CURRENT REVIEW

Impact of Future Elevated Carbon Dioxide on C₃ Plant Resistance to Biotic Stresses

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Before the end of the century, atmospheric carbon dioxide levels are predicted to increase to approximately 900 ppm. This will dramatically affect plant physiology and influence environmental interactions and, in particular, plant resistance to biotic stresses. This review is a broad survey of the current research on the effects of elevated CO₂ (eCO₂) on phytohormone-mediated resistance of C₃ agricultural crops and related model species to pathogens and insect herbivores. In general, while plants grown in eCO₂ often have increased constitutive and induced salicylic acid levels and suppressed induced jasmonate levels, there are exceptions that implicate other environmental factors, such as light and nitrogen fertilization in modulating these responses. Therefore, this review sets the stage for future studies to delve into understanding the mechanistic basis behind how eCO₂ will affect plant defensive phytohormone signaling pathways under future predicted environmental conditions that could threaten global food security to inform the best agricultural management practices.

Keywords: abscisic acid, aphid, beetle, biotroph, carbon dioxide, caterpillar, ethylene, jasmonates, necrotroph, pathogens, phytohormones, salicylic acid

Moderately conservative models predict tropospheric carbon dioxide levels to reach 900 to 1,100 ppm by 2100 (Arias et al. 2021); not only will this affect temperature and weather patterns but also plant physiology, with significant implications for food security. The majority of plant species conduct C₃ photosynthesis in which the first CO₂ fixation step is catalyzed by ribulose 1,5-bisphosphate carboxylase/oxygenase (rubisco). This enzyme catalyzes two reactions, a carboxylation reaction leading to two triose phosphates that can produce sugars through the Calvin-Benson-Bassham (CBB) cycle or the oxygenation reaction that generates one triose-phosphate to be used in the CBB cycle but

also produces a two carbon phosphoglycolate that must be salvaged through the photorespiration pathway. Though photorespiration was once thought of as a “wasteful” pathway because the regeneration of a triose phosphate from two molecules of phosphoglycolates requires ATP and NAD(P)H and depletes carbon skeletons from the productive CBB cycle (Ehlers et al. 2015; Timm et al. 2016), its importance to plant metabolism, linking photosynthesis with cellular redox homeostasis and other metabolic pathways, such as nitrogen and sulfur assimilation, is now well-recognized (Betti et al. 2016; Eisenhut et al. 2019). Through the cellular redox balance, photorespiration may also be linked to plant defensive phytohormone signaling in response to pathogen or herbivore attack (Kangasjärvi et al. 2012); thus, under elevated CO₂ (eCO₂), when the carboxylase activity of rubisco will be favored and photorespiration suppressed, the pressing question is will and, if so, how will plant defense responses to biotic stresses change under predicted future atmospheric CO₂ conditions?

This review summarizes current research on the effect of eCO₂ on plant resistance against pathogens and insect herbivores, focusing on C₃ agricultural crop and model plant systems. Even though, with predicted future climate change, there will be other critical abiotic issues that plants will need to contend with along with eCO₂, such as ozone, drought, salinity, and elevated temperature (Robinson et al. 2012), we have concentrated on the effect of eCO₂ on plant defense to biotic stress. eCO₂ will affect plant resistance, both plant structure and chemistry. For example, with rising CO₂ levels, we expect an adjustment in either stomatal density, conductance, or both across the leaf surface (Beerling and Chalonder 1993; Woodward and Kelly 1995); this will impact the access to the leaf for many foliar pathogens, possibly lowering infection. eCO₂ often positively affects plant growth and this has implications on the canopy and, thus, pathogen spread (Pangga et al. 2013; Pritchard et al. 1999). Also, in plants grown at eCO₂, phloem nutrients change, affecting phloem-feeding aphid performance (Kazan 2018; Ryan et al. 2015; Sun and Ge 2011). Additionally, foliar nitrogen levels are predicted to decrease, which may result in compensatory feeding from chewing herbivores (Bloom et al. 2014; Cornelissen 2011; Cotrufo et al. 1998; DeLucia et al. 2012; Zavala et al. 2013). eCO₂ levels may affect the types and levels of plant defensive compounds (specialized metabolites) and influence changes in cells or tissues that contain these compounds, such as modifying the density or distribution of trichomes, that also may affect plant-pathogen and -insect herbivore interactions (Bidart-Bouzat and Imeh-Nathaniel 2008; Fischer and Ward 2021; Kazan 2018; Ode et al. 2014). There also may be direct effects of eCO₂ on the virulence and aggressiveness of phytopathogenic organisms (Manning and Tiedemann 1995; Váry et al. 2015). These topics are covered in many excellent reviews and, thus, this review is a survey of the current literature on the effect of eCO₂ on plant resistance against pathogens and

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arthropod herbivores, with a focus on phytohormones and their signaling pathways, in C₃ crop plants and related model systems.

eCO₂: PLANT DEFENSE-RELATED PHYTOHORMONES

With remarkable sophistication, plants respond to insect herbivore and pathogen attack through the activation of phytohormone signaling pathways that interact and incorporate developmental and environmental information to ensure the appropriate allocation of resources to defense responses leading to resistance (Huot et al. 2014; Pieterse et al. 2009; Robert-Seilanianz et al. 2011). Even though we categorize responses to specific attackers by the primary phytohormone pathway they elicit, for example, resistance to necrotrophic pathogens is primarily mediated through the jasmonate/ethylene (ET) pathway, whereas biotrophic pathogen resistance is mediated through the salicylic acid (SA) pathway (Bürger and Chory 2019; Glazebrook 2005; Wang et al. 2019), we recognize that this is an oversimplification, though an appropriate starting point. At multiple signaling nodes, the SA and jasmonate/ET pathway interact (crosstalk), at times to enhance a response but more often in an antagonistic fashion to prioritize defensive responses (Ballaré 2011; Caarls et al. 2015; Shigenaga and Argueso 2016; Zhang et al. 2017). Unexpectedly, plants grown at eCO₂ often have altered constitutive and induced defense-related phytohormone levels (Supplementary Table S1), reflecting the complex and dynamic interactions between photorespiration, oxidative stress, and phytohormone signaling. In general, higher foliar constitutive SA levels are observed at eCO₂ (Supplementary Table S1) (Casteel et al. 2012b; Guo et al. 2016, 2017a; Huang et al. 2012; Li et al. 2019a and b; Martinez Henao et al. 2020; Mhamdi and Noctor 2016; Sun et al. 2013), whereas no change or lower levels are observed for jasmonates (i.e., 12-*oxo*-phytodienoic acid (OPDA), jasmonic acid [JA], and [$\pm$]-7-*iso*-jasmonoyl-L-isoleucine [JA-Ile]) or ET levels (Casteel et al. 2012a and b; Guo et al. 2012, 2017a; Hall et al. 2020; Huang et al. 2012; Johnson et al. 2020; Paudel et al. 2016; Qian et al. 2021; Sun et al. 2013; Zhang et al. 2020). However, there are exceptions. Some studies found that CO₂ levels did not affect constitutive SA levels (Casteel et al. 2012a; Gog et al. 2019; Jwa and Walling 2001; Martinez Henao et al. 2020; Mhamdi and Noctor 2016; Paudel et al. 2016; Qian et al. 2021) or even that JA levels are higher at eCO₂ (Zhang et al. 2020). These variations often reflect plant species or cultivars and ecotypes, photoperiod and light intensity, and fertilizer. Mhamdi and Noctor (2016) found that constitutive SA levels are elevated at eCO₂ in *Arabidopsis thaliana* (arabidopsis), *Phaseolus vulgaris* (bean), and *Triticum aestivum* (wheat) but not in *Hordeum vulgare* (barley). Enhanced rosette SA levels are observed in arabidopsis grown at eCO₂ and higher light intensity (Gog et al. 2019). Fertilizer also affects constitutive SA levels. Martinez Henao et al. (2020) observed higher foliar SA levels in arabidopsis fertilized with ammonium compared with nitrate, but this is only observed at ambient carbon dioxide (aCO₂). In general, foliar constitutive SA levels are often higher at eCO₂ with little effect on constitutive jasmonate levels, thus, one might expect enhanced plant resistance against viral and biotrophic pathogens.

eCO₂: PLANT RESISTANCE TO VIRAL PATHOGENS

The SA pathway is recognized as being critical for viral confinement, through the hypersensitive response as well as mediating systemic acquired resistance (Murphy et al. 2020). In plants, two pathways lead to SA biosynthesis from the phenolic shikimate, one via the amino acid phenylalanine (cytosolic pathway) and the other through isochorismate (plastid-associated pathway). In some plant species, notably arabidopsis, a divergence is present between

the virus-induced phenylalanine pathway and the bacterial-induced isochorismate pathway, whereas in other plant species, both pathways contribute to SA biosynthesis and pathogen resistance, for example in *Glycine max* (soybean) (Shine et al. 2016).

In studies on plant-viral interactions at eCO₂, in general, plants appear to be more resistant to viral infection (Fig. 1; Supplementary Table S2), experiencing either reduced viral levels compared with infected plants at aCO₂ or, in some cases (i.e., spring wheat and barley yellow dwarf virus), the increase in plant biomass at eCO₂ offsets losses due to viral infection (Fu et al. 2010; Guo et al. 2021; Trębicki et al. 2015, 2016). A number of these studies use aphids, the natural vector of some viruses, to introduce the infection; however, aphids also activate plant defensive pathways that may confound results (Malmström and Field 1997; Trębicki et al. 2015, 2017; Vandegheer et al. 2016; Vassiliadis et al. 2016).

In general, at eCO₂, plants infected with viral pathogens have increased SA with variable effects on jasmonate levels (Supplementary Table S1) (Guo et al. 2016; Huang et al. 2012; Zhang et al. 2015;). In fact, some research reports both induced SA and JA levels at eCO₂, suggesting that these two pathways may not act antagonistically in response to these viral infections at eCO₂ (Guo et al. 2016; Huang et al. 2012).

eCO₂: PLANT RESISTANCE TO BACTERIAL PATHOGENS

Many studies on understanding the underlying mechanisms of plant resistance to bacterial pathogens have focused on the arabidopsis– or tomato–*Pseudomonas syringae* pv. *tomato* DC3000 interaction. *P. syringae* enters the leaf through the stomata and rapidly multiplies to colonize the apoplast (Xin and He 2013). At this stage, the bacteria may be detected by receptors on the plant cell, injecting proteins into the cell through a type III secretion system. Recognition of general bacterial proteins (i.e., flagellin proteins) and specific pathogen effector proteins leads to plant pathogen-associated molecular pattern-triggered immunity and effector-triggered immunity responses that trigger SA-dependent resistance leading to a hypersensitive response and systemic acquired resistance (Jones and Dangl 2006). One effector produced by *P. syringae* is coronatine, a mimic of the phytohormone JA-Ile (Katsir et al. 2008). In response to recognition of a pathogen, plants often initiate jasmonate-dependent stomatal closure to limit bacterial entry (Melotto et al. 2006); *P. syringae*–produced coronatine has multiple effects on foliar guard cells, acting both to prevent jasmonate-dependent stomatal closure as well as interfering with SA levels and signaling (Gimenez-Ibanez et al. 2017).

Since SA signaling mediates plant resistance against *P. syringae* and other hemibiotrophic pathogens, it is expected that plant resistance against these pathogens will increase under future predicted eCO₂ levels (Fig. 2; Supplementary Table S3) (Noctor and Mhamdi 2017). However, whereas *Solanum lycopersicum* (tomato) appears to be more resistant to *P. syringae* pv. *tomato* attack with lower disease severity when grown at eCO₂ (Hu et al. 2021; Li et al. 2015; Zhang et al. 2015), arabidopsis shows an increased susceptibility to pathogen attack with higher pathogen levels (Zhou et al. 2017, 2019) (Fig. 2); this reflects the induced phytohormone levels and signaling pathways. In tomato grown at eCO₂ and challenged with *P. syringae* pv. *tomato*, even though levels of both SA and JA are induced, only an increase in SA-responsive gene expression is observed (Supplementary Table S1) (Zhang et al. 2015). In the *npr1* mutant that is impaired in the SA-signaling pathway, similar pathogen infection levels are observed whether plants are grown at aCO₂ or eCO₂ and the suppression of the jasmonate-responsive *PI II* gene expression is alleviated, supporting the involvement of SA $\times$ jasmonate crosstalk in tomato resistance against this pathogen at eCO₂. On the other hand, the susceptibility of arabidopsis to *P. syringae* pv.

tomato infection at eCO₂ is alleviated in the abscisic acid (ABA)-deficient *aba2-1* mutant, even though a pathogen-associated difference in foliar ABA level is not observed (Supplementary Table S1) (Zhou et al. 2017); the ABA × SA signaling antagonism to suppress plant systemic acquired resistance is well-established and may contribute to the susceptibility of arabidopsis to this pathogen at eCO₂ (Garcia-Andrade et al. 2020; Yasuda et al. 2008). These differences between arabidopsis and tomato responses to *P. syringae* pv. *tomato* at eCO₂ may reflect the photoperiod used in these experiments in which plant resistance is correlated with longer daylength or host-specific responses (Fig. 2) (Hu et al. 2021; Li et al. 2015; Mhamdi and Noctor 2016; Zhang et al. 2015; Zhou et al. 2017, 2019). *P. syringae* pv. *tomato* used in these studies was initially isolated from tomato and,

though it has become an important model to understand plant-pathogen interactions in arabidopsis, host-specific differences are recognized (Katagiri et al. 2002; Xin et al. 2018).

eCO₂: PLANT RESISTANCE TO OOMYCETE AND FUNGAL PATHOGENS

Biotrophs and hemibiotrophs.

Given the higher constitutive and induced SA levels observed in many plant species grown at eCO₂ (Supplementary Table S1) (Noctor and Mhamdi 2017), one would expect enhanced resistance to biotrophic and hemibiotrophic pathogens; this is coupled with the lower stomatal density or aperture that is also often observed in plants grown at eCO₂, which should further limit

Fig. 1. C₃ plants versus viral pathogens at elevated carbon dioxide (eCO₂). In general, C₃ plants grown at eCO₂ have higher constitutive and induced salicylic acid (SA) responses in response to viral pathogens, leading to enhanced plant resistance (Supplementary Tables S1 and S2). There were 20 constitutive phytohormone studies, four induced phytohormone studies, and 14 plant resistance studies.

Fig. 2. C₃ plants versus hemibiotrophic bacterial pathogens at elevated carbon dioxide (eCO₂). In general, C₃ plants grown at eCO₂ have higher constitutive salicylic acid (SA) levels (Supplementary Table S1). In the *Arabidopsis thaliana*–*Pseudomonas syringae* pv. *tomato* DC3000 system, plants are more susceptible to bacterial infection except in the presence of high CO₂ (3,000 ppm) and longer photoperiod (Supplementary Table S3). In contrast, tomato (*Solanum lycopersicum*), the natural host to this pathogen, is more resistant to *P. syringae* pv. *tomato* infection at eCO₂. There were 20 constitutive phytohormone studies, six plant resistance studies (three arabidopsis, three tomato). LD = long day, SD = short day.

entry of many pathogens (Beerling and Chalonder 1993; Woodward and Kelly 1995). Whether a plant is more or less susceptible to fungal and oomycete pathogens when grown at eCO₂ appears to be specific to the plant-pathogen interaction and likely reflects the complex and dynamic interactions of multiple signaling pathways in plant resistance (Figs. 3 and 4; Supplementary Table S4). In tomato grown at eCO₂, plants are more resistant to infection by the hemibiotrophic oomycete pathogen *Phytophthora parasitica* (Jwa and Walling 2001); however, a change in induced SA or ABA levels is not observed (Supplementary Table S1). There is also a hint that plant responses to biotrophic and hemibiotrophic pathogens at eCO₂ may be affected by the photoperiod, with plants being more resistant under long-day conditions (Chakraborty and Datta 2003; Gilardi et al. 2017; Gullino et al. 2020); however, there are also exceptions to this (Chakraborty et al. 2000; Gilardi et al. 2016a and b; Li et al. 2016; Pugliese et al. 2012).

Necrotrophs.

In plants grown at eCO₂, a suppression of stress-induced jasmonate biosynthesis is often observed (Martinez Henao et al. 2020; Paudel et al. 2016), therefore, plants may be more vulnerable to necrotrophic pathogens under future predicted atmospheric conditions. In the majority of studies on plant resistance to necrotrophic pathogens, this appears to be the case (Fig. 5; Supplementary Table S4). *Eruca vesicaria* (arugula) grown at eCO₂ had higher susceptibility to *Alternaria alternata* (Siciliano et al. 2017), though no difference in disease severity is noted on cauliflower or cabbage. Tomato is more susceptible to *Botrytis cinerea* infection (Hu et al. 2020; Zhang et al. 2015); this is reflected by increased pathogen-induced SA levels and lower JA levels with decreased gene expression of jasmonate-responsive transcripts at eCO₂ (Supplementary Table S1). Again, levels of pathogen infection and the suppression of the jasmonate-responsive markers *PI I* and *PI II* are alleviated in the *npr1* mutant that is impaired in SA signaling, which implicates SA × jasmonate crosstalk in the susceptibility of tomato to *B. cinerea* infection at eCO₂ (Zhang et al. 2015). In contrast, arabidopsis is more resistant to this pathogen

under conditions of extremely high eCO₂ (3,000 ppm) (Mhamdi and Noctor 2016). Rice, wheat, corn, and lettuce grown at eCO₂ are more susceptible to infections caused by pathogens in the *Fusarium* genus, such as *F. fujikuroi*, *F. graminearum*, and *F. oxysporum*, though cultivar-specific resistance is observed (Chitarra et al. 2015; Cuperlovic-Culf et al. 2019; Hay et al. 2020; Matić et al. 2021; Melloy et al. 2010; Váry et al. 2015; Vaughan et al. 2014; Vaughan et al. 2016). As well, rice and soybean grown in eCO₂ under free-air CO₂ enrichment conditions are more susceptible to *Rhizoctonia solani* and *Septoria glycines*, respectively (Eastburn et al. 2010; Kobayashi et al. 2006). These pathogens, *Fusarium* spp., *B. cinerea*, and *A. alternata*, are devastating crop pathogens recognized for severe economic damage and yield loss (Dean et al. 2012; Savary et al. 2012; Tralamazza et al. 2018).

eCO₂: PLANT RESISTANCE TO INSECT HERBIVORY

Chewing insect herbivores.

To assess the impact of eCO₂ on foliar dietary quality, both in terms of nutritional quality and constitutive defenses, insects were fed detached plant material (leaves, cotton bolls, wheat grains) (Supplementary Table S5) (Abdul Khadar et al. 2014; Chen et al. 2005, 2007; O'Neill et al. 2008; Sharma and Brar 2018; Wu et al. 2006, 2007; Xu et al. 2019; Yin et al. 2010). Nutritional indices (digestibility of the plant material, the efficiency of conversion of ingested food [ECI]) and the insect relative growth rate (RGR) are important criteria, to understand the efficiency of food usage by the insect, that reflect the ability of the herbivore to use diet for growth and development (Slansky 1985). In the majority of these studies, plants grown at eCO₂ had a negative effect on insect performance. Often there is an increase in consumption rate coupled with a decrease in ECI and insect RGR and increased mortality (Abdul Khadar et al. 2014; Chen et al. 2007; O'Neill et al. 2008; Wu et al. 2006, 2007; Xu et al. 2019; Yin et al. 2010). In plants grown at eCO₂, foliar levels of rubisco often decrease, resulting in lower protein levels, especially compared with the eCO₂-associated enhanced carbohydrate production (Cotrufo et al. 1998).

Fig. 3. C₃ plants versus biotrophic fungal and oomycete pathogens at elevated carbon dioxide (eCO₂). In general, C₃ plants grown at eCO₂ have higher constitutive salicylic acid (SA) levels (Supplementary Table S1). Plant resistance to fungal and oomycete biotrophic pathogens is highly variable but plants may be more vulnerable under predicted future CO₂ levels (Supplementary Table S4). There were 20 constitutive phytohormone studies, 12 plant resistance studies.

Since insects need to meet specific protein thresholds for development, a decrease in protein levels may result in compensatory feeding (Behmer 2009; Cornelissen 2011; DeLucia et al. 2012; Waldbauer and Friedman 1991). The decrease in insect performance may reflect the inability to easily attain sufficient dietary protein levels coupled with the increased exposure to potentially toxic plant-specialized metabolites in their diet (Bidart-Bouzat and Imeh-Nathaniel 2008; Cornelissen 2011; DeLucia et al. 2012; Ode et al. 2014).

In studies in which insects fed directly on plants grown at $e\text{CO}_2$, variability in terms of plant resistance is observed (Fig. 6; Supplementary Table S5). Many studies find that plants are more vulnerable to chewing herbivores due to compensatory

feeding. As well, in contrast with insects fed on detached plant tissues, an increase in insect performance is observed (Caulfield and Bunce 1994; Frew et al. 2017; Johnson et al. 2020; Karowe and Migliaccio 2011; Lu et al. 2018; Ryalls et al. 2013). This suggests that other factors involved with induced plant resistance to chewing herbivores are affected by $e\text{CO}_2$. Recent studies have shown that, whereas plant SA levels may be enhanced at $e\text{CO}_2$, the induced jasmonate burst, which is the primary defense resistance pathway against chewing insect herbivores such as beetles and caterpillars (Wang et al. 2019), is attenuated (Supplementary Table S1) (DeLucia et al. 2012; Martinez Henao et al. 2020; Noctor and Mhamdi 2017; Paudel et al. 2016; Zavala et al. 2013). In addition, as with some pathogens, insects

Fig. 4. C_3 plants versus hemibiotrophic fungal and oomycete pathogens at elevated carbon dioxide ($e\text{CO}_2$). In general, C_3 plants grown at $e\text{CO}_2$ have higher constitutive salicylic acid (SA) levels (Supplementary Table S1). Plant resistance to fungal and oomycete biotrophic pathogens is highly variable (Supplementary Table S4). There were 20 constitutive phytohormone studies, 11 plant resistance studies.

Fig. 5. C_3 plants versus necrotrophic fungal and oomycete pathogens at elevated carbon dioxide ($e\text{CO}_2$). In general, C_3 plants grown at $e\text{CO}_2$ have lower constitutive and weakened induced jasmonate (JA) responses (Supplementary Table S1), leading to a possible increased vulnerability of plants to necrotrophic fungal and oomycete pathogens (Supplementary Table S4). There were 19 constitutive phytohormone studies, two induced phytohormone studies, and 35 plant resistance studies.

manipulate plant defenses through activating antagonistic signaling pathways. For example, the SA $\times$ jasmonate pathways often suppress each other and may be manipulated for the advantage of the insect or pathogen (Ballaré 2011; Zhang et al. 2017). Effectors in insect oral secretions (labial saliva, mandibular saliva, regurgitant, ventral eversible gland [Acevedo et al. 2015; Basu et al. 2018]) may activate pathways to either enhance or attenuate plant defense responses. For example, regurgitant-derived fatty acid–amino acid conjugates activate pathways to induce the production and release of volatiles that attract natural enemies of the arthropod herbivore (Yoshinaga 2016). Glucose oxidase (GOX) is an effector found in the labial saliva of many pest caterpillars (Eichenseer et al. 2010). By catalyzing the oxidation of glucose to produce the signaling molecule hydrogen peroxide (H_2O_2) that leads to SA biosynthesis, caterpillars may activate the SA signaling pathway to attenuate the jasmonate-responsive pathway (Huot et al. 2014; Musser et al. 2002; Pieterse et al. 2009; Robert-Seilaniantz et al. 2011; Weech et al. 2008). In caterpillars of *Spodoptera exigua* (beet armyworm), dietary nutritional quality, both digestible carbohydrate and protein levels, affect the labial salivary gland gene expression and activity of this enzyme (Afshar et al. 2010; Babic et al. 2008; Merckx-Jacques and Bede 2005). A diet-associated labial salivary gland proteomic study suggests that a threshold level of dietary protein must be attained before this enzyme is secreted in the labial saliva (Afshar et al. 2013). Thus, as plant nutritional quality changes in response to eCO_2 , the lower foliar N content may result in compensatory feeding by insect herbivores and also affect the production and secretion of effectors that, in the case of GOX in the caterpillar labial saliva, may suppress plant defensive pathways (Afshar et al. 2010, 2013; Babic et al. 2008; Cornelissen 2011; DeLucia et al. 2012; Merckx-Jacques and Bede 2005). Therefore, to understand the effect of eCO_2 on the phytohormone signaling pathways without the confounding effects of herbivore-associated effectors, some studies have focused on plant responses to mechanical damage (Martinez Henao et al. 2020; Paudel et al. 2016). SA or ABA levels are not different in wounded arabidopsis grown at aCO_2 compared with eCO_2 (Supplementary Table S1) (Casteel et al. 2012b; Martinez Henao et al. 2020; Paudel et al. 2016); however, the nitrogen fertilization–related stimulation of the wound-induced jasmonate burst, observed at aCO_2 , is attenuated at eCO_2 (Martinez Henao et al. 2020). This suppressed jasmonate burst contributes to the enhanced vulnerability of plants to chewing herbivores, such as caterpillars and beetles, at eCO_2 (Guo et al. 2012; Johnson et al. 2020; Lu et al. 2018; Xu et al. 2019;

Zhang et al. 2020). Casteel et al. (2012a and b) also noted that SA levels are induced by beetle herbivory. Beetles are recognized to vector viruses in their saliva that may contribute to the stimulation of SA biosynthesis (Fulton et al. 1987). On the other hand, caterpillars are not believed to vector plant viruses in their saliva (Koch et al. 2020). In contrast, two studies found that plants have higher induced jasmonate levels in response to simulated caterpillar herbivory at eCO_2 (Lu et al. 2018; Zhang et al. 2020); both these studies used a tobacco system with herbivory simulated by wounding and adding *Spodoptera litura* (tobacco cutworm) caterpillar regurgitant. Though it must be noted that there is some contention regarding the amount of regurgitant that accurately represents the natural situation (Peiffer and Felton 2009).

From the leaf detachment feeding studies, plants grown at eCO_2 negatively affect insect performance and, thus, should have enhanced resistance; however, that is not necessarily the case when caterpillars feed directly on plants at eCO_2 (Supplementary Table S5). Johnson et al. (2020) have proposed, at least in the case of the caterpillars of the noctuid pest *Helicoverpa armigera* (cotton bollworm) feeding on *Medicago sativa* (alfalfa), that plant nutritional quality has little effect on caterpillar performance, but the suppression of jasmonate-related induced defenses observed in plants grown at eCO_2 plays an important role in the observed vulnerability of plants to chewing insect herbivores.

Aphids.

In contrast to chewing herbivores in which jasmonate-mediated defense is the major resistance pathway (Wang et al. 2019), activation of the SA signaling pathway leads to plant resistance against phloem feeders such as aphids (Morkunas et al. 2011; Smith and Boyko 2007). However, there is ever-increasing evidence supporting the role of jasmonate-mediated resistance in plant protection against aphids (Gao et al. 2007; Louis et al. 2012). For instance, in tomato, the SA pathway is critical for resistance against *Macrosiphon euphorbiae* (potato aphid) (Li et al. 2006), whereas in *Medicago truncatula* (barrel medic), soybean, and *Cucumis sativa* (cucumber), the jasmonate signaling pathway leads to resistance against *Acyrtosiphon kondoi* (blue-green aphid), *Aphis glycines* (soybean aphid), and *Aphis gossypii* (cotton-melon aphid), respectively (Chapman et al. 2018; Gao et al. 2007; Qi et al. 2020; Selig et al. 2016; Yates-Stewart et al. 2020). *Acyrtosiphon pisum* (pea aphid) restricted to nonhost plants also showed a strong correlation between jasmonate signaling and lower aphid performance, highlighting the role of jasmonates in aphid resistance (Sanchez-Arcos et al. 2016). In addition,

Fig. 6. C_3 plants versus chewing herbivores at elevated carbon dioxide (eCO_2). In general, C_3 plants grown at eCO_2 have weakened induced jasmonate (JA) responses to wounding or chewing herbivores (Supplementary Table S1). As a consequence, plants may be more vulnerable to chewing arthropods, such as caterpillars, beetles, and weevils (Supplementary Table S5). There were 19 constitutive phytohormone studies, 11 induced phytohormone (wounding and chewing herbivory) studies, and 15 plant resistance studies.

aphid salivary effectors or viruses vectored by aphids often elicit antagonistic phytohormone pathways (i.e., the SA pathway) to suppress the active plant defensive pathway (i.e., the jasmonate pathway) (De Vos and Jander 2009; Louis et al. 2012; Pan et al. 2021; Yates and Michel 2018). As well, host plant-aphid genotypes and factors such as aphid density, influence plant resistance (Sanchez-Arcos et al. 2016; Stewart et al. 2016). Therefore, plants with altered phytohormone pathways (i.e., mutants or gene silenced transgenic lines) coupled with exogenous treatment by phytohormones or mimics are critical to tease out these complex interactions. Particularly in the case of aphid infestation, eCO₂ will affect the phytohormones that are responsible for plant resistance and phloem nutritional quality, which greatly impacts aphid performance (Fig. 7; Supplementary Table S6) (Guo et al. 2017b; Sun et al. 2016).

In general, plants grown at eCO₂ are more susceptible to aphid infestation (Fig. 6; Supplementary Table S6). In studies with two closely related legumes, plants grown at eCO₂ are more susceptible to aphid attack; enhanced pea aphid performance and increased populations are observed on alfalfa and *M. truncatula* grown at eCO₂ (Guo et al. 2014a and b; Ryalls et al. 2015). In the *M. truncatula*–pea aphid interaction, higher SA-responsive gene expression and lower jasmonate/ET-responsive gene expression is observed in aphid-infested plants at eCO₂ (Supplementary Table S1) (Guo et al. 2014a and b; Guo et al. 2017a).

Plant resistance to *Brevicoryne brassicae* (cabbage aphid) is also correlated to jasmonate-mediated signaling; aphid infestation on arabidopsis *fou2* mutants, which have a hyperactivated jasmonate pathway, or the Cvi ecotype, which has high aphid-induced expression of genes encoding enzymes in the jasmonate biosynthesis pathway, have reduced cabbage aphid populations (Kuśnierczyk et al. 2007, 2011). In contrast, the Cvi host plant did not affect the population growth of the generalist *Myzus persicae* (green peach aphid) (Kuśnierczyk et al. 2007). When cabbage aphid or green peach aphids are reared on brassicaceous plants grown at eCO₂, in general, plants are more susceptible and aphid performance increases (Amiri-Jami et al. 2012; Bezemer et al. 1998; Fu et al. 2010; Guo et al. 2017b; Hughes and Bazzaz 2001; Stacey and Fellowes 2002; Sun et al. 2013).

In the arabidopsis–green peach aphid system, the increased vulnerability of plants grown at eCO₂ reflects the aphid-associated suppression of JA levels and JA-responsive gene expression and an increase in SA-responsive gene expression but no effect on ET release (Sun et al. 2013). However, overall, highly variable results are observed with plant-aphid interactions at eCO₂, highlighting that, in particular with these interactions, many factors are involved, such as aphid race and plant genotypes. One important element that is affected by eCO₂ is the plant phloem nutritional quality that has a profuse impact on aphid performance; therefore, particularly in the case of plant-aphid interactions, focusing on phytohormones alone may be an oversimplification.

Other arthropods.

In contrast to caterpillars, beetles, and aphids, research on the effect eCO₂ will have on plant resistance to other arthropods is scarce, making generalizations difficult (Supplementary Tables S7 and S8). For *Bemisia tabaci* (silverleaf whitefly) infestations, jasmonate-mediated signaling is critical for basal resistance (Zarate et al. 2007); in fact, infestation results in increased plant SA levels to antagonize the jasmonate-resistance pathway. For most studies with silverleaf whitefly, insect performance is not changed if the host plant is grown at eCO₂ (Cuperlovic-Culf et al. 2019; Guo et al. 2016). On eggplant grown at eCO₂, silverleaf whitefly spent more time ingesting sap and fecundity, measured as percent eggs hatched, increased (Peñalver-Cruz et al. 2012). In contrast, fecundity of *Trialeurodes vaporariorum* (greenhouse whitefly) decreased when reared on tomato grown at eCO₂. Application of the SA analog benzo[1,2,3]thiadiazole-7-carbothioic acid-S-methyl ester to tomato plants reduced greenhouse whitefly fecundity (Risal et al. 2008). Therefore, increased plant resistance against greenhouse whitefly may reflect elevated SA levels in plants at eCO₂.

Mites are arthropods that elicit a strong jasmonate response in plants as a result of feeding on epidermal or mesophyll cell contents (Blaazer et al. 2018; Kant et al. 2004). The reduced jasmonate response at eCO₂ supports the observation that the *Tetranychus urticae* (two-spotted mite) exhibits an increased rate of reproduction on white clover plants grown at eCO₂ (Heagle et al. 2002).

Fig. 7. C₃ plants versus aphids at elevated carbon dioxide (eCO₂). In general, C₃ plants grown at eCO₂ have higher constitutive or induced salicylic acid (SA) responses or both (Supplementary Table S1). Plant resistance to aphids is highly variable but plants may be more vulnerable under predicted future CO₂ levels (Supplementary Table S6). There were 20 constitutive phytohormone studies, 29 plant resistance studies.

Thrips are also cell-content feeders that elicit jasmonate-dependent signaling (Abe et al. 2008; Escobar-Bravo et al. 2017). As one would expect given the weakened jasmonate response at eCO₂, studies have found that either plants are less resistant to thrip attack or thrip performance increased (Heagle 2003; Hughes and Bazzaz 1997; Qian et al. 2021).

Given the intimate relationship between plants and leafminers, it is unsurprising that these insects manipulate plant phytohormones to minimize defense responses and maximize nutrient availability (Zhang et al. 2016). In plants grown at eCO₂, a decrease in leaf miner performance or infested leaf area is observed (Salt et al. 1995; Smith and Jones 1998). Little is known about the role of phytohormones and plant resistance in these specific systems, but, with *Liriomyza trifolii* (American serpentine leafminer fly), jasmonate signaling or application of methyl jasmonate conferred plant protection (Abe et al. 2013; Wei et al. 2021).

Plant resistance to phloem-feeding planthoppers is mediated primarily through the SA-signaling pathway (Pan et al. 2018); *Nilaparvata lugens* (brown planthoppers) manipulate plant brassinosteroid levels to decrease SA levels, resulting in decreased rice resistance to the pest. Ma et al. (2020) showed that activation of the ET pathway modulates rice jasmonate response, with low and high ET levels increasing or reducing plant resistance, respectively. Presumably, this reflects SA × jasmonate crosstalk in which high jasmonate levels will reduce SA signaling to weaken plant defense response (Broekgaarden et al. 2015; Caarls et al. 2015). Most studies have supported the idea that rice plants grown at eCO₂ are more susceptible to one or both infestation and yield loss due to brown planthoppers, *Laodelphax striatellus* (small brown planthopper), or *Sogatella furcifera* (white-backed planthopper) (Guru-Pirasanna-Pandi et al. 2018; Wan et al. 2014). In contrast, one study showed rice grown at eCO₂ is a poorer host for brown planthoppers, with the pest experiencing decreased adult female longevity and fecundity (Shi et al. 2014); this may reflect the photoperiod or the nitrogen fertilizer usage in comparison with the other studies.

CONCLUSION: THE IMPACT OF eCO₂ ON C₃ PLANT RESISTANCE TO BIOTIC STRESSES

Rising CO₂ levels will have multiple effects on C₃ crop plants that will affect their interactions with and resistance to pathogens and arthropod herbivores. For example, canopy structure, morphology, changes in nutritional quality, and specialized metabolites will all impact plant-pathogen and insect interactions (Beerling and Chalonder 1993; Bidart-Bouzat and Imeh-Nathaniel 2008; Cornelissen 2011; Cotrufo et al. 1998; DeLucia et al. 2012; Fischer and Ward 2021; Ode et al. 2014; Pangga et al. 2013; Pritchard et al. 1999; Ryan et al. 2015; Sun and Ge 2011; Woodward and Kelly 1995; Zavala et al. 2013). Phytohormone levels appear also to be altered in plants grown at eCO₂ (Fig. 8; Supplementary Table S1). Many studies have observed that, at eCO₂, plants have higher constitutive and induced SA levels, leading to a strong SA-responsive signaling pathway (Noctor and Mhamdi 2017). In contrast, an attenuation of the induced jasmonate burst is seen in plants grown at eCO₂ (DeLucia et al. 2012; Martinez Henao et al. 2020; Paudel et al. 2016). Therefore, we predict a stronger resistance against viral or (hemi)biotrophic pathogens and an increased vulnerability to necrotrophic pathogens and chewing herbivores. However, there are anomalies that indicate that phytohormone levels are affected by other environmental factors and we do not, yet, have the complete picture. For example, Bencze et al. (2017) infected the same cultivar of winter wheat (cv. Regiment) with *Fusarium culmorum* with slight changes in light or fertilizer and observed differences in pathogen resistance, showcasing the subtle, yet

important, impact of light intensity and fertilization on plant resistance at eCO₂. Light intensity affects phytohormone levels at eCO₂, often with a positive effect on SA levels (Gog et al. 2019; Lv et al. 2015). Gog et al. (2019) also found that caterpillar-induced SA levels are increased at eCO₂ under continuous but not dynamic light.

A few studies have suggested that there is a poorly defined relationship between N fertilization, atmospheric CO₂ levels, and plant resistance. Martinez Henao et al. (2020) observed a relationship between fertilization, particularly ammonium fertilization, and constitutive phytohormone levels. Higher constitutive and wound-induced SA levels are observed in plants fertilized with ammonium at aCO₂ but not eCO₂, whereas, at eCO₂, ammonium fertilization increased ABA levels. In mechanically damaged plants, the positive relationship between nitrogen fertilization rate and the level of wound-induced jasmonate phytohormones is attenuated at eCO₂. At aCO₂, a positive correlation exists between N fertilization rate and nematode density that is not seen at eCO₂ (Thakur et al. 2019). Additionally, at aCO₂, a greater population of the potato aphid is present on well-nitrogen fertilized *Solanum dulcamara* (bittersweet nightshade) plants that is not observed at eCO₂ (Sudderth et al. 2005). In contrast, a higher population of the brown planthopper is found on well-fertilized rice plants grown at eCO₂ (Liu et al. 2019). While it is likely that these observations, in part, reflect the nutritional quality of the host plant diet, one cannot discount the role of phytohormone levels leading to plant resistance pathways.

Fig. 8. Proposed model of plant phytohormone responses to biotic stresses at elevated carbon dioxide (eCO₂). C₃ plants grown at eCO₂ have lower photorespiration (PR) levels that contribute to maintaining cellular redox homeostasis, which affects phytohormone levels. In general, C₃ plants grown at eCO₂ have higher constitutive or induced salicylic acid (SA) responses, or both, and weakened induced jasmonate (JA) responses. Light (photoperiod, intensity, quality) and nitrogen appear to influence plant defense phytohormone levels. At ambient CO₂, the nitrogen (N) fertilization increase in the wound-induced jasmonate response is suppressed at eCO₂. Less is understood about the influence of light on phytohormone dynamics at eCO₂.

Future questions.

The literature survey suggests that under future predicted eCO₂ levels, we should see stronger resistance response to viral and biotrophic pathogens and a decreased resistance to necrotrophic pathogens and chewing herbivores, such as beetles and caterpillars. Though this generalization holds true in many cases, there are also anomalies that question whether we fully understand all the implications of eCO₂ on plant resistance. Many questions still need to be addressed:

- 1) What are the mechanisms underlying the elevated SA levels and suppression of induced jasmonates observed in plants grown at eCO₂? Research suggests that it is more complex than just SA × jasmonate crosstalk and that N assimilation and light (photoperiod, intensity, quality) play critical roles.
- 2) Changing environmental conditions involve environmental CO₂ levels as well as climate change, such as increased ozone, salinity, drought, and temperatures. These factors must be built into our understanding of plant-pathogen and herbivore resistance under future conditions.
- 3) This review focused on direct interactions between pathogens and pests and plant resistance. However, eCO₂ will affect tritrophic interactions. For example, with organisms in the rhizosphere, endophytes, and beneficial insects, to name a few.
- 4) As well, more studies of the direct effect of CO₂ on pathogens and insects, such as Melloy et al. (2010), Váry et al. (2015), Liu et al. (2017), and Vailla et al. (2019), are needed.
- 5) eCO₂ also affects pathogen and herbivore resistance in C₄ plants (Supplementary Table S9). Again, a deeper understanding of one or more underlying mechanisms is needed.

Given that atmospheric CO₂ levels are predicted to reach 700 ppm in the next 80 years (Meehl et al. 2007), it is critical that we understand how this will impact plant resistance for sustainable agricultural management practices. These are just some of the pressing concerns that must be addressed to ensure sustainable agriculture and future food security.

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