). With food-choice behavior, the negative effects of elevated CO₂ on the generalist insects may be buffered partially (Agrell et al., 2005). For many special insect herbivores, they also have many of the same options, but they only choose from a narrow range of suitable host plants (Hamilton et al.,

2004), and the shifts in host preference will encounter an evolutionary hurdle (Lindroth, 1996a).

5 Conclusions

A series of studies indicated that the elevated atmospheric CO₂ coupled with the indirect effects of the alteration in phytochemistry could affect the food consumption and growth of leaf-feeding insect individuals. Nevertheless, the direction and magnitude of the changes in insect performance can be affected by various factors. Although many researchers have focused on population dynamics of leaf-feeding forest insects and its feedback on the forest ecosystem and productivity under elevated CO₂, so far, only aphid populations have been studied time after time, and the changes in the population density of other forest insects were mostly speculated according to the reaction of insect individuals. Stiling et al. (2002, 2003) adopted indirect methods and detected that the population density of leaf-miners declined at the community level. However, at present, this conclusion cannot be affirmed if it is the same with other natural ecosystems and other kinds of insects. A large number of non-choice feeding trials with single plant species showed that the consumption of insect individuals increased under elevated CO₂. Thus, some scholars predicted that the pest damages to forests were likely to increase along with the continuous increase in the atmospheric CO₂ concentrations, while the studies on forest community-level found a consistent reduction in the levels of herbivory or pest damage. In addition, up to now, little is known about the responses of species over time, such as the acclimation of plant and the physiological and behavioral adaptation of insects to elevated CO₂. It is estimated that the magnitude of adaptive response would differ from that in short-term experiments. Therefore, long-term and large-scale field studies need to be conducted to further confirm the effects of elevated atmospheric CO₂ on herbivorous forest insects, the feedback effects of altered insect performance and population dynamics on forest. These researches on the response of other insects (such as xylem-feeders) and the tri-trophic interactions among plants, insects and natural enemies (predators, parasitoids and pathogens) under elevated CO₂ may be the hot issue in the future.

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