

Keynote review

Climate change: potential impact on plant diseases

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“Capsule”: *Climate change effects on plant disease incidence and severity are largely unknown.***Abstract**

Global climate has changed since pre-industrial times. Atmospheric CO₂, a major greenhouse gas, has increased by nearly 30% and temperature has risen by 0.3 to 0.6°C. The intergovernmental panel on climate change predicts that with the current emission scenario, global mean temperature would rise between 0.9 and 3.5°C by the year 2100. There are, however, many uncertainties that influence these predictions. Despite the significance of weather on plant diseases, comprehensive analysis of how climate change will influence plant diseases that impact primary production in agricultural systems is presently unavailable. Evaluation of the limited literature in this area suggests that the most likely impact of climate change will be felt in three areas: in losses from plant diseases, in the efficacy of disease management strategies and in the geographical distribution of plant diseases. Climate change could have positive, negative or no impact on individual plant diseases. More research is needed to obtain base-line information on different disease systems. Most plant disease models use different climatic variables and operate at a different spatial and temporal scale than do the global climate models. Improvements in methodology are necessary to realistically assess disease impacts at a global scale.

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Keywords: Climate change; Impact; Plant disease**1. Introduction**

Plant diseases are a significant constraint to the production of some 25 crops that stand between the rapidly expanding world population and starvation (Wittwer, 1995). World-wide losses from diseases range from 9 to 16% in rice, wheat, barley, maize, potato, soybean, cotton and coffee and in the USA alone, fungicides worth over US\$5 billion are used to control diseases (Oerke et al., 1994). In Australia, diseases cost an estimated Au\$1.3 billion annually in the six major agricultural commodities which are worth over Au\$10.9 billion (Chakraborty et al., 1998). The economic impact of disease stems from losses in productivity, the cost of disease management, and the economic penalty paid for having to grow less profitable alternative crops. Diseases such as Panama have resulted in the abandonment of entire banana plantations in Central America. The

Irish potato blight (1845–46) and the Bengal famine (1943) are grim reminders of the fact that the socio-political repercussions of major epidemics go far beyond simple economic impacts (Padmanabhan, 1973).

The classic disease triangle recognizes the role of physical environment in plant disease as no virulent pathogen can induce disease on a highly susceptible host if weather conditions are not favorable. Weather influences all stages of host and pathogen life cycles as well as the development of disease. Relationships between weather and disease are routinely used for forecasting and managing epidemics, and disease severity over a number of years can fluctuate according to climatic variation (Coakley, 1979; Scherm and Yang, 1995).

The interrelated climate, land, water, vegetation and human activity determine the ever-changing environment on Earth. Although change has always been a part of our world (e.g. Cheddadi et al., 1996), human activities are increasingly influencing the atmosphere, oceans, cryosphere and the terrestrial and marine biospheres, which together constitute the global climate system. Increased emissions of CO₂ and other radiatively active gases from industrial and agricultural development

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are changing the atmospheric composition. There is a strong interactive link between the large-scale clearing of forests in the humid tropics for logging and intensive agriculture, which alters global carbon balance and climate (IPCC, 1996a). Global change, including a changing climate, is one of the most critical issues facing our future today as terrestrial and aquatic ecosystems which sustain life on Earth are being increasingly affected by it. While the global population continues to rise, productive land resource, necessary for food production, shrinks. Uncertainties of climate change only magnify the challenge of increasing agricultural production to feed the expanding population.

A shift in the mean temperature or rainfall may appear to have a marginal impact, but the effects are greatly magnified at extreme values. For example, under a 2°C warming, the number of days over 35°C in Canberra, Australia, will increase from 4 to 10 days per summer, and the number of days less than 0°C in Ballarat decreases from 9 to 2 days per winter (Hennessy and Pittock, 1995). There will be changes in the intensity of rainfall to significantly impact on agriculture and on plant pathogens in particular. Changes in physical climate will interact with changes in plant morphology, physiology and chemistry due to increasing CO₂ concentrations to influence diseases. Undoubtedly the nature of host (e.g. annual vs. perennial, C3 vs. C4) and pathogen (e.g. root-infecting vs. shoot-infecting, biotroph vs. necrotroph) population and climate (e.g. asymmetric temperature shifts will have different effects from changes in both maxima and minima) will determine how the impacts of climate change will be felt. Consequently, climate change will reduce, increase or have no effect on a disease.

Except for early attempts to study impacts of elevated CO₂ on diseases (Gassner and Straib, 1930) and the impact of air pollution on diseases (Darley and Middleton, 1966; Coakley, 1995; Frankland et al., 1996; Sandermann, 1996), plant pathologists have only recently considered the influence of climate change on plant diseases. A coordinated international effort on the potential impact of climate change on pest, weeds and diseases commenced with the 1996 launch of activity 3.2.2 under the Global Change and Terrestrial Ecosystems core project of the International Geosphere–Biosphere Program (IGBP–GCTE) (Sutherst et al., 1996a). Recent reviews and other work (Clifford et al., 1996) reflect the growing concern in the community at large and within the international scientific community on global perspectives including the potential impacts of climate and air pollution changes on plant diseases (Prestidge and Pottinger, 1990; Atkinson, 1993; Coakley, 1995; Goudriaan and Zadoks, 1995; Manning and Tiedemann, 1995; Coakley and Scherm, 1996; Sutherst et al., 1996b; Chakraborty et al., 1998). In August 1998, over 15 invited and contributed papers on plant diseases

and climate change were presented at the VII International Congress of Plant Pathology. This keynote review was presented at this congress and mainly deals with impacts of climate change and changes in atmospheric composition that directly influence climate. More direct impacts of air pollutants are discussed in other papers in this issue (Paul et al., 2000; Sandermann, 2000; Tiedemann and Firsching, 2000).

2. Global climate is changing

The totality of the atmosphere, hydrosphere, biosphere and geosphere and their interactions via physical, biological and chemical processes constitute the climate system. Solar radiation is the driving force of global climate. A portion of the radiation reaching Earth's surface is scattered or reflected by clouds, aerosols, dust and other particles. Radiation reaching the planet is partly absorbed, causing the Earth to emit thermal radiation and part of the radiation is reflected back to the atmosphere. Water vapor and radiatively active CO₂, CH₄, N₂O and O₃, among others, partly trap the reflected radiation to warm the surface temperature from a frigid –18°C to about 15°C, a natural phenomenon known as the 'greenhouse effect'. Human activities have contributed to an increase in the concentration of radiatively active gases and added new greenhouse gases such as halocarbons (like chlorofluorocarbons) and hexafluoride (IPPC, 1997). Together with changes in land cover, this may have contributed to an enhanced greenhouse effect to cause global warming and other climatic changes.

General circulation models (GCMs) simulate climatic processes which operate at different temporal and spatial scales and more complex atmosphere–ocean GCMs (AOGCMs) represent the atmosphere and the oceans in three-dimensional grids to simulate climate. Although all GCMs show warming due to increased greenhouse gas concentration, uncertainties remain due to poor knowledge of cloud formation and feedback, ocean circulation and hydrological process (Rosenzweig and Hillel, 1998). With a resolution of 250×350 km, GCMs may not be very useful in explaining epidemic processes other than long distance transport of pathogens (Nagarajan and Singh, 1990). Downscaling of GCM outputs using mesoscale models (e.g. Russo and Zack, 1997) can generate more realistic outputs representing conditions at a 10–15 km grid resolution.

Between the late 18th century and 1994, CO₂ concentration has increased from 280 to 358 ppm, an increase of nearly 30%. During this period, concentration of N₂O has increased by 145% and CH₄ by 15%. Temperature has risen by about 0.3–0.6°C since the late 19th century. If CO₂ emissions were maintained at 1994 levels, its concentration would rise to about 550 ppm by

the end of the 21st century (IPCC, 1996a). Based on a range of emission scenarios for greenhouse gases and aerosol precursors, global mean temperature is projected to rise between 0.9 and 3.5°C by 2100, but the actual decadal changes would include considerable variability. All model simulations show increased winter precipitation at high latitudes. However, GCMs are better at simulating temperature, as precipitation is spatially and temporally discontinuous. For example, the two models used to simulate precipitation for Australia (Anon., 1996) show a pattern of decreased rainfall in winter but projection of summer rainfall changes according to the model used. This reflects a major systematic difference in regional response of the two models, and demonstrates the sensitivity of simulated rainfall change over Australia to oceanic processes. Future rainfall over Australia may also be affected by changes in large-scale atmospheric circulation due to increasing sulfate aerosols in Asia, and change in El Niño—southern oscillation (ENSO) behavior. Deficiencies in the current state of the science mean that the scenarios cannot make explicit allowance for these factors (Anon., 1996).

It is widely recognized that one of the most significant effects of climate change will be felt through changes in the frequency and magnitude of extreme events such as floods and droughts in Australia (Fowler and Hennesey, 1994) and other parts of the world (ICPP, 1996a).

3. Potential impacts on plant diseases

A consideration of potential impacts of global climate on plant population structure and dynamics, micro-evolutionary processes and plant community structure must be a prerequisite to the discussion of climate change impacts on plant diseases. Potential impacts are relatively easy to determine in monoculture that dominate intensive agricultural systems. Many assessments of potential impact on particular agricultural crops are available (IPCC, 1996b; Rosenzweig and Hillel, 1998). Some integrated studies for regions, countries or the world focus on the security of food supply under climate change (Rosenzweig and Parry, 1994; Harrison et al., 1995). Many only consider direct effects of changing mean climate, while some include the physiological effects of increasing CO₂ (e.g. Wang et al., 1992). In one of the most comprehensive studies using three different climate change scenarios and three general circulation models, Rosenzweig and Parry (1994) modeled the impact on wheat, maize, rice and soybean. The crop models were run for changes in +2 and +4°C, ±20% precipitation and for a doubling of CO₂. Average crop yields at +2°C warming increased by 10–15% in wheat and soybeans, and by 8% in rice and maize. Yields of all four crops were reduced at +4°C warming indicating a threshold of compensation for the direct effect of CO₂.

Similarly, in sorghum, yield increases due to CO₂ are masked by effects of elevated temperature resulting in an overall reduction in yield in drier regions of India (Rao et al., 1995). In the cotton-growing areas of the USA, above average temperature would mean that new cultivars, adapted to higher temperatures, will have to be developed to continue cotton production in areas currently in production (Reddy et al., 1995).

Impacts on more complex terrestrial ecosystems are less clearly understood. Considering a single step increase in atmospheric CO₂ level, Gifford et al. (1996) outlined a series of interconnected phenomena from simple physiological changes in individual plants to potential changes in species composition, which may occur over various timescales. However, only a small subset of species and physical processes are critical in forming the structure and overall behavior of complex terrestrial ecosystems (Holling et al., 1996). A major difficulty lies in the scaling-up from plant processes to processes that apply to vegetation in an ecosystem (Woodward, 1996).

Constraints from diseases, pests or weeds have not been considered to any significant extent in any impact assessment of natural or managed ecosystems despite recognition of their significance (e.g. Clifford et al., 1996; Rosenzweig and Hillel, 1998). For instance, a doubling of CO₂ has been conclusively shown to increase C3 crop yield by about 33% and C4 crop yield by about 10% in over 1000 studies (Kimball, 1985; Cure and Acock, 1986). Whether these benefits would still be realized in the presence of pests and diseases and other limiting factors is largely unknown. It has been suggested that climate change may have minor impact on diseases compared with the impact of crop management and genetic improvements in rice (Kropff et al., 1993) and in maize (Paruelo and Sala, 1994). Intensive agricultural systems regularly face major changes from introduction of new farming practices and cultivars. The apparent plasticity of some agricultural systems may help to minimize negative impacts of climate change through the adoption of new adapted cultivars and other practices. However, despite significant improvements in technology, diseases continue to impose significant constraints to production under the current climate. Disease may further restrict the limited range of crops/cultivars that are adapted to a changing climate. The emerging body of knowledge strongly suggests that climate change, especially changes in precipitation events, temperature and atmospheric composition, will significantly add to the complex interaction between technological and socio-economic changes in influencing plant diseases.

In dealing with climate change effects on global crop production, Rosenzweig and Hillel (1998) have devoted six pages on weeds, 12 pages on insect pests and a mere two pages on diseases. Although this does not represent

the relative level of knowledge in the three related disciplines since the authors have largely not cited published works, it demonstrates a paucity of knowledge on climate change impacts on diseases. Our review of available literature suggests that potential impacts will be felt in three areas: (1) changes in crop loss due to diseases; (2) effectiveness of management strategies; and (3) geographical distribution of diseases. Nevertheless, the limited information largely coming from experiments in controlled environment and modeling studies makes impact assessment difficult. In most cases, effects of a few chosen levels of environmental factors have been extrapolated to predict impacts that could potentially result from a slow and gradual climate change. In addition, there is a complete lack of information on host and pathogen adaptation to climate change. As a result, impact assessments must be treated with caution.

3.1. Changes in crop loss

As under current climate, crop loss from diseases in a changed climate will be determined by a large number of interacting factors that directly and indirectly influence plant diseases. Among direct effects, altered physiology and morphology of the host under elevated CO₂ would change the interception of light and precipitation, and modify canopy structure and microclimate to influence disease epidemiology. Some diseases can cause more severe reduction in plant growth under twice ambient compared to ambient CO₂ at least in controlled environments. For example, in barley powdery mildew, an acclimation of photosynthesis at elevated CO₂ and an infection-induced reduction in net photosynthesis caused larger reductions in plant growth at elevated CO₂ (Hibberd et al., 1996b). Growth of diseased plants is often reduced despite a lowering of disease severity at elevated CO₂ (Chakraborty et al., 1999). Similarly, the rust pathogen *Maravalia cryptostegiae*, used for the biological control of the woody weed rubber vine (*Cryptostegia grandiflora*), reduces growth enhancement of the weed under twice-ambient CO₂ from 24% to less than 16% (Chakraborty et al., unpublished data). Kaukoranta (1996) simulated yield loss in potato based on a 3-year long controlled environment study of late blight at ambient temperature and at 3°C higher than ambient. This study suggested that increases in yield loss of unprotected potato crop at the high temperature would wipe out any benefits from yield increases of around 2 t/ha dry matter per degree of warming. To protect this crop from late blight, fungicide application would need to be extended by 10–20 days for each degree of warming. While the significance of such growth reductions on yield can not be fully determined in the absence of field studies, these results suggest that predictions of bumper harvest due to CO₂ fertilization and increased water use efficiency (Wittwer, 1995) may be unrealistic.

Among indirect effects, ozone can predispose plants to result in losses greater than by a pathogen alone, while the effect of UV-B is inconsistent (Manning and Tiedemann, 1995). However, increased severity under climate change does not always lead to increased losses (Luo et al., 1995). Of the 10 biotrophic pathogens studied so far, disease severity was enhanced in six and reduced in four at high CO₂, and of the 15 necrotrophic pathogens, disease severity increased in nine, reduced in four and remained unchanged in the other two (Chakraborty et al., 1998).

Comprehensive analysis of how crop loss from diseases may be modified with a changing climate is presently unavailable. Preliminary assessments of the relative economic importance of diseases affecting major crops have been made for some countries and regions (Prestidge and Pottinger, 1990; Luo et al., 1995; Carter et al., 1996; Tiedemann, 1996; Chakraborty et al., 1998). Of these, Luo et al. (1995) considered temperature and rainfall in simulation studies to predict the impact of climate change on rice blast. Changes in rainfall were not important but temperature had significant effects in most of the 53 locations in five Asian rice-growing countries included in the simulations. Consequently, impacts varied with the agro-ecological zone and an increased risk of serious rice blast was predicted for cool, subtropical rice growing zones, such as Japan. In the humid tropics and subtropical zones, such as in the Philippines, blast development would be inhibited at higher temperatures.

3.2. Efficacy of management strategies

Effectiveness of most plant protection chemicals depends on prevailing climatic conditions. Changed duration, intensity and frequency of rainfall events would impact on the effectiveness of chemical control measures. Data from field experiments and modeling studies suggest precipitation during the post-application period (Wagenet et al., 1994; Schepers, 1996) is critical. Precipitation following fungicide application may improve its distribution (Schepers, 1996) but an increase in rainfall intensity can deplete fungicide residue on the foliage (Neuhaus et al., 1974). In addition to influences of the physical climate on biological control agents, changes in atmospheric composition will modify the community structure of phyllosphere and rhizosphere microflora (Manning and Tiedemann, 1995; Ayres et al., 1996). In the rhizosphere, elevated CO₂ would interact with nitrogen and other soil factors to modify the number and type of mycorrhizal fungi to influence root health and nutrient uptake. Some short-term studies under controlled conditions have shown that elevated CO₂ can stimulate mycorrhizal colonization (Staddon and Fitter, 1998) due to faster plant growth. Colonization of roots by arbuscular mycorrhizal fungi

is favored in soils of poor nutritional status (Klironomos et al., 1997). It is not clear if increases in soil carbon storage due to greater root and mycorrhizal growth under high CO₂ will influence mycorrhizal colonization.

Climate change will modify host–pathogen interaction to determine the outcome of many diseases. Consequently, the greatest impact of climate change will be on management strategies that utilize host resistance. Modification in Rubisco biochemistry, stomatal physiology, anatomy, morphology and phenology is well known under elevated CO₂ (Bowes, 1993; Wolfe, 1995). Many of these changes in host physiology can potentially enhance host resistance. Significant increase in rates of net photosynthesis allows increased mobilization of resources into host resistance at elevated CO₂ (Hibberd et al., 1996a). Other changes, including production of papillae and accumulation of silicon at sites of appressorial penetration (Hibberd et al., 1996a); greater accumulation of carbohydrates in leaves; more waxes, extra layers of epidermal cells and increased fiber content (Owensby, 1994); lowered nutrient concentration, leading to partitioning of nitrogen from photosynthetic proteins to metabolism that is limiting to plant growth (Baxter et al., 1994); and greater number of mesophyll cells (Bowes, 1993) can all influence host resistance. Reduced pathogen penetration results from a reduction in stomatal density (Chakraborty et al., 1999) and stomatal conductance at high CO₂ (Hibberd et al., 1996b). Thompson et al. (1993) reported a significant reduction in wheat powdery mildew at twice-ambient CO₂, but final severity was dependent on nitrogen and water status of plants. Increased lignification in some forage species at high temperatures (Wilson et al., 1991) can potentially enhance the level of resistance (Strange, 1993).

Whether changes in host physiology would equally influence susceptible and resistant cultivars or resistance in both traditionally bred and transgenic cultivars is not well known. In the tropical legume, *Stylosanthes scabra*, reduction in plant growth due to *Colletotrichum gloeosporioides*-induced anthracnose was more than compensated by growth enhancements at elevated CO₂ in a susceptible but not in a resistant cultivar. Anthracnose severity in the susceptible cultivar was reduced at elevated CO₂ but not in the resistant cultivar (Chakraborty et al., 2000). This suggests that some forms of resistance may be less effective under climate change.

Elevated temperature may cause the breakdown of temperature-sensitive resistance in oat cultivars with *Pg3* and *4* genes (Martens et al., 1967). Even if temperature change is well within the limits of current climatic variability, a modest warming can cause significant increase in heat sums above a critical temperature threshold to affect crop physiology and resistance to disease. Stress induced by extremes such as drought can exacerbate disease by species of *Armillaria* (Rishbeth, 1991), and the endophytic *Cryptostroma corticale*

can rapidly invade vascular and bark tissues in hot dry summers (Dickenson and Wheeler, 1981).

The biggest threat to the durability of host resistance would come from accelerated pathogen evolution. Changes will occur at all stages in the pathogen life cycle under elevated CO₂. Despite initial delays and reduction in host penetration, established colonies grow faster inside host tissues at elevated CO₂ (Lupton et al., 1995; Hibberd et al., 1996a; Chakraborty et al., 2000). Fecundity of both biotrophs and necrotrophs (Chakraborty et al., unpublished; Chakraborty et al., 2000) studied so far has increased under elevated CO₂. A combination of increased fecundity and a favorable microclimate within enlarged canopies will provide more opportunities for infection. There is evidence of adaptation for increased aggressiveness in some pathogens (Kolmer and Leonard, 1986) within three sexual generations and controlled crossing has shown that aggressiveness is heritable and may be polygenically controlled (Caten et al., 1984). For sexually reproducing pathogen populations with broad genetic diversity, increased population size and the number of generations in favorable microclimates would increase the probability of more damaging pathotypes evolving more rapidly (Sutherst et al., 1996b).

3.3. Changes in geographical distribution

Warming will generally cause a pole-ward shift of the agroclimatic zones and crops that grow in these zones. Carter et al. (1996) predicted that maize could be cultivated reliably in southern Finland by 2050 and warming will extend the northern limit for cereal cultivation. At the same time, risk of damage from late blight of potato would increase in all regions and potato nematodes may become a serious problem with additional generations per year. Similar predictions of northward migration and increased severity in areas of current distribution have been made for the oak decline pathogen, *Phytophthora cinnamomi* (Brasier and Scott, 1994; Brasier et al., 1996), and two plant parasitic nematodes (Boag et al., 1991). Pathogens will follow migrating host plants and their dispersal and survival between seasons and changes in host physiology and ecology in the new environment would largely determine how rapidly the pathogens establish in the new environment.

If only climatic effects are considered, changes in geographical distribution itself may not have a major economic impact on crop production. Impacts only become obvious when associated changes such as terrain, remnant vegetation, soil characteristics, etc., are considered. For example, in Australia, a southward shift in location of wheat may mean much of the existing winter rainfall dominant wheat belt would be in unfavorable terrain or offshore (Nix, 1990). A change in terrain may cause more die-back in highly susceptible

Eucalyptus spp. which presently grow on dry ridges in southeastern Australia (Burdon and Shattock, 1980).

Crops may continue to be grown in marginal climates for economic or other reasons and diseases, which are currently under check due to unfavorable weather, may suddenly become serious problems under a changing climate. Despite the presence of a *Eucalyptus* spp. susceptible to *Phytophthora cinnamomi*, impacts on forests in Tasmania, Australia, were minimal due to low ambient temperatures (Podger and Brown, 1989; Podger et al., 1990). Increase in wet periods with soil temperatures of 12–30°C would favor this disease in southeast Australia. Fast growing poplar clones grown in much of northern Europe are generally susceptible to thermophilic *Melampsora alli-populina*, but currently this pathogen does not constitute a major threat to poplar production (Somda and Pinon, 1981). A change to warmer climate may have serious implications for large areas where poplar is being grown as an alternative to producing agricultural surpluses (Lonsdale and Gibbs, 1996).

More aggressive strains of pathogens with broad host range, such as *Rhizoctonia*, *Sclerotinia*, *Sclerotium*, and other necrotrophic pathogens may migrate from agricultural crops to natural plant communities. Similarly, pathogens which are normally less aggressive in natural plant communities could devastate crop monocultures growing in close proximity. Pathogens, in particular unspecialized necrotrophs, may extend their host range to cause new disease problems in migrating crops. There are at least two well-known examples of an indigenous pathogen attacking an introduced plant when grown in close proximity. In its native habitat in the USA, the fire blight bacterium, *Erwinia amylovora*, attacks indigenous plants of the family Rosaceae without causing significant damage. When European settlers grew apples and pears in some regions, the bacterium caused serious losses. Similarly, the coffee rust epidemic in Asia during the late 1800s was facilitated by growing an introduced susceptible host, *Coffea arabica*, in a region where the native pathogen, *Hemileia vastatrix*, was already present on alternative hosts in the forests outlining the coffee plantations (Carefoot and Sprout, 1967). Expansion of host range may even occur in specialized biotrophs, as geographical proximity is as important as phylogenetic relatedness in influencing the host range of some rusts (Eshed and Dinor, 1981; Savile and Urban, 1982). As plants in both natural and agricultural communities can be symptomless carriers of pathogens, any early predictions of impending damage will be difficult (Katan, 1971; Dinor, 1974).

4. The future: a question of scale

As a discipline, plant pathology is dedicated to ensuring sustainable production in agricultural systems

through the management and improvement of plant health. In the foreseeable future, global change will impact on plant health and its management to influence productivity. The role of plant pathology must be to provide an assessment of how plant diseases will impact on agricultural systems under climate change in order to minimize loss to production and quality. Outcomes from this research will have important implications for decisions on amelioration and mitigation strategies.

Due to uncertainties in climate change predictions (IPPC, 1996a) a 'no regrets approach', where the proposed actions have definite and quantifiable benefits, with or without the effects of climate change factored in, should provide the rationale for this research. An example would be an improved understanding of a disease cycle; this will enhance our capacity to predict and manage the disease under current climatic conditions in addition to improving our capacity to respond to climate change.

Climate change may have positive, negative or neutral impact on diseases—research in this area is as much about identifying new opportunities as preparing to minimize negative impacts. Success will require an improved understanding of the causes, impacts and consequences of climate change from which will come amelioration and mitigation strategies. The shortage of critical epidemiological data on individual plant diseases needs to be addressed using experimental approaches. In the first instance, studies in a controlled environment may be used to formulate hypotheses and to determine critical relationships to help develop process-based approaches. Field-based research examining the influence of a combination of interacting factors (Senft, 1995; Norby et al., 1997) would be needed to provide a more realistic appraisal of impacts.

Methodology to model climate change impact has not been fully developed. Some of the impact assessments (Podger et al., 1990; Brasier and Scott, 1994) are 'first pass analysis' using climate-matching softwares such as BIOCLIM (Busby, 1991), HABITAT (Walker and Cocks, 1991) or CLIMEX (Sutherst and Maywald, 1985). Some have used and advocated the use of simulation models (Goudriaan and Zadoks, 1995; Luo et al., 1995; Teng et al., 1996). However, their use is currently limited due to a lack of hard data on impacts. Empirical procedures for assessing long-term climate and disease interactions are only just beginning to emerge (Calvero et al., 1994; Scherm and Yang, 1995; Coakley and Scherm, 1996). There is a need to look beyond the science of plant pathology to seek and invite concepts and ideas from other relevant disciplines for a reappraisal of priorities. Developments in information technology can help in the quest for knowledge and its dissemination (Bridge et al., 1998).

Knowledge needs to be acquired, synthesized and generalized at a scale relevant to an environmental unit.

Impact on an agricultural system must include on- and off-farm effects determined at a landscape scale of spatial resolution. Historically plant pathology research using site-specific knowledge of individual pathosystems has served well in understanding, predicting and managing diseases. Environmental variables at the microclimate level have been utilized at this spatial scale. In contrast, climate systems operate at a global scale and GCMs are better at explaining climate at this coarse level of resolution. As illustrated in Fig. 1, this difference in the level of understanding between plant pathology and biometeorology/climatology at the various spatial and temporal scales has hampered interdisciplinary interaction.

The need to bridge this gap in knowledge has been recognized (e.g. Kennedy, 1997). In recent years, a number of attempts have been made to downscale GCM outputs to a biologically relevant mesoscale (Martin et al., 1996; Bardossy, 1997; Russo and Zack, 1997). Lack of epidemiologically relevant weather variables has been an impediment to the application of GCMs and other climate models to plant disease modeling. Duration of surface wetness and relative humidity, which critically influence infection and disease development by many plant pathogens, have not been easily obtained from GCM output until recently (R.C. Seem, personal communication). Usefulness of remotely gathered site-specific wetness and other data for plant pathology research has been variable (Gleason et al.,

1997) and Seem et al. (2000) provide a more detailed discussion on this topic.

5. Concluding remarks

If changes in atmospheric composition and global climate continue in the future as predicted, there will be relocation of crops and their diseases and impacts will be felt in economic terms from crop loss. Changes in levels of CO₂, ozone and UV-B will influence disease by modifying host physiology and resistance. In addition, changes in temperature, precipitation and the frequency of extreme events will influence disease epidemiology. Changes in geographical distribution will potentially alter the relative importance and spectrum of diseases and new disease complexes may arise. Evolution of pathogen populations may accelerate from enhanced UV-B radiation and/or increased fecundity in elevated CO₂. As a result, host resistances may be overcome more rapidly. Disease management will be influenced due to altered efficacy of biological and chemical control options. Information gathered so far has been fragmented and a comprehensive analysis of climate change impacts on diseases is not possible with present knowledge. Experimental research on a diverse range of disease systems is necessary to improve comprehension of climate change impacts. Given the multitude of atmospheric and climatic factors, possible change scenarios and the number of disease systems, modeling approaches to impact assessment need to be strengthened. For instance, changes in both mean temperature and its variability are equally important in predicting the potential impact of climate change (Schermer and van Bruggen, 1994). Given that climate change is a global issue, the focus needs to shift from paddock-based assessment on specific diseases to a more ecologically relevant spatial unit (Schermer et al., 2000) to consider climate with other associated changes in land use and vegetation cover (Luo et al., 1995), among others.

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References

- Anon., 1996. Climate change scenarios for the Australian region. Climate Impact Group, CSIRO Division of Atmospheric Research, issued November 1996.
- Atkinson, D. (Ed.), 1993. Global climate change, its implication for crop protection. British Crop Protection Council Monograph No. 56. BCPC, Surrey, UK.

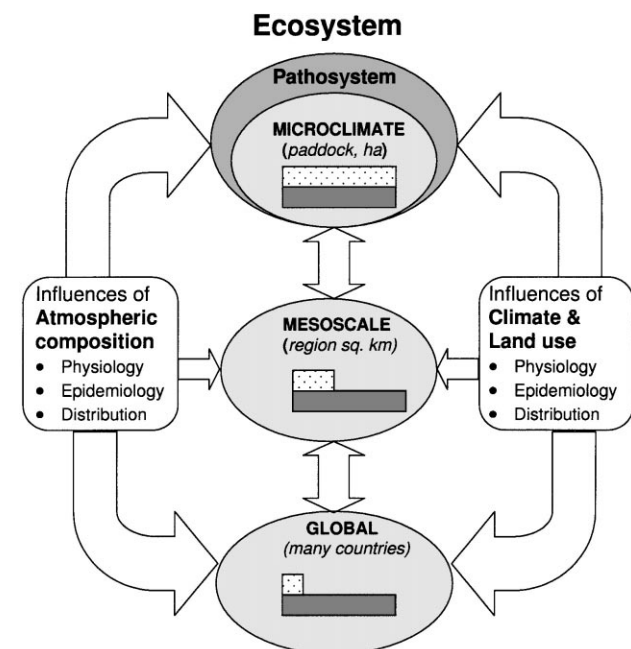


Fig. 1. A summary of major influences due to changes in atmospheric composition, land use and climate on plant diseases and the level of understanding of disease (▤) and climate (■). The understanding of disease and climate is highest at the paddock scale but the knowledge gap is wider at regional and global scales.

- Ayres, P.G., Gunasekera, T.S., Rasanayagam, M.S., Paul, N.D., 1996. Effects of UV-B radiation (280–320 nm) on foliar saprophytes and pathogens. In: Frankland, J.C., Magan, N., Gadd, G.M. (Eds.), *Fungi and Environmental Change*. Cambridge University Press, Cambridge, pp. 32–50.
- Bardossy, A., 1997. Downscaling from GCMs to local climate through stochastic linkages. *Journal of Environmental Management* 49, 7–17.
- Baxter, R., Ashenden, T.W., Sparks, T.H., Farrar, J.F., 1994. Effects of elevated CO₂ on three montane grass species. I. Growth and dry matter partitioning. *Journal of Experimental Botany* 45, 305–315.
- Boag, B., Crawford, J.W., Neilson, R., 1991. The effect of potential climatic changes on the geographical distribution of the plant parasitic nematodes *Xiphinema* and *Longidorus* in Europe. *Nematologia* 37, 312–323.
- Bowes, G., 1993. Facing the inevitable: plants and increasing atmospheric CO₂. *Annual Review of Plant Physiology and Plant Molecular Biology* 44, 309–332.
- Brasier, C.M., Scott, J.K., 1994. European oak decline and global warming: a theoretical assessment with special reference to the activity of *Phytophthora cinnamomi*. *EPPO Bulletin* 24, 221–232.
- Brasier, C.M., Dreyer, E., Aussenac, G., 1996. *Phytophthora cinnamomi* and oak decline in southern Europe. Environmental constraints including climate change. *Annales des Sciences Forestieres* 53, 347–358.
- Bridge, P., Jeffries, P., Morse, D.R., Scott, P.R. (Eds.), 1998. *Information Technology, Plant Pathology and Biodiversity*. CAB International, Wallingford, UK.
- Burdon, J.J., Shattock, R.C., 1980. Disease in plant communities. *Applied Biology* 5, 145–219.
- Busby, J.R., 1991. BIOCLIM—a bioclimate analysis and prediction system. *Plant Protection Quarterly* 6, 8–9.
- Calvero, S.B., Coakley, S.M., McDaniel, L.R., Teng, P.S., 1994. IRRI Discussion Paper Series No. 5, International Rice Research Institute, Manila, The Philippines.
- Carefoot, G.L., Sprott, E.R., 1967. *Famine on the Wind: Plant Diseases and Human History*. Angus & Robertson, Sydney.
- Carter, T.R., Nurro, M., Torkko, S., 1996. Global climate change and agriculture in the north. *Agriculture and Food Science in Finland* 5, 223–385.
- Caten, C.E., Person, C., Groth, J.V., Dhali, S.J., 1984. The genetics of pathogenic aggressiveness in three dikaryons of *Ustilago hordei*. *Canadian Journal of Botany* 62, 1209–1219.
- Chakraborty, S., Murray, G.M., Magarey, P.A., Yonow, T., O'Brien, R., Croft, B.J., Barbetti, M.J., Sivasithamparan, K., Old, K.M., Dudzinski, M.J., Sutherst, R.W., Penrose, L.J., Archer, C., Emmett, R.W., 1998. Potential impact of climate change on plant diseases of economic significance to Australia. *Australasian Plant Pathology* 27, 15–35.
- Chakraborty, S., Pangga, I.B., Lupton, J., Hart, L., Room, P.M., Yates, D., 2000. Production and dispersal of *Colletotrichum gloeosporioides* spores on *Stylosanthes scabra* under elevated CO₂. *Environmental Pollution* (this issue).
- Cheddadi, R., Yu, G., Guiot, J., Harrison, S.P., Prentice, I.C., 1996. The climate of Europe 6000 years ago. *Climate Dynamics* 13, 1–9.
- Clifford, B.C., Davies, A., Griffith, G., Froud-Williams, R.J., Harrington, R., Hocking, T.J., Smith, H.G., Thomas, T.H., 1996. UK climate change models to predict crop disease and pests threats. *Aspects of Applied Biology* 45, 269–276.
- Coakley, S.M., 1979. Climatic variability in the Pacific Northwest and its effect on stripe rust of winter wheat. *Climate Change* 2, 33–51.
- Coakley, S.M., 1999. Biospheric change: will it matter in plant pathology? *Canadian Journal of Plant Pathology* 17, 147–153.
- Coakley, S.M., Scherm, H., 1996. Plant disease in a changing global environment. *Aspects of Applied Biology* 45, 227–237.
- Cure, J.D., Accock, B., 1986. Crops response to carbon dioxide doubling: a literature survey. *Agricultural and Forest Meteorology* 38, 127–145.
- Darley, E.F., Middleton, J.T., 1966. Problems of air pollution in plant pathology. *Annual Review of Phytopathology* 4, 103–118.
- Dickenson, S., Wheeler, B.E.J., 1981. Effects of temperature and water stress in sycamore on growth of *Cryotostroma corticale*. *Transactions of the British Mycological Society* 76, 181–185.
- Dinoor, A., 1974. Role of wild and cultivated plants in the edipemiology of plant diseases in Israel. *Annual Review of Phytopathology* 12, 413–436.
- Eshed, N., Dinoor, A., 1981. Genetics of pathogenicity in *Puccinia coronata*: the host range among grasses. *Phytopathology* 71, 156–163.
- Fowler, A.M., Hennessy, K.J., 1994. Potential impacts of global warming on the frequency and magnitude of heavy precipitation. *Natural Hazards* 11, 283–303.
- Frankland, J.C., Magan, N., Gadd, G.M., 1996. *Fungi and Environmental Change*. Cambridge University Press, Cambridge.
- Gassner, G., Straib, W., 1930. Untersuchungen über die Abhängigkeit des Infektionsverhaltens der Getreiderostpilze vom Kohlensäuregehalt der Luft. *Journal of Phytopathology* 1, 1–30.
- Gifford, R.M., Barrett, D.J., Lutze, F.L., Samarakoon, A.B., 1996. Agriculture and global change: scaling direct carbon dioxide impacts and feedbacks through time. In: Walker, B., Steffen, W. (Eds.), *Global Change and Terrestrial Ecosystems*. Cambridge University Press, Cambridge.
- Gleason, M.L., Parker, S.K., Pitblado, R.E., Latin, R.X., Speranzini, D., Hazzard, R.V., Maletta, M.J., Cowgill Jr., W.P., Biederstedt, D.L., 1997. Validation of a commercial system for remote estimation of wetness duration. *Plant Disease* 81, 825–829.
- Goudriaan, J., Zadoks, J.C., 1995. Global climate change: modelling the potential responses of agro-ecosystems with special reference to crop protection. *Environmental Pollution* 87, 215–224.
- Harrison, P.A., Butterfield, R.E., Downing, T.E. (Ed.), 1995. *Climate Change and Agriculture in Europe*. Environmental Change Unit, University of Oxford Research Report No. 9.
- Hennessy, K.J., Pittock, A.B., 1995. Greenhouse warming and threshold temperature events in Victoria, Australia. *International Journal of Climatology* 15, 591–612.
- Hibberd, J.M., Whitbread, R., Farrar, J.F., 1996a. Effect of elevated concentrations of CO₂ on infection of barley by *Erysiphe graminis*. *Physiological and Molecular Plant Pathology* 48, 37–53.
- Hibberd, J.M., Whitbread, R., Farrar, J.F., 1996b. Effect of 700 µmol per mol CO₂ and infection of powdery mildew on the growth and partitioning of barley. *New Phytologist* 1348, 309–345.
- Holling, C.S., Peterson, G., Marples, P., Sendzimir, F., Redford, K., Gunderson, L., Lambert, D., 1996. Self-organization in ecosystems: lumpy geometries, periodicities and morphologies. In: Walker, B., Steffen, W. (Eds.), *Global Change and Terrestrial Ecosystems*. Cambridge University Press, Cambridge.
- IPCC, 1996a. *Climate Change 1995: The Science of Climate Change*. Houghton, J.T., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg A., Maskell, K. (Eds.), Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.
- IPCC, 1996b. *Agriculture*. In: Watson, R.T., Zinyowera, M.C., Moss, R.H. (Eds.), *Climate Change 1995: Impacts, Adaptation and Mitigation of Climate Change: Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- IPCC, 1997. *An introduction to Simple Climate Models Used in the IPCC Second Assessment Report*. Houghton, J.T., Filho, L.G.M., Griggs, D.J., Maskell, K. (Eds.), IPCC Secretariat.
- Katan, J., 1971. Symptomless carriers of the tomato *Fusarium* wilt pathogen. *Phytopathology* 61, 1213–1217.
- Kaukoranta, T., 1996. Impact of global warming on potato late blight: risks, yield loss and control. *Agriculture and Food Science in Finland* 5, 311–327.

- Kennedy, A.D., 1997. Bridging the gap between general circulation model (GCM) output and biological microenvironments. *International Journal of Biometeorology* 40, 119–122.
- Kimball, B.A., 1985. Adaptation of vegetation and management practices to a higher carbon dioxide world. In: Strain, B.R., Cure, J.D. (Eds.), *Direct Effects of Increasing Carbon Dioxide on Vegetation*. US Department of Energy, Washington, pp. 185–204.
- Klironomos, J.N., Rillig, M.C., Allen, M.F., Zak, D.R., Kubiske, M., Pregitzer, K.S., 1997. Soil fungal–arthropod responses to *Populus tremuloides* grown under enriched atmospheric CO₂ under field conditions. *Global Change Biology* 3, 473–478.
- Kolmer, J.A., Leonard, K.J., 1986. Genetic selection and adaptation of *Cochliobolus heterostrophus* to corn hosts with partial resistance. *Phytopathology* 76, 774–777.
- Kropff, M.J., Cassman, K.G., Penning de Vries, F.W.T., van Laar, H.H., 1993. Increasing the yield plateau in rice and the role of global climate change. *Journal of Agricultural Meteorology* 48, 795–798.
- Lonsdale, D., Gibbs, J.N., 1996. Effects of climate change on fungal diseases of trees. In: Frankland, J.C., Magan, N., Gadd, G.M. (Eds.), *Fungi and Environmental Change*. Cambridge University Press, Cambridge, p. 1019.
- Luo, Y., TeBeest, D.O., Teng, P.S., Fabellar, N.G., 1995. Simulation studies on risk analysis of rice blast epidemics associated with global climate in several Asian countries. *Journal of Biogeography* 22, 673–678.
- Lupton, J., Chakraborty, S., Dale, M., Sutherst, R., 1995. Assessment of the enhanced greenhouse effect on plant diseases—a case study of *Stylosanthes* anthracnose. In: *Proceedings of the 10th Biennial Australasian Plant Pathology Conference*, Lincoln University, New Zealand, 28–30 August.
- Manning, W.J., Tiedemann, A.V., 1995. Climate change: potential effects of increased atmospheric carbon dioxide (CO₂), ozone (O₃), and ultraviolet-B (UVB) radiation on plant diseases. *Environmental Pollution* 88, 219–245.
- Martens, J.W., McKenzie, R.H., Green, G.J., 1967. Thermal stability of stem rust resistance in oat seedlings. *Canadian Journal of Botany* 45, 451–458.
- Martin, E., Timbal, B., Brun, E., 1996. Downscaling of general circulation model outputs—simulation of the snow climatology of the French alps and sensitivity to climate change. *Climate Dynamics* 13, 45–56.
- Nagarajan, S., Singh, D.V., 1990. Long-distance dispersal of rust pathogens. *Annual Review of Phytopathology* 28, 139–153.
- Neuhaus, W., Stachewicz, H., Dunsing, M., 1974. Über den Einfluss von Niederschlägen auf die biologische Wirkung von Fungiziden zur Phytophthora-Bekämpfung. *Nachrichtenbl. Pflanzensch. DDR* 28, 149–153.
- Nix, H., 1990. Potential impacts of climate change on rural industries. In: *Rural Industries: Workshop on Climate Change*. Bureau of Rural Resources Report No. R/3/90. Department of Primary Industries and Energy, Canberra.
- Norby, R.J., Edwards, N.T., Riggs, J.S., Abner, C.H., Wullschlegel, S.D., Gunderson, C.A., 1997. Temperature-controlled open-top chambers for global change research. *Global Change Biology* 3, 259–267.
- Oerke, E.-C., Dehne, H.-W., Schonbeck, F., Weber, A., 1994. *Crop Production and Crop Protection, Estimated Losses in Major Food and Cash Crops*. Elsevier, Amsterdam.
- Owensby, C.E., 1994. Climate change and grasslands: ecosystem-level responses to elevated carbon dioxide. In: *Proceedings of XVII International Grassland Congress*, pp. 1119–1124.
- Padmanabhan, S.Y., 1973. The great Bengal famine. *Annual Review of Phytopathology* 11, 11–26.
- Paruelo, J.M., Sala, O.E., 1994. Effect of global change on maize production in the Argentinean Pampas. *Climate Research* 3, 161–167.
- Paul, N.D., Ayres, P.G., Rasanayagam, S., Royle, D.J., 2000. Stratospheric ozone depletion, UVB radiation and *Septoria tritici* infection of wheat. *Environmental Pollution* (this issue).
- Podger, F.D., Brown, M.J., 1989. Vegetation damage caused by *Phytophthora cinnamomi* on disturbed sites in temperate rainforest in Tasmania. *Australian Journal of Botany* 37, 443–480.
- Podger, F.D., Mummery, D.C., Palzer, C.R., Brown, M.L., 1990. Bioclimatic analysis of the distribution of damage to native plants in Tasmania by *Phytophthora*. *Australian Journal of Ecology* 15, 281–289.
- Prestidge, R.A., Pottinger, R.P. (Eds.), 1990. *The Impact of Climate Change on Pests, Diseases, Weeds and Beneficial Organisms Present in New Zealand Agricultural and Horticultural Systems*. MAF Technology, Ruakura Agricultural Centre, Hamilton, NZ.
- Rao, G.D., Katyal, J.C., Sinha, S.K., Srinivas, K., 1995. Impacts of climate change on sorghum production in India: simulation study. In: Rosenzweig, C., Allen, L.H., Harper, L.A., Hollinger, S.E., Jones, J.W. (Eds.), *Climate Change and Agriculture: Analysis of Potential International Impacts*. American Society of Agronomy, Madison, USA, pp. 325–337.
- Reddy, K.R., Hodges, H.F., McKinion, J.M., 1995. Cotton crop responses to a changing environment. In: Rosenzweig, C., Allen, L.H., Harper, L.A., Hollinger, S.E., Jones, J.W. (Eds.), *Climate Change and Agriculture: Analysis of Potential International Impacts*. American Society of Agronomy, Madison, USA, pp. 3–30.
- Rishbeth, J., 1991. *Armillaria* in an ancient broad leaved woodland. *European Journal of Forest Pathology* 21, 239–249.
- Rosenzweig, C., Parry, M.L., 1994. Potential impact of climate change on world food supply. *Nature* 367, 133–138.
- Rosenzweig, C., Hillel, D., 1998. *Climate Change and the Global Harvest*. Oxford University Press, New York.
- Russo, J.M., Zack, J.W., 1997. Downscaling GCM output with a mesoscale model. *Journal of Environmental Management* 49, 19–29.
- Sandermann Jr., H., 1996. Ozone and plant health. *Annual Review of Phytopathology* 34, 347–366.
- Sandermann Jr., H., 2000. Ozone and biotic disease interactions. *Environmental Pollution* (this issue).
- Savile, D.B.O., Urban, Z., 1982. Evolution and ecology of *Puccinia graminis*. *Preslia* 54, 97–104.
- Scherm, H., Newton, A., Harrington, R., 2000. Working on a global scale for global change impact assessment in plant pathology. *Environmental Pollution* (this issue).
- Scherm, H., van Bruggen, A.H.C., 1994. Global warming and non-linear growth: how important are changes in average temperature? *Phytopathology* 84, 1380–1384.
- Scherm, H., Yang, X.B., 1995. Interannual variations in wheat rust development in China and the United States in relation to the El Niño/Southern Oscillation. *Phytopathology* 85, 970–976.
- Schepers, H.T.A.M., 1996. Effect of rain on efficacy of fungicides on potato against *Phytophthora infestans*. *Potato Research* 39, 541–550.
- Seem, R.C., Magarey, R.D., Zack, J.W., Russo, J.M., 2000. Weather forecasts at the whole plant level: implications for estimating disease risk with global climate models. *Environmental Pollution* (this issue).
- Senft, D., 1995. FACE-ing the future. *Agricultural Research* 43, 4–6.
- Somda, B., Pinon, J., 1981. Ecophysiologie du state uredien de *Melampsora larici-populina* Kleb. et de *M. alli-populina* Kleb. *European Journal of Forest Pathology* 11, 243–254.
- Staddon, P.L., Fitter, A.H., 1998. Does elevated carbon dioxide affect arbuscular mycorrhizas? *Trends in Ecology and Evolution* 13, 455–458.
- Strange, R.N., 1993. *Plant Disease Control: Towards Environmentally Acceptable Methods*. Chapman and Hall, London.
- Sutherst, R.W., Maywald, G.F., 1985. A computerised system for matching climates in ecology. *Agriculture Ecosystems and Environment* 13, 281–299.

- Sutherst, R.W., Ingram, J.S.I., Steffen, W.L., 1996a. Global Change Impacts on Pests, Diseases and Weeds Implementation Plan. GCTE Core Project Office, Canberra, Australia.
- Sutherst, R.W., Yonow, T., Chakraborty, S., O'Donnell, C., White, N., 1996b. A generic approach to defining impacts of climate change on pests, weeds and diseases in Australasia. In: Bouma, W.J., Pearman, G.I., Manning, M.R. (Eds.), *Greenhouse, Coping with Climate Change*. CSIRO, Australia, pp. 281–307.
- Teng, P.S., Heong, K.L., Kropff, M.J., Nutter, F.W., Sutherst, R.W., 1996. Linked pest-crop models under global change. In: Walker, B., Will, S. (Eds.), *Global Change and Terrestrial Ecosystems*. Cambridge University Press, Cambridge, pp. 291–316.
- Thompson, G.B., Brown, J.K.M., Woodward, F.I., 1993. The effects of host carbon dioxide, nitrogen and water supply on the infection of wheat by powdery mildew and aphids. *Plant, Cell and Environment* 16, 687–694.
- Tiedemann, A.v., 1996. Global change of atmosphere and climate—what are the implications for plant protection? *Nachrichtenb. d. deutsch. Pflanzenschutzd.* 48, 73–79.
- Tiedemann, A.v., Firsching, K.H., 2000. Host–pathogen system in a changing atmosphere—case studies with fungal pathogens on wheat. *Environmental Pollution* (this issue).
- Wagenet, R.J., Hutson, J.L., Watson, D.G., Zazueta, F.S., Harrison, T.V., 1994. Computer simulation models as an aid in estimating the probability of pesticide leaching. *Computers in Agriculture* 1994, 786–794.
- Walker, P.A., Cocks, K.D., 1991. HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. *Global Ecology and Biogeography Letters* 1, 108–118.
- Wang, Y., Handoko, J., Rimmington, G., 1992. Sensitivity of wheat growth to increased air temperature for different scenarios of ambient CO₂ concentration and rainfall in Victoria, Australia—a simulation study. *Climate Research* 2, 131–149.
- Wilson, J.R., Deinum, B., Engels, F.M., 1991. Temperature effects on anatomy and digestibility of leaf and stem of tropical and temperate forage species. *Netherlands Journal of Agricultural Science* 39, 31–48.
- Wittwer, S.H., 1995. *Food, Climate and Carbon Dioxide—The Global Environment and World Food Production*. CRC Press, Boca Raton.
- Woodward, F.I., 1996. Developing the potential for describing the terrestrial biosphere's response to a changing climate. In: Walker, B., Steffen, W. (Eds.), *Global Change and Terrestrial Ecosystems*. Cambridge University Press, p. 619.
- Wolfe, D.W., 1995. Physiological and growth responses to atmospheric carbon dioxide concentration. In: Pessarakli, M. (Ed.), *Handbook of Plant and Crop Physiology*. Marcel Dekker, New York, pp. 223–242.