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REVIEW

Implications of climate change for diseases, crop yields and food security

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Abstract Accelerated climate change affects components of complex biological interactions differentially, often causing changes that are difficult to predict. Crop yield and quality are affected by climate change directly, and indirectly, through diseases that themselves will change but remain important. These effects are difficult to dissect and model as their mechanistic bases are generally poorly understood. A combination of integrated modelling from different disciplines and multi-factorial experimentation is needed to advance our understanding and prioritisation of the challenges. This will help prioritise breeding objectives. Food security brings in additional socio-economic, geographical and political factors. Enhancing resilience to the effects of climate change is important for all these systems and functional diversity, particularly in tolerance traits for abiotic and biotic stress, is one of the most effective targets for improved sustainability.

Keywords Resilience · Complex interactions · CO_2 · Ozone · Temperature · Extreme events · Quality

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Introduction

Climates continually change and there is evidence for the effect of recent accelerated warming on many biological systems (IPCC 2007). Not least of these are the effects on the geographic distributions of pests and pathogens (e.g. Woods et al. 2005; Admassu et al. 2008; Elphinstone and Toth 2008), with potentially serious implications for food security. However, cropping systems will also change in response to climate, with consequent impacts on their interactions with pests and pathogens.

The focus of many assessments of climate change effects on crops has been the direct effects on potential yields driven largely by changes in temperature, CO_2 and water (Gregory et al. 2009). Pests and pathogens have major effects in determining actual yields in practice (Gregory et al. 1999) and the effects of climate change on pests and pathogens have been evaluated in some experimental and modelling studies (Garrett et al. 2006), but their consequences for yield were rarely assessed (e.g. Evans et al. 2008). Although in intensive monoculture a few major pathogens tend to cause the dominant epidemics, most crops are not only affected by a single pest or pathogen, but each will be affected in different ways.

To evaluate effects of climate change effectively we should consider the whole crop system, recognising multiple trophic levels of organisms, each of which may be affected differently by climatic variables. Not least are the effects on the community of organisms in the soil upon which the overall health of the crop substantially depends. As these comprise complex and dynamic communities of pests, pathogens, mutualists and parasites (degrees of symbiosis) that change in response to environmental triggers (Newton et al. 2010b), one might expect difficulty in being able to predict the consequences of climate change and therefore difficulty in prioritising climate change breeding objectives. The complexity of these interactions is illustrated in an ecological context where, in an extensive synthesis of published studies, various sub-sets of microbe-plant interactions are placed in several strength/frequency influence scenarios (Tylianakis et al. 2008). However, as these show how the main drivers of change alter competitive interactions and generally increase pathogen infection, durable disease resistance will assume ever greater importance as an objective in crop breeding.

To grasp the true picture of the complexity of biological interactions in crop systems and how they might interact, and to contribute effectively to the food security and climate change debates, we must also comprehend issues of scale and how to translate findings at the plot-scale over a few seasons used in breeding and agronomic experimentation to larger spatial and temporal dimensions and subsequently their implications for food systems (Tubiello et al. 2007). The interacting driving forces of population increase, income growth, urbanization and globalization on food production, markets and consumption have changed food and agricultural systems worldwide (Von Braun 2007). Climate change and its increased variability compound the effects of these changes and have serious consequences for food production and food security (Parry et al. 2004).

In this paper, we review the effects of climate change on some diseases and on the incidence and severity of some pathogen vectors, focussing on implications for yield and how this information might affect crop breeding methodologies and objectives. In particular we consider crop systems where organisms interact, possibly resulting in outcomes that differ from those predicted from responses of the organisms singly. It is in this latter context that outcomes must be considered in terms of implications for food security which also encompass important geographic, socio-economic and political considerations.

Local scale climate effects on crop production systems

As climate change has already affected crop production and predictions are of accelerated effects, we will look at how climate change affected one region local to the authors (Scotland) where detailed records were kept since the 1960s (Barnett et al. 2006). These show not only changes in line with those predicted for Scotland, but also seasonal and regional shifts that can change field operations and thereby agricultural production in practice. For example, winters have become over twice as wet in western regions, but in the east the increase in precipitation has been smaller and restricted to the autumn. Summers have become drier in some regions, particularly the main arable areas, but there has been no change or an increase in rainfall in others. Temperature changes also vary both regionally and seasonally, with no change in western areas in autumn, but up to a 2°C increase in the south-east during winter. Air frost and days with snow cover also show spatial and temporal variation, with changes ranging from no reduction to around 40 days less.

In practice, this means longer growing seasons but the lack of chill can affect development of some crops. For example, blackcurrants suffer uneven bud break and therefore lack of synchrony in ripening due to insufficient cumulative temperature below 7°C (Jones and Brennan 2009). This can reduce yield and quality as the whole crop is harvested by machine on one date. Therefore cultivars with a lower chilling requirement have become an active breeding objective. High summer temperatures can cause sterility in wheat ears (Porter and Gawith 1999) so again this has become a breeding selection criterion. Wetter autumn or winters in some regions can affect access to the land for both harvest and sowing (Cooper et al. 1997), consequently it may not be possible to take advantage of the longer growing season and early-maturing cultivars retaining good yield have a clear market niche and therefore are a breeding criterion. Summer drought can also severely limit yield in sensitive crops like potato, and cause premature senescence, so water use-efficiency has gone on the breeder's selection priority agenda. The date of first or last frost also does not necessarily correlate with total frost days. The spatial variation in change may affect cropping patterns in different ways in different regions. Furthermore, year to year variability is very large so it is difficult to capitalise on changes over shorter periods. However, the requirements for breeding varieties suitable for resilience to such conditions are clear.

Macro-scale implications of climate change for agriculture and food security

Agricultural systems worldwide over the last 40–50 years have responded to the effects of the interacting driving forces of population increase, income growth, urbanization and globalization on food production, markets and consumption (Von Braun 2007). 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).

Although climate change may benefit crop production in northern latitudes above about 55°, where warmer temperatures may extend the growing season, in the developing world (especially sub-Saharan Africa) the projected changes are likely to have negative impact and will further complicate the achievement of food security. This is due to the observed and predicted deleterious impacts of climate change on agriculture, in particular in tropical and subtropical countries (Fischer et al. 2001; Parry et al. 2004; Stern 2007). Fischer et al. (2001) modelled the spatial variation in effects of climate change anticipated in 2050 on potential yields of rain-fed cereal crops worldwide and demonstrated that cereal producing regions of Canada, and northern Europe and Russia might be expected to increase production, while many other 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 rain-fed 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 under-nourished people, could drastically increase the number of those under-nourished.

There are three main factors underlying concerns about food security and climate change in the developing world. Firstly, many parts of the developing world are expected to experience significant changes in temperature and rainfall patterns. Climate assessments for southern Africa, for instance, conclude that the region will become warmer and drier (Hulme et al. 2001). A temperature increase of 2–5°C is predicted over coming decades (IPCC 2007) and increasingly variable rainfall is anticipated, with the region becoming generally drier, especially in the east (Scholes and Biggs 2004). An increase in extreme events (both droughts and floods) is also anticipated (Tyson et al. 2002). The consequence of these combined changes is expected to be reduced yields of several staple food crops (Jones and Thornton 2003; Lobell et al. 2008). It is noteworthy, though, that seasonal rainfall variation in semi-arid Africa is already large, raising the question as to whether, in the medium-term, farmers will have to cope with anything that they are not already dealing with (Cooper et al. 2009). Secondly, developing economies are particularly sensitive to the direct impacts of climate change given their often heavy dependence on agriculture and natural resources, and because of their high poverty levels and geographic exposure (Stern 2007). Thirdly, many people in the developing world depend directly on agriculture as their primary source of food, and negative impacts on crop yields will affect total crop production and thereby overall food supply at the local level.

How plant breeding can contribute directly to such large-scale problems is difficult to specify as the resilience requirements to cope with such variability are often not present in the germplasm used in elite breeding programmes. Biotechnological solutions together with agronomic practice changes may be offer some potential. However, landrace-based participatory breeding using germplasm from the regions already more stressed may represent valuable sources of resilient traits for exploitation in elite breeding programmes too (Ceccarelli 1994; Newton et al. 2010d).

Effects of climate change on crop diseases

Disease complexes

Taking a traditional pathologist's approach, we might focus on pathogens, the 'causal agents' of disease and the effect of climate change on them. However, crop loss is attributable to direct and indirect effects of pathogens together with the effects of other biotic and abiotic agents. Direct effects of pathogens or other organisms can be the induction of resistance or susceptibility and its associated cost or benefit to the host plant (Newton et al. 2010a). Disease symptoms such as development of necrotic lesions can be due to a combination of a pathogen or pathogenic complex and in some circumstances non-pathogens of that crop such as bacterial species, exploiting an advantageous trophic environment (Newton and Toth 1999; Newton et al. 2004). Each component of the host-pathogen/microbe interaction and the pathogenic complex will have a different interaction with the environment, and thus will change under different climates (e.g. Stonard et al. 2008; Xu and Nicholson 2009). However, such associations of organisms in the disease complex are very variable due to their opportunistic nature and therefore represent another area of uncertainty in predicting the effects of climate change. Deploying resistance reliably-affecting a broad spectrum of organisms with common trophic mechanisms (Newton et al. 2010b), where available, will be advantageous, but there is no effective substitute for selection under more extreme environments where these complexes occur naturally.

Many climate change experiments involve the manipulation of single parameters such as temperature or CO_2 and therefore do not simulate likely change scenarios where several parameters change simultaneously. These parameters will probably affect the host, disease and pathogen/pest complexes, in different ways through different mechanisms. Nevertheless, some trends can be shown that highlight where more resilience needs to be built into the system. Furthermore, the effects of many stresses are interactive, so it is frequently not possible to generalise.

For the major arable crops, particularly under intensive monoculture, a few pathogens often dominate. Epidemics can be both fast and severe where epidemiologically successful races of pathogens have adapted to the prevailing resistance mechanisms deployed. These are likely to have the most damaging economic impact, particularly rusts on cereals (Chakraborty et al. 2011) and are likely to have a large impact in terms of food security under climate change scenarios. The fact that the above examples are from monocultures under high input situations underlines the vulnerability of such systems to change. Polygenic resistance, where many genes each contribute small effects likely to be non-race-specific but together expressing effective resistance, should always be used by breeders in preference to major genes, where available. The major epidemiological and food security issues resulting from the spread of the stem rust race 'Ug99' (Chakraborty et al. 2011) demonstrate the serious consequences of relying on a very few major resistance genes, especially when a false sense of security was obtained from the medium-term durability of *Sr31*.

Temperature effects

There is evidence of the growing season being extended in many places, i.e. number of day-degrees (e.g. Barnett et al. 2006). In many countries this will enable earlier sowing and more crop species to be grown, but generally greater opportunities for increased disease pressure (Peltonen-Sainio et al. 2009). The effect of this is shown in the number of days after planting when the first outbreak of late blight occurs on potato in Finland, which decreased progressively over the 1990s (Hannukkala et al. 2007). However, it is difficult to find other examples of changes in disease incidence or severity that can be attributable directly to climate change rather than changes in cultivar, crop protection, agronomy or atmospheric pollution. For example, the abundance of the two common 'septoria' diseases of wheat, caused by *Phaeosphaeria nodorum* and *Mycosphaerella graminicola*, were studied from archive samples dating back to 1844 and, whilst seasonal variability could be attributable to weather factors, the only long-term variation was correlated with national SO_2 emissions (Shaw et al. 2008).

Many pathosystems, and it seems the cereal rusts in particular, are affected by temperature. At times about half of the wheat cultivars on the UK Recommended List (e.g. HGCA 2003) showed differential resistance expression when tested against isolates of brown rust (leaf rust) (caused by *Puccinia triticina*), either effective at 10°C and not at 25°C or vice versa (Jones and Clifford 1986–2002; Jones 2004–2007). The effect was not necessarily attributable simply to resistance gene expression response to temperature as isolates too showed differential temperature responses independent of resistance responses, and other authors reported similar effects (Dyck and Johnson 1983; Browder and Eversmeyer 1986). These differential responses to disease expression at different temperatures were also found against other rusts such as stripe rust (Gerechter-Amitai et al. 1984) and oat stem rust (Martens et al. 1967). In wheat stem rust the classical temperature sensitivity of the *Sr6* gene was extensively reported by Samborski and co-workers (e.g. Harder et al. 1979). However, such examples are not unique to rusts on cereals, but extend to other pathosystems involving monocot and dicot hosts and very different pathogens (Gregory et al. 2009). In rice, for example, some resistance genes, such as *Xa7* effective against some *Xanthomonas oryzae* pv. *oryzae* races, are more effective at high temperatures than low, whereas other resistance genes are less effective (Webb et al. 2010). There is a case for breeders to 'stress-test' their parental sources of resistance as well as advanced breeding lines under a range of possible temperatures as well as temperature extreme events. This should preferably be carried out together with likely scenarios for other environmental changes such as CO_2 concentration.

Greenhouse gas effects

In a majority of the examples reviewed by Chakraborty et al. (2000) disease severity increased with elevated CO_2 concentration, but in some examples it decreased. There can also be direct effects on pathogen growth; for example. the enhanced growth of *Colletotrichum gloeosporioides* infecting *Stylosanthes scabra* at high CO_2 (Chakraborty and Datta 2003). CO_2 can also affect pathogen fecundity which was shown to increase under elevated CO_2 levels leading to enhanced rates of pathogen evolution (Chakraborty and Datta 2003). *Arabidopsis thaliana* was more susceptible to *Erysiphe cichoracearum* under high CO_2 concentration, correlated with increased stomatal density and guard cell length, but there were inherent differences between ecotypes in this response (Lake and Wade 2009). In rice, enhanced susceptibility to *Magnaporthe oryzae* under elevated CO_2 was attributed to lower leaf silicon content (Kobayashi et al. 2006). Elevated CO_2 also reduced expression of induced resistance (Pangga et al. 2004) or affected expression of resistance more directly (Plazek et al. 2001; Plessl et al. 2005), but in resistant cultivars it also enhanced resistance by boosting phytoalexin production (Braga et al. 2006). In soybean elevated CO_2 increased *Septoria* brown spot but reduced downy mildew (Eastburn et al. 2010). Pathogen-specific effects are common, and different stages of infection can be affected differentially with the cumulative effects resulting in changed disease levels (Plazek et al. 2001; Plessl et al. 2005). These cumulative effects may be due to specific differential responses to climate change at different stages of infection (Hibberd et al. 1996).

Elevated ozone can have a similar range of effects (Plazek et al. 2001; Plessl et al. 2005), such as a 3- to 5-fold increase in rust infection on poplar, but this response is reduced by elevated CO_2 (Karnosky et al. 2002). However, wheat stem rust was found to be strongly inhibited by ozone but unaffected by CO_2 (Tiedemann and Firsching 2000). High CO_2 also compensated for the negative effects of ozone on plant growth, but not the negative effects of the rust on yield. Thus there are clearly no particular greenhouse gas tolerance traits that can be easily selected for in breeding programs. However, testing parental lines and advanced selections, although unlikely to be useful under greenhouse gas future climate change scenarios alone, would be worthwhile in conjunction with other likely parameter changes such as temperature.

Water, other effects and extremes

Debilitated crops under drought stress can have reduced impact or symptoms from pest or pathogen attack because they have reduced trophic value (Pennypacker et al. 1991; Huber and Gillespie 1992). However, resistance expression can also be changed and in particular reduced (Christiansen and Lewis 1982). Loss of resistance expression can be temporary due to stress or stress relief. For example, in barley a sudden relief of drought stress compromised the effectiveness of the *mlo* resistance gene against powdery mildew (caused by *Blumeria graminis* f. sp. *hordei*) (Newton and Young 1996). The significance of this is that speed of pathogen recognition and response is often crucial to effective defence and this effect is probably common to other resistance sources, but notably in *mlo* as it is particularly critical for its efficacy of expression.

Stress-related and defence-related gene expression were shown to be compromised in stress-relieved barley plants compared to 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). Enhanced levels of free radicals were found under drought-stressed conditions in the barley genotype showing the greatest loss of resistance, whereas other genotypes did not differ significantly (Goodman and Newton 2005). The same breakdown problem occurred in response to sudden relief of cold stress but not salt stress (Stewart 2002). We cannot therefore assume that resistance genes currently in use will continue to be equally effective under environments with changed abiotic stress such as water stress, as found in the temperature response of many rust resistance genes cited above.

Actions need to be taken to counter the effects of drought stress and to improve drought stress tolerance of crops generally, and the effects on resistance mechanism expression in particular. A first step will be for breeders to carry out more screening under stressed environments, and there is a degree of commonality at the molecular level between responses to a range of stress factors (Fujita et al. 2006). A limitation of such a strategy is that the pathogen isolates used will be current ones as opposed to adapted genotypes themselves arising from prolonged stress selection. However, we should also consider the role of other organisms in the crop environment or within the crop itself. For example, the grass *Elymus virginicus* was only half as much affected by drought if infected with an endophyte *Epichloe elymi* (Rudgers and Swafford 2009). Endophytes have largely been excluded by the approaches used in major crop breeding programs as well as common agronomic practices.

Pathogen adaptation

Plant pathogens are generally highly adaptable and likely to exploit any compromise in plant defence caused directly or indirectly by climate change. At a population level, the adaptive potential of pathogens may prove to be the most important predictors of the magnitude of climate change effects (Garrett et al. 2006). However, some changes, such as increased drought, may result in fewer periods with good infection conditions as the presence of free water, high humidity or open stomata is required by many pathogens for initial infection.

Instability of variation is common in many pathogens, although the mechanisms are often not known (Newton 1988). Under stressed conditions some organisms enhance their ability to generate variants by, for example, stimulation of retrotransposon activity in pathogens such as *Fusarium oxysporum, Ophiostoma ulmi* and *Ophiostoma nono-ulmi* (Anaya and Roncero 1996; Bouvet et al. 2008), and certain transposon activity regulation mechanisms in response to particular stress factors are known (Twiss et al. 2005). Elevated mutation rate mechanisms in response to stress have been found in other fungi (Hastings et al. 2000), particularly in response to increased reactive oxygen species (Blanco et al. 1995). Other mechanisms found in fungal pathogens might include alternative intron processing (Costanzo et al. 2007; Ho et al. 2007), alternate splicing of mRNA (Halterman et al. 2003) and other post-translational regulatory mechanisms, all of which may be a way of generating enhanced levels of variation for adaptation without adding to a disadvantageous mutation load (Newton 1988). This leads to enhanced genome plasticity enabling organisms to respond rapidly to environmental changes. Such changes can later become fixed through conventional mutation and recombination. In summary, pathogens are highly adaptable and they will often respond to climate change very rapidly within the limits of their fundamental biology (Gregory et al. 2009).

Effects of climate change on vectors of crop pathogens

The effect of climate change on invertebrate pests and vectors is gradually becoming better characterised, based largely on evidence from both historical records and experimental manipulation. In the case of historical records, the best studied examples have examined past trends for phenological events and prevailing air temperatures (Harrington et al. 1995; Zhou et al. 1995). In particular, aphid vectors of crop diseases have been recorded over several decades using suction traps across Europe (http://www.rothamsted.ac.uk/insect-survey/) (Harrington et al. 2007). This has established clear linkages between winter temperatures and first emergence of key aphid pests, with those that overwinter in non-egg stages (e.g. as adults or larvae) being particularly tightly correlated with winter temperatures (Harrington et al. 1995, 2007). For example, date of first recorded occurrence of the peach-potato aphid (*Myzus persicae*) was negatively correlated with mean January and February temperatures across 14 sites in the U.K. (Fig. 1). Amongst this extensive dataset, important vectors of cereal diseases include the bird cherry-oat aphid (*Rhopalosiphum padi*) and the grain aphid (*Sitobion avenae*). Since winter temperatures are widely predicted to increase (IPCC 2007), it seems inevitable that some aphid vectors will arrive, or become active, earlier (Harrington et al. 2007). In terms of managing plant diseases, this will require increasingly early pest management procedures (e.g. pesticide applications). This is problematic, not only because of increasingly restrictive pesticide legislation (e.g. Directive 91/414/EEC) (Copping 2008), but also the unfavourable logistics and costs of treating crops earlier in the season (e.g. water logged fields).

Whilst not explicitly concerned with crop pests and disease vectors, examination of historical records recently showed the earlier emergence of numerous animal and plant species between 1976 and 2005 (Thackeray et al. 2010). Many of the invertebrates included in the study were likely pests of crops and vectors of plants diseases, but many were also likely natural enemies and parasitoids which may help to control populations of such pests. In particular, this study suggested that such secondary consumers were slowest to respond to advances in timing, which may therefore lead to asynchrony between the life-cycles of predators and prey (Thackeray et al. 2010). To our knowledge, the effects of climate change on such eco-system services have not been explicitly considered, but understanding how populations of antagonists of crop pests will respond to changes in prey density and attendant changes in the climate must warrant further attention. Gregory et al. (2009) point to the dramatic escalation in the numbers of ladybird predators in the U.K. following increases in aphid numbers during particularly warm summers of 1975 and 1976, so the extent to which these will be affected by extreme events should also be considered.

In terms of experimental approaches to investigating how climate change will affect plant diseases vectored by insect pests, there are still surprisingly few examples (Gregory et al. 2009). However, there is evidence that elevated CO_2 could compromise crop resistance to some insect pests (Zavala et al. 2008, 2009). Most recently, this has been reported for resistance in red raspberry (*Rubus idaei*) to the European large raspberry aphid (*Amphorophora idaei*) (Martin and Johnson 2010). As a vector of at least four plant viruses (including black raspberry necrosis virus,

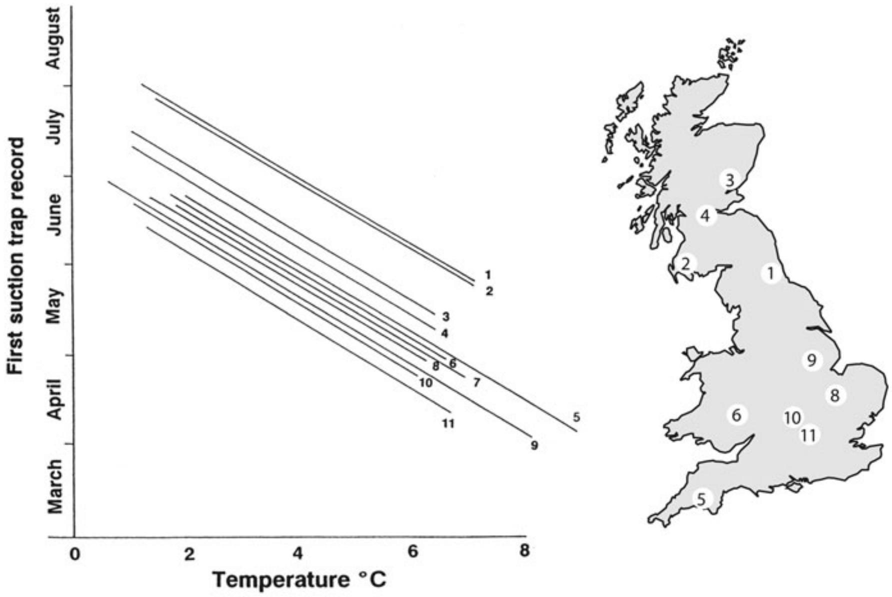

Fig. 1 Date of the first record of *Mysus persicae* (regression lines shown) in relation to mean temperature in January and February at different latitudes across the U.K., indicated on the map (1) 55.2° Newcastle, (2) 55.5° Ayr, (3) 56.5° Dundee, (4) 55.9° Edinburgh, (5) 50.6° Starcross, (6) 52.1° Hereford, (7) 51.2° Wye (8) 52.3° Broom's Barn, (9) 52.9° Kirkton, (10) 51.8° Rothamsted, and (11) 51.7° Writtle. Reproduced from Harrington et al. (1995)

raspberry leaf mottle virus, raspberry leaf spot virus and Rubus yellow net virus) *A. idaei* is considered to be the most significant disease vector of this crop (McMenemy et al. 2009). Martin and Johnson (2010) reported that under elevated CO_2, the number of aphids on a cultivar containing A_1 resistance (McMenemy et al. 2009) became equivalent to an entirely susceptible cultivar (Fig. 2a), with corresponding increases in body mass (Fig. 2b). Plants with A_{10} resistance (McMenemy et al. 2009) were seemingly more resistant at ambient and elevated carbon dioxide conditions (Fig. 2), but this still represents a potentially worrying development in terms of disease transmission in raspberry. This again illustrates the need for breeders to test putative resistant parental lines and selections under climate change scenario environments and stresses.

In cereals the trend will be for earlier and more severe aphid-borne virus losses as the climate

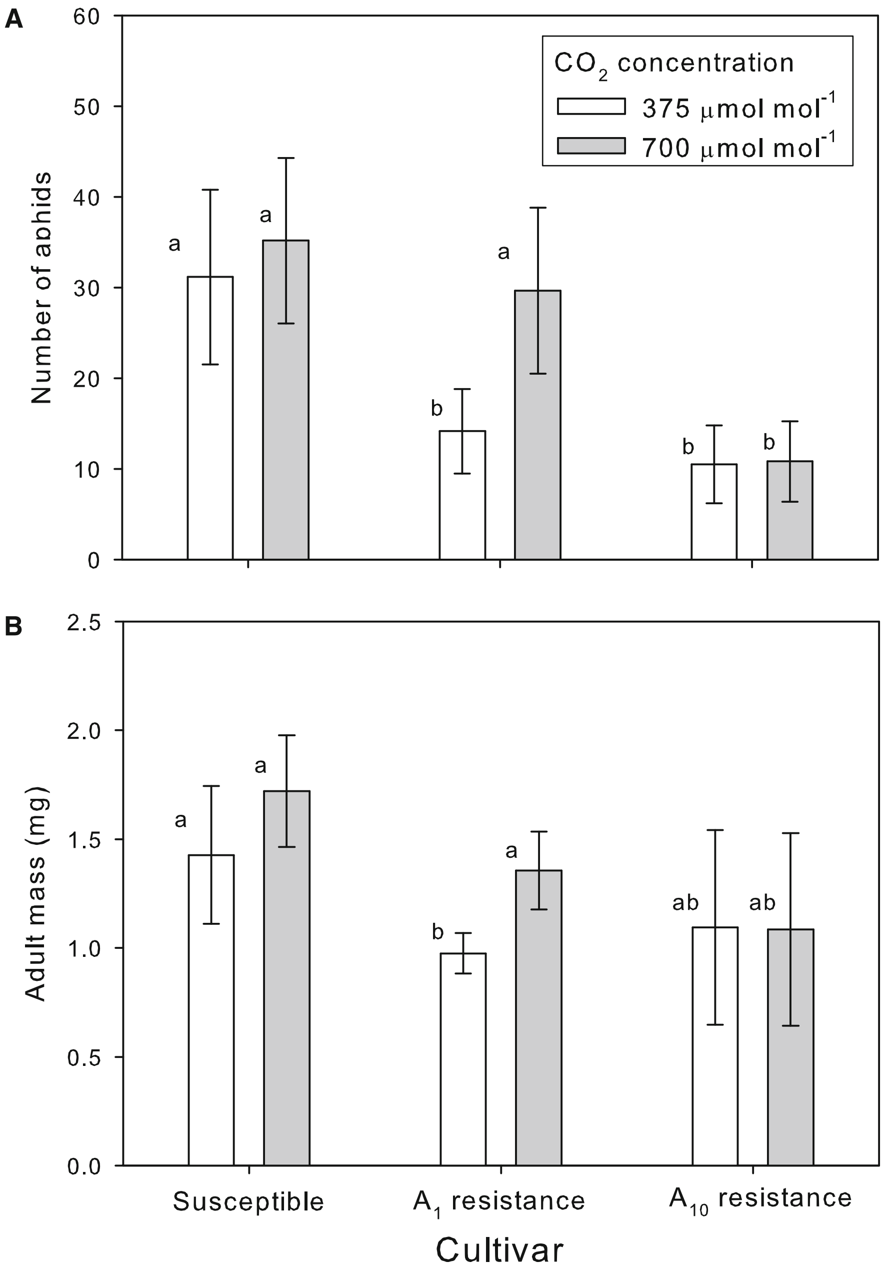

Fig. 2 Performance of European large raspberry aphid (*Amporophora idaei*) on three cultivars with different levels of resistance; susceptible (Malling Jewel), A1 gene (Glen Lyon) and A10 gene (Glen Rosa) at ambient and elevated CO_2 conditions. **a** Total population size and **b** Individual adult mass. Mean values ± SE shown ($N = 6$). Lowercase superscripts indicate statistically significant ($P < 0.05$) differences. Reproduced from Martin and Johnson (2010)

changes (Harrington et al. 1995, 2007). This may be balanced by the fecundity of parasitic wasps and other predatory insects that feed on them; however, the population dynamics of these species may not respond to climate in the same way. On cereals, damage is caused more from the viruses they carry, but like the wasps, these may multiply at different rates. In addition to the increased fecundity of the aphid vectors and viruses, elevated temperatures also will likely shorten virus acquisition, latent period, and transmission times, regardless of whether it is cultivated as an autumn or spring sown crop. Such effects of climate change on populations of vectors and hosts have recently been reviewed by Canto et al. (2009). In practice we have seen diseases such as Barley Yellow Dwarf Virus becoming much more severe and extensive in unusually warm summers, but aphid predators tend to lag in their increased numbers.

Multi-trophic effects on pathogen vectors

While the vectors of plant pathogens are the focus of this review, it should also be recognised that plants are seldom attacked by these vectors alone, and that other insect pests sharing a host plant may affect the behaviour and performance of such vectors. In particular, there are many examples of root-feeding insects changing the susceptibility of crops of vector aphids living aboveground (Johnson et al. 2008). For example in a cereal system, R. padi performance can be significantly increased when barley (*Hordeum vulgare*) is simultaneously attacked by root-feeding wireworms (*Agriotes* spp.) through changes to plant chemistry (Johnson et al. 2009). Likewise, virus vector aphids such as the large raspberry aphid, discussed above, can perform better when red raspberry (*R. idaeus*) is also fed on by root-feeding vine weevils (*Otiorhynchus sulcatus*) (McMenemy et al. 2009). Given that root-feeding insects are often influenced by climate change (Staley and Johnson 2008), it seems likely that they may moderate the effects of climate change in pathogen vectors. For example, vine weevils are negatively affected by elevated CO2 (Johnson et al. 2011) so it seems possible that the net effect of climate change on pathogen vectors is likely to influenced by the effects of climate change on other herbivores sharing the host crop too.

Direct effects of climate change on yield and quality

The major emphasis of climate change/food security research over recent years has been concerned with the impacts of climate change on crop yield. For example, 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. More recently, the modification of crops and management systems to cope with changed temperatures demonstrated what adaptation might be possible. For example, simulation of production for cropping systems in northern and central Italy showed that the combined effects of increased [CO_2] and climate change would depress crop yields by 10–40% if current management practices were unamended largely because the warmer air temperatures would accelerate the phenology of current cultivars (Tubiello et al. 2000). Through a combination of early planting of spring and summer crops and the use of slower-maturing winter cereal cultivars, though, the model indicated that it should be possible to maintain present yields. This demonstrates a clear breeding target for climate change adaptation. However, a major caveat to this conclusion was that 60–90% more irrigation water was required to maintain grain yields under conditions of climate change; this water was assumed to be available (Tubiello et al. 2000). More recently, elements of crop adaptation to extreme weather events have been explored with genotypic variation and adaptation able to compensate for several of the negative impacts on unadapted productivity (e.g. Fuhrer 2006; Challinor et al. 2007).

New cropping systems which are resilient to changed climate conditions are required. It is highly probable that the changes of climate and [CO_2] will occur sufficiently slowly that changes to sowing date, cultivar, crop and other management practices will allow at least some adaptation of the production system by farmers. Several adaptations are conceivable in the timescale available including:

- Crop selection to determine mechanisms and sources of durable disease resistance
- Crop selection to identify mechanisms and sources of resistance/resilience to abiotic stresses including drought and cold

- Genetic enhancement to cope with more variable growing conditions
- Development of new crops to take advantage of more favorable growing conditions

Extreme events may also become more frequent in the future increasing the risks to crop yields, although this is not always so and is often dependent on the precipitation scenario that is considered (Porter and Semenov 2005). 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. 2007). As a consequence, parts of the European Union such as the Po valley in Italy, reported a record reduction in maize yield of 36% (Ciais et al. 2005).

Whilst model predictions of crop responses to projected climate changes are numerous, relatively few assessments have been made of the effects on crop quality. Quality is a complex issue involving the whole food chain from growth through storage and processing to cooking and consumption (Porter and Semenov 2005) and its stability under climate change should be as a high priority as yield and disease resistance for breeders. One of the few quality traits investigated was that of rheological properties of wheat flour for bread-making (the Hagberg Falling Number, HFN). HFN is a measure of α-amylase activity in which a high HFN indicates a low activity—a desirable property of wheat for bread-making. Kettlewell et al. (1999) demonstrated how climate variation, expressed in terms of the North Atlantic oscillation (NAO, linked to sea surface temperatures) from year-to-year influenced the HFN of wheat in the U.K. during the period 1972 to 1996. HFN was positively correlated with NAO index for January and February and this had major consequences for the bread-making industry. In years of low NAO and HFN (wet years) about 45% of UK milling wheat was imported decreasing to 25% in years of high NAO and HFN.

Pests and diseases: implications for 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 factors and as early indicators of environmental changes because of their short generation times, high reproductive rates and efficient dispersal mechanisms. It is already clear that some pests will be able to invade new areas and become increasingly problematic for the maintenance of biodiversity, the functioning of ecosystems and the profitability of crop production. 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 dispersal abilities (Sutherst et al. 2007).

Many assessments of climate change effects on crops have focused on potential yields (e.g. Fischer et al. 2001) but factors such as pests and pathogens have major effects in determining actual yields (Gregory et al. 1999). The importance of including pathogens can be seen, for example, in the work of Butterworth et al. (2010). They combined a crop yield simulation model with a weather-based epidemiological model and showed that under 2020 and 2050 climate change scenarios fungicide-protected oilseed rape will increase in yield in Scotland by 15%, whereas in England yields could decrease by 50%.

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. 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 regional food security.

Another aspect of disease control is the CO_2 cost. Yield has a cost in terms of inputs that can be calculated in CO_2 equivalents per hectare. It therefore stands to reason that preventing yield loss increases efficiency that can be given a value. If it is achieved through use of crop protectants, their costs of production and application must be deducted, and similarly any additional cost of elite germplasm if it is achieved through plant resistance. It is calculated that control of disease in oilseed rape in the U.K. by fungicides reduces emissions by 100 kg CO_2 eq t^{-1} of seed (Mahmuti et al. 2009). For wheat it is estimated that in the U.K. fungicides save 59 kg CO_2 eq t^{-1} of grain and that a further 14 kg CO_2 eq t^{-1} could be achieved if all diseases were eliminated by fungicides or resistance that carries no yield penalty (Berry et al. 2008). It also means that the value of breeding durable resistance germplasm can be estimated in the same terms. Therefore efficient pest and disease control is important for both adaptation to, and mitigation of, climate change.

Managing crop systems for resilience

Biodiversity is regarded as a valuable source of novel resistance. Whilst undoubtedly true, major resistance genes obtained from alien germplasm are rarely durable, but their value should be measured by the opportunities they give for deployment, again potentially estimable in kg CO_2 eq t^{-1} of grain. This can be through combining several different and preferably contrasting genes into a single genotype, but also the ability to deploy many such different new cultivars. In the latter case, this lessens the selection pressure to overcome resistance in any one cultivar (Newton et al. 2009). Therefore, the scale of cultivar deployment should also be considered.

Epidemics are a feature of crop monocultures under high input situations. Contrast the opposite extreme of long-established natural ecosystems where plant, pests and pathogens are all found in much greater genotypic diversity, and we find small and localised epidemics but an absence of large epidemics. Under climate change we would expect such ecosystems to adapt, using the wealth of diversity to confer resilience on the system. We need to deploy this functional diversity intelligently in agricultural systems to confer resilience at appropriate scales (Newton et al. 2009). In the context of pests and pathogens, this means heterogeneity of deployment of resistance at scales appropriate to their dispersal mechanisms (Marshall et al. 2009). This can easily be implemented within field or between fields, but is difficult to implement at a regional scale since cultivar breeding has become more international.

Changes in land use will have many implications for climate change (Dale 1997). Introduction of crops to regions where they were previously not grown and consequent changes to crop rotations in response to climate change may also influence the future prevalence and importance of specific pathogens. An example would be growing maize for forage or grain in more northern latitudes. In a rotation with cereals this will leave residues in which pathogens such as *Fusarium* species could build up high levels of inoculum causing severe Fusarium Head Blight (FHB) on subsequent wheat and barley crops (Maiorano et al. 2008). Effective deployment of crop diversity across all scales from individual plant interactions to regions results in slowed progress of crop epidemics, improved resource utilisation and 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).

Phytosanitation will reduce Fusarium problems, but not eliminate them. Pesticides can and should be used in conjunction with effective resistance deployment strategies to reduce pest and pathogen populations, but not in a way that selects strongly for pesticide resistance. International phytosanitation measures, plant passports, and quarantine measures will slow the progress of pathogens entering new areas, but rarely prevent them for ever. However, all these measures—new disease resistance, deployment of resistance heterogeneously, and phytosanitation, all have roles to play in building resilience to changes likely to accelerate due to climate change. These need to be supported at local, national, regional and international levels through policy and extension service bodies where some degree of agreement and co-ordination would be desirable, including legislation (Fig. 3).

We noted above that a grass was only half as much affected by drought if colonised by an endophyte (Rudgers and Swafford 2009). Indeed endophytes may confer both abiotic and biotic stress tolerance in grasses, including cereals, and this feature could be targeted as a breeding objective (Newton et al. 2010a). Endophytes are a component of grassland breeding and development, and are widely recognised as conferring advantages for productivity. They are largely absent from major crop varieties and high soil disturbance agronomic approaches mitigate against their exploitation. However, in minimum and no-tillage systems

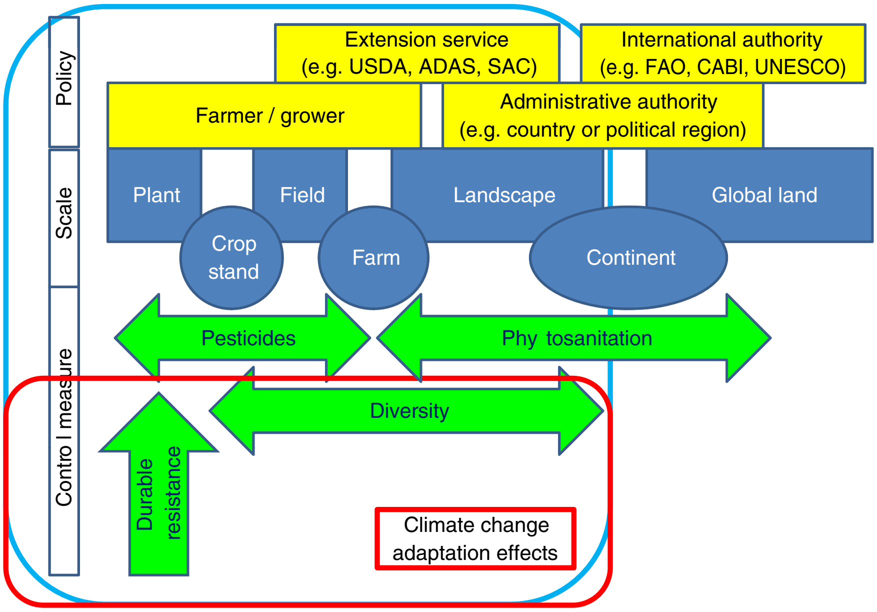

Fig. 3 Influences on pest and disease threat to food security. Yellow boxes are policy influences ranging from individuals to international organisations that can co-ordinate appropriate actions and transfer and exchange knowledge (KTE). Blue shapes are crop production scale relative to KTE bodies. Green arrows are strategies or measures that contribute to controlling disease that may be applied at different scales. The red box enclosed measures are particularly relevant to climate change effects, the blue box indicating the scale and relevant type of KTE bodies. Acronyms: *USDA* United States Department of Agriculture; *ADAS* Agricultural Development Advisory Service; *SAC* Scottish Agricultural College; *FAO* Food and Agriculture Organisation; *CABI* Commonwealth Agricultural Bureau International; *UNESCO* United Nations Educational, Scientific and Cultural Organization

they might be exploited to enhance resilience to abiotic stresses in general. Recent evidence show that under long-established reduced tillage situations many genotypes of barley respond differentially (Newton et al. 2010c). This is likely due not only to adaptation to changed soil physical conditions including water availability, but also the soil microbial environment and its component balance of pathogens, parasites and mutualists (symbionts) conferring enhanced resilience on some crop genotypes (Newton et al. 2010b).

Conclusions

The implications of climate change for crop pests and diseases cannot easily be summarised except to point out that they are highly adapted to exploit opportunities in general. Specific predictions will be difficult because of the complex multi-trophic relationships between many microbial organisms including pathogens, their vectors and their respective host plants. Nevertheless, such mechanistic understandings under likely multi-factorial climate change scenarios need to be obtained through linked experimentation and modelling.

The effects of disease on crops may be large but climate change will also have direct effects, complicating analyses. Diversity to give more options and build spatial and temporal heterogeneity into the cropping system, will enhance resilience to both abiotic and biotic stress challenges. Other resilience sources will include more robust genetic resistance and biochemical response mechanisms. This can be achieved through breeders selecting parental gerplasm proven to be resilient under likely climate change scenarios including extreme events. Resilient parameters should include not only pest and disease resistance and yield, but also quality. However, testing response to climate change-adapted pest and pathogen populations remains problematic. Broad host-range biotechnological solutions will play a part, as will participatory breeding selection in marginal and high stress environments. The biodiversity thus produced should be deployed at spatially heterogeneous scales to both maximise its efficacy and protect its longevity.

Food security is a complex issue as it is the summation of these effects and many other socio-economic, geographic and political factors. However, our understanding of the relative importance of these factors is improving, particularly as models hitherto discipline-bound are being linked together. Nevertheless, major epidemics in staple crops grown in non-resilient agricultural systems can have large and significant impacts on food security notwithstanding these complexities.

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References

Admassu B, Lind V, Freidt W, Ordon F (2008) Virulence analysis of *Puccinia graminis* f. sp. *tritici* populations in Ethiopia with special consideration of Ug99. Plant Pathol 58:362–369

Anaya N, Roncero MIG (1996) Stress-induced rearrangement of *Fusarium* retrotransposon sequences. Mol Gen Genet 253:89–94

Barker SJ (1998) The temporary breakdown of *mlo*-resistance in barley to powdery mildew. D.Phil Thesis, University of Oxford, U.K.

Barnett C, Hossell J, Perry M, Procter C, Hughes G (2006) A handbook of climate trends across Scotland. SNIFFER project CC03, Scotland & Northern Ireland Forum for Environmental Research, 62 pp

Berry PM, Kindred DR, Paveley ND (2008) Quantifying the effect of fungicides and disease resistance on greenhouse gas emissions associated with wheat production. Plant Pathol 57:1000–1008

Blanco M, Herrera G, Urios A (1995) Increased mutability by oxidative stress in oxyr-deficient Escherechia coli and Salmonella typhimurium cells–clonal occurrence of the mutants during growth on nonselective media. Mutat Res Lett 346:215–220

Bouvet GF, Jacobi V, Plourde KV, Bernier L (2008) Stress-induced mobility of OPHIO1 and OPHIO2, DNA transposons of the dutch elm disease fungi. Fungal Genet Biol 45:565–578

Braga MR, Aidar MPM, Marabesi MA, de Godoy JRL (2006) Effects of elevated CO_2 on the phytoalexin roduction of two soybean cultivars differing in the resistance to stem canker disease. Environ Exp Bot 58:85–92

Browder LE, Eversmeyer MG (1986) Interactions of temperature and time with some *Puccinia recondita: Triticum* corresponding gene pairs. Phytopathology 76:1286–1288

Butterworth MH, Semenov MA, Barnes A, Moran D, West JS, Fitt BDL (2010) North-South divide: contrasting impacts of climate change on crop yields in Scotland and England. J R Soc Interface 7:123–130

Canto T, Aranda MA, Fereres A (2009) Climate change effects on physiology and population processes of hosts and vectors that influence the spread of hemipteran-borne plant viruses. Glob Change Biol 15:1884–1894

Ceccarelli S (1994) Specific adaptation and breeding for marginal conditions. Euphytica 77:205–219

Chakraborty S, Datta S (2003) How will plant pathogens adapt to host plant resistance at elevated CO_2 under a changing climate? New Phytol 159:733–742

Chakraborty S, Tiedermann AV, Teng PS (2000) Climate change: potential impact on plant diseases. Environ Pollut 108:317–326

Chakraborty S, Luck J, Hollaway G, Fitzgerald G, White N (2011) Rust-proofing wheat for a changing climate. Euphytica. doi:10.1007/s10681-010-0324-7

Challinor AJ, Wheeler TR, Craufurd PQ (2007) Adaptation of crops to climate change through genotypic responses to mean and extreme temperatures. Agric Ecosyst Environ 119:190–204

Christiansen MN, Lewis CF (1982) Breeding plants for less favorable environments. Wiley, New York

Ciais P, Reichstein M, Viovy N, Granier A, Ogée J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grünwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533

Cooper G, McGechan MB, Vinten AJA (1997) The influence of a changed climate on soil workability and available workdays in Scotland. J Agric Eng Res 68:253–269

Cooper P, Rao KPC, Singh P, Dimes J, Traore PS, Rao K, Dixit P, Twomlow SJ (2009) Farming with current and future climate risk: advancing a “Hypothesis of Hope” for rainfed agriculture in the semi-arid tropics. J SAT Agric Res 7:1–19

Copping L (2008) The proposed revision of EC 91/414. Outlooks Pest Man 19:148–149

Costanzo S, Ospina-Giraldo MD, Deahl KL, Baker CJ, Jones RW (2007) Alternate intron processing of family 5 endoglucanase transcripts from the genus *Phytophthora*. Curr Genet 52:115–123

Dale VH (1997) The relationship between land-use change and climate change. Ecol Appl 7:753–769

Dyck PL, Johnson R (1983) Temperature sensitivity of genes for resistance in wheat to *Puccinia recondita*. Can J Plant Pathol 5:229–234

Eastburn DM, Degennaro MM, DeLucia EH, Dermody O, McElrone AJ (2010) Elevated atmospheric carbon dioxide and ozone alter soybean diseases at SoyFACE. Glob Change Biol 16:320–330

Elphinstone J, Toth IK (2008) *Erwinia chrysanthemi* (*Dikeya* spp.)—the facts. Potato Council, Oxford, U.K.

Evans N, Baierl A, Semenov MA, Gladders P, Fitt BDL (2008) Range and severity of a plant disease increased by global warming. J R Soc Interface 5:525–531

Fischer G, Shah M, van Velthuizen H, Nachtergaele FO (2001) Global agro-ecological assessment ain the 21st century. International Institute for Applied Systems Analysis, Laxenburg, Austria

Fischer G, Shah M, van Velthuizen H (2002) Climate change and agricultural vulnerability. Special Report as contribution to the World Summit on Sustainable Development, Johannesburg 2002. International Institute for Applied Systems Analysis, Laxenburg, Austria 152 pp

Fischer G, Shah M, Tubiello F, van Velhuizen H (2005) Socio-economic and climate change impacts on agriculture: an integrated assessment, 1990–2080. Philos Trans R Soc B 360:2067–2083

Fuhrer J (2006) Agricultural systems: sensitivity to climate change. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources 1, No 052

Fujita M, Fujita Y, Noutoshi Y, Takahashi F, Narusaka Y, Yamaguchi-Shinozaki K, Shinozaki K (2006) Crosstalk between abiotic and biotic stress responses: a current view from the points of convergence in the stress signaling networks. Curr Opin Plant Biol 9:436–442

Garrett KA, Dendy SP, Frank EE, Rouse MN, Travers SE (2006) Climate change effects on plant disease: Genomes to ecosystems. Annu Rev Phytopathol 44:489–509

Gerechter-Amitai ZK, Sharp EL, Reinhold M (1984) Temperature-sensitive genes for resistance to *Puccinia striiformis* in *Triticum dicoccoides*. Euphytica 33:665–672

Goodman BA, Newton AC (2005) Effects of drought stress and its sudden relief on free radical processes in barley. J Sci Food Agric 85:47–53

Gregory PJ, Ingram JSI, Campbell B, Goudriaan J, Hunt LA, Landsberg JJ, Linder S, Stafford Smith M, Sutherst RW, Valentin C (1999) Managed production systems. In: Walker B, Steffen W, Canadell J, Ingram JSI (eds) The terrestrial biosphere and global change: implications for natural and managed systems. Cambridge University Press, Cambridge, pp 229–270

Gregory PJ, Johnson SN, Newton AC, Ingram JSI (2009) Integrating pests and pathogens into the climate change/food security debate. J Exp Bot 60:2827–2838

Halterman DA, Wei FS, Wise RP (2003) Powdery mildew-induced Mla mRNAs are alternatively spliced and contain multiple upstream open reading frames. Plant Physiol 131:558–567

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 Pathol 56:167–176

Harder DE, Rohringer R, Samborski DJ, Rimmer SR, Kim WK, Chong J (1979) Electron-microscopy of susceptible and resistant near-isogenic (sr6-Sr6) lines of wheat infected by Puccinia graminis tritici. II. Expression of incompatibility in mesophyll and epidermal cells and the effect of temperature on host-parasite interactions in these cells. Can J Bot 57:2617–2625

Harrington R, Bale JS, Tatchell GM (1995) Aphids in a changing climate. In: Harrington R, Stork NE (eds) Insects in a changing environment. Academic Press, London, U.K., pp 126–155

Harrington R, Clark SJ, Welham SJ, Verrier PJ, Denholm CH, Hulle M, Maurice D, Rounsevell MD, Cocu N, European Union Examine C (2007) Environmental change and the phenology of European aphids. Glob Change Biol 13:1550–1564

Hastings PJ, Bull HJ, Klump JR, Rosenberg SM (2000) Adaptive amplification: an inducible chromosomal instability mechanism. Cell 103:723–731

HGCA (2003) www.hgca.com (Accessed 5th May 2010)

Hibberd JM, Whitbread R, Farrar JF (1996) Effect of elevated concentrations of CO_2 on infection of barley by *Erysiphe graminis*. Physiol Mol Plant Pathol 48:37–53

Ho EC, Cahill MJ, Saville BJ (2007) Gene discovery and transcript analyses in the corn smut pathogen *Ustilago maydis*: expressed sequence tag and genome sequence comparison. BMC Genom 8:334. http://www.biomedcentral.com/1471-2164/8/334

Huber L, Gillespie TJ (1992) Modeling leaf wetness in relation to plant disease epidemiology. Annu Rev Phytopathol 30:553–577

Hulme M, Doherty R, Ngara T, New M, Lister D (2001) African climate change: 1900–2100. Climate Res 17:145–168

Ingram JSI, Gregory PJ, Izac A-M (2008) The role of agronomic research in climate change and food security policy. Agric Ecosyst Environ 126:4–12

IPCC: Intergovernmental Panel on Climate Change (2007) Climate change 2007: the physical science basis. Summary for policymakers. Contribution of working group I and II to the third assessment report of the IPCC. IPCC Secretariat, Geneva, Switzerland

Johnson SN, Bezemer TM, Jones TH (2008) Linking aboveground and belowground herbivory. In: Johnson SN, Murray PJ (eds) Root Feeders—an ecosystem perspective. CABI, Wallingford, UK, pp 153–170

Johnson SN, Hawes C, Karley AJ (2009) Reappraising the role of plant nutrients as mediators of interactions between root- and foliar-feeding insects. Funct Ecol 23:699–706

Johnson SN, Barton AT, Clark KE, Gregory PJ, McMenemy LS, Hancock RD (2011) Elevated atmospheric carbon dioxide impairs the performance of root-feeding vine weevils by modifying root growth and secondary metabolites. Glob Change Biol 17:688–695

Jones ERL (2004–2007) Brown rust of wheat. United Kingdom Cereal Pathogen Virulence Survey 2003–2006 Ann Rep

Jones HG, Brennan RM (2009) Potential impacts of climate change on soft fruit production: the example of winter chill in *Ribes*. Acta Hortic 838:27–33

Jones ERL, Clifford BC (1986–2002) Brown rust of wheat. United Kingdom Cereal Pathogen Virulence Survey 1985–2001 Ann Rep

Jones PG, Thornton PK (2003) The potential impacts of climate change on maize production in Africa and Latin America in 2055. Glob Environ Change 13:51–59

Karnosky DF, Percy KE, Xiang BX, Callan B, Noormets A, Mankovska B, Hopkin A, Sober J, Jones W, Dickson RE, Isebrands JG (2002) Interacting elevated CO_2 and tropospheric O_3 predisposes aspen (*Populus tremuloides* Michx.) to infection by rust (*Melampsora medusae* f. Sp. *tremuloidae*). Glob Change Biol 8:329–338

Kettlewell PS, Sothern RB, Koukkari WL (1999) UK wheat quality and economic value are dependent in the North Atlantic oscillation. J Cereal Sci 29:205–209

Kobayashi T, Ishiguro K, Nakajima T, Kim HY, Okada M, Kobayashi K (2006) Effects of elevated atmospheric CO_2 concentration on the infection of rice blast and sheath blight. Phytopathology 96:425–431

Lake JA, Wade RN (2009) Plant-pathogen interactions and elevated CO_2: morphological changes in favour of pathogens. J Exp Bot 60:3123–3131

Lobell DB, Burke MB, Tebaldi C, Mastrandrea MD, Falcon WP, Naylor RL (2008) Prioritizing climate change adaptation needs for food security in 2030. Science 319:607–610

Mahmuti M, West JS, Watts J, Gladders P, Fitt BDL (2009) Controlling crop disease contributes to both food security and climate change mitigation. Int J Agric Sustain 7:189–202

Maiorano A, Blandino M, Reyneri A, Vanara F (2008) Effects of maize residues on the *Fusarium* spp. infection and deoxynivalenol (DON) contamination of wheat grain. Crop Prot 27:182–188

Marshall B, Newton AC, Zhan J (2009) Quantitative evolution of aggressiveness of powdery mildew in a two-cultivar barley mixture. Plant Pathol 58:378–388

Martens JW, McKenzie RIH, Green GJ (1967) Thermal stability of stem rust resistance in oat seedlings. Can J Bot 45:451–458

Martin P, Johnson SN (2010) Evidence that elevated CO_2 reduces resistance to the European large raspberry aphid in some raspberry cultivars. J Appl Ent. doi:10.1111/j.1439-0418.2010.01544.x

McMenemy LS, Mitchell C, Johnson SN (2009) Biology of the European large raspberry aphid (*Amphorophora idaei*): its role in virus transmission and resistance breakdown in red raspberry. Agric For Entomol 11:61–71

Newton AC (1988) Mutant instability in *Septoria nodorum*. Trans Brit Mycol Soc 91:607–610

Newton AC, Toth IK (1999) Helper bacteria and pathogenicity assessments. New Phytol 144:385–386

Newton AC, Young IM (1996) Temporary partial breakdown of Mlo-resistance in spring barley by the sudden relief of soil water stress. Plant Pathol 45:970–974

Newton AC, Toth IK, Neave P, Hyman L (2004) Bacterial inoculum from a previous crop affects fungal disease development on subsequent non-host crops. New Phytol 163:133–138

Newton AC, Begg G, Swanston JS (2009) Deployment of diversity for enhanced crop function. Ann Appl Biol 154:309–322

Newton AC, Gravouil C, Fountaine JM (2010a) Managing the ecology of foliar pathogens: ecological tolerance in crops. Ann Appl Biol 157:343–359

Newton AC, Fitt BDL, Daniell T, Atkins SD, Walters DR (2010b) Pathogenesis, mutualism and parasitism, in the trophic space of microbial-plant interactions. Trend Microbiol 18:365–373

Newton AC, Bengough AG, Guy DC, McKenzie BM, Hallett PD (2010c) Interactions between barley cultivars and soil cultivation—effects on yield and disease. Proc Crop Prot N Britain, 2010, pp 137–142

Newton AC, Aker T, Baresel JP, Bebeli P, Bettencourt E, Bladenopoulos KV, Czembor JH, Fasoula DA, Katsiotis A, Koutis K, Koutsika-Sotiriou M, Kovacs G, Larsson H, Pinheiro de Carvalho MAA, Rubiales D, Russell J, dos Santos TMM, Vaz Patto MC (2010d) Cereal landraces for sustainable agriculture: a review. Agron Sust Dev 30:237–269

Pangga IB, Chakraborty S, Yates D (2004) Canopy size and induced resistance in *Stylosanthes scabra* determine anthracnose severity at high CO_2. Phytopathology 94:221–227

Parry ML, Rosenzweig C, Iglesias A, Livermore M, Fischer G (2004) Effects of climate change on global food production under SRES emissions and socio-economic scenarios. Glob Environ Change 14:53–67

Peltonen-Sainio P, Jauhiainen L, Hakala K, Ojanen H (2009) Climate change and prolongation of growing season: changes in regional potential for field crop production in Finland. Agric Food Sci 18:171

Pennypacker BW, Leath KT, Hill JRR (1991) Impact of drought stress on the espression of resistance to *Verticillium albo-atrum* in alfalfa. Phytopathology 81:1014–1024

Plazek A, Hura K, Rapacz H, Zur I (2001) The influence of ozone fumigation on metabolic efficiency and plant resistance to fungal pathogens. J Appl Bot 75:8–13

Plessl M, Heller W, Payer HD, Elstner EF, Habermeyer J, Heiser I (2005) Growth parameters and resistance against *Drechslera teres* of spring barley (*Hordeum vulgare* L. cv. Scarlett) grown at elevated ozone and carbon dioxide concentrations. Plant Biol 7:694–705

Porter JR, Gawith M (1999) Temperatures and the growth and development of wheat: a review. Eur J Agron 10:23–36

Porter JR, Semenov MA (2005) Crop responses to climatic variation. Phil Trans R Soc B 360:2021–2031

Rudgers JA, Swafford AL (2009) Benefits of a fungal endophyte in *Elymus virginicus* decline under drought stress. Basic Appl Ecol 10:43–51

Scherm H, Sutherst RW, Harrington R, Ingram JSI (2000) Global networking for assessment of impacts of global change on plant pests. Environ Pollut 108:333–341

Scholes RJ, Biggs R (2004) Ecosystem services in Southern Africa: a regional assessment. Council for Scientific and Industrial Research, Pretoria, South Africa

Shaw MW, Bearchell SJ, Fitt BDL, Fraaije BA (2008) Long-term relationships between environment and abundance in wheat of *Phaeosphaeria nodorum* and *Mycosphaerella graminicola*. New Phytol 177:229–238

Staley JT, Johnson SN (2008) Climate change impacts on root herbivores. In: Johnson SN, Murray PJ (eds) Root Feeders—an ecosystem perspective. CABI, Wallingford, UK, pp 192–213

Stern NH (2007) The economics of climate change: the Stern review. Cabinet Office, Great Britain, Treasury, UK. Cambridge University Press, Cambridge, U.K.

Stewart KJ (2002) Abiotic stress and *mlo*-resistance breakdown to barley powdery mildew. D.Phil Thesis, University of Oxford, U.K.

Stonard JF, Marchant B, Latunde-Dada AO, Liu Z, Evans N, Gladders P, Eckert M, Fitt BDL (2008) Effect of climate on the proportions of *Leptosphaeria maculans* and

L. biglobosa in phoma stem cankers on oilseed rape in England. Asp Appl Biol 88:161–164

Sutherst R, Baker RHA, Coakley SM, Harrington R, Kriticos DJ, Scherm H (2007) Pests under global change—meeting your future landlords? In: Canadell JG (ed) Terrestrial ecosystems in a changing world. Springer, Berlin, Germany, pp 211–225

Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliott JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ & Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Glob Ch Biol 16:3304–3313

Tiedemann AV, Firsching KH (2000) Interactive effects of elevated ozone and carbon dioxide on growth and yield of leaf rust-infected versus non-infected wheat. Environ Pollut 108:357–363

Tubiello FN, Donatelli M, Rosenzweig C, Stockle CO (2000) Effects of climate change and elevated CO_2 on cropping systems: model predictions at two Italian locations. Eur J Agron 13:179–189

Tubiello F, Soussana J-F, Howden MS (2007) Crop and pasture response to climate change. Proc Natl Acad Sci USA 104:19686–19690

Twiss E, Coros AM, Tavakoli NP, Derbyshire KM (2005) Transposition is modulated by a diverse set of host factors in *Escherechia coli* and is stimulated by nutritional stress. Mol Microbiol 57:1593–1607

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363

Tyson P, Odada E, Schulze R, Vogel CI (2002) Regional-global change linkages: Southern Africa. In: Tyson P, Fuchs R, Fu C, Lebel L, Mitra AP, Odada E, Perry J, Steffen W, Virji H (eds) Global-regional linkages in the earth system. START/IHDP/IGBP/WCRP. Springer, Berlin & London

Von Braun J (2007) The world food situation: new driving forces and required actions. International Food Policy Research Institute, Washington D.C., USA

Webb KM, Ona I, Bai J, Garrett KA, Mew T, Vera Cruz CM, Leach JE (2010) A benefit of high temperature: increased effectiveness of a rice bacterial blight disease resistance gene. New Phytol 185:568–576

Woods A, Coates KD, Hamann A (2005) Is an unprecedented Dothistroma needle blight epidemic related to climate change? Bioscience 55:61–69

Xu XM, Nicholson P (2009) Community ecology of fungal pathogens causing wheat head blight. Annu Rev Phytopathol 47:83–103

Zavala JA, Casteel CL, DeLucia EH, Berenbaum MR (2008) Anthropogenic increase in carbon dioxide compromises plant defense against invasive insects. Proc Natl Acad Sci USA 105:5129–5133

Zavala JA, Casteel CL, Nabity PD, Berenbaum MR, DeLucia EH (2009) Role of cysteine proteinase inhibitors in preference of Japanese beetles (*Popillia japonica*) for soybean (*Glycine max*) leaves of different ages and grown under elevated CO_2. Oecologia 161:35–41

Zhou XL, Harrington R, Woiwod IP, Perry JN, Bale JS, Clark SJ (1995) Effects of temperature on aphid phenology. Glob Change Biol 1:303–313