

REVIEW ARTICLE

Anthropogenic increase in carbon dioxide modifies plant–insect interactionsJ.A. Zavala¹, L. Gog² & R. Giacometti¹¹ Cátedra de Bioquímica/Instituto de Investigación en Biociencias Agrícolas y Ambientales, Facultad de Agronomía, Universidad de Buenos Aires-Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina, Buenos Aires, Argentina² Department of Plant Biology, University of Illinois at Urbana-Champaign, Champaign, IL, USA**Keywords**

global change; herbivory; jasmonic acid; plant defences; plant–insect interactions; salicylic acid.

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Abstract

Industrialisation has elevated atmospheric levels of CO₂ from original 280 ppm to current levels at 400 ppm, which is estimated to double by 2050. Although high atmospheric CO₂ levels affect insect interactions with host plants, the impact of global change on plant defences in response to insect attack is not completely understood. Recent studies have made advances in elucidating the mechanisms of the effects of high CO₂ levels in plant–insect interactions. New studies have proposed that gene regulation and phytohormones regulate resource allocation from photosynthesis to plant defences against insects. Biochemical and molecular studies demonstrated that both defensive hormones jasmonic acid (JA) and ethylene (ET) participate in modulating chemical defences against herbivores in plants grown under elevated CO₂ atmosphere rather than changes in C:N ratio. High atmospheric CO₂ levels increase vulnerability to insect damage by down-regulating both inducible and constitutive chemical defences regulated by JA and ET. However, elevated CO₂ levels increase the JA antagonistic hormone salicylic acid that increases other chemical defences. How plants grown under elevated CO₂ environment allocate primary metabolites from photosynthesis to secondary metabolism would help to understand innate defences and prevent future herbivory in field crops. We present evidence demonstrating that changes in chemical defences in plants grown under elevated CO₂ environment are hormonal regulated and reject the C:N hypothesis. In addition, we discuss current knowledge of the mechanisms that regulate plants defences against insects in elevated CO₂ atmospheres.

Introduction

How populations of insect herbivores respond to rising CO₂ is not completely understood, yet the significance to natural environments and crop production is evident. Industrialisation has increased the concentration of atmospheric CO₂ from 280 ppm at the initiation of the Industrial Revolution to 400 ppm today and is estimated to rise twofold through this century (IPCC, 2013). Changes in environmental CO₂ concentration regulate the primary metabolism of C3 plants, with respect to use of carbon, nitrogen and water resources (Leakey *et al.*, 2009). By association with these alterations in their food source, insect herbivores can perceive higher CO₂ levels in the atmosphere that may elevate environmental

temperature as well (DeLucia *et al.*, 2008, 2012). Although many insects respond directly to peaks of CO₂, they do not respond to elevated constant concentrations of environmental CO₂ (Guerstein & Hildebrand, 2008), thus changes in atmospheric CO₂ levels affect insect populations through modifications of host plants that affect interactions with herbivores. Furthermore, to estimate insect population responses to elevated CO₂ atmosphere, studies should be focused around current knowledge of plant responses to insect damage, in particular, the understanding of mechanisms that regulate availability of primary resources to plant secondary metabolism in plants grown under environment with high CO₂ levels (Zavala *et al.*, 2013).

Exposing the biological connections between environmental CO₂ and plant–insect interactions could have some practical value. In the short term, better comprehension of the biochemical mechanisms that explain interactions of crops with insects will improve the understanding of the influences of elevated CO₂ on insect pest performance and host preferences. From the perspective of functional ecology, genetically modifying chemical defences of plants may present an alternative for maintaining crop production. Moreover, revealing how plants grown in atmosphere with high CO₂ levels assign primary metabolites to secondary metabolism could complement concurrent efforts to genetically modify plants for accelerated productivity (Zhu *et al.*, 2010). In this study, we present up-to-date knowledge of the mechanisms that regulate plants defences against insects in elevated CO₂ atmospheres.

Impacts of elevated CO₂ on plant ecophysiology and its effects on quality of foliage

Although carbon assimilation of C₄ and CAM plants is independent of atmospheric CO₂ concentrations, plants with C₃ metabolism increase the efficiency of photosynthesis as their availability of CO₂ is higher (Drake *et al.*, 1997). Boosting photosynthesis through increased concentration of CO₂ in the environment modifies the plant physiology, eventually reaching insect herbivores through two general pathways: Alterations in the character of plant tissue as a food source, and by changing the way plants induce chemical defences against biotic agents (Fig. 1). In one example of a change in character as food, changes in stomatal apertures that increase as consequences of high photosynthetic levels reduced transpiration rates, increasing foliar temperature and speeding the rate of herbivory by aphids (Ainsworth & Rogers, 2007; Bernacchi *et al.*, 2007; Hullé *et al.*, 2010). On the defence side, elevated CO₂ modifies the synthesis of the defence hormones jasmonic acid (JA) and salicylic acid (SA), thereby altering the vulnerability of plants to attack from biotic agents (Zhang *et al.*, 2015). Such strings of consequences starting with the substrate saturation of rubisco do not end with plant physiology, but can have some impacts in agroecosystems by changing balance in plant–insect interactions.

Leaves as food for insects

Herbivores are structured by the carbon and nitrogen of plant tissue. Since the proportion of carbon (C) in relation to nitrogen (N) in plant tissue is much higher than that of insects, N becomes restrictive to insect growth and development (Mattson, 1980). The increased production

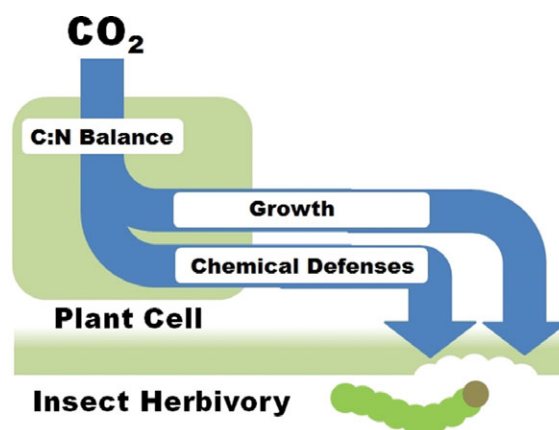


Figure 1 A model explaining carbon (C) and nutrient (N) allocation within plants. C:N ratio of foliage was hypothesised to regulate the way plants allocate resources between growth and secondary metabolism. Carbon-nutrient balance hypothesis, proposed that distribution of resources between growth and chemical defences were regulated by C:N balance.

of carbohydrates by plants grown under enriched CO₂ levels dilutes the N content of leaf tissue (Taub & Wang, 2008). However, the increase of starch content alone stimulates feeding rates in insect herbivores (Hamilton *et al.*, 2005). The high concentration of carbohydrate levels in soybean grown under elevated CO₂ augmented fertility of coleopterans *Popillia japonica* (O'Neill *et al.*, 2008). Eventually, insect herbivores need to compensate the low foliar N:C ratio by increasing consumption of foliage to achieve N requirements for growth and development (DeLucia *et al.*, 2008).

Although primary nutritional qualities of plant tissue are important for insects' growth and development, secondary metabolites can be regarded as a strategy of plants to make themselves indigestible to insects (Felton, 2005). In tobacco plants, for example, the toxicity of nicotine combined with the anti-nutritive qualities of trypsin protease inhibitors synergistically impede the growth of insect herbivores (Steppuhn & Baldwin, 2007). The content of secondary metabolites in plants influences the foraging behaviour of insect herbivores (Bernays, 1998; Singer, 2008) and the evolution of traits in insect populations (Futuyma & Agrawal, 2009). How rising CO₂ will influence this and other examples of host-plant switching and evolution of insect pest populations remains an open question (e.g. Aragon *et al.*, 2010).

Consequences of increasing photosynthesis on secondary metabolism: C:N balance and conceptual models

C:N ratio of foliage was once hypothesised to regulate the way plants allocate resources between growth

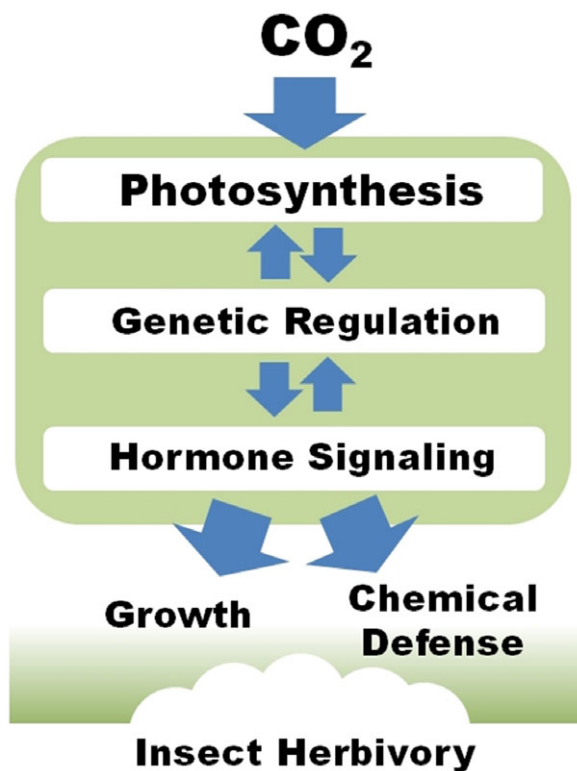


Figure 2 Plant resource allocation to defence is regulated by interconnections among photosynthesis, genetic regulation (regulation of gene expression) and hormone signalling. Understanding the interactions of these components may reduce the uncertainty in predicting the effects of elevated CO₂ on insect populations.

and secondary metabolism (Hamilton *et al.*, 2001). Several early models of the regulation of plant secondary metabolism, like the carbon-nutrient-balance hypothesis (Bryant *et al.*, 1983) and the resource availability hypothesis (Coley *et al.*, 1985), proposed the biological function of the amount of resources to be allocated as a main regulation of linking the growth rate of plants with the production of defensive secondary metabolites (Fig. 1). However, new studies have suggested that the resource utilisation to chemical defence has connections with photosynthesis (primary metabolism), control of gene expression and hormone regulation (for reviews see Kerchev *et al.*, 2012; Meldau *et al.*, 2012; Fig 2).

Although previous understanding of the influences of changing CO₂ environment on plant–insect interactions focused on the impacts of plant growth rate and foliage palatability on insect performance, they were not able to envisage the mechanisms of secondary metabolites production as a response to insect damage (Zavala *et al.*, 2013; Hamilton *et al.*, 2001). According to the carbon–nutrient balance hypothesis an increase in CO₂ supply induces high production levels of carbon-rich

defence compounds, like phenolics and terpenoids (Hamilton *et al.*, 2001); however, this prediction does not match results of secondary metabolite production from plants grown under conditions of elevated CO₂ environment (Lindroth, 2012).

Currently, models of the mechanisms of plant secondary metabolism consider hormonal regulation signalling to understand primary patterns based on the empirical data available for the impact of CO₂ on chemical defences against insects (Zavala *et al.*, 2013). Recent research would suggest that altered hormonal production underlies the observed shift in plant susceptibility to pathogens and insect herbivores in elevated CO₂ environments (Casteel *et al.*, 2012; Zhang *et al.*, 2015). Moreover, alterations in photosynthesis effect secondary metabolites production. Photosynthetic capacity reduction in *RuBPC*-silenced *Nicotiana attenuata* was accompanied with lower activity of trypsin protease inhibitors and concentration of diterpene glycosides (Mitra & Baldwin, 2008). *Vice-versa*, alterations in the hormonal control of secondary metabolism alters photosynthesis (Bilgin *et al.*, 2010). While caterpillar damage reduced gas exchange and increased defences against herbivores in wild-type of *N. attenuata*, plants unable to induce JA-regulated defences showed negligible inhibition of photosynthesis and no increase of chemical defences (Nabity *et al.*, 2013). A remaining area of uncertainty, then, centres on the regulatory connection between photosynthesis and plant secondary metabolism.

Plant secondary metabolites and volatile organic compounds

Elevated CO₂ atmosphere impacts on plant chemical defences and induce a variety of responses without clear explanation of the causes and consequences (Zavala *et al.*, 2013). Both phenolics and terpenoids have been the most studied carbon-based secondary metabolites with respect to elevated CO₂ (Lindroth, 2012). In general, phenolic compounds are not affected by changes in environmental CO₂ concentrations, only condensed tannins and some flavonoids vary extensively in response through species studied. Leaf damage produced by *Vanessa cardui* (Lepidoptera) on field-grown soybean-induced genistein, while coleopterans damage induced flavonols and flavones but not isoflavonoids (O'Neill *et al.*, 2010). Phenolic compounds can be toxic to herbivores because when they are oxidised to quinones covalently bind to proteins in the gut of insects and limit their availability as nutrients (Summers & Felton, 1994). These compounds can be oxidised in the leaf by the enzyme polyphenol oxidase, which is induced by insect damage (Casteel *et al.*, 2008). Equally, it has been suggested that increasing CO₂

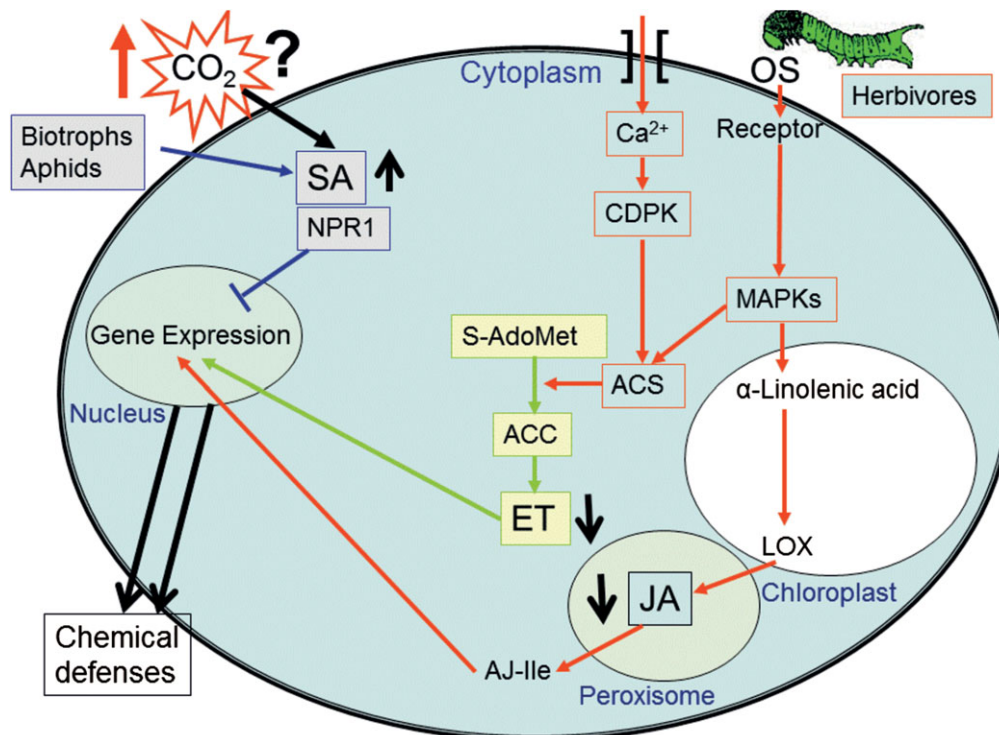


Figure 3 Different pathways responses induced by insect damage on cells of plants grown under high CO₂ environment. Oral secretions are perceived by a putative receptor and different kinases transmit the signal up-regulating both the ethylene (ET) and jasmonic acid (JA) pathways. Conversely, either pathogen or aphid attack induce the salicylic acid (SA) pathway that has an antagonistic effect on the JA pathway. While elevated CO₂ induces SA, also inhibits both the ET and JA pathway, making plants more vulnerable to insect damage.

concentration fluctuates terpenoids responses with no clear pattern among plant species (Lindroth, 2012). This unpredictability of plant responses under elevated CO₂ environment is similar among many kinds of secondary metabolites.

Besides to direct defences to deter herbivores, plants produce volatile organic compounds liberated to the neighbouring environment to affect indirect defences against insects (Karban, 2008). These complexes of volatile compounds comprised terpenoids, lipids and methyl-jasmonates defence hormones, which are normally liberated from plants damaged by insect herbivores (Karban, 2008; Howe & Jander, 2008). These volatiles have collective ecological effects that can induce chemical defences in adjacent plants (Karban *et al.*, 2010), or beckoning local predators of the insect herbivore feeding on the plant (Heil, 2008). Currently, although some data are available with respect to the effects of elevated CO₂ atmospheres on production of biogenic volatile organic compounds (BVOs) (Vuorinen *et al.*, 2004a, 2004b; Klaiber *et al.*, 2013), to comprehend biological influences of changes in CO₂ concentration on BVO emissions, more information is necessary.

Reducing uncertainty of chemical defence responses to herbivory

Herbivore damage generates specific signals through complex networks that produce chemical and biological adjustments within the plant, which can be influenced or regulated by changes in environmental CO₂ concentrations (Fig. 2). However, more studies are necessary to understand the mechanisms implicit in the effects of elevated CO₂ on plant interactions with insect herbivores. A pioneer study demonstrated the participation of phytohormones in down-regulation of plant chemical defences against herbivores in a regular soybean crop grown in an environment with high CO₂ levels (Zavala *et al.*, 2008). In the last years, explanations of the mechanisms of the effects of elevated CO₂ in plant–insect interactions have been reviewed (Zavala *et al.*, 2013; DeLucia *et al.*, 2012). What is more, recent molecular and biochemical advances have indicated the contribution of the defensive hormones JA, ethylene (ET) and SA (Fig. 3).

Herbivores disrupt plant tissues and insect oral secretions (OS) get in contact with presumed receptors that transfer the signal and induce the production of chemical defences. The fatty acid-amino acid conjugate Volicitin

[N-(17-hydroxylinolenoyl)-L-glutamine] is one of the most studied active compounds in OS, and was first identified and obtained from *Spodoptera exigua* (Alborn *et al.*, 1997). OS function as insect-derived elicitors and induce the synthesis of the defence hormone JA (Wasternack, 2013; Kallenbach *et al.*, 2010) and up-regulated many genes related with defences (Kandath *et al.*, 2007; Wu *et al.*, 2007).

Lipoxygenase (LOX) is the main regulation enzyme for the JA synthesis, the most important phytohormone related to plant defences against herbivores, and may be partially controlled by atmospheric CO₂ (e.g. Zavala *et al.*, 2008; Sun *et al.*, 2010, 2013; Casteel *et al.*, 2012). Field-grown soybean (*Glycine max*) under elevated CO₂ conditions showed that constitutive levels and elicitation of mRNA related with JA signalling by Japanese beetles (*P. japonica*) herbivory were down-regulated (Casteel *et al.*, 2008; Zavala *et al.*, 2008). Likewise, atmosphere with high CO₂ levels decreased the JA signalling pathway and synthesis in the wild-type of tomato and *Arabidopsis*, and also in an *Arabidopsis* genotype with high levels of JA (Sun *et al.*, 2011, 2013). Moreover, elevated CO₂ atmosphere not only reduced JA accumulation, but also emission of ET in different species of plant (Zavala *et al.*, 2008, 2009; Sun *et al.*, 2011, 2013).

Low ET levels allow the negative interaction between SA and JA, which is regulated by the protein NPR1 (NON-EXPRESSOR OF PATHOGENESIS-RELATED GENES1) (Giacometti *et al.*, 2016; DeLucia *et al.*, 2012) (Fig. 2). While elicitation of JA signalling may limit induction of SA-related defences (Brooks *et al.*, 2005; Uppalapati *et al.*, 2007), high levels of SA in plant tissue reduce JA-regulated defences (Felton & Korth, 2000; Spoel *et al.*, 2007). Elevated CO₂ environment reduced ET emission and caused antagonistic interaction between JA and SA, and this effect has been reported in diverse species, inducing the allocation of resources to SA- over JA-dependent defences (Sun *et al.*, 2011, 2013; Huang *et al.*, 2012; Guo *et al.*, 2014).

The mechanism of the mediation of elevated CO₂ concentration on the signalling pathways implicated in plant responses to insect attack and the JA/ET and SA biosynthesis still need to be revealed. However, the modifications produced in the accumulation of hormones in plant tissue by environments with high concentrations of CO₂ are reflected in the induction of genes that affect the quality of foliage as food for herbivores.

Consequences of hormonal regulation on chemical defences

Studies about the effects of high CO₂ concentration levels on chemical defences and their consequences on insect

growth and development are controversial. While it has been suggested that atmosphere with high CO₂ levels increases chemical defences against insects (e.g. Lindroth *et al.*, 1993; Holton *et al.*, 2003), other reports have shown that plants grown in an environment with high CO₂ levels are defenceless and preferred by herbivores (e.g. Zavala *et al.*, 2008, 2009; Hamilton *et al.*, 2005). Generally, traditional studies of the effects of elevated CO₂ atmosphere on plant defences against herbivore attack report only the effects on insect performance and some general information about chemical changes on plant tissue. Understanding chemical and biochemical responses of injured plants is the first step to establish the adaptive function of defences against herbivores (Karban & Baldwin, 1997) that are inhibited by atmosphere with high CO₂ levels.

Carbon-based defences are controlled by phytohormones affected by high CO₂ levels. Atmospheres with high CO₂ levels increased the C:N ratio of tissue by increasing flavonoids concentration, such as quercetin, kaempferol and fisetin, all three compounds regulated by SA, however, diminished the production of other carbon-based and JA-regulated phenolic compounds, such as genistein, another isoflavonoid and significant chemical defence against herbivores (Piubelli *et al.*, 2005; O'Neill *et al.*, 2010; Ghasemzadeh *et al.*, 2010; Figs 1 and 2). Plant hormones can discriminate within the shikimic acid pathway and synthesise both isoflavonoid and flavonol compounds differentially (Ferrer *et al.*, 2008). Though *N. attenuata* unable to synthesise JA did not produce phenolic conjugates after insect attack, flavonoids like rutin and chlorogenic acid were found in plant tissue (Demkura *et al.*, 2010; Hoffman-Campo *et al.*, 2001). Moreover, high CO₂ levels declined the accumulation of the triterpenoid cardenolides regulated by JA and normally produced by Milkweeds (*Asclepias syriaca*), an effective carbon-based defence against insect attack (Rasmann *et al.*, 2009; Vannette & Hunter, 2011).

Phytohormones also regulate nitrogen-based defences and can modify the ratio of C:N of plants (Figs 1 and 2). One of the first defences identified in plants against insects are protease inhibitors (PI), and these peptides are controlled by both JA and ET (Ryan, 1990). Leaf defences have co-evolved in significant ways with the digestive systems of insects (Farmer, 2014), like PIs that decrease the capacity of herbivores to digest proteins and thus amino acid assimilation (Birk, 2003; Zavala *et al.*, 2004). Elevated CO₂ increased the vulnerability of soybean to insects herbivores by decreasing activity and the accumulation of transcripts of cysteine proteinase inhibitors (CystPIs), these peptides have an important defensive function against Coleopteran insects (Zavala *et al.*, 2008, 2009; Sun *et al.*, 2011, 2013; Guo *et al.*, 2014). Elevated CO₂ concentrations

in the environment modulated the levels of glucosinolates by modifying the JA and SA defensive pathways. The defensive role of the glucosinolate–myrosinase combination is a consequence of liberating the toxic isothiocyanates when glucosinolates are hydrolysed by myrosinases on damaged tissue (Burrow *et al.*, 2007). Since glucosinolates are originated from amino acids, they are grouped into aliphatic- (methionine), aromatic- (phenylalanine) and indole-glucosinolates (tyrosine or tryptophan) (Halkier & Du, 1997). Broccoli (*Brassica oleracea*) and *Arabidopsis* cultivated under elevated atmospheric CO₂ conditions showed higher SA-regulated constitutive glucosinolates, such as aliphatic glucosinolates, methylsulfinylalkyl-glucosinolates glucoraphanin and glucoiberin (Schonhof *et al.*, 2007; Bidart-Bouzat *et al.*, 2005; Doughty *et al.*, 1991). In contrast, glucosinolates modulated by JA, like indole-glucosinolates declined in plants cultivated under environment with high CO₂ levels (Schonhof *et al.*, 2007; Brader *et al.*, 2001).

Likewise, emissions of BVOCs in plants are hormonal regulated. For example, cabbage (*Brassica oleracea*) grown under high CO₂ environment showed low emission levels of JA-regulated terpene volatiles (Vuorinen *et al.*, 2004a, 2004b). Terpene production was decreased in plants of *Brassica* after exposure to atmospheres with high CO₂ levels, reducing establishment of aphids (*Brevicoryne brassicae*) on plants and attraction of predators (Vuorinen *et al.*, 2004a; Klaiber *et al.*, 2013). In contrast, while high CO₂ levels induced the up-regulation of green leaf volatiles after insect damage (Vuorinen *et al.*, 2004b), as recently suggested JA is not involved in the regulation of these compounds (Halitschke & Baldwin, 2003; Allmann *et al.*, 2010). Considering the dissimilar responses of plants grown in atmosphere with high or ambient CO₂ levels to herbivory, and the variability of defensive compounds regulated idiosyncratically by hormones this study provides new vision into the mechanisms of how elevated CO₂ modulates plant defences to herbivory. In addition, the evidence presented here demonstrated that changes in chemical defences in plants grown under elevated CO₂ environment are hormonal regulated and reject the C:N hypothesis.

Modern agriculture in atmosphere with high CO₂ levels

It has been suggested that in the future crops may grow in an environment with twofold CO₂ concentration levels of those found nowadays (Prather *et al.*, 2001). Anthropogenic CO₂ emissions not only generate climate change, but also increase carbon assimilation and growth in important C3 crops, such as wheat and soybean and also the ratio of the rate of carbon assimilation to the rate

of transpiration in both types of crops, C3 and C4 (such as maize and millet) (Ainsworth & Long, 2005). Although it has been suggested the possibility of increasing agricultural production under elevated CO₂ environment, other changes than the fertilisation effects, such as higher insect pest attack levels may affect future crop yields (Long *et al.*, 2006; Müller, 2013). The indications that factors of climate change, such as elevated CO₂ will affect the secondary metabolites of crop plants and plant natural defences against insects pests (DaMatta *et al.*, 2010; Taub *et al.*, 2008; Zavala *et al.*, 2013), may also influence insecticide use to counterweigh the crop vulnerability to insect attack (Dermody *et al.*, 2008; Zavala *et al.*, 2008).

Plants grown in high CO₂ atmosphere are potentially more vulnerable to herbivores because the expression of JA-regulated defence traits is inhibited. Transgenic *N. attenuata* incapable to accumulate JA grown in a natural environment was more likely to be damaged by adapted insects and highly colonised by novel species, leading to even greater losses of foliage (Kessler *et al.*, 2004). Natural plant defences against insects as a way to increase crop resistance against insects has been considered to be applied in integrated pest management programmes. Overexpressing foreign genes in crops from resistant plants with inducible promoters could be an instrument to give protection against herbivory. In this scenario inducible defences might be affected and the important soybean defence CystPI will be down-regulated, making crops more susceptible to insect attack (Zavala *et al.*, 2008, 2013). Moreover, experiments performed at free-air carbon dioxide enrichment (FACE) demonstrated that the invasive Japanese beetles consuming leaves of soybean grown under elevated CO₂ lived longer and were more fecund (O'Neill *et al.*, 2008) and preferred to feed on plants grown under elevated CO₂ (Hamilton *et al.*, 2005). Thus, effects of elevated CO₂ on defence-signalling systems of host plants can be transferred to other trophic levels of agroecosystems, and exacerbate pest problems by affecting behaviour of predators.

The extent of CO₂ fertilisation effects on crop production and quality is difficult to assess and requires deeper scientific approach (Müller, 2013). Higher herbivore damage on younger leaves of cultivated soybean under environment with high CO₂ concentration found in Soy-FACE field experiments (Zavala *et al.*, 2009) may explain the compensation of the expected increases in crop yields induced by higher CO₂ levels in the atmosphere (Ainsworth & Long, 2005; Long *et al.*, 2006). However, low defended plants with high growth rate levels would increase plant tolerance to herbivory, which decrease selection pressure of crop resistant traits on insect pests (Núñez-Farfán *et al.*, 2007).

Concluding remarks

Broadly considered, plants transfer CO₂ into subsequent trophic levels. Since plants base their growth, development and chemical defences on photosynthesis, the character of interaction between phytophagous insects and C3 plants is affected by the concentration of atmospheric CO₂ (Zavala *et al.*, 2013; DeLucia *et al.*, 2012). While such observations are traditional to discussions of ecosystem management strategies (e.g. Odum, 1969), recent advances in genetic manipulation techniques allowed to explain changes in plant–insect interactions downstream from plant physiology.

New research has demonstrated that defences against insect pests damage in crops cultivated under environment with high CO₂ levels are regulated by plant hormones rather than by changes in flow of resources controlled by C:N ratio. However, evidence that anthropogenic elevation of atmospheric CO₂ concentration alters plant–insect interactions (e.g. Zavala *et al.*, 2008; DeLucia *et al.*, 2008) still leaves some questions in current knowledge of basic plant physiology and mechanisms of response to herbivore damage. How plants grown under elevated CO₂ environment allocate primary metabolites from photosynthesis to secondary metabolism would help to understand innate defences and prevent future herbivory in field crops.

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