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REVIEW

## **Insect–plant–pathogen interactions as shaped by future climate: effects on biology, distribution and implications for agriculture**

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**Abstract** Carbon dioxide (CO<sub>2</sub>) is the main anthropogenic gas which has drastically increased since the industrial revolution, and current concentrations are projected to double by the end of this century. As a consequence, elevated CO<sub>2</sub> is expected to alter the earth's climate, increase global temperatures and change weather patterns. This is likely to have both direct and indirect impacts on plants, insect pests, plant pathogens and their distribution, and is therefore problematic for the security of future food production. This review summarises the latest findings and highlights current knowledge gaps regarding the influence of climate change on insect, plant and pathogen interactions with an emphasis on agriculture and food production. Direct effects of climate change, including increased CO<sub>2</sub> concentration, temperature, patterns of rainfall and severe weather events that impact insects (namely vectors of plant pathogens) are discussed. Elevated CO<sub>2</sub> and temperature, together with plant pathogen infection, can considerably change plant biochemistry and therefore plant defence responses. This can have substantial consequences on insect fecundity, feeding rates, survival, population size, and dispersal. Generally, changes in host plant quality due to elevated CO<sub>2</sub> (e.g., carbon to nitrogen ratios in C3 plants) negatively affect insect pests. However, compensatory feeding, increased population size and distribution have also been reported for some agricultural insect pests. This underlines the importance of additional research on more targeted, individual insect–plant scenarios at specific locations to fully understand the impact of a changing climate on insect–plant–pathogen interactions.

**Key words** carbon dioxide; climate change; CO<sub>2</sub>; food security; pests; trophic interactions

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## Introduction

Carbon dioxide (CO<sub>2</sub>) concentrations have now surpassed 400 μmol/mol, with the industrial revolution acknowledged as the triggering point before when its concentration was at around 280 μmol/mol (IPCC, 2013). Carbon dioxide is an important gas, affecting global temperatures, weather patterns and directly altering many biological functions, particularly plant photosynthesis (Kimball, 2016). Therefore, changes in CO<sub>2</sub> concentrations will have significant impacts on all living organisms, including interactions between insects, plants and pathogenic microorganisms. Insects and pathogens transmitted by insects, despite the latest control strategies, can considerably reduce the yield and quality of all food crops (Chakraborty & Newton, 2011), posing great risks for future food security (Griffiths *et al.*, 2010; Luck *et al.*, 2010, 2011; Garrett *et al.*, 2006; Trebicki, 2016). The demand for food is expected to double by 2050 and likewise, CO<sub>2</sub> concentrations are predicted to continue to increase (Tilman *et al.*, 2011; Alexandratos & Bruinsma, 2012). Therefore, understanding the impacts of global climate change on insect, plant and pathogen interactions is imperative in order to sustain or increase future food production. Despite this, relatively few studies have examined the importance of climate change and its effect on the combined persistence of insects, microorganisms (viruses, bacteria and fungi) and plants. However, general conclusions can be made on the effects of either temperature or CO<sub>2</sub> concentrations on particular groups of insects, plants and to a lesser extent, pathogens.

The geographic distribution of plants, including food crops, are expected to shift as certain areas will become unsuitable for food production due to reduced rainfall and increased temperature under future climates. In addition, indirect changes to host plant biochemistry (facilitated by aspects of climate change) are likely to have a greater impact on insect herbivores and pathogens compared to the direct effects of CO<sub>2</sub> or temperature (Coviella &

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Trumble, 1999; Ben-Yakir & Fereres, 2016). Increased CO<sub>2</sub> levels are generally beneficial for C<sub>3</sub> plants, increasing biomass, yield and enhancing water use efficiency due to increased stomata closure and rates of photosynthesis (Conroy *et al.*, 1994; Aben *et al.*, 1999; Seneweera *et al.*, 2002; Ainsworth & Long, 2005; Fitzgerald *et al.*, 2010; Fitzgerald *et al.*, 2016). Additionally, eCO<sub>2</sub> (elevated CO<sub>2</sub>) has been documented to increase plant canopy temperatures, alter plant carbon (C) and nitrogen (N) ratios (C : N), and decrease grain protein content, nutritional value and baking quality (Myers *et al.*, 2014; Panozzo *et al.*, 2014; Fernando *et al.*, 2015; Kimball, 2016; Trębicki *et al.*, 2016). Conversely, increased temperatures can reduce or reverse the positive effects of eCO<sub>2</sub>, especially in agricultural regions where currently food production is proven to be extremely challenging (Wheeler *et al.*, 1996; Gibson & Paulsen, 1999; Nuttall *et al.*, 2012). The persistence and distribution of insects and pathogens will be further affected by changes in summer and winter temperatures, severity of drought, rain, humidity as well as cyclones and hurricanes (Cannon, 1998; Chakraborty *et al.*, 2000; Rosenzweig *et al.*, 2001; Jones, 2016). It is very likely that abiotic factors including temperature, CO<sub>2</sub> and rainfall will differentially affect insects, plants and pathogens under future climates. It is also reasonable to predict that the interactions between them may be altered, as was observed for aphids and virus in wheat (Trębicki *et al.*, 2016), leading to changes in the severity of both insects and pathogens on the host plant. Other pathogens (such as fungi), which are not necessarily transmitted by insects, but rather co-infect the host together with the insects, can also significantly impact the plant and/or the insect itself, however, these effects are not well understood. Furthermore, biocontrol agents, particularly predators and parasitoids, will also be altered by climate change, as will their interactions with their insect hosts. As an example, the combined effects of increased temperature and drought had a detrimental effect on the aphid parasitoid *Diaeretiella rapae* which resulted in a less efficient control of aphids (Romo & Tylianakis, 2013).

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This review aims to consolidate the current research regarding how climate change, specifically elevated CO<sub>2</sub> and temperature, may influence individual insect, plant and pathogens interactions with an emphasis on agricultural food production, thereby identifying important research gaps.

### **Insect vectors and plant pathogens**

Currently, it is well understood that insect pests and plant diseases can substantially reduce crop yield and quality, and increase input costs. Sap-sucking insects can inflict direct damage to plants and are also important vectors of many plant viruses, which further complicates control practices (Hull, 2013). There can be a very close relationship between insects and the plant viruses they transmit. Insects and viruses can modify plants to their advantage, by increasing host suitability by increasing vector populations and by reducing plant resistance. Plant viruses can also increase the attractiveness of host plants for their insect vectors by changing the plants' volatile profile and therefore increasing the probability of virus acquisition and subsequent spread (Eigenbrode *et al.*, 2002; Bosque-Pérez & Eigenbrode, 2011; Ingwell *et al.*, 2012; Fereres *et al.*, 2016). As a result of virus presence, aphid behaviour can also be changed; virus-free aphids have been shown to prefer virus-infected hosts, but viruliferous aphids preferred non-infected hosts (Ingwell *et al.*, 2012). Since eCO<sub>2</sub> can significantly alter plant biochemistry, further changes in insect-plant interactions are expected. This, for example, may include exacerbating insect/pathogen severity, favouring one over the other (insect or pathogen), or altering plant defences. Understanding how plants, insects or pathogens alone will respond to future climates will only partially provide

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appropriate information for future food security. Although there is limited information regarding the impacts of climate change (e.g. temperature and CO<sub>2</sub>) on vectors of important plant virus (Table 1), only extensive studies focused on bipartite or tripartite interactions will effectively increase our knowledge so that future food production can be maintained.

Based on the knowledge from plant systems and their responses to climate change, current research is quickly expanding into more complex systems including higher trophic levels. Current technologies such as controlled environment growth chambers, CO<sub>2</sub> tunnels, open top chambers, and more advanced systems like Free Air Carbon Enrichment (FACE) facilities (Kimball, 2016), are being used to understand insect, plant and pathogen interactions, with some studies showing both general and specific trends for particular insect, plant and pathogen combinations (Jones, 2016; Trębicki *et al.*, 2016; Trębicki *et al.*, 2017).

### **Direct effects of climate change**

The plant epidemic triangle illustrates the interactions between the environment, plant hosts and pathogens. Climate change can influence the environment from micro to macro scales (Jones, 2016), thereby altering the disease triangle in different ways (Fig. 1). These changes can either facilitate or reduce insect outbreaks, which are often specific to a particular insect exposed to a particular host. Increases in insect numbers, particularly vectors of plant pathogens, would likely increase the spread of viruses or bacteria that they transmit (Trębicki *et al.*, 2010, 2016; Jones, 2016). Predicting the direct effect of differential climate change scenarios on insect pests and plant diseases is complex. This is because the insect herbivores and their host plants are exposed to the same environmental conditions, yet they can respond to these changes differently. For example, changes in CO<sub>2</sub> concentration from ambient (400

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$\mu\text{mol/mol}$ ) to elevated ( $650 \mu\text{mol/mol}$ ) levels will not likely have a significant direct effect on insect herbivores (Coviella & Trumble, 1999), but it will have an indirect effect through changes to plant biochemistry. Hence, insect populations and pathogen spread can be impacted (Dáder *et al.*, 2016; Trębicki *et al.*, 2016) as relatively small changes to diet composition can significantly affect the insect (Trębicki *et al.*, 2009). In many cases, it is difficult to assess the impacts of climate change on insect herbivores and pathogens, when changes in plant biochemistry mediated by either temperature or  $\text{CO}_2$  overshadow the direct effects. However, use of artificial diet, or providing insects with fresh plants from those grown under ambient  $\text{CO}_2$  ( $\text{aCO}_2$ ) can be used to understand the direct effects of  $\text{eCO}_2$ .

Increased temperatures associated with future climate have been shown to directly affect chewing herbivores. As an example, *Pieris napi* L. larval developmental traits were affected by temperature, and larval time, pupal time and pupal mass were higher at lower temperatures, which resulted from increased leaf consumption at  $17^\circ\text{C}$  versus  $25^\circ\text{C}$  (Bauerfeind & Fischer, 2013a). Low temperature also caused higher adult stress resistance to desiccation and starvation in *P. napi*, *Spodoptera exigua* Hübner and the woodland butterfly *Bicyclus anynana* Butler (Pijpe *et al.*, 2007; Lee & Roh, 2010; Bauerfeind & Fischer, 2013b). The literature shows a variety of altered responses for sap-sucking insects to different aspects of climate change, but overall, aphid responses to temperature changes alone can be somewhat comparable. Aphids react strongly to small changes in temperatures due to their short generation times and great capacity for reproduction (Jones & Barbetti, 2012). Abundance of the green peach aphid, *Myzus persicae* Sulzer increased and its developmental time was reduced with increased temperature (Bezemer & Jones, 1998; Himanen *et al.*, 2008). Adult and progeny weights decreased for *Macrosiphum euphorbiae* Thomas and *M. persicae* at  $26^\circ\text{C}$  and  $24^\circ\text{C}$ , respectively, versus  $20^\circ\text{C}$  (Flynn *et al.*, 2006; Himanen *et al.*,

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2008). The lettuce aphid, *Nasonovia ribisnigri* had a much shorter developmental time at high temperatures but also a much higher mortality than at lower temperatures (Diaz & Fereres, 2005). Authors concluded that the lettuce aphid is better adapted to survive and reproduce at low (8°C) than at high (28°C) temperatures, and its best performance occurred within the 20–24°C range. The corn aphid *Rhopalosiphum maidis* Fitch had the highest intrinsic rate of increase under higher temperature (26°C) and increased CO<sub>2</sub> (750 μmol/mol) (Xie *et al.*, 2014).

In the context of global climate change, a small increase in temperature during winter can alter aphid peak densities and more importantly, cause aphid flights to occur earlier in the season, increasing the chance of virus pathogen outbreaks and altering the timing of outbreaks relative to crop development stage. Temperature increase will also favour the proportion of alate morphs over apterous morphs (Diaz & Fereres, 2005), which may expand virus disease epidemics over long distances. Higher temperature and CO<sub>2</sub> increased *R. maidis* alate production, which may enhance aphid migration and dispersal with subsequent spread of plant viruses (Xie *et al.*, 2014). These results indicate that the combined effects of both elevated temperature and CO<sub>2</sub> level on aphid biology may facilitate greater virus spread and exacerbate crop damage.

Whiteflies, especially *Bemisia tabaci* Gennadius, are serious pests and vectors of many plant pathogens, decreasing the yield and quality of fruit and plants, or killing the host altogether. Overall, it has been demonstrated that 28°C was most favourable for *B. tabaci* fitness; however reproduction parameters such as oviposition and nymphal survival were optimal between 28°C and 33°C, with net reproductive success declining at 33°C (Curnutte *et al.*, 2014). Therefore, rising temperatures would also increase the risk of epidemics of viral pathogens transmitted by whiteflies. Whiteflies have shown unchanged life history under

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eCO<sub>2</sub> (Curnutte *et al.*, 2014). However, the presence of *Tomato yellow leaf curl virus* (TYLCV) increased developmental rate and susceptibility to thermal stress in *B. tabaci* (Q biotype) (Pusag *et al.*, 2012).

The severity of virus infection can also be significantly altered by increased temperature. *Barley/Cereal yellow dwarf virus* (B/CYDV), a phloem restricted pathogen of cereals worldwide, is exclusively transmitted by aphids and can result in significant losses ranging from 9%–79% (Sward & Lister, 1987; McKirdy *et al.*, 2002). Incidence of B/CYDV depends on viruliferous aphid numbers and dispersal, which can be affected directly by temperature and wind. Additionally, timing of infection and virus titer can also influence the severity of this pathogen with early infection, significantly reducing yield and increasing virus titer and therefore the chance of disease spread. For example, future elevated temperatures predicted for grain growing regions of Australia were simulated in growth chamber experiments with results showing increased and earlier peak of virus titer associated with elevated temperature (Nancarrow *et al.*, 2014). In this case, the increased virus titer observed under higher temperature can further escalate disease progression resulting in greater yield losses, but above all, it can increase aphid prevalence and cause greater virus spread.

### **Indirect effects of climate change mediated through changes to plant hosts**

Plants encounter a variety of abiotic factors, such as extreme temperatures, CO<sub>2</sub> or drought, and biotic factors including insect herbivory and infection by viral, bacterial or fungal pathogens. These stresses can substantially alter the microclimate by influencing plant growth, water use and transpiration, and by modifying plant biochemistry to favour insects. Additionally, infection with a pathogen can modify host appearance and physiology, making

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it more attractive to vectors (Mauck *et al.*, 2010; Bosque-Pérez & Eigenbrode, 2011; Ingwell *et al.*, 2012; Fereres *et al.*, 2016).

Increasing CO<sub>2</sub> is not only the main driver for global climate change through trapping heat, it also plays an important role in plant growth and metabolism as it is the substrate for photosynthesis (Ziska, 2008). The main reported effects on plants include increased biomass and canopy size, earlier canopy development, higher photosynthetic rates and reduced stomatal conductance (Ainsworth & Long, 2005; Ainsworth & Rogers, 2007; Kimball, 2016). At the same time, eCO<sub>2</sub> causes chemical changes such as the accumulation of non-structural carbohydrates (Ainsworth *et al.*, 2008; Gao *et al.*, 2008; Johnson & Riegler, 2013; Ryan *et al.*, 2014a) and a decrease in plant N concentration and grain protein content (Taub & Wang, 2008; Ryan *et al.*, 2014b; Dáder *et al.*, 2016; Trębicki *et al.*, 2016). The reduction in stomatal conductance also leads to a decrease in micronutrients due to improved water uptake efficiency from the soil (Taub & Wang, 2008). Insects and pathogens depend on plant water and nutritional status for sustenance and habitat. Therefore, changes in host nutritional quality and resistance are likely to indirectly impact the performance and feeding behaviour of insect pests, the interactions between insects and pathogens (Hughes & Bazzaz, 2001; Himanen *et al.*, 2008; Sun *et al.*, 2009a; Oehme *et al.*, 2013; Stiling *et al.*, 2013), and also the incidence and severity of plant pathogens (Malmstrom & Field, 1997; Luck *et al.*, 2011; Jones & Barbetti, 2012; Trębicki *et al.*, 2015).

Among the sap-feeding insects, aphids have responded either positively or negatively to CO<sub>2</sub>-induced changes in plants without the presence of a pathogen (Coviella & Trumble, 1999; Newman *et al.*, 2003). Although, overall trends among insects reared on plants exposed to eCO<sub>2</sub> show either a negative effect on population growth or increased feeding rates to

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compensate for lower N content. Plant defoliator insects (such as some lepidopterans and coleopterans) can engage in compensatory feeding of low-quality food to meet critical nutrient requirements, which may induce greater herbivore damage to both managed and natural ecosystems as CO<sub>2</sub> continues to increase (Cornelissen, 2011).

Aphids are one of the few examples where eCO<sub>2</sub> can increase population abundance, but this is often species and host specific (Robinson *et al.*, 2012). For example, eCO<sub>2</sub> increased the abundance of *Aphis gossypii* Glover, on *Gossypium hirsutum* L., *Sitobion avenae* Fabricius on *Triticum aestivum* L. and *Acyrtosiphon pisum* Harris on *Medicago truncatula* Gaertn while *M. persicae* on *Solanum dulcamara* L. and *Arabidopsis thaliana* L. and *Rhopalosiphum maidis* on *Hordeum vulgare* L. (Chen *et al.*, 2004; Chen *et al.*, 2005; Sun *et al.*, 2013; Guo *et al.*, 2014b; Xie *et al.*, 2014). Elevated CO<sub>2</sub> also increased *R. padi* weight and growth rates on wheat (Sun *et al.*, 2009a; Oehme *et al.*, 2012; Oehme *et al.*, 2013). On the contrary, a negative response was found in *A. pisum* abundance on *Vicia faba* L. and *R. padi* on *Schedonorus arundinaceus* Schreb (Hughes & Bazzaz, 2001; Ryan *et al.*, 2014b) and wheat (Trębicki *et al.*, 2016). Results suggested that eCO<sub>2</sub> was also detrimental for *M. persicae* overall fitness and adult weight on brassicaceae and *A. gossypii* on *Capsicum annuum* L. ( Stacey & Fellowes, 2002; Himanen *et al.*, 2008; Oehme *et al.*, 2012; Oehme *et al.*, 2013; Dáder *et al.*, 2016). *Brevicoryne brassicae* L. colonised *Brassica oleraceae* var. *gemmifera* L. at a lower extent after long-term exposure to increasing CO<sub>2</sub> (Klaiber *et al.*, 2013). Several aphid species, such as *M. euphorbiae* and *Aulacorthum solani* Kaltenbach, have shown a neutral response (Hughes & Bazzaz, 2001; Flynn *et al.*, 2006 ). In addition, aphid responses seem to be host and even genotype-specific, and can be linked to quantitative and qualitative changes in foliar amino acids (Johnson *et al.*, 2014). Using the examples mentioned above, a similar species-specificity (including population size and feeding rates)

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was applied to other hemipteran insects such as planthoppers *Nilaparvata lugens* Stål, *Laodelphax striatellus* Fallen and *Sogatella furcifera* Horváth, which showed different abundance responses when raised on rice (*Oryza sativa*) under eCO<sub>2</sub> conditions (Wan *et al.*, 2014).

The feeding behavior of insect vectors, particularly aphids, has been monitored under rising CO<sub>2</sub> by the electrical penetration graph (EPG) technique (Dáder *et al.*, 2016; Trębicki *et al.*, 2016), which provides a live real time visualization of plant penetration by insect mouthparts (Tjallingii, 1978; Trębicki *et al.*, 2012). Decreased salivation into sieve elements, increased phloem sap ingestion and shorter non-pathway phase are among the responses observed for the aphid *A. pisum* on *M. truncatula* and *M. persicae* on *C. annuum* (Guo *et al.*, 2013; Dáder *et al.*, 2016). On non-infected wheat plants, *R. padi* phloem feeding significantly increased by 34% when the plants were grown under eCO<sub>2</sub>, but when infected with *Barley yellow dwarf virus* (BYDV, *Luteovirus*), no significant changes to feeding were observed as a result of increased CO<sub>2</sub> (Trębicki *et al.*, 2016).

Feeding of late-instar *Operophtera brumata* L. larvae increased on leaves of *Betula pendula* Roth under eCO<sub>2</sub> because of inadequate host nutrition (Lavola *et al.*, 1998). As a result of inferior host plant quality, herbivores were forced to consume more plant material to obtain necessary levels of nitrogen. Additionally, it has been demonstrated that the soil-dwelling insect *Xylotrupes gideon* L. has the potential to arrest the effects of eCO<sub>2</sub> on eucalypt physiology (Johnson & Riegler, 2013). Root damage caused by these insects impaired water uptake, which reduced photosynthesis activity and limited eucalyptus capacity for biomass accumulation under increasing CO<sub>2</sub>.

The plant stress hypothesis predicts that environmental stresses on plants decrease host resistance to pests or pathogens by altering biochemical relationships and foliar chemistry

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(Bauerfeind & Fischer, 2013b). Effects on host plant quality are expected to be more pronounced when temperatures are high, due to less efficient growth and reduced time for compensatory feeding. Furthermore, prolonged drought limits vector populations, causing a potential decrease in pathogen spread and economic losses. However, higher temperatures usually increase plant susceptibility to virus inoculation and the rate of virus multiplication within the host plant, which causes an earlier appearance of disease symptoms (Kassanis, 1952; Matthews, 1991). Other responses include alteration of secondary pathways and defense signaling routes. As mean global temperatures increase, viruses adapted to warm regions are likely to expand alongside with vectors. Additionally, vectors can be further affected by climate change as it can lead to heavy rainfall events that could wash insects off foliage or effect their establishment. Epidemics of viruses transmitted by fungi or nematodes in the soil are also predicted to change in response to altered rainfall patterns, potentially increasing in temperate regions, but decreasing in sub-tropical regions (Jones & Barbeti, 2012).

There is a limited body of literature on the indirect consequences of rising CO<sub>2</sub> on viral dynamics but the main assumption is that the larger amount of biomass (resulting from CO<sub>2</sub> fertilisation) could constitute an increased reservoir of infected tissue leading to a higher risk of virus transmission by insect vectors (Malmstrom & Field, 1997). Additionally, symptomatology of viruses can also be enhanced earlier or be more pronounced, expressed by increased virus titre and symptoms, making infected hosts more attractive to vectors (Trębicki *et al.*, 2015; Vassiliadis *et al.*, 2016). In this sense, BYDV incidence has been predicted to be greater in wheat (Trębicki *et al.*, 2015), which was recently show to increase by over 10% under eCO<sub>2</sub> under outdoor, FACE conditions (Trębicki *et al.*, 2017). On the other hand, a deviation of plant defences from viruses towards pests appears to take place (Fu

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*et al.*, 2010), causing resistance against infection with *Tobacco mosaic virus* (TMV, *Tobamovirus*) in *Solanum lycopersicum* L. (Zhang *et al.*, 2015), *Potato virus Y* (PVY, *Potyvirus*) (Matros *et al.*, 2006) in *Nicotiana tabacum* L. and *Cucumber mosaic virus* (CMV, *Cucumovirus*) in *N. tabacum* and *C. annuum* (Fu *et al.*, 2010; Dáder *et al.*, 2016).

Plant-pathogenic bacteria are most destructive under warm or moist climatic conditions, although prolonged heatwaves have the potential to diminish bacterial infections such as *Xanthomonas* and *Pseudomonas* species (Grondeau *et al.*, 1994). Most bacteria are spread through moisture films, therefore, altered timing and amount of rainfall patterns due to climate change could be a critical driving element because bacteria can be washed into natural openings or wounds (Jones & Barbetti, 2012). These films are present under high relative humidity conditions so dry microclimate of the leaf surface would be a disadvantage for pathogen movement. There are limited findings that show that eCO<sub>2</sub> may either accelerate or diminish bacterial epidemics (Ibe & Grogan, 1983; Shin & Yun, 2010). With regard to other pathogens, fungal epidemics could become less widespread in temperate regions where rainfall declines. However, eCO<sub>2</sub> has been shown to increase the fecundity and severity of fungal pathogens and increased plant biomass can exacerbate this further (Garrett *et al.*, 2006; Melloy *et al.*, 2010; Chakraborty & Newton, 2011). Although the importance of fungal pathogens is paramount, the question of future climates on their induced disease severities and aggressiveness has been addressed in limited studies. Additionally, little is known about how the changes mediated by increased CO<sub>2</sub>, temperature and fungal infection affect insect establishment, feeding damage and population structure. It is quite apparent that the interactions between insects and pathogens, including fungal pathogens which are not vectored by the insects, are unrepresented in light of the future climate; however, they can

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inhabit the same host and modify/respond to changes in temperature, rainfall and CO<sub>2</sub> in different ways, thus effecting each other.

Increasing CO<sub>2</sub> also implies further consequences for interactions between plants and endophytic microorganisms. Recent findings suggest that nutrient exchange dynamics are indispensable for maintaining the symbiotic relationship between fungal endophytes and their hosts and may be altered under eCO<sub>2</sub>, where endophyte presence is increased (Ryan *et al.*, 2014b). Enhanced photosynthetic rates allow for the translocation of more carbohydrates from leaves to roots, favouring nodule development and, at the same time, the presence of nitrogen-fixing rhizobial bacteria associated with roots. This enhances the rate of photosynthesis as a consequence of the increased sink (Ryalls *et al.*, 2013; Baslam *et al.*, 2014).

### **Plant metabolism and defence: insect pests and viruses**

Excess carbon resulting from CO<sub>2</sub> fertilization can be allocated to other carbon-based compounds (such as soluble carbohydrates), resulting in the dilution of other essential nutrients (Bartelt *et al.*, 1990; Awmack & Leather, 2002). This can lead to compensatory feeding and increased consumption rates. CO<sub>2</sub> enrichment has been shown to reduce the total concentrations of amino acids in barley and in cotton plants grown under CO<sub>2</sub> enrichment (Sicher, 2008; Sun *et al.*, 2009b). Similarly, amino acid concentrations have been found to decrease in the phloem of *Gossypium hirsutum* L. plants grown under elevated CO<sub>2</sub>, whilst increased amounts were found in cotton aphids (*A. gossypii*) after feeding on CO<sub>2</sub>-enriched cotton (Sun *et al.*, 2009a). Moreover, both feeding rates and ingestion efficiency of the sycamore aphid (*Drepanosiphum platanoidis* Schr.) increased as the amino acid

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concentrations of its host plant, sycamore (*Acer pseudoplatanus* L.), decreased (Dixon *et al.*, 1993).

Plant primary metabolism is also altered by the inclusion of virus and vector associations. Recent work has assessed the primary metabolism of wheat grown under eCO<sub>2</sub> (650 μmol/mol) and infected with BYDV (Vassiliadis *et al.*, 2016). Results showed that eCO<sub>2</sub> significantly enhances the composition of wheat carbohydrates, including fructose, mannitol and trehalose, irrespective of BYDV infection. Virus infection, however, enhanced amino acids such as histidine, lysine, phenylalanine and tryptophan, which are documented as being essential to aphid diet (Dadd, 1985), and this was irrespective of CO<sub>2</sub> concentration. Because the amino acid content in plants is species-specific, it is difficult to predict exactly how the amino acid content of important crop plants and their interactions with insect pests and pathogens will change under future atmospheric CO<sub>2</sub> conditions, thus further biochemical work is required.

Further, increased photosynthetic rates caused by greater CO<sub>2</sub> concentration can impact plant metabolism by re-allocating excess carbon to structural compounds such as pectin and cellulose or to carbon-based secondary metabolites such as phenolics, tannins and terpenoids (Sun *et al.*, 2009a). Such changes in biochemistry can modify how plants interact with insect pests and invading pathogens.

Secondary defence metabolites (allelochemicals) are produced by plants when attacked by herbivores, and this generally involves signalling by phytohormones such as salicylic acid (SA), jasmonic acid (JA) and ethylene (ET). Elevated CO<sub>2</sub> is likely to negatively impact JA and ET-mediated defences in plants, but positively enhances that of SA. For example, a down-regulation of the defence genes relating to the JA pathways has been observed in soybean (*Glycine max* L.) grown under eCO<sub>2</sub>, allowing increased susceptibility of the plants

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to herbivory by the Japanese beetle (*Popillia japonica* Newman) and the western corn rootworm (*Diabrotica virgifera virgifera* LeConte) (Zavala *et al.*, 2008; 2009; 2013). JA suppression is also known to benefit aphids by allowing them more time to locate the phloem, whilst enhanced SA signalling reduces phloem probing time, thereby reducing aphid fitness (Casteel *et al.*, 2012; Guo *et al.*, 2014a; Sun *et al.*, 2016).

This signalling cascade gives rise to alternative secondary defence metabolites which may also be impacted by CO<sub>2</sub> enrichment. Chickpea plants (*Cicer arietinum* L.) grown under eCO<sub>2</sub> (750  $\mu$ mol/mol) expressed higher levels of resistance to the pod borer, *Helicoverpa armigera* Hübner. Compared to ambient CO<sub>2</sub> (350  $\mu$ mol/mol), these plants also had greater levels of phenols, condensed tannins, and the defensive enzymes, peroxidase (POD), polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL) and tyrosine ammonia lyase (TAL) (Sharma *et al.*, 2016). DIMBOA (2,4-Dihydroxy-7-methoxy-1,4-benzoxazin-3-one), a major hydroxamic acid (benzoxazanoid) found in wheat and other cereals, has been shown to have toxic and anti-feeding properties towards aphids (Bohidar *et al.*, 1986; Thackray *et al.*, 1990; Nicol *et al.*, 1992; Givovich & Niemeyer, 1994; Elek *et al.*, 2013; Vaughan *et al.*, 2016). *R. padi* population sizes were negatively correlated with foliar concentrations of DIMBOA in wheat grown under elevated CO<sub>2</sub> (700  $\mu$ mol/mol) and elevated soil moisture levels (40% and 60% of field water capacity) (Zhang *et al.*, 2003).

The elicitation of plant defensive metabolites can also impact the way in which viruses are transmitted to host plants. For example, aphids were found to preferentially select wheat leaves with lower concentrations of hydroxamic acids and also spent more time attempting to reach the phloem vessels compared to those with higher concentrations (Givovich & Niemeyer, 1991). In turn, viruliferous aphids infected fewer plants, which had high levels of DIMBOA. It was suggested that plants expressing higher concentrations of hydroxamic acids

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under field conditions would be more tolerant to BYDV infection compared to those with lower concentrations (Givovich & Niemeyer, 1991). Nonetheless, viruses can modify their host plants to indirectly manipulate their vectors. This is achieved by altering sap amino acid compositions (Ajayi, 1986) and by modulating plant defence pathways (Ziebell *et al.*, 2011). Secondary metabolites emitted as volatile organic compounds (VOCs) are also induced by virus-infected plants and are important in aphid host selection and behaviour (Pickett *et al.*, 1992; Jan *et al.*, 1996; Visser *et al.*, 1996). For example, several studies have shown that non-viruliferous *R. padi* preferentially migrate towards BYDV-infected plants (Jiménez-Martínez *et al.*, 2004; Medina-Ortega *et al.*, 2009; Bosque-Pérez & Eigenbrode, 2011; Ingwell *et al.*, 2012). In contrast, methyl salicylate acts as a repellent to aphids and may be responsible for host discrimination during migration (Glinwood & Pettersson, 2000).

Since many viruses are dependent on insect vectors, it is difficult to separate the biochemical changes in plants caused by insect feeding or by the virus itself. For instance, research has shown that tobacco plants grown under eCO<sub>2</sub> (750  $\mu\text{mol/mol}$ ) produced greater secondary defence metabolites when infected with CMV, but the authors attributed this more strongly to aphid herbivory rather than virus infection, and these defences are thought to be transferred from the virus to aphids (Fu *et al.*, 2010). Alternative studies have, however, elucidated the biochemical impact of non-vectored viruses in plants. Accompanied by lower virus titres, phenylpropanoid levels including chlorogenic acid (CGA) and the coumarins, scopolin and scopoletin, were increased in the foliage of tobacco infected with PVY and grown under eCO<sub>2</sub> (1000  $\mu\text{mol/mol}$ ) (Matros *et al.*, 2006). Additionally, the phytohormone SA was dramatically enhanced in tomato plants infected with TYLCV and TMV when grown under eCO<sub>2</sub> (~750 and 800  $\mu\text{mol/mol}$  respectively) and this was mirrored by reduced disease incidence and severity (Huang *et al.*, 2012; Zhang *et al.*, 2015).

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Elevated temperatures have also been associated with increased disease symptoms and virus titre in wheat infected with BYDV (Nancarrow *et al.*, 2014). In contrast, increased resistance to *Potato virus X* (PVX) or PYV in tobacco plants (*N. glutinosa*) (Ma *et al.*, 2015), and to PVX in *N. benthamiana* (Aguilar *et al.*, 2015) has been documented with elevated temperatures. Furthermore, ozone (O<sub>3</sub>) also contributes to plant resistance against viruses. Soybean plants infected with *Soybean mosaic virus* (SMV) and exposed to elevated O<sub>3</sub> induced viral defence-related genes as well as genes synthesising flavonoid production. This resulted in elevated concentrations of quercetin and kaempferol derivatives, and was accompanied by lower disease severity (Bilgin *et al.*, 2008).

#### **Plant metabolism and defence: fungi and bacteria**

Climatic changes are also likely to impact the defence response of plants to invading bacterial and fungal pathogens. High temperatures have resulted in increased disease symptoms and inhibited resistance gene-mediated responses in *Arabidopsis* infected with *Pseudomonas syringae* pv. *tomato* (Wang *et al.*, 2009). Conversely, eCO<sub>2</sub> lowered the incidence and severity of disease induced by *P. syringae* in tomato plants, but enhanced the susceptibility of tomato to the fungal pathogen, *Botrytis cinerea*; and this was due to the silencing of SA and JA-mediated pathways (Zhang *et al.*, 2015). Furthermore, phenolic compounds such as flavonoids play an important role in plant resistance to microbes (Treutter, 2006). Soybean grown under eCO<sub>2</sub> and elicited with a fungal elicitor,  $\beta$ -glucan (from *Phytophthora sojae*), has been shown to accumulate high concentrations of glyceollins (phytoalexins) (dos Santos Kretschmar *et al.*, 2009).

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Recent work has assessed the acclimation of both fungal pathogens and plants to eCO<sub>2</sub> concentrations, with results showing increased *Fusarium* head blight and *Septoria tritici* blotch (STB) disease severities occurring in wheat infected with *Fusarium graminearum* and *Zymoseptoria tritici*, respectively (Váry *et al.*, 2015). Similarly, the combination of both eCO<sub>2</sub> and drought enhanced maize susceptibility to *F. verticillioides* (FV), producing higher levels of the carcinogenic mycotoxin, fumonisin (Vaughan *et al.*, 2016). A compromised host defence response was supported by the dampening of SA and JA response as well as reduced maize benzoxazanoid defence metabolites. In contrast, terpenoid phytoalexins were significantly influenced by the combined effects of elevated CO<sub>2</sub>, drought and infection, as observed by increased concentrations of zealexins and kauralexins (Vaughan *et al.*, 2016).

Plants exposed to differing climatic conditions will impact future pathogen and insect interactions. The continuing increases in atmospheric CO<sub>2</sub>, O<sub>3</sub> and temperature threaten agriculturally important crops. It is therefore critical to continue studying the alterations in plant biochemistry in association with different pests and pathogens to help mitigate disease spread and crop loss, and enhance food security in the future.

## Conclusions

Uncertainty around future climate, its effect on the Earth, the biosphere and specifically on humans, results in ever-increasing attention by governments, scientists and the general public. Agriculture and food security will be on the forefront, as the demand for food will increase and potentially, land and suitable climatic conditions will decrease. Identifying the difficulties which affect agriculture, including insect pests and plant pathogens associated with a changing climate, has progressed rapidly in the last decade, revealing a high level of

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scientific complexity. Changes to plant distribution, growth rates and biochemistry mediated by future climates will likely have a greater impact on insect and pathogen dispersal and spread compared to the direct impacts of climate change. Ongoing research is therefore required to further understand these interactions. However, since real-world situations are much more complex than common laboratory or field practices, additional research is needed to incorporate insects, plants and pathogens overlaid with different climatic variables, often for specific and for each pathosystem. General trends can be identified for plants, insects and pathogen when exposed to increased temperature and/or CO<sub>2</sub>. However, to protect specific crops against pests or diseases within particular geographic locations, direct and site specific approaches might be required; therefore, a detailed understanding of the biotic and abiotic factors for the particular location is needed to model the future effects of pests and diseases on the food crops.

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## References

- Aben, S.K., Seneweera, S.P., Ghannoum, O. and Conroy, J.P. (1999) Nitrogen requirements for maximum growth and photosynthesis of rice, *Oryza sativa* L. cv. Jarrah grown at 36 and 70 Pa CO<sub>2</sub>. *Functional Plant Biology*, 26, 759–766.
- Aguilar, E., Allende, L., Del Toro, F.J., Chung, B.N., Canto, T. and Tenllado, F. (2015) Effects of elevated CO<sub>2</sub> and temperature on pathogenicity determinants and virulence of *Potato virus X/Potyvirus*–associated synergism. *Molecular Plant–Microbe Interactions*, 28, 1364–1373.
- Ainsworth, E.A., Beier, C., Calfapietra, C., Ceulemans, R., Durand-Tardif, M. and Farquhar, G.D. *et al.* (2008) Next generation of elevated [CO<sub>2</sub>] experiments with crops: a critical investment for feeding the future world. *Plant, Cell & Environment*, 31, 1317–1324.
- Ainsworth, E.A. and Long, S.P. (2005) What have we learned from 15 years of free–air CO<sub>2</sub> enrichment (FACE)? A meta–analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytologist*, 165, 351–372.
- Ainsworth, E.A. and Rogers, A. (2007) The response of photosynthesis and stomatal conductance to rising [CO<sub>2</sub>]: mechanisms and environmental interactions. *Plant, Cell and Environment*, 30, 258–270.
- Ajayi, B.O. (1986) The effect of *Barley yellow dwarf virus* on the amino acid composition of spring wheat. *Annals of Applied Biology*, 108, 145–149.
- Alexandratos, N. and Bruinsma, J. (2012) World agriculture towards 2030/2050: the 2012 revision. ESA Working paper No. 12-03.
- Anhalt, M. and Almeida, R. (2008) Effect of temperature, vector life stage, and plant access period on transmission of *Banana bunchy top virus* to banana. *Phytopathology*, 98, 743–748.

This article is protected by copyright. All rights reserved.

- Awmack, C. and Leather, S. (2002) Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, 47, 817–844.
- Bartelt, R.J., Mcguire, M.R. and Black, D.A. (1990) Feeding stimulants for the European corn borer (Lepidoptera: Pyralidae): additives to a starch-based formulation for *Bacillus thuringiensis*. *Environmental Entomology*, 19, 182–189.
- Baslam, M., Antolín, M.C., Gogorcena, Y., Muñoz, F. and Goicoechea, N. (2014) Changes in alfalfa forage quality and stem carbohydrates induced by arbuscular mycorrhizal fungi and elevated atmospheric CO<sub>2</sub>. *Annals of Applied Biology*, 164, 190–199.
- Bauerfeind, S.S. and Fischer, K. (2013a) Targeting the right trait: The relative suitability of a host plant depends on the herbivore trait considered and ambient temperature. *Basic and Applied Ecology*, 14, 555–564.
- Bauerfeind, S.S. and Fischer, K. (2013b) Testing the plant stress hypothesis: stressed plants offer better food to an insect herbivore. *Entomologia Experimentalis et Applicata*, 149, 148–158.
- Ben-Yakir, D. and Fereres, A. (2016) The effects of UV radiation on arthropods: a review of recent publications (2010–2015). *Acta Horticulture*, 1134, 335–342.
- Bezemer, T.M. and Jones, T.H. (1998) Plant–insect herbivore interactions in elevated atmospheric CO<sub>2</sub>: quantitative analyses and guild effects. *Oikos*, 82, 212–222.
- Bilgin, D.D., Aldea, M., O'Neill, B.F., Benitez, M., Li, M. and Clough, S.J. *et al.* (2008) Elevated ozone alters soybean–virus interaction. *Molecular Plant–Microbe Interactions*, 21, 1297–1308.
- Bohidar, K., Wratten, S. and Niemeyer, H. (1986) Effects of hydroxamic acids on the resistance of wheat to the aphid *Sitobion avenae*. *Annals of Applied Biology*, 109, 193–198.

This article is protected by copyright. All rights reserved.



- Bosque-Pérez, N.A. and Eigenbrode, S.D. (2011) The influence of virus-induced changes in plants on aphid vectors: Insights from luteovirus pathosystems. *Virus Research*, 159, 201–205.
- Cannon, R.J.C. (1998) The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology*, 4, 785–796.
- Casteel, C.L., Segal, L.M., Niziolek, O.K., Berenbaum, M.R. and Delucia, E.H. (2012) Elevated carbon dioxide increases salicylic acid in *Glycine max*. *Environmental Entomology*, 41, 1435–1442.
- Chakraborty, S. and Newton, A.C. (2011) Climate change, plant diseases and food security: an overview. *Plant Pathology*, 60, 2–14.
- Chakraborty, S., Tiedemann, A. and Teng, P. (2000) Climate change: potential impact on plant diseases. *Environmental Pollution*, 108, 317–326.
- Chen, F., Ge, F. and Parajulee, M.N. (2005) Impact of elevated CO<sub>2</sub> on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossypii*, and *Leis axyridis*. *Environmental Entomology*, 34, 37–46.
- Chen, F., Wu, G. and Ge, F. (2004) Impacts of elevated CO<sub>2</sub> on the population abundance and reproductive activity of aphid *Sitobion avenae* Fabricius feeding on spring wheat. *Journal of Applied Entomology*, 128, 723–730.
- Chung, B.N., Canto, T., Tenllado, F., San Choi, K., Joa, J.H. and Ahn, J.J. *et al.* (2016) The effects of high temperature on infection by *Potato virus Y*, *Potato virus A*, and *Potato leafroll virus*. *The Plant Pathology Journal*, 32, 321.
- Conroy, J., Seneweera, S., Basra, A., Rogers, G. and Nissen-Wooller, B. (1994) Influence of rising atmospheric CO<sub>2</sub> concentrations and temperature on growth, yield and grain quality of cereal crops. *Functional Plant Biology*, 21, 741–758.

This article is protected by copyright. All rights reserved.

- Cornelissen, T. (2011) Climate change and its effects on terrestrial insects and herbivory patterns. *Neotropical Entomology*, 40, 155–163.
- Coviella, C.E. and Trumble, J.T. (1999) Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Conservation Biology*, 13, 700–712.
- Curnutte, L.B., Simmons, A.M. and Abd-Rabou, S. (2014) Climate change and *Bemisia tabaci* (Hemiptera: Aleyrodidae): impacts of temperature and carbon dioxide on life history. *Annals of the Entomological Society of America*, 107, 933–943.
- Dadd, R.H. (1985) Nutrition: Organisms. *Comprehensive Insect Physiology, Biochemistry and Pharmacology* (eds. G. Kerkut & L. Gilbert). Pergamon Press, Oxford, UK.
- Dáder, B., Fereres, A., Moreno, A. and Trębicki, P. (2016) Elevated CO<sub>2</sub> impacts bell pepper growth with consequences to *Myzus persicae* life history, feeding behaviour and virus transmission ability. *Scientific Reports*, 6, 19120.
- Diaz, B.M. and Fereres, A. (2005) Life table and population parameters of *Nasonovia ribisnigri* (Homoptera: Aphididae) at different constant temperatures. *Environmental Entomology*, 34, 527–534.
- Dixon, A., Wellings, P.W., Carter, C. and Nichols, J. (1993) The role of food quality and competition in shaping the seasonal cycle in the reproductive activity of the sycamore aphid. *Oecologia*, 95, 89–92.
- Dos Santos Kretzschmar, F., Aidar, M.P.M., Salgado, I. and Braga, M.R. (2009) Elevated CO<sub>2</sub> atmosphere enhances production of defense-related flavonoids in soybean elicited by NO and a fungal elicitor. *Environmental and Experimental Botany*, 65, 319–329.
- Eigenbrode, S.D., Ding, H., Shiel, P. and Berger, P.H. (2002) Volatiles from potato plants infected with potato leafroll virus attract and arrest the virus vector, *Myzus persicae* (Homoptera: Aphididae). *Proceedings of the Royal Society of London*, 269, 455–460.

This article is protected by copyright. All rights reserved.

Elek, H., Smart, L., Martin, J., Ahmad, S., Gordon - Weeks, R. and Welham, S. *et al.* (2013)

The potential of hydroxamic acids in tetraploid and hexaploid wheat varieties as resistance factors against the bird-cherry oat aphid, *Rhopalosiphum padi*. *Annals of Applied Biology*, 162, 100–109.

Fereres, A., Penaflor, M.F.G., Favaro, C.F., Azevedo, K.E., Landi, C.H. and Maluta, N.K. *et al.* (2016) Tomato infection by whitefly-transmitted circulative and non-circulative viruses induce contrasting changes in plant volatiles and vector behaviour. *Viruses*, 8, 225.

Fernando, N., Panozzo, J., Tausz, M., Norton, R., Fitzgerald, G. and Khan, A. (2015) Rising CO<sub>2</sub> concentration altered wheat grain proteome and flour rheological characteristics. *Food Chemistry*, 170, 448–454.

Fitzgerald, G., Norton, R., Tausz, M., O’Leary, G., Seneweera, S. and Posch, S. *et al.* (2010) Future effects of elevated CO<sub>2</sub> on wheat production—an overview of FACE research in Victoria, Australia. Proceedings 15th Agronomy Conference, pp.15–18.

Fitzgerald, G., Tausz, M., O’leary, G., Mollah, M., Tausz-Posch, S. and Seneweera, S. *et al.* (2016) Elevated atmospheric [CO<sub>2</sub>] can dramatically increase wheat yields in semi-arid environments and buffer against heat waves. *Global Change Biology*, 22, 2269.

Flynn, D.F., Sudderth, E.A. and Bazzaz, F. (2006) Effects of aphid herbivory on biomass and leaf-level physiology of *Solanum dulcamara* under elevated temperature and CO<sub>2</sub>. *Environmental and Experimental Botany*, 56, 10–18.

Fu, X., Ye, L., Kang, L. and Ge, F. (2010) Elevated CO<sub>2</sub> shifts the focus of tobacco plant defences from *Cucumber mosaic virus* to the green peach aphid. *Plant, Cell and Environment*, 33, 2056–2064.

This article is protected by copyright. All rights reserved.

- Gao, F., Zhu, S.R., Sun, Y.C., Du, L., Parajulee, M. and Kang, L. *et al.* (2008) Interactive effects of elevated CO<sub>2</sub> and cotton cultivar on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossypii*, and *Propylaea japonica*. *Environmental Entomology*, 37, 29–37.
- Garrett, K., Dendy, S., Frank, E., Rouse, M. and Travers, S. (2006) Climate change effects on plant disease: genomes to ecosystems. *Annual Review of Phytopathology*, 44, 489–509.
- Gibson, L. and Paulsen, G. (1999) Yield components of wheat grown under high temperature stress during reproductive growth. *Crop Science*, 39, 1841–1846.
- Givovich, A. and Niemeyer, H. (1991) Hydroxamic acids affecting *Barley yellow dwarf virus* transmission by the aphid *Rhopalosiphum padi*. *Entomologia Experimentalis et Applicata*, 59, 79–85.
- Givovich, A. and Niemeyer, H.M. (1994) Effect of hydroxamic acids on feeding behaviour and performance of cereal aphids (Hemiptera: Aphididae) on wheat. *European Journal of Entomology*, 91, 371–371.
- Glinwood, R.T. and Pettersson, J. (2000) Change in response of *Rhopalosiphum padi* spring migrants to the repellent winter host component methyl salicylate. *Entomologia Experimentalis et Applicata*, 94, 325–330.
- Griffiths, W., Aurambout, J., Parry, H., Trebicki, P., Kriticos, D. and O’Leary, G. *et al.* (2010) Insect–pathogen–crop dynamics and their importance to plant biosecurity under future climates: *Barley yellow dwarf virus* and wheat—a case study. Proceedings of 15th Agronomy Conference.
- Grondeau, C., Samson, R. and Sands, D. (1994) A review of thermotherapy to free plant materials from pathogens, especially seeds from bacteria. *Critical Reviews in Plant Sciences*, 13, 57–75.

This article is protected by copyright. All rights reserved.

- Guo, H., Sun, Y., Li, Y., Liu, X., Wang, P. and Zhu-Salzman, K. *et al.* (2014a) Elevated CO<sub>2</sub> alters the feeding behaviour of the pea aphid by modifying the physical and chemical resistance of *Medicago truncatula*. *Plant, Cell & Environment*, 37, 2158–2168.
- Guo, H., Sun, Y.C., Li, Y., Liu, X., Zhang, W. and Ge, F. (2014b) Elevated CO<sub>2</sub> decreases the response of the ethylene signaling pathway in *Medicago truncatula* and increases the abundance of the pea aphid. *New Phytologist*, 201, 279–291.
- Guo, H., Sun, Y.C., Li, Y., Tong, B., Harris, M. and Zhu-Salzman, K. *et al.* (2013) Pea aphid promotes amino acid metabolism both in *Medicago truncatula* and bacteriocytes to favor aphid population growth under elevated CO<sub>2</sub>. *Global Change Biology*, 19, 3210–3223.
- Himanen, S.J., Nissinen, A., Dong, W.X., Nerg, A., Stewart, C. and Poppy, G.M. *et al.* (2008) Interactions of elevated carbon dioxide and temperature with aphid feeding on transgenic oilseed rape: Are *Bacillus thuringiensis* (Bt) plants more susceptible to nontarget herbivores in future climate? *Global Change Biology*, 14, 1437–1454.
- Huang, L., Ren, Q., Sun, Y.C., Ye, L., Cao, H. and Ge, F. (2012) Lower incidence and severity of tomato virus in elevated CO<sub>2</sub> is accompanied by modulated plant induced defence in tomato. *Plant Biology*, 14, 905–913.
- Hughes, L. and Bazzaz, F.A. (2001) Effects of elevated CO<sub>2</sub> on five plant–aphid interactions. *Entomologia Experimentalis et Applicata*, 99, 87–96.
- Hull, R. (2013) *Plant Virology*. Academic press.
- Ibe, S. and Grogan, R. (1983) Effect of controlled oxygen and carbon dioxide atmospheres on bacterial growth rate and soft rot of tomato fruits caused by *Pseudomonas marginalis*. *Plant Disease*, 67, 1005–1008.
- Ingwell, L.L., Eigenbrode, S.D. and Bosque-Pérez, N.A. (2012) Plant viruses alter insect behavior to enhance their spread. *Scientific Reports*, 2, 1–6.

This article is protected by copyright. All rights reserved.

- IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.
- Jan, P., Andres, Q. and Elham, F.A. (1996) Aphid antixenosis mediated by volatiles in cereals. *Acta Agriculturae Scandinavica B-Plant Soil Sciences*, 46, 135–140.
- Jiménez-Martínez, E.S., Bosque-Pérez, N.A., Berger, P.H., Zemetra, R.S., Ding, H. and Eigenbrode, S.D. (2004) Volatile cues influence the response of *Rhopalosiphum padi* (Homoptera: Aphididae) to *Barley yellow dwarf virus*-infected transgenic and untransformed wheat. *Environmental Entomology*, 33, 1207–1216.
- Johnson, S., Ryalls, J. and Karley, A. (2014) Global climate change and crop resistance to aphids: contrasting responses of lucerne genotypes to elevated atmospheric carbon dioxide. *Annals of Applied Biology*, 165, 62–72.
- Johnson, S.N. and Riegler, M. (2013) Root damage by insects reverses the effects of elevated atmospheric CO<sub>2</sub> on eucalypt seedlings. *PLoS ONE*, 8, e79479.
- Jones, R.A. and Barbetti, M.J. (2012) Influence of climate change on plant disease infections and epidemics caused by viruses and bacteria. *Plant Sciences Reviews*, 22, 1–31.
- Jones, R.A.C. (2016) Future scenarios for plant virus pathogens as climate change progresses. *Advances in Virus Research* (eds. K.M.M. Kielian & C.M. Thomas). Academic Press.
- Kassanis, B. (1952) Some effects of high temperature on the susceptibility of plants to infection with viruses. *Annals of Applied Biology*, 39, 358–369.
- Kimball, B.A. (2016) Crop responses to elevated CO<sub>2</sub> and interactions with H<sub>2</sub>O, N, and temperature. *Current Opinion in Plant Biology*, 31, 36–43.

This article is protected by copyright. All rights reserved.

- Klaiber, J., Najar-Rodriguez, A.J., Piskorski, R. and Dorn, S. (2013) Plant acclimation to elevated CO<sub>2</sub> affects important plant functional traits, and concomitantly reduces plant colonization rates by an herbivorous insect. *Planta*, 237, 29–42.
- Lavola, A., Julkunen-Tiitto, R., Roininen, H. and Aphalo, P. (1998) Host-plant preference of an insect herbivore mediated by UV-B and CO<sub>2</sub> in relation to plant secondary metabolites. *Biochemical Systematics and Ecology*, 26, 1–12.
- Lee, K.P. and Roh, C. (2010) Temperature–by–nutrient interactions affecting growth rate in an insect ectotherm. *Entomologia Experimentalis et Applicata*, 136, 151–163.
- Luck, J., Aurambout, J.P., Finlay, K., Chakraborty, S., Parry, H. and Griffiths, W. *et al.* (2010) An integrative approach to understanding the pest and disease threats to agricultural biosecurity under future climates. Building sustainable rural futures: the added value of systems approaches in times of change and uncertainty. 9th European IFSA Symposium, Vienna, Austria, 4–7 July 2010., Citeseer, 1379–1388 pp.
- Luck, J., Spackman, M., Freeman, A., Trebicki, P., Griffiths, W. and Finlay, K. *et al.* (2011) Climate change and diseases of food crops. *Plant Pathology*, 60, 113–121.
- Ma, L., Huang, X., Yu, R., Jing, X., Xu, J. and Wu, C. *et al.* (2015) Elevated ambient temperature differentially affects virus resistance in two tobacco species. *Phytopathology*, 106, 94–100.
- Malmstrom, C.M. and Field, C.B. (1997) Virus–induced differences in the response of oat plants to elevated carbon dioxide. *Plant, Cell and Environment*, 20, 178–188.
- Matros, A., Amme, S., Kettig, B., Buck-Sorlin, G.H., Sonnewald, U. and Mock, H.P. (2006) Growth at elevated CO<sub>2</sub> concentrations leads to modified profiles of secondary metabolites in tobacco cv. Samsun NN and to increased resistance against infection with potato virus Y. *Plant, Cell and Environment*, 29, 126–137.
- Matthews, R.C.F. (1991) *Plant Virology*. San Diego, Academic Press.

This article is protected by copyright. All rights reserved.

- Mauck, K.E., De Moraes, C.M. and Mescher, M.C. (2010) Deceptive chemical signals induced by a plant virus attract insect vectors to inferior hosts. *Proceedings of the National Academy of Sciences USA*, 107, 3600–3605.
- Mckirdy, S.J., Jones, R.A.C. and Nutter, F.W.J. (2002) Quantification of yield losses caused by *Barley yellow dwarf virus* in wheat and oats. *Plant Disease*, 86, 769–773.
- Medina-Ortega, K.J., Bosque-Pérez, N.A., Ngumbi, E., Jiménez-Martínez, E.S. and Eigenbrode, S.D. (2009) *Rhopalosiphum padi* (Hemiptera: Aphididae) responses to volatile cues from *Barley yellow dwarf virus*-infected wheat. *Environmental Entomology*, 38, 836–845.
- Melloy, P., Hollaway, G., Luck, J., Norton, R., Aitken, E. and Chakraborty, S. (2010) Production and fitness of *Fusarium pseudograminearum* inoculum at elevated carbon dioxide in FACE. *Global Change Biology*, 16, 3363–3373.
- Myers, S.S., Zanobetti, A., Kloog, I., Huybers, P., Leakey, A.D. and Bloom, A.J. *et al.* (2014) Increasing CO<sub>2</sub> threatens human nutrition. *Nature*, 510, 139–142.
- Nancarrow, N., Constable, F.E., Finlay, K.J., Freeman, A.J., Rodoni, B.C. and Trębicki, P. *et al.* (2014) The effect of elevated temperature on *Barley yellow dwarf virus*-PAV in wheat. *Virus Research*, 186, 97–103.
- Newman, J., Gibson, D., Parsons, A. and Thornley, J. (2003) How predictable are aphid population responses to elevated CO<sub>2</sub>? *Journal of Animal Ecology*, 72, 556–566.
- Nicol, D., Copaja, S., Wratten, S. and Niemeyer, H. (1992) A screen of worldwide wheat cultivars for hydroxamic acid levels and aphid antixenosis. *Annals of Applied Biology*, 121, 11–18.
- Nuttall, J., O'leary, G., Khimashia, N., Asseng, S., Fitzgerald, G. and Norton, R. (2012) 'Haying-off' in wheat is predicted to increase under a future climate in south-eastern Australia. *Crop and Pasture Science*, 63, 593–605.

This article is protected by copyright. All rights reserved.



- Oehme, V., Högy, P., Franzaring, J., Zebitz, C. and Fangmeier, A. (2012) Response of spring crops and associated aphids to elevated atmospheric CO<sub>2</sub> concentrations. *Journal of Applied Botany and Food Quality*, 84, 151.
- Oehme, V., Högy, P., Zebitz, C.P. and Fangmeier, A. (2013) Effects of elevated atmospheric CO<sub>2</sub> concentrations on phloem sap composition of spring crops and aphid performance. *Journal of Plant Interactions*, 8, 74–84.
- Panozzo, J.F., Walker, C.K., Partington, D.L., Neumann, N.C., Tausz, M. and Seneweera, S. *et al.* (2014) Elevated carbon dioxide changes grain protein concentration and composition and compromises baking quality. A FACE study. *Journal of Cereal Science*, 60, 461–470.
- Pickett, J., Wadhams, L., Woodcock, C. and Hardie, J. (1992) The chemical ecology of aphids. *Annual Review of Entomology*, 37, 67–90.
- Pijpe, J., Brakefield, P.M. and Zwaan, B.J. (2007) Phenotypic plasticity of starvation resistance in the butterfly *Bicyclus anynana*. *Evolutionary Ecology*, 21, 589–600.
- Pusag, J.C.A., Jahan, S.H., Lee, K.S., Lee, S. and Lee, K.Y. (2012) Upregulation of temperature susceptibility in *Bemisia tabaci* upon acquisition of *Tomato yellow leaf curl virus* (TYLCV). *Journal of Insect Physiology*, 58, 1343–1348.
- Robinson, E.A., Ryan, G.D. and Newman, J.A. (2012) A meta-analytical review of the effects of elevated CO<sub>2</sub> on plant–arthropod interactions highlights the importance of interacting environmental and biological variables. *New Phytologist*, 194, 321–336.
- Romo, C.M. and Tylianakis, J.M. (2013) Elevated temperature and drought interact to reduce parasitoid effectiveness in suppressing hosts. *PLoS ONE*, 8, e58136.
- Rosenzweig, C., Iglesias, A., Yang, X., Epstein, P.R. and Chivian, E. (2001) Climate change and extreme weather events; implications for food production, plant diseases, and pests. *Global Change & Human Health*, 2, 90–104.

This article is protected by copyright. All rights reserved.

- Ryalls, J.M.W., Riegler, M., Moore, B.D., Lopaticki, G. and Johnson, S.N.J. (2013) Effects of elevated temperature and CO<sub>2</sub> on aboveground–belowground systems: a case study with plants, their mutualistic bacteria and root/shoot herbivores. *Frontiers in Plant Science*, 4, 445.
- Ryan, G.D., Emiljanowicz, L., Haerri, S.A. and Newman, J.A. (2014a) Aphid and host–plant genotype x genotype interactions under elevated CO<sub>2</sub>. *Ecological Entomology*, 39, 309–315.
- Ryan, G.D., Rasmussen, S., Xue, H., Parsons, A.J. and Newman, J.A. (2014b) Metabolite analysis of the effects of elevated CO<sub>2</sub> and nitrogen fertilization on the association between tall fescue (*Schedonorus arundinaceus*) and its fungal symbiont *Neotyphodium coenophialum*. *Plant, Cell and Environment*, 37, 204–212.
- Seneweera, S.P., Ghannoum, O., Conroy, J.P., Ishimaru, K., Okada, M. and Lieffering, M. *et al.* (2002) Changes in source–sink relations during development influence photosynthetic acclimation of rice to Free Air CO<sub>2</sub> Enrichment (FACE). *Functional Plant Biology*, 29, 947–955.
- Sharma, H.C., War, A.R., Pathania, M., Sharma, S.P., Akbar, S.M. and Munghate, R.S. (2016) Elevated CO<sub>2</sub> influences host plant defense response in chickpea against *Helicoverpa armigera*. *Arthropod-Plant Interactions*, 10, 171–181.
- Shin, J.W. and Yun, S.C. (2010) Elevated CO<sub>2</sub> and temperature effects on the incidence of four major chili pepper diseases. *The Plant Pathology Journal*, 26, 178–184.
- Sicher, R.C. (2008) Effects of CO<sub>2</sub> enrichment on soluble amino acids and organic acids in barley primary leaves as a function of age, photoperiod and chlorosis. *Plant Science*, 174, 576–582.
- Stacey, D.A. and Fellowes, M.D. (2002) Influence of elevated CO<sub>2</sub> on interspecific interactions at higher trophic levels. *Global Change Biology*, 8, 668–678.

This article is protected by copyright. All rights reserved.

- Stiling, P., Moon, D., Rossi, A., Forkner, R., Hungate, B.A. and Day, F.P. *et al.* (2013) Direct and legacy effects of long-term elevated CO<sub>2</sub> on fine root growth and plant–insect interactions. *New Phytologist*, 200, 788–795.
- Sun, Y.C., Guo, H. and Ge, F. (2016) Plant–aphid interactions under elevated CO<sub>2</sub>: some cues from aphid feeding behavior. *Frontiers in Plant Science*, 7, 502.
- Sun, Y.C., Guo, H., Zhu-Salzman, K. and Ge, F. (2013) Elevated CO<sub>2</sub> increases the abundance of the peach aphid on Arabidopsis by reducing jasmonic acid defenses. *Plant Science*, 210, 128–140.
- Sun, Y.C., Chen, F.J. and Ge, F. (2009a) Elevated CO<sub>2</sub> changes interspecific competition among three species of wheat aphids: *Sitobion avenae*, *Rhopalosiphum padi*, and *Schizaphis graminum*. *Environmental Entomology*, 38, 26–34.
- Sun, Y.C., Jing, B.B. and Ge, F. (2009b) Response of amino acid changes in *Aphis gossypii* (Glover) to elevated CO<sub>2</sub> levels. *Journal of Applied Entomology*, 133, 189–197.
- Sward, R. and Lister, R. (1987) The incidence of *Barley yellow dwarf viruses* in wheat in Victoria. *Australian Journal of Agricultural Research*, 38, 821 – 828.
- Taub, D.R. and Wang, X. (2008) Why are nitrogen concentrations in plant tissues lower under elevated CO<sub>2</sub>? A critical examination of the hypotheses. *Journal of Integrative Plant Biology*, 50, 1365–1374.
- Thackray, D., Wrattent, S., Edwards, P. and Niemeyer, H. (1990) Resistance to the aphids *Sitobion avenae* and *Rhopalosiphum padi* in Gramineae in relation to hydroxamic acid levels. *Annals of Applied Biology*, 116, 573–582.
- Tilman, D., Balzer, C., Hill, J. and Befort, B.L. (2011) Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences USA*, 108, 20260–20264.

This article is protected by copyright. All rights reserved.

- Tjallingii, W. (1978) Electronic recording of penetration behaviour by aphids. *Entomologia Experimentalis et Applicata*, 24, 721–730.
- Trebicki, P. (2016) Plant viruses threaten crops as climate warms. *Australasian Science*, 37, 36.
- Trębicki, P., Harding, R., Rodoni, B., Baxter, G. and Powell, K. (2010) Vectors and alternative hosts of *Tobacco yellow dwarf virus* in southeastern Australia. *Annals of Applied Biology*, 157, 13–24.
- Trębicki, P., Harding, R.M. and Powell, K.S. (2009) Anti-metabolic effects of *Galanthus nivalis* agglutinin and wheat germ agglutinin on nymphal stages of the common brown leafhopper using a novel artificial diet system. *Entomologia Experimentalis et Applicata*, 131, 99–105.
- Trębicki, P., Nancarrow, N., Bosque-Pérez, N.A., Rodoni, B., Aftab, M. and Freeman, A. *et al.* (2017) Virus incidence in wheat increases under elevated CO<sub>2</sub>: A 4-year study of *Yellow dwarf viruses* from a Free Air Carbon Dioxide facility. *Virus Research* (in press).
- Trębicki, P., Nancarrow, N., Cole, E., Bosque-Pérez, N.A., Constable, F.E. and Freeman, A.J. *et al.* (2015) Virus disease in wheat predicted to increase with a changing climate. *Global Change Biology*, 21, 3511–3519.
- Trębicki, P., Tjallingii, W.F., Harding, R.M., Rodoni, B.C. and Powell, K.S. (2012) EPG monitoring of the probing behaviour of the common brown leafhopper *Orosius orientalis* on artificial diet and selected host plants. *Arthropod–Plant Interactions*, 6, 405–415.
- Trębicki, P., Vandegeer, R.K., Bosque-Pérez, N.A., Powell, K.S., Dader, B. and Freeman, A. J. *et al.* (2016) Virus infection mediates the effects of elevated CO<sub>2</sub> on plants and vectors. *Scientific Reports*, 6, 22785.

This article is protected by copyright. All rights reserved.

- Treutter, D. (2006) Significance of flavonoids in plant resistance: a review. *Environmental Chemistry Letters*, 4, 147–157.
- Vandeger, R.K., Powell, K.S. and Tausz, M. (2016) *Barley yellow dwarf virus* infection and elevated CO<sub>2</sub> alter the antioxidants ascorbate and glutathione in wheat. *Journal of Plant Physiology*.
- Váry, Z., Mullins, E., Mcelwain, J.C. and Doohan, F.M. (2015) The severity of wheat diseases increases when plants and pathogens are acclimatized to elevated carbon dioxide. *Global Change Biology*, 21, 2661–2669.
- Vassiliadis, S., Plummer, K., Powell, K., Trebicki, P., Luck, J. and Rochfort, S. (2016) The effect of elevated CO<sub>2</sub> and virus infection on the primary metabolism of wheat. *Functional Plant Biology*, 43, 892–902.
- Vaughan, M.M., Huffaker, A., Schmelz, E.A., Dafoe, N.J., Christensen, S.A. and Mcauslane, H.J. *et al.* (2016) Interactive effects of elevated [CO<sub>2</sub>] and drought on the maize phytochemical defense response against fycotoxigenic *Fusarium verticillioides*. *PLoS ONE*, 11, e0159270.
- Visser, J., Piron, P. and Hardie, J. (1996) The aphids' peripheral perception of plant volatiles. *Entomologia Experimentalis et Applicata*, 80, 35–38.
- Wan, G., Dang, Z., Wu, G., Parajulee, M.N., Ge, F. and Chen, F. (2014) Single and fused transgenic *Bacillus thuringiensis* rice alter the species-specific responses of non-target planthoppers to elevated carbon dioxide and temperature. *Pest Management Science*, 70, 734–742.
- Wang, Y., Bao, Z., Zhu, Y. and Hua, J. (2009) Analysis of temperature modulation of plant defense against biotrophic microbes. *Molecular Plant-Microbe Interactions*, 22, 498–506.

This article is protected by copyright. All rights reserved.

- Wheeler, T., Hong, T., Ellis, R., Batts, G., Morison, J. and Hadley, P. (1996) The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L.) in response to temperature and CO<sub>2</sub>. *Journal of Experimental Botany*, 47, 623–630.
- Xie, H., Zhao, L., Wang, W., Wang, Z., Ni, X. and Cai, W. *et al.* (2014) Changes in life history parameters of *Rhopalosiphum maidis* (Homoptera: Aphididae) under four different elevated temperature and CO<sub>2</sub> combinations. *Journal of Economic Entomology*, 107, 1411–1418.
- Zavala, J.A., Casteel, C.L., Delucia, E.H. and Berenbaum, M.R. (2008) Anthropogenic increase in carbon dioxide compromises plant defense against invasive insects. *Proceedings of the National Academy of Sciences USA*, 105, 5129–5133.
- Zavala, J.A., Casteel, C.L., Nability, P.D., Berenbaum, M.R. and Delucia, E.H. (2009) Role of cysteine proteinase inhibitors in preference of Japanese beetles (*Popillia japonica*) for soybean (*Glycine max*) leaves of different ages and grown under elevated CO<sub>2</sub>. *Oecologia*, 161, 35–41.
- Zavala, J.A., Nability, P.D. and Delucia, E.H. (2013) An emerging understanding of mechanisms governing insect herbivory under elevated CO<sub>2</sub>. *Annual Review of Entomology*, 58, 79–97.
- Zhang, J., Xing, G., Liao, J., Hou, Z., Wang, G. and Wang, Y. (2003) Effects of different atmospheric CO<sub>2</sub> concentrations and soil moistures on the populations of bird cherry–oat aphid (*Rhopalosiphum padi*) feeding on spring wheat. *European Journal of Entomology*, 100, 521–530.
- Zhang, S., Li, X., Sun, Z., Shao, S., Hu, L. and Ye, M. *et al.* (2015) Antagonism between phytohormone signalling underlies the variation in disease susceptibility of tomato plants under elevated CO<sub>2</sub>. *Journal of Experimental Botany*, eru538.

This article is protected by copyright. All rights reserved.

Ziebell, H., Murphy, A.M., Groen, S.C., Tungadi, T., Westwood, J.H. and Lewsey, M.G. *et al.*

(2011) Cucumber mosaic virus and its 2b RNA silencing suppressor modify plant-aphid interactions in tobacco. *Scientific Reports*, 1, 187.

Ziska, L.H. (2008) Rising atmospheric carbon dioxide and plant biology: the overlooked paradigm. *DNA and Cell Biology*, 27, 165–172.

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**Table 1** Aphid (Hemiptera: Aphididae), plant and virus interaction studies under different climatic scenarios.

Insect vector	Host plant	Virus	Climatic scenario	Main focus	Main outcome	Reference
<i>M. persicae</i>	<i>Nicotiana benthamiana</i> , <i>Physalis floridana</i>	<i>Potato virus Y-O</i> , <i>Potato virus A</i> , <i>Potato leafroll virus</i>	Temperature	Plant–insect–virus	Optimum temperatures for proliferation of PVY-O/PVA and PLRV differed.	Chung <i>et al.</i> , 2016
<i>Pentalonia nigronervosa</i>	Banana	<i>Banana bunchy top</i>	Temperature	Plant–insect	Adult aphids transmit	Anhalt & Almeida, 2008

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			<i>virus</i>		d virus more efficiently at 25°C and 30°C than at 20°C.	
<i>Rhopalosiphum padi</i>	Wheat	<i>Barley yellow dwarf virus</i>	Temperature	Plant–virus	Virus titre increased under higher temperature.	Nancarrow <i>et al.</i> , 2014
<i>M. persicae</i>	Tobacco	<i>Cucumber mosaic virus</i>	Elevated CO <sub>2</sub>	Plant–insect–virus	Aphid density increased on infected plants under aCO <sub>2</sub> , but not under eCO <sub>2</sub> .	Fu <i>et al.</i> , 2010
<i>M. persicae</i>	Bell pepper	<i>Cucumber mosaic virus</i>	Elevated CO <sub>2</sub>	Plant–insect–virus	eCO <sub>2</sub> reduced aphid fecundity and CMV transmission.	Dáder <i>et al.</i> , 2016
<i>R. padi</i>	Oat	<i>Barley yellow dwarf virus</i>	Elevated CO <sub>2</sub>	Plant–virus	Biomass increased in infected oats grown under eCO <sub>2</sub> .	Malmström & Field, 1997
<i>R. padi</i>	Wheat	<i>Barley yellow dwarf virus</i>	Elevated CO <sub>2</sub>	Plant–virus	Virus titre increased in wheat under eCO <sub>2</sub> .	Trębicki <i>et al.</i> , 2015
<i>R. padi</i>	Wheat	<i>Barley yellow dwarf virus</i>	Elevated CO <sub>2</sub>	Plant–insect–virus	Aphid fecundity was reduced on virus-free plants, but	Trębicki <i>et al.</i> , 2016

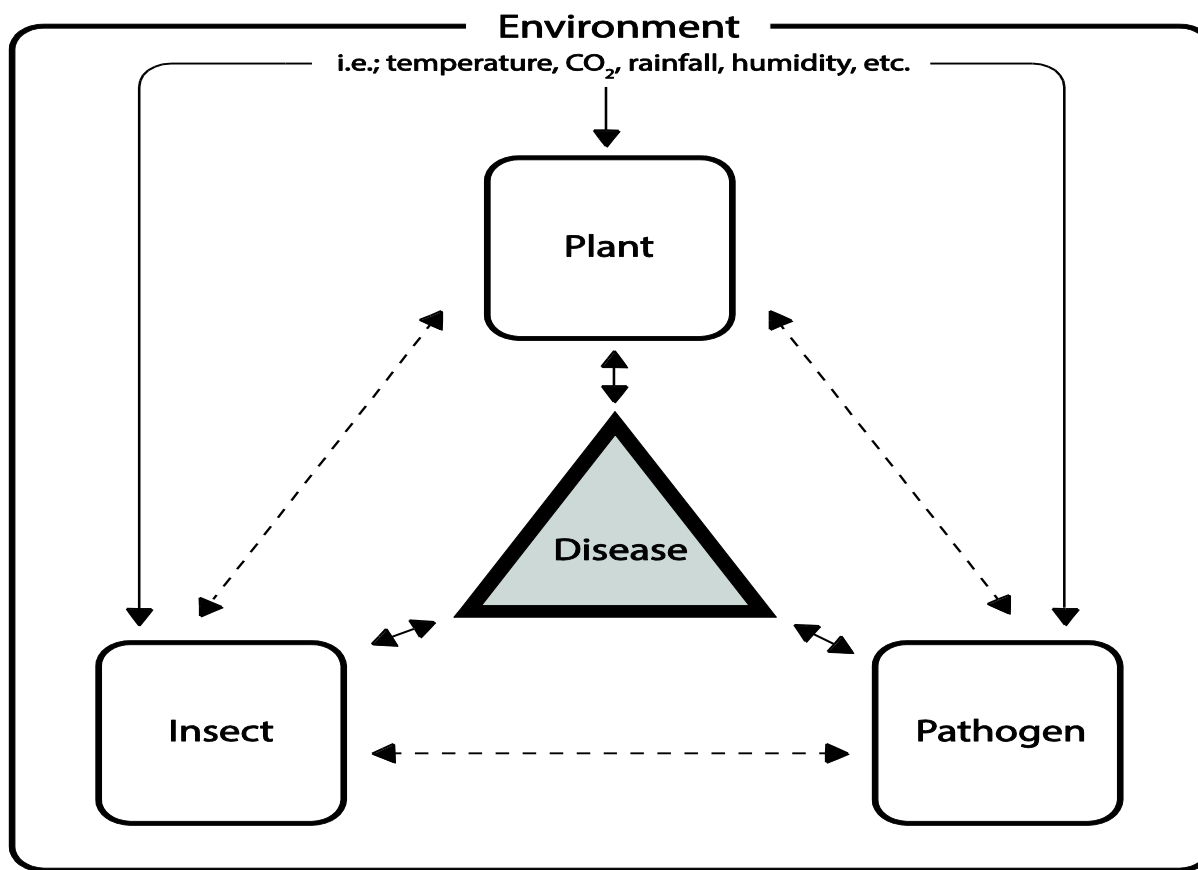
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					not on virus-infected plants. Increased feeding observed on virus-free plants under eCO <sub>2</sub> .	
<i>R. padi</i>	Wheat	<i>Barley yellow dwarf virus</i>	Elevated CO <sub>2</sub>	Plant-virus	ECO <sub>2</sub> decreased the fraction of oxidised ascorbate in plants.	Vandegeer <i>et al.</i> , 2016
<i>R. padi</i>	Wheat	<i>Barley yellow dwarf virus</i>	Elevated CO <sub>2</sub>	Plant-virus	Virus and eCO <sub>2</sub> changes primary plant metabolism and early virus symptom expression	Vassiliadis <i>et al.</i> , 2016
<i>R. padi</i>	Wheat	<i>Yellow dwarf virus</i>	Elevated CO <sub>2</sub>	Plant-virus	Natural incidence of yellow dwarf viruses (including BYDV) increased in the field (FACE) by over 10% as a result of eCO <sub>2</sub> .	Trębicki <i>et al.</i> , 2017

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## Figure legend



**Fig. 1** Illustration of the tripartite interactions (disease triangle) between plant, insect and pathogens, influencing one another and by different environmental factors. Solid lines represent direct effects of elevated CO<sub>2</sub> (eCO<sub>2</sub>), dashed lines represent indirect effects of eCO<sub>2</sub> changes via plant biochemistry or changes mediated through virus or insect vectors.

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