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Potential impact of climate change on plant–pathogen interactions

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Preamble

How a rapidly changing climate may influence plant pathogens and the diseases they cause gained international prominence after Manning and Tiedemann (1995) first reviewed the impact of changing atmospheric CO_2, O_3 and UV-B on plant diseases. Two other publications considering changes in the biosphere and climate rapidly followed (Coakley 1995; Coakley and Scherm 1996). However, the effect of changing climate on plant diseases was assessed for New Zealand (Prestidge and Pottinger 1990) and the United Kingdom (Atkinson 1993) well before this and similar assessments have continued for other countries (Chakraborty *et al.* 1998), specific diseases/pathogens (Brasier and Scott 1994; Luo *et al.* 1995; Kaukoranta 1996; Bergot *et al.* 2004) and regions (Boland *et al.* 2004). Climate change effects on plant diseases have featured at many international meetings, including the Global Change and Terrestrial Ecology (GCTE) meeting at Reading in 1999 (http://mwnta.nmw.ac.uk/GCTEFocus3/FoodandForest/99progr.htm). GCTE offers coordination among international groups for impact assessment (Scherm *et al.* 2000) on specific diseases such as potato late blight (Hijmans *et al.* 2000). Awareness among the plant pathology community was boosted by a session on this topic at the 7th International Congress of Plant Pathology (ICPP) in Edinburgh in 1998 (Chakraborty *et al.* 2000*b*). Since then there has been a session at the ICPP 2003 in Christchurch (Scherm and Coakley 2003) and one is planned for Turino in 2008. In Australia, a national workshop in 1997 addressed climate change impacts on economically significant plant diseases and a review was published in the *Australasian Plant Pathology* (Chakraborty *et al.* 1998).

Although the topic has not yet sparked widespread interest among plant pathologists, new findings have continued to appear in plant pathology literature (Pangga *et al.* 2004) including novel approaches to impact modelling (Scherm 2004). Notable among recent empirical studies are diseases in natural plant communities using free air CO_2 enrichment (FACE) (Percy *et al.* 2002), a field study on elevated temperature (Roy *et al.* 2004) and pathogen evolution (Chakraborty and Datta 2003). There have been important political developments too, none more significant than signing of the landmark Kyoto protocol and the recently announced 'Asia-pacific partnership on clean development and climate' between Australia, China, India, Japan, The Republic of Korea and the United States of America (http://www.pm.gov.au/news/media_releases/media_Release1482.html).

A plenary presentation by the author at the 15th Australasian Plant Pathology Society Conference, 26–29 September, 2005 in Geelong offered an opportunity to review current research and development in this area. This commentary reintroduces climate change to plant protection specialists, updates knowledge on its potential impacts on host-pathogen interactions to critically review progress and touches on future research needs in Australia to better manage diseases under a changing climate.

Climate change

Solar radiation mediates interactions between atmosphere, hydrosphere, cryosphere and biosphere to drive global climate. Infrared radiation heating up the earth surface is partly radiated back to space. Radiatively active water vapour, CO_2, CH_4, N_2O and O_3 in the atmosphere trap reflected radiation, acting like the glass of a greenhouse and hence called greenhouse gases, to warm the earth surface that supports life. Covering over 70% of the earth's surface, the oceans absorb solar energy and transports heat from the equator towards the Poles, regulating global temperature. Snow and ice reflect 60–90% of the solar energy they receive to cool the earth. The biosphere influences climate through CO_2 sequestration and shielding the earth surface from radiation. Global climate is modelled using rules that describe interactions between the atmosphere, land, water,

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ice and vegetation. These models are now more accurate in their representation of the reality (IPCC 2001), but uncertainties remain.

Palaeoclimatic records show an ever-changing global climate (Sabin and Pisias 1996) and continental glaciers had melted rapidly between 8,000 and 15,000 years ago to warm the earth (Cheddadi *et al.* 1996). Human activities such as fossil fuel burning and deforestation have accelerated some changes. 'Vostok' ice core data show atmospheric CO_2 fluctuated between 180 and 280 ppm for the past 420 000 years (Petit *et al.* 1999; Souchez *et al.* 2003), but increased to 367 ppm in just over 200 years. Since the late 19th century, the average earth surface temperature has risen by $0.6 \pm 0.2°C$ with minimum temperatures increasing at twice the rate of maximum temperatures (0.2 *v.* 0.1°C/decade) (IPCC 2001). Consequently, glaciers that cover 10% of the land area and contain some 70% of the global freshwater have shrunk and the average sea level has risen. Rainfall has increased in the middle and high latitudes of the Northern Hemisphere and decreased over the sub-tropics.

Global climate predictions for 2100 are available from the Intergovernmental Panel on Climate Change (IPCC 2001). For Australia, the annual average temperature may rise by 0.4–2°C by 2030, while rainfall in south-western Australia will change by -20 to $+5$% and in other parts of south-west and Queensland by -10 to $+5$% (CSIRO 2001).

The Kyoto protocol and carbon trading

The United Nations Framework Convention on Climate Change adopted the Kyoto protocol (www.unfccc.de) to reduce greenhouse gas emissions of industrialised nations by 5% below 1990 levels by 2008–2012. It entered into force on February 16, 2005. Carbon sources and sinks from agricultural land and forestry are included in the calculation of carbon stocks. Grasslands (Jones and Donnelly 2004) and forests (Stainback and Alavalapati 2002) sequester and store atmospheric carbon in pools of varying lifetime but vegetation type, atmospheric CO_2 and management practices influence this. Croplands can also store carbon and 90–120 Mt C per year is estimated for Europe (Smith 2004).

The trading of carbon and other emissions provides economic incentive for reducing greenhouse gas emissions. Companies and organisations are allocated annual limits and those exceeding limits may buy 'credits' from groups which stay below theirs. Technology that reduces emission gives 'surplus' credits. A proportion of the emission from each traded credit is retired to achieve overall reduction. Markets in the USA and the European Union offer carbon trading. In Australia, carbon trading is through the Sydney Futures Exchange, but the local $11.50 spot price is less than the $30 European Union price.

Climate change and plant disease

Climate-induced change to species ecology is already evident from pole-ward range expansion in temperate regions, changes in morphology, abundance and life cycle traits (Root *et al.* 2003; Parmesan and Yohe 2003). But examples of fingerprint and harbingers do not include plant pathogens as long-term data are lacking or confounded by changing varieties and management. Linking SO_2 emissions to the relative abundance of two wheat pathogens using DNA analysis of archived infected wheat over 160 years is an exception (Bearchell *et al.* 2005). Other examples are (i) link between El Niño-Southern Oscillation (ENSO) and severe wheat scab in eastern China (Zhao and Yao 1989), (ii) a 2–10 year periodicity between Southern Oscillation Index, a measure of ENSO intensity and wheat stripe rust in China and a 6–8 year periodicity of stem rust in the USA (Scherm and Yang 1995), and (iii) co-oscillation of severe stripe rust in China with the Western Atlantic teleconnection pattern (Scherm and Yang 1998).

Diseases and insect pests rob humanity of 42% of the attainable yield of the eight most important food crops worldwide (Oerke *et al.* 1994). Weather is a key driver of endemic and emerging fungal and bacterial diseases (Anderson *et al.* 2004) but limited empirical knowledge restricts prediction of crop loss under changing climate. The limited data are mostly from growth chamber studies where increased production of ethylene and its precursor (Grodzinski 1992) influence plant response to CO_2.

Interactive effects of elevated CO_2 and other factors are best studied under free air CO_2 enrichment (FACE) with at least four facilities studying plant diseases (Table 1). There are two FACE facilities in Australia; OZFACE near Townsville, started in 2001 to study climate change and tropical Savannas (Stokes *et al.* 2003) and TasFACE near Hobart, started in 2002 to study native grasslands/vegetation (http://www.utas.edu.au/docs/plant_science/Ecophys/TasFACE.html) but none has been used to study plant diseases.

Modelling studies are essential (Coakley and Scherm 1996) and commonly used to predict range expansion and distribution (Bergot *et al.* 2004; Luo *et al.* 1995; Brasier and Scott 1994). Scherm (2004) and Bourgeois *et al.* (2004) have recently summarised modelling approaches. The key challenge of selecting appropriate spatial and temporal scale for weather and disease remains. Downscaling weather predictions to a spatial mesoscale appropriate for disease forecasting (Seem 2004) and predicting weather at the level of plant organs (Chelle 2005) are two approaches. Pathogens can change species composition and size structure of forests affecting CO_2 flux and heat transfer creating feedbacks to climate (Ayres and Lombardero 2000) and models must include higher level ecological interactions. Uncertainties

Table 1. Research facilities and groups studying plant disease and climate change under realistic field experiments

No.	Facility/group	Areas of research	Key reference/website
1	Aspen FACE site, USDA Forest Service, Wisconsin	Forests; elevated CO_2 & O_3 impacts	Percy *et al.* (2002); Karnosky *et al.* (2002)
2	'Meadow warming' experiment, Rocky Mountains, Colorado	Pathogens and pests in natural plant communities	Roy *et al.* (2004)
3	Konza Prairie Biological Station, Manhattan, KS	Pathogens in prairie	Garrett and Bowden (2002)
4	BioCON FACE, Cedar Creek Natural History area, University of Minnesota	Perennial grassland, Elevated CO_2	Mitchell *et al.* (2003)
5	Duke FACE, Duke University, North Carolina	Forest pest and pathogens	http://face.env.duke.edu/fertilization.cfm, Palmroth *et al.* (2005)
6	FACE, Tohoku National Agricultural Experiment Station, Japan	Rice blast	http://tohoku.naro.affrc.go.jp/e-index.html

and nonlinear thresholds are other issues where Monte-Carlo simulation, fuzzy arithmetic (Scherm *et al.* 2000) and artificial neural network (Chakraborty *et al.* 2004) can help.

Finding parallels among diseases of marine and terrestrial hosts including plants and wildlife, Harvell *et al.* (2002) identified four priorities including collecting baseline data on diseases of wild populations, and separating effects of multiple climate variables on disease. Baseline data can help detect fingerprints of climate change for diseases of natural ecosystems where human interference has not confounded trends, but such data are not available.

Pathogens in natural ecosystems

Historically, diseases in natural plant communities have been a neglected area but significant research and reviews in the 1980s and 1990s have recognised pathogens as a strong force which influences the structure, function and dynamics of plant communities (Gilbert 2002; Fuhrer 2003; Mitchell 2003). Changes in pathogen prevalence in forests under changing climate and atmospheric composition are predicted (Ayres and Lombardero 2000) but empirical studies have only recently appeared in the literature. At the Aspen FACE in northern Wisconsin, Percy *et al.* (2002) found increased *Melampsora medusae* infection of *Populus tremuloides* under elevated CO_2 and O_3 that stimulated cuticular wax production, fatty acids, hydrocarbons, and altered the composition of phenolic glycosides to change host plant resistance. Changes in leaf surface properties at elevated O_3 alone or with CO_2 predisposed aspen to rust infection by 3- to 5-fold (Karnosky *et al.* 2002). At a FACE site in Minnesota, the abundance of 16 pathogenic fungi increased under elevated CO_2, nitrogen fertilisation in C_4 grasses and where plant diversity decreased in a grassland ecosystem (Mitchell *et al.* 2003).

In a 12-year-old natural montane meadow where the top 12 cm soil was heated to 1.5°C above ambient temperature, plants in the warmer plots were more heavily damaged and attacked by many more pathogens and herbivores (Roy *et al.* 2004). But the effects are specific and some pathogens performed better in cooler temperatures. Recent field studies at the Konza Prairie Biological Station, Manhattan, Kansas on the influence of rainfall patterns matching climate change projections show that infection decreases with decreasing precipitation for most, but not all, of the 23 common tallgrass prairie species studied (Karen Garret, personal communication). *Puccinia dioicae* on the forb *Solidago* spp. was significantly reduced by drought in both years of a study (Dendy *et al.* 2001). Similarly, incidence of *Uropyxis petalostemonis* was higher in irrigation plots where it affected fitness and fecundity of white prairie clover (*Dalea candida*).

Pathogens in managed ecosystems

Pathogens of agricultural crops have received greater attention but nearly all data are from growth room experiments. Severity has increased in the majority of 26 diseases studied thus far (Chakraborty and Pangga 2004). High CO_2 changes host anatomy, morphology and phenology to influence resistance (Hartley *et al.* 2000; Hibberd *et al.* 1996), pathogen life cycle (Chakraborty *et al.* 2000*a*; Chakraborty and Datta 2003), host-pathogen interaction and disease epidemiology (Pangga *et al.* 2004). Detailed case studies, arguments, discussions and research priorities have appeared in recent reviews (Coakley *et al.* 1999; Chakraborty 2001; Scherm and Coakley 2003; Runion 2003; Chakraborty and Pangga 2004).

Two important trends appear for diseases at high CO_2; the enlarged plant canopy (Idso and Idso 1994) with a microclimate conducive to disease development offers more infection sites and some fungal pathogens produce more spores (Chakraborty *et al.* 2000*a*; Hibberd *et al.* 1996) but enhanced host resistance slows host invasion (Pangga *et al.* 2004). An increased pathogen fecundity and many more spores trapped by the enlarged canopy lead to twice as many lesions at high CO_2 (Pangga 2002). Mutation, selection and other evolutionary processes act on the massive pathogen population and new strains can evolve after only

25 sequential infection cycles (Chakraborty and Datta 2003). Although host resistance is expected to keep pace with a changing pathogen, the predicted rates of evolutionary response are slower than the rate of current climate change (Etterson and Shaw 2001). Baseline studies on changing host and its interaction with an evolving pathogen are lacking.

Only the rice blast pathogen *Magnaporthe grisea* has been studied in a FACE facility by Nakajima and co-workers at the Tohoku National Agricultural Experiment Station, Japan (http://tohoku.naro.affrc.go.jp/e-index.html). Their preliminary results indicate that high CO_2 predisposes rice to blast. Rice at twice-ambient CO_2 had higher lesion numbers with higher incidence and severity of panicle blast.

Outlook

This brief overview highlights a clear lack of knowledge for model host-pathogen interactions that must be met through baseline empirical studies. Models can then be used to extrapolate, predict and validate potential impacts. The latest report on climate change risk and vulnerability asserts that Australian agricultural systems have historically shown considerable capacity to adapt to climate and management changes. This capacity will help in responding and adapting to climate change and there may be some gains from longer growing seasons, fewer frosts, higher rainfall in northern Australia and CO_2 fertilisation (Commonwealth of Australia 2005). Research and development to alleviate production constraints imposed by pest and diseases in a changing climate surely is a prerequisite to realise these projected gains.

New FACE facilities fostering multi-disciplinary research on climate change in cropping systems is a priority in Australia and research on pest and diseases must be a part of this. Change in atmospheric concentration or temperature is gradual, yet most climate change studies routinely use one or more discrete CO_2 and or temperature levels. Using a transient scenario of gradually increasing greenhouse gas concentrations (Reilly *et al*. 2003) will provide more realistic assessments.

Australia has an international reputation for its disease-free, clean and 'green' agricultural produce. Introduction of alien plant pathogens is one of the major causes of emerging plant diseases worldwide and increasing travel and trade increases this (Anderson *et al*. 2004). A great deal of resources is directed to keep exotic pests and diseases from entering Australia. All pest risk analyses must examine and quantify potential risks within the context of a changing climate as this can make conditions more favourable for some exotic pests and pathogens to establish in Australia.

In recent years, there has been a slow but steady stream of publications on climate change and plant pathogens including some from FACE facilities in the USA and Japan. If this represents an increasing level of awareness of this important issue in the plant pathology community, it can only lead to sustainable disease management in the future. Currently our key constraint is a lack of understanding of the underlying mechanisms as to how climate change influences host-pathogen interaction so as to generate simple 'rules of thumb'.

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