

An Emerging Understanding of Mechanisms Governing Insect Herbivory Under Elevated CO₂

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Abstract

By changing the chemical composition of foliage, the increase in atmospheric CO₂ is fundamentally altering insect herbivory. The responses of folivorous insects to these changes is, however, highly variable. In this review we highlight emerging mechanisms by which increasing CO₂ alters the defense chemistry and signaling of plants. The response of allelochemicals affecting insect performance varies under elevated CO₂, and results suggest this is driven by changes in plant hormones. Increasing CO₂ suppresses the production of jasmonates and ethylene and increases the production of salicylic acid, and these differential responses of plant hormones affect specific secondary chemical pathways. In addition to changes in secondary chemistry, elevated CO₂ decreases rates of water loss from leaves, increases temperature and feeding rates, and alters nutritional content. New insights into the mechanistic responses of secondary chemistry to elevated CO₂ increase our ability to predict the ecological and evolutionary responses of plants attacked by insects.

Allelochemicals:
biochemical substances produced by plants, typically not involved in primary metabolism, that negatively affect the growth, survival, or reproduction of other organisms

INTRODUCTION

Insect herbivory affects native and agricultural ecosystems, reducing productivity and economic yields and altering the biogeochemical cycling of nitrogen and other important elements (25, 122). The amount of plant material consumed by phytophagous insects is intimately associated with its suitability and nutritional quality; in addition to increasing growth rates, elevated CO₂ in the atmosphere dramatically alters these plant traits. Prior to the Industrial Revolution, the concentration of atmospheric CO₂ was stable for the previous 1,000 years at ~270 μl liter⁻¹ (64) and well below 300 μl liter⁻¹ for more than 20 Mya (103). The increase in anthropogenic emissions caused primarily by combustion of fossil fuels is driving a dramatic increase in CO₂. Today, the atmosphere is ~390 μl liter⁻¹ and by end of the century it will be twice the pre-Industrial level (64). The response of plants to this change in the atmosphere is fundamentally altering their relationship with herbivorous insects.

Many insects, particularly hematophagous insects, respond directly to CO₂ (50). However, elevated CO₂ affects folivorous arthropods indirectly by altering leaf chemistry (30, 85, 114). Elevated CO₂ typically causes carbohydrates to accumulate, increasing the carbon:nitrogen ratio (C:N) (116). This change in the nutritional quality of foliage provided the foundation for the compensatory feeding hypothesis, in which increased feeding compensates for poor nutritional quality (84, 120). Its simplicity is attractive but also has limited the ability of the compensatory feeding hypothesis to predict the diverse responses of insects to food sources developed under elevated CO₂. This hypothesis does not, for example, address the role of changes in plant secondary metabolism and the different nutritional requirements affecting insect feeding. This review is, in part, an attempt to move beyond the compensatory feeding hypothesis and to consider new information about the molecular and biochemical mechanisms governing herbivory in a high CO₂ world.

The effects of elevated CO₂ on insect herbivory, operating through changes in leaf chemistry, have been reviewed extensively (18, 30, 86, 116, 130). An emerging conclusion from these reviews developed in this paper is that changes in primary metabolism affecting the suitability of plant biomass to herbivores is relatively predictable, whereas changes in plant secondary metabolism and its corresponding effects on insect feeding, survivorship, and reproduction are highly variable. This variation poses a significant challenge to developing credible predictions about the responses of herbivory to further increases in atmospheric CO₂. In this review we highlight overlooked processes and new discoveries that may reduce this uncertainty. We review a small but growing literature demonstrating a direct effect of elevated CO₂ on plant hormones, particularly jasmonates and salicylic acid that modulate defense responses. Finally, recognizing the consistent responses of plant primary metabolism to elevated CO₂, we speculate how these changes may alter the ecology of plant-insect interactions and further how they will shape the evolution of phytophagous insects.

ECOPHYSIOLOGICAL RESPONSES OF PLANTS TO ELEVATED CO₂

Half of all insects, including the majority of the Orthoptera, Hemiptera, and Lepidoptera, often in their larval forms, feed on plants and the amount of plant material consumed is largely dependent on its nutritional quality. Although a multitude of factors determine the nutritional quality of plants (124), nitrogen is of primary importance (94). The C:N of plant materials typically is many times greater than that of insects, resulting in severe dietary limitations. As a result of the complex coevolutionary relationships between herbivorous insects and plants, insects also must contend with a diverse array of allelochemicals produced by plants. Up to atmospheric concentrations of ~500 μl liter⁻¹, the rate of photosynthesis in plants using the C₃ photosynthetic pathway—the

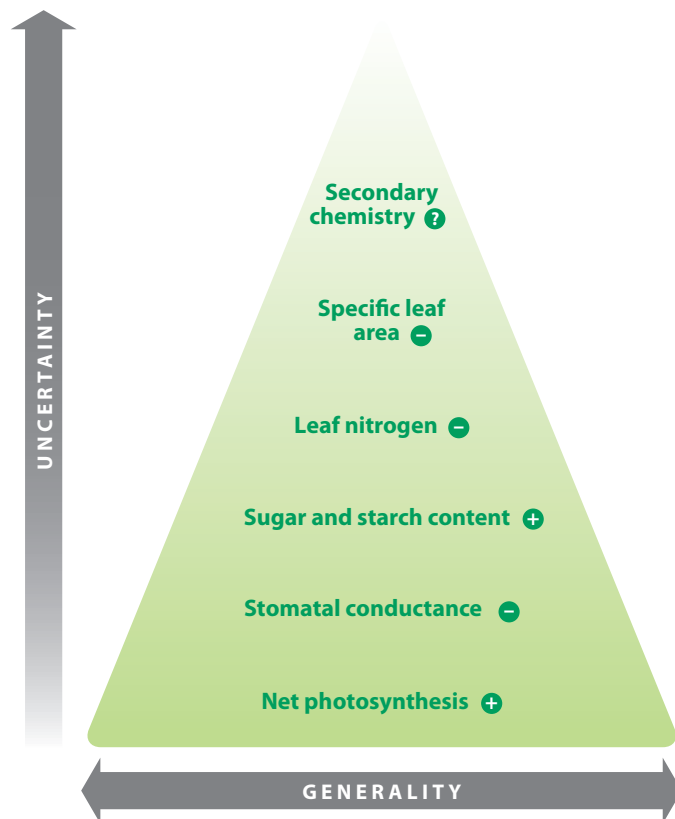


Figure 1

Exposure to elevated CO_2 affects many facets of leaf chemistry and physiology with important implications for herbivory. Whereas the stimulation of photosynthesis and accumulation of nonstructural carbohydrates, and the decrease in leaf nitrogen, stomatal conductance, and specific leaf area, are relatively consistent among plant species, changes in plant secondary chemistry are highly variable.

majority of plant species, including trees and many broadleaf crops—is highly responsive to CO_2 (88). This stimulation in the rate of photosynthesis caused by elevated CO_2 propagates through plant metabolism, affecting the nutritional quality and secondary metabolism of plants and consequently the suitability of plant material to insect herbivores.

Increases in atmospheric CO_2 associated with global change affect two aspects of plant physiology with consequences for herbivory: photosynthesis and stomatal conductance. The mechanisms by which elevated CO_2 stimulates photosynthesis are well known. By stimulating the carboxylase reaction and reducing the oxygenase reaction of the primary carboxylating enzyme responsible for assimilating CO_2 into carbohydrates in C_3 plants (ribulose-1,5-bisphosphate carboxylase oxygenase; RuBisCO), the increase in CO_2 from ~ 360 to $560 \mu\text{l liter}^{-1}$ stimulates net carbon uptake by over 20% (2), driving an increase in biomass production (2, 32, 36, 88). How this stimulation in photosynthesis affects the suitability of plant material to herbivorous insects has been extensively reviewed (e.g., 77, 86, 116, 130, 158). Emerging from these reviews is the general conclusion that whereas the response of plant primary metabolism to elevated CO_2 affecting the nutritional quality of plants is relatively predictable, the response of allelochemicals and biogenic volatile organic compounds (BVOCs) is highly variable (**Figure 1**).

Stomatal conductance:

the capacity of the stomatal pores on leaves to permit diffusion of water vapor, CO_2 , and other gases between the leaf interior and the atmosphere

C3 plants: plants in which the first step in reducing CO_2 during photosynthesis produces a three-carbon acid

BVOC: biogenic volatile organic compound

TNC: total nonstructural carbohydrates

SLA: specific leaf area

C4 plants: plants in which the first step in reducing CO₂ during photosynthesis produces a four-carbon acid

Chemical Properties of Leaves

The stimulation of photosynthesis under elevated CO₂ almost invariably increases the concentration of total nonstructural carbohydrates (TNC; starch and soluble sugars) (**Figure 1**). Starch concentrations can increase by more than 40%, twice as high as pre-Industrial CO₂ concentrations; increases in sugars are somewhat less (130). As carbohydrates are increasingly invested in plant cell walls, growth under increasing CO₂ also causes a decline in specific leaf area—the ratio of leaf area per unit leaf mass (SLA) (1, 31, 130). Both increasing TNC and decreasing SLA effectively dilute leaf nitrogen concentration. The reduction in N concentration across a broad range of species can exceed 14%, with C3 plants responding more than C4 plants, and little response by nitrogen-fixing species (1, 116, 130). The reduction in N concentration is not simply passive, however. A substantial proportion of leaf N is invested in RuBisCO (38), and because the carboxylation reaction becomes increasingly stimulated by elevated CO₂, there is evidence that N invested in this enzyme is increasingly allocated elsewhere to rebalance resource acquisition by plants (125, 135). The net effect of increasing TNC, decreasing SLA, and reallocation of leaf N is to widen the difference between the C:N of plants and that of herbivorous insects, and in some cases to reduce water content, further reducing the nutritional quality of plant material.

Changes in leaf properties stemming from the stimulation of photosynthesis vary by species and environment, but there is general consistency in the direction of the responses (116). The response of plant secondary metabolism, responsible for producing myriad defensive chemicals, is, however, far from predictable (**Figure 1**).

While specialist herbivores should be highly responsive to changes in leaf carbohydrates and N caused by elevated CO₂, the feeding responses of generalists to variation in leaf quality will be strongly modulated by defensive phytochemicals. There is, however, scant evidence for a generalized response of phytochemistry to elevated CO₂ (**Figure 1**). One class of allelochemicals that tends to respond predictably is phenolics. These compounds as well as terpenoids are important defenses against herbivory, particularly in woody plants (39, 115), and the concentration of phenolics tends to increase under elevated CO₂ (77, 104).

Phenolic compounds are formed from phenylalanine via the shikimic acid pathway and are regulated by phenylalanine ammonia-lyase activity (142). Although phenolics are ubiquitous in plants and this group is composed of a large variety of compounds with different biological functions, in general only a few studies of the impact of elevated CO₂ on plant chemistry report changes in compounds other than tannins, some flavonoids (simple phenolics), or total phenolics. Recent reviews have reported that plants grown under elevated CO₂ environments increased total phenolics by 19%, condensed tannins by 22%, and flavonoids by 27% (116).

Tannins often are present in high concentrations in vascular plants and bind with their phenolic hydroxyl groups to soluble proteins in the insect gut, inhibiting protein hydrolysis and decreasing the nutritional value of plant tissues. Whereas hydrolyzable tannins are limited to angiosperms, nonhydrolyzable (condensed) tannins are widespread throughout the plant kingdom. Some phenolics function as defense against herbivory, reducing consumption of plant tissue (53) as well as growth and survivorship of insect herbivores (54, 69); other phenolics, such as antioxidant flavonoids, can have positive effects on insect performance, i.e., stimulate feeding and promote herbivore growth (102, 118).

Elevated CO₂ increased the concentration of flavonoids with antioxidant properties, such as quercetin, kaempferol, and fisetin in leaves and rhizomes of two ginger varieties, and exhibited more enhanced free radical scavenging power (45). In soybean (*Glycine max*), elevated CO₂ increased quercetin-to-kaempferol ratios but decreased concentration levels of the isoflavonoid genistein (101). Whereas genistein is an important defense compound against herbivores in

soybeans (109), quercetin may be acting as an antioxidant for these plants, quenching reactive oxygen species (ROS) (11, 112).

In contrast to phenolics, data for terpenoids are more variable. A review of 17 plant species (104) reported a trend of increasing terpenoid concentration with elevated CO₂. A recent meta-analysis, however, indicates a small (−13%) but statistically significant decrease (116). The triterpenoid cardenolides are important steroidal toxins against herbivores because they inhibit Na⁺/K⁺-ATPases, which are important for maintenance of membrane potential in most animal cells. Elevated CO₂ decreased cardenolide levels in plant tissue of four different genotypes of milkweed (*Asclepias syriaca*) (140). Terpenoids are built from isoprene units (C₅H₈) through either the mevalonate pathway in the cytosol or the methylerythritol phosphate pathway in plastids (147).

There is some indication that the mevalonic acid and methylerythritol phosphate pathways leading to the production of terpenoids tend to be less stimulated by elevated CO₂ than the shikimic acid pathway producing phenolics (86). The responses of other classes of phytochemicals to elevated CO₂ defy generalization. The nitrogen-based glucosinolates produced by brassicoids, for example, can increase or decrease in response to elevated CO₂ (18, 70). Total glucosinolate content increased in broccoli (*Brassica oleracea*) and *Arabidopsis thaliana* grown at elevated CO₂ as a result of a strong increase in aliphatic glucosinolates and the methylsulfinylalkyl glucosinolates glucoraphanin and glucoiberin (19, 123). In contrast, indole glucosinolates decreased simultaneously in plants grown under elevated CO₂ environments, predominantly because of a reduction of glucobrassicin and 4-methoxy-glucobrassicin contents (123).

Plants emit BVOCs, including isoprene, terpenoids, green leaf volatiles, phenylpropanoids, benzenoids, and methyl-esters of plant hormones, many of which act as indirect defenses by summoning parasites or predators to the site of herbivore damage, in addition to playing important roles in pollinator attraction, plant-plant communication, and plant-pathogen interactions (71, 79). The emission of BVOCs is sensitive to increasing temperature, but relatively little is known about the response to elevated CO₂ (105, 153). Elevated CO₂ may increase the production of BVOCs by increasing plant biomass. It is, however, unclear how elevated CO₂ directly affects the synthesis of BVOCs and models suggest that the effect of temperature will dominate (56, 153). There is some indication that the production of isoprene is decreased (110, 117) but other BVOCs are increased under elevated CO₂ (90). Elevated CO₂ typically induces a decrease in stomatal conductance; insofar as the emission of BVOCs from foliage is regulated by diffusion, this reduction in conductance may contribute to a lower flux. As with allelochemicals, the response of BVOC emission to elevated CO₂ is highly idiosyncratic, varying with individual species.

Leaf Energy Balance and Herbivory

A less appreciated consequence of elevated CO₂ for herbivory is through its effect on plant stomata, the small pores on leaves that regulate the diffusion of CO₂ and water vapor. Stomata are dynamic, opening and closing in response to environmental and endogenous cues. Stomatal conductance is determined by the pore size of individual stomata together with their number per unit leaf area. As evaporation of water inside the leaf and subsequent diffusion to the atmosphere (transpiration) increase, latent heat flux causes the leaf to cool. Folivorous insects, particularly leaf miners, including larvae of moths (Lepidoptera), beetles (Coleoptera), sawflies (Hymenoptera), flies (Diptera), aphids (Hemiptera), and mites (Arachnida), that are in intimate contact with leaves are closely coupled to leaf temperature (108), thereby establishing a link between the functional properties of leaf stomata and insect metabolism.

The concentration of CO₂ in the atmosphere during leaf development as well as variation on shorter timescales often reduces stomatal conductance, either by decreasing the number of

Concentration of CO₂: the volumetric mixing ratio CO₂ in the atmosphere, currently 392 ppm

stomata in developing leaves (16, 43, 150) or by decreasing their pore size (3, 58). Reductions of up to 35% have been reported as CO₂ is doubled from pre-Industrial levels, with an average decrease of 21–22% (3, 96).

The reduction in stomatal conductance and increase in leaf temperature are not always proportional because of feedbacks in the soil-plant-atmosphere system (14), but they can be substantial. In maize grown at 750 μl liter⁻¹ CO₂, canopy evapotranspiration was reduced by 22% and leaf temperature increased by an average of 1°C compared with plants grown at 370 μl liter⁻¹ (73). Although increases in leaf temperature with a doubling of pre-Industrial CO₂ concentrations typically range from 0.2°C to 2.0°C (15, 34, 136), values as high as 3°C have been reported (91).

The feeding rates of ectotherms are intimately dependent on temperature; generally, insect feeding rate (74), foraging (129), and metabolism (62) increase with increasing temperature up to a thermal maximum. Even relatively small increases in leaf temperature caused by elevated CO₂ can strongly affect consumption rates. As temperature increased by 3°C, the consumption rate of *Manduca sexta* L. (75) and *Popillia japonica* Newman (98) increased by ~50%.

Plants growing under elevated CO₂ vary in their susceptibility to folivorous insects, and some of this variation may be an indirect response to increasing temperature. A number of reports have demonstrated increased feeding or population growth rates for aphids on plants grown under elevated CO₂ (e.g., 6, 55, 83), but as with chewing insects this response is variable (17, 59, 97). Aphids are particularly sensitive to temperature (63), and the indirect effect of elevated CO₂ on leaf temperature may explain some of this variation.

For example, increasing concentration of the phenolic aldehyde, gossypol, has a demonstrable negative effect on chewing insects and aphids on cotton, and the concentration of this compound increases when cotton is grown under elevated CO₂ (44). But, contrary to expectation, the survivorship of *Aphis gossypii* increased on plants grown under elevated CO₂ (44). When the effect of elevated CO₂ on leaf temperature was removed by offering bird cherry oat aphids (*Rhopalosiphum padi*) leaf disks of wheat grown under elevated and ambient CO₂ in a laboratory setting, elevated CO₂ had little effect (131). Furthermore, no effect of elevated CO₂ was resolved on aphids (*Cepegillettea betulaefoliae*) feeding on paper birch under otherwise natural field conditions (7), and it may not be coincidental that these trees were in the minority of studies showing an increase rather than a decrease in leaf conductance under elevated CO₂ (138). Reduction in stomatal conductance and increase in leaf temperature were not examined in these studies and in each case may explain the anomalous results on aphid performance.

In the only direct test published to date, O'Neill et al. (100) demonstrated the indirect effect of CO₂ operating through increased leaf temperature. Under field conditions, aphid infestation in an outbreak year was twice as high on soybean grown under elevated CO₂ (34), and soybean leaves are on average 0.2°C, but as great as 3°C, higher under elevated CO₂ (14, 34). By growing soybean under controlled environmental conditions, O'Neill et al. (100) demonstrated that increased population growth of alate soybean aphids (*Aphis glycines* Matsumura) on soybean grown under elevated CO₂ could be completely removed by eliminating differences in leaf temperature between ambient and elevated CO₂. Although elevated CO₂ changes myriad leaf chemical and structural characteristics affecting herbivory, this indirect effect on leaf temperature is not well appreciated and may explain some of the diverse responses reported in the literature.

EMERGING MOLECULAR AND BIOCHEMICAL MECHANISMS OF PLANT RESPONSES TO INSECT ATTACK

The lack of a widely supported conceptual model that embraces the complexities of plant metabolism and relates the production of phytochemicals to variation in resource availability

poses a significant challenge to a deeper understanding of how elevated CO₂ will affect plant-insect interactions. Prominent hypotheses that purport to explain how variation in resources affects secondary metabolism include the carbon-nutrient balance hypothesis and the growth differentiation hypothesis (24, 29, 57). Although both hypotheses are conceptually attractive and in some cases consistent with observed changes in defensive chemistry associated with elevated CO₂ (77), they do not consider genetically based plant allocation strategies and the intricacies of metabolic regulation (13, 52). Understanding how the production of allelochemicals is altered by elevated CO₂ requires in-depth knowledge of how primary and secondary metabolism are coordinated. New information about the response of plant hormones may unravel the complex and variable responses of allelochemicals and herbivory to elevated CO₂.

Plants attacked by herbivores generate specific hormonal signals through intricate networks that elicit downstream changes in biochemistry and physiology (8, 61, 151). Emerging data suggest that exposure to elevated CO₂ modulates these hormonal signals and, further, that differential responses of plant hormones may explain some of the variation in the observed responses of allelochemicals.

Early Responses and Regulation of Jasmonates

The synthesis and signaling of jasmonic acid (JA) compose a complex network that is regulated in part by CO₂ (**Figure 2**). Leaf damage increases (<30 min) accumulation of JA at the site of wounding (95). Herbivore attack is associated with direct contact of insect oral secretions with putative cell receptors, which transduce the alarm signal and induce the accumulation of defensive metabolites (**Figure 2**). Fatty acid–amino acid conjugate obtained from *Spodoptera exigua* oral secretions contributes to the Ca²⁺ influxes by forming ion channels in planar lipid bilayer membranes (4, 92). The intracellular Ca²⁺ binds to different proteins, including calmodulins and calcium-dependent protein kinases (80) (**Figure 2**). Herbivory and application of *Manduca sexta* oral secretions to wounded leaves of *Nicotiana attenuata* (coyote tobacco) and *Solanum lycopersicum* (tomato) elicit both salicylic acid–induced protein kinase and wound-induced protein kinase, which induce transcriptional regulation of many defense-related genes (67, 152). Elevated CO₂ may inhibit protein kinase activation, decreasing plant response to herbivore attack.

JA is synthesized via the octadecanoid pathway, from which nearly all biosynthetic enzymes have been identified in *Arabidopsis* and characterized in several other species (51, 121, 137). SIPK regulates the activity of chloroplastic GLA1 phospholipase and releases linolenic acid from lipids of chloroplast membranes (66), which is transformed through a series of reactions to 12-oxophytodienoic acid (OPDA) by the enzymes, lipoxygenase (LOX), allene oxide synthase (AOS), and allene oxide cyclase (AOC). Then in the peroxisomes, after three steps of β-oxidation, OPDA is converted to JA (149) (**Figure 2**). Elevated CO₂ downregulates constitutive and herbivory-induced levels of key transcripts in soybean (*Glycine max*) associated with the JA pathway, LOX7, LOX8, AOS, AOC (27, 155), and this downregulation corresponds with lower JA levels in soybean foliage (26). Similar results have been observed in tomato (132).

Although mechanistic understanding of how elevated CO₂ alters JA is lacking, carbon has a direct role in modulating JA. JA patterns are circadian regulated, reaching peaks during the day (49) at a time when photosynthesis is at its highest and intercellular CO₂ (C_i) is at its lowest. Conversely, JA titers decrease as C_i rises at night. Insofar as C_i tracks JA concentrations in plants, circadian regulation of other variables such as assimilated carbon and light may also influence JA; however, the cumulative suppression in JA under increasing CO₂ increases herbivory in field and chamber conditions (27, 132, 155).

JA: jasmonic acid

LOX: lipoxygenase

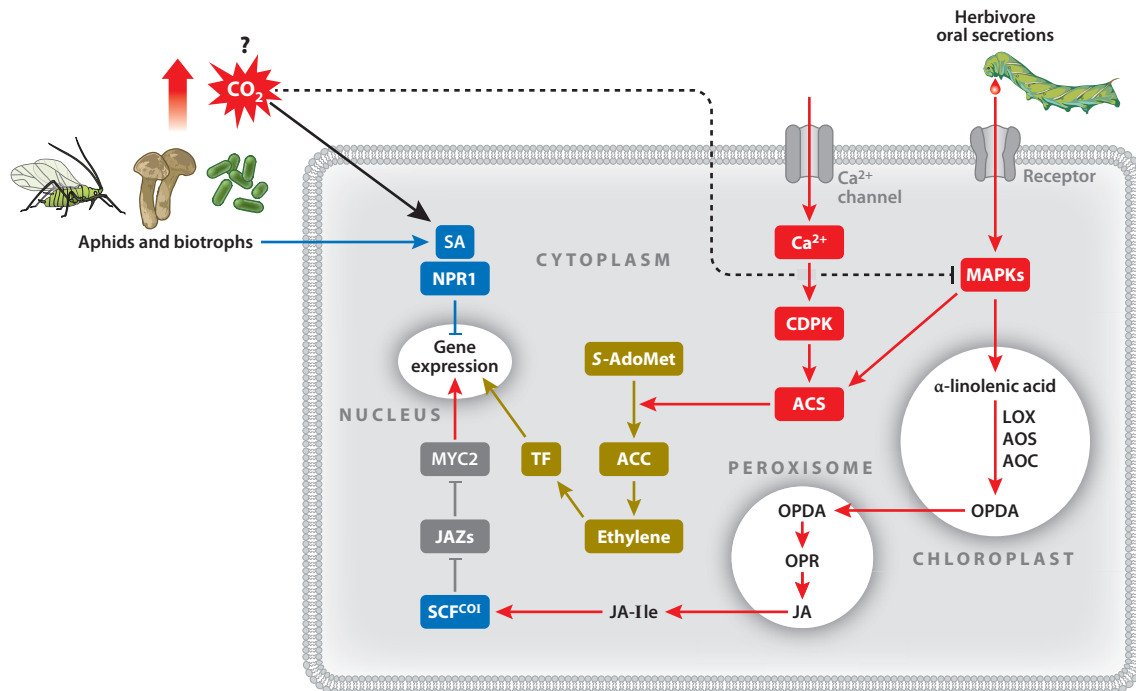


Figure 2

A model summarizing the effects of elevated CO_2 on early signaling events in a cell as a response of herbivore attack. Herbivore oral secretions are perceived by unidentified receptors and trigger the activation of Ca^{2+} channels, resulting in Ca^{2+} influxes. Ca^{2+} binds to calmodulins and CDPKs. MAPKs, such as SIPK and WIPK, are also rapidly activated and trigger the biosynthesis of JA and thus JA-Ile. JA-Ile binds to the COI1 receptor that leads to the degradation of JAZ proteins, resulting in the release of their inhibitory effect on MYC2, which induces defense genes in the nucleus. MAPK and CDPK phosphorylate ACS proteins and increase ethylene production, which leads to the increased activity of ethylene-responsive transcription factors, inducing defense genes. Elevated CO_2 induces SA accumulation and NPR1 activation by changing redox status in the cytosol by inducing thioredoxins and glutathione S-transferase (black arrow). The activated NPR1 functions as a TF in the nucleus and inhibits JA-induced defense gene expression. In addition, we hypothesize that elevated CO_2 may decrease MPK4 activity and activate downstream genes of SA signaling (black arrow). The inhibition of early signaling events by elevated CO_2 decreases the accumulation of metabolites that function as a defense against herbivores. Abbreviations: ACC, 1-aminocyclopropane-1-carboxylic acid; ACS, 1-aminocyclopropane-1-carboxylic acid synthase; OPDA, 12-oxo-phytodienoic acid; OPR, OPDA reductase; LOX, lipoxygenase; AOS, allene oxide synthase; AOC, allene oxide cyclase; TF, transcription factor; SA, salicylic acid; JA, jasmonic acid; MAPK, mitogen-activated protein kinase; CDPK, calcium-dependent protein kinase; SIPK, salicylic acid-induced protein kinase; WIPK, wound-induced protein kinase; NPR1, NONEXPRESSOR OF PATHOGENESIS-RELATED GENES1.

Cross Talk Among Defense Pathways

Elevated CO_2 increased the susceptibility of soybean to Japanese beetle (*Popillia japonica*) and western corn rootworm (*Diabrotica virgifera virgifera*) by downregulating JA and ET (ethylene), which in turn reduced the production of cysteine proteinase inhibitors (CystPIs) (27, 155, 156). ET is an important modulator of JA-induced defense (143), affecting the induction of certain antiherbivore defenses, such as protease inhibitors (PIs) in tomato (99). ET and JA are synergistic in that they activate a common transcription factor (TF) (89, 93, 111). The ET pathway is initiated by the synthesis of S-adenosylmethionine from methionine, which, after being oxidized by 1-aminocyclopropane-1-carboxylic acid (ACC) oxidase, is converted to the ET precursor ACC by ACC synthase (Figure 2). ACC synthesis is considered to be rate limiting for ET biosynthesis,

ET: ethylene

CystPI: cysteine protease inhibitor

TF: transcription factor

which can be inhibited in plants grown under elevated CO₂ (27, 155). JA and ET are important modulators for chewing insects, and the salicylic acid (SA) pathway is activated by plants in response to attack by phloem-feeding insects, such as aphids and silverleaf whiteflies, and biotrophic pathogens (146).

The JA and SA pathways often are antagonistic (76, 78, 141). While the elicitation of the JA pathway may repress SA defense responses (22, 139), SA pathway-inducing insects and biotrophic pathogens inhibit JA-dependent defenses (40, 128, 154) (**Figure 2**). This antagonism appears to be expressed under elevated CO₂. In tomato, elevated CO₂ enhances induced defenses derived from the SA-signaling pathway, such as the pathogenesis-related (PR) protein, and reduces JA signaling and defenses (132). Moreover, elevated CO₂ increases SA levels in field-grown soybeans (26) and in leaves and rhizomes in two varieties of ginger (*Zingiber officinale*) (45).

The SA-signaling pathway initiates the synthesis of defense compounds against plant pathogens (47), and elevated CO₂ attenuates this pathogenicity (37). The mechanism by which elevated CO₂ alters the hormonal response to herbivory is not known. Although SA is suggested to decrease JA biosynthesis and sensitivity (126), priming plants with JA diminishes the capacity of SA to reciprocally downregulate JA (82). The protein component of the SA-signaling pathway NPR1 (NONEXPRESSOR OF PATHOGENESIS-RELATED GENES1) is required for the suppressive effects of SA on pathogen-induced JA accumulation and JA-induced defense gene expression (48, 126) (**Figure 2**), and increased production of NPR1 may be responsible for downregulating JA-related defenses and increasing susceptibility to herbivory in plants grown under CO₂ enrichment (**Figure 2**). Experiments on *Arabidopsis* demonstrated that NPR1 is required for the suppressive effects of SA on pathogen-induced JA accumulation and JA-induced defense gene expression. In addition, these experiments indicated that the effects of SA on JA signaling are mediated through the activity of NPR1 in the cytosol to function as TF in the nucleus (48, 126). NPR1 is activated by redox changes that lead to reduction of the oxidized disulfide bonds in NPR1, a reaction catalyzed by thioredoxins (133).

Elevated CO₂ alters the transcripts regulating the redox status of soybeans by inducing thioredoxins and glutathione *S*-transferase (27). Moreover, elevated CO₂ alters ascorbate or glutathione, albeit with some degree of plant specificity (46, 106), and may allow TFs to interact with reduced NPR1 and facilitate efficient DNA binding for induction of immune signaling (127). In addition, alterations in these redox control hubs may interfere with sugar signaling (42).

NPR1 may be responsible for downregulating JA-related defenses and increasing susceptibility to herbivory in plants grown in enriched CO₂ (**Figure 2**). However, the early signal perceived by plants that is responsible for upregulating the SA pathway still is not known. Recent experiments demonstrated that SA and ROS accumulation and PR expression were increased in mitogen protein kinase 4 (*MPK4*)-silenced soybeans and *Arabidopsis* (87, 107) (**Figure 2**). Expression of *WRKY33* increased 16-fold in *MPK4*-silenced soybeans, suggesting that *MPK4* negatively controls *WRKY33* at both the posttranslational and transcriptional levels (87). *MPK4* functions to sequester *WRKY33* in the nucleus and prevent it from activating downstream genes of SA signaling (112). The mechanism of the interference of CO₂ on the early signaling steps involved in the perception of the attack by herbivores and the activation of JA biosynthesis remains to be elucidated.

Hormonal Regulation of Chemical Defenses

Studies have started to address the effects of elevated CO₂ on chemical defenses and the relationships between elevated CO₂ and hormonal regulation. Elevated CO₂ downregulates JA and ET pathways and increases susceptibility to herbivore attack by disrupting both constitutive and

SA: salicylic acid

NPR1:
NONEXPRESSOR
OF
PATHOGENESIS-
RELATED
GENES1

Enriched CO₂ atmosphere: the increase above the pre-Industrial CO₂ concentration of ~290 ppm caused largely by the combustion of fossil fuels

Phytohormones: chemicals, typically active at very low concentrations, that regulate plant growth and metabolism

inducible chemical defenses against certain insects; however, enriched atmospheric CO₂ increases SA, which increases other chemical defense pathways not regulated by JA (e.g., 45, 132). The chemical response of damaged plants is integral to understanding adaptive antiherbivore defenses (68) disrupted by elevated CO₂ and should be investigated in concert with predictable changes in CO₂-driven plant traits.

Hormones affected by elevated CO₂ regulate carbon-based defenses. Enriched CO₂ atmosphere increased the concentration of SA-regulated phenolics, such as flavonoids with antioxidant properties (quercetin, kaempferol, and fisetin) (45), but decreased the concentration of JA-regulated isoflavonoids such as genistein (101), an important defense against herbivores (109). Although both isoflavonoids and flavonols are produced through the phenylpropanoid pathway (41), phytohormonal regulation discriminates among different phenolic compounds. *Nicotiana attenuata* impaired in JA biosynthesis was unable to accumulate phenolic conjugates after herbivory; however, these plants produced rutin (a flavonoid) and chlorogenic acid (33, 60). In addition, elevated CO₂ decreased the JA-regulated triterpenoid cardenolides in four different genotypes of milkweed (113, 140).

Nitrogen-based defenses also are regulated by phytohormones (61). One of the first defenses against herbivores studied and regulated by JA are PIs in tomato (119). PIs impair the ability of insects to digest proteins and assimilate amino acids (20, 157). Elevated CO₂ increases the susceptibility of soybean foliage to herbivores by downregulating the constitutive and inducible expression of genes related to JA and ET; these in turn decrease the constitutive and induced expression and activity levels of CystPIs, the principal defense against coleopteran herbivores (132, 155, 156).

Differential responses in the levels of glucosinolates may also be explained by differential responses of the JA- and SA-signaling pathways to elevated CO₂. Elevated atmospheric CO₂ increases constitutive glucosinolates regulated by SA, such as aliphatic glucosinolates, and the methylsulfinylalkyl glucosinolates glucoraphanin and glucoiberin in broccoli, and these compounds were induced in *Arabidopsis* after herbivory by diamondback moths (*Plutella xylostella*) (19, 35, 123). In contrast, indole glucosinolates regulated by JA decreased in plants grown under elevated CO₂, predominantly because of a reduction of glucobrassicin and 4-methoxy-glucobrassicin contents, which are regulated by JA (21, 123).

Similarly, differential responses of plant BVOCs may depend on whether JA or SA regulates them. For example, elevated CO₂ decreased the emission of JA-regulated terpene volatile compounds in cabbage (*Brassica oleracea*) (144, 145). In contrast, the upregulation of green leaf volatiles (GLVs) following herbivory was enhanced by elevated CO₂ (144, 145), and it appears that the regulation of these compounds does not rely on JA signaling (5, 51). The differential responses among pathways producing allelochemicals to JA/ET and SA might provide new insights into how elevated CO₂ modulates plant defenses against herbivory.

AGRICULTURAL AND ECOLOGICAL PERSPECTIVES

The accumulation of starch and sugars in plants grown under elevated CO₂ is reproducible (**Figure 1**), and this increase in plant C content directly alters patterns of herbivory relative to how insects optimize target nutrient uptake. When faced with nutrient imbalances, insects alter their feeding behavior to avoid the deleterious effects of excess. Too much protein can reduce life span (e.g., 81); too much carbohydrate can increase lipid stores that reduce fitness (e.g., 148). Excess C relative to protein in food results in compensatory feeding for some chewing insects (e.g., 65) and increases aphid populations by supplying their bacterial endosymbionts with greater availability of resources under elevated CO₂ (12). Conversely, dilution of protein increases

grasshopper assimilation efficiency of protein from C3 grasses (10). To this end, grasshoppers can experience extreme population growth, achieving outbreak status and influencing community- or ecosystem-level productivity (28).

Among insects, caterpillars preferentially consume more protein relative to C in ratios greater than 2:1, whereas grasshoppers and aphids favor equal or less protein than C (12). Although it is tempting to hypothesize that increasing C levels in C3 relative to C4 plants, for example, will favor host switching among herbivores, it is more plausible that herbivores will acclimate and adapt to their current hosts over generations. Compensatory feeding by the leaf beetle *Gastrophysa viridula* on *Rumex obtusifolius* grown under elevated CO₂ reduces survival and fecundity in subsequent generations reared on the same plants (23). Similarly, caterpillars reduce assimilation efficiency of C when consuming C-enriched plants grown under elevated CO₂ (9). When plant defenses are removed from this test by supplying caterpillars with artificial diets, exposure over generations reduces lipid storage without changes in consumption (148). That the opposite occurs (i.e., lipid storage increases under diets low in C) illustrates a strong selective environment for insect optimization of nutrition. For adaptation to leaves with higher C:N, it is possible that insect excretion, respiration, or increases in thermogenesis may reduce lipid storage; however, these mechanisms have not been verified. Nonetheless, insects readily adapt to diets high in C over generations, but the degree to which secondary chemistry modulates this selective environment may be equally important.

The known shifts in primary metabolism under elevated CO₂ appear to modulate downstream defense production, but the mechanisms regulating these processes are less well understood. Our current understanding is that elevated CO₂ interacts with hormone signaling and suppresses LOX-dependent defenses. Field studies of *N. attenuata* with suppressed LOX defenses linked defense status to insect herbivore host switching and verified that new herbivores will feed on defense-suppressed plants (72). Moreover, starch-modified mutants of *Arabidopsis* maintain different glucosinolate profiles (134). These patterns stress the intimate association between C metabolism and defense signaling and production. As a result, continual effort to elucidate the regulatory mechanisms linking the dynamics of C metabolism to defense signaling will provide greater insights into plant-insect adaptation to changing climate.

CONCLUSIONS

We provide evidence indicating that changes in allelochemical production induced by increased atmospheric CO₂ concentration are regulated by hormones not by changes in the C:N, and thereby suggest a testable hypothesis that future plant-herbivore relations will be mediated by hormones as a consequence of transcriptional regulators. These predictions can be tested by modern molecular biology and biochemistry methods and will help elucidate the mechanisms involved in allelochemical production under an elevated CO₂ environment. We also suggest that the effects of elevated CO₂ on insect behavior will be regulated not only by changes in chemical properties of leaves but also by changes in leaf temperature, a subject in need of further investigation.

SUMMARY POINTS

1. The increase in atmospheric CO₂ is altering insect herbivory by changing the chemical composition and energy balance of foliage.
2. The reduction of water loss under elevated CO₂ increases leaf temperature, stimulating the metabolism and feeding rate of insects in close association with leaf surfaces.

3. Whereas the increase in carbohydrates and the reduction in C:N of leaves grown under elevated CO₂ are fairly reproducible, changes in the content of allelochemicals affecting the suitability of foliage for insects are highly idiosyncratic.
4. JA synthesis and signaling compose a complex network that is regulated in part by CO₂. Elevated CO₂ downregulates constitutive and herbivory-induced levels of key transcripts associated with the JA pathway.
5. Elevated CO₂ enhances induced defenses derived from the SA-signaling pathway, such as the PR protein, and reduces signaling and defenses based on JA. NPR1 may be responsible for downregulating JA-related defenses and increasing susceptibility to herbivory in plants grown in enriched CO₂.
6. The differential responses among pathways producing allelochemicals to JA/ET and SA might provide new insights into how elevated CO₂ modulates plant defenses against herbivory.
7. Insects will likely acclimate and adapt over generations to changes in C:N in foliage, but the influence of secondary chemistry will modulate this selection.
8. Carbon supply remains inexplicably linked to defense-hormone signaling and, under increasing atmospheric CO₂, will differentially alter the synthesis of allelochemicals. Elucidating this link will enhance our understanding of plant-insect adaptation amid a changing climate.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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