

REVIEW PAPER

Integrating pests and pathogens into the climate change/food security debate

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Abstract

While many studies have demonstrated the sensitivities of plants and of crop yield to a changing climate, a major challenge for the agricultural research community is to relate these findings to the broader societal concern with food security. This paper reviews the direct effects of climate on both crop growth and yield and on plant pests and pathogens and the interactions that may occur between crops, pests, and pathogens under changed climate. Finally, we consider the contribution that better understanding of the roles of pests and pathogens in crop production systems might make to enhanced food security. Evidence for the measured climate change on crops and their associated pests and pathogens is starting to be documented. Globally atmospheric [CO₂] has increased, and in northern latitudes mean temperature at many locations has increased by about 1.0–1.4 °C with accompanying changes in pest and pathogen incidence and to farming practices. Many pests and pathogens exhibit considerable capacity for generating, recombining, and selecting fit combinations of variants in key pathogenicity, fitness, and aggressiveness traits that there is little doubt that any new opportunities resulting from climate change will be exploited by them. However, the interactions between crops and pests and pathogens are complex and poorly understood in the context of climate change. More mechanistic inclusion of pests and pathogen effects in crop models would lead to more realistic predictions of crop production on a regional scale and thereby assist in the development of more robust regional food security policies.

Key words: Crop–pathogen interactions, crop–pest interactions, crop productivity, yield.

Introduction

The last 40–50 years have seen major changes to agricultural systems worldwide that have contributed to, and interacted with, new food systems. Von Braun (2007) highlighted the transforming role of the interacting driving forces of population increase, income growth, urbanization, and globalization on food production, markets, and consumption. To these forces can be added the twin elements of climate variability and climate change which have direct effects on both food production and food security (Parry *et al.*, 2004). It is well known that the sensitivity of agricultural systems to climate differs between systems depending on whether they are temperature- or water-limited, and whether they are operating near their optimum or not. Fuhrer (2006) concluded that there

was ample evidence to demonstrate the sensitivity of agricultural systems to climate change, and that the range of effects on potential productivity was from extremely negative in areas that were already water-limited to positive in areas that were temperature-limited. Similarly, the effects of climate variability and change on food security are also location-specific and, more importantly, societally-specific with countries and groups with low income and limited adaptive capacity facing significant threats to food security (von Braun, 2007). In particular, food insecurity in Sub-Saharan Africa will be increased by climate change although the size of the effect is affected more by socio-economic factors than by climate change *per se* (Easterling *et al.*, 2007).

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Although many studies have detailed considerable progress in understanding the sensitivities of plants and of crop yield to climate variables and change, a major challenge for the agricultural research community is to relate these findings to the broader societal concern with food security. Food security (defined as when all people, at all times, have physical and economic access to sufficient, safe, and nutritious food to meet their dietary needs and food preferences for an active and healthy life, FAO) is concerned not only with food availability (production, distribution, and exchange) but also with access to, and utilization of, food so that studies which focus only on agricultural production only provide a partial assessment of food security/climate change relationships (Gregory *et al.*, 2005; Ericksen, 2008).

Gregory *et al.* (2005) demonstrated that climate variation is only one of several interacting factors that affect food security. In studies of household food security in southern Africa, Misselhorn (2005) found that climate/environment was only one of some 33 drivers mentioned in surveys as important by householders, so that in all communities many interacting factors resulted in vulnerability to food shortages. However, climate/environment was one of the seven most frequently cited factors influencing food security, because of its role both as an ongoing issue (57% of cases where it was mentioned) and as a 'shock' (43%; Scholes and Biggs, 2004). The effects of sudden shocks such as drought are felt, then, on top of other ongoing, long-term stresses. The result is that the long-term stresses deplete household resilience so that the employment of coping strategies that might be available to other better-prepared communities to deal with sudden shocks, is at too high a cost or, simply, unavailable. For example, reliance on purchased food typically increases in drought years due to losses in food production leading to an increase in poverty due to the synergistic action of other drivers such as rising food prices and unemployment. Scholes and Biggs (2004) noted that the food security crisis in southern Africa in 2002–2003 was not simply a result of drought alone and, indeed, climatic stress was not as severe as in many previous years. Maize production during the preceding growing season was only 5.5% less than the previous 5-year average so food stocks at the start of the climatic shock were not unusually low. However, a range of regional and global political and economic factors including high food prices, legacies of structural adjustment, government policies, conflict, and war, policies on genetically-modified foods, and poor responses to the HIV/AIDS pandemic (Vogel and Smith, 2002) reduced the resilience of the communities to cope with the shock of drought. The moderate climatic shock intensified food insecurity and the long-term vulnerability of the region.

While many agricultural systems are a mix of crop, pasture, tree, and animal production, this paper focuses on crops. Ingram *et al.* (2008) outlined three major challenges for agronomic research in the climate/food security debate: (i) to understand better how climate change will affect cropping systems (as opposed to crop productivity); (ii) to assess technical and policy options for reducing the deleterious impacts of climate change on cropping systems

while minimizing further environmental degradation; and (iii) to understand how best to address the information needs of policy-makers and report and communicate agronomic research results in a manner that will assist the development of food systems adapted to climate change. In addition, to contribute effectively to the food security/climate change debate, the agricultural research community should think more about the issues of scale and how to translate findings at plot-scale over a few seasons to larger spatial and temporal scales and to the issues of food security.

Many assessments of climate change effects on crops have focused on potential yields, but factors such as pests and pathogens have major effects in determining actual yields (Gregory *et al.*, 1999). This paper reviews the direct effects of climate on crop growth and yield and the evidence that existing change or variation has affected production. The effects of climate on plant pests and pathogens and the interactions that may occur between crops, pests, and pathogens under changed climate are also reviewed. Finally, the contribution that better understanding of the roles of pests and diseases in crop production systems might make to enhanced food security in changed climates is considered.

Climate, crop growth, and yield

Current research suggests that while many crops may respond positively to increased atmospheric CO₂ concentrations in the absence of climate changes (Long *et al.*, 2004), the associated effects of higher temperatures and altered patterns of precipitation will probably combine to reduce yields (Easterling *et al.*, 2007). Estimates of the CO₂ fertilization effect vary depending on which experimental approach is used (Long *et al.*, 2006; Tubiello *et al.*, 2007a; Ziska and Bunce, 2007; Ainsworth *et al.*, 2008), but current estimates for increases in crop yield are 10–20% for C₃ crops and 0–10% for C₄ crops (Ainsworth and Long, 2005). However, it is widely recognized that these figures are likely to represent an overestimate in actual field and farm level responses because they are derived from experiments and crop models that do not necessarily take limiting factors such as pests and pathogens, competition, nutrient competition, and soil water fully into account (Gregory *et al.*, 1999; Tubiello *et al.*, 2007b).

Because of the fundamental effects of radiation, temperature, and water on the growth of plants (Hay and Porter, 2006), it is unsurprising that there has been considerable research to understand the effects of climate and climate change on crop production. Gregory *et al.* (1999) summarized experimental findings on wheat and rice crops that indicated decreased crop duration (and hence yield) of wheat as a consequence of warming, and reductions in yields of rice of about 5% per °C rise above 32 °C. Similarly, simulations of maize production in Africa and Latin America using climate data from the Hadley Climate Model 2 to generate characteristic daily weather data for 2055 predicted an overall reduction of 10%, although there

was considerable variability within and between countries with some areas benefitting from changed climate (Jones and Thornton, 2003). The likelihood of some regions benefitting from changed climate while others suffer has been highlighted by a number of modelling exercises that combine biophysically based crop models with global simulations of climate. For example, Fischer *et al.* (2001) modelled the global variation in effects of climate change anticipated in 2050 on potential yields of rainfed cereal crops and demonstrated that cereal-producing regions of Canada, and northern Europe and Russia might be expected to increase production, while many parts of the world would suffer losses, including the western edge of the USA prairies, eastern Brazil, Western Australia, and many, though not all, parts of Africa. Overall, the results of this and subsequent work demonstrated that climate change would benefit the cereal production of developed countries more than the developing countries, even if cropping practices evolved to allow more than one rainfed crop per year (Fischer *et al.*, 2002, 2005). They concluded that production losses in some 40 poor, developing countries (mainly in Sub-Saharan Africa) with a combined population of 2 billion, including 450 million undernourished people, may drastically increase the number of those undernourished.

While model predictions of crop responses to projected climate changes are numerous, relatively few assessments have been made of the effects of the measured changes in climate that have already occurred in the last 50 years or so, a period in which the global mean air temperature has increased by 0.13 °C per decade (IPCC, 2007). Gregory and Ingram (2008) show that the majority of such assessments have been made on temperate cereals grown in northern mid-latitudes with very little information available for crops in the tropics. Although the results were variable, there were some common features including (i) a measured increase in mean temperature at many locations across the globe of about 1.0–1.4 °C over the last 30–40 years often with a larger change in minimum than maximum temperatures but with no detected trend in precipitation; (ii) warmer temperatures have resulted in phenological change and there is some evidence for changes to disease incidence and to farming practices; (iii) the effects of changed temperatures (not all were warmer) on crops is complex because different species have different base and optimum temperatures for development, some processes are daytime only (e.g. photosynthesis) while others occur throughout the day (e.g. respiration), and many processes are non-linearly related to temperature; (iv) typically, the climate effects were small relative to the increased yields resulting from technological improvements, but they can be regionally significant; and (v) use of crop models combined with climatic data suggests that, for vegetative crops grown in areas where higher temperatures permit earlier sowing and hence increased duration of green leaf area, crop yields may have increased. No such effects were found for crops such as wheat which forms a distinct reproductive structure because while warming may advance flowering, it reduces the period of grain filling and thereby does not benefit yield.

Climate and crop pests

CO₂ effects

Few studies addressing the impacts of climate change on crop yield have incorporated the effects of crop pests. For example, when reviewing how elevated [CO₂] might affect crop yields, Ziska and Bunce (2007) listed only two papers that considered how insect pests might modify the predictions. This is despite the wealth of studies that address the impacts of climate change variables on insect pests using growth chambers, open-top chambers and free air carbon dioxide enrichment (FACE) approaches (see reviews by Bezemer and Jones, 1998; Bale *et al.*, 2002). Most studies continue to address the responses of crop pests to separate variables (usually elevated [CO₂] or temperature), but some studies have illustrated the importance of combining climatic variables for more realistic climate change scenarios (Zvereva and Kozlov, 2006). For example, Newman (2004) presented a model for cereal aphid (*Rhopalosiphum padi*) dynamics under elevated CO₂ concentrations and warmer temperatures, and demonstrated that, while under optimal conditions elevated CO₂ was likely to promote aphid populations, this effect was negated by predicted increases in temperature. However, even though *R. padi* did not become more prevalent under simultaneously elevated CO₂ and temperature, Newman (2004) pointed out that the 10% earlier timing of population peaks and the 10% increase in winged forms could result in greater spread and incidence of barley yellow dwarf virus for which this aphid is a vector.

While crop biomass is predicted to increase in response to elevated CO₂ concentrations under many circumstances, it is also recognized that crops and soils may subsequently become nutrient limited, especially in terms of nitrogen availability (Diaz *et al.*, 1993). The increased use of legumes within arable rotations has therefore been of considerable interest (Tubiello *et al.*, 2007b) since legumes can increase N₂ fixation in response to elevated CO₂ (Soussana and Hartwig, 1996). However, soil-dwelling *Sitona* spp. weevil larvae are known to target legume root nodules (which house the N₂-fixing bacteria) which potentially reduces N₂ fixation in the plant (Murray *et al.*, 1996). Recent findings suggest that elevated CO₂ promotes *Sitona* spp. larvae (Staley and Johnson, 2008). In this example, root nodules of white clover (*Trifolium repens*) became both more numerous and larger in size, which was accompanied by larger populations of *Sitona lepidus* larvae that developed at a much faster rate (Table 1). More root nodules were damaged as a consequence and nitrogen concentrations in the roots declined (Table 1). Any accompanying increase in such pests could therefore compromise the perceived benefits of legumes in arable rotations under future climate scenarios.

Temperature effects

In addition to empirical studies and models of effects of climate change variables on crop pests, extrapolations based on responses of crop pests to recent changes in climate

Table 1. Impacts of elevated CO₂ on a legume and an insect pest

Responses of *T. repens* root nodules to ambient (380 $\mu\text{l l}^{-1}$) and elevated (700 $\mu\text{l l}^{-1}$) concentrations of atmospheric CO₂, together with responses of soil-dwelling *S. lepidus* larvae which target root nodules during the early stages of their life-cycle. Mean values \pm standard error shown (adapted from Staley and Johnson, 2008).

Atmospheric CO ₂ concentration ($\mu\text{l l}^{-1}$)	Insect treatment	Root nodule responses		Insect responses			Root N concentration (mg g^{-1} dry mass)
		Number of root nodules	Root nodule size (mm)	Number of larvae recovered	Developmental instar (1–5)	Number of damaged nodules	
380	Control	67.87 \pm 5.54	2.20 \pm 0.06	–	–	–	36.01 \pm 0.11
	Insects	64.64 \pm 6.04	2.01 \pm 0.08	34.07 \pm 2.54	2.04 \pm 0.12	38.96 \pm 4.36	30.21 \pm 0.08
700	Control	150.13 \pm 12.78	2.60 \pm 0.05	–	–	–	34.84 \pm 0.07
	Insects	167.07 \pm 13.75	2.58 \pm 0.06	46.86 \pm 2.25	3.37 \pm 0.17	85.57 \pm 8.35	28.13 \pm 0.10
	CO ₂	F _{1,54} =117.97 P<0.001	F _{1,54} =63.86 P<0.001	F _{1,26} =14.16 P<0.001	F _{1,26} =41.93 P<0.001	F _{1,26} =24.50 P<0.001	F _{1,51} =3.05 P=0.087
	Insect	F _{1,54} =0.15 P=0.69	F _{1,54} =2.94 P=0.09	–	–	–	F _{1,51} =45.68 P<0.001
	CO ₂ × insect	NS	NS	–	–	–	NS

(referred to as climate change fingerprinting) have also been attempted (Schermer, 2004). One of the most detailed examples of this approach is the use of historical flight phenology records of aphids in the UK (Fleming and Tatchell, 1995). These have shown reduced overwintering mortality of some aphids due to increasing temperatures, resulting in flight phenologies occurring as much as a month earlier (Zhou *et al.*, 1995). Like the models presented by Newman (2004), these fingerprint studies suggest that climate change is likely to increase the spread of plant pathogens spread by aphid vectors in a number of crops (Harrington *et al.*, 2007) which could ultimately reduce yields. Again in the UK, warmer winters have already resulted in aphids being detected in suction traps in Scotland several weeks earlier than previously, and the aphid populations themselves, previously of a few clonal genotypes, are becoming much more variable (Malloch *et al.*, 2006). The current Scottish Seed Potato industry is dependent on the virus-free status of its crops which has historically been sustained through the absence of the aphid vectors early in the season; this status is increasingly under threat.

Rainfall

Rainfall can have substantial effects on insect populations. For example, Staley *et al.* (2007) investigated the impacts of enhanced summer rainfall and drought conditions on soil-dwelling *Agriotes lineatus* (wireworms) in grassland plots. Wireworms are damaging pests of crops such as potatoes, especially when planted on land taken out of grass (Johnson *et al.*, 2008) and there is speculation that they are likely to become more of a problem as a result of climate change (Parker and Howard, 2001). Staley *et al.* (2007) found that there was a rapid increase in the population of wireworms in the upper soil as a consequence of enhanced summer rainfall events compared to ambient and drought conditions (Fig. 1). In Sub-Saharan Africa, there is already increasing evidence that changes in rainfall patterns are driving migratory

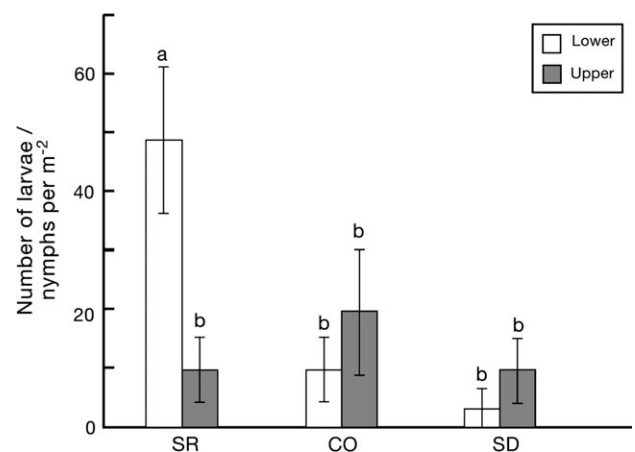


Fig. 1. Abundance of *Agriotes lineatus* larvae (mean \pm standard error) m^{-2} in plots under enhanced summer rainfall (SR), summer drought (SD), and control (CO) treatments. Samples were taken from upper (0–5 cm) and lower (5–10 cm) soil zones. For each species, treatments with different letters are different from each other at $P < 0.05$ (adapted from Staley JT, Hodgson CJ, Mortimer SR, Morecroft MD, Masters GJ, Brown VK, Taylor ME. 2007. Effects of summer rainfall manipulations on the abundance and vertical distribution of herbivorous soil macro-invertebrates. *European Journal of Soil Biology* **43**, 189–198., Copyright Elsevier. Reproduced with permission).

patterns of the desert locust (*Schistocerca gregaria*), which devastates crops in Africa, the Middle East, and Asia (Cheke and Tratalos, 2007). Hulme *et al.* (2001) suggest that precipitation patterns in Southern Africa are likely to decrease in December–February, but increase in June–August when this will most benefit *S. gregaria* and lead to further problems.

Crop–pest interactions

While many observations of insect responses to elevated CO₂ and temperature have been made in natural ecosystems, a feature of insect herbivores in agro-ecosystems is that crops

that they graze have usually been selected for pest resistance and therefore have specific traits that reduce pest damage (Russell, 1978). This may involve traits that directly deter or inhibit herbivory, or traits that result in the production of compounds that recruit antagonists of the pest. There are now several examples of climate change compromising such crop resistance to pests. In soybean, elevated CO₂ caused a down-regulation of genes that produce cysteine proteinase inhibitors, which are specific deterrents to coleopteran herbivores (Zavala *et al.*, 2008). This resulted in increased crop susceptibility to western corn rootworm (*Diabrotica virgifera virgifera*) and Japanese beetle (*Popilla japonica*), both of which have significant impacts on yields. Indirect resistance (e.g. recruitment of pest antagonists) can also be affected by climate change. For example, elevated CO₂ altered the production of volatile defence compounds in white cabbage (*Brassica oleracea*) responsible for recruiting natural enemies (*Cotesia plutellae*) of the diamond back moth (*Plutella xylostella*), resulting in lower searching efficacy of *C. plutellae* (Vuorinen *et al.*, 2004).

Elevated CO₂ and temperature can affect the production of plant secondary compounds with pharmacological impacts on crop–pest interactions. For example, Ziska *et al.* (2008a) found that elevated CO₂ increased concentrations of nicotine in tobacco and scopolamine in jimson weed (*Datura stramonium* L.), but had no effect on atropine concentration in tobacco. Because growth was enhanced in both plant species, the amount of all three secondary compounds was increased on a per plant basis. Likewise elevated CO₂ increased production per plant of morphine, codeine, papaverine, and noscapine in wild poppy (*Papaver setigerum*; Ziska *et al.*, 2008b). The consequences for herbivory were not determined.

Climate and crop pathogens

There are several reports of changes in disease incidence or severity in response to components of climate change, although their usefulness is limited because the experiments normally involved only single parameters and thus do not fully capture the possible change scenarios. Furthermore, most environmental variables will affect both host and pathogen, and affect them in different ways through different mechanisms. Also, in crop stands, there are further complex interactions that are not captured in controlled environment chambers. Consequently, most studies to date only provide some indicative trends which mainly serve to highlight where more resilience needs to be built into the system. Nevertheless, there are reports of some diseases occurring earlier in the growing season as a consequence of warming. For example, the number of days after planting when the first outbreak of late blight occurs in Finland, decreased progressively over a decade in the 1990s (Hannukkala *et al.*, 2007; Fig. 2).

CO₂ effects

While elevated CO₂ has direct effects on plant growth, it can also result in indirect effects such as reduced expression

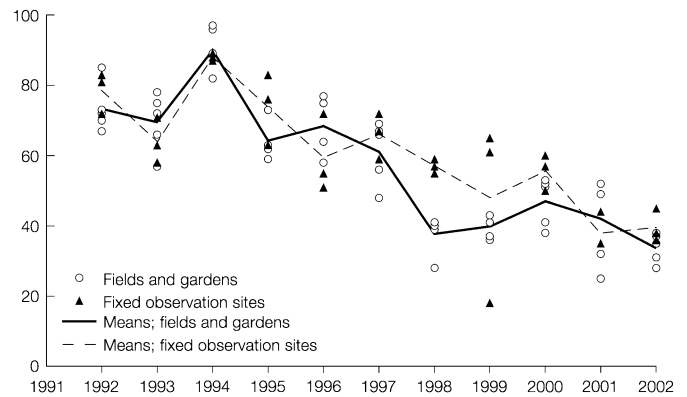


Fig. 2. Changes between 1992 and 2002 in the three earliest observations of potato late-blight (expressed as days after planting – d.a.p. vertical axis) at fixed sites (filled triangles), and the three to five earliest observations in potato fields or home gardens (open circles) at less than 50 km from fixed observation sites in Finland. Figure reproduced from Hannukkala AO, Kaukoranta T, Lehtinen A, Rahkonen A. 2007. Late-blight epidemics on potato in Finland, 1933–2002; increased and earlier occurrence of epidemics associated with climate change and lack of rotation. *Plant Pathology* **56**, 167–176. Copyright © 2007 John Wiley and Sons Ltd. Reproduced with permission.

of induced resistance (Pangga *et al.*, 2004). Elevated levels of both ozone and CO₂ can also affect expression of resistance more directly (Plazek *et al.*, 2001; Plessl *et al.*, 2005). There can also be direct effects on pathogen growth, for example, the enhanced growth of *Colletotrichum gloeosporioides* infecting *Stylosanthes scabra* at high CO₂ (Chakraborty and Datta, 2003). Pathogen-specific effects are common, and different stages of infection can be affected differentially with the cumulative effects resulting in the observed disease (Hibberd *et al.*, 1996). However, perhaps as important as both the direct and indirect effects of CO₂ on pathogen growth and subsequent disease is the effect on pathogen fecundity, which has been shown to increase under elevated CO₂ levels leading to enhanced rates of pathogen evolution (Chakraborty and Datta, 2003). Elevated ozone can have a similar range of effects (such as a 3–5-fold increase in rust infection on poplar), but this response is reduced by elevated CO₂ (Karnosky *et al.*, 2002).

Overall, the effects of elevated CO₂ concentration on plant disease can be positive or negative, although in a majority of the examples reviewed by Chakraborty *et al.* (2000), disease severity increased. Similarly, the effects of ozone and other abiotic stresses can be in either direction and the effects of many stresses are interactive, so it is not possible to generalize.

Temperature and drought effects

Disease resistance can be differentially affected by temperature. For example, cultivars of wheat on the UK Recommended List (HGCA, 2003, www.hgca.com) were routinely tested against isolates of brown rust (leaf rust) (*Puccinia*

recondita) at 10 °C and 25 °C for 20 years (Jones and Clifford, 1986–2002; Jones, 2004–2007). Generally about half showed differential resistance expression, either effective at 10 °C and not at 25 °C or vice versa (Jones, 2003). Browder and Eversmeyer (1986) also reported similar differential temperature responses in the same host–pathogen system, and both groups also demonstrated that the effect was not necessarily attributable simply to resistance gene expression as isolates showed differential responses too. Similar temperature sensitivities have been reported previously to the same rust (Dyck and Johnson, 1983), to *Puccinia striiformis* (Gerechter-Amitai *et al.*, 1984), and to *Puccinia tritici* in oats (Martens *et al.*, 1967). Expression of resistance to broomrape in sunflower (Eizenberg *et al.*, 2003), black shank resistance in tobacco (Sanden and Moore, 1978) and rice resistance to *Xanthomonas oryzae* pv. *oryzae* (Webb *et al.* in Garrett *et al.*, 2006) provide other examples of temperature sensitivity.

Under drought stress, pathogens can have reduced impact or symptoms (Huber and Gillespie, 1992; Pennypacker *et al.*, 1991), but resistance expression can also be reduced (Christiansen and Lewis, 1982). Resistance genes can also show temporary loss of expression due to stress or stress relief. For example, the sudden relief of drought stress resulted in a loss of effectiveness of the *mlo* resistance gene against powdery mildew (*Blumeria graminis* f.sp. *hordei*) in barley (Newton and Young, 1996). This was probably not specific to the *mlo* gene but rather to the speed of resistance gene response which is critical for the efficacy of *mlo* gene expression. A possible mechanism for the changed levels of resistance is that enhanced levels of free radicals were found under drought-stressed conditions in the barley genotype which expressed most loss of resistance, whereas other genotypes did not differ significantly (Goodman and Newton, 2005). Stress-related and defence-related gene expression were shown to be compromised in stress-relieved barley plants compared with non-stressed plants (Barker, 1998) with the differences in accumulation of defence gene transcripts correlated with levels of resistance breakdown in different barley genotypes (Stewart, 2002). The same breakdown problem occurred in response to sudden relief of cold stress but not salt stress (Stewart, 2002). Together, these findings suggest that the efficacy of current resistance genes may be compromised under more extreme and variable climatic conditions.

Crop–pathogen interactions

Many pathogens exhibit so much capacity for generating, recombining, and selecting fit combinations of variants in key pathogenicity, fitness, and aggressiveness traits that there is little doubt that any new opportunities which result from crop responses to climate change will be exploited by them. However, there is also evidence that, under stressed conditions, some organisms enhance their ability to generate variants. For example, stress can stimulate the activity of retrotransposons thereby enhancing the generation of variability in pathogens such as *Fusarium oxysporum*

(Anaya and Roncero, 1996). Similarly, in the Dutch elm disease fungi, *Ophiostoma ulmi* and *Ophiostoma nono-ulmi*, the mobility of its transposons is activated by stress (Bouvet *et al.*, 2008). Organisms have genes which regulate such transposon activity in response to particular stress factors (Twiss *et al.*, 2005).

There is evidence for adaptive mutation and amplification as routes for inducible genetic instability which allow more rapid evolution under stress and an escape from growth inhibition (Hastings *et al.*, 2000). Enhanced mutation rate is specifically related to an increased background of reactive oxygen species characteristically produced in stress responses (Blanco *et al.*, 1995). Fungal pathogens such as *Phaeosphaera nodorum* and *Phytophthora infestans* have been observed to generate very high levels of variability and Newton (1988) suggested that the mechanisms described facilitated mutant instability as a means of generating enhanced levels of variation for adaptation without disadvantageous mutation load (Newton, 1988). In higher plants, alternate splicing of mRNA is another mechanism which can give different gene products in response to stress, and stresses such as pathogen infection can induce this (Halterman *et al.*, 2003). Alternative intron processing has also been reported in the pathogens themselves, such as in the Oomycetes *Phytophthora* species (Costanzo *et al.*, 2007) and true fungi such as *Ustilago maydis* (Ho *et al.*, 2007). Clearly these and other post-translational regulatory mechanisms may contribute to adaptive response to climate. In these ways enhanced genome plasticity can be achieved for response to environmental changes affecting gene expression levels and achieving ectopic recombination—changes which can later become fixed through conventional mutation and recombination.

Most models used to investigate the probable changes in pathogen prevalence are relatively simple and frequently employ climate-matching approaches. Others improve predictions by combining climate change models with other models such as a weather-based disease forecasting models. This approach, used to simulate the effects of climate change on *Phoma* stem canker on oilseed rape, has been modelled with respect to both its severity and spread over the next 10–20 years. The results clearly indicate not only increased severity across its existing range, but also rapid progress into more northern areas where the crop is largely disease-free at present (Evans *et al.*, 2008). Another example of this type of model is the increased range of stem rust, and, in particular, the race known as Ug99 which has virulence towards the *Sr31* resistance gene (1B/IR translocation) which is used extensively in wheat varieties across the world (Admassu *et al.*, 2009). Barley is generally susceptible to Ug99 but hitherto not generally exposed to suitable climatic conditions. About 30 wild barley accessions have already been identified in a screen for effective resistance (B Steffenson, personal communication). There are several other examples where the distribution ranges of pathogens have been shown to change in response to climatic variables such as, for example, *Puccinia striiformis* f.sp. *tritici* in response to rainfall patterns in South Africa

(Boshoff *et al.*, 2002). Similarly, the northward extension of the range of needle blight (*Dothistroma septosporum*) is attributed to climate warming (Woods *et al.*, 2005).

While such models are useful indicators of potential new diseases in hitherto disease-free areas, the effects of covariates and the details of complex interactions at other trophic levels are usually absent. For example, although populations of aphids may increase on cotton, the response of predators, such as wasps, is unknown (Zamani *et al.*, 2006). Similarly, while a combination of heat and drought may reduce the population of cereal aphids in southern Britain, if aphid predators are affected to an even greater degree, then the predicted reduction in aphids may be negated (Newman, 2005). Changes in crop rotations in response to climate change may also influence the future importance of specific pathogens. For example, if warming of northern latitudes enables forage maize to be grown in the rotation then this will leave residues in which pathogens such as Fusarium Head Blight (FHB) could build up high levels of inoculum for subsequent wheat and barley crops (Maiorano *et al.*, 2008). Changes in land use will have many such implications for climate change (Dale, 1997). Effective deployment of crop diversity across all scales, from individual plant interactions to regions, results in the reduced progress of crop epidemics, improved resource utilization, and the enhanced stability of yield and quality. These, in turn, combine to enhance crop resilience to the effects of climatic stress, and stresses in general, thereby improving crop performance (Newton *et al.*, 2009).

Extreme events and crop pests and pathogens

Extreme events may become more frequent in the future, increasing the risks to crop yields. However, this is not always so and the consequence for yield is often dependent on the particular scenario that is considered (Porter and Semenov, 2005). Two main types of extreme events can be characterized either as (i) exceeding normal maxima or minima parameter ranges by a rare magnitude, or (ii) maintaining a normal maxima or minima for an unusually long duration. Events which do not normally occur in a region such as violent storms or floods can be included in these categories. Extreme parameters can include temperature (including lack of, or occurrence of, unseasonal frosts), precipitation (including snow, hail or extreme intensity), wind, light (e.g. lack of intensity due to cloud or dust), humidity, or any unusual sequences of such extremes or even unusual combinations, none of which is extreme on its own. The effect of extremes is illustrated by events in the summer of 2003 in parts of Europe, where temperatures were 6 °C warmer than long-term means and precipitation deficits of up to 300 mm were recorded (Tubiello *et al.*, 2007b). As a consequence, parts of the EU such as the Po valley in Italy, reported record reductions in maize yield of 36% (Ciais *et al.*, 2005). For the EU as a whole, uninsured losses were estimated at 13 billion Euros for 2003 (Sénat,

2004; Tubiello *et al.*, 2007b). In many respects, rapid changes in the climate caused by extreme events are likely to be more devastating for crop production if they lead to sudden pest outbreaks and disease epidemics because control measures are difficult to apply quickly enough or on a sufficiently large scale to contain the problem.

When addressing how climate change will affect pests, experimentalists have conventionally focused on long-term climate changes such as elevated global CO₂ concentration and air temperatures (reviewed above) but there are several examples of extreme events having impacts on pest incidence in the shorter term (see Collier *et al.*, 2008). Historically, there are also many examples of invertebrate food webs responding to short-term changes in climatic conditions. For example, conditions in the UK in 1975 and 1976 were particularly beneficial for aphids in terms of early development and reduced overwintering mortality, leading to large increases in aphid populations, including the cereal aphids *Sitobion avenae* and *Metopolophium dirhodum* (Jones, 1979). This caused an explosion in populations of predatory ladybirds (*Adalia* spp.) which fed on the abundant prey in early spring and developed to adult stage rapidly (Majerus and Kearns, 1989). Indeed, populations became so abundant that there were widespread reports of ladybirds biting humans when they had exhausted supplies of their aphid prey (Majerus and Kearns, 1989).

Extreme events can also have indirect or secondary consequences as illustrated by outbreaks of potato late-blight in Canada. The epidemics in 1994 to 1996 were due to genotypes of *Phytophthora infestans* from distant regions which were associated with the unusual tropical storm tracks moving up the eastern seaboard of the USA (Peters *et al.*, 1999). In the UK, the unusually wet season of 2007, coinciding with the prevalence of epidemiologically-fit new pathotypes of *P. infestans*, resulted in an unprecedented number of outbreaks of late-blight (www.eucablight.org). This was also reflected in the number of isolates and their genotypes (Fig. 3).

Crops, pests and diseases in the context of food security

The impacts of pests and diseases on yield in current conditions are well known, but the consequences of climate change on pests and diseases are complex and, as the preceding descriptions attest, are still only imperfectly understood. Scherm *et al.* (2000) highlighted the importance of pests and diseases both as important yield-reducing components and as early indicators of environmental changes because of their short generation times, high reproductive rates, and efficient dispersal mechanisms. Attempts have been made to model the effects of changing climate on the distribution of pests and pathogens particularly using climatic mapping to delineate potential distributions based on the concept of the fundamental niche (Baker *et al.*, 2000). While such approaches are open to criticism because climate alone does not determine distribution and

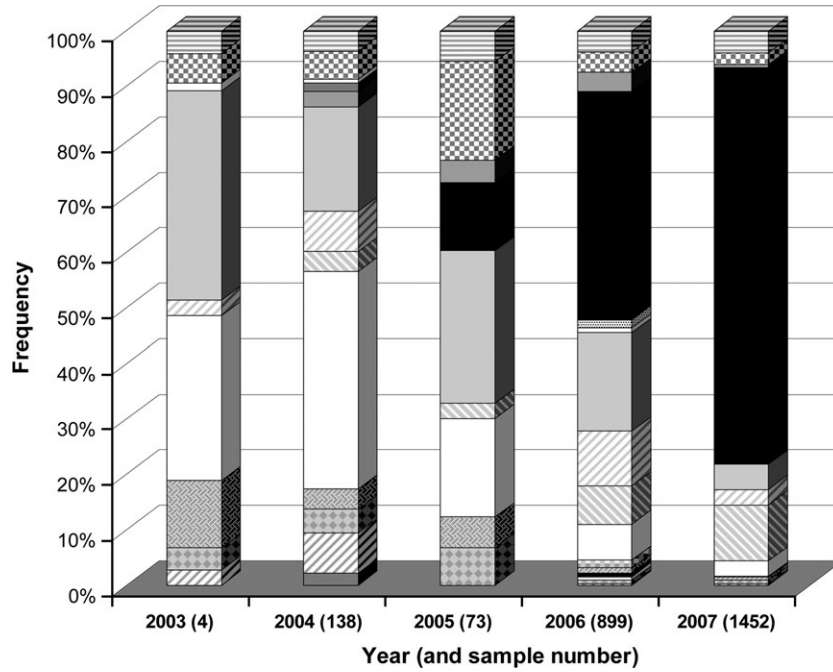


Fig. 3. The frequency of different genotypes of *Phytophthora infestans*, indicated by the different shaded sections of the bars, over five successive sampling years in the UK. Note the increased sample number together with increased frequency of a new fit genotype (black bar) in the unusually wet summer of 2007, when an unprecedented number of outbreaks of potato late-blight were reported. Figure courtesy of DELI Cooke, SCRI.

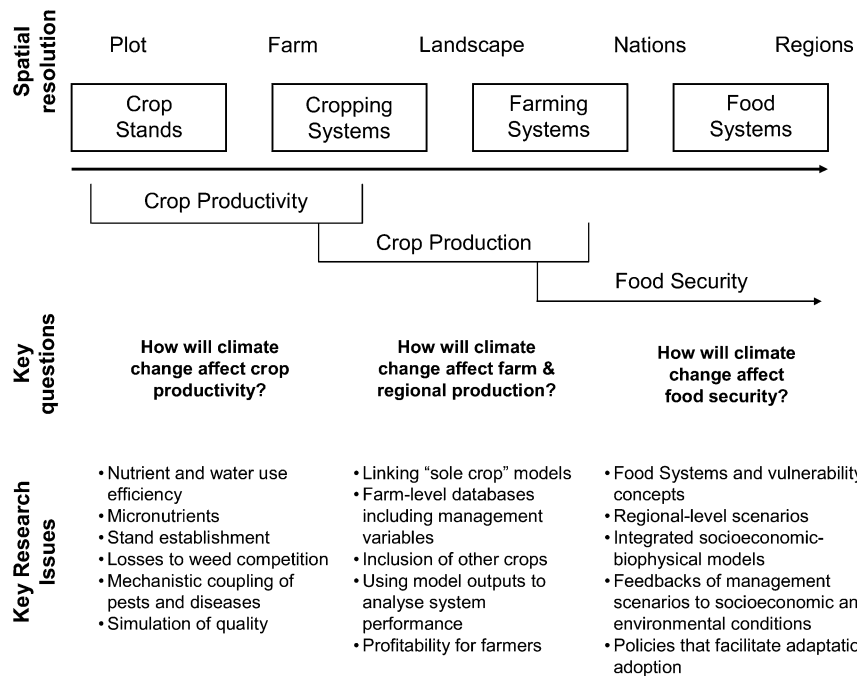


Fig. 4. Effects of scale on elements of food systems contributing to food security and the various questions and research issues appropriate to different scales (from Ingram JSI, Gregory PJ, Izac A-M. 2008. The role of agronomic research in climate change and food security policy. *Agriculture, Ecosystems and Environment* **126**, 4–12. Copyright Elsevier, Reproduced with permission.)

species interactions are ignored (Davis et al., 1998), climatic mapping provides a pragmatic means of investigating the potential for exotic pests and pathogens to establish in new areas (Baker et al., 2000) and a basis for implementing phytosanitary controls to restrict the entry, for example, of

karnal bunt (*Tilletia indica*) into Europe (Sansford et al., 2008). Changing climate has already affected the geographical distribution of some crop pests and pathogens [e.g. *Puccinia graminis* f.sp. *tritici* (stem rust) and *Dickea dianthicola*; Woods et al., 2005; Admassu et al., 2009;

Elphinstone and Toth, 2008)] and advanced the appearance in the growing season of others [(e.g. late blight in Finland (Hannukkala *et al.*, 2007) and *Myzus persicae* aphids in Scotland (Malloch *et al.*, 2006)]. Some pests which are already present, but only occur in small areas or at low densities, may be able to exploit the changing conditions by spreading more widely and reaching damaging population densities. Aphids, for instance, key pests of agriculture, horticulture, and forestry throughout the world, are expected to be particularly responsive to climate change because of their low developmental threshold temperature, short generation time, and considerable dispersal abilities (Sutherst *et al.*, 2007). Together, the effects of changing climate and more variable weather suggest that pest and pathogen attacks are likely to be more unpredictable and the amplitude larger. The consequences for other elements of agro-ecosystems and crop yields are still uncertain and greater effort is required to integrate this science into estimates of actual crop productivity (Ingram *et al.*, 2008).

The ability to include realistic impacts of pests and diseases in future climates has a direct link to considerations of food security (Fig. 4). Ingram *et al.* (2008) point out that more mechanistic inclusion of pests and disease effects on crops would lead to more realistic predictions of crop production on a regional scale and thereby assist in the development of more robust regional food security policies. As described in the introduction, economic and social issues are often dominant determinants of household food security, but changed pest and disease incidence under climate change is an essential influence on future food security. The currently limited ability to model crop and pest and pathogen interactions, coupled with increased unpredictability of future pest and pathogen attacks means that systematic monitoring, increased research on the biology of the organisms, breeding of durable resistance in crops, and improved modelling of the many interacting processes, would be an essential underpinning investment for future food security.

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