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REVIEW

IMPACTS OF CLIMATE CHANGE ON CROP PRODUCTION, PESTS AND PATHOGENS OF WHEAT AND RICE

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KEYWORDS

climate change, pest, pathogen, food security

HIGHLIGHTS

- An overview of impacts of climate change on wheat and rice crops.
- A review on impacts of climate change on insect pests and fungal pathogens of wheat and rice.
- A selection of adaptation strategies to mitigate impacts of climate change on crop production and pest and disease management.

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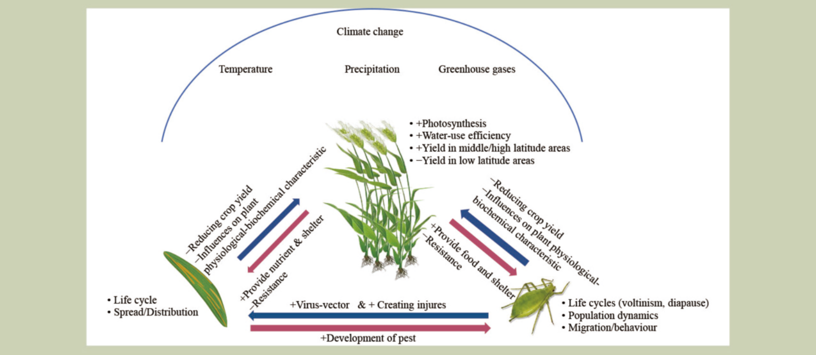
GRAPHICAL ABSTRACT



ABSTRACT

Ongoing climate change is expected to have impacts on crops, insect pests, and plant pathogens and poses considerable threats to sustainable food security. Existing reviews have summarized impacts of a changing climate on agriculture, but the majority of these are presented from an ecological point of view, and scant information is available on specific species in agricultural applications. This paper provides an overview of impacts of climate change on two staple crops, wheat and rice. First, the direct effects of climate change on crop growth, yield formation, and geographic distribution of wheat and rice are reviewed. Then, the effects of climate change on pests and pathogens related with wheat and rice, and their interactions with the crops are summarized. Finally, potential management strategies to mitigate the direct impacts of climate change on crops, and the indirect impacts on crops through pests and pathogens are outlined. The present overview aims to aid agriculture practitioners and researchers who are interested in wheat and rice to better understand climate change related impacts on the target species.

1 INTRODUCTION

The climate is changing across the globe. Such changes can affect the agricultural system through impacts on crops and their pests and pathogens. The effect of climate change on agricultural productivity has been studied for more than two decades. These studies, relevant to crop production and climate change, have generally focused on three subjects: crops, pests and pathogens, but rarely focus on all three factors at the same time or on interactions between them. Abundant evidence from these studies indicates that climate change can have direct negative impacts on crop yields[1–4]. Also, climate change can have indirect impacts on crop productivity through effects on pests, pathogens, weeds and other biotic factors such as natural enemies of agricultural pests[5] (Fig. 1). Like crops, pests and pathogens that negatively affect crop growth, development, and yield formation, can be sensitive to climate change[6–9]. To date, few studies have focused on the impact of climate change on the interaction between crops, pests and pathogens[10]. A good understanding of the effects of these interactions, and the impacts of climate change, on crop productivity, especially of the most important global food crops, is imperative for global food security.

Wheat and rice are the two most important food crops for mankind. The impacts of climate change on yields of these two crops, and their pests and pathogens, have received considerable attention from scientists. In this paper, we focus on these two primary staple food crops, and their major pests and pathogens. We first summarize the studies on impacts of climate change on crops, pests, and pathogens separately, point out potential mitigation strategies in pest and disease management and identify research gaps. We then discuss the diverse ways how climate change will influence interactions between these crops, their pests and pathogens (Fig. 1) and provide some insights for future perspectives as well as some avenues for future research. With our review, we aim to contribute toward obtaining a comprehensive understanding of how climate change will impact food crops and their insect pests and pathogens, which will help scientists and decision makers to identify and design mitigation strategies to reduce negative impacts on crop production.

2 IMPACT OF CLIMATE CHANGE ON WHEAT AND RICE PRODUCTION

2.1 Wheat

Wheat, ranking first in total harvested area worldwide (about 216 Mha in 2019)[11], is the most important grain crop for

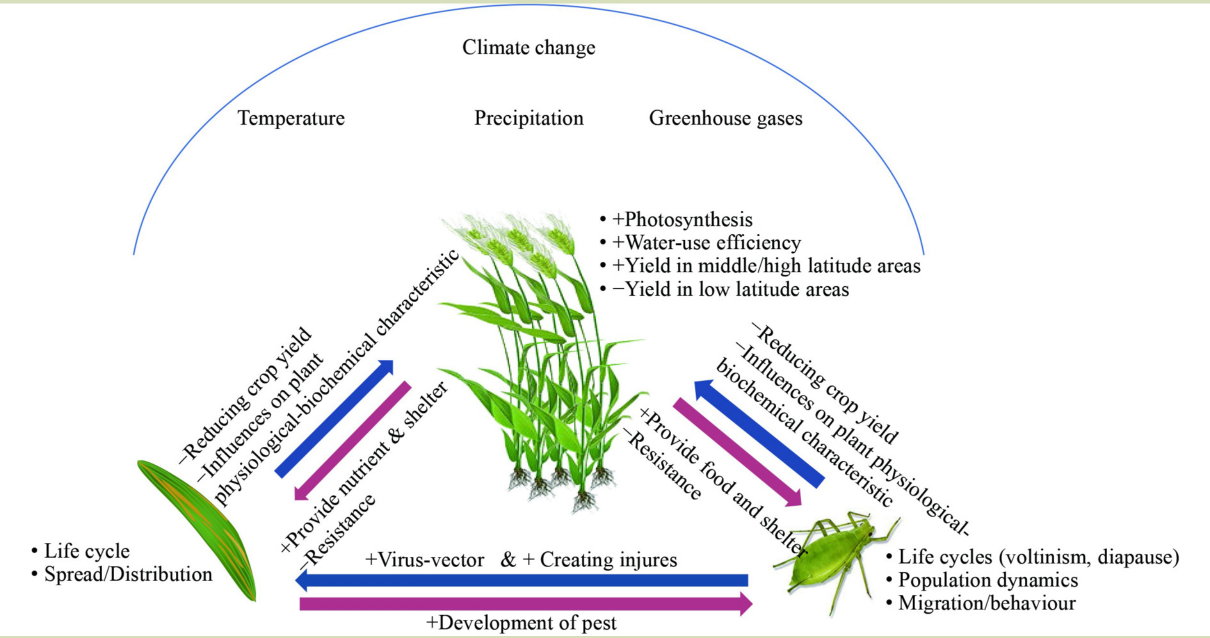


Fig. 1 A conceptual illustration of how multiple trophic levels (crop-pest-pathogen) respond to climate change and the interaction between them in farmland ecosystems. Changes in temperature, precipitation and concentrations of greenhouse gases caused by climate change can bring about positive or negative impacts on crops, and pests and pathogens of crops. Plus signs indicate that the interaction will benefit another organism (red arrow), and minus signs indicate that the interaction will inhibit another organism (blue arrow).

humans. In general, a climate change related increase in temperature will have negative effects on wheat yield on a global scale according to a number of recent studies[1–4]. Although effects on yields show regional and seasonal variations, without considering fertilization effects of carbon dioxide, effective adaptation, and genetic improvement, a 1 °C increase in global mean temperature could reduce global wheat yields by 6.0%[1]. However, average yields have increased across Europe since the 1960s due to lengthening of the growing season due to rising temperatures[12]. Also, expansion of the cultivatable area is projected to occur in northern Europe and Asia[12], while in most developing countries, located at lower latitudes, the cultivatable area is projected to decrease.

The physiological mechanisms of yield and quality reduction by climate change have been explored in many studies. An increase in atmospheric CO_2 concentration has a beneficial effect on wheat since it is a precursor in photosynthesis. An elevated atmospheric CO_2 concentration can increase photosynthetic rate, promote growth, and consequently change yield levels[13]. However, an increase in temperature can impact all physiological processes of wheat, also negatively affecting yield. Wheat benefits from a mild (10–24 °C) temperature for growth and development[14]. The suitable range of temperature varies for different developmental stages from germination and seedling growth to heading and flowering[14]. Wheat can stop forming new seeds when the temperature rises above the suitable range of temperature for these processes[14]. Porter and Gawith[15] summarized the temperature ranges for different phenological phases of wheat plants. Recent studies showed that wheat, as a C_3 plant (with a Calvin-Benson cycle), has a considerable ability to adjust its photosynthetic capacity to respond to rising temperatures[16]. Nevertheless, high temperatures can still limit the growth and development of wheat through changing metabolic processes[16]. Several studies and reviews examined the effects of climate change on wheat quality[17,18]. An ongoing increase in CO_2 concentration and temperature will have negative impacts on wheat quality. For example, the protein content of wheat flour has been shown to decrease significantly with increasing CO_2 concentrations[19]. In addition, grain yield, grain weight, protein yield, globulin content and total starch accumulation have been shown to decline under temperature stress[18].

2.2 Rice

Rice (*Oryza sativa*) is the second most important crop in the world after wheat, with about 755 Mt of yield from 162 Mha in 2019[11]. Similar to wheat, increases of atmospheric CO_2 concentrations have positive impacts on rice yield due to its stimulation of photosynthesis[20]. Impacts of temperature increase on rice yield are also similar to wheat at a global scale, causing 5.6% ± 2% loss with an increase of 1 °C based on a global data set of field warming experiments[4]. Especially in tropical regions, nighttime temperature increase can greatly affect rice yields, for example, with 10% for every 1 °C increase in the minimum temperature during the growing season over a period of 25 years (1979–2003) in the Philippines[21]. Therefore, yield increase by elevated CO_2 concentration can be partially counteracted by temperature increase, although the magnitude of this counteraction remains uncertain[4].

The physiological basis for yield and quality reduction in rice caused by climate change is also linked to growth and developmental processes[21–23]. Rice is vulnerable to changes in the temperature during its developmental phases. The optimal temperature for rice development ranges from 22 to 28 °C[22]. Several studies report potential impacts of high temperatures on growth and development, performances of traits, yield components and grain quality in rice[22]. The growth rate of seedlings increases linearly as the temperature increases from 22 to 31 °C, but declines sharply when the temperature exceeds 35 °C, and the seedlings will die above 40 °C[22]. In addition, extreme climate events, like the El Niño-southern oscillation, are projected to exert a negative impact on rice agriculture by delayed rainfall in the main rice-growing regions of Indonesia[24]. Also, rice chilling injuries during summer has occurred more frequently and more seriously over the past two decades in some regions (which is reported to relate with climate change), such as Heilongjiang Province, China, and caused a huge reduction in rice yield[23]. Likewise, rice grain quality (such as color, texture, surface abnormalities and milling characteristics) is also susceptible to extreme temperatures. High temperatures during the ripening phase often lead to an increase in the percentage of chalky rice but a decrease in head rice[22], reducing the price of rice significantly.

2.3 Implications for crop production

In general, climate change can generate both positive and negative impacts on crops. Previous studies have elucidated the impacts of climate change related changes in temperature, atmospheric CO_2 and soil moisture on crop productivity. However, these studies are limited to local surveys or used a combination of models[1,3], making it difficult to generalize or extrapolate results to a larger scale. Results from one study site might fail to reflect the real situation in other regions, especially considering uncontrollable socioeconomic conditions[25]. The extent to which the positive impact of CO_2 elevation can compensate the negative impacts of climate warming remains relatively understudied[4]. As extreme climate events are projected to occur more frequently, more comprehensive studies involving a variety of natural thermal regimes, rather than simply a gradual increase in mean temperature, is needed to better understand the mechanisms underlying physiological thermal responses of crops. In addition, there has been insufficient study of the development of crop genotypes that can cope with multiple environmental stressors simultaneously. A genetic × environment × management interaction framework within crop models can be a powerful approach to help tackle challenges brought about by climate change, although there are limitations to such a framework[26].

It is clear that climate change poses a large challenge for agriculture. To mitigate potential negative effects or even to utilize the positive effects of climate change, adaptive management should be considered. Possible measures include (1) adjusting the sowing date to cope with changing crop phenology due to climate change; (2) developing heat or drought tolerant cultivars to maintain or enhance crop yields; (3) planting cultivars that originally grow at lower latitudes at higher latitudes; (4) adopting suitable cultivation practices such as adjusting the planting density, adding N fertilizer, irrigation and rotation; (5) developing new planting patterns to utilize climate resources more efficiently, such as rotation of two crops in the same year; and (6) promoting water-saving technologies and conservation tillage to respond to drought stress.

3 IMPACT OF CLIMATE CHANGE ON PESTS

Biological processes like development, reproduction and survival rates of insect pests are influenced by environmental conditions such as temperature, humidity and atmospheric CO_2 concentration. A growing amount of research focuses on how crop pests respond to climate change through chamber or field studies or through process-based models such as phenological models and niche models. The main effects of climate change on insect pests that have been identified are: (1) advances in phenology, (2) increases in voltinism and shortened generation time, (3) expanding geographic ranges, (4) changing phenological synchronization between crops, pests and natural enemies, (5) increasing abundance and population size, and (6) increasing the risks of invasive species and outbreaks of secondary pests. However, climate change induced impacts of pests on the final grain production remain largely unknown. Here, we summarize individual studies published in the past 10 years on the potential effects of climate change on wheat and rice pests (Table 1 and Table 2), give an overview on research progress, and pinpoint research gaps.

3.1 Climate change and wheat pests

Wheat is impacted by more than 100 arthropod pests, however only a few species are of economic importance[7,51]. Among them, cereal aphids are the most economically important and widespread pests of wheat in the world. In the USA, the estimated annual economic loss caused by greenbug (*Schizaphis graminum*) to wheat production can reach 100 million USD[33]; in China, two dominant aphids, English grain aphid (*Sitobion avenae*) and the bird cherry-oat aphid (*Rhopalosiphum padi*) have been responsible for infesting up to 17 Mha of wheat crops[52]; the Russian wheat aphid (*Diuraphis nociva*) can cause from 80% to 100% yield loss through direct feeding and virus transmission[53]. Therefore, these species have received more attention than other insect pests such as wheat midges (*Sitodiplosis mosellana*), oriental armyworm (*Mythimna separata*), the brown wheat mite (*Petrobia latens*) and winter grain mite (*Penthaleus major*), although these latter species are regionally or temporally also important (Table 1). Several reviews have synthesized the impacts of climate change on wheat pests from the perspective of key climate change elements, such as drought, high temperatures and rising concentration of atmospheric CO_2[7,54]. Studies on the effects of climate change on wheat pests generally focus on four aspects (from individual, population, community to multitrophic systems). (1) Effects on fitness-related life history traits or behavior. For example, both *S. avenae* and *R. padi* show heat-escape behavior and this behavior can be affected by heat stress due to climate warming[29]. Also, elevated CO_2 concentrations and temperature combined has been shown to decrease *R. padi* fecundity and development time[27]. (2) Effects on population dynamics and geographical distribution. Rising temperatures on the North China Plain were reported to cause a northward range shift of about 5.9 $km \cdot yr^{-1}$ for *S. mosellana* from the 1950s to the 2010s, and the population density of *S. mosellana* was positively correlated with total precipitation in early spring in China[55]. (3) Effects on community structure. A recent study showed that high-temperature events can shift the pest dominance hierarchy of *S. avenae* and *R. padi*[28]. (4) Effects on multitrophic systems. For example, increasing nocturnal temperatures have shown to alter predator–prey interactions[32].

The Climate Change Biology Research Group of the Chinese Academy of Agricultural Sciences studies demographic and

Table 1 Summary of studies on effects of climate change on common global wheat pests

Species	Region	Research question	Main finding	Reference
Bird cherry-oat aphid (*Rhopalosiphum padi*)	Australia	Multi-trophic interactions	Elevated CO_2 and temperature decrease development time	[27]
	China	Dominance hierarchy shift	High-temperature events affected per capita growth rate of *Sitobion avenae* but not *R. padi*, driving a dominance shift	[28]
	China	Heat-escape behavior	Brief thermal history influenced aphids' heat-escape behavior	[29]
	China	Life history traits and fitness	Sporadic short mild periods during a long extreme hot event could improve aphids' life history traits; night warming reduced aphid survival	[30,31]
	China	Predator–prey interactions	Night warming alter the interaction between predator and prey	[32]
	China	Heat-escape behavior	Brief thermal history influenced aphids' heat-escape behavior	[29]
	China	Dominance hierarchy shift	High-temperature events affected per capita growth rate of *S. avenae* but not *R. padi*, driving a dominance shift	[28]
Greenbug (*Schizaphis graminum*)	Worldwide	Potential distribution	Shift northward	[33]
Rose-grain aphid (*Metopolophium dirhodum*)	UK	Abundance	Increased abundance with mean annual precipitation	[34]
Russian wheat aphid (*Diuraphis nociva*)	USA	Abundance	Abundance negatively correlated with increasing temperatures after removing inter-annual density-dependent effects	[35]
Hessian fly (*Mayetiola destructor*)	USA	Effects of El Nino-southern oscillation	Hessian fly infestation and yield losses were greatest during the La Nina and least during the El Nino phase	[36]
Wheat stem sawfly (*Cephus cinctus*)	Canada	Abundance and distribution	Relative abundance would increase in the future	[37]
Wheat midge (*Sitodiplosis mosellana*)	North America	Distribution and relative abundance	Shift north and abundance was predicted to increase	[38]
Wheat armyworm (*Mythimna sequax*)	Brazil	Voltinism	Voltinism increased in the future	[39]
Cotton bollworm (*Helicoverpa armigera*)	China	Population dynamic	A shift to early eclosion of diapausing pupae due to global warming; elevated CO_2 and temperature increased foliar consumption	[40]

abundance responses of wheat aphids, and their interactions with predators, to varying temperature regimes that reflect (future) natural fluctuations, using historical data sets, simulations in climatic chambers, laboratory and field observations, and meta-analyses[30,31,56–62]. From their studies we can conclude that thermal extremes are critical in pest management and biodiversity conservation. They further stress that it is imperative to include all important characteristics of thermal extremes when studying the demographic performances, population and community structure, such as night warming on hot days[30], daytime warming[57,58], frequency and intensity of high temperatures[57], alternating patterns of high and normal temperatures[59], and sporadic short temperature events[31].

Most studies only assess the effects of single climate factors on wheat pests based on laboratory simulation studies or long-term sampling efforts using suction traps. Few studies have assessed the effects of multiple climatic factors and management strategies on insects[63]. Xing et al.[64] assessed the effects of multiple climatic factors on *R. padi*. They report the impacts of elevated CO_2 and soil water on population dynamics, fecundity and development of *R. padi* by affecting its host plant (wheat) characteristics[64]. They found that high N input could increase the fecundity and plant N content, but did not counteract the negative effects of elevated CO_2 on total fecundity of *R. padi* and wheat N content.

3.2 Climate change and rice pests

Rice is a host for over 800 insect pests of which only 15–20 species currently cause serious damage. Rice pests can be divided into four types including leaf-feeders such as rice leaf folder (*Cnaphalocrocis medinalis*); steam-borers such as rice stem borer (*Chilo suppressalis*); grain-suckers such as brown planthopper (*Nilaparvata lugens*), white back planthopper (*Sogatella furcifera*), small brown planthopper (*Laodelphax *striatellus*), and southern green stink bug (*Nezara viridula*) and root-feeders, such as mole cricket (*Neoscapteriscus borellii*). Studies on the effects of these pests on rice cover individual, population, community and multitrophic systems levels, but usually emphasize only one aspect. The number of climate-relevant studies are quite unbalanced between pest species (Table 2). Grain-suckers, especially *N. lugens*, have received most attention, involving effects on their physiology at the individual level, their distribution at the population level, and the efficacy of pesticides at pest management level. Regarding the effect of climate change on the physiology of grain suckers; increasing the maximum temperature caused more old nymphs of *N. lugens* to die. When temperatures exceed 34 °C, no nymphs of *N. lugens* emerged[65]. Elevated CO_2 increased fecundity and honeydew excretion of *N. lugens* and exhibited a negative effect on rice yield[66]. Regarding pest distribution; Chaoxing et al. analyzed the effects of climate change on the overwintering boundary of *N. lugens* in China and predicted that the overwintering boundary would move northward with about 50 km between 2010 and 2039[67]. Regarding pesticide efficacy; it was found that under elevated CO_2, the control efficacy of triazophos for *N. lugens* decreased[44].

For other rice pests, studies gave more attention to the individual and population levels, including physiological responses and acclimation to thermal stress[46], behavioral adaptation[47], occurrence and distribution[68], and population dynamics[65]. For example, thermal tolerance of rice leaf folders (*C. medinalis*) was enlarged after two or three generations of heat selection[46]. Rice leaf folders were also observed to have behavioral thermoregulation such as laying eggs on the lower surfaces of rice leaves under heat stress[48], and preferring to build multileaf overlapping shelters, while at the optimal temperature they chose to build single-leaf longitudinal shelters[47]. Regarding pest occurrence and distribution; Morimoto et al. have shown that climate change is anticipated to shift the geographic distribution ranges of several rice pests in Japan[68]. The northern boundaries of *C. suppressalis* were estimated to shift northward with about 300 km by 2100 if temperatures rise by 2 °C[68]. Studies on rice stem borer focus on population level dynamics and abundance. For example, the climate change related increase of winter temperature was estimated to enhance the abundance of *C. suppressalis* in Japan, in 2031–2050 compared to 1981–2000, which even enables previously harmless species to become harmful[69]. Overall, few studies have investigated the impacts from the perspective of community to multitrophic systems for rice pests, except for some recent examples in viruses transmitted by small brown planthoppers[70] and interspecific interactions between coexisting rice planthoppers (i.e., *N. lugens* and *S. furcifera*)[71].

Like studies focusing on wheat pests, scientists in climate change biology of rice pests should consider studying how the multifaceted aspects of climate change, such as intensity and frequency of irregular extreme events that happen on a fine temporal scale (e.g., daily maximum and minimum

Table 2 Summary of studies on effects of climate change on common global rice pests

Species	Region	Research questions	Main findings	Reference
Brown planthopper (*Nilaparvata lugens*)	China	Growth and development	High temperatures decreased the survival rate of nymphs	[41]
	Philippines	Oviposition and nymph performance	*S. furcifera* had lower the most suitable temperatures for oviposition than for *N. lugens*	[42]
	Malaysia	Thermal tolerance	Occasional extreme high temperature events are likely to affect the survival and distribution of *N. lugens*	[43]
	China	Biochemical control	Control efficacy of triazophos decreased elevated CO_2	[44]
White back planthopper (*Sogatella furcifera*)	Philippines	Oviposition and nymph performance	*S. furcifera* had lower the most suitable temperatures for oviposition than for *N. lugens*	[42]
Small brown planthopper (*Laodelphax striatellus*)	China	Survival and wing dimorphism	Climate affected wing-form of planthoppers	[45]
Rice leaf folder (*Cnaphalocrosis medinalis*)	China	Physiological response	Heat selection increased survival and fecundity of larvae	[46]
	China	Shelter-building behavior	Larvae tended to build multileaf overlapping shelters under heat stress	[47]
	China	Behavioral adaptation	Shelter size decreased as the temperature increased	[48]
Black rice bug (*Scotinophara lurida*)	Korea	Penology of insects and plants	Temperature increase advanced the immigration time	[49]
Striped stem borer (*Chilo suppressalis*)	China	Heat tolerance	Adult fertility was more sensitive to heat stress than adult survival	[50]

temperatures; the number of hot days during a given period; and the time duration between extreme hot events)[9], affect rice pests at population and community levels.

4 Impact of climate change on pathogens

Crop pathogens are important components in agroecosystems and can directly damage the health of crops and consequently decrease crop productivity. Plant pathogens include bacteria, fungi, nematodes, oomycetes and viruses. The fungi are the most important among these plant pathogens. Pathogenic microorganisms and their infection processes are highly sensitive to climate change related changes in precipitation regimes, rising temperatures and atmospheric CO_2 levels. Plant pathogens can be divided into two categories: (1) necrotrophs, which obtain nutrients from dead host tissues, and (2) biotrophs, which derive nutrients from living host cells. Climate change can alter necrotrophic pathogens through accelerating tissue death; in contrast, it can shift biotrophic pathogens through influencing the growth of crops. Here, we give an overview of the effects of climate change on wheat and rice pathogens and identify some research gaps.

4.1 Climate change and wheat pathogens

Wheat stripe rust (*Puccinia striiformis* f. sp. *tritici*), wheat leaf rust (*Puccinia recondita* f. sp. *tritici*), wheat powdery mildew (*Blumeria graminis* f. sp. *tritici*) and Fusarium head blight (*Fusarium graminearum*) occur widely and seriously affect the yield and quality of wheat across the globe. The impact of climate change on these pathogens has been widely studied (summarized in Table 3). It is generally predicted that under climate change the prevalence and severity of the diseases caused by these pathogens will increase[82]. However, some studies indicated that future climate change might limit the development of powdery mildew on wheat[79] and can have negative impacts on the evolution of leaf blotch (*Zymoseptoria tritici*)[77]. Environmental conditions, especially weather conditions such as relative humidity or moisture, temperature, CO_2 concentration, wind and a combination of these factors, affect epidemics of wheat pathogens[80]. High moisture content during the growing season of wheat might, for example, enhance the infection of wheat with stripe rust and Fusarium head blight[81]. However, particularly high humidity can reduce

Table 3 Summary of studies on effects of climate change on common global wheat diseases

Species	Region	Research question	Main finding	Reference
Leaf rust (*Puccinia recondita* f. sp. *tritici*)	Poland	Relationship between latency period and temperature	Latency period of wheat leaf rust is going to decrease which may result in increase of wheat leaf rust incidence	[72]
	France	Disease earliness, intensity, and disease dynamics	Disease severity is forecasted to be increased with climate change	[73]
Stripe rust (*Puccinia striiformis* f. sp. *tritici*)	USA and Canada	Race evolution on the epidemiology and ecology	Changes taking place in *P. striiformis* f. sp. *tritici* ecology and epidemiology over the last decade	[74]
	China	Relationship of diseases overwintering potential to winter temperatures	*P. striiformis* f. sp. *tritici* winter survival is related to temperatures in the coldest period from mid-December to late January	[75]
	Denmark, France, and USA	The susceptibility	At low temperatures, vernalisation reduced the susceptibility of seedlings exposed to the 'Warrior' race	[76]
Leaf blotch (*Zymoseptoria tritic*)	China	Temperature-dependent evolution of aggressiveness	Global warming may have a negative effect on the evolution of pathogens	[77]
Powdery mildew (*Blumeria graminis* f.sp. *tritici*)	China	Epidemics	Percent acreage of the disease would increase in the future	[78]
	Italy	Development	Future global warming scenarios may limit the development of powdery mildew on wheat	[79]
Fusarium head blight (*Fusarium graminearum*)	China	Severity	The key factor affecting Fusarium head blight severity was weather condition during the heading and anthesis stages of winter wheat	[80]
	China	Excess precipitation	Excess precipitation can induce Fusarium head blight	[81]
Wheat take-all (*Gaeumannomyces graminis* var. *tritici*), and wheat crown rot (*Fusarium* spp.)	New Zealand	Disease expression	Increased drought is expected to increase disease expression	[82]

summer spore survival and dispersal of stripe rust due to adhesion to leaves.

Temperature affects each stage in a pathogen life cycle and consequently affects the pathogenicity, dispersal and disease epidemics in aerial and soilborne pathogens[6]. Many pathogens are quite sensitive to temperature fluctuations[76]. Not only the warming trend will affect wheat pathogens, but extreme climate events, like spells of extremely high temperature, droughts, and torrential rains affect fungal infections as well. Also, elevated CO_2 levels have direct effects on fungal pathogens. Some studies have shown that disease severity and mycotoxins can accelerate the rate of pathogen evolution[83].

Recent literature on impacts of climate change on wheat pathogens mainly focuses on the effects of climatic variables on prevalence and severity of diseases and few studies consider the evolution of pathogens themselves in response to warming (see exceptions in Chen et al.[77], Liu et al.[83], Lyon B and Broders K[74]). Thus, we suggest that future research should also focus on the adaptation of pathogens themselves to obtain a deeper understanding of the adaptive ability of wheat pathogens and to allow for a better prediction of where and when epidemics of wheat pathogens might occur.

4.2 Climate change and rice pathogens

There are about 80 diseases reported for rice. Fungal diseases, blast (caused by *Magnaporthe oryzae*), brown spot (caused by *Bipolaris oryzae*), sheath blight (caused by *Rhizoctonia solani*) and bakanae disease (caused by *Fusarium fujikuroi*) are considered the principal diseases of rice and can substantially decrease its yield and quality (see details in Table 4). Climate change related alterations in temperature and precipitation regimes and atmospheric CO_2 concentrations can impact rice pathogens in various ways. However, it is still uncertain how rice diseases will be affected in general. The actual impacts will depend highly on the type of diseases and regional climatic conditions. Some studies showed that diseases like rice blast will become more severe under elevated CO_2 concentrations and temperature in lower latitudes[88]. However, other studies predict that the severity of leaf blast will decline in countries like Tanzania[86] and Japan[89]. Model simulations indicated that rising temperature will result in a higher risk of blast epidemics in cool subtropical zones, such as northern China, while the risk will be lower in humid tropics and warm humid subtropics[91].

Like wheat fungal diseases, rice fungal diseases also favored by humid conditions, and epidemics and prevalence of leaf fungal pathogens are predicted to increase under high moisture conditions[86]. Sheath blight has a high infection rate under high temperature microclimatic conditions (28–32 °C), thus rising temperatures can favor the rapid spread of hypha. High temperature coincides with high incidence and severity of many diseases, such as leaf smut, stack burn, bakanae disease, sheath spot, false smut and grain spot[90]. An elevated CO_2 concentration has shown to increase the number of leaf blast lesions and the infection proportion of diseased plants

Table 4 Summary of studies on effects of climate change on common global rice diseases

Species	Region	Research question	Main finding	Reference
brown spot (*Bipolaris oryzae*)	Brazil	Biochemical defenses of rice	Biochemical defenses of rice against *B. oryzae* increase with high atmospheric concentration of CO_2	[84]
Blast disease (*Magnaporthe oryzae*)	South Korea, Korea	Potential epidemics	The incidence of epidemics was simulated to decrease toward 2100	[85]
	Tanzania	Yield losses	Losses due to leaf blast is predicted to decline in Tanzania	[86]
	Brazil	Severity	The disease was more severe under high CO_2 concentration	[87]
	India	Infection ability	Leaf blast is projected to increase during the winter season (December–March) in 2020 (2010–2039) and 2050 (2040–2069) climate scenarios due to temperature rise, particularly in lower latitudes	[88]
	Japan	Rice leaf wetness	The infection risk was estimated to decrease for Japan	[89]
Sheath blight (*Rhizoctonia solani*)	South Korea, Korea	Potential epidemics	The incidence of epidemics was simulated to gradually decrease toward 2100	[85]
Bakanae disease (*Fusarium fujikuroi*)	Italy	Severity	Combined and single effects of elevated CO_2 and high temperatures seem to be favorable for bakanae disease development in the Mediterranean Basin	[90]

damaged by the sheath blight in a FACE experiment (around 200–280 μmol·mol^{-1} above ambient CO_2). This indicates that potential risks for infection and epidemics of leaf blast and sheath blight will increase in future if CO_2 concentrations keep rising[92]. However, recent studies have failed to address the effects of multiple interacting climatic factors (synergistic, antagonistic or additive effects) on rice pathogens, or the integrated response of multiple pathogens to the same climate scenarios. Such studies are needed to reflect the real conditions rice pathogens experience.

5 IMPACT OF CLIMATE CHANGE ON SPECIES INTERACTIONS

Crops, pests, pathogens and even their natural enemies do not exist alone in agroecosystems but interact with each other (Fig. 1). Climate change does not only impact the biological performance of these components themselves but also their interactions. Impact of climate change on these interactions has been explored for crop-pathogen, crop-pest and even for tritrophic systems, such as plant-pest-predator. Results from molecular studies on crop-pathogen interactions suggest that extreme climate conditions can lead to fungal pathogens generating variants in pathogenicity and aggressiveness, and in turn induce host plants to produce new gene products in response to this change[93]. Elevated atmospheric CO_2 could also affect interactions between plant and insect herbivores. Bezemer and Jones[94] analyzed data from 43 insect herbivores and found that enhanced CO_2 could change the biochemistry of plants, such as reduced leaf nitrogen content and increased carbohydrates. The results also show that herbivores in different feeding guilds (e.g., leaf-chewers, leaf-miners and phloem-feeders) respond in different ways in response to elevated CO_2. For example, the food consumption of leaf-chewers and leaf-miners increased to compensate for the reduction of nitrogen content in the plant whereas the abundance of phloem-feeders increased under elevated CO_2 conditions. Changing temperatures regimes might also affect the interaction between herbivores such as leaf-miners. A study by for instance Rodríguez-Castañeda et al.[95] found a temperature mediated competitive exclusion interaction between two cosmopolitan leaf-miner species. Also, parasitoids had a host-plant-dependent negative effect on the leaf-miners. They hypothesized that under future climatic change the presence/dominance of the leaf-miner species will depend on (1) the presence of suitable host plants, (2) the success of parasitoids in regulating leaf-miner hosts, and (3) the local temperature regime, also highlighting the importance of studying multiple interacting factors while assessing future crop productivity.

There are some studies and reviews that assess the effects of climate change on multiple components, for example, interactions between insects and pathogens, plants and pathogens[5], tripartite interactions between viruses, pests and host plants, and between plants, herbivores and natural enemies[5]. In addition, the triangle to illustrate the interactions between plants, insects and pathogens under environmental changes has recently been extended by adding evolutionary time, which is potentially an important consideration for future research on rapid evolution. However, few researchers have done systematic research into the interaction between insect pests and fungal pathogens (lower arrows the bottom line in Fig. 1). Recently, a small number of studies investigated co-infection of insect pests and pathogens, and the results showed that fungal infection (powdery mildew) suppressed the performance of an insect pest (*S. avenae*) and another insect pest (*R. padi*) preferred healthy leaves that had not been infected by fungal pathogens (*Parastagonospora nodorum*)[96]. The asymmetric warming during nighttime can result in opposite effects on biological control of wheat aphids and their predators[32]. Given the complexity of multiple trophic levels, the interaction between multiple species in agricultural ecosystems under climate change under different management regimes still needs further research.

6 IMPLICATIONS FOR PEST AND DISEASE MANAGEMENT

The widely accepted and adopted practice of integrated pest management (IPM) is currently facing great but relatively unpredictable challenges from climate change. IPM was defined as a holistic strategy to beat pests and diseases using all available methods, meanwhile minimizing the use of chemical agents to control pest populations below economical thresholds. This is often presented in the IPM triangle, which is composed of three main elements: abiotic control, such as mechanical, physical and cultural control; biological control, such as intrinsic heritable plant resistance, biocontrol agents (predators, parasitoids and biopesticides) and biorational synthetic volatiles; and chemical pesticides[97]. Recently, the IPM triangle has been modified to optimize it by combining traditional and novel IPM strategies into a conceptual framework[97] and even integrating an evolutionary perspective to address unwanted evolution of resistance in pests[98]. As climate change imposes important effects on crop pests and pathogens, we argue that policymakers and practitioners should consider the impact of climate change when adopting IPM strategies.

Here, we provide several suggestions on how to modify current IPM strategies to respond to climate change. First, pest monitoring needs to be strengthened in order to provide more accurate information for estimating economic thresholds. Specifically, more attention should be given to developing an intense spatiotemporal monitoring network with fine-scale monitoring units of pests and pathogens based on existing field surveys in order to detect the often overlooked impacts of extreme high temperatures. Both nocturnal and diurnal monitoring should be conducted to identify the potential effects of night warming as described above. In addition to the traditional well known pests, the monitoring of secondary pests and invasive insect pests should be strengthened to avoid yield losses caused by unexpected outbreaks. This is especially important as, with climate change, secondary pests can become primary pests. Second, regarding abiotic control, changing planting systems by increasing the spatial and temporal diversity of crop species and cultivars can contribute to mitigate the possible negative effects induced by climate change. This might be especially important in light of the large uncertainty about the precise direction climate change will take and the frequency with which rare events like heat waves will occur. Some strategies are particularly useful, for example, adopting intercropping system based on the push-pull concept, viz., growing repellant plants around a crop and trap plants at a distance from the corp, or planting cultivars that currently can only grow in southern regions in more northern regions to respond to warming trends. Diversification is a strategy suggested in other sectors (e.g., in the forestry sector[99]) to increase resilience. Third, for biological control, developing cultivars resistant to pests or pathogens should consider the desirable traits of wild species to cope with extreme climates and to keep a balance between pest/pathogen resistant traits and extreme climate-resistant traits and ultimately find the optimal combination of resistance genes. Stress-tolerant biocontrol agents should be released at appropriate times to fit phenological synchronization to increase the control efficacy under extreme climate conditions; biorational synthetic volatiles should be applied after fully understanding how pests are affected by climate change. Lastly, for chemical pesticides, the local climate regimes should be considered when applying pesticides and fungicides to increase the control efficacy and potentially reduce the dose of pesticides. For example, recent studies have shown that changes in daily temperature fluctuations can make the pesticide more toxic[100], thus we can take advantage of this to reduce the dose of pesticides in the context of global warming.

7 FUTURE PERSPECTIVES

Climate change is identified as one of the major risks to agriculture and food security, and thus it is imperative that crops, insect pests and crop pathogens, as well as their interactions are included in future climate change studies. Despite a large number of studies on the topic, there is still no adequate answer to the question of how climate change will shape the relationship between crops, pests and pathogens, and ultimately affect crop productivity. To better answer this question, we advocate that future studies put increased effort into the following three factors: including controlled laboratory experiments and models, controlled field experiments, and strategies of the IPM.

First, regarding controlled laboratory experiments and models, the current knowledge on the effect of extreme climatic events on crops, pests and pathogens is not sufficient to characterize the effects of increased frequency of the extreme climate events across temporal and spatial scales. Neglecting important characteristics such as daily maximum and minimum temperatures, and time elapsed between each subsequent extreme climate event can generate misleading model predictions on the individual physiological and biochemical responses of crops, pests and pathogens to climate change[9]. Therefore, future research should investigate the impacts of ecological relevant extreme climates on crops and their pests and pathogens more in detail, which could, for example, be done in laboratory settings. Second, results from current controlled field practices have generally been unable to adequately represent real-world complex conditions[10]. Also, results from local or regional experiments cannot accurately be extrapolated at a larger scale. We are therefore in need of additional, preferably, large-scale and long-term, studies to better explore real field environments across a range of latitudinal and altitudinal gradients. Third, interactions between crops, pests and pathogens are highly complex and particularly sensitive to IPM strategies. There remain large gaps in our knowledge on the impact of different agricultural practices, such as intercropping, changing planting dates, and use of pesticide and fungicide, on pests and pathogens and their interaction with crops. Also, no matter which IPM strategies are taken to control pests, these strategies will also affect the beneficial organisms (biological control agents) and subsequent IPM strategies[97]. The combined effect of multiple climatic stressors and IPM strategies on crop production, and crop pests and pathogens, as well as the interaction between them, is still uncertain. Cross-tolerance phenomena might exist when facing multiple stressors, which might mean that increased tolerance to one stressor can also increase the tolerance to other stressors, or vice versa. Thus, further research is needed to address the complex problems of multi-factors to ultimately realize the full potential of IPM.

In conclusion, under the dual pressure of climate change and socioeconomic development, additional studies that involve interactions among crops, pests, pathogens and agricultural practices under climate change are required to help agriculturists, practitioners, farmers and scientists to better understand the effects of a changing climate on crop production. Only once the whole picture of how climate change will impact crop pests and pathogens is formed, farmers can take effective measures to control crop pests and pathogens, adapt the use of pesticides and fungicides, and mitigate negative effects of climate change. Although future climate change is full of uncertainty and it is difficult to generalize, current work has started to elucidate a uniform trend of how insect pests, pathogens, crops and their interactions respond to climate change.

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Compliance with ethics guidelines

Bing-Xin Wang, Anouschka R. Hof, and Chun-Sen Ma declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any study with human or animal subjects performed by any of the authors.

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