
The impact of climate change on wheat insect pests: current knowledge and future trends

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1 Climate change and insect pests: the global perspective

Historical trends and models suggest that sustained wheat production will be more difficult under projected climate change (Asseng et al., 2014; Challinor et al., 2014; Wilcox and Makowski, 2014). Unfortunately, these projections are limited in that they do not incorporate constraints on production from diseases, weeds and insect pests. Incorporating these factors is a significant challenge because information is limited. For insect pests, although trends noted for insects in general (e.g. Parmesan and al, 1999; Parmesan and Yohe, 2003; Parmesan, 2006; Bebber, 2015) might apply, specifics will vary widely because the potentially contributing mechanisms are diverse. These include changes to survival rates in winter and summer, population growth rates, shifts in phenology and changes in interspecific interactions (Kiritani, 2013). Effects that can

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come into play include direct effects of warming and increasing atmospheric CO₂ on pest fecundity and population dynamics (Dyer et al., 2013), shifts in geographic or elevational ranges of pests (Bebber et al., 2013; Bebber, 2015), expression of plant resistance factors affecting pests (Tyler and Hatchett, 1983; Currie et al., 2014), changes to feeding behaviour, phenology and voltinism (Ziter et al., 2012), and alterations to trophic interactions and biological control mechanisms (Gutierrez et al., 2008; Romo and Tylianakis, 2013; Thomson et al., 2010; Gillespie, et al. 2013; Eigenbrode et al., 2015).

Thus, although warming temperatures might generally be expected to increase pest pressure in agriculture (e.g. Patterson et al., 1999; Roos et al., 2011), the direction and level of pest responses to a changing climate vary among insect pest species, especially for pests of annual crops. In addition, for many pests, data are insufficient to make reliable projections of their responses to future climate change (Finlay et al., 2011; Seidel, 2014). For others, a growing literature relies on models that require additional validation (e.g. Newman, 2005, 2006; Ulrichs and Hopper, 2008; Wolfe et al., 2008; Gebauer et al., 2015). Long-term data sets tracking insect pest abundance through periods of climate change are useful, but are rare (e.g. Folcher et al., 2011, Bell et al., 2014; Brabec

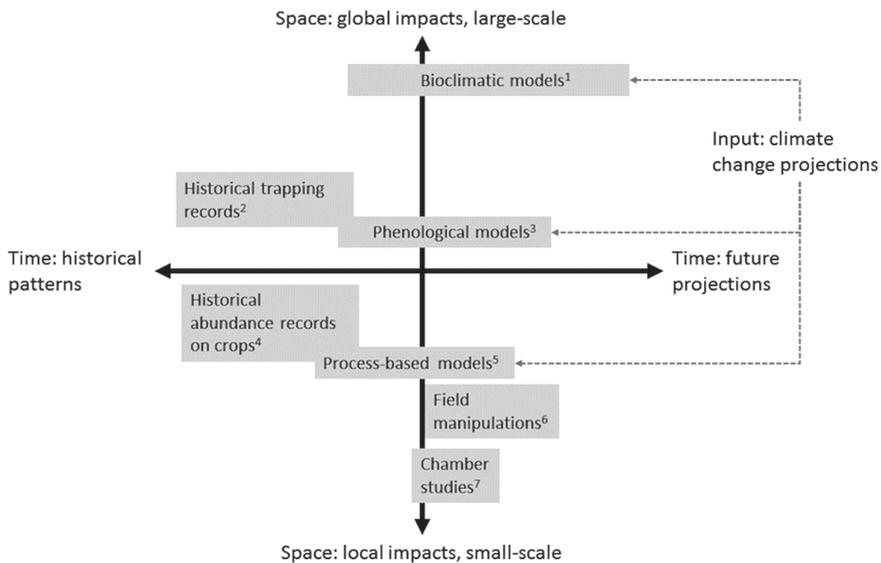


Figure 1 The range of tools and techniques used to assess potential climate change impacts on invertebrate pests. Their positions on the axes illustrate the time and space scale at which they can be used to draw conclusions. Examples of each technique in relation to wheat include: ¹(Olfert et al., 2004; Newman, 2006; Olfert and Weiss, 2006; Olfert et al., 2015), ²(Bommarco et al., 2007; Hullé et al., 2010; Bell et al., 2014; Davis et al., 2014; Sheppard et al., 2015), ³(Guo et al., 2009; Nufio et al., 2010), ⁴(Folcher et al., 2011; Evans et al., 2012; Brabec et al., 2014; Wang et al., 2015), ⁵none we could find relevant to wheat, ⁶(Dong et al., 2013), ⁷(Oehme et al., 2011; Le Lann et al., 2014).

et al., 2014; Davis et al., 2014), and projections based on those are uncertain because anticipated rates of climate change in most regions are greater than historical trends (Collins et al., 2013). These limitations pertain for insect pests of all production systems, including wheat.

The range of tools and techniques used to assess potential climate change impacts on invertebrate pests include those that assess insect responses to specific drivers experimentally through chamber studies and field manipulations, historical records of abundance in crops or in regional trapping networks. Coupled with climate models, these data records can inform process-based models, phenological models and bioclimatic or niche models (Fig. 1, and references cited therein). All of these approaches have been used to anticipate climate change effects on various insect pests of wheat at varying degrees. In this chapter, we summarize what is known about climate change and its implications for principal insect pests of wheat worldwide, and the tools and techniques that have been used to assess the potential impact of climate change on these species. Finally, we highlight directions for future research that may overcome some of the challenges. Most of the work that we summarize has focused on the impact of climate change on the pest species itself, and then has drawn conclusions on how this may impact yield loss in wheat (i.e. by increasing or decreasing the risk of damage from the pest). This chapter considers pests, construed as comprising insect pests, with the exception of viruses transmitted by aphids.

2 Cereal aphids

Wheat systems are attacked by several cosmopolitan aphid species important as direct phloem-feeding pests and as vectors of plant viruses (Blackman and Eastop, 2008). These pests can respond to climate variability through changes in the timing and abundance of their annual migrations, which can affect their arrival into fall and spring planted crops, with implications for viral disease epidemiology. Given the relatively abundant historic data and importance of these pests, aphids, especially cereal aphids, have received considerable attention in the context of climate change. The species receiving the greatest attention worldwide have been *Rhopalosiphum padi* L., *Metopolophium dirhodum* (Walker) and *Sitobion avenae* F. (Table 1). Less studied species are *Schizaphis graminum* (Rodani) and *Diuraphis noxia* (Kurduinov) (Hemiptera: Aphididae). Approaches to assess climate change impacts on aphids have included experimental chamber studies, free-air carbon enrichment field trials, analysis of long-term sampling data sets coupled with climate records and modelling based on these parameters (all those listed in Fig. 1). Therefore, this pest group offers the most comprehensive information for making generalizations and therefore predictions about climate change impacts.

Long-term suction trap networks have documented aphid migrations in the United Kingdom, Europe, and the Pacific Northwest (PNW) and Midwestern United States operated over different periods have detected changes in migrations related to warming. In Europe, a warming trend over 25 years has been associated with increased aphid diversity and earlier flight periods for cereal aphids (Hullé et al., 2010). In contrast, data from 17-year time-series from the PNW trapping network (Davis et al., 2014) detected different responses from the three most abundant species in the record. *D. noxia*

Table 1 Synopsis of studies reviewed on projected effects of climate change on some of the common global pests of wheat

Species	Key findings	Approach	Impact on pest*	Citation
<i>Rhopalosiphum padi</i>	Plant nitrogen concentration was affected by virus infection under elevated CO ₂ . Reduced aphid population size and increased feeding damage on non-infected plants grown in elevated CO ₂ . No changes to aphid population and feeding on virus-infected plants.	Laboratory study	±	Trebicki et al., 2016
	Reduced pest pressure in Southern Britain with elevated CO ₂ .	Coupled modelling	-	Newman, 2005
	Timing of arrival into wheat plots was earlier and increased aphid densities under warmer temperatures.	Historical 24-year sampling in the crop, western Czech Republic	+	Brabec et al., 2014
	No change in abundance with warming trend over last 50 years.	Historical 50-year suction trap samples, UK	±	Bell et al., 2014
<i>Metopolophium dirhodum</i>	No change in abundance with warming trend over last 50 years.	Historical 17-year suction trap, Idaho	±	Davis et al., 2014
	No change in abundance with warming trend over the last 50 years. Aphids caught in suction traps in the UK.	Historical 50-year suction trap samples, UK	±	Bell et al., 2014
	Timing of arrival into wheat plots was earlier and increased aphid densities under warmer temperatures.	Historical 24-year sampling in the crop, western Czech Republic	+	Brabec et al., 2014
	Increased abundance with mean annual precipitation.	Historical 17-year suction trap, Idaho	+	Davis et al., 2014
<i>Sitobion avenae</i>	Warming of wheat plots significantly increased the numbers of aphid in comparison to control plots in year one of the study. In year two, aphid populations did not differ between warmed and control plots, but there were parasitoids three times as abundant in warmed plots as in control ones. The rate of parasitism increased in the warmed plots.	Experimental manipulation in the field, eastern China	±	Dong et al., 2013
	Biological control by a principal parasitoid disrupted under increased temperatures.	Laboratory study	+	Le Lann et al., 2014
	Increased aphid density with higher temperatures and elevated CO ₂ .	Laboratory study	+	Adaros and Heimbach, 1997
	No change in abundance with warming trend over 50-year historical period.	Historical 50-year suction trap samples, UK	±	Bell et al., 2014

	Timing of arrival into wheat plots was earlier and increased aphid densities under warmer temperatures.		Historical 24-year sampling in the crop, western Czech Republic	+	Brabec et al., 2014
	Peak in migration phenology between aphids and parasitoids is broadly synchronized within a season, regardless of temperature.		Historical 50-year suction trap samples, UK	±	Perez-Rodriguez et al., 2015
<i>Diuraphis noxia</i>	Abundances negatively correlated with increasing temperatures after removing inter-annual density-dependent effects.		Historical 17-year suction trap, Idaho	+	Davis et al., 2014
Viruses transmitted by aphids	Lower aphid populations on non-infected plants under elevated CO ₂ , but no change or increased aphid populations on virus-infected plants, therefore more virus spread under elevated CO ₂ .		Laboratory study	+	Trebicki et al., 2016
<i>Sitodiplosis mosellana</i>	Synchrony between pest and parasitoids may be maintained under increased temperatures.		Laboratory study	±	Chavalle et al., 2015
<i>Mayetiola destructor</i>	Bioclimatic model suggests distributional range will expand in the future. The effectiveness of one pest resistance gene in cereals is weakened by heat stress.		Bioclimatic modelling Laboratory study	+	Olfert et al., 2015 Zhu et al., 2010; Currie et al., 2014
	Decreasing La Niña frequencies will make conditions less suitable for pest.		Historical 20-year records in South-eastern United States	-	Woli et al., 2014
<i>Oulema melanopus</i>	Bioclimatic models suggest increased suitability of habitats and northward range expansion under warmer climates. Decreases in peak parasitism rates in years with warm springs.		Bioclimatic modelling for North America Historical 10-year records in Utah	+	Olfert and Weiss, 2006; Olfert et al., 2004 Evans et al., 2012
<i>Helicoverpa armigera</i>	No effect of elevated CO ₂ on interaction between pest and parasitoid. Elevated CO ₂ and temperature increased foliar consumption and therefore may cause more damage to crop production. Increased temperatures enhance survival of overwintering pupae.		Laboratory study Laboratory study Historical 17-year records, northwest China	± + +	Yin et al., 2009 Akbar et al., 2016 Huang et al., 2015

*+ Study provided evidence for increased abundance, survival, development or severity of the pest with a climatic trend and/or elevated CO₂. – study provided evidence for decreased abundance, survival, development or severity of the pest with a climatic trend and/or elevated CO₂. ± study was neutral or equivocal concerning pest response to a climatic trend. Note: there will be a publication bias towards studies that show some impact.

abundances in traps were negatively correlated with increasing temperatures in the absence of density-dependent effects. This period included the initial decade of outbreak dynamics for *D. noxia*, followed by the more stable dynamics that ensued after 1995. *R. padi* abundances were unrelated to climate variables irrespective of population feedbacks, whereas *M. dirhodum* abundances were positively correlated with increasing cumulative precipitation in the presence of density-dependent effects (Davis et al., 2014). Similarly, long-term suction trap data from the United Kingdom (Bell et al., 2014) indicate that the two most prominent cereal aphid species, *M. dirhodum* and *S. avenae*, showed little response to warming trends over a 50-year period. Working with the same data set as Bell et al. (2014), Sheppard et al. (2015) showed that the cereal aphid species, among other pestiferous aphids, exhibited changes in spatial synchrony of first-flight dates associated with spatial synchrony in winter temperatures in the United Kingdom.

In a long-term study at a smaller spatial scale, the abundance of *M. dirhodum*, *S. avenae* and *R. padi* on plots of winter wheat was recorded over 24 years at a location in the western Czech Republic (Brabec et al., 2014). The data showed that temperature affects timing of arrival of aphid populations into cereal stands and that aphid densities respond positively to temperature (the duration and accumulated heat units during the season). In a study of the cereal production systems in China spanning 23 years from 1987 to 2010, a trend of increasing pest damage by cereal aphids (collectively) and rising temperatures in February during the same period suggest a causal link (Wang et al., 2015).

Bioclimatic models can be used to project potential geographic changes in pest species distributions based on their temperature and moisture requirements (reviewed in Hill and Thomson, 2015). Using the bioclimatic model CLIMEX (Hearn Software), Svobodova et al. (2014) concluded that *R. padi* could expand its range northward in Europe, above 55°N by mid-twentieth-first century, and that changing temperature and moisture may allow the development of more generations per year of both *R. padi* and *S. avenae* in Northern Europe. Bioclimatic models can be improved by incorporating indirect effects that arise from climate effects on host plants. Newman (2006) used a mechanistic model incorporating grass growth physiology, aphid population dynamics and climate projections (Hadley Centre HadCM3 global circulation model) to project northward shifts in the range of cereal aphid populations in Canada accompanied by declines in aphid abundance in continental regions and increases in the coastal regions.

Indirect effects of climate change on the host plant can influence herbivores, and this is a particularly important result of the increasing concentrations of atmospheric CO₂ that affect plant growth. Most studies indicate greater population growth of phloem feeders, including cereal aphids, on plants grown under elevated CO₂ in growth chambers (Whittaker, 1999; Sun et al., 2016). For example, a chamber study with *S. avenae* projected increases in densities of the aphid with increased temperature (mean of 20 vs 17°C) and CO₂ (1000 ppm vs 400 ppm) (Adaros and Heimbach, 1997). In another example, *R. padi* increased in biomass by approximately 20% on spring wheat grown in growth chambers under enhanced CO₂ (400 ppm and 600 ppm) over two years (Oehme et al., 2011). In a meta-analysis, Robinson et al. (2012) found increased survival and abundance of Homoptera (which includes aphids) under elevated CO₂. Thus, comprehensive projections for aphid abundance with changing climates must incorporate temperature, precipitation and CO₂ in combination. Putting these factors together can result in complex outcomes. Newman (2003) showed that although elevated CO₂ and temperature each separately produce increases in cereal aphid population sizes, when both changes are imposed together (and assuming that soil nitrogen levels are adequate), projected aphid population dynamics

are more similar to current conditions. Newman (2005) used parameterized models that projected declining pest status of cereal aphid populations with increasing CO₂ in Southern Britain, with temperature and precipitation as the overriding drivers. It seems likely that the combined effects of climate and CO₂ will have different effects on aphid abundance and timing of their flights in different settings. Newman et al. (2003) showed that 'idiosyncratic' behaviour among aphids in response to CO₂ could be explained based on interactions between this factor and responses of each species to nutrients and crowding. Determining what factors contribute to climate change effects on cereal aphids for a particular system and how these interact will be necessary to generate reliable projections.

In addition to these bottom-up effects of climate change on aphids (and other pests), the influence of natural enemies can also be substantial. Multi-year records of aphid populations taken in suction traps often reveal strong inter-annual biotic feedback (Bommarco et al., 2007; Davis et al., 2014), which can be more pronounced than the climate signal (Davis et al., 2014). These could be caused by resource limitation or predators, parasitoids, or pathogens, which in turn are affected by climate. Evidence for such effects is weak or mixed. Biological control of *S. avenae* by its parasitoid, *Aphidius rhopalosiphi*, was disrupted by increased temperatures in a growth chamber experiment because the two species responded differently in terms of their resting metabolic rate (Le Lann et al., 2014). A semi-field-scale experiment in a temperate wheat-growing region in China (Dong et al., 2013) reported that artificial warming over two years (increase of 1.1 to 1.6°C in soil temperatures) caused >50% increase in abundance of *S. avenae* in one year with very low parasitism, with parasitism rates similar between the imposed climate regimes. In the second year, however, the warmed plots had a higher percentage of parasitism of aphids (and about three times the abundance of parasitoids), but aphid populations sizes did not differ among the soil temperature treatments. The study is difficult to interpret because the warmed subplots were small (just 2 m x 2 m) but the different effects in different years may represent the complex dynamics that could occur. Using a model that incorporated aphid and parasitoid responses, Hoover and Newman (2004) showed that climate change should not alter biological control of cereal aphids. Consistent with this, based on suction trap samples from 1976 to 2013 from two sites in Southern England, simple regression models showed that the peak parasitoid abundance was correlated with peak aphid abundance in this record (Perez-Rodriguez et al., 2015). Together, and based on the reports so far, there is little evidence that parasitism of aphids will be disrupted by climate change. Aphids are subject to many other natural enemies that can be at least as important as parasitoids, but these do not appear to have been studied in a climate change context.

Together, the available studies on cereal aphids and climate change do not permit robust generalizations because of the variable responses exhibited by different aphid species in the same regions or locations, or different responses of the cereal aphid species complex in different regions. Certainly more studies are needed to clarify projections and refine approaches for generating them.

3 Vector-borne plant viruses

The seriousness of aphid pests of wheat derives largely from their role as vectors of destructive viruses, especially the Barley yellow dwarf virus (BYDV) species complex (Parry

et al., 2012). Finlay and Luck (2011) review the various factors that could affect the spread of BYDV by one of its principal vectors, *R. padi*, including direct effects of warming, elevated CO₂ and changes in precipitation on the performance and migration of the aphid and its natural enemies, and the effects of warming and CO₂ on virus transmission. The authors conclude that significant research gaps exist for all of these aspects of the pathosystem and its potential response to climate change. In simple terms, virus spread and disease incidence are proportional to vector abundance, as expected from epidemiological models (Jeger et al., 2004; Sisterson, 2008, 2009). Other effects on these systems include the influence of climatic factors on virus titer within the plant, which can also influence spread. In a chamber study, BYDV-infected plants reached higher virus titer in growth chambers under elevated CO₂, and the authors concluded that virus spread could be greater under future atmospheric conditions (Trebicki et al., 2015). A follow-up study projected lower aphid populations on healthy plants but no change or increased aphid numbers on infected plants that together could alter virus epidemiology (Trebicki et al., 2016). The environmental effects on BYDV can extend to temperature as well. Wheat plants grown at substantially higher temperatures (increase of 5°C) and infected with BYDV had significantly higher virus titers (Nancarrow et al., 2014). Virus spread is also influenced by the behaviour of the vectors, which in turn is influenced by chemical cues characteristic of infection status, a phenomenon that is well documented in several systems, including BYDV infection in wheat (Eigenbrode et al., 2002; Jimenez-Martinez et al., 2004; Ingwell et al., 2012). The manner in which these sorts of interactions are influenced by temperature or CO₂ have yet to be examined.

Effects at the interface of BYDV, its vectors, host plant and climate may have another level of complexity. Recent studies have shown that drought and virus infection effects interact in wheat, such that wheat infected with BYDV exhibits greater tolerance to drought stress, a phenomenon related to the plant's stress response mechanisms (Davis et al., 2015a,b). Furthermore, the infected plants under drought were better hosts than non-infected plants for *R. padi*, which exhibited greater population growth on the infected plants under drought (Davis et al., 2015a). Thus, although the effects of climate change on BYDV are indicated, specifics are difficult to project from the information available and are likely complex. Climate change effects on other vector-borne pathogens of cereals have not been well documented (Juroszek and von Tiedemann, 2013).

4 Hessian fly and orange wheat blossom midge

4.1 Hessian fly

The Hessian fly [*Mayetiola destructor* (Say)] is a univoltine pest in the northern parts of its range in North America, but it can have up to six generations in the southern latitudes (Wellso, 1991). In warmer climates, Hessian fly exhibits summer estivation, whereas in cooler ones, the fly overwinters in a diapausing pupal stage. Warming trends may shift voltinism of Hessian fly through this continuum, which would change the timing of infestations at different latitudes. Across parts of the Midwestern United States, recommendations for Hessian fly management include delaying planting of winter wheat until after a prescribed 'fly-free date' after the winter estivation has begun (e.g. Boyd and Bailey, 2000). Climate warming could undermine the fly-free-date method by extending oviposition beyond the period when producers can realistically delay planting due to other factors affecting wheat crop development and yield (Zheng et al., 2012).

Climate drivers have other effects on the likelihood of Hessian fly outbreaks across larger spatial and temporal scales that have been detected using long-term data sets. Over a 20-year period in the South-eastern United States, Hessian fly infestation and yield losses were greatest during years with wetter, cooler August–September conditions and warmer drier October–February conditions, both of which tended to occur under the ‘La Niña’ years of the El Niño Southern Oscillation or ENSO (Woli et al., 2014). Climate change-related trends in ENSO patterns suggest increasing frequency and intensity of El Niño years (Cobb et al., 2013), which if accompanied by decreasing La Niña frequencies could reduce pressure from Hessian fly in South-eastern United States (Table 1).

The most important means of managing Hessian fly globally is through the use of host plant resistance (HPR). Resistance to Hessian fly in wheat has been known for more than two centuries, and there are 32 known resistance genes that can readily be transferred into wheat varieties to match virulence genes in Hessian fly populations (Ratcliffe and Hatchett, 1997). The biology and genetics of resistance to Hessian fly is better understood than for any insect pest (Harris et al., 2003; Stuart et al., 2012). Presumably HPR to Hessian fly will remain largely robust under climate change, but interactions between climate and the efficacy of HPR are feasible and well documented in other systems (e.g. temperature-dependent resistance to fungal pathogens [Barrett et al., 2009]). Indeed, the effectiveness of at least one Hessian fly resistance gene is weakened in plants exposed to heat stress near the time of insect attack (Zhu et al., 2010; Currie et al., 2014). These effects have not been widely documented, and the mechanisms are unclear, but merit further study.

4.2 Orange wheat blossom midge

Phenology of the midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae), is responsive to temperature, or temperature in combination with precipitation, in field studies from different locales (Elliott et al., 2009; Jacquemin et al., 2014). Reliability of phenological models was validated for current conditions in these locals, but might not be robust under future conditions or different locales. Indeed, degree-day requirements for midge emergence differ considerably among published models (Jacquemin et al., 2014). Similar responses of the midge and its parasitoids to climatic factors in controlled chamber studies (Chavalle et al., 2015) indicate that synchrony should be maintained under projected changes in climate, although this requires additional study and verification (Table 1). Bioclimatic models (Olfert et al., 2015) indicate that the distribution of the midge in North America is unlikely to expand westward or southward from its current range under changing climate, but northward expansion is projected, especially across the Canadian Prairie Provinces, including areas where wheat currently is not grown but may be in the future.

5 Cereal leaf beetle, cotton bollworm and other pest species affecting wheat

5.1 Cereal leaf beetle

The cereal leaf beetle, *Oulema melanopus* L. (Coleoptera: Chrysomelidae), has been studied in terms of its potential response to climate change. During its initial invasion of North America, a number of exhaustive studies were conducted to document and model

its phenology and responses to climate drivers (Haynes and Gage, 1981; Bailey et al., 1991; Roberts and Walenta, 2012). This information was used to develop a bioclimatic model to project the extent of its potential invaded range under current climates of North America, and to estimate its range under hypothetical incremental increases in mean annual temperatures in Canada (Olfert and Weiss, 2006). Together, these studies indicated that warming temperatures will increase the suitability of cropping system habitats for the beetle under warming climates (Table 1).

There is also evidence that biological control of the cereal leaf beetle will be altered under climate change. Using observed observations from Utah's Cache Valley over a 10-year period, Evans et al. (2012) detected sharp decreases in the maximum parasitism rate of *O. melanopus* by its principal introduced parasitoid, *Tetrastichus julis*, during warm springs. Using downscaled climate projections, Evans et al. (in prep) show that under projected climates in the PNW, the frequency of years when parasitism is substantially weakened will increase, coupled with the previously projected increases in suitability of the climate for the beetle. Together, these trends could exacerbate the severity of this pest, which is currently held in check by biological control across much of its range in western North America.

5.2 Cotton bollworm

The cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), is a highly polyphagous pest species that undergoes facultative diapause and exhibits large-scale seasonal migration events. This species attacks a range of crops in Asia, Australia, Africa and Europe, and has recently expanded its range into South America (Kriticos et al., 2015). Long-term time-series data on overwintering of *H. armigera* in China showed how increases in winter and spring temperatures may alter phenology (Huang and Li, 2015; Ouyang et al., 2016). Increasing average overwinter temperatures has resulted in early eclosion of pupae and extended the duration of the first generation of moths, which then increases damage to early wheat crops (Table 1). A small field cage study demonstrated that the early eclosion of moths had a significant effect on wheat biomass due to larval feeding. In an open-topped chamber study, Yin et al. (2009) showed that for the first generation of *H. armigera* reared on wheat plants grown in elevated CO₂, there was no impact on the generation time or rate of increase. However, the second generation experienced longer generation times and slower rates of increase. A parasitoid wasp (*Microplitis mediator* Haliday) of *H. armigera* was included in the study but was unaffected by elevated CO₂. Other studies have illustrated that increased CO₂ can alter larval feeding behaviour. Akbar et al. (2016) showed that elevated CO₂ and temperature increased consumption of an artificial diet by *H. armigera* larvae, a unique result since most studies of CO₂ effects on herbivore are indirect, mediated by CO₂ effects on plants' quality. If such effects are also seen in commercial cereal fields, then there may be more damage to crops from this pest under elevated CO₂ conditions in the future.

5.3 Other pest species affecting wheat

The catalogue of pests affecting cereal systems (Duveiller et al., 2012) includes many species for which their potential responses to climate change have yet to be assessed. Grasshopper species (Orthoptera: Acrididae), including locusts [*Locusta migratoria* (L.) and *Schistocerca* spp.] and other species (*Melanoplus* spp.), can become pests of wheat

in different regions of the world (Capinera, 2008). There are few explicit studies of these species as cereal pests in the context of climate change, but studies with rangeland grasshopper communities indicate that changes in developmental responses to warming will differ among species (Nufio et al., 2010). Grasshopper species in grasslands differ in their phenological responses to warming and precipitation (Guo et al., 2009; Nufio et al., 2010), suggesting this may also be the case in agricultural systems. For example, although the first appearance of adults of ten different grasshopper species has advanced in response to a 50-year warming trend in Colorado, the first appearance of adults of *Melanoplus sanguinipes* (F.), a pest of wheat in the Great Plains, has been delayed over the same period (Nufio et al., 2010). On the other hand, a bioclimatic model suggests that *M. sanguinipes* may have increased range and relative abundance in northern regions of North America in the future (Olfert et al., 2011).

There appears to be no scientific information on the possible effects of climate change on the wheat stem maggot, *Meromyza americana* Fitch (Diptera: Chloropidae); the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae); or on the various species of stinkbugs (Hemiptera: Pentatomidae), cutworms and armyworms (Lepidoptera: Noctuidae), thrips (Thysanoptera), white grubs (Coleoptera: Scarabidae) and wireworms (Coleoptera: Elateridae) that can affect cereal crops to varying degrees in different regions.

6 Climate change effects on biological pest control in wheat systems

Pest abundance in agroecosystems is strongly influenced by the abundance and effectiveness of natural enemies. Climate change potentially influences biological control through various mechanisms, including changes in the phenology and geographic ranges of predators and their prey, that can alter the degree of synchronicity between predators and prey in time and space, and changes in the physiology of host plants or prey that can influence efficacy of natural enemies (Gutierrez, 2000; Thomson et al., 2010; Eigenbrode et al., 2015). Changes in farming practices to adapt to climate change (e.g. changes in sowing dates, stubble retention) can also alter biological control through altering natural enemy abundance, diversity or activity (Thomson et al., 2010).

Examples in which such effects have been examined rigorously are rare, including those specifically focused on cereal systems. As reviewed above, for aphids, data and models available suggest that parasitism will not be disrupted by climate change (Hoover and Newman, 2004; Dong et al., 2013; Perez-Rodriguez et al., 2015). On the other hand, the study of cereal leaf beetle (Evans et al., 2012) suggests warming trends could strongly reduce larval parasitism of this pest.

Most biological control in cereal systems is *conservation biological control*, which is provided by the entire community of natural enemies that are present in these systems. Insect communities within agroecosystems will be affected by climate change through effects on individual species and their interactions, changing community structure and abundance. Drivers for these changes are numerous and include changes in plant defensive responses that influence the insects, changes in predation rates and interspecific competition. Studies suggest that higher trophic levels are most sensitive to climate change (Stireman et al., 2005; Gilman et al., 2010). Climate change has caused

the extinction of many species in natural systems (usually due to a constriction in suitable habitat), and more are threatened (Sala et al., 2000; Tylianakis et al., 2008). If natural enemy communities in production systems also have fewer species as climates warm, and more species-rich communities exert more control as has generally been determined (Hooper et al., 2005; Cardinale et al., 2006, 2013; Crowder et al., 2010; Snyder et al., 2006), then a weakening of biological control in agroecosystems, including cereal systems, with warming is a reasonable concern.

Unfortunately, the effects of climate change on natural enemies have not been rigorously documented in broad-acre cereal production systems; all the examples in this section are from other systems (e.g. natural systems, forestry, orchards and vegetable production systems). An exception to this was conducted in a cereal production system in the United Kingdom. Berthe et al. (2015) examined the effects on abundance of higher taxa of Coleoptera (mostly predators) in response to artificial warming (increase of 2°C), enhanced precipitation (increase of 10%) or both, during a single season. Diversity indices, based on eight taxonomic groupings, decreased as a result of warming but were unaffected by extra precipitation. Warming increased pitfall trapping (activity-density) of the four most abundant predaceous species. Unfortunately, the short duration and small plot size (2 m x 2 m) make it difficult to interpret these results, and no measurements were taken of prey densities to assess effects on biological control. More work of this kind is merited.

7 Other considerations: interaction of stress factors, extreme events and pest behaviour

7.1 Interactions between pest and multiple stressors

The interaction between multiple abiotic factors in the crop environment and biotic factors such as pest incidence and severity might also change under climate change (Kaunisto et al., 2016). For example, an acute exposure to cold temperature stress rendered wheat plants more susceptible to colonization by apterous *R. padi* (Lacoste et al., 2015). As described above, temperature sensitivity of insect and pathogen resistance genes potentially will increase vulnerability of systems to warming. Different stressors can interact in a number of ways that may lead to synergistic or antagonistic outcomes. Kaunisto et al. (2016) note that although we have described how some insects respond to single stressors, few studies have looked at multiple stressors in combination. Similarly studies that examined the combined impacts of CO₂ enrichment and increased temperatures on invertebrate pests are rare (although we have given some notable examples for aphids above; see Robinson et al., 2012). Methods such as the free-air carbon enrichment trials (e.g. Fitzgerald et al., 2016) can be used to address this question for immobile pest species; for other species closed chambers will be necessary.

7.2 Extreme events

All of the work on pests in wheat systems has been premised on understanding species responses to projected climate trends, which necessitate the averaging of climate data across time and space (usually with a large spatial and temporal resolution, Fig. 1). The climate science community is increasingly interested in the implications of 'extreme events', which could be very different from those of trends, even though extreme event

frequencies may be projected to change. Extreme events include storms and heat waves that cause mortality of individuals and put stress on pest populations, usually for short periods. Extreme events in turn will have varying effects on crop yield and quality. For example, based on simulation models, grain protein in wheat responds not only to change in mean temperature and precipitation, but also their variability (Porter and Semenov, 2005). In a relevant study which combined a laboratory experiment with a six-year observational field study, meta-analysis of three aphid species, namely *R. padi*, *S. avenae* and *S. graminum*, showed differing responses to extreme high temperature (EHT) events (defined as temperature spikes to 34 or 38°C, at two different frequencies) (Ma et al., 2015). All methods showed consistent results, with *R. padi* exhibiting an ability to compensate and thereby recover from EHT events, whereas the other two species were unable to do so (also see De Barro and Maelzer, 1993). This pattern appears to explain the relative prevalence of the three aphids in different wheat-producing regions of the world. It also suggests that increased frequencies of EHT events, that may be part of future climate systems, will shift aphid community composition, not in response to means, but in response to thermal variability (Ma et al., 2015). In another study involving cereal aphids in growth chambers, heat stress regimes extended the development period, and reduced fecundity of *S. avenae*, while cold stress regimes reduced population growth rates, but not fecundity, per se (Jefferies and Leather, 2014).

7.3 Pest behavior

Extrapolating from chamber studies to climate change projections carries risks in that chambers fail to incorporate behavioural aspects of insect responses to climate change (Sun et al., 2016). *R. padi*, as compared with *M. dirhodum* and *S. avenae*, better survives winter temperatures in the field at the Long Term Ecological Research site in north-western France, despite its relatively poor low-temperature thermal tolerance in chambers, indicating the species is able to mediate its exposure behaviourally (Alford et al., 2014). The different responses of cereal leaf beetle and its parasitoid, *T. julis*, to warm springs in Utah (Evans et al., 2012) might not have been anticipated based on chamber studies since the differences evidently stem from the beetle's basking behaviour, which accelerates its accumulation of thermal units in cooler conditions early in the spring, in contrast to the parasitoid, which is not mobile during that part of the season.

8 Conclusions

Wheat growers may be faced with greater challenges from insect pest management under future climates, but projections are incomplete and varied among important pest species, and we currently have an incomplete understanding of the causes of the variability that is evident. Consistent with the situation for all the major crops, understanding of the ongoing and potential effects of climate change on insect pests of wheat remains fragmentary. First, the number of species that have been studied in the context of climate change is limited. Table 1 summarizes results for nine species that are prominently represented in the literature on wheat pests and climate change, but more than 30 species are important pests of wheat worldwide (Duveiller et al., 2012). Second, long-term data sets to allow tracking insect responses to historical climate trends are scarce. Such studies have the advantage of revealing pest responses as an outcome of changes to the production

system. Unfortunately, of the 23 studies listed in Table 1, just nine are based on long-term records. Even these data sets have limitations in that projected trends may be more severe than historical trends, and factors other than climate could have influenced the historical trends. The remaining examples in Table 1 are laboratory or small plot studies, or outputs from bioclimatic modelling, which often are parameterized with laboratory data. These sorts of studies are subject to modelling assumptions and experimental conditions imposed and controlled in the laboratory.

Nonetheless, despite these limitations, there appears to be a general trend towards climate change exacerbating pest problems in wheat systems that have been studied, with 13 instances of greater abundance or severity, nine instances of equivocal effects and just one instance projecting decreased abundance or severity (Table 1). Although this trend may not persist with additional research, it indicates the need for investment in research to delineate the potential threat to food security that increasing pest pressure in wheat systems may present. The variability in the types and direction of responses within (across studies) and among species is striking, even in this small number of available studies. It is likely that this variability will prevail as additional data accumulate. Most of the studies pertain to one or a few pests within a particular system or region. We do not have data or studies across the full spatial and temporal range needed for a comprehensive picture (i.e. all the tools and techniques shown in Fig. 1) for any single species (Table 1), let alone pest complexes like those affecting wheat. The way forward is therefore challenging. We suggest the following specific research gaps that require attention:

- *Obtaining additional long-term records of pest abundance or pest injury and coupling these with historical climate records.* Data sets of pest abundance or pest injury in wheat systems might exist that have yet to be analysed in conjunction with historical climate records. Several of the publications cited in Table 1, although relatively recent, draw upon such archival records (Bell et al., 2014; Brabec et al., 2014; Davis et al., 2014; Woli et al., 2014; Huang et al., 2015; Perez-Rodriguez et al., 2015). Where such historical records are lacking, they should be initiated without delay to enable projections as climate change progresses.
- *Incorporating pests and natural enemies into niche overlap and phenological models.* To improve on simple bioclimatic simulations, the effects of interacting species, especially natural enemies of pests, should be incorporated (Sutherst et al., 2007; Sutherst et al., 2011, and references in Aurambout et al., 2009; Gilman et al., 2010; Dyer et al., 2013). We have yet to see natural enemies of pests routinely incorporated into climate change projections. For common natural enemies affecting wheat systems worldwide, we should make a greater effort to incorporate their effects explicitly into climate change models.
- *Focusing on mechanisms.* Although systems and species will certainly differ, common mechanistic principles that can help improve the reliability of projections should be pursued. Wheat systems worldwide share many of the same pest species, which is an advantage that can be exploited. Different species respond differently to the same drivers. It is to be hoped that a greater understanding of mechanisms will untangle the idiosyncratic differences among species to various aspects of climate change and help establish principles that can be applied more generally to different production systems (Newman, 2005; Andrew et al., 2013).
- *Employing complementary, comprehensive approaches for individual pest species.* Based on Table 1, studies of individual pest species are fragmentary. Some have

been examined based on models, while others based on long-term records and yet others through chamber or laboratory studies, the approaches are represented in (Fig. 1). These methods can be complementary when employed together, but that sort of comprehensive study is lacking for any pest of wheat. There are opportunities to do so using existing data sets and approaches that should be exploited.

- *More comprehensive study of whole systems.* Future studies must incorporate system-specific pest complexes affecting wheat. Virtually all of the studies have focused on a particular pest in a production region under climate change but have not considered the suite of pest herbivores. This extension to a system perspective can include recognizing that climate change affects insects and their natural enemies directly, but also indirectly through effects of temperature, moisture and CO₂ on the wheat plant that in turn influence herbivores and natural enemies.
- *Anticipating changes in farmer practices in response to climate change and agronomy that might significantly alter pest complexes.* We know that agricultural practices are continually changing in response to a range of drivers, and these will impact pest communities independent of climate change (Ewald et al., 2015). There are also a range of management practices that may exacerbate or ameliorate climate change impacts on pests (e.g. pesticide use, stubble retention and reduced tillage, changes to planting dates, changes to crop rotations). We can study some of these now to see what impact they may ultimately have on pest risk. Improvements in the tools and techniques currently available will be required (e.g. Pearson and Dawson, 2003; Elith et al., 2006; Alford et al., 2016), along with a re-framing of the climate change research questions we assess (i.e. from what is the impact to how can we manage for a range of responses).
- *Providing timely information for farmers.* While this research agenda is important in the medium and long term, growers are seeking ways to adapt to potential climate change impacts now, and we have a responsibility to use our knowledge to assist them in meeting this challenge. Abbott et al. (2014) showed that predicting qualitative effects of climate change is possible with only basic knowledge about a production system. Decision-making by growers that relies more on empirically derived thresholds and simple guidelines will be important in any response to climate change-induced effects on pest abundance. Since pests may respond in various ways to climate change, with some becoming less severe regionally or even locally, and others more severe, there will be no substitute for prudent and effective application of integrated pest management principles and tools. Continued development and promulgation will be an important part of helping farmers cope with insect pests of wheat as climates change worldwide.

9 Where to look for further information

Adapting Agriculture to Climate Change. Edited book (Stokes and Howden, 2010) that summarises climate change scenarios for Australia and considerations for adapting to climate change in various agricultural sectors. <http://www.publish.csiro.au/book/6170/>

Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., Butterfield, J., Buse, A., Coulson, J. C., Farrar, J., Good, J. E., Harrington, R., Hartley, S. E., Jones, T. H., Lindroth, R. L., Press, M. C., Symnioudis, I., Watt, A. D. and Whittaker, J. B. (2002), 'Herbivory in global climate change research: direct effects of rising temperature

on insect herbivores', *Global Change Biol.*, 8, 1–16., a key reference pertinent to insect pest responses to warming.

Bjorkman, C. and Niemela, P. (2015) *Climate change and insect pests*. CABI, Oxon, UK., an edited volume with 14 chapters covering climate change effects on insect pests of forestry and agriculture - see <http://www.cabi.org/bookshop/book/9781780643786>

Climate Change in Australia, a comprehensive site covering climate change projections, impacts and adaptations, sponsored by the Department of the Environment and CSIRO, <https://www.climatechangeinaustralia.gov.au/en/>

Climate Change in Australia, a comprehensive site covering climate change projections, impacts and adaptations, sponsored by the Department of the Environment and CSIRO, see <https://www.climatechangeinaustralia.gov.au/en/>

Primary Industries Climate Change Center, Australia, focuses on the effects of rising CO₂ for agriculture, <http://piccc.org.au/research/project/252>

Primary Industries Climate Change Center, Australia, focuses on the effects of rising CO₂ for agriculture, also has information about the FACE site <http://piccc.org.au/research/project/252>

Regional Approaches to Climate Change for PNW Agriculture, a web site housing information generated by a large transdisciplinary climate change project focused on wheat systems of the American Northwest. <http://reachpna.org>

Transitioning Cereal Systems to Adapt to Climate Change, a 2015 conference on climate change and semi-arid production systems. Program and talks is archived at the University of Idaho. <https://aridcereals.nkn.uidaho.edu>

Walshall, C.L. et al. (2012), *Climate Change and Agriculture in the United States: Effects and Adaptation*. USDA Technical Bulletin 1935. [https://www.usda.gov/oce/climate_change/effects_2012/CC%20and%20Agriculture%20Report%20\(02-04-2013\)b.pdf](https://www.usda.gov/oce/climate_change/effects_2012/CC%20and%20Agriculture%20Report%20(02-04-2013)b.pdf)

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