Review

Effects of Elevated Atmospheric Carbon Dioxide on Insect-Plant Interactions

CARLOS E. COVIELLA*† AND JOHN T. TRUMBLE*

*Department of Entomology, University of California, Riverside, CA 92521, U.S.A., email carlos. coviella@ucr.edu
†Laboratorio de Ecología, Departamento de Ciencias Básicas, Universidad Nacional de Luján, (6700) Luján, Buenos Aires, Argentina

Abstract: *In the enriched carbon dioxide atmosphere expected in the next century, many species of herbivorous insects will confront less nutritious host plants that will induce both lengthened larval developmental times and greater mortality. The limited data currently available suggest that the effect of increased atmospheric CO_2 on herbivory will be not only highly species-specific but also specific to each insect-plant system. Several scenarios can be predicted, however: (1) local extinctions will occur; (2) the endangered species status as well as the pest status of some insect species will change; (3) geographic distributions for some insect species will shift with host-plant ranges; and (4) changes in the population dynamics of affected insect species will influence their interactions with other insects and plants. For insect conservation purposes, it is critical to begin long-term studies on the effects of enhanced CO_2 levels on insect populations. An analysis of the available literature indicates that many orders containing insect species important for ecosystem conservation, and even those important as agricultural or medical pests, have not been examined. Without a major increase in research on this topic, we will be unprepared for the species changes that will occur, we will lose the opportunity to document just how some insects adapt to elevated CO_2 levels, and we will lack the information necessary for effective conservation efforts.*

Efectos de Elevados Niveles de Dióxido de Carbono Atmosférico en Interacciones Planta-Insecto

Resúmen: *En la atmósfera con elevado CO_2 que se espera para el próximo siglo, muchas especies de insectos herbívoros se enfrentarán a plantas hospedadoras de menor calidad nutritiva, las cuales inducirán tiempos de desarrollo larval mas prolongados y mortalidad mas alta. Los limitados datos de que se dispone actualmente, sugieren que el efecto del aumento del CO_2 en la herbivoría podría ser no solo altamente especie-específico, sino tambien específico para cada sistema planta-insecto. Varios escenarios pueden predecirse: (1) ocurrirán extinciones locales; (2) cambiará la situación de especies en peligro de extinción asi como de especies plaga, de algunas especies de insectos; (3) las distribuciones geográficas de algunas especies de insectos, se verán afectadas por cambios en la distribucion geográfica de sus plantas hospedadoras; y (4) cambios en la dinámica poblacional de las especies de insectos afectadas, modificarán sus interacciones con otros insectos y plantas. Para propósitos de conservación, resulta crítico el incrementar los estudios a largo plazo sobre los efectos de los altos niveles de CO_2 sobre las poblaciones de insectos. El análisis de la literatura disponible, indica que muchos de los órdenes que contienen especies de insectos importantes para la conservación de ecosistemas específicos, o aún como plagas de la agricultura o de importancia médica no han sido examinados. Si no se produce un gran aumento en la investigación sobre este tema, no estaremos preparados para los*

cambios que ocurrirán en muchas especies de insectos, perderemos la oportunidad de documentar los procesos de adaptación de algunos insectos a elevado CO_2 y careceremos de la necesaria información para llevar adelante esfuerzos de conservación.

Introduction

Global atmospheric carbon dioxide levels are increasing. Most of the earth's CO_2 now resides in carbonates (Hunten 1993), mainly due to weathering processes (Berner 1992) and biological activity (Watson et al. 1991). Beginning with the increasing fossil fuel use associated with the industrial revolution, however, CO_2 concentration in the atmosphere has increased from 270–280 ppm (volume) to the current level of 364 ppm (Bazzaz 1990; Houghton et al. 1990, 1992; R. M. White 1990; Berner 1993; Sarmiento 1993; Tans & Bakwin 1995; Houghton et al. 1996b; Watson et al. 1996; Keeling & Whorf 1998). This represents an increase of approximately 32% in a relatively short period of geological and evolutionary time.

Accurate predictions about future CO_2 levels and their potential biological and physical effects are the subject of considerable scientific, economic, and political debate (Thuillier 1992; Kerr 1996; Azar & Rodhe 1997). In 1996 the Intergovernmental Panel on Climate Change (IPCC) published six different trajectories leading to stabilization of atmospheric CO_2 in the range of 350–1000 ppm (Houghton et al. 1996b). According to some interpretations, however, even the median emission scenario from the IPCC report (scenario IS92a) suggests that we are in a trajectory leading toward a rapid quadrupling of the preindustrial CO_2 atmospheric concentration (Mahlman 1997). Although a preliminary agreement was reached in December of 1997 in Kyoto, Japan, for reductions in anthropogenic CO_2 emissions, it remains to be seen what effect this will have in terms of establishing a new equilibrium level.

Even though long-range extrapolations are the result of various possible scenarios (Caldeira & Kasting 1993), the best approximations for the range of atmospheric CO_2 levels that will occur by the years 2040–2100 are bounded by a low of 700 ppm to the remarkably high value of 2100 ppm (Sundquist 1993). This high concentration assumes the burning of all the estimated reserves of carbon fossil fuel (Tans & Bakwin 1995). In any case, most published studies indicate that CO_2 levels will at least double in the next few decades and that anthropogenic CO_2 represents a biogeochemical perturbation of global proportions (Sundquist 1993). Even though the potential effects of such an increase are still the subject of serious disagreements, it is clear that elevated CO_2 will have profound effects on many biological systems.

Even the best-case predictions suggest that new equilibrium levels ensuing from these activities are likely to last several hundred years and that their potential effects will have ample time to manifest themselves.

Potential Effects of Elevated Atmospheric CO_2 Levels

The biological effects of global climate change are among the most important issues in ecological research. In April 1991, the Ecological Society of America (ESA) published the "Ecological Research Agenda for the 1990s," in which a call was made to ecologists to focus basic research on environmental problems. One of the categories the ESA deemed most important was global change. They indicated that more research should focus on and more money be invested in examining the effects that global climate change will have on our complex ecological systems (Gibbons 1991). Such new data are critical because our knowledge of the structure and function of ecosystems on a global scale is not adequate to predict even a majority of the consequences of climate change either on the ecosystems themselves or on the interacting causal agents (Mooney 1991).

Recent reports indicate that the potential effects of a doubling or tripling of the current atmospheric CO_2 levels could be substantial. In the short time scale of 100–1000 years, increasing atmospheric CO_2 levels may affect a variety of abiotic attributes of the Earth: (1) temperature (higher mean temperatures may precipitate the greenhouse effect; reviewed by Handell & Risbey 1992); (2) precipitation patterns (Smith et al. 1992); (3) precipitation acidity (Berner 1992), (4) ocean levels (higher sea level will inundate low lying areas); and (5) climatic regions (shifts in climatic zones would lead to changes in ecosystem composition and distribution of plants and animals; Emanuel et al. 1985; Parry & Carter 1985; Warrick et al. 1986; Bazzaz 1990; Smith et al. 1992; Kondrasheva et al. 1993). In addition, elevation of CO_2 is predicted to change patterns of organic matter turnover (Kirschbaum 1993; Woodwell 1993) and to reduce soil moisture (Manabe & Wetherald 1986; Manabe et al. 1992). Such changes are expected to influence biodiversity (Rochefort & Woodward 1992; Pimm et al. 1995) through alteration of photosynthesis rates, plant species composition, and ultimately plant competitive ability (Besford 1990; Besford et al. 1990; Bazzaz & Williams

1991; Bazzaz & Fajer 1992; Ahmed et al. 1993; Hall & Allen 1993).

Because the predicted changes are likely to occur over large areas, the implications for many organisms may be substantial. The combined effect of higher temperatures, altered rainfall, and decreased soil moisture will probably lead to a range adjustment of plants and trees toward higher latitudes, possibly following the same pattern that plants and trees exhibited when similar migrations occurred after the last glacial period. Shifts from desert to tundra in high latitudes and from desert to grasslands in temperate and tropical regions are likely. The environmental changes are occurring hundreds of times faster than they did after the last glacial period; so some plants, which have generation times on the order of tens of years or more, will not be able to adapt quickly and may be subject to extinction (Bazzaz & Williams 1991). Differential rates of range adjustment, and local extinctions, will affect the distribution and survival of insects and other animals. In fact, some recent studies have suggested that such shifts in insect distributions are already in progress (Parmesan 1996; Kuchlein & Ellis 1997; Woiwod 1997).

Interactions between plant species will be affected, as will interactions between cultivars within species and plants within cultivars. Using selected lines of cowpea (*Vigna unguiculata*), Ahmed et al. (1993) demonstrated that temperature differentially affects the reproductive success of its various cultivars. The availability of CO_2 and high temperatures have complex interactive physiological effects, and both factors are likely to change in the years to come.

All of these effects can substantially alter the interactions between herbivores and plants (Lincoln et al. 1986; Osbrink et al. 1987; Fajer 1989; Fajer et al. 1989; Johnson & Lincoln 1990; Mitchell et al. 1993; Caulfield & Bunce 1994). Further, modifications in herbivore-plant interactions, particularly those associated with suitability and nutritional status, could reasonably be expected to have significant effects on natural enemies (Price et al. 1980; Hare 1992; Roth & Lindroth 1995). From the point of view of insect diversity, distribution, and conservation, the biological effects of high CO_2 levels may be initially compartmentalized into the effect on plants, the subsequent impact on herbivorous insects, and the cumulative effects on parasitic and predatory insects.

Effects on Plants

The most evident and best studied effect of elevated atmospheric CO_2 is the so called "fertilization effect" (LaMarche et al. 1984). Carbon dioxide availability generally has a positive effect on photosynthesis and photo-synthate production. This effect has been observed repeatedly for various plant species by several researchers (Osbrink et al. 1987; Besford 1990; Groninger et al. 1996). The short-term responses that are typically measured may be different from long-term responses (Hall & Allen 1993), however. Under elevated CO_2 levels, photosynthesis rates increase initially but after a period of time may decrease (Poorter et al. 1988; Yelle et al. 1989; Besford 1990; Besford et al. 1990; Dugal et al. 1990; Idso 1990; Idso & Kimball 1991; Goudriaan 1992; but see Idso & Kimball 1992; Hall & Allen 1993). There is also evidence of reduced dark respiration (El Kohen et al. 1991) and photorespiration rates.

Despite some acclimatization, augmented photosynthesis and reduced photorespiration under enhanced CO_2 levels generate plants with lower total nitrogen, higher ratios of carbon to nitrogen (C:N; Lawler et al. 1997), and increased carbohydrate levels (Osbrink et al. 1987; Yelle et al. 1989; Ahmed et al. 1993; Mitchell et al. 1993). This leads to greater root and shoot dry weight and greater root length (Davis & Potter 1989; Johnson & Lincoln 1990) and occasionally to improved yields (Allen et al. 1991; Stockle et al. 1992*a*; but see Mitchell et al. 1993). Because increased photosynthesis rates can result in more biomass accumulation, the sustainability of elevated photosynthetic activity and the potential compensatory response to insect feeding depend strongly on the availability of nutrients for plant growth (Trumble et al. 1993). In long-term exposure experiments in open-top chambers, Idso and Kimball (1992) found that after 3.5 years, sour orange trees had substantially increased leaf, trunk, and branch volume and had more fruit rind than the ambient-treatment trees. Thus, growth effects may be most dramatic in agricultural systems, where nutrients are less limiting than in natural systems, which often are depauperate in key nutrients. Such growth effects have important implications for insects.

Experimentally determining the specific effects of elevated CO_2 on photosynthetic processes is not always simple. Many interactive factors are believed to influence photosynthesis rates, and these factors have different effects depending on plant species and environmental conditions. Bazzaz and Williams (1991), working in a mixed deciduous forest in England, found that CO_2 concentrations show strong seasonal and daily variations. They also demonstrated that CO_2 concentration varies with height, so trees of different ages (and therefore heights) are exposed to different levels of CO_2. Similarly, the leaves of the same tree at different heights would be exposed to different concentrations, raising questions about experiments employing a single CO_2 concentration on large plants. Further, this may create a mosaic in plant suitability for insect herbivores. Although mobile insects may be able to exploit increased variability within large host plants, sessile insects such as scale insects may be at a disadvantage.

The competitive interactions between plants that use the Calvin cycle for photosynthetic CO_2 fixation (C_3 plants) and plants that use the Hatch-Slack photosynthetic pathway (C_4 plants) are also expected to change in response to CO_2 elevation (Kondrasheva et al. 1993). A review of 770 experimental observations of numerous crops documented 14% and 34% average yield increases for C_4 and C_3 plants, respectively, grown in elevated CO_2 atmospheres (Stockle et al. 1992b). Under ambient CO_2 levels, C_4 plant species had an advantage over C_3 plants, especially in regions of high irradiance, high temperature, and water stress. As CO_2 levels rise, C_4 plants may lose this advantage. Some studies have shown that in elevated CO_2 levels, C_3 plants can out-compete C_4 plants (Bazzaz & Fajer 1992), leading to potentially important changes in the floristic composition of natural ecosystems and changes in the status of certain agriculturally important plants and their relationships with weeds. On a prairie in North Dakota with a mixture of C_3 and C_4 plants, Ode et al. (1980) demonstrated that seasonality of production relies on the presence of both groups of plants because the primary productive periods of C_3 and C_4 plants are staggered over time. Early in the season, new biomass production on the prairie is almost entirely due to C_3 plants, whereas during midsummer the contributions of C_4 plants are most important.

These variable responses of C_3 and C_4 plants to elevated CO_2 may result in asymmetrical effects on herbivory, and the response of insects that feed on C_4 plants may be different from that of those feeding on C_3 plants. The C_3 plants are likely to be positively affected by increased CO_2 and negatively affected by the insect response, whereas C_4 plants are less responsive to higher CO_2 and thus will be less affected by changes in the feeding behavior of insects (Lincoln et al. 1984).

Interactions of Plants and Herbivorous Insects

Lincoln et al. (1993) and Watt et al. (1995) showed that little research had been conducted on plant-insect interactions under high CO_2, and the situation has not changed since (Bezemer & Jones 1998). The majority of insects studied have been lepidopterans (Table 1), which are represented by only nine families. Of these, the economically important Noctuidae have received the most attention. Most other orders are represented by only one or two species, nearly all of which are economically important agricultural pests. Remarkably, only three species in two families have been examined in the largest insect order, the Coleoptera, and Diptera is represented by just two species in two families. In addition, most of the pests belong to either the phloem feeder or foliage feeder guilds. Only a single parasitoid species has been studied (Roth & Lindroth 1995). Thus, essentially

no information is available on the effects of elevated CO_2 on insects in natural systems, and information is limited on the diversity of insects that occur in agricultural systems. Not surprisingly, most of these insect studies were conducted on a relatively small number of plant species, most of which are of economic importance (Table 1). Nonetheless, several general observations can be made regarding plant and insect interactions in enhanced CO_2 environments.

Several studies have shown that insect herbivores consistently respond to changes in plant quality induced by enriched CO_2 environments by consuming more foliage (Lincoln et al. 1986; Osbrink et al. 1987; Fajer 1989; Marks & Lincoln 1996) and perhaps with reduced growth (Lincoln et al. 1986; Fajer 1989). Lincoln et al. (1984) showed that insect larvae consume up to 80% more leaves from high CO_2 treatments. In other experiments with lepidopterans, Fajer (1989) found that insect weight gain is positively correlated with nitrogen concentration in the plant material offered and that the amount of foliage consumption is negatively correlated with foliar nitrogen concentration. In addition, insects that feed on plants grown in elevated CO_2 levels have a reduced efficiency of ingested food. This result was confirmed by Marks and Lincoln (1996) and is consistent with reduced nitrogen content in a food source (T.R.C. White 1984).

Any potential effect of altered C:N ratios may be modified by the within-plant distribution of the nitrogen. Lawler et al. (1997) showed for *Eucalyptus tereticornis* (Smith) that the C:N ratio of the leaves is more affected by far than that of the plant as a whole. Akey et al. (1988) found that lepidopterans fed on bolls of cotton plants are not affected because C:N in bolls is not changed by elevated CO_2. If this trend proves generally true and reproductive structures out-compete other plant parts for limited nitrogen, then insects could be stimulated to feed more frequently on these structures. The implications of these results are considerable for insect conservation, the pest status of insects, and host plant fitness in both agricultural and natural systems.

The net result of either slower growth or increased consumption by insects is likely to be increased mortality at the population level. Reduced developmental rates increase the chances that biological (predators, parasites) or environmental hazards will be encountered (Fajer 1989; but see Caulfield & Bunce 1994). Consumption of additional foliage increases the probability of ingestion of pathogenic bacteria and viruses, which can cause reduced fecundity or death (e.g., *Bacillus thuringiensis*; Entwistle 1993). Marks and Lincoln (1996) demonstrated that when lepidopterans are fed on plants infected with Balansiae fungal endophytes, the increased consumption associated with elevated CO_2 exacerbates the negative effects of the fungus on both growth and survival of the insects.

Table 1.   Published reports of the effects of elevated CO_2 on insects.

Order/family/species	Insect feeding guild	Host plant species	Reference
Thysanoptera			
Thripidae			
Frankliniella occidentalis (Pergande)	foliage feeder	*Asclepias syriaca*	Hughes & Bazzaz 1997
Frankliniella spp.	foliage feeder	*Gossypium hirsutum*	Butler 1985; Butler et al. 1986
Orthoptera			
Acrídidae			
Melanoplus differentialis (Thomas)	foliage feeder	*Artemisa tridentata*	Johnson & Lincoln 1990, 1991
Melanoplus sanguinipes (Fabricius)	foliage feeder	*Artemisa tridentata*	Johnson & Lincoln 1990, 1991
Homoptera			
Aleyrodidae			
Bemísia tabaci (Gennadius):	phloem feeder	*Gossypium hirsutum*	Butler 1985; Butler et al. 1986
Trialeurodes vaporariorum (Westwood)	phloem feeder	*Lycopersicon esculentum*	Tripp et al. 1992
Cicadéllidae			
Empoasca spp.	xylem feeder	*Gossypium hirsutum*	Butler 1985; Butler et al. 1986
Fagocyba cruenta Herrich-Schäffer	phloem feeder	*Fagus sylvatica*	Docherty et al. 1997
Ossiannilssonola callosa (Then)	phloem feeder	*Acer pseudoplatanus*	Docherty et al. 1997
Aphididae			
Aphis fabae fabae	phloem feeder	*Cardamine pratensis*	Salt et al. 1996
Aphis rumicis (L.)	phloem feeder	*Rumex obtusifolius*	Brooks 1995
Aulacorthum solani (Kalt.)	phloem feeder	*Vicia faba*	Awmack et al. 1997
Periphyllus testudinaceus (Ferni)	phloem feeder	*Acer pseudoplatanus*	Docherty et al. 1997
Drepanosiphum platanoidis (Schrank)	phloem feeder	*Acer pseudoplatanus*	Docherty et al. 1997
Phyllaphis fagi L.	phloem feeder	*Fagus sylvatica*	Docherty et al. 1997
Sitobion avenae (F.)	phloem feeder	*Triticum aestivum*	Awmack 1997; Awmack et al. 1997
Cercopidae			
Phylaenus spumarius (L.)	phloem feeder	*Rumex obtusifolius*	Brooks 1995
Neophilaneus lineatus (L.)	phloem feeder	*Juncus squarrosus*	Brooks 1995
Pemphigidae			
Pemphigus populitransversus	phloem feeder	*Cardamine pratensis*	Salt et al. 1996
Lepidoptera			
Lymnantriidae			
Lymantria dispar (L.)	foliage feeder	*Quercus alba*	Williams & Lincoln 1994
		Pinus taeda	Williams & Lincoln 1993
		Acer saccharum	Lindroth 1991; Lindroth et al. 1993*a*
		Populus tremuloides	Lindroth et al. 1993*b*
		Quercus rubra	Lindroth et al. 1993*b*
		Populus tremuloides	Hemming & Lindroth 1994
		Betula papyrifera	Roth & Lindroth 1994*a*
		Pinus strobus	Roth & Lindroth 1994*a*
		Populus tremuloides	Roth & Lindroth 1995
		Betula papyrifera	Roth & Lindroth 1995
		Acer saccharum	Roth & Lindroth 1995
		Betula allegheniensis	Traw et al. 1996
		Betula populifolia	Traw et al. 1996
		Populus tremuloides	Kinney et al. 1997
		Acer saccharum	Kinney et al. 1997
		Quercus rubra	Kinney et al. 1997
Lasiocampidae			
Malacosoma disstria Hübner	foliage feeder	*Acer saccharum*	Lindroth 1991
		Populus tremuloides	Lindroth 1991
		Quercus rubra	Lindroth 1991
		Populus tremuloides	Hemming & Lindroth 1994
		Betula papyrifera	Roth & Lindroth 1994*b*
		Pinus strobus	Roth & Lindroth 1994*b*
		Populus tremuloides	Roth et al. 1996, 1997
		Acer saccharum	Lindroth et al. 1996; Roth et al. 1997

Table 1.   (continued)

Order/family/species	Insect feeding guild	Host plant species	Reference
Pyralidae			
Cactoblastis cactorum (Berg)	foliage feeder	*Opuntia stricta*	Stange et al. 1995; Stange 1997
Gallèria mellonella (L.)	foliage feeder	no plants involved	Lewis et al. 1993
Saturniidae			
Hyalophora cecropia (L.)	foliage feeder	*Betula papyrifera*	Lindroth et al. 1995
Actias lùna (L.)	foliage feeder	*Betula papyrifera*	Lindroth et al. 1995
Antheracea polyphemus (Cramer)	foliage feeder	*Betula papyrifera*	Lindroth et al. 1995
Tortricidae			
Choristoneùra occidentalis Freeman	foliage feeder	mixed forest tree species	Williams & Liebhold 1995
Noctuidae			
Spodoptera exigua (Hübner)	foliage feeder	*Gossypium hirsutum*	Akey & Kimball 1989
		Beta vulgaris	Caulfield & Bunce 1994
		Amaranthus hybridus	Caulfield & Bunce 1994
Spodoptera frugiperda (J.E.Smith)	foliage feeder	*Festuca arundinacea*	Marks & Lincoln 1996
Spodoptera eridania (Cramer)	foliage feeder	mixed plant community	Arnone et al. 1994, 1995
		Mentha piperita	Lincoln & Couvet 1989
Trichoplusia ni (Hübner)	foliage feeder	*Phaseolus lunatus*	Osbrink et al. 1987
Pseudoplusia includens Walker	foliage feeder	*Glycine max*	Lincoln et al. 1984, 1986
Nymphalidae			
Junonia coenia Hübner	foliage feeder	*Plantago lanceolata*	Fajer 1989; Fajer et al. 1989, 1991
Geometridae			
Operophtera brumata	foliage feeder	*Quercus robur*	Buse & Good 1996
			Lavola et al. 1998
Gelechíidae			
Pectinophora gossypiella (Saunders)	foliage feeder	*Gossypium hirsutum*	Butler 1985; Butler et al. 1986
		Gossypium hirsutum	Akey et al. 1988
Coleoptera			
Chrysomelidae			
Chaetocnema ectypa Horn	foliage feeder	*Gossypium hirsutum*	Butler 1985; Butler et al. 1986
Chrysophartha flaveola (Chapuis)	foliage feeder	*Eucalyptus tereticornis*	Lawler et al. 1997
Curculionidae			
Rhynchaenus fagi (L.)	foliage feeder	*Fagus sylvatica*	Docherty et al. 1997
Diptera			
Agromizidae			
Chromatomyia syngenesia Hardy	leaf feeder	*Sonchus oleraceus*	Smith & Jones 1998
Anthomiidae			
Pegomya nigritarsis Zetterstadt	leaf feeder	*Rumex obtusifolius*	Salt et al. 1995
		Rumex crispus	Salt et al. 1995
Hymenoptera			
Apidae			
Apis mellifera L.	pollen/nectar feeder	no plants involved	Harris et al. 1996
Diprionidae			
Neodíprion lecontei (Fitch)	foliage feeder	*Pinus taeda*	Lincoln & Thomas 1991
			Williams & Lincoln 1992, 1993
			Williams et al. 1994, 1997
Bracónidae			
Cotesia melanoscela (Ratz).	parasitoid	*Populus tremuloides*	Roth & Lindroth 1994*b*, 1995
		Betula papyrifera	Roth & Lindroth 1994*a*, 1995
		Acer saccharum	Roth & Lindroth 1994*b*, 1995

One of the outcomes of this increased feeding rate is that insects will also ingest more defensive compounds from plants. The carbon-nutrient balance hypothesis (Bryant et al. 1983; Tuomi et al. 1988) predicts that elevated CO_2 will allow plants to allocate more carbohydrate resources to secondary metabolism, generating higher concentrations of defensive compounds active against insects. Some studies have shown that under elevated CO_2 many carbon-based defensive compounds do increase (Lavola & Julkunen-Tiitto 1994; Peñuelas & Es-

tiarte 1998). This plant response is stronger for soluble phenolic compounds, especially the condensed tannins (but see Lindroth et al. 1993*b*; Peñuelas et al. 1997; Poorter et al. 1997; Peñuelas & Estiarte 1998). These compounds are known to strongly affect non-adapted herbivorous insects (Hagerman & Butler 1991).

Other reports indicate, however, that plants grown in elevated CO_2 do not generate increased concentrations of carbon-based defensive compounds. Johnson and Lincoln (1990) showed that allelochemical concentrations

are not affected by increased CO_2 and that grasshoppers feeding on sagebrush (*Artemisia tridentata* var. *tridentata*) are not affected. Reitz et al. (1997) demonstrated that celery (*Apium graveolens*) plants grown in elevated CO_2 did not have increased concentrations of linear furanocoumarins, even though the plants had higher C:N. Lincoln and Couvet (1989) found no differences in total volatile leaf mono- and sesquiterpenes in peppermint (*Mentha piperita*) between plants grown in ambient and elevated CO_2 atmospheres. A decline in the phenolic ellagitannin was observed for red oak (*Quercus rubra*) trees grown in elevated CO_2 atmospheres (Lindroth et al. 1993b). Thus, generalizations regarding elevated CO_2 and plant defensive chemistry do not appear possible at this time; the potential effects of changes in plant chemistry that can influence insect population dynamics will need to be evaluated on a case-by-case basis.

There may be special conditions in which insect populations would benefit from the effect of increased CO_2. For example, the water-use efficiency of plants is improved under high CO_2 conditions. Normally, the uptake of CO_2 entails a cost to the plant. For every molecule of carbon dioxide that enters the stomata, between 100 and 400 molecules of water are lost (Bazzaz & Fajer 1992). In a CO_2–enriched atmosphere, the CO_2 gradient between the exterior and the interior of the plant is lower, so the plants can absorb the same amount of CO_2 with smaller stomatal openings or in shorter periods, resulting in less water loss. In fact, increased stomatal resistance is commonly observed in plants grown under high CO_2 levels (Nijs et al. 1989; Dugal et al. 1990; Goudriaan 1992; Groninger et al. 1996). This can lead to increased plant water content (Osbrink et al. 1987, but see Idso et al. 1988; Reitz et al. 1997). Increased water availability is beneficial to most herbivorous insects (Scriber & Slansky 1981) because it aides in the digestion and assimilation of nutrients, particularly nitrogen (Scriber 1984). In addition, more efficient use of water would extend the life of plants in the drought conditions of late spring and summer, providing longer periods of habitat suitability for transient insect species. It is likely that endemic insect species would receive the plant-derived cues to enter aestivation or summer diapause somewhat later. This may allow smaller late-season larvae time to reach the stage of growth needed to survive. Thus, at least in the short term, elevated CO_2 concentrations resulting in better water-use efficiency by drought-stressed plants would benefit the herbivores.

Direct Effects of Elevated CO_2 on Insects

None of the studies we have examined suggest that elevated CO_2, at the predicted levels of 700 to 1100 ppm, has a direct effect on insect growth and development if

the effect through the host plant is eliminated. The ability to locate host plants of some herbivores may be affected, however. Some insects locate hosts using minute changes in CO_2 concentrations. The labial palps of *Helicoverpa armigera* (Hübner) are able to detect fluctuations in CO_2 density as small as 0.14% or 0.5 ppm (Stange 1992). Other insects are able to locate their plant hosts following the plume of slightly higher CO_2 concentrations, as does the moth *Cactoblastis cactorum* (Bergroth) with its host plant *Opuntia stricta* (Stange 1992; Stange et al. 1995). *Diabrotica virgifera virgifera* (LeConte) uses CO_2 concentrations in soil to locate corn roots (Strnad et al. 1986; Bernklau & Bjostad 1998). The extent to which host plant location may be affected by changes in atmospheric CO_2, and how readily insects might adapt to such changes, needs to be examined in future studies.

Elevated CO_2 and Natural Enemies

Even though changes in insect-plant interactions are likely to have consequences for higher trophic levels, published information is relatively sparse. Price et al. (1980) argued that the development of theories of insect-plant interactions cannot progress realistically without consideration of the third trophic level. Even at an elementary level, this assertion appears reasonable: there is considerable evidence that the fitness of herbivorous insects varies with the quality of their diet and that dietary differences have corresponding effects on their parasitoids (Barbosa et al. 1982). Greenblatt et al. (1982) found that differences in weight of the parasitoid species *Brachymeria intermedia* (Ness) (Hymenoptera: Chalcididae) and *Coccigomimus turionellae* (L.) (Hymenoptera:Ichneumonidae) are associated with host diet. In the special case of egg parasitoids, the size of the adult depends on two factors: the size of the host egg and the number of conspecifics that emerge with it (Bai et al. 1992). Size is critical because increased size is correlated with increased fecundity (Hohmann et al. 1988; Bai et al. 1992). Size will influence reproductive success and therefore alter the parasitoid population biology. Thus, any dietary differences that prolong developmental time, increase food consumption, and reduce growth by herbivores serve to increase the susceptibility of herbivores to natural enemies (Roth & Lindroth 1995). On the other hand, poor host nutrition could also decrease parasitoid fitness (Barbosa et al. 1982).

Nutrient deficiencies are also suspected to reduce defenses against endoparasitoids (Barbosa et al. 1982). Of the nutrient-derived elements of plant defensive chemistry, nitrogen is by far the most widely incorporated (Waterman & Mole 1989). Therefore, a nitrogen shortage due to a reduction in nitrogen per unit of plant tissue with high CO_2 concentrations might also affect nitrogen

use by herbivores. Because one strategy of herbivorous insects is the sequestration of toxins to which they have evolved tolerance (Vinson 1994), modified secondary metabolism in their host plants may affect the suitability of herbivores to their parasitoids. Similarly, variation in the quality and composition of food consumed, which is likely to result in differences in the chemical composition of the herbivore, can affect its susceptibility to predator attack (Price et al. 1980).

Host size and quality also affect the rate of attack by natural enemies. Small hosts are usually allocated few eggs that develop into small adults because of nutrient supply (Barrett & Schmidt 1991). Parasitoids usually lay progressively more eggs and more female-biased clutches as the size of the host increases (Murdoch et al. 1997). Some studies of *Trichogramma minutum* Riley, for example, have shown that female parasitoids can adjust clutch size according to host volume (Schmidt & Smith 1987). Also, ovipositing *Trichogramma* are sensitive to variations in host quality. Amino acid production in the host is dependent on nitrogen availability, and the presence of specific amino acids in the host is known to be an oviposition stimulant. Hosts with slightly reduced levels of these amino acids are unlikely to be accepted or will stimulate reduced rates of oviposition (Barrett & Schmidt 1991). On the other hand, some aphids are known to have reduced responses to alarm pheromones under elevated CO_2 (Awmack et al. 1997) and thus are more susceptible to natural enemy attack.

In addition, the rate of attack depends also on how conspicuous the host is to natural enemies. Changes in the secondary metabolism of plants associated with elevated CO_2 will affect utilization by the natural enemies of semiochemical-associated cues such as synomones or kairomones, thereby disrupting or affecting the ability of the natural enemies to locate their hosts. Thus, both the parasitoid's reproductive success and its effectiveness as a biological control agent may be affected (Hare & Luck 1994).

Survival of the natural enemies will also be affected under high CO_2 conditions. Roth and Lindroth (1995) found that parasitoid mortality increased in elevated CO_2. In other systems, enhanced parasitoid mortality occurs in response to a nutrient imbalance in the host (Vinson & Barbosa 1987). At the population level, the mortality effects of natural enemies on some plant-insect associations will decrease under the high CO_2 levels expected in the near future (Roth & Lindroth 1995). On the other hand, increased survival of their hosts could be beneficial if the host is endangered.

Additional effects of elevated CO_2 on tritrophic interactions can be anticipated. If elevated CO_2 levels increase global temperatures, this could enhance differences within parasitoid species; the response to different temperatures is actually used as a characterization of different biotypes for some species (Botto et al. 1988). Such changes might affect the distribution of biotypes that vary in performance (Powell & Shepard 1982). These changes are likely to be species-specific. Therefore, the differential effects of temperature changes might disrupt the spatial co-distribution between herbivore and natural enemy, thus affecting the population dynamic of both.

Because plant influences on the effectiveness of natural enemies have important evolutionary consequences for the herbivores involved (Price et al. 1980), there will be important evolutionary effects on the natural enemies as well. The evolutionary fitness of an animal depends significantly upon a diet optimal in both quantity and quality (Hassell & Southwood 1978). The expected changes in CO_2 concentrations will probably last for centuries. Thus, given the relatively short generation times and potential for rapid genetic turnover in many insect species, an extended period of elevated CO_2 will be a strong evolutionary force.

Conclusions

Most insect species are herbivores and are affected by the physiological and nutritional state of their host plants. Thus, changes in growth patterns and quality of host plants can be expected to affect the survival and population dynamics of these herbivores. Insects that are parasitic or predaceous on herbivorous insects also can be affected by the quality of the food provided to their hosts (Reitz & Trumble 1997). Thus, understanding the effects of increased atmospheric CO_2 on plants is necessary for predicting its potential effects on insects.

As shown in many of the studies cited, the elevated CO_2 expected in the next century will lower the host plant quality for many species of herbivorous insects. This lower host quality will induce both lengthened larval developmental times and greater mortality. These effects may be strong enough to constitute an evolutionary force; the insects that do survive may adapt by either increasing ingestion rates (Fajer et al. 1989) or by developing an increased efficiency of conversion of ingested nitrogen. In spite of the limited data currently available, several scenarios are probable. Local extinctions, changes in endangered species status, and altered pest status will almost certainly result. Geographic distributions will be affected by shifts in host-plant ranges. Changes in the population dynamics of affected insect species will influence their interactions with other insects as well as plants. Therefore, even insect species that will not be directly affected by elevated CO_2 may be affected by the changes in other insect species. Such changes will be substantial for predators and parasites, and addressing this issue in long-term, multi-trophic research is necessary.

From the point of view of insect conservation efforts, it is critical to expand long-term studies on the effect of

enhanced CO_2 levels on insect populations. An analysis of the insect species that have been examined so far (Table 1) indicates that many orders containing insect species important for conservation, or even as agricultural or medical pests, have not been investigated. For example, Coleoptera, the largest order of insects, is represented in Table 1 by only three species, Diptera is represented by only two leafminer species, and Hymenopterans are represented by two species. Only one species of parasitoid has been studied, and no information has been published regarding CO_2 effects on any predaceous insect. Entire insect orders have been completely ignored in CO_2 research. Of the feeding guilds, leaf-chewing insects are the most studied group, although orthopterans are poorly represented by just two species. Parasites, gall-feeders, pollinators, parasitoids, and leaf-miners also are represented by few, if any, species.

For conservation purposes, research should start to focus on endangered species and then on species that may become threatened as CO_2 levels increase. Until now, the majority of studies on the effect of CO_2 on insects examined effects from a bottom-up perspective (Bizina 1997), focusing on herbivorous insects. It may be instructive to include a top-down perspective as well.

In any case, a major increase in research on this topic will be necessary to provide an understanding of the changes that will occur within the next few decades. Without a concerted effort to begin studies as soon as possible, we will lose the opportunity to document how some plant-insects systems will adapt to an environment with elevated CO_2. Finally, a better understanding of the changes we expect in the decades to come is crucial to making wise decisions about present and future conservation efforts in our rapidly changing environment.

Acknowledgments

Literature Cited

Ahmed, F. E., A. E. Hall, and M. A. Madore. 1993. Interactive effects of high temperature and elevated carbon dioxide concentration on cowpea [*Vigna unguiculata* (L.) Walp.]. Plant Cell and Environment **16:**835–842.

Akey, D. H., and B. A. Kimball. 1989. Growth and development of the beet armyworm on cotton grown in an enriched carbon dioxide atmosphere. Southwestern Entomologist **14:**255–260.

Akey, D. H., B. A. Kimball, and J. R. Mauney. 1988. Growth and development of the pink bollworm, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae) on bolls of cotton grown in enriched carbon dioxide atmospheres. Environmental Entomology **17:**452–455.

Allen, L. H., Jr., E. C. Bisbal, K. J. Boote, and P. H. Jones. 1991. Soybean dry matter allocation under subambient and superambient levels of carbon dioxide. Agronomy Journal **83:**875–883.

Arnone, J. A. I., J. G. Zaller, C. Korner, C. Ziegler, and H. Zandt. 1994. Insect herbivory in model tropical plant communities after 1.5 years exposure to elevated CO_2. Bulletin of the Ecological Society of America **75:**5–6.

Arnone, J. A., III, J. G. Zaller, C. Ziegler, H. Zandt, and C. Korner. 1995. Leaf quality and insect herbivory in model tropical plant communities after long-term exposure to elevated atmospheric CO_2. Oecologia (Berlin) **104:**72–78.

Awmack, C. S. 1997. Aphid-plant interactions at ambient and elevated CO_2. Ph.D. thesis. University of London, London.

Awmack, C. S., C. M. Woodcock, and R. Harrington. 1997. Climate change may increase vulnerability of aphids to natural enemies. Ecological Entomology **22:**366–368.

Azar, C., and H. Rodhe. 1997. Targets for stabilization of atmospheric CO_2. Science **276:**1818–1819.

Bai, B. R., R. F. Luck, L. Forster, B. Stephens, and J. A. M. Janssen. 1992. The effect of host size on quality attributes of the egg parasitoid, *Trichogramma pretiosum*. Entomologia Experimentalis Et Applicata **64:**37–48.

Barbosa, P., J. A. Saunders, and M. Waldvogel. 1982. Plant-mediated variation in herbivore suitability and parasitoid fitness [*Apanteles congregatus*, biological control, *Manduca sexta*, *Myzus persicae*]. Pages 63–71 in Proceedings of the fifth international symposium on insect-plant relationships. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Barrett, M., and J. M. Schmidt. 1991. A comparison between the amino acid composition of an egg parasitoid wasp and some of its hosts. Entomologia Experimentalis et Applicata **59:**29–42.

Bazzaz, F. A. 1990. The response of natural ecosystems to the rising global carbon dioxide levels. Annual Review of Ecology and Systematics **21:**167–196.

Bazzaz, F. A., and E. D. Fajer. 1992. Plant life in a carbon dioxide rich world. Scientific American **266:**68–74.

Bazzaz, F. A., and W. E. Williams. 1991. Atmospheric carbon dioxide concentrations within a mixed forest: implications for seedling growth. Ecology **72:**12–16.

Berner, R. A. 1992. Weathering, plants, and the long-term carbon cycle. Geochimica et Cosmochimica Acta **56:**3225–3231.

Berner, R. A. 1993. Paleozoic atmospheric CO_2: importance of solar radiation and plant evolution. Science **261:**68–70.

Bernklau, E. J., and L. B. Bjostad. 1998. Behavioral responses of first-instar western corn rootworm (Coleoptera: Chrysomelidae) to carbon dioxide in a glass bead bioassay. Journal of Economic Entomology **91:**444–456.

Besford, R. T. 1990. The greenhouse effect: acclimation of tomato plants growing in high CO_2, relative changes in Calvin cycle enzymes. Journal Of Plant Physiology **136:**458–463.

Besford, R. T., L. J. Ludwig, and A. C. Withers. 1990. The greenhouse effect: acclimation of tomato plants growing in high CO_2, photosynthesis and ribulose-1,5-bisphosphate carboxylase protein. Journal of Experimental Botany **41:**925–931.

Bezemer, T. M., and T. H. Jones. 1998. Plant-insect herbivore interactions in elevated atmospheric CO_2: quantitative analyses and guild effects. Oikos **82:**212–222.

Bizina, E. V. 1997. The relative strength of top-down versus bottom-up factors in the regulation of community structure and functioning: review of hypotheses. Zhurnal Obshchei Biologii **58:**26–45.

Botto, E. N., D. Gonzalez, and T. Bellows. 1988. Effect of temperature on some biological parameters of two populations of *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae). Pages 367–377 in V.K. Gupta, editor. Proceedings of the meeting on advances in parasitic hymenoptera research. E.J. Brill, Lieden, New York.

Brooks, G. L. 1995. The effects of elevated CO_2 on herbivorous insects. Ph.D. thesis. Lancaster University, Lancaster, United Kingdom.

Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos **40:**357–368.

Buse, A., and J. E. G. Good. 1996. Synchronization of larval emergence in winter moth (*Operophtera brumata* L.) and budburst in pedunculate oak (*Quercus robur* L.) under simulated climate change. Ecological Entomology **21:**335–343.

Butler, G. D., Jr. 1985. Populations of several insects on cotton [*Gossypium hirsutum* cultivar Deltapine 61] in open-top carbon dioxide enrichment chambers. Southwestern Entomologist **10:**264–267.

Butler, G. D., Jr., B. A. Kimball, and J. R. Mauney. 1986. Populations of *Bemisia tabaci* (Homoptera: Aleyrodidae) on cotton [*Gossypium hirsutum* cultivar Deltapine 61] grown in open-top field chambers enriched with carbon dioxide. Environmental Entomology **15:**61–63.

Caldeira, K., and J. F. Kasting. 1993. Insensitivity of global warming potentials to carbon dioxide emission scenarios. Nature **366:**251–253.

Caulfield, F., and J. A. Bunce. 1994. Elevated atmospheric carbon dioxide concentrations affects interactions between *Spodoptera exigua* (Lepidoptera: Noctuidae) larvae and two host plant species outdoors. Environmental Entomology **23:**999–1005.

Davis, T. D., and J. R. Potter. 1989. Relations between carbohydrate, water status and adventitious root formation in leafy pea cuttings rooted under various levels of atmospheric CO_2 and relative humidity. Physiologia Plantarum **77(2):**185–190.

Docherty, M., F. A. Wade, D. K. Hurst, J. B Whittaker, and P. J. Lea. 1997. Responses of tree sap-feeding herbivores to elevated CO_2. Global Change Biology **3:**51–59.

Dugal, A., S. Yelle, and A. Gosselin. 1990. Influence of CO_2 enrichment and its method of distribution on the evolution of gas exchanges in greenhouse tomatoes. Canadian Journal of Plant Science **70:**345–356.

El Kohen, A., J. Y. Pontailler, and M. Mousseau. 1991. Effect of doubling of atmospheric CO2 concentration on dark respiration in aerial parts of young chestnut trees (*Castanea sativa* Mill). Comptes Rendus De L Academie Des Sciences Serie Iii-Sciences De La Vie **312:**477–481.

Emanuel, W. R., H. H. Shugart, and M. P. Stevenson. 1985. Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. Climate Change **7:**29–43.

Entwistle, P. F. 1993. *Bacillus thuringiensis*, an environmental biopesticide: theory and practice. Wiley, New York.

Fajer, E. D. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions: growth responses of larvae of the specialist butterfly, *Junonia coenia* (Lepidoptera: Nymphalidae). Oecologia (Berlin) **81:**514–520.

Fajer, E. D., M. D. Bowers, and F. A. Bazzaz. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. Science **243:**1198–1200.

Fajer, E. D., M. D. Bowers, and F. A. Bazzaz. 1991. The effects of enriched carbon dioxide atmospheres on the buckeye butterfly *Junonia-Coenia.* Ecology **72:**751–754.

Gibbons, A. 1991. Ecologists set broad priorities for 1990s. Science **252:**504.

Goudriaan, J. 1992. El papel de la vegetación. Mundo Científico **12:**686–692.

Greenblatt, J. A., P. Barbosa, and M. E. Montgomery. 1982. Host's diet effects on nitrogen utilization efficiency for two parasitoid species: *Brachymeria intermedia* and *Coccygomimus turionellae.* Physiological Entomology **7:**263–267.

Groninger, J. W., J. R. Seiler, S. M. Zedaker, and P. C. Berrang. 1996. Photosynthetic response of loblolly pine and sweetgum seedling

stands to elevated carbon dioxide, water stress, and nitrogen level. Canadian Journal of Forest Research **26:**95–102.

Hagerman, A. E., and L. G. Butler. 1991. Tannins and lignins. Pages 355–358 in G. A. Rosenthal and M. R. Berenbaum, editors. Herbivores: their interactions with secondary plant metabolites. The chemical participants. I. Academic Press, San Diego.

Hall, A., and L. H. Allen Jr. 1993. Designing cultivars for the climatic conditions of the next century. Pages 291–297 in D.R. Buxton and L.H. Allen, editors. International crop science I. International Crop Science Congress. Crop Science Society of America, Madison, Wisconsin.

Handell, M. D., and J. S. Risbey. 1992. An annotated bibliography on the greenhouse effect and climate change. Climate Change **21:**91–255.

Hare, J. D. 1992. Effects of plant variation on herbivore-natural enemy interactions. Pages 278–298 in R. S. Fritz and E. L. Simms, editors. Plant resistance to herbivores and pathogens: ecology, evolution, and genetics. University of Chicago Press, Chicago.

Hare, J. D., and R. F. Luck. 1994. Environment variation in physical and chemical cues used by the parasitic wasp, *Aphytis melinus,* for host recognition. Entomologia Experimentalis et Applicata **72:**97–108.

Harris, J. W., J. Woodring, and J. R. Harbo. 1996. Effects of carbon dioxide on levels of biogenic amines in the brains of queenless worker and virgin queen honey bees (*Apis mellifera*). Journal of Apicultural Research **35:**69–78.

Hassell, M. P., and T. R. E. Southwood. 1978. Foraging strategies of insects. Annual Review of Ecology and Systematics **9:**75–98.

Hemming, J. D. C., and R. L. Lindroth. 1994. Changes in the carbon-nutrient balance of aspen: effects on gypsy moths and forest tent caterpillars. Bulletin of the Ecological Society of America **75:**92.

Hohmann, C. L., R. F. Luck, and E. R. Oatman. 1988. A comparison of longevity and fecundity of adult *Trichogramma platneri* (Hymenoptera: Trichogrammatidae) reared from eggs of the cabbage looper and the angoumois grain moth, with and without access to honey. Journal of Economic Entomology **81:**1307–1312.

Houghton, J. T., et al., editors. 1990. Climate change. The intergovernmental panel on climate change scientific assessment. Report of the Working Group 1. Cambridge University Press, Cambridge, United Kingdom.

Houghton, J. T., et al., editors. 1992. Climate change 1992. The supplementary report to the intergovernmental panel on climate change scientific assessment. Cambridge University Press, Cambridge, United Kingdom.

Houghton, J. T., et al., editors. 1996*a.* Climate change 1994. Radiative forcing of climate change and an evaluation of the intergovernmental panel on climate change IS92 emission scenarios. Cambridge University Press, Cambridge, United Kingdom.

Houghton, J. T., et al., editors. 1996*b.* Climate change 1995. the science of climate change. Contribution of the Work Group I to the second assessment report. Cambridge University Press, Cambridge, United Kingdom.

Hughes, L., and F. A. Bazzaz. 1997. Effect of elevated CO_2 on interactions between the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae) and the common milkweed, *Asclepias syriaca.* Oecologia **109:**286–290.

Hunten, D. M. 1993. Atmospheric evolution of the terrestrial planets. Science **259:**915.

Idso, S. B. 1990. Interactive effects of carbon dioxide and climate variables on plant growth. Pages 61–69 in ASA special publication 53. American Society of Agronomy, Madison, Wisconsin.

Idso, S. B., and B. A. Kimball. 1991. Downward regulation of photosynthesis and growth at high carbon dioxide levels: no evidence for either phenomenon in three-year study of sour orange trees. Plant Physiology **96:**990–992.

Idso, S. B., and B. A. Kimball. 1992. Aboveground inventory of sour orange trees exposed to different atmospheric carbon dioxide concentrations for 3 full years. Agricultural and Forest Meteorology **60:**145–151.

Idso, S. B., B. A. Kimball, and J. R. Mauney. 1988. Atmospheric carbon dioxide enrichment and plant dry matter content. Agricultural and Forest Meteorology **43:**171–181.

Johnson, R. H., and D. E. Lincoln. 1990. Sagebrush and grasshopper responses to atmospheric carbon dioxide concentration. Oecologia **84:**103–110.

Johnson, R. H., and D. E. Lincoln. 1991. Sagebrush carbon allocation patterns and grasshopper nutrition: the influence of carbon dioxide enrichment and soil mineral limitation. Oecologia (Berlin) **87:**127–134.

Keeling, C. D., and T. P. Whorf. 1998. Atmospheric CO_2 concentrations (ppmv) derived from in situ air samples collected at Mauna Loa Oservatory, Hawaii. Available from http://cdiac.esd.ornl.gov/trends /co$_2$/sio-mlo.htm.

Kerr, R. A. 1996. Sky-high findings drop new hints of greenhouse warming. Science **273:**34.

Kinney, K. K., R. L. Lindroth, S. M. Jung, and E. V. Nordheim. 1997. Effects of CO_2 and NO_3 availability on deciduous trees: phytochemistry and insect performance. Ecology **78:**215–230.

Kirschbaum, M. U. F. 1993. A modelling study of the effects of changes in atmospheric CO_2 concentration, temperature and atmospheric nitrogen input on soil organic carbon storage. Tellus Series B—Chemical and Physical Meteorology **45:**321–334.

Kondrasheva, N. Y., K. I. Kobak, and I. E. Turchinovich. 1993. Possible responses of terrestrial vegetation to increasing CO_2 concentration in atmosphere and global warming. Lesovedenie **4:**71–76.

Kuchlein, J. H., and W. N. Ellis. 1997. Climate-induced changes in the microlepidoptera fauna of the Netherlands and the implications for nature conservation. Journal of Insect Conservation **1:**73–80.

LaMarche, V. C., D. A. Grabyll, H. C. Fritts, and M. R. Rose. 1984. Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. Science **225:**1019–1021.

Lavola, A., and R. Julkunen-Tiitto. 1994. The effect of elevated carbon dioxide and fertilization on primary and secondary metabolites in birch, *Betula pendula* (Roth). Oecologia **99:**315–321.

Lavola, A., R. Julkunen-Tiitto, H. Roininen, and P. Aphalo 1998. Host-plant preference of an insect herbivore mediated by UV-B and CO_2 in relation to plant secondary metabolites. Biochemical Systematics and Ecology **26:**1–12.

Lawler, I. R., W. J. Foley, I. E. Woodrow, and S. J. Cork. 1997. The effects of elevated CO_2 atmospheres on the nutritional quality of Eucalyptus foliage and its interaction with soil nutrient and light availability. Oecologia **109:**59–68.

Lewis, E. E., R. Gaugler, and R. Harrison. 1993. Response of cruiser and ambusher entomopathogenic nematodes (Steinernematidae) to host volatile cues. Canadian Journal of Zoology **71:**765–769.

Lincoln, D. E., and D. Couvet. 1989. The effect of carbon supply on allocation to allelochemicals and caterpillar consumption of peppermint. Oecologia **78:**112–114.

Lincoln, D. E., and R. B. Thomas. 1991. Responses of pine sawfly larvae to loblolly pine seedlings grown in elevated carbon dioxide under differing nitrogen supply regimes. Bulletin of the Ecological Society of America **72:**176.

Lincoln, D. E., D. Couvet, and N. Sionit. 1986. Response of an insect herbivore to host plants grown in carbon dioxide enriched atmospheres. Oecologia **69:**556–560.

Lincoln, D. E., N. Sionit, and B. R. Strain. 1984. Growth and feeding response of *Pseudoplusia includens* (Lepidoptera: Noctuidae) to host plants grown in controlled carbon dioxide atmospheres. Environmental Entomology **13:**1527–1530.

Lincoln, D. E., E. D. Fajer, and R. H. Johnson. 1993. Plant insect herbivore interactions in elevated CO_2 environments. Trends in Ecology and Evolution **8:**64–68.

Lindroth, R. L. 1991. Consequences of elevated atmospheric carbon dioxide for deciduous trees phytochemistry and insect resistance. Bulletin of the Ecological Society of America **72** (supplement):176–177.

Lindroth, R. L., S. M. Jung, and A. M. Feuker. 1993*a*. Detoxication activity in the gypsy moth: effects of host carbon dioxide and nitrate availability. Journal of Chemical Ecology **19:**357–367.

Lindroth, R. L., K. K. Kinney, and C. L. Platz. 1993*b*. Responses of deciduous trees to elevated atmospheric carbon dioxide: productivity phytochemistry and insect performance. Ecology **74:**763–777.

Lindroth, R. L., G. E. Arteel, and K. K. Kinney. 1995. Responses of three saturniid species to paper birch grown under enriched CO_2 atmospheres. Functional Ecology **9:**306–311.

Lindroth, R. L., S. Roth, E. L. Kruger, and J. C. Volin. 1996. Consequences of enriched atmospheric CO_2 and defoliation for tree-insect interactions. Bulletin of the Ecological Society of America **77:**267.

Mahlman, J. D. 1997. Anticipated climate changes in a high-CO_2 world: implications for long term planning. U. S. Global Change Research Program Seminar Series, Washington D.C. Available from www.usgcrp.gov/usgcrp/9799DD.html

Manabe, S., and R. T. Wetherald. 1986. Reduction in summer soil wetness induced by an increase in atmospheric carbon dioxide. Science **232:**626–628.

Manabe, S., M. J. Spelman, and R. J. Stouffer. 1992. Transient responses of a coupled ocean atmosphere model to gradual changes of atmospheric CO_2. 2. Seasonal response. Journal of Climate **5:**105–126.

Marks, S., and D. E. Lincoln. 1996. Antiherbivore defense mutualism under elevated carbon dioxide levels: a fungal endophyte and grass. Environmental Entomology **25:**618–623.

Mitchell, R. A. C., V. J. Mitchell, S. P. Dirscoll, J. Franklin, and D. W. Lawlor. 1993. Effects of increased carbon dioxide concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. Plant Cell and Environment **16:**521–529.

Mooney, H. A. 1991. Biological response to climate change: an agenda for research. Ecological Applications **1:**112–117.

Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 1997. Dynamical effects of host size and parasitoid-state dependent attacks by parasitoids. Journal of Animal Ecology **66:**542–556.

Nijs, I., I. Impens, and T. Behaeghe. 1989. Leaf and canopy responses of *Lolium perenne* to long-term elevated atmospheric carbon dioxide concentration. Planta (Heidelberg) **177:**313–320.

Ode, D. J., L. L. Tieszen, and J. C. Lerman. 1980. The seasonal contribution of C3 and C4 plant species to primary production in a mixed prairie. Ecology **61:**1304–1311.

Osbrink, W. L. A., J. T. Trumble, and R. E. Wagner. 1987. Host suitability of *Phaseolus lunatus* for *Trichoplusia ni* (Lepidoptera: Noctuidae) in controlled carbon dioxide atmospheres. Environmental Entomology **16:**639–644.

Parmesan, C. 1996. Climate and species range. Nature **382:**765–766.

Parry, M. L., and T. R. Carter. 1985. The effect of climatic variations on agricultural risk. Climatic Change **7:**95–110.

Peñuelas, J., and M. Estiarte. 1998. Can elevated CO_2 affect secondary metabolism and ecosystem function? Trends in Ecology and Evolution **13:**20–24.

Peñuelas, J., M. Estiarte, and J. Llusià. 1997. Carbon-based secondary compounds at elevated CO_2. Photosynthetica **33:**313–316.

Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. Science **269:**341–350.

Poorter, H., Y. Van Berkel, R. Baxter, J. Den Hertog, P. Dijkstra, R. M. Gifford, K. L. Griffin, C. Roumet, J. Roy, and S. C. Wong. 1997. The effect of elevated CO_2 on the chemical composition and construction costs of leaves of 27 C_3 species. Plant Cell and Environment **20:**472–482.

Poorter, H., S. Pot, and H. Lambers. 1988. The effect of an elevated atmospheric carbon dioxide concentration on growth, photosynthesis and respiration of *Plantago major*. Physiologia Plantarum **73:**553–559.

Powell, J. E., and M. Shepard. 1982. Biology of Australian and United States strains of *Trissolcus basalis*, a parasitoid of the green vegetable bug *Nezara viridula*. Australian Journal of Ecology **7:**181–186.

Price, P. W., C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson,

and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annual Review of Ecology and Systematics **11:**41–65.

Reitz, S. R., and J. T. Trumble. 1997. Effects of linear furanocoumarins on the herbivore *Spodoptera exigua* and the parasitoid *Archytas marmoratus*: host quality and parasitoid success. Entomologia Experimentalis et Applicata **84:**9–16.

Reitz, S. R., D. N. Karowe, M. M. Diawara, and J. T. Trumble. 1997. Effects of elevated atmospheric carbon dioxide on the growth and linear furanocoumarin content of celery. Journal of Agricultural and Food Chemistry **45:**3642–3646.

Rochefort, L., and F. I. Woodward. 1992. Effects of climate change and a doubling of CO_2 on vegetation diversity. Journal of Experimental Botany **43:**1169–1180.

Roth, S. K., and R. L. Lindroth. 1994*a*. Effects of CO_2-mediated changes in paper birch and white pine chemistry on gypsy moth performance. Oecologia (Berlin) **98:**133–138.

Roth, S. K., and R. L. Lindroth. 1994*b*. Elevated atmospheric carbon dioxide: effects on tritrophic interactions. Bulletin of the Ecological Society of America **75:**197–198.

Roth, S. K., and R. L. Lindroth. 1995. Elevated atmospheric CO_2 effects on phytochemistry, insect performance and insect parasitoid interactions. Global Change Biology **1:**173–182.

Roth, S., R. L. Lindroth, J. C. Volin, and E. L. Kruger. 1996. Consequences of enriched atmospheric CO_2 and defoliation for tree-insect interactions. II. Insect performance. Bulletin of the Ecological Society of America **77** (supplement):381.

Roth, S. K., E. P. McDonald, and R. L. Lindroth. 1997. Atmospheric CO_2 and soil water availability: consequences for tree-insect interactions. Canadian Journal of Forestry Research **27:**1281–1290.

Sarmiento, J. L. 1993. Ocean carbon cycle; most of the carbon released from fossil fuels will end up in the oceans, where a complex cycle of circulation and other processes control its fate. Chemical and Engineering News **71:**30–44.

Salt, D. T., G. L. Brooks, and J. B. Whittaker. 1995. Elevated carbon dioxide affects leaf-miner performance and plant growth in docks (*Rumex* spp.). Global Change Biology **1:**153–156.

Salt, D. T., P. Fenwick, and J. B. Whittaker. 1996. Interespecific herbivore interactions in a high CO_2 environment: root and shoot aphids feeding on *Cardamine*. Oikos **77:**326–330.

Schmidt, J. M., and J. J. B. Smith. 1987. The measurement of exposed host volume by the parasitoid wasp *Trichogramma minutum* and the effects of wasp size. Canadian Journal of Zoology **65:**2837–2845.

Scriber, J. M. 1984. Host plant suitability. Pages 159–202 in R. T. Carde and W. J. Bell, editors. Chemical ecology of insects. Chapman and Hall, London.

Scriber, J. M., and F. Slansky Jr. 1981. The nutritional ecology of immature insects. Annual Review Entomology **26:**183–211.

Smith, P. H., and T. H. Jones 1998. Effects of elevated CO_2 on the chrysanthemum leaf miner *Chromatomyia synchenesiae*: a greenhouse study. Global Change Biology **4:**287–291.

Smith, T. S., R. Leemans, and H. H. Shugart. 1992. Sensitivity of terrestrial carbon storage to carbon dioxide–induced climate change: comparison of four scenarios based on general circulation models. Climatic Change **21:**367–384.

Stange, G. 1992. High resolution measurement of atmospheric carbon dioxide concentration changes by the labial palp organ of the moth *Heliothis armigera* (Lepidoptera: Noctuidae). Journal of Comparative Physiology A: Sensory Neural and Behavioral Physiology **171:**317–324.

Stange, G. 1997. Effects of changes in atmospheric carbon dioxide on the location of hosts by the moth, *Cactoblastis cactorum.* Oecologia **110:**539–545.

Stange, G., J. Monro, S. Stowe, and C. B. Osmond. 1995. The CO_2 sense of the moth *Cactoblastis cactorum* and its probable role in the biological control of the CAM plant *Opuntia stricta.* Oecologia **102:**341–352.

Stockle, C. O., J. R. Williams, N. J. Rosenberg, and C. A. Jones. 1992*a*. A method for estimating the direct and climatic effects of rising atmospheric carbon dioxide on growth and yield of crops. Part 1. Modification of the EPIC model for climate change analysis. Agricultural Systems **38:**225–238.

Stockle, C. O., P. T. Dyke, J. R. Williams, C. A. Jones, and N. J. Rosenberg. 1992*b*. A method for estimating the direct and climatic effects of rising atmospheric carbon dioxide on growth and yield of crops. Part 2. Sensitivity analysis at 3 sites in the midwestern USA. Agricultural Systems **38:**239–256.

Strnad, S. P., M. K. Bergman, and W. C. Fulton. 1986. First-instar western corn rootworm (Coleoptera: Chrysomelidae) response to carbon dioxide. Environmental Entomology **15:**839–842.

Sundquist, E. T. 1993. The global carbon dioxide budget. Science **259:**934–941.

Tans, P. P., and P. S. Bakwin. 1995. Climate change and carbon dioxide forever. Ambio **24:**376–378.

Thuillier, P. 1992. La humanidad ante el efecto invernadero. Mundo Cientifico **12:**603–605.

Traw, M. B., R. L. Lindroth, and F. A. Bazzaz. 1996. Decline in gypsy moth (*Lymantria dispar*) performance in an elevated CO_2 atmosphere depends upon host plant species. Oecologia **108:**113–120.

Tripp, K. E., W. K. Kroen, M. M. Peet, and D. H. Willits. 1992. Fewer whiteflies found on CO_2 enriched greenhouse tomatoes with high C:N ratios. Hortscience **4:**1079–1080.

Trumble, J. T., D. M. Kolodny-Hirsch, and I. P. Ting. 1993. Plant compensation for arthropod herbivory. Annual Review of Entomology **38:**93–119.

Tuomi, J., P. Niemela, F. S. Chapin III, J. P. Bryant, and S. Siren. 1988. Defensive responses of trees in relation to their carbon/nutrient balance. Pages 57–72 in W. J. Mattson, J. Levieux, and C. B. Dagans, editors. Mechanisms of woody plant defenses against insects: search for pattern. Springer-Verlag, New York.

Vinson, S. B. 1994. Physiological interactions between egg parasitoids and their hosts. Pages 201–211 in E. Wajenberg and S. A. Hassans, editors. Biological control with egg parasitoids. CAB International, Wallingford, Oxon, United Kingdom.

Vinson, S. B., and P. Barbosa. 1987. Interrelationships of nutritional ecology of parasitoids. Pages 673–698 in F. Slansky Jr. and J. G. Rodriguez, editors. Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley, New York.

Warrick, R. A., H. H. Shugart, and M. J. Antonovski. 1986. The effects of increased CO_2 on increased terrestrial ecosystems. Pages 363–392 in B. Bolin et al., editors. The greenhouse effect, climatic change, and ecosystems. Wiley, Chichester, United Kingdom.

Waterman, P. G., and S. Mole. 1989. Extrinsec factors influencing production of secondary metabolites in plants. Pages 107–134 in E. A. Bernays, editor. I. Insect-plant interactions. CRC Press, Boca Raton, Florida.

Watson, A. J., C. Robinson, J. E. Robinson, P. J. L. B. Williams, and M. J. R. Fasham. 1991. Spatial variability in the sink for atmospheric carbon dioxide in the North Atlantic. Nature **350:**50–53.

Watson, R. T., et al., editors. 1996. Climate change 1995. Impacts, adaptations and mitigation of climate change: scientific-technical analyses. Contribution of the Work Group II to the second assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom.

Watt, A. D., J. B. Whittaker, M. Docherty, G. Brooks, E. Lindsay, and D. T. Salt. 1995. The impact of elevated atmospheric CO_2 on insect herbivores. Pages 197–217 in R. Harrington and M.E. Stork, editors. Insects in a changing environment. Academic Press, San Diego, California.

White, R. M. 1990. The great climate debate. Scientific American **263:**36–43.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia **63:**90–105.

Williams, D. W., and A. M. Liebhold. 1995. Forest defoliators and climatic change: potential changes in spatial distribution of outbreaks of western spruce budworm (Lepidoptera: Tortricidae) and gypsy moth (Lepidoptera: Lymantriidae). Environmental Entomology **24:**1–9.

Williams, R. S., and D. E. Lincoln. 1992. Effects of loblolly pine grown under elevated carbon dioxide and different nutrient levels on performance of red-headed pine sawfly larvae. Bulletin of the Ecological Society of America **73:**390.

Williams, R. S., and D. E. Lincoln. 1993. Compensatory responses of early instar red-headed pine sawfly larvae to loblolly pine grown in enriched carbon dioxide atmospheres. Bulletin of the Ecological Society of America **74:**489.

Williams, R. S., and D. E. Lincoln. 1994. Potential effects of global change on an important plant-insect interaction: white oak and gypsy moth. Bulletin of the Ecological Society of America **75:**250.

Williams, R. S., D. E. Lincoln, and R. B. Thomas. 1994. Loblolly pine grown under elevated CO_2 affects early instar pine sawfly performance. Oecologia **98:**64–71.

Williams, R. S., R. B. Thomas, B. R. Strain, and D. E. Lincoln. 1997. Effects of elevated CO_2, soil nutrient levels, and foliage age on the performance of two generations of *Neodiprion lecontei (*Hymenoptera: Diprionidae) feeding on loblolly pine. Environmental Entomology **26:**1312–1322.

Woiwod, I. P. 1997. Detecting the effects of climate change on Lepidoptera. Journal of Insect Conservation **1:**149–158.

Woodwell, G. M. 1993. Balancing the carbon budget. Trends in Ecology and Evolution **8:**381.

Yelle, S., R. C. Beeson Jr., M. J. Trudel, and A. Gosselin. 1989. Acclimation of two tomato species to high atmospheric carbon dioxide. I. Sugar and starch concentrations. Plant Physiology **90:**1465–1472.