Author running head: *P. Trębicki et al.*

Title running head: *Insects, plants and pathogens under future climate*

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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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This is an Accepted Article that has been peer-reviewed and approved for publication in the Insect Science but has yet to undergo copy-editing and proof correction. Please cite this article as [doi: 10.1111/1744-7917.12531](https://doi.org/10.1111/1744-7917.12531).

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Trębicki, P., Dáder, B., Vassiliadis, S., Fereres, A. (2017). Insect-plant-pathogen interactions as shaped by future climate: effects on biology, distribution, and implications for agriculture. *Insect Science*, 24 (6), 975-989. , DOI : 10.1111/1744-7917.12531

Abstract Carbon dioxide (CO₂) 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 CO₂ 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 CO₂ concentration, temperature, patterns of rainfall and severe weather events that impact insects (namely vectors of plant pathogens) are discussed. Elevated CO₂ 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 CO₂ (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; CO₂; food security; pests; trophic interactions

Introduction

Carbon dioxide (CO₂) concentrations have now surpassed 400 $\mu\text{mol/mol}$, with the industrial revolution acknowledged as the triggering point before when its concentration was at around 280 $\mu\text{mol/mol}$ (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 CO₂ 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, CO₂ 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 CO₂ 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 CO₂ or temperature (Coviella &

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Trumble, 1999; Ben-Yakir & Fereres, 2016). Increased CO₂ levels are generally beneficial for C₃ 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, eCO₂ (elevated CO₂) 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 eCO₂, 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, CO₂ 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 CO₂ 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 eCO₂ 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 CO₂) 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, CO₂ 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 CO₂ 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 CO_2 overshadow the direct effects. However, use of artificial diet, or providing insects with fresh plants from those grown under ambient CO_2 ($a\text{CO}_2$) can be used to understand the direct effects of $e\text{CO}_2$.

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°C versus 25°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 & Barbeti, 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°C and 24°C , respectively, versus 20°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 CO₂ (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 CO₂ 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 CO₂ 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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eCO₂ (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, CO₂ 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 CO₂ 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, eCO₂ 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; Däder *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 CO₂-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 eCO₂ 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 CO₂ continues to increase (Cornelissen, 2011).

Aphids are one of the few examples where eCO₂ can increase population abundance, but this is often species and host specific (Robinson *et al.*, 2012). For example, eCO₂ 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 CO₂ 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 eCO₂ 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 CO₂ (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 eCO₂ conditions (Wan *et al.*, 2014).

The feeding behavior of insect vectors, particularly aphids, has been monitored under rising CO₂ 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 eCO₂, but when infected with *Barley yellow dwarf virus* (BYDV, *Luteovirus*), no significant changes to feeding were observed as a result of increased CO₂ (Trębicki *et al.*, 2016).

Feeding of late-instar *Operophtera brumata* L. larvae increased on leaves of *Betula pendula* Roth under eCO₂ 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 eCO₂ 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 CO₂.

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 CO₂ on viral dynamics but the main assumption is that the larger amount of biomass (resulting from CO₂ 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 eCO₂ 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 eCO₂ 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, eCO₂ 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 CO₂, 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 CO₂ in different ways, thus effecting each other.

Increasing CO₂ 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 eCO₂, 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 CO₂ 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. CO₂ enrichment has been shown to reduce the total concentrations of amino acids in barley and in cotton plants grown under CO₂ 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 CO₂, whilst increased amounts were found in cotton aphids (*A. gossypii*) after feeding on CO₂-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 eCO₂ (650 μ mol/mol) and infected with BYDV (Vassiliadis *et al.*, 2016). Results showed that eCO₂ 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 CO₂ 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 CO₂ conditions, thus further biochemical work is required.

Further, increased photosynthetic rates caused by greater CO₂ 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 CO₂ 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 eCO₂, 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 CO₂ enrichment. Chickpea plants (*Cicer arietinum* L.) grown under eCO₂ (750 µmol/mol) expressed higher levels of resistance to the pod borer, *Helicoverpa armigera* Hübner. Compared to ambient CO₂ (350 µmol/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 CO₂ (700 µmol/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 eCO₂ (750 μ 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 eCO₂ (1000 μ mol/mol) (Matros *et al.*, 2006). Additionally, the phytohormone SA was dramatically enhanced in tomato plants infected with TYLCV and TMV when grown under eCO₂ (~750 and 800 μ 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 (O₃) also contributes to plant resistance against viruses. Soybean plants infected with *Soybean mosaic virus* (SMV) and exposed to elevated O₃ 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, eCO₂ 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 eCO₂ and elicited with a fungal elicitor, β -glucan (from *Phytophthora sojae*), has been shown to accumulate high concentrations of glyceollins (phytoalexins) (dos Santos Kretzschmar *et al.*, 2009).

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Recent work has assessed the acclimation of both fungal pathogens and plants to eCO₂ 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 eCO₂ 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 CO₂, 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 CO₂, O₃ 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 CO₂. 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.

Acknowledgments

We thank Agriculture Victoria, Bioscience Research and the Grains Research and Development Corporation (GRDC), Australia for support. We also thank Institute of Agricultural Sciences-CSIC, Madrid, Spain; and INRA, Campus International de Baillarguet, Montpellier, France for in-house funding to support this review. B.D. is supported by the AgreeSkills fellowship program which has received funding from the EU's Seventh 470 Framework Program under grant agreement No. FP7-609398 (AgreeSkills+ contract). Additionally, we thank Nilsa Bosque-Perez, Narelle Nancarrow, Hollie Riley and Glenn Fitzgerald for comments on early versions of the manuscript.

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Manuscript received October 31, 2016

Final version received August 6, 2017

Accepted August 7, 2017

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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virus

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 ₂	Plant–insect–virus	Aphid density increased on infected plants under aCO ₂ , but not under eCO ₂ .	Fu <i>et al.</i> , 2010
<i>M. persicae</i>	Bell pepper	<i>Cucumber mosaic virus</i>	Elevated CO ₂	Plant–insect–virus	eCO ₂ 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 ₂	Plant–virus	Biomass increased in infected oats grown under eCO ₂ .	Malmström & Field, 1997
<i>R. padi</i>	Wheat	<i>Barley yellow dwarf virus</i>	Elevated CO ₂	Plant–virus	Virus titre increased in wheat under eCO ₂ .	Trębicki <i>et al.</i> , 2015
<i>R. padi</i>	Wheat	<i>Barley yellow dwarf virus</i>	Elevated CO ₂	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 ₂ .	
<i>R. padi</i>	Wheat	<i>Barley yellow dwarf virus</i>	Elevated CO ₂	Plant-virus	ECO ₂ 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 ₂	Plant-virus	Virus and eCO ₂ 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 ₂	Plant-virus	Natural incidence of yellow dwarf viruses (including BYDV) increased in the field (FACE) by over 10% as a result of eCO ₂ .	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 CO₂ (eCO₂), dashed lines represent indirect effects of eCO₂ changes via plant biochemistry or changes mediated through virus or insect vectors.