

Impacts of climate change on plant diseases—opinions and trends

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Accepted: 5 January 2012
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Abstract There has been a remarkable scientific output on the topic of how climate change is likely to affect plant diseases. This overview addresses the need for review of this burgeoning literature by summarizing opinions of previous reviews and trends in recent studies on the impacts of climate change on plant health. Sudden Oak Death is used as an introductory case study: Californian forests could become even more susceptible to this emerging plant disease, if spring precipitations will be accompanied by warmer temperatures, although

climate shifts may also affect the current synchronicity between host cambium activity and pathogen colonization rate. A summary of observed and predicted climate changes, as well as of direct effects of climate change on pathosystems, is provided. Prediction and management of climate change effects on plant health are complicated by indirect effects and the interactions with global change drivers. Uncertainty in models of plant disease development under climate change calls for a diversity of management strategies, from more participatory approaches to interdisciplinary science. Involvement of stakeholders and scientists from outside plant pathology shows the importance of trade-offs, for example in the land-sharing vs. sparing debate. Further research is needed on climate change and plant health in mountain, boreal, Mediterranean and tropical regions, with multiple climate change factors and scenarios (including our responses to it, e.g. the assisted migration of plants), in relation to endophytes, viruses and mycorrhiza, using long-term and large-scale datasets and considering various plant disease control methods.

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Keywords Adaptive ecosystem management · Biotic interactions · Landscape pathology · *Phytophthora ramorum* · Plant disease epidemiology · Tree fungal pathogens

Up to the 1990s, there was little information about climate change impacts on plant disease. For example,

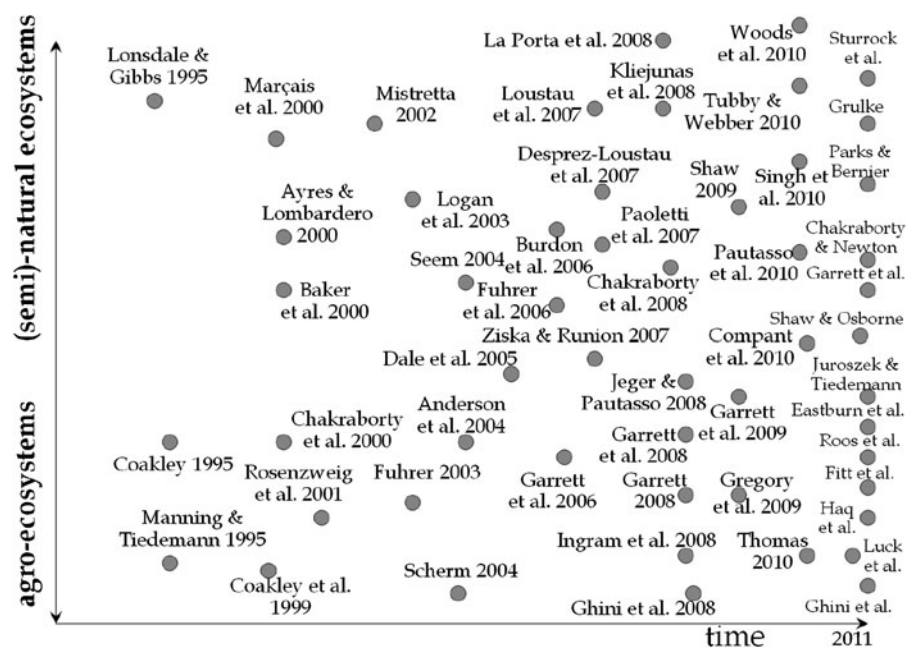
in a review on the impacts on plant health of increasing atmosphere concentrations of ozone, SO₂ and CO₂, Coakley (1995) stated that disease development may increase, decrease or remain stable depending on the particular pollutant and host-pathogen interaction. Similarly, Manning and von Tiedemann (1995) recognized that, at that time, there was limited knowledge about observed and predicted impacts of climate change on plant epidemics. However, plant pathologists already realized in the 1990s that climate change was clearly set to pose a challenge to many pathosystems. Referring to tree fungal pathogens, Lonsdale and Gibbs (1995) made the point that environmental change, especially when combined with pathogen and host introductions, may result in unprecedented effects. This statement has been re-iterated many times since (e.g. by Wingfield et al. 2010).

It is now recognized that climate change will affect plant diseases together with other components of global change, i.e. anthropogenic processes such as air, water and soil pollution, long-distance introduction of exotic species and urbanization (Gurr et al. 2011; Bradley et al. 2012; Matyssek et al. 2012; Régnière 2012). Predictions on how changes in climate will affect plant health at various spatio-temporal scales (from seasons to centuries, from the genetic to the ecosystem level, from farms to watersheds and entire continents) are based on: (i) already observed effects of climate change on plant diseases, (ii) extrapolation from expert knowledge and

experimental studies, and (iii) computer models. It is widely acknowledged that climate change is likely to be pervasive across the planet, and will thus be relevant to most of the many existing (and yet to arise) plant health issues. Past reviews on the topic agree that climate change is a challenge that needs to be addressed together with the several problems already faced in agriculture, forestry, landscape management and nature conservation. It is important to study the interconnections among climate change and other drivers of global change in affecting plant health, also because declining plant health may result in climate change feedbacks (through changes in carbon sequestration and albedo patterns; O'Halloran et al. 2012).

Many reviews of the literature on plant diseases and climate change have recently appeared (Fig. 1), so that there is the need for an overview providing an update of this growing literature. Our focus is on plant pathosystems, but similar arguments can be made also for invertebrate pests. We start from (1) the case study of *Phytophthora ramorum*, provide (2) a summary of the main observed and forecasted climate changes, and describe (3) selected studies on the effect of single variables on the health of pathogens or plants. We then move to (4) indirect effects and interactions among global change factors, discuss (5) the issue of plant health predictability, modelling and extrapolation under climate change, and argue (6) that a diversity of

Fig. 1 Recent literature reviews on climate/global change and plant health (the figure was prepared in February 2011 and is not exhaustive, but merely illustrative; see reference list for bibliographic details)



approaches is needed to make plant disease management more sustainable in the face of climate change. We also point out (7) the need for interdisciplinarity, stakeholder involvement and consideration of trade-offs, introduce (8) the debate on land-sparing vs. -sharing in the context of climate change effects on plant health, and conclude with (9) some take-home messages and research opportunities. There are many other aspects relevant to the issue of climate changes and plant health, but we believe that the selected topics can provide a good point of entry into the relevant literature.

A case study: climate change and *Phytophthora ramorum*

Although there is still uncertainty about the direction of change for many regions (Shaw and Osborne 2011), climate change is expected to be omnipresent. It is thus likely to affect most plant pathosystems, included those that are already troublesome or out of control under current climate conditions. As an example, take Sudden Oak Death, caused by the generalist oomycete *Phytophthora ramorum* (Rizzo et al. 2011). The pathogen is a newly introduced invasive species in the USA and Europe and currently causes large-scale mortality in a range of tree and shrub species in California. Climate change could make forests on the West Coast of the USA even more susceptible to this pathogen, in case of warmer temperatures during spring precipitations (Venette 2009). *P. ramorum*-inoculated branch cuttings of coast live oaks (*Quercus agrifolia*) developed larger lesions in spring, a result interpreted to suggest a role of synchronicity between host cambium activity and pathogen colonization rate (Dodd et al. 2008). Such co-occurrences between host phenology and pathogen sporulation are likely to be affected by climate shifts (Donnelly et al. 2011).

At the same time, climate change may modify the pattern of susceptibility to *P. ramorum* in ecosystems not currently affected but at risk due to the presence of potentially sporulating hosts (e.g. plantations of Japanese larch, *Larix kaempferi*), from the Appalachians to the Mediterranean, from New Zealand to Japan (Brasier and Webber 2010; Tubby and Webber 2010). Even if the change in climate may turn out not to be favourable everywhere to *P. ramorum*, e.g. because of a lower amount of precipitation during the period of main activity of the pathogen, there could still be negative consequences for plant health. Such negative impacts of

climate change can be expected when a mismatch between plants and their environment leads to an increased vulnerability to biotic agents (Ayres and Lombardero 2000; Lonsdale and Gibbs 2002). Therefore, there is today little doubt that future ecosystems will experience altered disturbance patterns and that, in general, new plant health problems will become more frequent (Marçais et al. 2000).

A summary of observed and predicted climate changes

It is useful to summarize current knowledge on climate change before moving to the main potential effects of climate change on plant pathosystems. For example, Chakraborty et al. (2008) remind us that the current CO₂ concentration in the atmosphere ([CO₂], which is set to exceed 400 ppm in a few years) is higher than the range of concentrations (180–300 ppm) measured from ice cores going back 650,000 years. The main causes of this global [CO₂] increase are fossil fuel burning and land-use changes (mainly deforestation) (Cerri et al. 2007; Paterson and Lima 2010). The increase in [CO₂] and the concentration of other greenhouse gases has already resulted in an increase in the global average temperature of 0.6–0.7°C over the last century (Mann et al. 1998; Walther et al. 2002; Benvenuti 2009). This average increase has been translated in a trend in many regions towards shorter and warmer winters (Quarles 2007). There is widespread evidence that such seasonal shifts have already affected the phenology, abundance and distribution of many species (Kömer and Basler 2010; Matesanz et al. 2010).

The documented evidence of recent climate changes is dwarfed by the magnitude of the forecasted further shifts during the 21st century and beyond (with a best estimate of +2 to 4°C in global average temperatures by the end of the century; Milad et al. 2011). Some ecoregions will be more affected than others by climate changes (Engler et al. 2011; Heyder et al. 2011; Teixeira et al. 2012), with the most biodiverse ecoregions particularly at risk (Beaumont et al. 2011). In Europe, Southern regions are predicted to be more sensitive to climate change than Northern ones, due to increases in summer drought (Küdelä 2009). In North America, the temperature increase is expected to be greater than the global average, particularly in boreal and mountainous regions (Bentz et al. 2010). Although

tropical regions are predicted to experience a lower absolute increase in temperatures, tropical metabolic rates are likely to be affected more strongly than at extra-tropical latitudes, given the non-linear influence of temperature on metabolic rates (Dillon et al. 2010). Metabolic rates are key determinants also of the activity of plant pathogens. Many tropical crops show yield reductions in the presence of warmer temperatures, as current temperatures are already close to the maximum physiological limit (Cerri et al. 2007). Also relevant to plant health is the forecasted increase in extreme weather events, from floods to drought, from heat waves to severe wind, rain, and hail storms (Boland et al. 2004; Hegerl et al. 2011; Peng et al. 2011): floods can make the spread of water-borne pathogens easier, droughts and heat waves can predispose plants to infection, storms can enhance wind-borne dispersal of spores.

Direct effects of climate change on plant pathosystems

Plant pathologists have long considered environmental influences in their study of plant diseases: the classic disease triangle emphasizes the interactions between plant hosts, pathogens and environment in causing disease (Garrett 2008; Klopfenstein et al. 2009; Grulke 2011). Climate change is just one of the many ways in which the environment can move in the long term from disease-suppressive to disease-conducive or vice versa (Baker et al. 2000; Fuhrer 2003; Truscott and Gilligan 2003; Perkins et al. 2011). Therefore, plant diseases could be even used as indicators of climate change (Logan et al. 2003; Garrett et al. 2009), although there may be other bio-indicators which are easier to monitor. Long-term datasets on plant disease development under changing environmental conditions are rare (Scherin 2004), but, when available, can demonstrate the key importance of environmental change for plant health (Jeger and Pautasso 2008; Fabre et al. 2011). For example, analysis of archive samples from the Rothamsted long-term (1850s–) wheat production and fertilizer experiment shows that historical records of SO₂ emissions are well correlated with the ratio of two pathogens (*Phaeosphaeria nodorum*/*Mycosphaerella graminicola*) (Bearchell et al. 2005; Fitt et al. 2011).

Plant health is predicted to generally suffer under climate change through a variety of mechanisms, from accelerated pathogen evolution and shorter incubation

periods to enhanced abiotic stress due to mismatches between ecosystems and their climate and the more frequent occurrence of extreme weather events (Chakraborty and Datta 2003; Chakraborty 2005; Chakraborty et al. 2011; Ghini et al. 2011b; Newton et al. 2011; Sutherst et al. 2011). Drought is expected to lead to increased frequency of tree pathogens, mainly through indirect effects on host physiology (Desprez-Loustau et al. 2006). Drier conditions may also have direct effects on pathogens, as shown by the invasive exotic species *Heterobasidion irregulare* in central Italy, which appears better adapted to dispersal in the Mediterranean climate than the native *H. annosum* species (Garbelotto et al. 2010). Reduction in frost due to increased average minimum temperatures implies the removal of a limiting factor for pathogens such as *Fusarium circinatum* (the causal agent of pine pitch canker), with consequent enlargement of the area at risk, particularly in Europe (Watt et al. 2011). Conversely, for pathogens that take advantage of frost-wounds in order to infect the host (e.g. *Seiridium cardinale* on cypress species), a decreased occurrence of frost could lead to reduction in disease incidence (Garbelotto 2008). In the case of insect-vectorized diseases: if warmer temperatures translate into additional insect generations (as they often do), obviously this will increase transmission rates of the invasive pathogen (Dobson 2009; Robinet et al. 2011).

Already observed climate warming appears to have been associated with shifts in plant hosts for some fungi (Gange et al. 2011). Some regional consequences of climate change on plant health are already present: for example, although changes in cropping practices may also be playing a role, there have been progressively earlier and more frequent observations of *Phytophthora infestans* in Finland (Hannukkala et al. 2007). In forests of Canada and the Western USA, warmer temperatures have been associated with large-scale outbreaks of bark beetles (Bentz et al. 2010; Woods et al. 2010; Woods 2011). Plant pests are already causing substantial crop losses in most regions of the world (Rosenzweig et al. 2001; Barnes et al. 2010; Haq et al. 2011). An increase in extreme weather events and a trend towards warmer temperatures may well worsen these impacts (Roos et al. 2010; Thomas 2010; Hakala et al. 2011; Madgwick et al. 2011; West et al. 2012). Regional tree declines due to drought, new pathogens and existing pests, and the interactions between these factors, can have negative repercussions on biodiversity (Fischer et al. 2010; Parks and Bernier 2010; Tomback and Achuff 2010; Carnicer

et al. 2011; McDowell et al. 2011). However, they can also in some cases help increase the supply of deadwood across forests, where management has resulted in a decline of this important requirement for biodiversity conservation (Calder and Kirkpatrick 2008; Lonsdale et al. 2008; Cobb et al. 2012).

Climate change is indeed not only going to threaten plant health, but may in some cases enhance it. For example, in Scotland, models predict in the mid-term a lower impact of oilseed rape diseases such as *Leptosphaeria maculans* and *Pyrenopeziza brassicae* (Fitt et al. 2011). In Northern Germany, however, oil seed rape pathogens such as *Alternaria brassicae*, *Sclerotinia sclerotiorum*, and *Verticillium longisporum* are predicted to be favoured by average warmer temperatures, particularly when taking a long-term (2071–2100) view (Siebold and von Tiedemann 2012). Warmer climates and more frequent extreme events are likely to increase the magnitude of forest fires, which could act as purging factor for some diseases in woodland. Nonetheless, in many cases an increased frequency and severity of fires can decrease the ability of forests to provide goods and services (Sturrock et al. 2011). It is also possible that warmer temperatures may make it easier to deploy biological control in some cases, although there is still little available information on the impacts of climate change on plant disease biological control (Ghini et al. 2008; Compant et al. 2010).

Interactions among global change factors

Direct effects on plant health of climate warming, increased pollutants and CO₂ concentrations (Kliejunas et al. 2008; McElrone et al. 2010; Davies et al. 2011; Eastburn et al. 2011) will be accompanied by the easier introduction of exotic invasive species (Chakraborty et al. 2000; Lonsdale and Gibbs 2002; Ganley et al. 2011; Chytrý et al. 2012). Introductions of novel plant pathogens have already occurred in many regions (Brown and Hovmøller 2002; Dehnen-Schmutz et al. 2010; Stenlid et al. 2011; Fig. 2), but climate changes are likely to often facilitate their further establishment and spread (Anderson et al. 2004; Shaw 2009; Hannukkala 2011). There is a consensus that prediction and management of climate change effects on plant health are complicated by interactions between globalization, shifts in climate, pollution and increasing numbers of invasive plants,

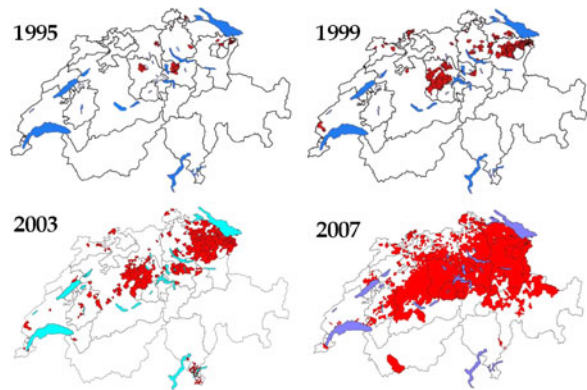


Fig. 2 Development of the fire blight epidemic (due to the bacterium *Erwinia amylovora*) in Switzerland, 1995–2007. The pathogen was introduced into Switzerland from South-West Germany in the 1980s (this explains why the climatically more suitable Ticino has been less affected by fire blight than northern Swiss Cantons). It affects tree and shrub species of the family Rosaceae (e.g. *Malus*, *Pyrus*, *Crataegus*) and is favoured by humid and mild springs, as was the case in 2007, when the epidemic reached unprecedented levels (from Holdenrieder et al. 2008)

pests and pathogens (Mistretta 2002; Desprez-Loustau et al. 2007a; Danon et al. 2011; Fig. 3).

Ensuring that landscape management incorporates the many insights from new studies on global change impacts on plant health will be important to improve the sustainability and security of food production, and to make biodiversity conservation more successful (Dale et al. 2005; Fletcher et al. 2009; Pautasso et al. 2010; Geyer et al. 2011). Assessing the ecological consequences of climate change requires an understanding of biotic interactions (Tylianakis et al. 2008; Médiène et al. 2011), including the evolution of plant pathogens and their hosts at the interface between fields and surrounding remnant semi-natural ecosystems (Burdon and Thrall 2008). Although some studies of multiple global change factors are appearing (e.g. Matesanz et al. 2009; Baeten et al. 2010), these analyses have rarely involved plant pathogens (e.g. *Phytophthora citricola* on *Fagus sylvatica* seedlings under elevated CO₂ and N fertilization; Fleischmann et al. 2010). Free-Air CO₂ Enrichment (FACE) facilities can deliver useful insights on how plant pathosystems are likely to be affected by the interactions among global change factors (Eastburn et al. 2009, 2011). There is a need to include in such studies various plant disease management approaches, including

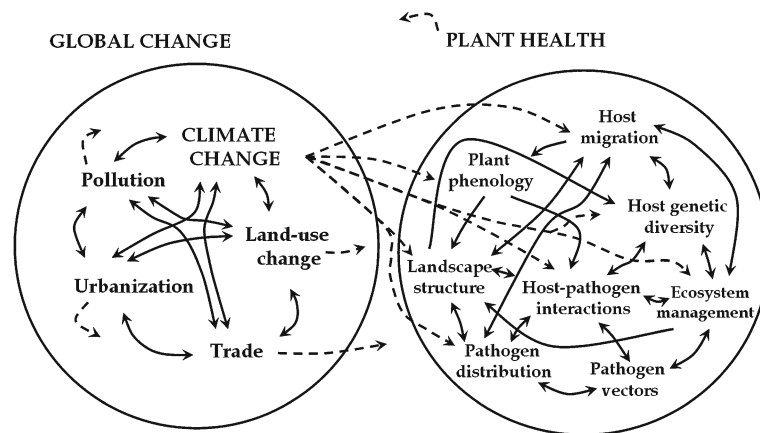


Fig. 3 Global change impacts on plant health. Global change is composed of the interactions of various drivers (climate change, increased trade, land-use change, pollution, urbanization). All these factors will have an impact on plant health, through direct effects on host-pathogen interactions, and via indirect effects on host migration, genetic diversity and phenology, as well as on

disease distribution, insect pests, vectors and landscape structure. There is a feedback from plant health to global change. To be successful in the face of global change, ecosystem management will have to consider this complexity of interactions (modified from Pautasso 2012)

organic agriculture (Crowder et al. 2010), biocontrol mixtures (Xu et al. 2011), and the design of agricultural landscapes for natural pest control (Steingröver et al. 2010).

Predictability, modelling and extrapolation

The many factors involved in determining plant health under a changing climate, their direct and indirect effects, interactions and feedback loops raise the question of whether a predictive understanding of these complex systems is achievable (Garrett et al. 2011). Predictability is a key condition to the design of solutions to the many new plant health problems likely to arise, or to old problems becoming more severe. Many reviews available on the topic of plant diseases and climate change agree that there is a need for more empirical data on the subject (Loustau et al. 2007; Ziska and Runion 2007; Chakraborty et al. 2008; Ingram et al. 2008; Chakraborty and Newton 2011; Luck et al. 2011). The assumption is that more and better data will make prediction more accurate and/or reliable (Shaw and Osborne 2011). In these efforts, documented impacts of environmental change on plant pathosystems need to be complemented by predictions based on expert knowledge and common sense (Marçais and Desprez-Loustau 2007; Roos et al. 2010) as well as on computer simulations (Bergot et al. 2004; Desprez-

Loustau et al. 2007b; La Porta et al. 2008; Watt et al. 2010; Seidl et al. 2011).

For example, according to models, predicted climate change will have different effects on phoma stem canker (*Leptosphaeria maculans*) on oilseed rape in the north and south of the UK (Butterworth et al. 2010). Although there is still a challenge in extrapolating from individual studies to epidemics over entire regions (Burdon et al. 2006; Garrett et al. 2006), the phoma study shows that statements about regional patterns in future disease development under climate change are possible. Nonetheless, their direct test in reality will have to wait. There is an increased appreciation that understanding of the interactions among weather and the spatial distribution of susceptible/resistant host patches are keys to managing plant diseases across entire landscapes (Seem 2004; Skelsey et al. 2010). The integration of multi-scale epidemic simulations with climate change scenarios is indeed one of the outstanding challenges in landscape epidemiology (Holdenrieder et al. 2004; Pinkard et al. 2010).

Despite these advances in the understanding of the interactions between pathosystems and a changing climate, it is important to make clear the inherent uncertainty in models of plant disease development under climate change. The prediction from climate research that climate is going to be more variable, i.e. less predictable, is matched by the motto of plant pathologists involved with exotic organisms (“expect

the unexpected"; Webber 2010). What is needed in such paradoxical and idiosyncratic situations, in addition to continuing research into the biological mechanisms underlying plant health under novel conditions, is the development of agricultural and forestry systems that can cope with change. This is not impossible. Even if—due to our limitations in data availability, epidemiological understanding, funding, time, computing power, and knowledge of future climate—we are unable to predict the trajectory of each pathosystem under climate change accurately, some general guidelines for action can be identified. For example, there is agreement that adaptive management is an important strategy to develop, because of its in-built monitoring and iterative learning process (Yousefpour et al. 2012). Similarly important is the development of a range of different predictive techniques, so as to be able to take advantage of a diversity of analytical approaches. Equally, the greater integration of plant diversity in production systems is expected to buffer against the unpredicted or unpredictable alterations that pathosystems will experience in a changing climate (Østergård et al. 2009; Brummer et al. 2011; Döring et al. 2011; Jarvis et al. 2011).

Plant health management strategies: diversity is needed

As a consequence of all these potential impacts of climate change on the health of plants and their associated organisms, there is increasing recognition that we need to develop strategies for long-term adaptation and insurance in agriculture and silviculture (Fuhrer et al. 2006; Ciscar et al. 2011). The importance of adaptive management is also stressed from the point of view of North American forest management by Millar et al. (2007), who point out that future climate change challenges will not be met by a single solution, but by a mix of different approaches adapted to different situations. As an example (for an invasive pathogen under current climate), whilst there has been an effort at eradication of the single *P. ramorum* outbreak in Oregon forests, the similarly isolated Humboldt county outbreak in Northern California was left to follow its course, so that now we have a rough idea (without replication) of the likely medium-term outcomes of both approaches. Even if developing landscape-scale experiments remains a challenge (even more so when considering climate change), such an approach is essential to

validate models and risk analysis (Körner 2003; Petter et al. 2010; Venette et al. 2010). The spread of invasive plant diseases in regions of naive host populations (i.e. with no history of co-evolution) is a likely outcome of climate warming and calls for increased monitoring and modelling (Loustau et al. 2007; Moricca and Ragazzi 2009). In their international overview, Ogden and Innes (2007) agree, but deplore the lack of action so far, inasmuch as climate considerations have been rarely adopted by forest managers in strategic and operational plans yet.

Wherever pathosystems are already difficult to deal with, it is to be expected that climate change will make the opportunities for sustainable disease management even more remote (Coakley et al. 1999). In this case, diversification alone will not be adequate without the support of the whole range of current and novel management approaches. For example, according to models taking into account climate change, it has been suggested that it may become necessary to increase the number of fungicide treatments against *Plasmopara viticola* in wine-producing regions of Northern Italy over the next decades (Salinari et al. 2006). However, an increase of extension activities that prevent abuse and misuse of pesticides should also be considered (Savary et al. 2011b). The current reliance on economically attractive management approaches may well be challenged in the future, not just because of climate change, but also due to developments in society, for example an enhanced awareness of environmental issues, see e.g. the new pesticide regulations due to enter in force in the European Community (Erlacher and Wang 2011; Mills et al. 2011). Moreover, preventive measures such as the use of cultivar mixtures in fields and the preservation of tree species diversity in forests are still likely to make sense also in the presence of novel climates (Finckh and Wolfe 1996; Garrett and Mundt 1999; Zhu et al. 2000; Pautasso et al. 2005; Bodin and Wiman 2007; Keesing et al. 2010; Quijas et al. 2010; Juroszek and von Tiedemann 2011). In addition, new approaches will be needed, from pest risk assessments including climate change and economic considerations (Yemshanov et al. 2009), to involvement of the stakeholders for a certain plant pathosystem in the development of strategies to cope with the disease (for *P. ramorum* without considering climate change, Alexander and Lee 2010), from spatio-temporal analysis of known occurrences of a plant pathogen in the plant trade and the semi-natural environment (Xu et al. 2009) to the use of network theory tools in targeting control and predicting

climate change impacts (Araújo et al. 2011; Chadès et al. 2011; Moslonka-Lefebvre et al. 2011). Innovative approaches in plant disease management will be required also given the likely increased importance of novel agro-ecosystems (e.g. biofuel crops: Fitt 2011; Newton et al. 2011).

Interdisciplinarity, stakeholder involvement and trade-offs

One problem here is that climate and global change will not act on plant health in isolation, but in addition to other worldwide processes, from dwindling fossil energy sources to a still growing global human population, from sea-level rise to freshwater scarcity, from attempts to improve food safety/security to those trying to arrest biodiversity loss/homogenization (Gregory et al. 2009; Flood 2010; Chimera et al. 2010; Kulakowski et al. 2011; Reganold et al. 2011; Savary et al. 2011b). Multiple, interconnected processes such as these will require interdisciplinary science, long-term funding and the increased use of meta-analysis (e.g. Zvereva and Kozlov 2006; Blankinship et al. 2011; Fischer et al. 2011; Kozlov and Zvereva 2011; Rohr et al. 2011). At the same time, there is a need for the evolution of plant health regulatory frameworks to catch up with the latest scientific developments, from taxonomic advancements (e.g. the identification of novel *Phytophthora* species: Jung et al. 2011; Vettraino et al. 2011) to network epidemiology (Jeger et al. 2007; Keller et al. 2011) and digital pest diagnostics and severity estimation (Bock et al. 2010; Norton and Taylor 2010). The involvement of the many stakeholders in plant health (Furstenau et al. 2007; Macleod et al. 2010) deserves repetition in more than one section of this review, as it can be beneficial not just to adapt the regulatory framework, but also to improve dissemination of plant health knowledge (Jacobi et al. 2011; Rebaudo and Dangles 2011) and to devise effective response strategies to new invasive pathogens (Crall et al. 2010).

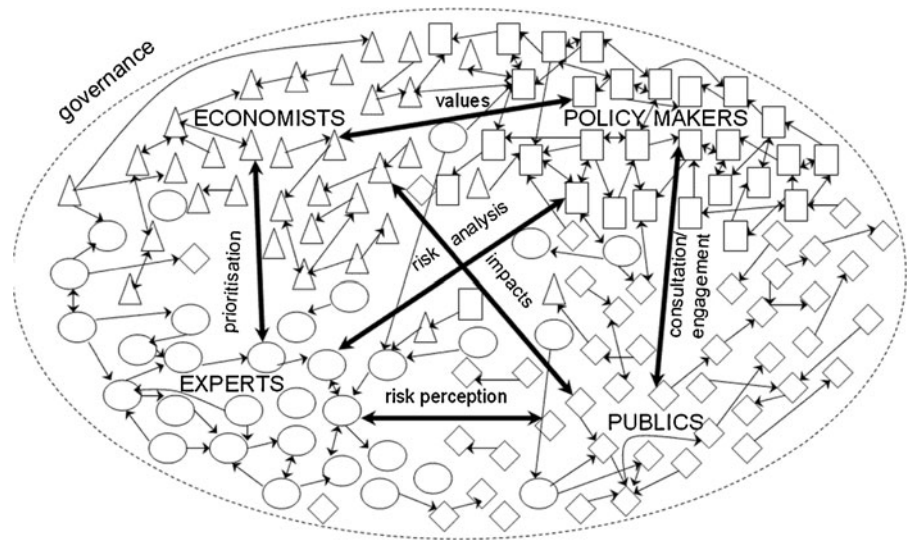
For example, citizen-science can help in the identification of host resistance in selected locations or throughout distributional ranges (Ingwell and Preisser 2011). According to a recent participatory process, ‘finding the most technically and financially effective ways of identifying, monitoring and controlling invasive species, pests and disease’ is one of the top policy-relevant research questions in the UK forestry sector (Petrokofsky

et al. 2010). This aim is complicated by concurrent objectives in biodiversity conservation. For instance, habitat fragmentation is often considered to affect in a negative way meta-populations of species of conservation interest, but could make dispersal of plant pathogens more difficult across the shifting distributional ranges of their old and new hosts (Margosian et al. 2009), unless long-distance links are provided by plant trade (Harwood et al. 2009). This kind of trade-offs makes it important to involve economists in the formulation of plant health policy under uncertainty (Horan and Lupi 2010; Ndeffo Mbah et al. 2010; Moore et al. 2010; Bradford and D’Amato 2012).

Plant health and climate change: land sparing or sharing?

Cross-talk between plant health policy-makers, the publics and economists will need not only to involve scientists active in pest surveillance and monitoring, as well as epidemic analysis and modeling, but also those from outside plant pathology (Fig. 4). For example, in biodiversity conservation there is currently a debate on how best to meet the additional food needs due to the growing human population and changing dietary habits of many countries without jeopardizing biodiversity conservation efforts. On the one hand, increasing the intensity of cultivation may make it possible to save some natural ecosystems from conversion into cropland (land sparing). On the other hand, decreasing the intensity of cultivation may enable the coexistence of biodiversity and crops in agro-ecosystems, but would allow remnant patches of natural ecosystems to shrink (land sharing) (Ewers et al. 2009; Clough et al. 2011; Lambin and Meyfroidt 2011; Lin 2011; Phalan et al. 2011; Fitter 2012). Little attention has been paid to how this issue will be influenced by the effects of climate change on plant health, or whether one or the other strategy is more advisable to better cope with such effects (Jones 2009; Jeger et al. 2011; Savary et al. 2011b). Land sharing between food production and biodiversity conservation has the advantage of a more diverse composition of croplands, which would make them more adaptable to new conditions. At the same time, this strategy may make (semi)-natural ecosystems and their plant health more vulnerable to climate change, due to the lower size, quality and connectivity of habitat patches. Conversely, land sparing may increase the

Fig. 4 Network of interactions among experts (*circles*), economists (*triangles*), publics (*diamonds*) and policy makers (*rectangles*) in the plant health governance landscape. For a successful management of plant health problems in a changing environment, there is need for better information flow among the components of this network. Modified from Mills et al. (2011)



chances of adaptation in semi-natural forest, woodland, scrubland and grassland, but may result in more pronounced plant health problems in intensively managed ecosystems. Although this issue is often presented in terms of a dichotomy, a diversity of strategies may be a good way to proceed also in this case, also given the continuum between intensive cultivation and pristine ecosystems. Nonetheless, the land-sharing vs. sparing debate may benefit from incorporating both climate change and plant health considerations.

Similarly, both the land-sparing vs -sharing debate and the many contributions to how to improve plant health management under climate change will need to recognize the importance of soil health, both in terms of its function as habitat for soil-borne plant pathogens, and in relation to the multiple roles of soil microbes in promoting plant health and productivity (French et al. 2009; Singh et al. 2010). There is a consensus that we have currently less knowledge about potential impacts of climate change on soil-borne pathogens compared to foliar pathogens (Eastburn et al. 2011). Progress in our understanding of how both groups of plant pathogens will respond to climate change will be facilitated by the application of emerging genetic techniques (Pritchard 2011). Genetic analyses will be instrumental in devising strategies to cope with an increased pressure from established and new diseases as a result of better suitability of the climatic conditions and/or more intense and far-reaching trade (Bawa and Dayanandan 1998; Archie et al. 2008; Jombart et al. 2011). For example, there is genetic evidence that some ash trees (*Fraxinus excelsior*)

in Denmark are resistant against the emerging fungal pathogen *Chalara fraxinea* (McKinney et al. 2011; Kjær et al. 2012), which is now reported to cause ash dieback throughout Europe, from Poland to France and from Sweden to Switzerland (Bengtsson et al. 2012; Gross et al. 2012). For this pathosystem, there are also data on the genetic variability of the pathogen in lowland vs. highland Poland (Kraj et al. 2012) and in the Åland islands, mainland Finland, Estonia and Latvia (Rytkönen et al. 2011). Although there is increasing attention to the patterns in species genetic diversity across landscapes and distributional ranges (including studies of plant fungal pathogens, e.g. Barrès et al. 2008; Baumgartner et al. 2010; Dutech et al. 2010; King et al. 2010; Dale et al. 2011; De Simone et al. 2011; Tsui et al. 2012), there is still little inclusion of such important data in models predicting climate change impacts on plant health, as well as in studies of the land-sparing vs. -sharing issue.

Plant health and climate change: conclusions and research gaps

Climate change effects on plant health are likely to be ubiquitous, both in terms of direct and indirect impacts. Maintaining plant health across the planet, in turn, is a key requirement for climate change mitigation, as well as the conservation of biodiversity and the provision of ecosystem services under global change. Since there are inherent limits in our understanding of plant pathosystems and their interactions with future climates, it is likely

that a diversity of management strategies, including learning from our mistakes, is a better choice than a single, inflexible solution. As an exception, adding diversity to our fields, plantations, forests, and landscapes appears as a commendable insurance policy which may increase the adaptation potential of a range of managed ecosystems. To maintain ecosystem health and services under variable, unpredictable or unknown conditions, we need more resilient systems, decentralization, participatory research and breeding networks. At the same time, increased involvement of the many stakeholders and scientists from outside plant pathology shows the importance of considering trade-offs with other objectives. Increasing diversity would be in favour of a land-sharing approach, but may be relevant also to land-sparing scenarios (e.g. at the margin of fields), depending on the spatial and temporal scale and the type of diversity (genetic, species, species turnover, ecosystem) considered. Within and beyond the European level, there is certainly the scope to integrate plant health considerations into agri-environment schemes, biosecurity regulation, and research across the network of the world's botanic gardens (Britton et al. 2010; Golding et al. 2010; Webber 2010).

Research gaps in this rapidly developing area include effects of climate change on plant pathosystems:

- of mountain and boreal ecosystems (Roy et al. 2004; Rohrs-Richey et al. 2011; Witzell et al. 2011);
- of Mediterranean and tropical regions (Garbelotto 2008; Zocca et al. 2008; Thompson et al. 2010; Savary et al. 2011a, b);
- with climate change aspects other than temperature (e.g. precipitation: Hawkes et al. 2011);
- with multiple climate change factors (Paajanen et al. 2011);
- in relation to endophytes and viruses, two key factors for plant health (Jones 2009; Brosi et al. 2010);
- in relation to mycorrhiza diversity and productivity (Deslippe et al. 2010; Egli 2011);
- with long-term datasets (Hannukkala et al. 2007; Fitt et al. 2011);
- under various climate change scenarios (Watt et al. 2011);
- following various climate change management options (e.g. assisted migration of plant species; McDonald-Madden et al. 2011; Garbelotto and Pautasso 2012);
- and considering various plant disease control methods (Ghini et al. 2011a).

More research on the role of feedbacks is needed too (Paoletti et al. 2007; Garrett et al. 2011): not only will climate change affect plant health, but a regionally-to-globally declining plant health may in turn accelerate climate change because of the additional carbon emissions due to increased plant mortality and soil organic matter mineralization, so that plant disease management, by maintaining plant health, has a role in reducing and preventing greenhouse gas emissions (Mahmuti et al. 2009; Lovett et al. 2010; Busby and Canham 2011; but see Bernier et al. 2011). Most importantly, research on climate change and plant health needs to reflect the variety of levels affected and the many viewpoints involved and tools available, from the molecular to the landscape scale, using network theory, meta- and risk analysis, in collaboration with various stakeholders, the publics and scientists outside plant health science.

Acknowledgements Many thanks to K. Dehnen-Schmutz, T. Harwood, O. Holdenrieder, A. MacLeod, P. Mills, M. Moslonka-Lefebvre, M. Shaw, J. Webber, M. Wolfe and X. Xu for insights and discussions, and to T. Matoni and anonymous reviewers for helpful comments on a previous draft. This review was partly funded by the Rural Economy and Land Use Programme (RELU), UK, and by the French Foundation for Research on Biodiversity (FRB) and is partly based on a presentation at the Climate Change and Plant Disease Management Conference, University of Evora, Portugal, 10–12 November 2010.

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