Impacts of Anthropogenic Carbon Dioxide Emissions on Plant-Insect Interactions

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Abstract

Human industrialization has steadily raised atmospheric levels of CO_2 from 280 ppm prior to industrialization to current levels at 400 ppm and by 2050 are expected levels of 550 ppm. Climate change has important impacts on plant-insect interactions, and gaps in current understanding of plant responses to herbivory exist. Lately new empirical data has started to illuminate the mechanisms of the effects of elevated CO_2 in plant-insect interactions. Research has shown that the resource allocation to allelochemicals is interconnected among photosynthesis, genetic regulation, and hormonal signaling. Recent molecular approaches have revealed that insect damage is perceived by plants, and the signal is amplified by the participation of regulatory elements modulated by JA and ET, which induce plant responses to increase chemical defenses against herbivores. Elevated CO_2 inhibits JA and ET pathways and increases susceptibility of plants to herbivore attack by decreasing both constitutive and inducible chemical defenses against certain insects. Conversely, enriched atmospheric CO_2 increases SA, which increases other chemical defense pathways that are not regulated by JA. Identifying how atmospheres with high CO_2 levels moderate resource allocation to secondary metabolism would help to avoid any interference in natural plant defenses. In this chapter, we discuss current understanding of the mechanisms controlling insect herbivory pertaining to the global rise in atmospheric CO_2 concentrations.

Keywords

Elevated CO_2 • Global change • Plant insect-interactions • Plant defenses • Secondary metabolites

10.1 Introduction

At the beginning of the twenty-first century, the scientific literature outlines global boundary limits to agricultural production. Estimates of land use, for instance, hold that croplands, pastures, and planted forests occupy between 4000 and 5000 million hectares of land on Earth, with a

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predicted addition of 120–280 million hectares by 2030 (Lambin and Meyfroidt 2011). The ceiling on energy efficiency of plants is known as well: Zhu et al. (2008) calculate that at contemporary CO_2 concentrations, C3 plants are up to 4.6 % efficient at capturing solar energy as chemical bonds, while C4 plants are 6 %. Before that energy can be appropriated for anthropic purposes, however, herbivory by insects annually deducts up to 13 % from global agricultural yield, at an estimated economic cost of 400 billion dollars (Pimental 2004).

Responses of insect populations to rising anthropogenic CO_2 emissions are a topic of uncertainty and important to agriculture. Human industrialization has steadily raised atmospheric levels of CO_2 from 280 ppm prior to industrialization to current levels at 400 ppm and by 2050 are expected levels of 550 ppm (IPCC 2007). Atmospheric CO_2 concentration modulates the overall physiology of C3 plants (Leakey et al. 2009) and changes the quality of foliage, which makes herbivore insects sensitive to the rise in atmospheric CO_2 (DeLucia et al. 2008). Since climate change influences insect populations through their interactions with host plants, predicting how insect populations will respond to climate change centers on understanding of plant physiology responses to herbivory. Especially, the physiological mechanisms controlling allocation of resources to defenses against herbivores in plants grown under elevated CO_2 are most uncertain (Zavala et al. 2013).

Understanding the physiological mechanisms that lie beneath plant-insect interactions in elevated CO_2 environments could help to predict the impacts of climate change on insect populations. Yet adjusting plant chemical defenses to changing environment could be an option for managing the stability of agroecosystems. Additionally, understanding how plants allocate resources to secondary metabolism under elevated CO_2 environment would help to prevent any interference on the innate defenses in genetically modified plants. In this chapter, we discuss current understanding of the mechanisms controlling insect herbivory pertaining to the global rise in atmospheric CO_2 concentrations.

10.2 Role of Plant Ecophysiology on Quality of Foliage

10.2.1 Photosynthesis and Stomata Closure

Photosynthesis can be imagined as the initial stage of a process that distributes carbon and energy through interactions between plants and herbivore insects to culminate in considerable portion of the terrestrial ecosystem (Weisser and Siemann 2008). The carbon fixation enzyme ribulose bisphosphate carboxylase/oxidase (rubisco) is responsible for fixing atmospheric CO_2, and it is situated at the beginning of this process. Competitive substrate binding between CO_2 and O_2 at the active site of rubisco accounts for the sensitivity of photosynthesis to changes in levels of atmospheric CO_2. Although some grasses and arid succulents (C4 and CAM plants) fix carbon independent of atmospheric CO_2 concentrations, the majority of plants (those which possess C3 metabolism) photosynthesize with increasing efficiency as their supply of CO_2 becomes more concentrated (Leakey et al. 2009).

The stimulation of photosynthesis by rising CO_2 levels has proliferant consequences on the general physiology of plants. For instance, stomatal apertures constrict as photosynthetic capacity increases, which leads to reduced transpiration rates, resulting in increased foliar temperature (Ainsworth and Rogers 2007; Bernacchi et al. 2007). The substrate saturation of rubisco by CO_2 assimilation not only influences plant physiology by increasing starch accumulation and sucrose signaling but also extends into the ecological dynamic between plants and insect herbivores.

10.2.2 The Impact of Leaf Quality on Folivores

The main source of N for insects comes from rubisco, the dominant protein in the leaves of most plants and also the main source of valuable amino acids. Leaves contain up to nearly 40 % of amino acids and this is a potentially greater source of energy than a few micrograms of starch

(Farmer 2014). The ratio of carbon (C) to nitrogen (N) in plant tissue is higher than that of insects and converts N a limiting factor to the growth of insect herbivores (Mattson 1980). Although insects in general tend to compensate the lack of N in the diet by consuming more foliage, some insects are phagostimulated by high levels of carbohydrates (Hamilton et al. 2005). In one study, the CO_2-driven increase of carbohydrates in soybean increased fecundity of Japanese beetles (O'Neill et al. 2008).

Although insects want nutritional resources from leaves, plants need to conserve these same resources for their own growth and reproduction. While the plant nutritional resources support insect growth, many plant secondary metabolites specifically reduce herbivore feeding efficiency (Felton 2005). Optimal defense theory predicts that the products of primary metabolism are balanced against the products of secondary metabolism in plant tissue, such that plant fitness is maximized under challenge by insect herbivores (McKey 1974). When considering the effects of elevated CO_2 on insect populations, both the nutritional content and the titer of chemical defenses must be taken into account.

10.2.3 Consequences on Plant Growth Rate

Increasing atmospheric CO_2 accelerates plant growth. Elevated CO_2 environment spurns plants to assimilate carbon at a greater rate, leading to increased carbohydrate content as well as a shift to lower specific leaf areas (Stiling and Cornelissen 2007). The acceleration of plant growth rate can result a form of tolerance to insect herbivores by decreasing the relative foliar N content (Fornoni 2011). At the same time, the reduction in ratio of N to C obliges insect herbivores to compensate by consuming more plant tissue to meet their basic dietary N requirements (DeLucia et al. 2008).

The phenology of plants also can be affected by the environmental concentration of CO_2; the timing and extent of developmental stages of plants are typically delayed with rising CO_2 atmospheres. Soybeans grown under elevated CO_2, for instance, begin to flower later than their control counterparts grown in ambient CO_2 atmosphere (Castro et al. 2009). Likewise, senescence is both delayed in onset and prolonged in duration for plants exposed to elevated CO_2 levels (Taylor et al. 2008). This shift in phenological timing can lead to developmental mismatches between plants and their insect counterparts (DeLucia et al. 2012). Stages in the life cycles of insect pollinators, in particular, often are synchronized with the flowering times of plants they frequent and can drift out of temporal overlap under elevated CO_2 (DeLucia et al. 2012).

10.2.4 Consequences of Ecophysiology Changes on Secondary Metabolism

10.2.4.1 C:N Balance and Plant-Insect Interactions

The carbon-nutrient balance hypothesis postulates that the nutrition status (C:N) of plants directly controls allocation of secondary metabolites (Bryant et al. 1983). Similarly, the resource availability hypothesis (Coley et al. 1985) predicated the physiological role of resource availability as a control point connecting the plant's primary growth with its chemical defenses against insect herbivores (Fig. 10.1). Based on these hypotheses, one can predict that plants grown under elevated CO_2 environment produce more carbon-based secondary metabolites because the higher CO_2 assimilated is diverted to the production of these types of metabolites. This prediction, however, has been disputed by many empirical observations on the production of carbon-based secondary metabolites by plants grown under conditions of enriched CO_2 (Lindroth 2010). Continuous progresses in understanding patterns of synthesis of secondary metabolites have shown that resource allocation is interwoven among at least three physiological operators: photosynthesis, genetic regulation, and hormonal signaling (Kerchev et al. 2012; Fig. 10.2).

While the earlier models of plant responses to elevated CO_2 clearly conceptualize the effects of plant growth habit and nutrition on insect populations, they unsuccessfully predict the

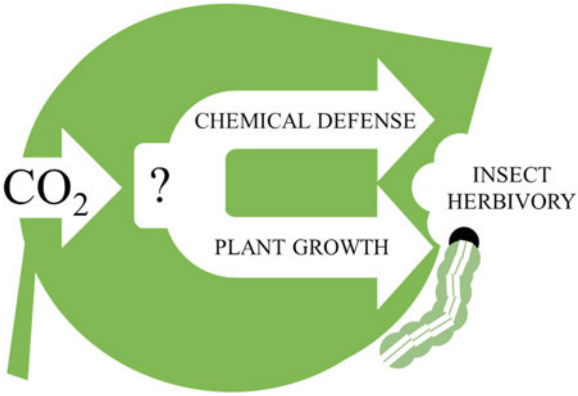

Fig. 10.1 Early conceptual models of resource allocation in plants, such as the carbon-nutrient balance hypothesis, based the partitioning of resources to growth and chemical defenses on only a few physiological operators, such as C:N balance. However, the variable influence of elevated CO_2 on the production of plant secondary metabolites against insect herbivory suggests that the task of resource allocation in plants is more complex than previously supposed

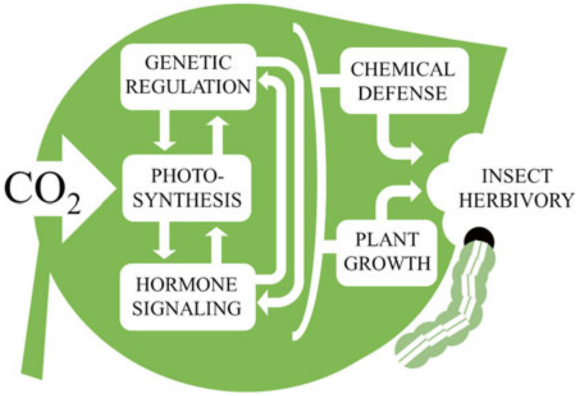

Fig. 10.2 The physiological function of resource allocation is now understood to be interwoven among at least three operators: photosynthesis, genetic regulation, and hormone signaling. The uncertainty in predicting how CO_2 influences populations of insect herbivores lies in the way these components interact with one another to yield plant growth and defense

production of secondary metabolites in defense against insect herbivory (Zavala et al. 2013; Hamilton et al. 2001). Existing mechanistic models of plant secondary metabolism regulation by environmental CO_2 have yet to discern underlying patterns among the empirical data available. Evidence suggests that photosynthesis plays a direct regulatory role in the mobilization of plant chemical defenses against herbivores. Under biotic stress, for instance, plants universally downregulate genes related to photosynthesis (Bilgin et al. 2010). The redox state within the chloroplast is thought to link photosynthesis with secondary metabolism; under attack from herbivore insects, plants interrupt the electron transport chain in photosynthesis, leading to a rapid accumulation of reactive oxygen species within the chloroplast (Kerchev et al. 2012). In turn, metabolic pathways responsible for the synthesis of several defense hormones are sensitive to the redox state of the cell (Kerchev et al. 2012).

10.2.4.2 Unpredictability of CO_2 Effects on Secondary Metabolism

Secondary metabolites are both diverse and idiosyncratic in that their distribution does not always follow phylogenetic relationships among the plants that produce them (Wink 2003). This characteristic unpredictability remains consistent in response to rising atmospheric CO_2; the influence of CO_2 on plant chemical defenses results in a range of responses without any apparent pattern (Zavala et al. 2013). Of the classes of compounds studied with regard to CO_2, phenolics and terpenoids represent the majority (Lindroth 2010). Phenolic compounds appear largely unaffected by carbon dioxide, with the exception of condensed tannins which vary widely in response across species studied. Likewise, the response of terpenoids to rising CO_2 concentration varies without pattern by species of plant (Lindroth 2010). The unpredictability of secondary compound production in plants grown under elevated CO_2 remains much the same for other studied classes of secondary compounds.

In addition to inducing direct chemical defenses against insects, herbivore attack on plants elicits the release of airborne compounds that interact with the surrounding ecosystem and function as a potential indirect defense (Karban 2008). The “bouquet” of volatiles can be composed of terpenoids, lipids, and methyl-esterated defense hormones typically released from herbivore-induced wounds in plant tissue (Karban 2008). Some of the potential ecological effects of these biogenic volatile organic compounds (BVOCs) are from activating chemical defenses in neighboring plants (Karban et al. 2010), to recruit natural predators of herbivores challenging the plant (Heil 2008). BVOCs emission can reduce the herbivore attack of the plant by more than 90 % because it attracts predators and reduces herbivore oviposition rates (Kessler and Baldwin 2001). Although some studies are available regarding to the impacts of atmospheric CO_2 on BVOCs production (Vuorinen et al. 2004a, b; Klaiber et al. 2013), more studies are required to understand biological impacts of elevated CO_2 environments on BVOC emissions.

10.2.5 Consequences of Stomata Closure

10.2.5.1 Transpiration and Leaf Temperature

In addition to altering the nutritive and chemical properties of leaves to prospective herbivore insects, elevated CO_2 also influences the hydraulic and thermal characteristics of leaves by reducing transpiration rates through closure of stomata (Bernacchi et al. 2007). As phloem feeders, aphid populations are especially sensitive to changes in the rate of nutrient translocation within their host plants (Hullé et al. 2010). Lowering transpiration rates in the plant could reduce the growth of insect populations with piercing/sucking mouthparts.

As an effect of reduced evapotranspiration due to lowered stomatal conductance, leaf temperatures rise under elevated CO_2. As ectotherms, insects in close contact with leaf surfaces experience increased metabolic rates as the temperature of the leaf rises (Pincebourde and Woods 2012). This principle especially applies to aphids, whose feeding rates and population growth can be expected to steepen as leaf temperatures increase (O’Neill et al. 2011).

10.3 Solving the Ambiguity of Induced Chemical Defenses to Insect Damage

In the last years, many new studies have been published suggesting that elevated CO_2 modifies plant chemical defenses against insects and alters their performance (Zavala et al. 2013). Insect damage is perceived by plants and induces signals through different pathways, which further produce biochemical and physiological changes that can be affected or modulated by variations in environmental CO_2 concentrations (Fig. 10.2). These changes in damaged leaves induce the production of plant secondary metabolites and decrease insect performance. However, it is not clear how high environmental CO_2 levels can interfere with the production of plant chemical defenses and its effects on plant-insect interactions. An earlier study on field-grown soybean demonstrated that changes in plant defenses against herbivore attack in plants grown in elevated CO_2 atmosphere are regulated by phytohormones (Zavala et al. 2008). Lately, new progress has been done in revealing the mechanisms of the influences of atmosphere with high CO_2 levels on plant defense elicitation by herbivore damage, which has been recently reviewed (DeLucia et al. 2012; Zavala et al. 2013). Although our understanding of the plant-herbivore interphase is limited, recent molecular approaches have revealed the participation of regulatory elements, such as Ca^{2+} ion fluxes, mitogen-activated protein kinases (MAPKs), jasmonic acid (JA), ethylene (ET), and reactive oxygen species (ROS), which detect insect damage, amplify the signal, and induce plant responses to increase chemical defenses against herbivores (Fig. 10.3).

10.3.1 Early Responses to Herbivory

Since plant defenses against insect attack are costly for plants, they must avoid wasting defensive resources and differentiate insect feeding from simple mechanical damage (Zavala et al. 2004; Zavala and Baldwin 2004). Herbivore attack is commonly associated with wounding of plant tissues and direct contact of insect oral secretions (OS) with putative cell receptors, which transduce the alarm signal and induce the accumulation of defensive metabolites. Volicitin [N-(17-hydroxylinolenoyl)-L-glutamine], the first identified fatty acid-amino acid conjugates (FACs) and herbivore-derived elicitor, was obtained from *Spodoptera exigua* OS (Alborn et al. 1997). FACs are not only present in OS of

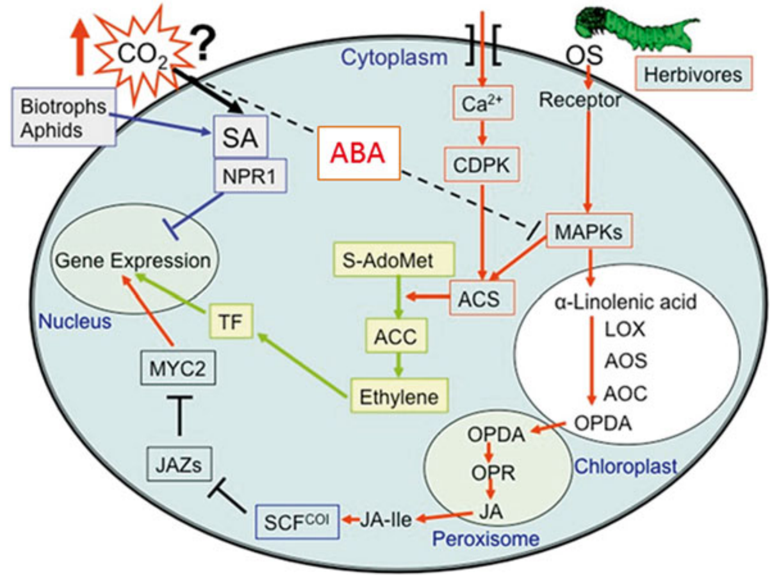

Fig. 10.3 A simplified model of the effects of elevated CO_2 on signaling events in a cell as a response of herbivore attack (Modified from Zavala et al. 2013). In ambient CO_2 herbivore oral secretions are perceived by unidentified receptors and trigger the activation of Ca^{2+} channels, resulting in Ca^{2+} influxes. Ca^{2+} binds to calmodulins and calcium-dependent protein kinases (*CDPKs*). Mitogen-activated protein kinases (*MAPKs*) are also rapidly activated and trigger the biosynthesis of jasmonic acid (*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. However, elevated CO_2 induces salicylic acid (*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 transcription factor (*TF*) in the nucleus and inhibits JA-induced defense gene expression. In addition, we hypothesize that elevated CO_2 increases ABA concentration, which decrease ethylene emission. In addition elevated CO_2 decreases MPK4 activity and activates downstream genes of SA signaling (*dashed black arrow*). The inhibition of early signaling events by elevated CO_2 decreases the accumulation of metabolites that function as defense against herbivores.

some lepidopteran species (Halitschke et al. 2001; Pohnert et al. 1999; Spiteller and Boland 2003; Spiteller et al. 2004) but also in OS of fruit flies (*Drosophila melanogaster*) and crickets (*Teleogryllus taiwanemma*) (Yoshinaga et al. 2007). A new study has demonstrated that plants can differentiate specialists from generalist insects by the amount of FAC present in the OS; this identification of the attacker allows plants to upregulate specific defenses accordingly (Hettenhausen et al. 2013).

Membrane depolarization is one of the earliest cellular responses to damage by herbivory. Bites of *Spodoptera littoralis* larvae on leaves of *Phaseolus lunatus* (lima bean) produced large membrane depolarization (Maffei et al. 2004). Since Ca^{+2} fluxes across the cell membranes' change membrane potentials, this ion has been implicated as a second messenger in many plant signaling pathways, including responses to herbivory (Maffei et al. 2007). Larva FACs contribute to the Ca^{+2} influxes by forming ion channels in planar lipid bilayer membranes (Maischak et al. 2007). It has been suggested that calcium-dependent protein kinases are part of plant defense system against herbivores because these Ca^{+2}-dependent protein kinases regulate the production of reactive oxygen species (ROS) in potato, which in turn upregulate plant defenses (Kobayashi et al. 2007).

Activation of mitogen-activated protein kinase (MAPK) cascades is a common response of plants to abiotic and biotic stimuli, including pathogens and herbivory (Romeis et al. 2001; Zhang and Klessig 2001; Wu et al. 2007). Herbivory and application of *Manduca sexta* OS to wounded leaves of *Nicotiana attenuata* and *Solanum lycopersicum* (tomato) highly elicit both salicylic acid-induced protein kinase (SIPK) and wound-induced protein kinase (WIPK), which induced transcriptional regulation of many defense-related genes (Wu et al. 2007; Kandoth et al. 2007). In potato the homologous SIPK and WIPK are involved in Mi-1-mediated resistance to aphids (Li et al. 2006). The *Arabidopsis* orthologous MPK3 and MPK6 to tobacco (*Nicotiana*) WIPK and SIPK, respectively (Zhang and Klessig 2001; Ichimura et al. 2002; Ren et al. 2002), phosphorylate the transcription factor WRKY33 and induce important plant defenses (Mao et al. 2011). In addition, SIPK regulates the activity of chloroplastic GLA1 phospholipase and releases polyunsaturated fatty acids, such as linolenic acid, from the plastidial membranes (Kallenbach et al. 2010). Linolenic acid can be used to the synthesis of the defense hormone JA, the most important phytohormone that controls plant defenses against herbivores (Wasternack 2007).

10.3.2 Jamonates Regulation as Key of Inducing Defenses

Variations of atmospheric CO_2 levels can modify jasmonic acid (JA) accumulation in plant tissues and alter plant chemical defenses against herbivore insects (e.g., Zavala et al. 2008; Sun et al. 2010, 2013; Casteel et al. 2012). Leaf damage inflicted by chewing insects or mechanical damage increases (<30 min) accumulation of JA at the site of wounding; this key cellular signal is involved in the activation of the immune responses to most insect herbivores and necrotrophic microorganisms (Farmer 2014). JA is synthesized via the octadecanoid pathway, from which nearly all jasmonate biosynthetic enzymes have been identified in *Arabidopsis* and characterized in several species (Schaller et al. 2005; Halitschke and Baldwin 2003; Fig. 10.3). The linolenic acid liberated by phospholipases from lipids of chloroplast membranes is transformed to a series of reactions to 12-oxo-phytodienoic acid (OPDA) by the enzymes, lipoxygenase (LOX), allene oxide synthase (AOS), and allene oxide cyclase (AOC) (Fig. 10.3). Then in the peroxisomes, after three steps of β-oxidation, OPDA is converted to JA (Wasternack 2007).

Studies using microarray analysis and RT-PCR of field-grown soybean (*Glycine max*) showed that constitutive and inducible levels of key transcripts associated with JA pathway, LOX7 and LOX8, AOS, and AOC, were downregulated under elevated CO_2 (Casteel et al. 2008; Zavala et al. 2008). Downregulation of JA pathway resulted in lower level of chemical defenses in soybean foliage after 24 h of Japanese beetle (*Popillia japonica*) herbivory (Casteel 2010). Similar results were found in tomato and *Arabidopsis*; elevated CO_2 levels reduced the JA pathway and accumulation in the wild-type plants and in a genotype in which the JA pathway is constitutively upregulated (Sun et al. 2011, 2013).

The new insights into the mechanisms of JA bioactive perception and signal transduction into the activation of defense transcriptional responses have been discussed in several review papers and suggest that the core signal transduction chain is composed for relative few links (Ballaré 2011; Wu and Baldwin 2010; Wasternack and Hause 2013). The first step is conjugation of JA to isoleucine (Ile), which is required for direct defense response against herbivores, such as caterpillar feeding (Kang et al. 2006). The ubiquitin ligase SCFCOI1 complex perceives the jasmonoyl-isoleucine (JA-Ile), and the F-box protein CORONATINE-INSENSITIVE1 (COI1) recognizes JA-Ile, which triggers the ubiquitination and subsequent proteosomal degradation of JASMONATE ZIM DOMAIN (JAZ) proteins. Degradation of the JAZ repressors releases the expression of MYC2 transcription factor (TF). Therefore, MYC2 TF induces downstream defense responses related to JA burst. Interestingly, increases of JA synthesis (possibly via MYC2) induce the transcription of JAZ repressors (Thines et al. 2007; Chico et al. 2008), controlling the levels of signal transduction and production of chemical defenses (Fig. 10.3). Since rapid resynthesis of JAZ repressors restrains the expression of genes related with defenses, this negative feedback presumably avoids the synthesis of energetically costly compounds once insect attack is finished and allows plants to save energy.

10.3.3 Cross Talk among Defense Pathways

Plants grown in elevated CO_2 atmosphere presented low JA accumulation and emission of ET, which reduced antiherbivore defenses and increased insect attack (Zavala et al. 2008, 2009; Sun et al. 2011, 2013). ET and JA have synergistic effects on upregulating plant defenses against herbivores, such as the upregulation of protease inhibitors (PIs) in tomato (O'Donnell et al. 1996). It has been demonstrated that both ET and JA can activate common TF in *Arabidopsis* and sunflower (*Helianthus annuus*) (Manavella et al. 2008; Lorenzo et al. 2003; Pre et al. 2008), explaining the synergistic effect. The synergistic cross talk between JA and ET is known to occur preferentially for the response to necrotrophic pathogens (Pieterse et al. 2012). Two central TFs of ET signaling, ETHYLENE-INSENSITIVE3 (EIN3) and EIN3-like (EIL1), bind JAZ1, JAZ3, and JAZ9 via the Jas domain of JAZs, resulting in the suppression of EIN3/EIL1 activity (Zhu et al. 2011).

ET pathway is initiated by the synthesis of S-adenosylmethionine from methionine, which after being oxidized by 1-aminocyclopropane-1-carboxylic acid (ACC) oxidases is converted to the ET precursor ACC by ACC synthase (ACCs) (Fig. 10.3). Since ACC forms ET, ACC synthesis is considered to be rate limiting of ET biosynthesis, which can be inhibited in plants grown under elevated CO_2, increasing herbivory susceptibility. Both constitutive and inducible expression levels of *acc* are diminished in foliage of field-grown soybeans under elevated CO_2 atmosphere (Casteel et al. 2008; Zavala et al. 2008). In addition, elevated CO_2 environment decreased both the accumulation of JA and the emission of ET in *Arabidopsis* (Sun et al. 2013). While JA and ET are important modulator for chewing insects, salicylic acid (SA) pathway is activated by plants in response to attack by phloem feeding insects, such as aphids and silver leaf whiteflies and biotrophic pathogens (Walling 2000).

One of the most studied cross talk is the antagonistic interaction between the JA and SA pathways (Pieterse et al. 2009; Kunkel and Brooks 2002). Upregulation of JA pathway can repress SA defense responses (Brooks et al. 2005; Uppalapati et al. 2007), and conversely, induction of SA by biotrophic pathogens inhibits defenses regulated by JA (Felton and Korth 2000; Spoel et al. 2007). Similar antagonistic interaction between JA and SA was observed in different plant species grown under enriched CO_2 atmosphere, increasing the allocation of resources to SA-dependent over JA-dependent defenses. Elevated CO_2 increased the induce defenses based on SA pathway in tomato, such as the pathogenesis-related protein (PR), and decreased JA-regulated defenses, such as PIs (Sun et al. 2011; Huang et al. 2012). Similar results were found in *Arabidopsis* growing in open chambers with elevated CO_2 atmosphere (Sun et al. 2013). Field-grown soybeans under elevated CO_2 amplified SA-regulated defenses and pathway and diminished gene expression of JA pathway and JA accumulation compared to ambient-grown plants (Casteel et al. 2008, 2012; Zavala et al. 2008).

Synthesis of defense compounds against plant pathogens is regulated by SA signaling pathway and can be modulated by CO_2 (Glazebrook 2005; Zarate et al. 2007). Recently, it has been demonstrated that some soybean pathogens are reduced in elevated CO_2 treatments at SoyFACE (Eastburn et al. 2010). In addition, elevated CO_2 increased SA and decreased JA accumulation in tomato, enhancing resistant to tomato yellow leaf curl virus (Huang et al. 2012). The mechanism by which elevated CO_2 alters the hormonal response to herbivory is not known, but the antagonism between SA and JA responses is discussed in several recent reviews (Pieterse et al. 2009, 2012).

SA can decrease JA biosynthesis and sensitivity through a negative interaction (Spoel et al. 2003). NPR1 (NONEXPRESSOR OF PATHOGENESIS-RELATED GENES1) is an important protein component of SA pathway and activated by SA (Fig. 10.3). Some NPR1 multimers monomerize by SA-induced changes of the redox state via thioredoxin followed by the transport of the monomeric forms into the nucleus. Here, they bind as activators to TGA TFs specific for SA-inducible genes and phosphorylated them and induce transcription (Fu et al. 2012). Elevated CO_2 alters the transcripts regulating the redox status of soybeans by inducing thioredoxins and glutathione S-transferase (Casteel et al. 2008). Moreover, elevated CO_2 alters ascorbate or glutathione, albeit with some degree of plant specificity (Gillespie et al. 2011; Perez-Lopez et al. 2009), and may allow TFs to interact with reduced NPR1 and facilitate efficient DNA binding for induction of immune signaling (Spoel and Loake 2011).

Assuming that NPR1 may be responsible for downregulating JA-related defenses and increasing herbivory susceptibility in plants grown in enriched CO_2 environment, what is the early signal perceived by plants that upregulate the SA pathway? Recent experiments demonstrated that SA and ROS accumulation and PR expression were increased in MPK4-silenced soybeans and *Arabidopsis* (Liu et al. 2011; Petersen et al. 2000). Interestingly, expression of WRKY33 increased 16-fold in MPK4-silenced soybeans, suggesting that MPK4 negatively control WRKY33 at both the posttranslational and transcriptional level (Liu et al. 2011). MPK4 functions to sequester WRKY33 in the nucleus and prevent it to activating downstream genes of SA signaling (Qiu et al. 2008). Conversely, the cross talk between JA with other hormones can also interfere with either JA or ET pathway.

Atmosphere of elevated CO_2 concentration increases ABA levels during leaf development and promotes stomatal closure, reducing stomatal conductance by decreasing pore size in developing leaves (Ainsworth and Rogers 2007; Herrick et al. 2004). ABA and SA signaling required for stomatal closure (Pieterse et al. 2012) are modulated by MAPK4 (Hettenhausen et al. 2013). Upon wounding or herbivory, ABA production increases and antagonizes the ERF pathway, compromising ET signaling and perception (Abe et al. 2003; Anderson et al. 2004; Fig. 10.3). ET can play a critical role during SA-JA interaction, and the final outcome of this signal cross talk can be shaped by levels of ET. When ET signal is high, JA-SA antagonisms are diluted, while with low ET levels in plant tissue, the JA-SA antagonistic relationship becomes greater (Pieterse et al. 2012).

In summary, we suggest that elevated CO_2 atmosphere induces changes in gene expression and activity of MAPK4 and the production of ABA in leaves, which induces SA signaling and inhibits ET emission and pathway that increases the JA-SA antagonistic relationship. Thus, in plants grown in elevated CO_2 environment, levels of SA increase and production of JA and ET decrease compared to ambient-grown plants (Casteel et al. 2007; Zavala et al. 2008; Casteel et al. 2008, 2012; Sun et al. 2011; Huang et al. 2012). Although the mechanism of the impact of elevated CO_2 on the early signaling steps involved in the perception of insect damage and the activation of JA biosynthesis remain to be elucidated, some advances have been done to explain CO_2 regulation on secondary metabolite production. Elevated CO_2 alters hormonal responses that are transduced into the activation of transcriptional responses and affect plant-insect interactions.

10.3.4 CO_2 Regulates Chemical Defenses through Phytohormones

Many empirical studies about the consequences of elevated CO_2 on plant chemical responses to insect damage and their effects on herbivore performance seem to be contradictory. Whereas some studies report that plants grown under elevated CO_2 environment are more defensed against herbivores (e.g., Lindroth et al. 1993; Holton et al. 2003), field studies demonstrated that elevated CO_2 atmosphere diminished plant defenses against some herbivore insects (e.g., Zavala et al. 2008; 2009; Hamilton et al. 2005). Recently new research has started to study the mechanisms of the consequences of elevated CO_2 on chemical defenses and its relationships with hormonal regulation rather than just study the effects of defenses on herbivore performance (Zavala et al. 2013; DeLucia et al. 2012). Although elevated CO_2 increases SA in plant tissue and increases chemical defense pathways that are not regulated by JA (e.g., Sun et al. 2011; Ghasemzadeh et al. 2010; Casteel et al. 2012), plants grown in enriched atmospheric CO_2 downregulate JA and ET pathways and increase susceptibility to herbivore attack by disrupting both constitutive and inducible important chemical defenses (Zavala et al. 2008, 2009); Interestingly, a new study has proposed that an unknown JA-independent defense pathway may defend *Nicotiana attenuata* against larvae of *M. sexta* (Hettenhausen et al. 2013).

Revealing the regulation of plant chemical defenses in response to herbivory will allow us to determine the adaptive function of anti-herbivore defenses (Karban and Baldwin 1997) that are modified by elevated CO_2 and these modifications should be investigated in concert with predictable changes in CO_2-driven plant traits.

Phytohormones differentiate among phenolic pathways and synthesize both isoflavonoids and flavonols compounds in accordance to environmental cues (Ferrer et al. 2008). Although *Nicotiana attenuata* impaired in JA biosynthesis was unable to produce phenolic conjugates after damage produced by herbivores, these plants were able to produce rutin (a flavonoid) and chlorogenic acid (Demkura et al. 2010; Hoffman-Campo et al. 2001). The production of carbon-based defenses is modified by hormones affected by elevated CO_2. Elevated CO_2 levels increased C:N ratio and concomitantly the production of SA-regulated flavonoids in plants, such as quercetin, kaempferol, and fisetin (Ghasemzadeh et al. 2010), but decreased the concentration of JA-regulated isoflavonoids such as genistein (O'Neill et al. 2010), an important antiherbivore defense (Piubelli et al. 2005; Figs 10.1 and 10.2). In addition, elevated CO_2 decreased the JA-regulated triterpenoid cardenolides in four different genotypes of milkweed (*Asclepias syriaca*) another important chemical defense against herbivores (Vanette and Hunter 2011; Rasmann et al. 2009).

One of the first defenses against herbivores studied is protein proteases inhibitors (PIs) in tomato, which are regulated systemically and locally by JA (Ryan 1990). PIs damage the ability of insects to digest proteins and decrease amino acid assimilation (Birk 2003; Zavala et al. 2004). The accumulation of these nitrogen-based defenses also can change C:N ratio in plant tissue (Howe and Jander 2008; Figs. 10.1 and 10.2). Foliage of field-grown soybean had low constitutive and induced expression and activity levels of cysteine proteinase inhibitors (CystPIs) in an atmosphere with high CO_2 levels, the principal antiherbivore defenses against coleopteran herbivores (Zavala et al. 2008, 2009; Sun et al. 2011). CystPIs are typically regulated by the defense hormones JA and ET that are downregulated by elevated CO_2 (Zavala et al. 2008; Sun et al. 2013). Glucosinolates, another nitrogen-based defense and regulated by JA and SA signaling pathways, are differentially regulated by concentration levels of CO_2 in the atmosphere. Plants grown in atmosphere with high CO_2 levels had incremented constitutive glucosinolates regulated by SA, such as aliphatic glucosinolates and methyl sulfinylalkyl glucosinolates glucoraphanin and glucoiberin in broccoli (*Brassica oleracea*), and these metabolites were induced in *Arabidopsis* by diamondback moths (*Plutella xylostella*) herbivory (Schonhof et al. 2007; Bidart-Bouzat et al. 2005; Doughty et al. 1991). Conversely, JA-regulated indole glucosinolates decreased in plants grown under elevated CO_2, predominantly because of a reduction of glucobrassicin and 4-methoxy-glucobrassicin contents, which are regulated by JA (Schonhof et al. 2007; Brader et al. 2001).

Analogously, levels of plant BVOC emission depend on whether they are regulated by JA or SA. Downregulation of JA levels by elevated CO_2 environment decreased the emission of terpene volatile compounds in cabbage (*Brassica oleracea*; Vuorinen et al. 2004a, b). Plants exposed to elevated CO_2 exhibited a great reduction of terpene emission, decreasing aphid (*Brevicoryne brassicae*) colonization and attraction of herbivores' natural enemies (Vuorinen et al. 2004a; Klaiber et al. 2013). However, emission of GLV following herbivory was enhanced in plants grown under elevated CO_2 environment (Vuorinen et al. 2004b), and it appears that the regulation of these compounds does not rely on JA signaling (Halitschke and Baldwin 2003; Allmann et al. 2010). Based on the empirical evidence presented here, we suggest that JA/ET and SA may provide new insights into how elevated CO_2 modulates plant chemical responses to herbivory.

10.4 Impact of Atmosphere with High CO_2 Levels on Agriculture

By 2050 crops will grow in an atmosphere with CO_2 levels 50 % higher than today (Prather et al. 2001) and by that date the projected world population will be about 9 billion (Ray et al. 2013). Although it has been suggested that global crop production needs to increase twice the present rate to meet global food demand, climate change is likely to worsen the situation by increasing infestation of diseases and insects on crops (Khoury et al. 2014). As a consequence of anthropogenic global change, elevated levels of atmospheric CO_2 can greatly modify the interactions between crops and insect pests and may promote the rapid establishment of invasive species (Zavala et al. 2008; 2013).

Whereas higher atmospheric CO_2 concentrations stimulate photosynthetic activity in C3 plants (such as wheat and soybean), elevated CO_2 increases water-use efficiency in both C3 and C4 plants (such as maize and millet), suggesting a potential increment in yield of crops (Ainsworth and Long 2005). However, field experiments demonstrated that the projections of increasing agricultural production under climate change cannot be reached, probably because of insect herbivory, an aspect that was not considered in open chambers (Muller 2013; Long et al. 2006). New studies have suggested that climate change may affect plant natural defenses against insects, especially when they are grown under elevated atmospheric CO_2 concentrations (DaMatta et al. 2010; Taub et al. 2008; Zavala et al. 2013). Downregulation of natural plant defenses may also affect pesticide use, to compensate the altered chemical composition changes that increase susceptibility of crops to insect damage (Dermody et al. 2008; Zavala et al. 2008).

One of the main components of integrated pest management programs is the utilization of natural plant defenses against insect pest, which together with the expression of foreign genes with inducible promoters has been suggested as an important tool to protect crops against insect herbivores. However, the ability of insect to adapt to plant defenses may limit the extent of those programs (Bolter and Jongsma 1995). In addition, high CO_2 levels in the atmosphere in the future may restrain inducible defenses of crops, such as CystPI in soybean, which will be downregulated and may compromise defenses against insects (Zavala et al. 2008, 2013). Elevated CO_2 may affect the expression of JA-regulated defenses of soybean, which include not only CystPIs but also serine proteinase inhibitors, isoflavonoid content, or polyphenol oxidase activity, potentially making plants more vulnerable to herbivores other than beetles and leading to even greater losses. *Nicotiana attenuata* unable to produce JA planted into native habitats was more vulnerable to adapted herbivores and also was more colonized at a higher rate by novel herbivore species, which fed and reproduced successfully (Kessler et al. 2004). On the other side, insect herbivores preferred to feed on younger leaves of plants grown under elevated CO_2 in FACE experiments (Zavala et al. 2009), which is a potential mechanism to explain the offset of the predicted increases in agricultural productivity associated with greater levels of CO_2 in the atmosphere (Ainsworth and Long 2005; Long et al. 2006). Furthermore, it is likely that the impacts of elevated CO_2 atmosphere on plant chemical defenses reported here also affect communities of natural enemies and the entire trophic structure of agroecosystems (Richards et al. 2015), potentially exacerbating pest problems by multiple mechanisms. Additional scientific attention is necessary to understand and evaluate the impact of CO_2 fertilization on agricultural productivity and crop quality (Muller 2013).

10.5 Concluding Remarks

Recent evidence has demonstrated that anthropogenic elevation in CO_2 concentration alters plant-insect interactions by altering hormonal regulation that in turn change chemical defenses of plants against herbivore insects (e.g., Zavala et al. 2008, DeLucia et al. 2008). However, many aspects of the mechanisms that regulate the impact of elevated CO_2 atmosphere on defense metabolisms are still to be elucidated. As recent review articles have remarked, the task of predicting how insect populations respond to changes in host plant growth habits and nutritive composition would be easier if the basic regulatory connections between plant primary and secondary metabolism were better understood.

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