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Combining climate change, crop growth and crop disease models to predict impacts of climate change on crop diseases can guide planning of climate change adaptation strategies to ensure future food security. This review summarises recent developments in modelling climate change impacts on crop diseases, emphasises some major challenges and highlights recent trends. The use of multi-model ensembles in climate change modelling and crop modelling is contributing towards measures of uncertainty in climate change impact projections but other aspects of uncertainty remain largely unexplored. Impact assessments are still concentrated on few crops and few diseases but are beginning to investigate arable crop disease dynamics at the landscape level.

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The importance of modelling impacts of climate change on arable crop diseases

Climate change threatens crop yields, both directly through changes in plant growth and production and indirectly through impacts on crop diseases. It has been estimated that changes in climate have already been reducing global agricultural production by 1-5% per decade over the last 30 years [1]. The greatest yield reductions have been observed in tropical cereals such

as maize and rice. The trend of reduced production is projected to continue in the future [2]. However, world demand for staple crop products is predicted to increase by 60% to feed the population expected by 2050 [3].

Food production is also being impacted by adaptations towards a more sustainable biosphere, such as the expansion of biofuel crops and solar farms that compete with edible crops for land suitable for food production and the decrease in chemical inputs in order to decrease risks to ecosystem services.

Arable crop diseases cause yield losses estimated at 16% globally for unprotected crops [4]. The control of crop diseases therefore has a crucial role to play in enabling high yields from crops and ensuring food security in the future. As risks of decreases in crop yields increase due to climate change and more variable weather patterns, it is essential that crop disease losses are minimised.

Plant breeding for resistance and the development of new chemical or biological controls for crop diseases are not short-term processes. Therefore, decades can be needed for strategies to be implemented. To guide strategies for adaptation by the agricultural industry, it is essential to project the impacts of climate change on severity of crop disease epidemics.

Findings from recent climate change disease projection work have been reviewed by Elad and Pertot [5] and by Juroszek and von Teidemann [6^{••}]. Climate change impacts will differ between crops, diseases and geographic locations, with disease severity increasing in some areas/crops and decreasing in others.

This review first summarises developments in modelling climate change impacts on arable crop diseases over the last two years. We then emphasise some of the major challenges in crop disease modelling and recent work that addresses these. Finally, we highlight a recent trend to develop tools to investigate arable crop disease dynamics at the landscape level.

Developments in modelling impact of climate change on arable crop diseases

Climate change models are now readily available for a series of standard climate change scenarios resulting from different levels of anthropogenic CO_2 release driven by a new set of emission scenarios corresponding to new Representative Concentration Pathways (RCPs) [7].

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These can be used to generate climate projections from a series of different Global Circulation Models (GCMs) to form multi-model ensembles. Temperature projections are more robust than precipitation projections [8].

To account for expected variability in future weather [9], crop and disease modellers are generating future 'weather' rather than using mean climate shifts (e.g. in crop modelling [10–13]; in crop disease modelling: see Table 1 and Figure 1). Uncertainties resulting from the projections of future climate change are being addressed in crop disease modelling through the use of multiple GCMs because climate change projections vary with different climate models [14]. These projections by GCMs need to be downscaled using weather generators and fed into process-based crop simulation and disease models in order to account for local variations in the weather. Weather generators now available (e.g. LARS-WG [13];

Figure 1

PRECIS [15]) allow 'weather variables' to be generated at regional/local daily scales as inputs for crop and disease models [16]. Launay *et al.* [17^{••}] investigated five foliar fungal diseases and concluded that use of weather variables over several years rather than overall mean changes in climate was 'crucial to model the effects of these variations'. Projections of extreme weather events, however, are still in their infancy [7], although researchers are recognising that extreme weather events will have large impacts on disease severity and yield loss [18].

Climate change affects pathogen biology not only directly but also indirectly through effects on host development and phenology. Therefore, crop models are frequently included within climate change impact assessments for crop diseases in order to enable interactions between crop phenology and pathogen development to be deduced and impacts of diseases on crop yield to be examined [19–21].



An illustration of how climate, crop growth and disease models can be combined to produce projections of crop growth stages and disease incidence/severity for different climate change scenarios. (1) Observed data for weather (e.g. daily minimum and maximum temperature (°C), total rainfall (mm) and solar radiation (MJ day⁻¹)), crop growth stage and disease incidence can be collated from a number of sources for different regions for a period of years. (2) The crop growth stages predicted using the crop growth model can be validated by comparing predicted crop growth stages, generated by the model using observed weather data, with observed crop growth stages for the same sites for a given period. (3) A disease model can be developed from data for disease incidence from sites within a certain distance of the site for which there is observed weather for a given period. (4) Predictions of disease incidence can be validated by comparing predicted weather to observed disease incidence data for a given period for different regions. (5) Weather data can be generated for each of the sites for each climate scenario. (6) The crop growth stages can be projected for each site for each site for each climate scenario using the crop growth model, allowing maps to be generated to show the effect of climate change on crop growth. (7) Using the weather generated and crop growth stage projected using the crop growth model for each of the sites for each of the climate scenarios.

Table	1
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Pathogen group	Disease	Pathogen	Model components	Comments	Reference [68]
Fungi	Various diseases on various hosts	Fusarium oxysporum f. spp.	$Two\;GCM\toCLIMEX$	Climate change impacts on global distribution of a pathogenic species complex.	
Fungi	Fusarium head blight on wheat	Fusarium spp.	One GCM → simulated weather + crop model + disease model.	Climate change impacts in China.	[21]
Fungi	Fusarium head blight on wheat	ht Fusarium culmorum 11 GCM ensemble + anthesis model + mycotoxin model.		Climate change impacts on mycotoxin levels in Scotland.	[32*]
Fungi	Brown rust on wheat	Puccinia recondita	15 GCM \rightarrow simulated weather + disease model.	Climate change impacts in Luxembourg.	[24]
Fungi	Six soil-borne fungi: three affecting cereals, three affecting spring-sown herbaceous crops	Fusarium nivale Fusarium culmorum Bipolaris sorokiniana Pythium ultimum Sclerotinia minor Macrophomina phaseolina	One GCM + soil conditions model + disease model.	Climate change impacts in Europe.	[69]
Fungi Bacteria	Leaf blast on rice Leaf blight on rice	Magnaporthe oryzae Xanthomonas oryzae pv. oryzae	One GCM → simulated weather + crop model + disease model.	Climate change impacts in Tanzania. Same disease can increase in severity in some areas and decrease in others.	[19]
Fungi Bacteria	Leaf blast on rice Leaf blight on rice	Magnaporthe oryzae Xanthomonas oryzae pv. oryzae	One GCM \rightarrow simulated weather + disease model.	Climate change impacts in South Korea.	[26*]
Fungi Bacteria	Leaf blast on rice Leaf blight on rice	Magnaporthe oryzae Xanthomonas oryzae	11 GCMs and ensemble → simulated weather + disease model	Climate change impacts in South Korea.	[31]
Fungi	Phoma stem canker on oilseed rape Brown rust on wheat Net blotch on barley	Leptosphaeria maculans Puccinia recondita Pyrenophora teres	One GCM \rightarrow simulated weather + infection model.	Climate change impacts in France for five foliar pathogens.	[17**]
Oomycetes	Downy mildew on grape Potato late blight	Plasmopara viticola Phytophthora infestans			
Oomycetes	Downy mildew on grape	Plasmopara viticola	One GCM → simulated weather + crop model + disease model.	Climate change impacts in France.	[25]
Oomycetes	Potato late blight	Phytophthora infestans	3 GCM \rightarrow monthly means + crop model + disease model.	Global climate change impacts.	[20]
Oomycetes	Potato late blight	Phytophthora infestans	Weather data + 3 disease models.	Not strictly a climate change impact paper but a comparison of different disease models.	[70]

For example, when climate change impacts on *Fusarium* head blight in UK wheat were first considered, projected drier weather at current anthesis dates in June suggested that disease severity would decrease [22]. However, the addition of a crop model showed that the susceptible growth stage (anthesis) would occur 2 weeks earlier, when rainfall was still sufficient to facilitate infection.

Crop models are frequently process-based in design [23], while both empirical [21,24] and process-based [25,26[•]] disease models are in general use. Juroszek and von Tei-

demann [6^{••}] found that temperature was the most widely used environmental parameter in disease models, with leaf wetness duration or another variable representing moisture used if necessary. Process-based disease models are particularly well-developed for inoculum potential and infection success because of the need to enable farmers to reduce costs and crop losses by making appropriate interventions at optimal timings. Models that predict yield loss are comparatively less reliable, partly because they require accurate mathematical descriptions of all aspects of disease epidemiology, crop physiology and host-pathogen

Table 2

Examples of experimentation in free-air CO ₂ enrichment (FACE), controlled-environment (CE) or glasshouse facilities that will e	nhance
parameterisation of crop disease models	

Experimental facility	Climate change aspects			Crop	Disease and pathogen	Comments	Reference
laointy	Temp	CO ₂	Ozone				
FACE		1		Coffee	Coffee rust (<i>Hemileia vastatrix</i>) Cercospora leaf spot (Cercospora coffeicola)	No effect of elevated CO ₂ on disease incidence	[71]
CE	~	~	~	Barley	Powdery mildew (<i>Blumeria</i> graminis) Spot blotch (<i>Bipolaris</i> sorokiniana)	Elevated CO ₂ , O ₃ and temperature, when applied in isolation, gave different effects on the two diseases Unexpected interactions between elevated CO ₂ , O ₃ and temperature	[72*]
CE				Barley	Yellow dwarf virus	Elevated temperature	[73]
CE		~		Maize	Fusarium verticillioides	Elevated CO ₂ increased maize susceptibility and fungal biomass Mycotoxin levels unaltered	[56]
Glasshouse	-	/		Wheat	Fusarium crown rot (Fusarium pseudograminearum)	Elevated CO ₂ increased disease severity	[53]
Glasshouse	~			Wheat	Fusarium crown rot (Fusarium pseudograminearum)	Elevated temperature reduced disease severity	[55]

interactions. Controlled environment, glasshouse and free-air CO_2 enrichment (FACE) experiments continue to facilitate more accurate parameterisation of both crop and disease models through investigation of temperature, CO_2 and ozone effects (Table 2).

The formation of the Agricultural Model Intercomparison and Improvement Project (AgMIP [27,28]) has increased interest in the use of multi-model ensembles. Ensembles have been used in climate projections for some years. The first large scale multi-model ensemble work has been done for wheat growth models [10,29]. The median of a series of models, calibrated for the same cropping area, was the most reliable predictor of grain yield [30], whereas the mean gave the most reliable prediction for grain protein concentration. Other published ensembles for maize [11] and rice [12] have shown that model-ensembles give more reliable predictions than single models alone.

Climate model ensembles have already been used for disease modelling [24,31,32°]. The use of disease-model ensembles has not yet been implemented but this was discussed at a satellite meeting to the 5th AgMIP Global Workshop in Florida in February 2015 (Advancing Pest and Disease Modelling: http://conference.ifas.ufl.edu/pest/index.html).

Major challenges for modelling impacts of climate change on arable crop diseases

The fact that multi-model ensembles are possible for some crop and disease models emphasises the concentration of research on few diseases of relatively few major crops, especially those of wheat, grape and oilseed rape [6^{••}]. Most work has been done on fungal pathogens although some recent work has been done with viral [33] and bacterial [19] pathogens and on disease vectors [34[•]]. To some extent, efforts and time are being wisely directed to major staple crops. However, all are predominantly temperate crops. Population expansion is greatest in the developing world, where other staple crops are grown and climate change impacts on food security are likely to be greatest [1]. In fact, climate change impacts are already being experienced in Africa [35]. This region has already been recognised as having the world's greatest proportion of food-insecure people.

In the southern hemisphere, it is likely that efforts are being concentrated on solutions to current disease and pest problems rather than directed at projections for the future. A recent Climate Change, Agriculture and Food Security (CCAFS) working paper [36] highlights the need for trained plant pathologists, data gathering, modelling of crop diseases and pests, and pre-emptive crop resistance against serious new disease and pest threats to give Africa the best support to maintain its food security. It does not suggest research on climate change impacts on individual diseases. This may be wise advice, since agricultural catastrophes such as the world-wide loss of Gross Michel bananas to Fusarium wilt, the threat of Fusarium oxy*sporum* subtropical race 4 to Cavendish bananas [37] and the arrival of maize lethal necrosis in new areas have had much larger effects on family and regional food security and economies than gradual climate-related changes in disease severity. Many of the worst crop

disease problems currently occurring in Africa are the result of 'first encounter' events, including *Phytophthora megakarya* on cocoa, cassava mosaic virus and cassava brown streak virus [36].

The arrival of new pathogens highlighted in recent papers [38,39] has been attributed to new climatic conditions [40], trade movements [41,42], host shifts $[43^{\bullet\bullet},44]$ and lack of indigenous host resistance [45] all contributing to a trend towards pathogen saturation in both crops and natural ecosystems [38]. Combined climate, crop growth and disease modelling has been implemented in areas where pathogens are not already present to emphasise the need for quarantine procedures, pathologist training and the introduction of crop resistance to slow the entry and establishment of pathogens in new countries [45]. Modelling to predict new disease threats is expected to be beneficial since many years are needed to prepare appropriate solutions. In Africa, for example, the development time for a control practice for a new disease is estimated to be 10-15 years [36]. A major challenge for plant pathologists is to expand work to include the major diseases of a worldwide range of staple crops. Recent attempts to group pathogens with similar epidemiological traits [17^{••},46] and to develop generic disease risk assessments may help to predict what will happen to a greater number of diseases under climate change. However, disease severity is often conditional on one or more absolutely critical co-occurrences in host and pathogen phenology that are difficult to include in generic models.

Another major challenge is the fact that the uncertainty and reliability of models continues to be poorly reported or inadequately emphasised. A special issue of Agricultural and Forest Meteorology on Agricultural prediction using climate model ensembles recently highlighted uncertainty in crop and disease modelling. The use of multiple 'years' of generated weather data partially accounts for uncertainty in climate projections but there are few other instances of stochastic modelling in disease work [47]. Gouache et al. [48], examining climate change impacts on Zymoseptoria tritici leaf blotch on winter wheat in France, used multiple GCMs to generate climatic projections. Three sources of uncertainty were considered: uncertainty in climate projections, uncertainty in disease parameter estimation and the variance of residual error. Uncertainty in climate projections contributed most to uncertainty in disease predictions but interactions between causes of uncertainty also made 'a major contribution to overall variance'. This appears to contradict the findings of the AgMIP multi-model ensemble work on wheat [29] and on rice [12], where the largest contribution to uncertainties was due to variation among crop models rather than among climate models. However, Gouache et al. [48] did not use a crop model in their work.

Several other crop disease studies have now included multiple GCMs (see Table 1). Adoption of a technique by Mendlik and Gobiet [49[•]] for reducing the number of GCMs in a climate model ensemble while maintaining variability in model designs may increase the use of multiple GCMs in modelling climate change impacts on crop diseases.

Frequently, researchers have used different methods to describe the fit of their models to their construction and validation data without further attempts to quantify the reliability of model predictions. Zhang et al. [21] examined their empirical model's predictive capability for both construction and validation data sets to show that model performance was consistent but did not comment that the model over-predicts low disease incidence. The need for models to be assessed for their usability and validity was highlighted by Cunniffe et al. [50^{••}]. Kim et al. [26[•]] tested their parameterisation of the process-based model EPIR-ICE by examining whether the model exceeded a pre-set tolerance threshold selected to assess whether the model 'was sufficiently accurate for its intended purpose'. Yet for findings from modelling to be of use for planners, clear statements of the usefulness and reliability of model outputs need to be made.

Some other aspects of climate change impacts have received little attention to date and, therefore, offer additional challenges to crop disease modellers. These include the effects of climate change on host resistance against pathogens [51–56]; the effects of climate change on pathogen insensitivity to fungicides [57] and the genetic adaptation of pathogens to changes in climate [44,58]. An interesting tool has been published to examine management of fungicide resistance over time [59°] but the model does not incorporate climate change impacts that may modify the response of pathogens.

Work has begun at the crop level to examine impacts of climate change on the balance between interacting pathogen species. Different pathogens can become dominant because new pathogens reach new locations or new hosts or because a previously unimportant pathogen becomes dominant. Shifts in competition between organisms, both pathogenic and commensal, both within the host and in the host's immediate environment, are beginning to receive attention [60] but the interactive ecology of microbial communities is difficult to study. Kemen [43^{••}] summarised process-based work done in this area and discussed progress made at the microbe community level, proposing that host-microbe interactions are strongly affected by the presence and/or participation of other microbes. Incorporating findings from microbial interactions as they become available will offer another challenge to disease modellers.

Inter-disciplinary collaboration is challenging but is especially important in modelling impacts of climate change on crop diseases. There is a need to incorporate advances in climate change and crop modelling into disease models; to continue to construct models for new host-pathogen systems; to calibrate and validate these models through experimentation and long-term data collections: to examine how pathogens, hosts and landscapes might change in the future; and to take account of pathosystem interactions with other organisms. To facilitate information exchange, scientists should consider carefully the use of keywords in publications. During the search for recent relevant papers for this article, the keywords 'climate change' and 'plant disease' reliably returned review articles but failed to locate much of the relevant primary research. A move amongst research funders to make project outcomes publicly available is driving the expanding use of open access publishing but has not yet resulted in the easy availability of research data. An increase in free data repositories, which offer not only safe storage of research data but also easy access through DOI links publishable in primary research papers, should aid future research.

Modelling impacts of climate change on arable crop diseases at the landscape scale

Modelling is producing tools for policy planners that will facilitate investigation of possible consequences of human adaptation to the threats to food security of climate warming and diseases. This investigation needs to be done at the landscape level since disease inoculum is often widely dispersed.

Much has been said in recent reviews of food security [61] about the need for sustainable systems, including natural and agricultural ecosystems. With the almost certain [7] increase in extreme weather, resilience is likely to involve adaptation through diversification. This will produce changes at the landscape and farm scales that will have effects on disease incidence and severity. Cropping changes will also occur due to the introduction of new crops adapted to the changed climate, with or without the loss of current crops. Skelsey and Newton [32[•]] modelled the effects on *Fusarium* mycotoxin levels in wheat of introducing maize into cropping rotations in Scotland as the climate becomes more favourable for maize. They estimated that projected decreases in rain during wheat anthesis should offset the increased risk resulting from maize debris being a more potent source of Fusarium inoculum than wheat or barley debris. Although it is difficult to foresee the effects of crop yield, product demand and economics on farmer decision-making [62], modelling offers strategic planners the opportunity to experiment with different cropping regimes across a landscape to estimate potential impacts on crop diseases.

A group from INRA, the French National Institute for Agricultural Research, have developed a modelling

framework that allows planners to assess the effects of different crops and different crop aggregations within the landscape on wind-dispersed foliar pathogens [63[•],64]. Their model can also simulate the effects on epidemics of spatial deployment strategies for cultivars with complete or partial resistance. Although not vet expanded to examine effects over several years, the modelling suggests that complete resistance results in best disease control when it is deployed in mixed landscapes whereas partial resistance is most effective when the crop host is aggregated in different regions [64]. This finding is illustrated by the effective deployment in Australia of oilseed rape resistant R gene-mediated resistance against Leptosphaeria maculans (phoma stem canker) through deployment of different R gene combinations in different cropping regions [65]. Since virulent races exist for all R genes deployed, the cultivars with pyramided R genes can be described as partially resistant. Similarly, Fabre et al. [66] considered resistance deployment in the landscape. Modelling the effects of R gene resistance deployment in the landscape showed that using a mixture of resistant and susceptible cultivars was effective in controlling foliar pathogens that were spread by wind from sources outside the field. Modelling over a series of years showed that deploying a mixture of resistant and susceptible cultivars across the landscape also reduced the likelihood of pathogen adaptation to deployed resistance. Pathosystems with different epidemiological traits react differently at the landscape level [67]. It is important that these traits can be accurately represented in climate change impact assessments.

Conclusions

Climate change impacts on crop disease are still being studied for relatively few crops and few pathogens. Uncertainties resulting from the projections of future climate change are being addressed through the use of multiple GCMs and multiple weather years. However, other uncertainties inherent in crop disease models remain largely unexplored and unreported. There is still a need to find methods to clearly describe the reliability of projections to planners and climate change adaptation strategists.

Other aspects of arable crop disease modelling, such as the effects of interactions between pathogens and other microbes, will require inter-disciplinary collaboration.

Recently developed tools that enable changes at landscape level to be incorporated into disease predictions have already been used to investigate changes in crop patterns and alternative deployments of host resistance. Future studies to expand these landscape investigations to include the effects of more adaptation strategies are needed for climate change impact assessments for arable crop diseases to contribute more widely to future needs in food and environmental security.

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