

Global Atmospheric Change and Trophic Interactions: Are There Any General Responses?

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Abstract Increasing atmospheric CO₂ is hypothesized to alter plant physiology and metabolism, which may have important implications for species interactions. In this chapter, we review published studies on the effects of elevated atmospheric CO₂ on plant-derived allelochemicals and the possible effects of CO₂-mediated changes on higher trophic levels such as herbivores, parasitoids, and predators. We provide a critical assessment of conventional ecological theories used to predict phytochemical responses to CO₂ and we make some suggestions as to how this field may be expanded and improved.

1 Introduction

Atmospheric carbon dioxide levels have risen by approximately 100 ppm since the onset of the industrial revolution to the present level of 385 ppm. The Intergovernmental Panel on Climate Change (IPCC) predicts that levels of CO₂ in the atmosphere will rise to between 500 and 975 ppm in the next century depending on economic growth and energy use scenarios (IPCC 2000), though recent projections suggest that these estimates may be conservative (Raupach et al. 2007). Elevated CO₂, along with increased emissions of other greenhouse gases such as methane and ozone, is primarily due to anthropogenic activities such as fossil fuel

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consumption and forest clearing. Greenhouse gas emissions are projected to cause increases in surface air temperatures of between 1 and 4°C in this century, along with changes in precipitation and cloud cover. While the predictions regarding climatic changes have been debated, levels of atmospheric CO₂ are unequivocally rising. This will have important implications for plant growth and development. The effects of increasing CO₂ on plant physiology are complex and have been extensively reviewed (Bazzaz 1990; Bowes 1993; Drake and González-Meler 1997; Makino and Mae 1999; Medlyn et al. 2001; Woodward 2002; Nowak et al. 2004; Ainsworth and Long 2005). Plants exposed to elevated CO₂ experience enhanced photosynthesis, reduced photorespiration, decreases in stomatal conductance, decreased transpiration rates and subsequent enhanced water-use efficiency, and alterations in resource allocation, phenology and reproductive biology (as reviewed in Bazzaz 1990). In addition, decreases in plant nitrogen content, increases in the carbon to nitrogen ratio (C:N), alterations in the concentrations of defensive compounds and overall changes in plant quality are likely to directly impact herbivores. Changes in allocation to secondary metabolites can also have both direct and indirect (herbivore-mediated) effects on higher trophic levels, which may have broad implications for community structure. As we see in the next section, plant-derived allelochemicals are a critical component in shaping ecosystems in general. Thus, plant responses to increased photosynthate production under elevated CO₂ and subsequent changes in antiherbivore phytochemical production are among the critical impacts of rising CO₂ on plant growth (Bazzaz 1990).

This chapter explores the ways in which elevated CO₂ may impact resource allocation to plant allelochemicals – where an allelochemical may be defined as “any nonnutritional chemical produced by an individual of one species that affects the growth, health, behavior or population biology of another species” (Schoonhoven et al., 2005). We then examine the potential effects of these changes on higher trophic levels. Several excellent reviews have been produced on the general effects of CO₂ on ecosystems (Bazzaz 1990; Coley 1998; Coviella and Trumble 1999; Hunter 2001; Lindroth and Dearing 2005). We focus primarily on literature that addresses CO₂ effects in terms of plant secondary chemistry. The projected increase in atmospheric CO₂ is unlikely to have direct physiological effects on insect herbivores (Fajer et al. 1991) or their enemies, so effects are expected to be plant-mediated. Here, we examine the current body of literature on this topic and evaluate empirical studies in light of theoretical predictions, which consider how altered resource allocation may change the production and concentration of allelochemicals. We assess empirical studies within the framework of the prevailing ecological theory and we also discuss the limitations of such models. Where pertinent, discussions include factors associated with primary plant metabolism, especially when evaluating the effects of elevated CO₂ on host quality for herbivores. This chapter is structured to address the effects of CO₂ at increasing trophic levels starting with the effects on plant-derived allelochemicals, the implications for insect herbivores, and in turn the direct and indirect effects on herbivore enemies such as parasitoids and predators.

2 Climate Change and Plant-Derived Allelochemicals

2.1 *Plant-Derived Allelochemicals as a Driving Force for Community Structure*

Plants and their herbivores collectively comprise a large proportion of global species diversity, with these two groups representing almost 50% of all identified species on earth (Strong et al. 1984). The quality of host plants for herbivorous insects is dependent on a number of factors including plant metabolism (nutritional make-up and production of defenses) and morphology (physical defenses). Although the definition of plant quality depends on factors intrinsic to the herbivore in question (e.g., nutrient requirements and sensitivity to plant defenses), many generalizations can be made about the requirements of insect herbivores. In this section, we give an overview of the ways in which plant-derived allelochemicals can shape ecosystems and why predicting changes in plant chemicals are a critical part of understanding how ecosystems may function in the future. Plants produce a vast range of secondary metabolites such as alkaloids, terpenoids, saponins, flavonoids, and tannins, (Futuyama 1983) which are critically important to the reproductive fitness of plants and serve as protection against herbivores, viruses, bacteria, fungi, and competing plants.

Herbivores can encounter secondary metabolites at many levels during the process of searching for, and feeding on, plant food. Prior to feeding, herbivores may encounter plant volatile organic compounds (VOCs) in the headspace surrounding the potential host, and these compounds (e.g., monoterpenes, sesquiterpenes, aldehydes, alcohols and ketones) may provide the insect with information about the suitability of the plant as a host (Pickett et al. 1998; Bruce et al. 2005). Deciphering the effects of plant volatiles on insect herbivores can be challenging as these volatiles can act as both attractants and deterrents. The effects of specific compounds will likely be dependent on the herbivore group in question and it has been demonstrated that the peripheral receptors of phytophagous insects are tuned to the detection of specific host plant “blends” of ubiquitous VOCs, rather than any one single VOC (Fraser et al. 2003; Birkett et al. 2004).

Once a herbivore has commenced feeding, it may be exposed to a diverse array of internal plant compounds such as phenolics (e.g., tannins and flavonoids), nitrogenous compounds (e.g., alkaloids, amines, cyanogenic glycosides, and glucosinolates), terpenoids, organic acids, lipids and sulfur-containing compounds (Futuyama 1983; Howe and Jander 2008; Rasmann and Agrawal 2009). Some insects have adapted to these plant-produced defensive compounds and in some cases may exploit them for their own needs. For example, propenylbenzenes, coumarins, and polyacetylene produced in the surface wax of plants are known to be growth inhibitors for a number of taxa including fungi, bacteria and many generalist herbivores. However the same compounds have been shown to stimulate oviposition in the carrot fly *Psila rosae* (Städler and Buser 1984). Many insects can

also sequester toxic plant compounds, e.g., pyrrolizidine alkaloids and cardenolides, which are stored in specialized insect tissues, and protect the insect from predators (Brower and Fink 1985; Narberhaus et al. 2005; Opitz and Müller 2009). Plant secondary chemicals can vastly alter the physiology of insect hosts and can induce complex behaviors associated with host location, oviposition, deterrence and attraction. Secondary metabolites are a crucial component in determining host-quality for insect herbivores and ingested secondary metabolites can have profound and diverse effects on feeding herbivores including the disruption of digestion, metabolism, growth, and development.

Plant-produced allelochemicals can also affect higher trophic levels either directly or indirectly (via herbivores) and thus can serve a multitude of functions in the broader ecosystem context. The induction of plant VOC release by feeding herbivores can signal the presence of herbivores to natural enemies such as predators and parasitoids which are then attracted to the damaged plant (Kessler and Baldwin 2001; Rasmann et al. 2005; Schnee et al. 2006). Damage-induced VOCs can also be perceived by neighboring plants which are alerted to the presence of herbivores and may subsequently alter their secondary chemistry (Baldwin and Schultz 1983; Karban and Shiojiri 2009). Volatiles released from different plant parts may serve different functions. For example, pollinators are attracted to emissions from flowers, while seed dispersers can recognize and orient towards volatiles released from developing fruit (Dudareva et al. 2006). The diversity of chemical groups and the types of responses they elicit are extremely complex and are beyond the scope of this chapter. However this section serves to highlight the importance of allelochemicals in community structure and function and to emphasize the importance in predicting changes in allelochemical production in a high CO₂ atmosphere.

2.2 Elevated CO₂ and Resource Allocation to Allelochemicals

Plants have a finite capacity to acquire necessary resources such as carbon, mineral nutrients and water. Plants may allocate photosynthates and nutrients to reproduction, growth, storage or defense (Ayres 1993) depending on the needs of the plant and the availability of these resources. Increased atmospheric CO₂ is expected to have a stimulatory effect on the production of photosynthates though this effect is generally stronger for C₃ plants than for C₄ plants (Stitt and Krapp 1999; Ainsworth and Long 2005). How these additional resources are allocated depends on the evolutionary history of the plant (i.e., genotypic response) and the range of strategies allowed for within the physiological constraints of the plant (i.e., phenotypic response). Changes in allocation to chemical defenses under elevated CO₂ are expected to have important implications for herbivores and to have both direct effects and indirect herbivore-mediated effects on higher trophic levels. In the search for a “general theory of plant defense” ecologists have formulated several hypotheses which have been used to predict resource allocation to allelochemicals under altered environmental conditions such as changes

in light, water and nutrient inputs and sink/source relationships. These can be extended to predictions of resource allocation and allelochemical production under elevated CO₂. Among the most widely used of these are: (1) the Optimal Defense (OD) Hypothesis; (2) the Growth-Differentiation Balance (GDB) Hypothesis; and (3) the Carbon-Nutrient Balance (CNB) Hypothesis. Many of the predictions invoked by these hypotheses broadly overlap and all contain the same basic assumption, that allocation of finite plant resources constitutes a trade-off between secondary defenses (morphological and chemical defenses and cellular differentiation) and primary metabolism (photosynthesis, respiration and growth) (Cronin and Hay 1996).

The optimal defense hypothesis:

The OD (McKey 1979; Strauss et al. 2004), which incorporates aspects from the coevolution theory (Ehrlich and Raven 1964) and from the plant apparency theory (Feeny 1975, 1976; Rhoades 1979; Rhoades and Cates 1976; Cornell and Hawkins 2003) attempts to explain how the defensive needs of a plant (as defined by the plant's risk of attack by herbivores) determine the evolution of defensive secondary metabolites. The ODH comprises two central hypotheses: (1) "organisms evolve and allocate defenses in a way that maximizes individual inclusive fitness" and (2) "defenses are costly in terms of fitness" (Rhoades 1979; Stamp 2003; Strauss et al. 2002, 2004). Hypothesis 2 encompasses four subhypotheses which are (1) "organisms evolve defenses in direct proportion to their risk from predators and in inverse proportion to the cost of defense," (2) "within an organism, defenses are allocated in proportion to risk of the plant part and value of it to plant fitness, and in inverse proportion to the cost of defense," (3) "defense is decreased when enemies are absent and increased when they are present (i.e., allocation pattern of constitutive and inducible defenses)," and (4) "there is a trade-off between defense and other plant functions (growth and reproduction) such that stressed individuals are less defended" (Rhoades 1979; Stamp 2003). While some of the assumptions of the ODH are implicit in studies of plant responses to elevated CO₂, its hypotheses have not generally been formally tested in climate change scenarios. The principle of optimal defense makes different predictions about defense allocation under elevated CO₂ depending on assumptions concerning the defensive strategies of plants (Ayres 1993). The Plant Apparency Hypothesis (Feeny 1975, 1976; Rhoades 1979) predicts that plants generally have one of two defensive strategies: (1) "quantitative" (apparent plants) or (2) "qualitative" (unapparent plants). So-called "apparent" plants (e.g. long-lived woody species) are readily found by herbivores and therefore invest heavily in plant defenses that are effective against a broad range of herbivorous animals. Apparent plants produce quantitative defenses (e.g., tannins and lignins); their effects are dose dependent and they act to reduce plant tissue digestibility to herbivores. Unapparent plants on the other hand can readily escape herbivores in time and space and as a result invest much less in defensive compounds, producing low doses of overtly toxic chemicals such as glucosinolates, cyanogenic glycosides and alkaloids. If the benefits of defense increase linearly with investment in secondary chemistry (as in the case of apparent plants) and if the cost of quantitative defenses decreases under elevated CO₂, then the ODH

would predict that increased CO₂ would result in increased concentrations of allelochemicals in apparent plants. On the other hand if plants are maximally protected with low concentrations of qualitative compounds (i.e., unapparent plants) then the ODH predicts no change in allelochemical production under elevated CO₂ (Ayres 1993).

Growth Differentiation Balance Hypothesis:

The GDB (Loomis 1932, 1953; Herms and Mattson 1992) is a framework for explaining resource allocation to growth vs. differentiation processes under environmental perturbations such as alterations in water and nutrient inputs. Growth can be defined as the irreversible increase in plant size due to cell division and enlargement, while differentiation refers to processes that occur after cell expansion that often (but not always) have an antiherbivore function. Processes such as deposition of lignin, leaf thickening, production of trichomes and thorns, production of secondary metabolites, and development of reproductive organs are examples of differentiation. The GDB hypothesis is based on the premise that plant growth is inversely proportional to differentiation representing a trade-off in resource allocation to different sinks. The GDB hypothesis simply states that limitations in any resource that inhibits growth more than it does photosynthesis will increase the pool of resources that can be allocated to differentiation. Empirical studies show that net photosynthesis is not as sensitive to shortages of nutrients and water, as growth processes (reviewed by Herms and Mattson 1992). Applied to climate change studies (Mattson et al. 2005; Gayler et al. 2008) the GDB hypothesis predicts that increases in atmospheric CO₂, which stimulate photosynthesis causing an increase in the C:N ratio and a decrease in plant nitrogen (Cotrufo et al. 1998), will result in a shunting of photosynthates into differentiation. Hence the production of secondary metabolites is expected to increase under elevated CO₂. As we will see, predictions based on the GDB hypothesis broadly overlap with those of the CNB (below) but the two hypotheses differ in their explanations of predicted results and only the GDB hypothesis addresses cellular development.

The Carbon-Nutrient Balance Hypothesis:

The CNB (Bryant et al. 1983) has been the most widely used of the available defense allocation models in climate change studies (Fajer et al. 1992; Roth and Lindroth 1995; Kinney et al. 1997; Hemming and Lindroth 1999; Bezemer et al. 2000; Coviella et al. 2000; Schädler et al. 2007), in part owing to the simplicity of empirical tests of its predictions. As previously mentioned the predictions of the CNB broadly overlap with those of the GDB hypothesis. However while the GDB makes predictions about changes in any resource, the CNB hypothesis addresses changes in nutrient levels only. Under the CNB framework a similar prediction can be made for elevated CO₂ whereby increased photosynthetic rates and consequential increases in the C:N ratio result in carbon products in excess of those needed for primary metabolic functions and as such result in increased carbon-based secondary metabolites (Fig. 1). A related prediction is that nitrogen limitations resulting from plant growth under elevated CO₂ will result in a decrease of N-based secondary metabolites (Karowe et al. 1997). Both the GDB and the CNB hypotheses predict that allocation to secondary metabolites under elevated CO₂ will depend critically on

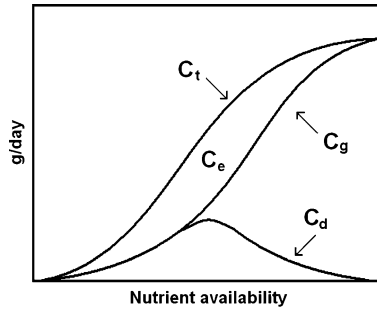


Fig. 1 The carbon–nutrient balance hypothesis: (C_t) = total available carbon, (C_g) = carbon diverted to growth, (C_e) = excess carbon, (C_d) = carbon-based allelochemicals. Nutrient limitations limit growth more than photosynthesis resulting in a net excess of carbon resources. Carbon-based plant defenses are highest where excess carbon is highest as carbon is shunted from primary metabolism to secondary metabolism. Redrawn from Stamp (2003)

other plant resource inputs such as nutrients and light, and there is much empirical evidence to support this (Johnson and Lincoln 1991; Hättenschwiler and Schafellner 1999; McDonald et al. 1999; Agrell et al. 2000; Saxon et al. 2004).

2.3 *C and N Allocation to Biosynthetic Classes of Secondary Metabolites*

We performed a literature search using the search terms: (plant) + (antiherbivory, alkaloids, cyanogenic glycosides, terpenoids, phenolics, secondary metabolites, defense) + (elevated, increased) + (climate change, CO₂) in Google Scholar. The search returned 101 relevant studies (Appendix 1) with measurements of 608 plant secondary metabolites under elevated CO₂ from 191 plants representing 102 species. Measurements of secondary metabolites under elevated CO₂ were recorded and placed into one of four chemical classes (phenolics, terpenoids, nitrogen-based compounds, and volatiles). Since some studies measured several individual allelochemicals, while others reported only totals (e.g., total phenolics), studies with a greater number of measured allelochemicals are thus overrepresented here relative to single allelochemical reports. The phytochemicals surveyed here represent constitutively produced compounds, however, the production of allelochemicals can be induced in response to damage by herbivores (see Chapter “Within-Plant Signalling by Volatiles Triggers Systemic Defences”). The dynamics of herbivore induction of plant allelochemicals may be altered under elevated CO₂. For example Bidart-Bouzat et al. (2005) found that herbivores induced increases in glucosinolate levels under elevated CO₂, but not in ambient conditions.

Figure 2 shows the proportion of measured allelochemicals in each of the four chemical classes that showed increases, decreases or no change in concentration. For all classes except phenolics the majority of studies found no change under

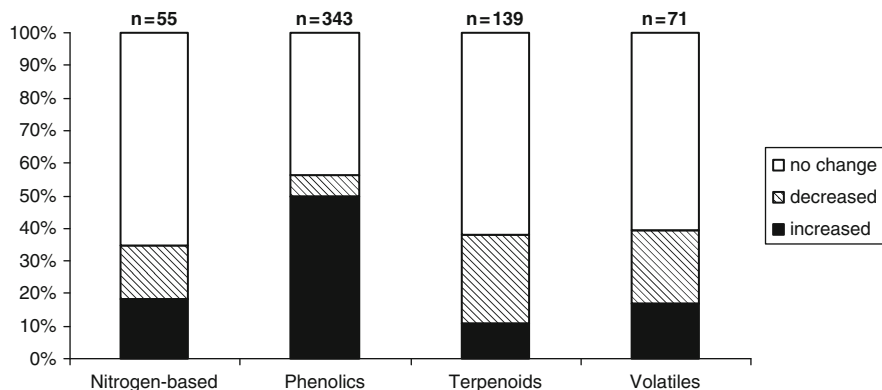


Fig. 2 The percentage of plant-derived allelochemicals that increased, decreased or showed no change under elevated CO_2 for four chemical classes: nitrogen-based compounds ($n = 55$), phenolics ($n = 343$), terpenoids ($n = 139$) and volatiles ($n = 71$). N values represent a single measured chemical compound except in cases where only the change for a specific group was given (e.g., “total phenolics”). “Elevated” CO_2 ranged from 500 to 1,400. Some terpenoids (e.g., some monoterpenes and sesquiterpenes) which can be classified as both terpenoids and volatiles, were placed in the “terpenoid” category when expressed as a concentration (mass compound/unit mass plant tissue) and were placed in the “volatile” category when expressed as an emission rate (mass compound/unit plant area/unit time). Studies which measured allelochemicals derived from plant endosymbionts, or where concentrations of plant-derived allelochemicals were measured in an interacting nonplant species (e.g., insect tissues) were excluded. In the cases where allelochemical response to CO_2 depended on an interacting factor, we attempted to characterize significant effects based on subjective “ambient” conditions in order to examine the effects of CO_2 alone (e.g., ambient temperatures)

elevated CO_2 . This may be because the null hypothesis is true, or it may be the result of type II (β) statistical error due to low sample sizes (and hence a lack of statistical power). It may also be an artifact of the way in which these results are usually considered. Plant chemical concentrations are usually expressed on a dry weight basis and the accumulation of predominantly total *nonstructural* carbohydrates (TNC) under elevated CO_2 might mask changes in concentrations of carbon-based secondary or structural compounds (CBSSC). When concentrations of CBSSC were expressed on a *structural* dry weight basis, nonsignificant average increases of flavonoids and soluble phenolics became significant (Porter et al. 1997; Peñuelas and Estiarte 1998). The two main predictions of the CNB: an increase in C-based allelochemicals and a decrease in N-based allelochemicals are not met. Under elevated CO_2 N-based compounds increased (18% of cases) more often than they decreased (16% of cases). For the carbon-based terpenoids, concentrations increased in 11% of cases and decreased in 27%. The same was true for the C-based volatile class with increases in 17% of cases and decreases in 23% of cases. Again, these decreases in carbon-based secondary metabolites under elevated CO_2 do not support the CNB. In the phenolic class however, allelochemicals increased in 50% of cases with decreases in only 7% of cases. It has been suggested that the predictive power of the CNB hypothesis is greater for certain

chemical classes or subclasses over others (Reichardt et al. 1991; Lerdaу and Coley 2002). For example, the CNB hypothesis may better predict allocation to stable end products and may be less effective for unstable or transient metabolic intermediates. Reichardt et al. (1991) showed that metabolite turnover determined which secondary metabolites could be predicted using the CNB framework and suggest that “dynamic” or transient intermediates (e.g. monoterpenes, sesquiterpenes, and phenolic glycosides) are less predictable than “stable” metabolic end products such as tannins and lignin. Predictions may be dependent on the biochemical pathways involved and appear to be much less conclusive for terpenes (products of the DOXP (1-deoxy-D-xylulose-5-phosphate and mevalonic acid pathways) and alkaloids (multiple pathways) (Lerdaу and Coley 2002). Even within a given biochemical pathway, predictions may be more robust for stable metabolic endpoints. Figure 3 shows the breakdown of three subclasses of phenolics: tannins, phenolic glycosides and phenolic acids, from the literature search described above. Tannins are generally thought to be stable endpoints of the shikimic acid biochemical pathway while phenolic glycosides and phenolic acids are transient intermediates. The prediction that C-based secondary metabolites increase under elevated CO₂ was met only for the tannin subclass where less than 2% of measurements showed decreases in tannins while increases were shown in over 60% of cases. Results are much more varied for metabolic intermediates, which corroborates the view that predictions may be dependent on the stability of metabolites. In addition, compounds such as phenolic acids and other metabolic intermediates of the shikimic acid pathway generally represent only a small proportion of plant biomass (Koricheva 2002) and previous work has suggested that caution should be taken in applying a cost-benefit approach to compounds which are found in only very low concentrations (Gulmon and Mooney 1986).

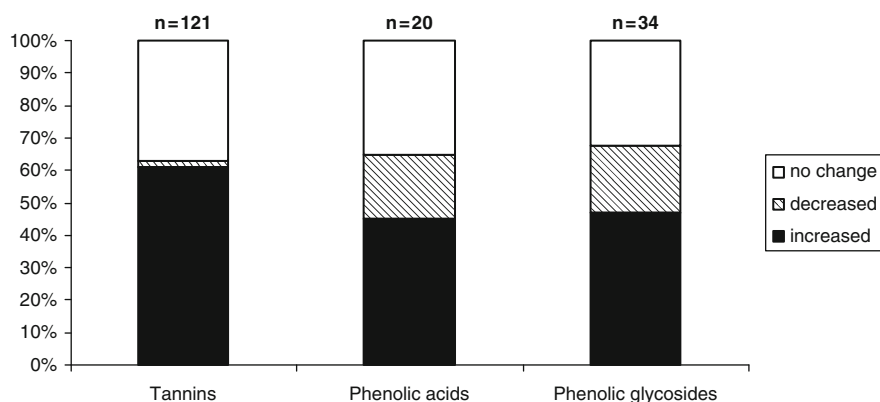


Fig. 3 The percentage of plant-derived allelochemicals that increased, decreased or showed no change under elevated CO₂ for three subclasses of phenolic compounds: tannins ($n = 121$), phenolic acids ($n = 20$) and phenolic glycosides ($n = 34$). n values represent a single measured chemical compound. Tannins are so called stable or “static” metabolic endpoints while phenolic glycosides and phenolic acids are classified as intermediate or “dynamic” metabolites

A stipulation of the CNB and GDB frameworks is that changes in allelochemical allocation are predominantly driven by nutrient limitations that cause excess photosynthates to be shunted into secondary metabolism. We therefore wished to consider simultaneous changes in nitrogen and allelochemicals. Our literature search resulted in 378 studies of carbon-based allelochemical changes for which nitrogen concentrations were measured simultaneously. Figure 4 shows the N x allelochemical contingency table for these results and the number of measurements showing the specified changes in nitrogen and allelochemicals. In 69% of cases the nitrogen concentration decreased under elevated CO₂ as predicted. Only a single study found an increase in N concentration and those that did not detect a statistical change in N concentrations generally showed a trend towards decreased nitrogen. For the CNB to be a good predictor we would expect most of the data points to consolidate in the top right cell corresponding to decreased N and increased C-based allelochemicals. However, decreased nitrogen and increased allelochemical production accounted for only 32% of all possible combinations. In only 6% of cases did decreased plant nitrogen show a simultaneous decrease in C-based allelochemicals. When only tannins were considered, 52 out of 106 cases (49% – not shown in figure) reported simultaneous decreases in nitrogen and increases in tannins. Thus, even when nitrogen concentrations are considered, the results of empirical studies of allelochemical allocation under elevated CO₂ are only weakly predicted by existing frameworks such as the CNB, except maybe for tannins.

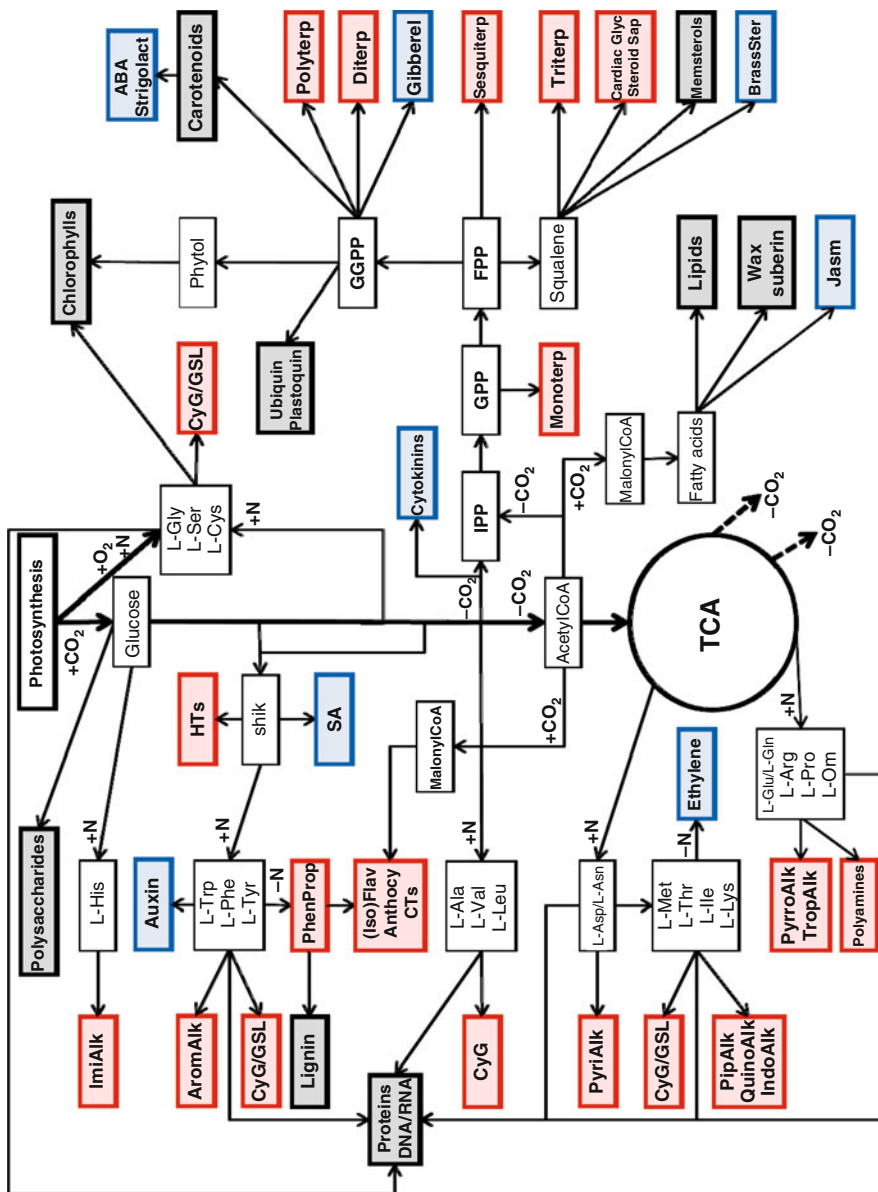
Generally, the usefulness of the CNB hypothesis as a predictive and explanatory tool has been widely debated (Hamilton et al. 2001; Koricheva 2002; Lerda and Coley 2002; Stamp 2003). Some suggest that the CNB has outlived its usefulness (Hamilton et al. 2001) while others suggest that the limitations of the CNB framework arise from a lack of understanding of the model's fundamental assumptions (Stamp 2003). One criticism of the CNB hypothesis is that it ignores the complexities of the biochemical machinery involved in the production of plant defenses (Hamilton et al. 2001). This has resulted in the generation of more

| | | [Nitrogen] | | | TOTAL |
|------------------|---|------------|-----|-----|-------|
| | | + | 0 | - | |
| [Allelochemical] | + | 1 | 18 | 119 | 138 |
| | 0 | 0 | 68 | 122 | 190 |
| | - | 0 | 29 | 21 | 50 |
| TOTAL | | 1 | 115 | 262 | 378 |

Fig. 4 Nitrogen concentration × allelochemical concentration contingency table for $n = 378$ measurements which simultaneously measured carbon-based plant allelochemicals and nitrogen concentration under elevated CO₂. Each cell represents the percentage of studies with the corresponding change in allelochemical and nitrogen concentrations. (+) = increased concentration under elevated CO₂, (0) = no change in concentration under elevated CO₂, (-) = decreased concentration under elevated CO₂. Data exclude N-based allelochemicals

mechanistic hypotheses that consider biochemical intermediates rather than simple cause and effect relationships between the composition of resource inputs and metabolic endpoints. For example, the Protein Competition Model (PCM) of phenolic allocation (Jones and Hartley 1999) predicts the allocation and concentration of phenolics in leaves of terrestrial higher plants based on biochemical pathways and regulatory mechanisms. Specifically, the model predicts that protein and phenolic synthesis compete for the common, limiting resource phenylalanine (PHE), such that protein and phenolic production are inversely correlated. Under elevated CO₂ the concentration of phenolic compounds can thus be predicted from the effects of increased carbon on leaf functions that create competing demands for proteins vs. phenolics. However, it should be noted here that the classification of defense compounds into “C-based” (e.g., tannins) and “N-based” (e.g., alkaloids) might not be justified *per se*, as the production of e.g. alkaloids might be equally or even more C-costly in terms of required glucose as is the production of phenolics (3.24 vs. 2.11 g of glucose per gram of alkaloid vs. phenolic; Gershenson 1994; Schoonhoven et al. 2005). Furthermore, the production of tannins requires a large suite of enzymes (>10; Winkel-Shirley 2001), which are very N-costly, whereas the biosynthesis of the N-based tyrosine derived cyanogenic glycoside dhurrin requires only three enzymes (Nielsen et al. 2008). Furthermore, not only phenylalanine derived phenolics compete with the production of growth-related proteins, but so do all N-based secondary metabolites which require amino acids as precursors. Figure 5 shows the biochemical pathways involved in secondary metabolite production, phytohormone production (see Sect. 2.4, this chapter) and primary metabolic endpoints. The complexity of these biochemical pathways illustrates how simple predictions based on chemical composition may be misleading.

Even more confounding is the fact that classifications of compounds based on their biosynthetic origin might not be relevant in the context of defense (or differentiation) vs. growth allocation. The compound class “phenolics” in fact represents a wide array of possible structures which are all derived from the aromatic amino acid phenylalanine produced in the shikimic acid pathway. However, the major “phenolic” in most plants is lignin, a very complex and large, more or less inert polymer. Lignin is essential for xylem and cell wall development and so plays a critical role in all processes related to water transport including photosynthesis and mineral nutrient transport, as well as in structural support for land plants. Even though one might argue that xylem and secondary cell wall formation is already “differentiation” as opposed to “growth,” and lignin should therefore be seen as a “secondary metabolite” it is also clear that the absence of lignin would lead to the cessation of any growth in land plants. Another example is the even larger class of isoprene derived terpenoids which comprises molecules critical for photosynthesis (carotenoids, terpenoid side chain of chlorophylls), electron carriers (e.g., side chains of plasto- and ubiquinones), membrane structures (sterols), and plant development related phytohormones (abscisic acid, gibberellins) – all essential for and not separable from plant growth. We suggest therefore that models of resource allocation should not be based on chemical structure of metabolites *per se*, but rather on functionality of these metabolites.



2.4 *Phytohormones: The Molecular Link Between Physiological Responses to Elevated CO₂ and Secondary Metabolite Production?*

A metaanalysis of responses of photosynthesis, canopy properties and plant production to elevated CO₂ has shown general trends of increases in light-saturated carbon uptake, diurnal C assimilation, growth, and above-ground production, and decreases in specific leaf area and stomatal conductance (Ainsworth and Long 2005). It has also been shown that, on average, stomatal density decreases under elevated CO₂ (Woodward 1987; Woodward and Bazzaz 1988), resulting in reduced transpiration rates and improved water use efficiency (Woodward 2002; Teng et al. 2006). It has been proposed that the signaling of CO₂ and the induction of these physiological responses is mediated by shifts in the biosynthesis and accumulation of phytohormones, in particular abscisic acid, ethylene, jasmonates, and cytokinins (Yong et al. 2000; Lake et al. 2002; Teng et al. 2006). Furthermore, sugars like e.g. glucose can act as signaling molecules and influence the biosynthesis of these phytohormones (Léon and Sheen 2003; Gibson 2004, 2005; Rolland et al. 2006; Bossi et al. 2009), and increased hexose levels in plants under elevated CO₂ might affect these signaling processes as well.

Phytohormones are also closely linked to the biosynthesis of a wide range of secondary metabolites involved in plant defenses. Figure 5 shows some of the pathways involved in secondary metabolite and phytohormone production. Jasmonates in particular have been linked to plant defense and immunity, and recent excellent reviews have summarized molecular mechanisms of their action as signal transducers in plant–herbivore interactions (Howe and Jander 2008; Browse 2009). Evidence for herbivore-induced production of jasmonates and for their roles in plant immunity is largely based on studies with jasmonate mutants that are compromised in resistance against a wide range of insect herbivores (see references in: Howe and Jander 2008; Browse 2009). It has also been demonstrated that jasmonates interact with other phytohormones like ABA and ethylene, as well as sugar signals (Gazzarrini and McCourt 2001), and that cross-talk between ethylene and jasmonate signaling pathways determine the activation of specific defense responses (Lorenzo et al. 2003).

Jasmonates are formed from the fatty acid linolenic acid in the octadecanoic pathway (Schaller et al. 2004). Several intermediates of this pathway as well as the resulting jasmonates have been shown to induce the biosynthesis of terpenoids in conifers (Martin et al. 2002) and tomatoes (Ament et al. 2004), terpenoid indole alkaloids in *Catharanthus rosea* (Menke et al. 1999), and terpene volatiles in

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Fig. 5 Schematic overview of plant metabolic pathways (simplified and plant specific modified version of KEGG overview of biosynthetic pathways); <http://www.genome.jp/kegg/pathway/map/map01010.html>) from primary metabolites (*black open*) to secondary metabolites (*red shaded*), primary “end” metabolites (*black shaded*) and phytohormones (*blue shaded*). ±CO₂ and N represent the regions where biochemical processes lead to the incorporation (+) or release (–) of CO₂ or N. See Appendix 2 for a list of abbreviations

Brassica oleraceae (Bruinsma et al. 2009). A study on terpene volatile induction in lima beans also reported that early and late intermediates of the octadecanoic pathway induce the accumulation of different terpenoids, resulting in a different “blend” of volatiles (Koch et al. 1999).

Only a few studies tested a relationship between elevated CO₂, phytohormone production, and plant defense responses, but it has been demonstrated that elevated CO₂ down-regulated genes involved in ethylene and jasmonate production, and that in turn resulted in the down-regulation of the expression of genes for an antiherbivorous cysteine proteinase inhibitor and enzymes of the phenylpropanoid pathway in soybean, compromising the plants’ resistance against some insect herbivores (Zavala et al. 2008, 2009). We propose therefore that studies on phytohormones may provide a molecular link between physiological responses to elevated CO₂ and plant secondary metabolites and should be studied in more detail to unravel mechanisms of changes in defense metabolite production under elevated CO₂.

3 Trophic Interactions and Climate Change

3.1 Plant–Herbivore Interactions and Elevated CO₂

Changes in the quality of host plants for phytophagous insects in an atmosphere with higher levels of CO₂ will likely be driven by two predominant factors: allelochemicals and nitrogen. As discussed in Sect. 2.2 nitrogen decreases under elevated CO₂ are almost ubiquitous in plants, whereas carbon-based allelochemicals are expected to increase, albeit with many exceptions. Thus, a general prediction emerges whereby simultaneous decreases in nitrogen and increases in allelochemicals will have a net negative effect on herbivorous insects. As we will see below, this simple prediction is also subject to many exceptions and dependent on many interacting factors. Understanding the impact of CO₂-mediated changes in plant quality on insect herbivores, and how herbivory in turn will affect plant growth, is dependent on understanding how these changes affect insect performance parameters at both the individual and population levels.

Empirical studies:

For the literature search described in Sect. 2.3, a subset of studies ($n = 38$) also reported herbivore responses to CO₂-induced changes in secondary metabolites. Figures 6 and 7 below are derived from these reports. It should be noted however that correlation analyzes between insect performance parameters and allelochemical production were reported in only a minority of these studies. As such, the covariation of allelochemical concentration and insect performance presented here do not necessarily imply causation and these data should thus be interpreted with caution. Insect performance was typically measured using life history traits such as survival, body size, development time, fecundity, and growth rate. As predicted by life history theory, many of these traits typically covaried. For example decreased body size was often associated with increased development

time. An overall performance score (increased, decreased or no change) was given to each study based on these traits. Again plant chemistry data must be interpreted with caution as they are based on simultaneous measurements of allelochemicals and insect performance, and as such, performance of a given insect is overrepresented here in cases where multiple allelochemicals are measured in a single study.

Figure 6a shows the contingency table derived from these data for insect performance vs. allelochemical concentration ($n = 216$). Insect performance decreased in 44% of cases (96 out of 216), was unchanged in 43% of cases (92 out of 216) and increased in 13% of cases (28 out of 216). In cases where allelochemicals increased (80 out of 216) insect performance decreased 48% of the time (38 out of 80). In some cases insect performance was negatively correlated with increases in specific groups of allelochemicals such as phenolic glycosides (Lindroth et al. 1997; McDonald et al. 1999). However, where allelochemicals decreased (19 out of 216) surprisingly more often than not insect performance also

a

| | | Insect performance | | | |
|------------------|---|--------------------|----|----|-------|
| | | + | 0 | - | TOTAL |
| [Allelochemical] | + | 9 | 33 | 38 | 80 |
| | 0 | 16 | 53 | 48 | 117 |
| | - | 3 | 6 | 10 | 19 |
| TOTAL | | 28 | 92 | 96 | 216 |

b

| | | Insect performance | | | |
|------------|---|--------------------|----|----|-------|
| | | + | 0 | - | TOTAL |
| [Nitrogen] | + | 0 | 0 | 0 | 0 |
| | 0 | 2 | 9 | 3 | 14 |
| | - | 5 | 17 | 23 | 45 |
| TOTAL | | 7 | 26 | 26 | 59 |

Fig. 6 (a) Insect performance \times allelochemical concentration contingency table for $n = 216$ measurements which simultaneously measured allelochemical concentration and insect performance under elevated CO_2 and (b) Insect performance \times nitrogen concentration contingency table for $n = 59$ measurements. Each cell represents the number of measurements with the corresponding change in allelochemical concentration, N concentration and insect performance. (+) = increased concentration or performance under elevated CO_2 , (0) = no change in concentration or performance under elevated CO_2 , (-) = decreased concentration or performance under elevated CO_2 . Insect performance was classified as negative in cases where decreases in survival, mass, growth rate or fecundity, or increases in development time or mortality were reported. The opposite was used to denote decreases in performance. Where none of the above performance parameters changed, overall insect performance was counted as unchanged

decreased (53% of cases) which suggests that factors other than allelochemicals may be strong determinants of insect performance under elevated CO₂. We examined the effect of nitrogen on insect performance in the same way (Fig. 6b). As expected, nitrogen did not increase in any of the 59 observations but decreased, as predicted, in 76% of cases. Where nitrogen decreased, insect performance decreased in 23 of 45 cases (51%). Thus, several generalities can be made from the effect of CO₂ on nitrogen and allelochemicals, and their subsequent effect on insect herbivores, however some of the conceptual and theoretical models proposed here are only weakly predictive. The variable nature of these data is likely to occur for several reasons. Firstly, the predictive frameworks explained here, and those often used in climate change biology, are often far too simplistic to capture the complexities of species interactions in heterogeneous environments. These interactions will depend critically on the environmental context in which they occur and will be subject to several interacting variables. For example, changes in the interactions between plants and insects under elevated CO₂ are dependent on light regime (McDonald et al. 1999; Agrell et al. 2000), soil nutrient status (Johnson and Lincoln 1991; Hättenschwiler and Schafellner 1999; Saxon et al. 2004), atmospheric ozone levels (Kopper et al. 2001; Kopper and Lindroth 2003), temperature (Veteli et al. 2002; Williams et al. 2003) and plant and insect genotype (Goverde et al. 2004; Saxon et al. 2004). The plant-mediated effects on insect herbivores will also depend on herbivore sensitivity to such changes. Just as plants have a range of plastic responses to elevated CO₂, herbivores too can alter or compensate for elevated CO₂-mediated changes in plant quality by altering feeding rates and efficiency.

Compensatory feeding:

In many cases, insect herbivores can compensate for decreases in the nutritional quality of plants grown under elevated CO₂ by increasing their food intake (Johnson and Lincoln 1990; Lindroth et al. 1993; Kinney et al. 1997; Mansfield et al. 1999; Agrell et al. 2000). Figure 7a shows the herbivore consumption rate vs. nitrogen concentration contingency table generated from the reports described above. This table summarizes insect plastic feeding response to elevated CO₂-induced nutrient deficiencies. In no cases did consumption decrease under elevated CO₂ suggesting that food intake rate is critical for insects feeding on elevated CO₂-grown plants. In the 30 cases where N decreased, increased consumption rates occurred in 57% (17) of observations. However, increased intake did not always correlate with insect performance in the studies examined here and compensatory feeding did not always result in full N intake compensation. For example, Hättenschwiler and Schafellner (1999) found that nun moth larvae that increased their relative consumption rates on N-deficient plants grown under elevated CO₂ still consumed on average 33% less nitrogen.

Consumption rates were unchanged in 43% of cases where plant N decreased (Fig. 7a). In some cases compensatory feeding was shown to be limited by the presence of different classes of allelochemicals such as terpenoids (Johnson and Lincoln 1990, 1991) and phenolic glycosides (Roth et al. 1998). Figure 7b shows the contingency table for allelochemicals vs. consumption. In cases where

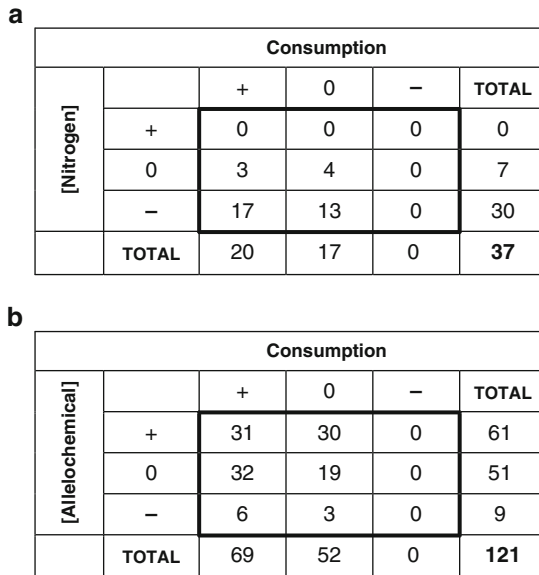


Fig. 7 (a) Insect herbivore consumption \times nitrogen concentration contingency table for $n = 37$ measurements which simultaneously measured nitrogen concentration and consumption rates under elevated CO_2 . **(b)** Insect herbivore consumption \times allelochemical concentration contingency table for $n = 121$ measurements which simultaneously measured carbon-based plant allelochemicals and consumption rates under elevated CO_2 . Each cell represents the number of studies with the corresponding change in allelochemical concentrations, consumption rates and nitrogen concentrations. (+) = increased concentration under elevated CO_2 , (0) = no change in concentration under elevated CO_2 , (-) = decreased concentration under elevated CO_2

allelochemicals increased under elevated CO_2 , compensatory feeding occurred about half of the time, where allelochemicals did not change compensatory feeding occurred in 63% of cases and where allelochemicals decreased compensatory feeding occurred in 67% of cases. This suggests that allelochemical concentration may have an effect on compensatory feeding though this is difficult to assess as cases where allelochemicals decreased were low (9 out of 121 measurements). Herbivores may also compensate for decreases in nutritive value of host plants in ways that alter food processing efficiency. For example, larvae of the red-headed pine sawfly increased their nitrogen utilization efficiency under elevated CO_2 in response to declines in nitrogen concentration in loblolly pine (Williams et al. 1994). In addition, it has been shown that insect herbivores exposed to multiple species of plants may offset the negative effects associated with elevated CO_2 by partial host shifts or by feeding on alternative plant parts (Williams et al. 1997; Agrell et al. 2005).

In agricultural systems, compensatory feeding may have implications for crop yields. Insects that increase their consumption due to high C:N ratios under elevated CO_2 can increase their exposure to pesticides resulting in increased mortality (Coviella and Trumble 2000). It is generally predicted that elevated CO_2 will have a net positive effect on agricultural yields and increased efficacy of insecticides

could potentially augment this result. However, assessing the net impact of elevated CO₂ on agricultural systems is subject to several considerations. In many cases compensatory feeding has been shown to occur in response to decreases in the nutritional quality of plants under elevated CO₂ with no corresponding changes in insect performance (Johnson and Lincoln 1990; Lindroth et al. 1993; Williams et al. 1994; Docherty et al. 1996; Kinney et al. 1997; Roth et al. 1998). However, the net effect on plant productivity will depend on whether increases in plant biomass can ameliorate increases in defoliation (Hunter 2001). Other factors may also influence herbivore feeding rates under elevated CO₂. For example, Hamilton et al. (2005) found that the leaf area of soybean plants removed by insect herbivores increased by up to 57% under elevated CO₂ due to the phagostimulatory effect of sugar which increased in concentration. However, since CO₂-mediated resource allocation in plants is likely to depend critically on nutrient inputs (Johnson and Lincoln 1991; Hättenschwiler and Schafellner 1999; Saxon et al. 2004), this means that some of these effects may be buffered by controlling fertilization levels in agricultural contexts.

A challenge for climate change ecologists is the ability to broadly predict the effects of elevated CO₂ on plant–insect interactions which can in turn have profound effects on ecosystems as a whole. It may be possible that generalities can be made and models derived at specific levels of ecosystem complexity. Plant variables which are likely to be strong determinants of ecosystem responses and which should be incorporated into mechanistic models are photosynthetic machinery (C3 vs. C4), growth rates (fast vs. slow growing species), symbiotic associations (e.g., rhizobia and N₂ fixation; fungal endophytes and their antiherbivorous toxins; mycorrhizae and P uptake), agricultural vs. natural ecosystems and plant chemical profiles. Insect responses in turn will depend on levels of insect specialization, guild effects, sensitivity to changing plant quality and capacity to compensate for nutritive deficits.

3.2 The Effects of Elevated CO₂ on Higher Trophic Levels

Global atmospheric change can be reasonably expected to have consequences, not just for plants and their herbivores, but for ecosystems as a whole. Changes in primary productivity are expected to alter an array of community interactions and ecosystem functions. For example, increased lignin:nitrogen and C:N ratios in the litter of deciduous trees grown under elevated CO₂ can cause decreases in decomposition and respiration rates (Cotrufo et al. 1994). Elevated CO₂ has also been shown to affect soil microbial composition and activity (Runion et al. 1994). Changes in the biotic and abiotic structure of soils are likely to have profound effects on ecosystems via feedbacks to primary production. Plant–fungal interactions are likely to also be affected by elevated CO₂. Symbiotic fungal endophytes of grasses can impact the primary metabolic response of the host plant to elevated CO₂ which in turn is expected to affect other trophic levels. Recent studies have shown

that endophyte infection can buffer the plant’s nitrogen metabolism response to elevated CO₂ in both tall fescue (Newman et al. 2003) and perennial ryegrass (Hunt et al. 2005). For soil fungi, increases in the hyphal length and activity of saprophytic fungi, along with increases in mycorrhizal infection of roots, have been reported (Dhillon et al. 1996). Increasing atmospheric CO₂ may also have consequences for plant–plant communication though to our knowledge this has never been explicitly tested. Baldwin and Schultz (1983) demonstrated that herbivory can induce volatile cues in plants that signal the presence of herbivores to other plants. Nearby plants then alter their secondary chemistry in a way that makes them less palatable to herbivores, and this response is likely to depend on the genetic relatedness of plants (Karban and Shiojiri 2009). Thus, plant–plant communication may be affected by CO₂-induced changes in volatile emissions which have been demonstrated in several studies (Tognetti et al. 1998; Constable et al. 1999; Loreto et al. 2001; Kreuzwieser et al. 2002; Rapparini et al. 2004; Vuorinen et al. 2004a; Himanen et al. 2009). Figure 8 shows the number of studies that have examined the effects of CO₂-induced changes in plant defensive chemistry on several important community interactions. Studies have been dominated by the effects of elevated CO₂ on plant secondary chemistry, are common for subsequent effects on herbivores and decrease in number with higher trophic levels, highlighting the need for investigation of elevated CO₂ on broader community interactions. Recent studies suggest that changes in plant defensive chemistry under elevated CO₂ may have profound consequences for herbivore enemies.

The effects of elevated CO₂ on the production of plant allelochemicals may influence higher trophic levels either directly or indirectly (herbivore-mediated)

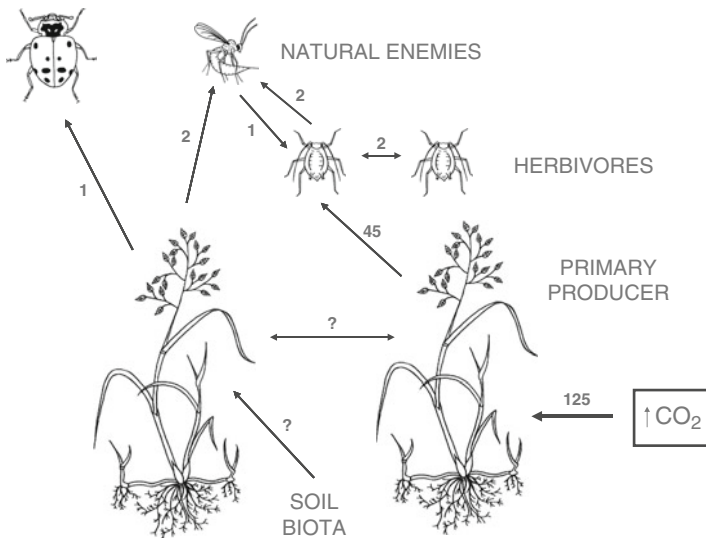


Fig. 8 The number of publications located on the effects of elevated CO₂ on plant secondary chemicals and the subsequent effects on higher trophic levels

(see Fig. 8). Higher trophic levels are attracted by herbivore-induced damage volatiles which signal to natural enemies (predators and parasitoids) that herbivores are present (direct effect). Changes in emission rates and composition of plant-derived VOCs under elevated CO_2 may alter the fitness of natural enemies through alterations in this olfactory cue and the subsequent capability of natural enemies to locate herbivores. Vuorinen et al. (2004b) found changes in the orientation behavior of a generalist predator *Podisus maculiventris* in the presence of herbivore-damaged cabbage plants grown under elevated CO_2 . In the same study it was found that the specialist parasitoid *Cotesia plutellae* was unable to orient itself towards herbivore-damaged plants grown under elevated CO_2 . At ambient CO_2 levels both species are able to detect herbivore presence via herbivore-induced plant volatiles. Thus herbivore-induced damage response by higher trophic levels may be diminished under elevated CO_2 . This is expected to have profound effects for herbivore enemies in changing atmospheres particularly in light of the suggestion that herbivore-induced volatiles are the single most reliable prey location cue for generalist predators (Vet and Dicke 1992). Research suggests that natural enemy attraction may depend on the concentration of volatiles released. For example, transgenic *Arabidopsis thaliana* plants engineered to overexpress a terpene synthase gene were found to increase in attractiveness to the parasitic wasp *C. marginiventris* when plants were damaged by lepidopteran larvae (Schnee et al., 2006). However data on volatile emission rates under elevated CO_2 have been highly inconsistent and may covary with other plant variables sensitive to CO_2 -induced changes. Compensatory feeding by herbivores on nutrient deficient plants grown under elevated CO_2 may cause increases in inducible defenses such as VOC emissions (Himanan et al. 2009) which could alter enemy behavior. However, changes in orientation behavior may be dependent on the sensitivity of herbivore enemies to changes in plant volatiles. For example, Himanan et al. (2009) found that damage-induced volatiles from *B. napus* plants increased under elevated CO_2 but there was no difference in the orientation behavior of the endoparasitoid *C. vestalis* between the treatments.

The effects of elevated CO_2 on plant defensive chemistry may also affect higher trophic levels indirectly through ingestion of plant chemicals by herbivores that in turn may alter parasitoid or predator survival. However, few studies have examined the indirect effects of CO_2 -induced changes in plant chemistry on higher trophic levels. Roth and Lindroth (1995) found that the effect of parasitism on gypsy moth performance did not change under elevated CO_2 . However, parasitoid mortality increased, especially on aspen grown under elevated CO_2 where sensitivity of parasitoids to the accumulation of phenolic glycosides by the gypsy moth due to compensatory feeding may have been a factor. In a similar study elevated CO_2 had little effect on the survivorship of the dipteran parasitoid *Compsilura concinnata* when its host *Malacosoma disstria* was fed on aspen grown under elevated CO_2 (Holton et al. 2003).

Elevated CO_2 may also have implications for plant-mediated production and perception of alarm responses of herbivores. For example, in potato aphids (*Aulacorthum solani*) feeding on broad bean (*Vicia faba*) grown in elevated CO_2 it

was found that the ability to produce alarm pheromone in the presence of a disturbance was reduced, as was the ability of the recipient to detect the pheromone (Awmack et al. 1997). Diminished escape responses by aphids under elevated CO₂ have also been demonstrated in subsequent studies (Mondor et al. 2004). It has been hypothesized that the ability of herbivores to detect conspecific alarm signals may depend on the surrounding chemical environment produced by the plant (Dill et al. 1990). Thus CO₂-induced changes in volatile emissions may have implications for herbivore–herbivore communication.

4 Conclusions

Here we examined the effect of elevated CO₂ on plant allocation to secondary defense and subsequent effects on higher trophic levels. A great deal of empirical studies have been undertaken at the level of the plant and some general patterns have emerged from these investigations. In general carbon-based secondary metabolites have a tendency to increase, though this is likely to be pathway dependent. Thus, more mechanistic models are needed in order to help us understand some of this complexity. If we are to predict the effects of CO₂ on plant chemistry we will need to be able to determine where generalities can be made, where they cannot and what can be learned from exceptions to these generalities. Although we have focused on secondary metabolites here, the primary metabolic response will also have broad implications for bottom–up interactions in a high CO₂ atmosphere. In addition, interacting factors are likely to profoundly affect the response to elevated CO₂. We have already seen that changes in plant chemistry and nutrient status are the most common determinants of herbivore responses and subsequent responses of higher trophic levels. In general, insect herbivores are expected to have decreased performance if nitrogen concentrations decrease and plant defenses increase. However, plant responses and subsequent herbivore responses will likely depend on factors such as temperature, ozone, nutrients, water availability and light availability.

The possible role of evolution in species' responses to CO₂ and other climate change projections in the next century is often precluded from discussions of climate change impacts and the majority of studies assess only the plastic response of organisms. Thus it is generally accepted that species will either adjust to perturbations within their physiological range or become extinct. This is true for many of the long-lived woody plant species which tend to dominate the literature on elevated CO₂. However, in many cases herbivorous insects may fit the criteria for rapid evolutionary adaptation, that is: large population sizes ($>10^5$ – 10^6), short generation times (e.g. <1 year) and high intrinsic rates of increase (e.g. $r_m > 0.5$ /generation) (Kingsolver 1996). For example, genetic changes in fruit flies have been associated with adaptation to climate warming (Umina et al. 2005; Balanyá et al. 2006). Thus there is a need for longer term studies on the community effects of CO₂. Even in the absence of adaptation per se, plants have the potential to

acclimatize to changing conditions over time and studies have shown that plants can exhibit a high level of adaptive plasticity. For example, for some plants, changes in photosynthetic rates associated with elevated CO₂ may be transient (Bazzaz 1990). Also, the single-step increase in elevated CO₂ adopted in the design of most experiments is not representative of the gradual increases seen in reality and this may have implications for observed changes. For example, Klironomos et al. (2005) showed that long term gradual increases in elevated CO₂ resulted in no change in the diversity of mycorrhizal fungi relative to ambient but an abrupt step increase reduced diversity due to the sensitivity of some species to this change.

Ecosystem-wide responses to increasing CO₂ will be difficult to predict given the complexity of interactions which exist in even the most elementary ecosystems. More research is needed to even begin to formulate general principles with regard to responses of higher trophic levels. Even then, individual responses may not predict the response of communities as a whole. Differences in the physiological sensitivities of certain groups or species and the differential ability of organisms to adjust to atmospheric changes might reasonably be expected to alter relative abundances, which in turn may have consequences for ecosystem diversity and function. Figure 8 highlights the gaps in our knowledge with respect to community effects of elevated CO₂ and reveals the scarcity of studies on higher trophic levels, below ground effects and intraspecific communication. The complexity of communities necessitates the identification of those variables which are likely to be of utmost importance. Ecosystem-wide studies will benefit from technologies such as free-air carbon enrichment (FACE) and open-topped chambers (OTC) which will be of great importance in assessing effects on natural communities.

References

- Agrell J, McDonald EP, Lindroth RL (2000) Effects of CO₂ and light on tree phytochemistry and insect performance. *Oikos* 88:259–272
- Agrell J, Kopper B, McDonald EP, Lindroth RL (2005) CO₂ and O₃ effects on host plant preferences of the forest tent caterpillar (*Malacosoma disstria*). *Glob Chang Biol* 11:588–599
- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytol* 165:351–372
- Ament K, Kant MR, Sabelis MW, Haring MA, Schuurink RC (2004) Jasmonic acid is a key regulator of spider mite-induced volatile terpenoid and methyl salicylate emission in tomato. *Plant Physiol* 135:2025–2037
- Awmack CS, Woodcock CM, Harrington R (1997) Climate change may increase vulnerability of aphids to natural enemies. *Ecol Entomol* 22:366–368
- Ayres MP (1993) Plant defense, herbivory and climate change. In: Kareiva PM, Kingsolver JG, Huey RB (eds) *Biotic interactions and global change*. Sinauer Associates, Sunderland, MA, pp 75–94
- Balanyá J, Oller JM, Huey RB, Gilchrist GW, Serra L (2006) Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science* 313:1773–1775

- Baldwin JT, Schultz JC (1983) Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. *Science* 221:277–279
- Bazzaz FA (1990) Response of natural ecosystems to the rising global CO₂ level. *Annu Rev Ecol Syst* 21:167–196
- Bezemer TM, Jones TH, Newington JE (2000) Effects of carbon dioxide and nitrogen fertilization on phenolic content in *Poa annua* L. *Biochem Sys Ecol* 28:839–846
- Bidart-Bouzat MG, Mithen R, Berenbaum MR (2005) Elevated CO₂ influences herbivory-induced defense responses of *Arabidopsis thaliana*. *Oecologia* 145:415–424
- Birkett MA, Bruce TJA, Martin JL, Smart LE, Oakley J, Wadhams LJ (2004) Responses of female orange wheat blossom midge, *Sitodiplosis mosellana*, to wheat panicle volatiles. *J Chem Ecol* 30:1319–1328
- Bossi F, Cordoba E, Dupré P, Mendoza MS, San Román C, León P (2009) The *Arabidopsis* ABA-INSENSITIVE (ABI) 4 factor acts as a central transcription activator of the expression of its own gene, and for the induction of *ABI5* and *SBE2.2* genes during signaling. *Plant J* 59:359–374
- Bowes G (1993) Facing the inevitable: plants and increasing atmospheric CO₂. *Annu Rev Plant Physiol, Plant Mol Biol* 44:309–32
- Brower LP, Fink LS (1985) A natural toxic defense system – cardenolides in butterflies versus birds. *Ann N Y Acad Sci* 443:171–188
- Browse J (2009) Jasmonate passes muster: a receptor and targets for the defense hormone. *Annu Rev Plant Biol* 60:183–205
- Bruce TJA, Wadhams LJ, Woodcock CM (2005) Insect host location: a volatile situation. *Trends Plant Sci* 10:269–274
- Bruinsma M, Posthumus MA, Mumm R, Mueller MJ, van Loon JJA, Dicke M (2009) Jasmonic acid-induced volatiles of *Brassica oleraceae* attract parasitoids: effects of time and dose, and comparison with induction by herbivores. *J Exp Bot* 60:2575–2587
- Bryant JP, Chapin FS III, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40:357–368
- Coley PD (1998) Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Clim Change* 39:455–472
- Constable JVH, Litvak ME, Greenberg JP, Monson RK (1999) Monoterpene emission from coniferous trees in response to elevated CO₂ concentration and climate warming. *Glob Chang Biol* 5:255–267
- Cornell HV, Hawkins BA (2003) Herbivore responses to plant secondary compounds: a test of phytochemical theory. *Am Nat* 161:507–522
- Cotrufo MF, Ineson P, Rowland AP (1994) Decomposition of tree leaf litters grown under elevated CO₂: effect of litter quality. *Plant Soil* 163:121–130
- Cotrufo MF, Ineson P, Scott A (1998) Elevated CO₂ reduces the nitrogen concentration of plant tissues. *Glob Chang Biol* 4:43–54
- Coviella CE, Trumble JT (1999) Effects of elevated atmospheric carbon dioxide on insect–plant interactions. *Conserv Biol* 18:700–712
- Coviella CE, Trumble JT (2000) Effect of elevated atmospheric carbon dioxide on the use of foliar application of *Bacillus thuringiensis*. *Biocontrol* 45:325–336
- Coviella CE, Morgan DJW, Trumble JT (2000) Interactions of elevated CO₂ and nitrogen fertilization: effects on production of *Bacillus thuringiensis* toxins in transgenic plants. *J Econ Entomol* 93:781–787
- Cronin G, Hay ME (1996) Within-plant variation in seaweed palatability and chemical defenses: optimal defense theory versus the growth-differentiation balance hypothesis. *Oecologia* 105:361–368
- Dhillion SS, Roy J, Abrams M (1996) Assessing the impact of elevated CO₂ on soil microbial activity in a Mediterranean model ecosystem. *Plant Soil* 187:333–342
- Dill LM, Fraser AHG, Roitberg BD (1990) The economics of escape behaviour in the pea aphid, *Acyrtosiphon pisum*. *Oecologia* 83:473–478

- Docherty M, Hurst DK, Holopainen JK, Whittaker JB, Lea PJ, Watt AD (1996) Carbon dioxide-induced changes in beech foliage cause female beech weevil larvae to feed in a compensatory manner. *Glob Chang Biol* 2:335–331
- Drake BG, González-Meler MA (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Annu Rev Plant Physiol Plant Mol Biol* 48:609–639
- Dudareva N, Negre F, Nagegowda DA, Orlova I (2006) Plant volatiles: recent advances and future perspectives. *Crit Rev Plant Sci* 25:417–440
- Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. *Evolution* 18:586–608
- Fajer ED, Bowers MD, Bazzaz FA (1991) The effects of enriched CO₂ atmospheres on the Buckeye Butterfly, *Junonia coenia*. *Ecology* 72:751–754
- Fajer ED, Bowers MD, Bazzaz FA (1992) The effect of nutrients and enriched CO₂ environments on production of carbon-based allelochemicals in plantago: a test of the carbon/nutrient balance hypothesis. *Am Nat* 140:707–723
- Feeny P (1975) Biochemical coevolution between plants and their insect herbivores. In: Gilbert LE, Raven PH (eds) *Coevolution of animals and plants*. University of Texas Press, Austin, TX, pp 3–19
- Feeny P (1976) Plant apparency and chemical defense. In: Wallace JW, Mansell RL (eds) *Recent advances in phytochemistry*, vol 10. Plenum, New York, pp 1–40
- Fraser AM, Mechaber WL, Hildebrand JG (2003) Electroantennographic and behavioural responses of the sphinx moth *Manduca sexta* to host plant headspace volatiles. *J Chem Ecol* 29:1813–1833
- Futuyama DJ (1983) Evolutionary interactions among herbivorous insects and plants. In: Futuyama DJ, Slatkins M (eds) *Coevolution*. Sinauer, Sunderland, MA, pp 207–231
- Gayler S, Grams TEE, Heller W, Treutter D, Priesack E (2008) A dynamical model of environmental effects on allocation to carbon-based secondary compounds in juvenile trees. *Ann Bot* 101:1089–1098
- Gazzarrini S, McCourt P (2001) Genetic interactions between ABA, ethylene and sugar signaling pathways. *Curr Opin Plant Biol* 4:387–391
- Gershenzon J (1994) Metabolic costs of terpenoid accumulation in higher plants. *J Chem Ecol* 20:1281–1328
- Gibson SI (2004) Sugar and phytohormone response pathways: navigating a signalling network. *J Exp Bot* 55:253–264
- Gibson SI (2005) Control of plant development and gene expression by sugar signaling. *Curr Opin Plant Biol* 8:93–102
- Goverde M, Erhardt A, Stocklin J (2004) Genotype-specific response of a lycaenid herbivore to elevated carbon dioxide and phosphorous availability in calcareous grassland. *Oecologia* 139:383–391
- Gulmon SL, Mooney HA (1986) Costs of defense on plant productivity. In: Givnish TJ (ed) *On the economy of plant form and function*. Cambridge University Press, Cambridge, pp 681–698
- Hamilton JG, Zangerl AR, DeLucia EH, Berenbaum MR (2001) The carbon–nutrient balance hypothesis: its rise and fall. *Ecol Lett* 4:86–95
- Hamilton JG, Dermody O, Mihai A, Zangerl AR, Rogers A, Berenbaum MR, DeLucia EH (2005) Anthropogenic changes in tropospheric composition increase susceptibility of soybean to insect herbivory. *Environ Entomol* 32:479–485
- Hättenschwiler S, Schafellner C (1999) Opposing effects of elevated CO₂ and N deposition on *Lymantria monacha* larvae feeding on spruce trees. *Oecologia* 118:210–217
- Hemming JDC, Lindroth RL (1999) Effect of light and nutrient availability on aspen: growth, phytochemistry and insect performance. *J Chem Ecol* 25:1687–1714
- Herns DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. *Q Rev Biol* 67:283–335
- Himanen SJ, Nerg AM, Nissinen A, Pinto DM, Stewart CN Jr, Poppy GM, Holopainen JK (2009) Effects of elevated carbon dioxide and ozone on volatile terpenoid emissions and multitrophic communication of transgenic insecticidal oilseed rape (*Brassica napus*). *New Phytol* 181:174–186

- Holtan MK, Lindroth RL, Nordheim EV (2003) Foliar quality influences tree–herbivore–parasitoid interactions: effects of elevated CO₂, O₃, and plant genotype. *Oecologia* 137:233–244
- Howe GA, Jander G (2008) Plant immunity to insect herbivores. *Annu Rev Plant Biol* 59:41–66
- Hunt MG, Rasmussen S, Newton PCD, Parsons AJ, Newman JA (2005) Near-term impacts of elevated CO₂, nitrogen and fungal endophyte infection on perennial ryegrass: growth, chemical composition and alkaloid production. *Plant Cell Environ* 28:1345–1354
- Hunter MD (2001) Effects of elevated atmospheric carbon dioxide on insect–plant interactions. *Agric For Entomol* 3:153–159
- IPCC Special Report on Emissions Scenarios (SRES), Nakicenovic N, Swart R (eds) (2000) Special report on emissions scenarios, working group III, intergovernmental panel on climate change (IPCC). Cambridge University Press, Cambridge
- Johnson RH, Lincoln DE (1990) Sagebrush and grasshopper responses to atmospheric carbon dioxide concentration. *Oecologia* 84:103–110
- Johnson RH, Lincoln DE (1991) Sagebrush carbon allocation patterns and grasshopper nutrition: the influence of CO₂ enrichment and soil mineral limitation. *Oecologia* 87:127–134
- Jones CG, Hartley SE (1999) A protein competition model of phenolic allocation. *Oikos* 86:27–44
- Karban R, Shiojiri K (2009) Self-recognition affects plant communication and defense. *Ecol Lett* 12:502–506
- Karowe DN, Seimens DH, Mitchell-Olds T (1997) Species-specific response of glucosinolate content to elevated atmospheric CO₂. *J Chem Ecol* 23:2569–2582
- Kessler A, Baldwin IT (2001) Defensive function of herbivore-induced plant volatile emissions in nature. *Science* 291:2141–2144
- Kingsolver JG (1996) Physiological sensitivity and evolutionary responses to climate change. In: Körner C, Bazzaz FA (eds) *Carbon dioxide, populations and communities*. Academic, San Diego, CA, pp 3–12
- Kinney KK, Lindroth RL, Jung SM, Nordheim EV (1997) Effects of CO₂ and NO₃⁻ availability on deciduous trees: phytochemistry and insect performance. *Ecology* 78:215–230
- Klironomos JN, Allen MF, Rillig MC, Pietrowski J, Makvandi-Nejad S, Wolfe BE, Powell JR (2005) Abrupt rise in atmospheric CO₂ overestimates community response in a model plant–soil system. *Nature* 433:621–624
- Koch T, Krumm T, Jung V, Engelberth J, Boland W (1999) Differential induction of plant volatile biosynthesis in the lima bean by early and late intermediates of the octadecanoid-signaling pathway. *Plant Physiol* 121:153–162
- Kopper BJ, Lindroth RL (2003) Effects of elevated carbon dioxide and ozone on the phytochemistry of aspen and performance of an herbivore. *Oecologia* 134:95–103
- Kopper BJ, Lindroth RL, Nordheim EV (2001) CO₂ and O₃ effects on paper birch (*Betula papyrifera*) phytochemistry and whitemarked tussock moth (*Lymantriidae: Orgyia leucostigma*) performance. *Environ Entomol* 30:1119–1126
- Koricheva J (2002) The carbon–nutrient balance hypothesis is dead; long live the carbon–nutrient balance hypothesis? *Oikos* 98:537–539
- Kreuzwieser J, Cojocariu C, Jüssen V, Rennenberg H (2002) Elevated atmospheric CO₂ causes seasonal changes in carbonyl emissions from *Quercus ilex*. *New Phytol* 154:327–333
- Lake JA, Woodward FI, Quick WP (2002) Long-distance CO₂ signalling in plants. *J Exp Bot* 53:183–193
- Léon P, Sheen J (2003) Sugar and hormone connections. *Trends Plant Sci* 8:110–116
- Lerdau M, Coley PD (2002) Benefits of the carbon–nutrient balance hypothesis. *Oikos* 98:534–536
- Lindroth RL, Dearing MD (2005) Herbivory in a world of elevated CO₂. In: Ehleringer JR, Cerling TE, Dearing MD (eds) *A history of atmospheric CO₂ and its effects on plants, animals and ecosystems*. Springer, Berlin, pp 468–486
- Lindroth RL, Kinney KK, Platz CL (1993) Responses of deciduous trees to elevated atmospheric CO₂: productivity, phytochemistry, and insect performance. *Ecology* 74:763–777

- Lindroth RL, Roth S, Kruger EL, Volin JC, Koss PA (1997) CO₂-mediated changes in aspen chemistry: effects on gypsy moth performance and susceptibility to virus. *Glob Chang Biol* 3:279–289
- Loomis WE (1932) Growth-differentiation balance vs carbohydrate–nitrogen ratio. *Proc Am Soc Hort Sci* 29:240–245
- Loomis WE (1953) Growth and differentiation – an introduction and summary. In: Loomis WE (ed) *Growth and differentiation in plants*. State College Press, Ames, IA, pp 1–17
- Lorenzo O, Piqueras R, Sánchez-Serrano JJ, Solano R (2003) Ethylene response factor1 integrates signals from ethylene and jasmonate pathways in plant defense. *Plant Cell* 15:165–178
- Loreto F, Fischbach RJ, Schnitzler JP, Cicciolo P, Brancaleoni E, Calfapietra C, Seufert G (2001) Monoterpene emission and monoterpene synthase activities in the Mediterranean evergreen oak *Quercus ilex* L. grown at elevated CO₂ concentrations. *Glob Chang Biol* 7:709–717
- Makino A, Mae T (1999) Photosynthesis and plant growth at elevated levels of CO₂. *Plant Cell Physiol* 40:999–1006
- Mansfield JL, Curtis PS, Zak DR, Pregitzer KS (1999) Genotypic variation for condensed tannin production in trembling aspen (*Populus tremuloides*, Salicaceae) under elevated CO₂ and in high- and low-fertility soil. *Am J Bot* 86:1154–1159
- Martin D, Tholl D, Gershenzon J, Bohlmann J (2002) Methyl jasmonate induces traumatic resin ducts, terpenoid resin biosynthesis, and terpenoid accumulation in developing xylem of Norway spruce stems. *Plant Physiol* 129:1003–1018
- Mattson WJ, Julkunen-Tiitto R, Herms DA (2005) CO₂ enrichment and carbon partitioning to phenolics: do plant responses accord better with the protein competition or the growth-differentiation balance models? *Oikos* 111:337–347
- McDonald EP, Agrell J, Lindroth RL (1999) CO₂ and light effects on deciduous trees: growth, foliar chemistry, and insect performance. *Oecologia* 119:389–399
- McKey DB (1979) The distribution of secondary compounds within plants. In: Rosenthal JA, Janzen DH (eds) *Herbivores: their interactions with secondary plant metabolites*. Academic, New York, pp 55–133
- Medlyn BE, Barton CVM, Broadmeadow MSJ, Ceulemans R, De Angelis P, Forstreuter M, Freeman M, Jackson SB, Kellomäki S, Laitat E, Rey A, Roberntz P, Sigurdsson BD, Strassmeyer J, Wang K, Curtis PS, Jarvis PG (2001) Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentration: a synthesis. *New Phytol* 149:247–264
- Menke FLH, Champion A, Kijne JW, Memelink J (1999) A novel jasmonate- and elicitor-responsive element in the periwinkle secondary metabolite biosynthetic gene *Str* interacts with a jasmonate- and elicitor-inducible AP2-domain transcription factor, ORCA2. *EMBO J* 18:4455–4463
- Mondor EB, Tremblay NM, Awmack CS, Lindroth RL (2004) Divergent pheromone-mediated insect behaviour under global atmospheric change. *Glob Chang Biol* 10:1820–1824
- Narberhaus I, Zintgraf V, Dobler S (2005) Pyrrolizidine alkaloids on three trophic levels – evidence for toxic and deterrent effects on phytophages and predators. *Chemoecology* 15:121–125
- Newman JA, Abner ML, Dado RG, Gibson DJ, Brookings A, Parsons AJ (2003) Effects of elevated CO₂, nitrogen and fungal endophyte infection on tall fescue: growth, photosynthesis, chemical composition and digestibility. *Glob Chang Biol* 9:425–437
- Nielsen KA, Tattersall DB, Jones PR, Møller BL (2008) Metabolite formation in dhurrin biosynthesis. *Phytochemistry* 69:88–98
- Nowak RS, Ellsworth DS, Smith SD (2004) Functional responses of plants to elevated atmospheric CO₂: do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytol* 162:253–280
- Opitz SEW, Müller C (2009) Plant chemistry and insect sequestration. *Chemoecology* 19:117–154
- Peñuelas J, Estiarte M (1998) Can elevated CO₂ affect secondary metabolism and ecosystem function? *Trends Ecol Evol* 13:20–24

- Pickett JA, Wadhams LJ, Woodcock CM (1998) Insect supersense: mate and host location by insects as model systems for exploiting olfactory interactions. *Biochemist* 20:8–13
- Poorter H, Van Berkel Y, Baxter R, Den Hertog J, Dijkstra P, Gifford RM, Griffin KL, Roumet C, Roy J, Wong SC (1997) The effect of elevated CO₂ on the chemical composition and construction costs of leaves of 27 C₃ species. *Plant Cell Environ* 20:472–482
- Rapparini F, Baraldi R, Miglietta F, Loreto F (2004) Isoprenoid emission in trees of *Quercus pubescens* and *Quercus ilex* with lifetime exposure to naturally high CO₂ environment. *Plant Cell Environ* 27:381–391
- Rasmann S, Agrawal AA (2009) Plant defense against herbivory: progress in identifying synergism, redundancy, and antagonism between resistance traits. *Curr Opin Plant Biol* 12:473–478
- Rasmann S, Köllner TG, Degenhardt J, Hiltbold I, Toepfer S, Kuhlmann U, Gershenzon J, Turlings TCJ (2005) Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature* 434:732–737
- Raupach MR, Marland G, Ciais P, Le Quéré C, Canadell JG, Klepper G, Field CB (2007) Global and regional drivers of accelerating CO₂ emissions. *Proc Natl Acad Sci USA* 104:10288–10293
- Reichardt PB, Chapin FS III, Bryant JP, Mattes BR, Clausen TP (1991) Carbon/nutrient balance as a predictor of plant defense in Alaskan balsam poplar: potential importance of metabolite turnover. *Oecologia* 88:401–406
- Rhoades DF (1979) Evolution of plant chemical defense against herbivores. In: Rosenthal GA, Janzen DH (eds) *Herbivores: their interaction with secondary plant metabolites*. Academic, New York, pp 1–55
- Rhoades DF, Cates RG (1976) Toward a general theory of plant antiherbivore chemistry. In: Wallace JW, Mansell RL (eds) *Recent advances in phytochemistry*, vol 10. Plenum, New York, pp 168–213
- Rolland F, Baena-Gonzalez E, Sheen J (2006) Sugar sensing and signaling in plants: conserved and novel mechanisms. *Annu Rev Plant Biol* 57:675–709
- Roth SK, Lindroth RL (1995) Elevated atmospheric CO₂: effects on phytochemistry, insect performance and insect–parasitoid interactions. *Glob Chang Biol* 1:173–182
- Roth S, Lindroth RL, Volin JC, Kruger EL (1998) Enriched atmospheric CO₂ and defoliation: effects on tree chemistry and insect performance. *Glob Chang Biol* 4:419–430
- Runion GB, Curl EA, Rogers HH, Backman PA, Rodriguez-Kabana R, Helms BE (1994) Effects of free-air CO₂ enrichment on microbial populations in the rhizosphere and phyllosphere of cotton. *Agric For Meteorol* 70:117–130
- Saxon ME, Davis MA, Pritchard SG, Runion GB, Prior SA, Stelzer HE, Rogers HH, Dute RR (2004) Influence of elevated CO₂, nitrogen, and *Pinus elliottii* genotypes on performance of the redheaded pine sawfly, *Neodiprion lecontei*. *Can J Res* 34:1007–1017
- Schädler M, Roeder M, Brandl R (2007) Interacting effects of elevated CO₂, nutrient availability and plant species on a generalist invertebrate herbivore. *Glob Chang Biol* 13:1005–1015
- Schaller F, Schaller A, Stintzi A (2004) Biosynthesis and metabolism of jasmonates. *J Plant Growth Regul* 23:179–199
- Schnee C, Kollner TG, Held M, Turlings TCJ, Gershenzon J, Degenhardt J (2006) The products of a single maize sesquiterpene synthase form a volatile defense signal that attracts natural enemies of maize herbivores. *Proc Natl Acad Sci USA* 103:1129–1134
- Schoonhoven LM, van Loon JJA, Dicke M (2005) *Insect–plant biology*, 2nd edn. Oxford University Press, Oxford
- Städler E, Buser H-R (1984) Defense chemicals in leaf surface wax synergistically stimulate oviposition by a phytophagous insect. *Experientia* 40:1157–1159
- Stamp N (2003) Out of the quagmire of plant defense hypotheses. *Q Rev Biol* 78:23–55
- Stitt M, Krapp A (1999) The interaction between elevated carbon dioxide and nitrogen nutrition: the physiological and molecular background. *Plant Cell Environ* 22:583–621
- Strauss SY, Rudgers JA, Lau JA, Irwin RE (2002) Direct and ecological costs of resistance to herbivory. *Trends Ecol Evol* 17:278–285

- Strauss SY, Irwin RE, Lambrix VM (2004) Optimal defence theory and flower petal colour predict variation in the secondary chemistry of wild radish. *J Ecol* 92:132–141
- Strong DR, Lawton JH, Southwood TRE (1984) *Insects on plants: community patterns and mechanisms*. Blackwell, Oxford
- Teng N, Wang J, Chen T, Wu X, Wang Y, Lin J (2006) Elevated CO₂ induces physiological, biochemical and structural changes in leaves of *Arabidopsis thaliana*. *New Phytol* 172:92–103
- Tognetti R, Johnson JD, Michelozzi M, Raschi A (1998) Response of foliar metabolism in mature trees of *Quercus pubescens* and *Quercus ilex* to long-term elevated CO₂. *Environ Exp Bot* 39:233–245
- Umina PA, Weeks AR, Kearney MR, McKechnie SW, Hoffmann AA (2005) A rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science* 308:691–693
- Vet LEM, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. *Annu Rev Entomol* 37:141–172
- Veteli TO, Kuokkanen K, Julkunen-Tiitto R, Roininen H, Tahvanainen J (2002) Effects of elevated CO₂ and temperature on plant growth and herbivore defensive chemistry. *Glob Chang Biol* 8:1240–1252
- Vuorinen T, Reddy GVP, Nerg AM, Holopainen JK (2004a) Monoterpene and herbivore-induced emission from cabbage plants grown at elevated atmospheric CO₂ concentration. *Atmos Environ* 38:675–682
- Vuorinen T, Nerg AM, Ibrahim MA, Reddy GVP, Holopainen JK (2004b) Emission of *Plutella xylostella*-induced compounds from cabbages grown at elevated CO₂ and orientation behavior of the natural enemies. *Plant Physiol* 135:1984–1992
- Williams RS, Lincoln DE, Thomas RB (1994) Loblolly pine grown under elevated CO₂ affects early instar pine sawfly performance. *Oecologia* 98:64–71
- Williams RS, Lincoln DE, Thomas RB (1997) Effects of elevated CO₂-grown loblolly pine needles on the growth, consumption, development, and pupal weight of red-headed pine sawfly larvae reared within open-topped chambers. *Glob Chang Biol* 3:501–511
- Williams RS, Lincoln DE, Norby RJ (2003) Development of gypsy moth larval feeding on red maple saplings at elevated CO₂ and temperature. *Oecologia* 137:114–122
- Winkel-Shirley B (2001) Flavonoid biosynthesis. A colorful model for genetics, biochemistry, cell biology, and biotechnology. *Plant Physiol* 126:485–493
- Woodward FI (1987) Stomatal numbers are sensitive to increase in CO₂ from pre-industrial levels. *Nature* 327:617–618
- Woodward F (2002) Potential impacts of global elevated CO₂ concentrations on plants. *Curr Opin Plant Biol* 5:207–211
- Woodward FI, Bazzaz FA (1988) The responses of stomatal density to CO₂ partial pressure. *J Exp Bot* 39:1771–1781
- Yong JWH, Wong SC, Letham DS, Hocart CH, Farquhar GD (2000) Effects of elevated [CO₂] and nitrogen nutrition on cytokinins in the xylem sap and leaves of cotton. *Plant Physiol* 124:767–779
- Zavala JA, Casteel CL, DeLucia EH, Berenbaum MR (2008) Anthropogenic increase in carbon dioxide compromises plant defense against invasive insects. *Proc Natl Acad Sci USA* 105:5129–5133
- Zavala JA, Casteel CL, Nability PD, Berenbaum MR, DeLucia EH (2009) Role of cysteine proteinase inhibitors in preference of Japanese beetles (*Popillia japonica*) for soybean (*Glycine max*) leaves of different ages and grown under elevated CO₂. *Oecologia* 161:35–41

Appendix 1

References Used for (Figs. 11.2–11.4, 11.6, and 11.7)

- Agrell J, McDonald EP, Lindroth RL (2000) Effects of CO₂ and light on tree phytochemistry and insect performance. *Oikos* 88:259–272
- Agrell J, Anderson P, Oleszek W, Stochmal A, Agrell C (2004) Combined effects of elevated CO₂ and herbivore damage on alfalfa and cotton. *J Chem Ecol* 30:2309–2324
- Agrell A, Kopper B, McDonald EP, Lindroth RL (2005) CO₂ and O₃ effects on host plant preferences of the forest tent caterpillar (*Malacosoma disstria*). *Glob Change Biol* 11:588–599
- Bazin A, Goverde M, Erhardt A, Shykoff (2002) Influence of atmospheric carbon dioxide enrichment on induced response and growth compensation after herbivore damage in *Lotus corniculatus*. *Ecol Entomol* 27:271–278
- Bezemer TM, Jones TH, Newington JE (2000) Effects of carbon dioxide and nitrogen fertilization on phenolic content in *Poa annua* L. *Biochem Syst Ecol* 28:839–846
- Bidart-Bouzat MG, Mithen R, Berenbaum MR (2005) Elevated CO₂ influences herbivory-induced defense responses of *Arabidopsis thaliana*. *Oecologia* 145:415–424
- Booker FL (2000) Influence of carbon dioxide enrichment, ozone and nitrogen fertilization on cotton (*Gossypium hirsutum* L.) leaf and root composition. *Plant Cell Environ* 23:573–583
- Booker FL, Maier CA (2001) Atmospheric carbon dioxide, irrigation, and fertilization effects on phenolic and nitrogen concentration in loblolly pine (*Pinus taeda*) needles. *Tree Physiol* 21:609–616
- Castells E, Roumet C, Penuelas J, Roy J (2002) Intraspecific variability of phenolic concentrations and their responses to elevated CO₂ in two Mediterranean perennial grasses. *Environ Exp Bot* 47:205–216
- Causin HF, Ruffy TW, Reynolds JF (2006) Gas exchange and carbon metabolism in two *Prosopis* species (Fabaceae) from semiarid habitats: effects of elevated CO₂, N supply, and N source. *Am J Bot* 93:716–723
- Centritto M, Nascetti PN, Petrilli L, Raschi A, Loreto F (2004) Profiles of isoprene emission and photosynthetic parameters in hybrid poplars exposed to free-air CO₂ enrichment. *Plant Cell Environ* 27:403–412
- Chen F, Wu G, Ge F, Parajulee MN, Shrestha RB (2005) Effects of elevated CO₂ and transgenic Bt cotton on plant chemistry, performance, and feeding of an insect herbivore, the cotton bollworm. *Entomol Exp Appl* 115:341–350
- Cipollini ML, Drake BG, Whigham D (1993) Effects of elevated CO₂ on growth and carbon/nutrient balance in the deciduous woody shrub *Lindera benzoin* (L.) Blume (Lauraceae). *Oecologia* 96:339–346
- Coley PD, Massa M, Lovelock CE, Winter K (2002) Effects of elevated CO₂ on foliar chemistry of saplings on nine species of tropical tree. *Oecologia* 133:62–69
- Constable JVH, Litvak ME, Greenberg JP, Monson RK (1999) Monoterpene emission from coniferous trees in response to elevated CO₂ concentration and climate warming. *Glob Change Biol* 5:255–267
- Comelissen T, Stiling P, Drake B (2003) Elevated CO₂ decreases leaf fluctuating asymmetry and herbivory by leaf miners on two oak species. *Glob Change Biol* 10:27–36
- Coviella CE, Stipanovic RD, Trumble JT (2002) Plant allocation to defensive compounds: interactions between elevated CO₂ and nitrogen in transgenic cotton plants. *J Exp Bot* 53:323–331
- Davey MP, Bryant DN, Cummins I, Ashenden TW, Gates P, Baxter R, Edwards R (2004) Effects of elevated CO₂ on the vasculature and phenolic secondary metabolism of *Plantago maritima*. *Phytochemistry* 65:2197–2204
- Diaz S, Fraser LH, Grime JP, Falczuk (1998) The impact of elevated CO₂ on plant-herbivore interactions: experimental evidence of moderating effects at the community level. *Oecologia* 117:177–186

- Dury SJ, Good JEG, Perrins CM, Buse A, Kaye T (1998) The effects of increasing CO₂ and temperature on oak leaf palatability and the implications for herbivorous insects. *Glob Change Biol* 4:55–61
- Estiarte M, Penuelas J, Kimball BA, Hendrix DL, Pinter PJ Jr, Wall GW, LaMorte RL, Hunsaker DJ (1999) Free-air CO₂ enrichment of wheat: leaf flavonoid concentration throughout the growth cycle. *Physiol Plant* 105:423–433
- Fajer ED (1989) The effects of enriched CO₂ atmospheres on plant-insect herbivore interactions: growth responses of larvae of the specialist butterfly, *Junonia coenia* (Lepidoptera: Nymphalidae). *Oecologia* 81:514–520
- Fajer ED, Bowers MD, Bazzaz FA (1992) The effect of nutrients and enriched CO₂ environments on production of carbon-based allelochemicals in plantago: a test of the carbon/nutrient balance hypothesis. *Am Nat* 140:707–723
- Gebauer RLE, Strain BR, Reynolds JF (1998) The effect of elevated CO₂ and N availability on tissue concentrations and whole plant pools of carbon-based secondary compounds in loblolly pin (*Pinus taeda*). *Oecologia* 113:29–36
- Gleadow RM, Foley WJ, Woodrow IE (1998) Enhanced CO₂ alters the relationship between photosynthesis and defense in cyanogenic *Eucalyptus cladocalyx* F. Muell. *Plant Cell Environ* 21:12–22
- Goverde M, Bazin A, Shykoff JA, Erhardt A (1999) Influence of leaf chemistry of *Lotus corniculatus* (Fabaceae) on larval development of *Polyommatus icarus* (Lepidoptera, Lycaenidae): effects of elevated CO₂ and plant genotype. *Funct Ecol* 13:801–810
- Goverde M, Erhardt A, Niklaus PA (2002) In situ development of a satyrid butterfly on calcareous grassland exposed to elevated carbon dioxide. *Ecology* 83:1399–1411
- Goverde M, Erhardt A, Stocklin J (2004) Genotype-specific response of a lycaenid herbivore to elevated carbon dioxide and phosphorous availability in calcareous grassland. *Oecologia* 139:383–391
- Hall MC, Stiling P, Moon DC, Drake BG, Hunter MD (2005) Effects of elevated CO₂ on foliar quality and herbivore damage in a scrub oak ecosystem. *J Chem Ecol* 31:267–286
- Haring DA, Komer CH (2004) CO₂ enrichment reduces the relative contribution of latex and latex-related hydrocarbons to biomass in *Euphorbi lathyris*. *Plant Cell Environ* 27:209–217
- Hartley SE, Jones CG, Couper GC, Jones TH (2000) Biosynthesis of plant phenolic compounds in elevated atmospheric CO₂. *Glob Change Biol* 6:497–506
- Hattas D, Stock WD, Mabusela WT, Green IR (2005) Phytochemical changes in leaves of subtropical grasses and fynbos shrubs at elevated atmospheric CO₂ concentrations. *Glob Planet Change* 47:181–192
- Hättenschwiler S, Schafellner C (1999) Opposing effects of elevated CO₂ and N deposition on *Lymantria monacha* larvae feeding on spruce trees. *Oecologia* 118:210–217
- Heyworth CJ, Iason GR, Temperton V, Jarvis PG, Duncan AJ (1998) The effect of elevated CO₂ concentration and nutrient supply on carbon-based plant secondary metabolites in *Pinus sylvestris* L. *Oecologia* 115:344–350
- Himanan SJ, Nissinen A, Auriola S, Poppy GM, Stewart CNJ, Holopainen JK, Nerg A (2008) Constitutive and herbivore-inducible glucosinolate concentrations in oilseed rape (*Brassica napus*) leaves are not affected by *Bt CryIAC* insertion but change under elevated atmospheric CO₂ and O₃. *Planta* 227: 427–437
- Himanan SJ, Nerg AM, Nissinen A, Pinto DM, Stewart CN Jr, Poppy GM, Holopainen JK (2009) Effects of elevated carbon dioxide and ozone on volatile terpenoid emissions and multitrophic communication of transgenic insecticidal oilseed rape (*Brassica napus*). *New Phytol* 181:174–186
- Holten MK, Lindroth RL, Nordheim EV (2003) Foliar quality influences tree-herbivore-parasitoid interactions: effects of elevated CO₂, O₃, and plant genotype. *Oecologia* 137:233–244
- Huang W, He X, Chen W, Chen Z, Ruan Y, Xu S (2008) Influence of elevated carbon dioxide and ozone on the foliar nonvolatile terpenoids in *Ginkgo biloba*. *Bull Environ Contam Toxicol* 81:432–435

- Johnson RH, Lincoln DE (1990) Sagebrush and grasshopper responses to atmospheric carbon dioxide concentration. *Oecologia* 84:103–110
- Johnson RH, Lincoln DE (1991) Sagebrush carbon allocation patterns and grasshopper nutrition: the influence of CO₂ enrichment and soil mineral limitation. *Oecologia* 87:127–134
- Julkunen-Tiitto R, Tahvanainen J, Silvola J (1993) Increased CO₂ and nutrient status changes affect phytomass and the production of plant defensive secondary chemicals in *Salix myrsinifolia* (Salisb.). *Oecologia* 95:495–498
- Kainulainen P, Holopainen JK, Holopainen T (1998) The influence of elevated CO₂ and O₃ concentrations on Scots pine needles: changes in starch and secondary metabolites over three exposure years. *Oecologia* 114:455–460
- Karowe DN, Seimens DH, Mitchell-Olds T (1997) Species-specific response of glucosinolate content to elevated atmospheric CO₂. *J Chem Ecol* 23:2569–2582
- Kerslake JE, Woodin SJ, Hartley SE (1998) Effects of carbon dioxide and nitrogen enrichment on a plant-insect interaction: the quality of *Calluna vulgaris* as a host for *Operophtera brumata*. *New Phytol* 140:43–53
- Kinney KK, Lindroth RL, Jung SM, Nordheim EV (1997) Effects of CO₂ and NO₃⁻ availability on deciduous trees: phytochemistry and insect performance. *Ecology* 78:215–230
- Knepp RG, Hamilton JG, Mohan JE, Zangerl AR, Berenbaum MR, DeLucia EH (2005) Elevated CO₂ reduces leaf damage by insect herbivores in a forest community. *New Phytol* 267:207–218
- Koike T, Tobita H, Shibata T, Matsuki S, Konno K, Kitao M, Yamashita N, Maruyama Y (2006) Defense characteristics of seral deciduous broad-leaved tree seedlings grown under differing levels of CO₂ and nitrogen. *Popul Ecol* 48:23–29
- Kopper BJ, Lindroth RL (2003) Effects of elevated carbon dioxide and ozone on the phytochemistry of aspen and performance of an herbivore. *Oecologia* 134:95–103
- Kopper BJ, Lindroth RL, Nordheim EV (2001) CO₂ and O₃ effects on Paper Birch (Betulaceae: *Betula papyrifera*) phytochemistry and Whitemarked Tussock Moth (Lymantriidae: *Orgyia leucostigma*) performance. *Environ Entomol* 30:1119–1126
- Kreuzwieser J, Cojocariu C, Jüssen V, Rennenberg H (2002) Elevated atmospheric CO₂ causes seasonal changes in carbonyl emissions from *Quercus ilex*. *New Phytol* 154:327–333
- Kuokkanen K, Julkunen-Tiitto R, Keinänen M, Niemela P, Tahvanainen J (2001) The effect of elevated CO₂ and temperature on the secondary chemistry of *Betula pendula* seedlings. *Trees* 15:378–384
- Kuokkanen K, Yan S, Niemela P (2003) Effects of elevated CO₂ and temperature on the leaf chemistry of birch *Betula pendula* (Roth) and the feeding behaviour of the weevil *Phyllobius maculicornis*. *Agric For Entomol* 5:209–217
- Lavola A, Julkunen-Tiitto R (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, Julkunen-Tiitto R, de la Rosa TM, Lehto T, Aphalo PJ (2000) Allocation of carbon to growth and secondary metabolites in birch seedlings under UV-B radiation and CO₂ exposure. *Physiol Plant* 109:260–267
- Lawler IR, Foley WJ, Woodrow IE, Cork SJ (1997) The effects of elevated CO₂ atmospheres on the nutritional quality of eucalyptus foliage and its interaction with soil nutrient and light availability. *Oecologia* 109:59–68
- Lincoln DE, Couvet D (1989) The effect of carbon supply on allocation to allelochemicals and caterpillar consumption of peppermint. *Oecologia* 78:112–114
- Lindroth RL, Kinney KK (1998) Consequences of enriched atmospheric CO₂ and defoliation for foliar chemistry and gypsy moth performance. *J Chem Ecol* 24:1677–1695
- Lindroth RL, Kinney KK, Platz CL (1993) Responses of deciduous tree to elevated atmospheric CO₂: productivity, phytochemistry, and insect performance. *Ecology* 74:763–777
- Lindroth RL, Arteel GE, Kinney KK (1995) Responses of three saturniid species to paper birch grown under enriched CO₂ atmospheres. *Funct Ecol* 9:306–311

- Lindroth RL, Roth S, Kruger EL, Volin JC, Koss PA (1997) CO₂-mediated changes in aspen chemistry: effects on gypsy moth performance and susceptibility to virus. *Glob Change Biol* 3:279–289
- Lindroth RL, Kopper BJ, Parsons WFJ, Bockheim JG, Karnosky DF, Hendrey GR, Pregitzer KS, Isebrands JG, Sober J (2001) Consequences of elevated carbon dioxide and ozone for foliar chemical composition and dynamics in trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). *Environ Pollut* 115:395–404
- Lindroth RL, Wood SA, Kopper BJ (2002) Response of quaking aspen genotypes to enriched CO₂: foliar chemistry and tussock moth performance. *Agric For Entomol* 4:315–323
- Loreto F, Fischbach RJ, Schnitzler JP, Cicciolo P, Brancaleoni E, Calfapietra C, Seufert G (2001) Monoterpene emission and monoterpene synthase activities in the Mediterranean evergreen oak *Quercus ilex* L. grown at elevated CO₂ concentrations. *Glob Change Biol* 7:709–717
- Mansfield JL, Curtis PS, Zak DR, Pregitzer KS (1999) Genotypic variation for condensed tannin production in trembling aspen (*Populus tremuloides*, Salicaceae) under elevated CO₂ and in high- and low-fertility soil. *Am J Bot* 86:1154–1159
- Matros A, Amme S, Kettig B, Buck-Sorlin GH, Sonnewald U, Mock HP (2006) Growth at elevated CO₂ concentrations leads to modified profiles of secondary metabolites in tobacco cv. SamsunNN and to increased resistance against infections with potato virus Y. *Plant Cell Environ* 29:126–137
- Mattson WJ, Kuokkanen K, Niemela P, Julkunen-Tiitto R, Kellomaki S, Tahvanainen J (2004) Elevated CO₂ alters birch resistance to *Lagomorpha* herbivores. *Glob Change Biol* 10:1402–1413
- Mattson WJ, Julkunen-Tiitto R, Herms DA (2005) CO₂ enrichment and carbon partitioning to phenolics: do plant responses accord better with the protein competition or the growth-differentiation balance models? *Oikos* 111:337–347
- McDonald EP, Agrell J, Lindroth RL (1999) CO₂ and light effects on deciduous trees: growth, foliar chemistry, and insect performance. *Oecologia* 119:389–399
- Peltonen PA, Vapaavuori E, Julkunen-Tiitto R (2005) Accumulation of phenolic compounds in birch leaves is changed by elevated carbon dioxide and ozone. *Glob Change Biol* 11:1305–1324
- Penuelas J, Llusia J (1997) Effects of carbon dioxide, water supply, and seasonality on terpene content and emission by *Rosmarinus officinalis*. *J Chem Ecol* 23:979–993
- Penuelas J, Estiarte M, Kimball BA, Idso SB, Pinter PJ Jr, Wall GW, Garcia RL, Hansaker DJ, LaMorte RL, Hendrix DL (1996) Variety of responses of plant phenolic concentration to CO₂ enrichment. *J Exp Bot* 47:1463–1467
- Pritchard S, Peterson C, Runion GB, Priorj S, Rogers H (1997) Atmospheric CO₂ concentration, N availability, and water status affect patterns of ergastic substance deposition in longleaf pine (*Pinus palustris* Mill.) foliage. *Trees* 11:494–503
- Räisänen T, Ryyppö A, Julkunen-Tiitto R, Kellomaki S (2008) Effects of elevated CO₂ and temperature on secondary compounds in the needles of Scots pine (*Pinus sylvestris* L.). *Trees* 22:121–135
- Rapparini F, Baraldi R, Miglietta F, Loreto F (2004) Isoprenoid emission in trees of *Quercus pubescens* and *Quercus ilex* with lifetime exposure to naturally high CO₂ environment. *Plant Cell Environ* 27:381–391
- Reddy GVP, Tossavainen P, Nerg AM, Holopainen JK (2004) Elevated atmospheric CO₂ affects the chemical quality of *Brassica* plants and the growth rate of the specialist, *Plutella xylostella*, but not the generalist, *Spodoptera littoralis*. *J Agric Food Chem* 52:4185–4191
- Reitz SR, Karowe DN, Diawara MM, Trumble JT (1997) Effects of elevated atmospheric carbon dioxide on the growth and linear furanocoumarin content of celery. *J Agric Food Chem* 45:3642–3646
- Rossi AM, Stiling P, Moon DC, Cattell MV, Drake BG (2004) Induced defensive response of myrtle oak to foliar insect herbivory in ambient and elevated CO₂. *J Chem Ecol* 30:1143–1152

- Roth SK, Lindroth RL (1994) Effects of CO₂-mediated changes in paper birch and white pine chemistry on gypsy moth performance. *Oecologia* 98:133–138
- Roth SK, Lindroth RL (1995) Elevated atmospheric CO₂: effects on phytochemistry, insect performance and insect-parasitoid interactions. *Glob Change Biol* 1:173–182
- Roth S, McDonald EP, Lindroth RL (1997) Atmospheric CO₂ and soil water availability: consequences for tree-insect interaction. *Can J For Res* 27:1281–1290
- Roth S, Lindroth RL, Volin JC, Kruger EL (1998) Enriched atmospheric CO₂ and defoliation: effects on tree chemistry and insect performance. *Glob Change Biol* 4:419–430
- Sallas L, Kainulainen P, Utriainen J, Holopainen T, Holopainen JK (2001) The influence of elevated O₃ and CO₂ concentrations on secondary metabolites of Scots pine (*Pinus sylvestris* L.) seedlings. *Glob Change Biol* 7:303–311
- Sallas L, Luomala EM, Utriainen J, Kainulainen P, Holopainen JK (2003) Contrasting effects of elevated carbon dioxide concentration and temperature on Rubisco activity, chlorophyll fluorescence, needle ultrastructure and secondary metabolites in conifer seedlings. *Tree Physiol* 23:97–108
- Saxon ME, Davis MA, Pritchard SG, Runion GB, Prior SA, Stelzer HE, Rogers HH, Dute RR (2004) Influence of elevated CO₂, nitrogen, and *Pinus elliottii* genotypes on performance of the redheaded pine sawfly, *Neodiprion lecontei*. *Can J For Res* 34:1007–1017
- Scholefield PA, Doick KJ, Herbert BMJ, Hewitt CNS, Schnitzler JP, Pinelli P, Loreto F (2004) Impact of rising CO₂ on emissions of volatile organic compounds: isoprene emission from *Phragmites australis* growing at elevated CO₂ in a natural carbon dioxide spring. *Plant Cell Environ* 27:393–401
- Schonhof I, Kläring HP, Krumbein A, Schreiner M (2007) Interaction between atmospheric CO₂ and glucosinolates in broccoli. *J Chem Ecol* 33:105–114
- Snow MD, Bard RR, Olszyk DM, Minster LM, Hager AN, Tingey DT (2003) Monoterpene levels in needles of Douglas fir exposed to elevated CO₂ and temperature. *Physiol Plant* 117:352–358
- Staudt M, Joffre R, Rambal S, Kesselmeier J (2001) Effects of elevated CO₂ on monoterpene emission of young *Quercus ilex* trees and its relation to structural and ecophysiological parameters. *Tree Physiol* 21:437–445
- Tognetti R, Johnson JD, Michelozzi M, Raschi A (1998) Response of foliar metabolism in mature trees of *Quercus pubescens* and *Quercus ilex* to long-term elevated CO₂. *Environ Exp Bot* 39:233–245
- Veteli TO, Kuokkanen K, Julkunen-Tiitto R, Roininen H, Tahavanainen J (2002) Effects of elevated CO₂ and temperature on plant growth and herbivore defensive chemistry. *Glob Change Biol* 8:1240–1252
- Veteli TO, Mattson WJ, Niemela P, Julkunen-Tiitto R, Kellomaki S, Kuokkanen K, Lavola A (2007) Do elevated temperature and CO₂ generally have counteracting effects on phenolic phytochemistry of boreal trees? *J Chem Ecol* 33:287–296
- Vuorinen T, Reddy GVP, Nerg AM, Holopainen JK (2004) Monoterpene and herbivore-induced emission from cabbage plants grown at elevated atmospheric CO₂ concentration. *Atmos Environ* 38:675–682
- Vuorinen T, Nerg AM, Vapaavuori E, Holopainen JK (2005) Emission of volatile organic compounds from two silver birch (*Betula pendula* Roth) clones grown under ambient and elevated CO₂ and different O₃ concentrations. *Atmos Environ* 39:1185–1197
- Wang XW, Ji LZ, Zhang QH, Liu Y, Wang GQ (2009) Effects of elevated CO₂ on feeding preference and performance of the gypsy moth (*Lymantria dispar*) larvae. *J Appl Entomol* 133:47–57
- Williams RS, Lincoln DE, Thomas RB (1994) Loblolly pine grown under elevated CO₂ affects early instar pine sawfly performance. *Oecologia* 98:64–71
- Williams RS, Lincoln DE, Thomas RB (1997) Effects of elevated CO₂-grown loblolly pine needles on the growth, consumption, development, and pupal weight of red-headed pine sawfly larvae reared within open-topped chambers. *Glob Change Biol* 3:501–511

- Williams RS, Lincoln DE, Norby RJ (1998) Leaf age effects of elevated CO₂-grown white oak leaves on spring-feeding lepidopterans. *Glob Change Biol* 4:235–246
- Williams RS, Norby RJ, Lincoln DE (2000) Effects of elevated CO₂ and temperature-grown red and sugar maple on gypsy moth performance. *Glob Change Biol* 6:685–695
- Williams RS, Lincoln DE, Norby RJ (2003) Development of gypsy moth larval feeding on red maple saplings at elevated CO₂ and temperature. *Oecologia* 137:114–122
- Wu G, Chen FJ, Ge F, Sun YC (2007) Effects of elevated carbon dioxide on the growth and foliar chemistry of transgenic Bt Cotton. *J Integr Plant Biol* 49:1361–1369
- Ziska LH, Emche SD, Johnson EL, George K, Reed DR, Sicher RC (2005) Alterations in the productions and concentration of selected alkaloids as a function of rising atmospheric carbon dioxide and air temperature: implications for ethno-pharmacology. *Glob Change Biol* 11:1798–1807

Appendix 2

List of Abbreviations for Fig. 11.5

Alkaloids (red)

| | |
|----------|---|
| ImiAlk | Imidazole alkaloids |
| AromAlk | Aromatic alkaloids |
| | Quinazoline alkaloids (from anthranilate, precursor of L-Trp) |
| | Quinoline alkaloids (from anthranilate, precursor of L-Trp) |
| | Acridine alkaloids (from anthranilate, precursor of L-Trp) |
| | Indole alkaloids (from L-Trp) |
| | Quinoline alkaloids (from L-Trp) |
| | Tetrahydroisoquinoline alkaloids (from L-Tyr) |
| | Benzylisoquinoline alkaloids (from L-Tyr) |
| | Amarylidaceae alkaloids (from L-Tyr) |
| PyrAlk | Pyridine alkaloids (from nicotinate, product of L-Asp) |
| PipAlk | Piperidine alkaloids (from L-Lys) |
| QuinoAlk | Quinolizidine alkaloids (from L-Lys) |
| IndoAlk | Indolizidine alkaloids (from L-Lys) |
| PyrroAlk | Pyrrolizidine and pyrrolidine alkaloids (from L-Orn) |
| TropAlk | Tropane alkaloids |

Other secondary metabolites (red)

| | |
|-----------|--|
| CyG | Cyanogenic glycosides |
| GSL | Glucosinolates |
| PhenProp | Phenylpropanoids (includes hydroxycinnamic acids, e.g. caffeic acid, and their esters, e.g. chlorogenic acid; also hydroxycinnamic aldehydes and alcohols) |
| (Iso)Flav | Isoflavonoids and flavonoids |
| Anthocy | Anthocyanins |

| | |
|-------------|--|
| CTs | Condensed tannins |
| HTs | Hydrolyzable tannins, e.g. ellagitannins |
| ...terp | ...terpene |
| CardiacGlyc | Cardiac glycosides |
| SteroidSap | Steroid saponins |

Phytohormones (blue)

| | |
|------------|------------------|
| SA | Salicylic acid |
| ABA | Abscisic acid |
| Strigolact | Strigolactone |
| Gibberel | Gibberellins |
| BrassSter | Brassinosteroids |
| Jasm | Jasmonates |

Polymeric (essential) metabolites (gray)

| | |
|------------|--|
| Ubiquin | Ubiquinones |
| Plastoquin | Plastoquinones |
| MemSterols | Membrane sterols like e.g. cholesterol |

Intermediates (no fill)

Amino acids

| | |
|-------|-----------------|
| L-His | L-Histidine |
| L-Trp | L-Tryptophan |
| L-Phe | L-Phenylalanine |
| L-Tyr | L-Tyrosine |
| L-Ala | L-Alanine |
| L-Val | L-Valine |
| L-Leu | L-Leucine |
| L-Asp | L-Aspartate |
| L-Asn | L-Asparagine |
| L-Met | L-Methionine |
| L-Thr | L-Threonine |
| L-Ile | L-Isoleucine |
| L-Lys | L-Lysine |
| L-Glu | L-Glutamate |
| L-Gln | L-Glutamine |
| L-Arg | L-Arginine |
| L-Pro | L-Proline |
| L-Orn | L-Ornithine |
| L-Gly | L-Glycine |

| | |
|-------------------------------------|-----------------------------|
| L-Ser | L-Serine |
| L-Cys | L-Cysteine |
| Isoprenoid/terpene intermediates | |
| IPP | Isopentenylpyrophosphate |
| GPP | Geranylpyrophosphate |
| FPP | Farnesylpyrophosphate |
| GGPP | Geranylgeranylpyrophosphate |

Others

Shik Shikimate