

## Rust-proofing wheat for a changing climate

Sukumar Chakraborty<sup>1,5</sup>, Jo Luck<sup>2,5</sup>, Grant Hollaway<sup>3</sup>, Glenn Fitzgerald<sup>4</sup>, Neil White<sup>6</sup>

<sup>1</sup>*CSIRO Plant Industry, 306 Carmody Road, St Lucia, Queensland 4067 Australia.*

<sup>2</sup>*Biosciences Research Division, Department Primary Industries Victoria, Knoxfield, Victoria*

<sup>3</sup>*Biosciences Research Division, Department Primary Industries Victoria, Private Bag 260, Horsham, Victoria 3401, Australia.*

<sup>4</sup>*Future Farming Systems Research, Department Primary Industries Victoria, Private Bag 260, Horsham, Victoria 3401, Australia.*

<sup>5</sup>*Cooperative Research Centre for National Plant Biosecurity, Innovation Centre, University of Canberra, Bruce ACT 2617, Australia.*

<sup>6</sup>*Agri-Science Queensland, Department of Employment, Economic Development and Innovation, 203 Tor St, Toowoomba, Queensland 4350*

*e-mail: sukumar.chakraborty@csiro.au*

**Abstract** This paper offers projections of potential effects of climate change on rusts of wheat and how we should factor in a changing climate when planning for the future management of these diseases. Even though the rusts of wheat have been extensively studied internationally, there is a paucity of information on the likely effects of a changing climate on the rusts and hence on wheat production. Due to the lack of published empirical research we relied on the few published studies of other plant diseases, our own unpublished work and relevant information from the vast literature on rusts of wheat to prepare this overview. Potential risks from a changing climate were divided into three major groups: increased loss from wheat rusts, new rust races evolving faster and the reduced effectiveness of rust resistances. Increased biomass of wheat crops grown in the presence of elevated CO<sub>2</sub> concentrations and higher temperatures will increase the leaf area available for attack by the pathogen. This combined with increased speed of the pathogen's life cycle, may increase the rate of epidemic development in many environments. Likewise, should the effects of climate change result in more conducive conditions for rust development there will also be a corresponding increase in the rate of evolution of new and presumably virulent races. The effectiveness of some rust resistance genes are influenced by temperature, crop development stage and even nitrogen status of the host. It is likely that direct and indirect changes on the host from climate change may influence the effectiveness of some of these resistance genes. Currently the likely effects of climate change on the effectiveness of disease resistance is not known and since disease resistance breeding is a long term strategy it is important to determine if any of the important genes may become less effective due to climate change. Studies must be made to acquire new information on the rust disease triangle to increase the adaptive capacity of wheat under climate change. BGRI leadership is needed to broker research on rust evolution and the durability of resistance under climate change.

**Keywords** climate change, elevated CO<sub>2</sub>, epidemiology, evolution of virulence, rust resistance, wheat rust

### Introduction

According to the latest assessment by the Intergovernmental Panel on Climate Change, atmospheric concentration of radiatively active gases including CO<sub>2</sub> has risen rapidly since 1750 (IPCC 2007). These gases trap solar radiation creating a 'greenhouse effect', which along with other factors increase the surface temperature of the earth. Changing rainfall patterns and the frequency and severity of extreme weather events, such as droughts, floods, heat waves, and hurricanes, are among other effects of climate change. Rising CO<sub>2</sub> concentrations and perturbations in climate are increasingly influencing agriculture (Stern 2007) by shifting crop growing regions and affecting food production.

Depending on nutrient and water supply, crop yields can increase by up to 30% from a ‘fertilization effect’ at elevated atmospheric CO<sub>2</sub> (Ainsworth and Long 2005) and increases of 20% are common for wheat (Norton et al. 2008; Högy et al. 2009). These projections do not consider the effect of other climatic factors or the impacts of pest and diseases. Changes in temperature, for example, can potentially reduce wheat productivity in regions such as the high yielding Indo-Gangetic Plains (Ortiz et al. 2008). In Australia, the likely impacts of increased CO<sub>2</sub> concentrations and associated temperature and rainfall changes on wheat yields will vary among regions, with significant yield reductions in Western Australia, but a moderate yield increase in north-eastern Australia (Howden and Jones 2004). Similarly, pests and diseases will interact with crops to limit yield increases with rising CO<sub>2</sub> but how this might affect future food security has not been addressed (Gregory et al. 2009; Mahmuti et al. 2009).

Climate influences the frequency and severity of disease epidemics and some studies link the abundance of wheat pathogens to changing atmospheric composition (Shaw et al. 2008). Wheat scab (caused by *Fusarium graminearum*) and wheat stripe rust (*Puccinia striiformis* f. sp. *tritici*) severity in China and stem rust (*P. graminis* f. sp. *tritici*) severity in the USA have been linked to the El Niño-Southern Oscillation Index (Scherm and Yang 1995), and the prevalence/severity of wheat diseases, including leaf rust and stripe rust in Sweden (Wiik and Ewaldz 2009) to long-term climatic conditions. Among diseases of other crop plants, changes in the severity of potato late blight (Hannukkala et al. 2007) and pine needle blight (Woods et al. 2005) severities were also linked to long-term climate changes. These studies indicate that climate change modifies disease and pest risks and increases uncertainty in risk predictions associated with climate change.

Models predicting changes in geographical distribution of host plants and their diseases under a changing climate can serve as a guide to future disease prevalence (Bergot et al. 2004). However, whether current disease management strategies including the use of resistant varieties will be effective cannot be ascertained without detailed knowledge of host-pathogen biology under conditions simulating future climates. New rust pathogen races, such as *Puccinia graminis* f. sp. *tritici* race ‘Ug99’ (Pretorius et al. 2000), can pose significant threats to global wheat production. This race is virulent to the resistance gene *Sr31* that has been effective worldwide for more than 30 years (Wanyera et al. 2006). For example, with a 10% yield loss, damage from Ug99 could amount to US\$1–2 billion in Asia alone (Duveiller et al. 2007). Screening of advanced lines in East Africa combined with a program to pyramid resistance genes is now underway through the Borlaug Global Rust Initiative (BGRI, <http://www.globalrust.org>). Because there has been no research on rust micro-evolution under rising temperatures and CO<sub>2</sub> levels, future appearance of new races under climate change cannot be predicted from current knowledge. Little is known about the potential effect of changing atmospheric composition or physical climate on the biology of cereal rusts, rust resistance of the host plant or the host-pathogen interaction and no assessments of climate change impacts on wheat rusts could be found in the literature. There were only a few published empirical studies on diseases other than rusts under realistic field conditions. The effects of elevated CO<sub>2</sub> in these studies varied with the host-pathogen combination (Karnosky et al. 2002; McElrone et al. 2005; Kobayashi et al., 2006; Eastburn et al. 2010; Melloy et al. 2010), but none addressed wheat rusts. Therefore, it is difficult to project ‘generalized effects’ of climate change on the rusts of wheat.

In a recent two-year scoping study we considered some aspects of wheat stripe rust biology in the Australian Grains Free Air CO<sub>2</sub> Enrichment (AGFACE) facility. This paper gives an overview from this and other relevant studies on the potential effects of climate change, and suggests research needs to address climate change in combating the threat of wheat rusts.

### **Direct effects of climate change and variability**

Changes in atmospheric composition and the physical climate including temperature, rainfall and humidity will no doubt affect the economic importance, geographical distribution and management of rusts of wheat ultimately effecting wheat production and food security. These effects are conveniently grouped in two classes. Firstly, changes in the effectiveness of host plant resistance and pathogen

fitness due to modified host and pathogen biology, and host-pathogen interaction. The effectiveness of resistance in wheat varieties could change under a changed climate and/or resistance may be overcome quickly by new races, which may evolve at a different rate in a changing climate. Secondly, geographical distribution of wheat rusts and consequently their relative economic importance may change. If the new environments are highly suitable for wheat, the rusts may become more damaging further increasing economic importance. If however, wheat growing regions become less suitable for wheat growth, rusts may become less important. Changes in host plants, pathogen populations, host-pathogen interactions and the geographical distribution of wheat cropping areas will each potentially affect the economic importance and management of rusts.

### ***Effects mediated through changes in the host plant***

Plants grown at elevated CO<sub>2</sub> have changed morphology, anatomy, chemical composition and gene expression profiles in addition to increased biomass and yield. For instance, the stimulation of photosynthesis at elevated CO<sub>2</sub> levels lead to increased production and accumulation of carbohydrates in plant organs, generally leading to reduced protein in grain (Kimball et al. 2000), which can influence bread-making quality of wheat flour (Rogers et al. 1998). However, changes in fiber and protein content of wheat do not change forage quality or digestibility (Akin et al. 1994). Increased starch and decreased protein concentration in the grain coincide with increased width of chloroplasts, whose shape changes from elliptical in ambient to round in elevated CO<sub>2</sub> (Sinha et al. 2009). The implications of these changes are not clearly understood. Stomatal density and conductance, wax and epidermal cell layers, number of mesophyll cells and fiber content are among other changes occurring at elevated CO<sub>2</sub> concentrations (Wittwer 1995). These changes are modulated by rising temperature and other changes in climate including the microclimate of an enlarged wheat canopy (Pinter et al. 2000), but insufficient knowledge makes any impact assessment speculative. Wheat varieties differ in their response to elevated CO<sub>2</sub> but this has only been considered in a very few recent studies (Ziska 2008).

The physiology, biochemistry and molecular biology of host-pathogen interactions have been extensively studied in the rusts of wheat and many reviews are available (Eversmeyer and Kramer 2000; Line 2002; Singh et al. 2002; Leonard and Szabo 2005). In stem rust, for example, a urediniospore germinates to produce a germ tube, which swells to form an appressorium over stomatal openings. Further development is dependent on a reduction of CO<sub>2</sub> concentration in the stomata among other factors and penetration can be inhibited by high CO<sub>2</sub> (Yirgou and Caldwell 1968). Infection by *P. graminis* alters the direction of phloem transport and massive accumulation of cytokinins and sugars in the lesion area resulting from highly regulated host and pathogen signaling. Detailed studies on how altered host plant physiology at elevated CO<sub>2</sub> concentrations influence rust infection are lacking, but reduced stomatal density, production of papillae and accumulation of silicon at the sites of appressorial penetration (Hibberd et al. 1996a) and changed leaf chemistry at high CO<sub>2</sub> concentrations increased resistance to powdery mildew (*Blumeria graminis*) in barley (Hibberd et al. 1996b) and other pathogens in other crops (McElrone et al. 2005; Hassan et al. 2008). In some crops, increased production of secondary metabolites at elevated CO<sub>2</sub> has been linked to increased disease resistance. At high CO<sub>2</sub> phenylpropanoids, coumarin scopolin and scopoletins are significantly increased to enhance resistance to potato virus Y in tobacco (Matros et al. 2006); and in soybean, phytoalexin glyceollin production is stimulated in a resistant, but not in a susceptible variety (Braga et al. 2006).

In wheat, the expression of many genes for resistance to leaf rust (*P. triticina*) (Kolmer 1996), stripe rust (Singh et al. 2000; Datta et al. 2009) and stem rust (Leonard and Szabo 2005) is influenced by temperature and/or plant developmental stage. Some resistances may become less effective at high temperature. For example, rust reaction of wheat varieties with the stem rust resistance gene *Sr15* can change from resistant at 15°C to nearly fully-susceptible at 20°C (Roelfs 1988). Anecdotal evidence of a weakening of stripe rust resistance and pathogen adaptation due to temperature increases has come from annual race surveys in the Eastern USA (Markell and Milus 2008), but these findings may

also reflect a change in the pathogen population, described in the following section. Conversely some stripe rust resistance genes, such as *Yr18*, are known to be temperature mediated and become more effective at higher temperatures (Park et al. 1992), therefore in varieties with this resistance there may be an enhancement of the effectiveness of resistance in a warming climate.

Changes in plant physiology, morphology, anatomy and gene expression will also influence the effectiveness of other rust control measures including the use of fungicides. The crucial role of plant physiology and morphology in the uptake and translocation of fungicides is well known (O'Leary and Jones 1987) as is the influence of systemic fungicides on plant physiology including photosynthesis and gas exchange (Grubler et al. 2009). Effectiveness of systemic fungicides could be reduced by changes such as smaller stomatal opening or thicker epicuticular waxes that slow down uptake rates. On the other hand, increased metabolic rates at high temperature could increase uptake, but empirical studies are lacking to allow realistic predictions. Other climatic factors will also interact, including more frequent rainfall events that will wash away residues of contact fungicides, triggering more frequent applications. Currently the potential effect of climate change on the efficacy of foliar applied fungicides for the control of rusts of wheat is not known. It is likely that should any changes in the host due to climate change reduce the efficacy of fungicides, higher rates will be warranted.

### ***Effects mediated through changes in the pathogen / host-pathogen interaction***

In a growth cabinet study of wheat, Tiedemann and Firsching (2000) observed strong inhibition of leaf rust development at elevated O<sub>3</sub>, but not at elevated CO<sub>2</sub>. By enhancing photosynthesis, elevated CO<sub>2</sub> compensated for the adverse effects of high O<sub>3</sub> in both leaf rust-inoculated and non-inoculated plants. Pflieger et al. (1999) contended that whether a disease is influenced by O<sub>3</sub> depends on the timing of pollutant exposure and the infective periods of a particular host/pathogen combination. These authors concluded that while obligate parasitism is generally inhibited by elevated O<sub>3</sub>, infection by facultative pathogens can increase, decrease, or remain unchanged. Ozone predisposition of plants to pests and diseases was recently summarized by Chakraborty et al. (2008) and is not considered here.

During the 2007 and 2008 wheat seasons we studied progress of stripe rust development and changes in the biology of *P.f. sp. tritici* on adult plant susceptible H45, the partially resistant Janz with the adult plant resistance genes *Yr18*, and others grown at ambient (380 ppm) and elevated (820 ppm) CO<sub>2</sub> concentrations in the AGFACE facility at Horsham, Victoria, with or without irrigation. Description of the AGFACE facility appears in Mollah et al. (2009). Stripe rust was induced by inoculating a section of each row. Latent period was assessed as the number of days from inoculation to the appearance of the first visible stripe rust lesion.

Stripe rust severity was visually assessed over time as the percentage of leaf area affected enabling determination of the area under the disease progress curve for each treatment. The partially resistant cultivar significantly reduced disease severity, and while the application of irrigation increased disease severity, this effect was not significant in either season. CO<sub>2</sub> did not have a significant effect on disease severity in either 2007 (Fig. 1) or in 2008. The strong varietal effect and the smaller irrigation effect on disease progress were as expected. There was no interaction between CO<sub>2</sub> and variety to indicate any change in the ranking of the two varieties and the effectiveness of the partial resistance within the cultivar Janz was not changed in the presence of elevated CO<sub>2</sub>. This is important information for plant breeders developing wheat cultivars for future climates, particularly with increased effort in the breeding of wheat with multiple genes conferring partial resistance. In this experiment total leaf area, and total spore production, was not measured, so it is not known if the increased leaf area from the elevated CO<sub>2</sub> concentrations resulted in increased spore production from the crop canopy.

FIGURE 1 HERE

Latent period, determined from the 2008 season only, remained unchanged at 14 days at both CO<sub>2</sub> concentrations for both varieties. This result was unexpected, because, even in the absence of elevated CO<sub>2</sub>, the two varieties otherwise were expected to differ in latent period and the study needs to be repeated.

For fecundity assessment infected leaves were sampled and the cumulative number of urediniospores per unit pustule area was determined by washing and counting spores using a haemocytometer. Following the first wash, leaves were incubated in the field in moist Petri dish for 24 h at the respective CO<sub>2</sub> concentrations and a further urediniospore suspension was recovered. The daily rate of urediniospore production was similarly determined from the second suspension. Leaf segments were blotted dry, scanned and the area covered by pustules was calculated and analysed using 'Image Tool' image analysis software from the University of Texas Health Science Center at San Antonio and downloadable from the web. Results from 2007 showed no significant differences between CO<sub>2</sub> concentrations or wheat varieties. Similar findings came from the 2008 data with no significant difference between CO<sub>2</sub> concentrations, but the susceptible H45 produced significantly more urediniospores per day than the partially resistant Janz. However, as with stripe rust severity, at a plant or paddock level *P. striiformis* f. sp. *tritici* inoculum would increase many fold even though urediniospore production per unit leaf area did not increase.

Previous growth chamber studies with rubber vine rust (caused by *Maravalia cryptostegiae*, Chakraborty et al. unpublished) and the anthracnose pathogen, *Colletotrichum gloeosporioides* (Chakraborty et al. 2000) showed significant increases in fecundity at high CO<sub>2</sub> for both pathogens. The AGFACE results highlight the difficulty in obtaining precise data on fecundity and latent period from the variable field environment and future studies should consider using more controlled environments. However, even with no intrinsic change in fecundity, a 20-30% increase in wheat biomass under elevated CO<sub>2</sub> (Kimball et al. 1995) will significantly increase inoculum size to potentially increase their dispersal and severity, but further studies are required to test this hypothesis.

It is likely that rusts of wheat will be able to adapt to increased temperature associated with climate change. Recent studies suggest that rust pathogens can adapt to different optimal temperatures. Annual race surveys in the Eastern USA showed that contemporary *P. striiformis* f. sp. *tritici* races have different temperature optima and virulence profiles than races collected before 2000 (Markell and Milus 2008). Latent period and spore germination studies indicated that the contemporary population was better adapted to high temperature (Milus et al. 2006). Both populations had similar latent period and spore germination rates at 12°C, but at 18°C, isolates of the new population had shorter latent periods and higher germination rates than the old isolates. Such adaptation may have been responsible for the more widespread stripe rust epidemics covering at least 20 central and southern states of the USA in 2000 (Milus et al. 2006). Further studies showed that recent severe stripe rust epidemics were most likely magnified by increased pathogen aggressiveness at higher temperature. This demonstrates adaptation of *P. striiformis* f. sp. *tritici* to warmer temperatures to cause severe disease in previously unfavorable environments (Milus et al. 2009).

In parts of Canada, where rusts do not survive winter temperatures, milder winters may allow overwintering and/or earlier starts to rust epidemics, potentially making them more severe (Boland et al. 2004). In a similar way, increased out-of-season rainfall will provide increased opportunities for over-summering of rusts in parts of Australia. Changes in the ability of rust pathogens to survive from one season to the next need to be considered when determining the effects of a changing climate on rust severity.

At a larger scale and longer time-frame, changes in wheat rust severities are associated with temporal scale characteristic of the El Niño-Southern Oscillation Index (SOI), with a 2-10 year periodicity between SOI intensity and stripe rust in China (41 years data from 1950 to 1990) and a 6-8 year periodicity of stem rust in the USA (42 years data from 1921 to 1962) (Scherm and Yang 1995). Further analyses of this data showed that a mid-latitude atmospheric circulation pattern, the Western Atlantic teleconnection, better described the observed association between SOI and severe stripe rust in China (Scherm and Yang 1998). These examples serve to illustrate how changes in circulation

pattern in the upper atmosphere influence dispersal of rusts in the northern hemisphere. Increasing climate variability projected under climate change will make these associations harder to predict.

### ***Effect of changed geographical distribution of wheat and its rusts***

A coupling of crop simulation and climate change models for the year 2050 scenario predicts significant shifts in wheat mega-environments (Ortiz et al. 2008). The 12 or so mega-environments for spring wheat are demarcations of wheat growing regions of the world based on biotic and abiotic constraints, cropping systems and other characteristics (Braun et al. 1996). Mega-environment 1, comprising 32 million hectares of northwestern Mexico, the Indo-Gangetic plains and Nile valley, for example, has high yield potential. According to the simulation study, mega-environment 1 would suffer a 51% reduction in area by 2050 whereas the high latitude mega-environment 6, covering the cool temperate regions of North America and northern Eurasia and bound by the 55°N latitude, would shift northwards to 65°N (Ortiz et al. 2008).

At the very least, the major breeding targets would need to change in order to reflect changes in relative importance of diseases within each altered mega-environment. If these shifts in climatic suitability are not matched by soil fertility, farming systems, infrastructure and other agricultural inputs, crops could suffer from chronic water, nutrient and other stresses. Alternatively, if crops continue to be grown in areas that no longer have an ideal climate, but have the necessary soil, infrastructure and other inputs, they could also suffer chronic stress. Necrotrophic and soil-borne pathogens, among others, may become more damaging to stressed plants. Biotrophic pathogens like rust fungi associated with particular wheat varieties will follow the geographical shift in mega-environments. Migrating pathogens will interact with organisms endemic to the region. New disease complexes and/or novel biological control opportunities may arise as a consequence. Breeding targets (Ortiz et al. 2008) will change for each mega-environment with changing pathogen spectra, disease dynamics and relative economic values.

Predicted shifts in the distribution of forests and their pathogens in response to global warming are expected to be upwards along altitudinal gradients and towards the poles (reviewed by Chakraborty et al. 2008). Other modelling studies predict range shifts with rising temperature and other weather variables for important crop pathogens such as those for black sigatoka (*Mycosphaerella fijiensis*) in banana (Ghini et al. 2008), grapevine downy mildew (*Plasmopara viticola*) (Salinari et al. 2007), and phoma stem canker (*Leptosphaeria maculans*) on oilseed rape (Evans et al. 2008). We found no published modeling study on changed geographical distribution of wheat rust pathogens as a result of climate change, although with long distance inter-continental dispersal, uredinial inocula will easily keep up with changes in the distribution of cropping regions. In discussing the effect of climate changes on stripe rust development, Line (2002) summarized research on modeling the weather-dependency of stripe rust epidemics, but did not predict stripe rust severity, prevalence or distribution under future climate scenarios.

Using a process-based modeling tool, Dymex (Maywald et al. 2000), Chakraborty et al. (2002) linked a wheat growth model (O'Leary and Connor 1996) to *P. striiformis* f. sp. *tritici* life cycle through damage functions. The model outputs were validated using data collected at selected wheat-growing regions in New South Wales, Australia, and were further extended to study the potential effect of changed climate scenarios according to a CSIRO model for the period 1990 – 2100 (CSIRO 1996). The *P. striiformis* f. sp. *tritici* model included three stages in the life cycle: viz. spores, infective stages and lesions, each with parameters dealing with mortality, growth and state transfer functions. The leaf area and lesion area were linked through various feedbacks that limit lesion growth and also reduce the transpiration efficiency of the host plant. A location effect was clear with diseased leaf area decreasing under future climates in some areas, but stripe rust levels were generally higher for 2070 at many sites (Fig. 2). Yield loss resulted from an interaction between the change in climate, cultivar phenology and effect of disease.

FIGURE 2 HERE

These models did not include interacting factors such as host-pathogen adaptation and temperature sensitivity of host resistance and thus can only be used for broad guidance. Temperature sensitivity of *P. striiformis* f. sp. *tritici* may be a limiting factor, and one assessment has predicted reduced stripe rust incidence for some regions and cultivars under climate change (Chakraborty et al. 2002). Nevertheless, higher winter and lower spring temperatures in the Pacific Northwest of the USA were implicated for increased frequency and severity of stripe rust epidemics (Coakley 1979), possibly due to pathogen adaptation to high temperature (Milus et al. 2009).

### ***Evolution of virulence***

The histories of stripe rust in Australia and New Zealand (Steele et al. 2001; Wellings 2007) and the USA (Line 2002) illustrate how rust pathotypes evolve. Similar evolutionary trends were reviewed for *P. graminis* f. sp. *tritici* in Australia (Park 2007). Since the initial introduction of wheat stripe rust to Australia in 1979 at least two further introductions occurred in 1999 and 2002. A fourth stripe rust incursion in Australia in 1998 involved a putative *forma specialis* adapted to barley grass (*Hordeum murinum* complex) (Wellings 2007). Over the 28 years many new pathotypes were detected, and a subset of these became economically important and dominant components of the pathogen population (Wellings 2007).

Following exotic introduction to particular areas new pathotypes arose presumably by mutation and possibly somatic hybridization between or within the immigrant and local populations (Wright and Lennard 1980; Steele et al. 2001). Although sexual reproduction was recently reported with the discovery of *Berberis* spp. as alternate hosts (Jin et al. 2010), mutation is probably the most prevalent evolutionary force in the stripe rust pathogen (Line 2002). Similar exotic incursions followed by mutation and/or other asexual means of reproduction are the main sources of variation as appropriate alternative hosts are rarely present in cultivation areas for any of the three wheat rusts (Leonard and Szabo 2005; Bolton et al. 2008). For *P. graminis* f. sp. *tritici* the frequency of mutants were estimated at  $8.3 \times 10^{-6}$  per uredinial generation for a heterozygous locus dominant for avirulence to  $6.9 \times 10^{-11}$  for a homozygous locus (Schafer and Roelfs 1985). Mutation rate varies with the avirulence gene (reviewed by Leach et al. 2001). Mutation of avirulence to virulence in *P. graminis* f. sp. *tritici* is a case in point, where genes corresponding to *Sr5*, *Sr15* and *Sr21* had very high mutation rates whereas those for genes like *Sr13*, *Sr24* and *Sr27* rarely mutated (Luig 1979). A pathotype can also evolve at different rates at different locations; for example, two mutants of *P. striiformis* f. sp. *tritici* pathotype 134 were recorded in Australia since its detection in 2002 (Wellings 2007) and another two ('Jacky' and the 'Jacky + *Yr27*') strains were recorded since the 2007 publication. In contrast, at least 17 variants appeared in the USA within 4 years of its arrival in 2000 (Chen 2005). However, the success or failure of a new pathotype depends on several factors including the relative fitness of virulent mutants (Leonard and Czochoz 1980; Leach et al. 2001).

The probability of mutation to virulence increases with increasing population size. Although there are only a few studies on pathogen biology under elevated CO<sub>2</sub> concentrations, the majority have demonstrated increased fecundity in both biotrophic and necrotrophic pathogens. Fecundity was significantly increased at high CO<sub>2</sub> levels in the rubber vine rust (*Maravalia cryptostegiae*, Chakraborty et al. unpublished), barley powdery mildew (Hibberd et al. 1996a), anthracnose (*Colletotrichum gloeosporioides*, Chakraborty et al. 2000) and crown rot (*Fusarium pseudograminearum*, Melloy et al. 2010) pathogens. However, fecundity was not increased in *P. striiformis* f. sp. *tritici* in the present AGFACE study. In the case of the anthracnose pathogen, increased fecundity was characteristic of newly isolated highly aggressive strains with a novel molecular haplotype after 25 sequential infection cycles at high CO<sub>2</sub> levels (Chakraborty and Datta 2004).

Rising atmospheric CO<sub>2</sub> and temperature will extend the wheat growing season, enlarge crop canopy to increase the amount of susceptible tissue and make the canopy micro-climate more conducive to rust development. Temperature is an important factor that controls rate of reproduction and sporulation in rusts (Clifford and Harris 1981; Dennis 1987). High CO<sub>2</sub> and temperature will also

influence host plant resistance. A combination of these and other factors including raised pathogen fecundity, will increase the number of uredinial generations to potentially accelerate the evolution of new pathotypes. Any assessment of future risk must anticipate changes in host-pathogen biology and evolution under climate change. With plant breeders controlling the evolution of wheat crops, pathogen evolution must be an important component of any fact-based risk assessment.

### Summary of potential effects

Only four diseases of field crops have been studied under realistic field conditions in a FACE facility (Kobayashi et al. 2006; Eastburn et al. 2009; Melloy et al. 2010). The unpublished study on stripe rust summarized here, is the only empirical study dealing with climate change and a rust of wheat in a FACE. This is despite the economic importance of rusts, the massive global investment in rust management, advanced understanding of the genetic and molecular bases of host-pathogen interaction and the wealth of knowledge on the effects of atmospheric composition and climate on wheat production (Kimball et al. 2000; Ziska 2008). Many studies consider the effect of elevated CO<sub>2</sub> on pathogens and diseases in greenhouse and growth cabinets and one has studied the influence of elevated CO<sub>2</sub> and ozone levels on leaf rust (Tiedemann and Firsching 2000). However, given the variable responses of pathogens and host-pathogen interactions to altered atmospheric composition and climate for diseases studied so far, the only option is to undertake empirical studies to gather new knowledge on the rusts. Based on current understanding, there are no ‘rules of thumb’ for determining the specific effects of wheat rusts under a changing climate. We essentially have a ‘best guess scenario’ that is certainly not definitive.

Predicted effects on rusts of wheat will apply equally to endemic pathotypes as well as to exotic races, such as Ug99, yet to get a foothold in many new regions. The risks can be outlined as follows:

1. *Risk of increased loss from wheat rusts.* Increased over-summering / overwintering, enlarged crop canopy and extended growing season, among others, will increase rust inoculum to increase yield loss. Effectiveness of management options using fungicides may be reduced and/or frequency of applications may increase. Self-sown wheat and other grasses in new and existing areas opened up for wheat growth due to changing climate will serve as reservoirs of inoculum.
2. *Risk of new pathogen races evolving faster.* Large pathogen populations from increased crop biomass and increased wheat areas may undergo increased numbers of infection cycles in expanded wheat growing season to accelerate pathogen evolution on large spatial scales. If there is increased pathogen fecundity, this will further contribute to the population size.
3. *Risk of reduced effectiveness of rust resistance.* Effectiveness of some temperature-sensitive rust resistance genes may be reduced; pathogen strains adapted to higher temperature may inflict more damage and other potential physiological, structural and genetic changes may make some rust resistances ineffective.

### Research needs

A lack of empirical knowledge means that the potential effects of climate change on rusts of wheat are far from clear. Studies must be made to acquire new information on the host-pathogen-environment interaction for better impact assessments. However, research must expand beyond impact assessment to develop adaptation strategies, such as new varieties and/or other rust management options that will retain their effectiveness under a changing climate thus increasing the adaptive capacity of wheat (Chakraborty et al. 2008). Whether current rust management strategies will deliver this outcome can only be determined from a rigorous scrutiny via targeted R&D and assessing the impacts of climate change will be an essential component of this.

Changes in atmospheric composition and climate will not happen quickly but will occur gradually and plant breeding and other research on rust management is expected to keep pace with gradual changes in host-pathogen interaction due to climate change. For instance, if new races evolve

at a frequency that has been driving the well-known 'boom and bust' cycles (Eversmeyer and Kramer 2000), then current breeding efforts should be adequate to cope with the new variants. If on the other hand, combinations of high temperature and CO<sub>2</sub>, altered crop physiology, increased inoculum, and increased numbers of infection cycles lead to explosive changes in the wheat rust pathosystem, current breeding programs may not be able to keep pace with the accelerated evolution of new pathotypes. Potential changes in farming systems due to climate change will also bring new challenges.

Research on the following areas are essential to project realistic effects of climate change on rusts of wheat and to better plan and manage the threat of wheat rusts under a changing climate:

### ***Rust evolution***

As evident from the heightened global concern over Ug99, the appearance of new rust pathotypes with new virulence combinations is the biggest risk facing agriculture and food security. Even before Ug99, management of wheat rusts was one of the best examples of internationally-coordinated research efforts with perhaps the most significant investment in all cereal producing countries. Currently there is limited information available as to the likely effects of a changed climate on the evolution of rusts of wheat and therefore the likely rate of development of new pathotypes with new virulence combinations. Empirical research on rust micro-evolution under a changing climate is needed to predict future appearance of new races and this must be an essential component of any risk assessment from rust under a changing climate so that the international plant breeding community can respond accordingly.

### ***Effectiveness of rust management strategies***

Much of the current debate is on how agriculture and food security may be affected by shifting disease dynamics under climate change (Gregory et al. 2009; Mahmuti et al. 2009), but there is little on strategies that will prove effective in managing diseases. For instance, whether the current physical, chemical and biological control tactics including disease resistant varieties would offer effective protection or whether there is a need to develop and deploy new management strategies has never been addressed. Changing farming systems will influence rust epidemiology and additional measures will be necessary to reduce pathogen over-summering / overwintering opportunities. Likewise, the efficacy of fungicides in crops with altered physiology and under changing physical weather conditions, including temperature and rainfall, must be determined. Most wheat cultivars maintain resistance for five or more years (Singh et al. 2002), which is about the agronomic lifespan of a common cultivar. Some resistance genes in cultivars have failed before they were used extensively, and some genes have lasted many years (Leach et al. 2001). Testing the performance of rust resistant wheat varieties under rising CO<sub>2</sub> and temperature levels is essential to ascertain their longevity under future climates. Pre-emptive breeding can commence to replace resistance sources once the most vulnerable genes/gene combinations are identified (McIntosh and Brown 1997). Long distance dispersal of urediniospores on continental scales means that R&D efforts must be globally coordinated, perhaps following a similar model to the BGRI, to evaluate risks from both endemic and exotic pathotypes. Led by the late Nobel Laureate Dr. Norman E. Borlaug, the BGRI, among other activities, currently supports screening of advanced germplasm and lines in East Africa combined with a research program to combine resistance genes.

### ***Breeding for resistance***

The probability of a rust pathotype to acquire simultaneous mutations in several avirulence genes is small (Schafer and Roelfs 1985), thus the reasoning that durability can be achieved with multiple effective resistance genes. Research in Australia is aimed at developing triple adult plant resistances to rusts by combining stripe rust, leaf rust and stem rust resistance genes through marker-assisted

selection (Bariana et al. 2007). Another approach has been the use of cloned resistance genes in cassettes of linked transgenes and novel genes to develop transgenic plants with multiple rust resistance genes at a single locus (Ellis et al. 2007). Genetic improvements for rust management under changing climates will need to rely on both traditional selection/breeding and genetic transformation routes. Knowledge of host-pathogen interaction at a molecular level can lead to the identification of novel resistance genes and recent studies on secondary metabolites (Matros et al. 2006; Braga et al. 2006) and gene expression (Miyazaki et al. 2004; Zou et al. 2007; Lake and Wade 2009; Leakey et al. 2009;) at elevated CO<sub>2</sub> levels can serve as a guide to similar studies on rust resistance.

### ***Rust biology and epidemiology under changing farming systems.***

Changes in geographical distribution of cropping areas can alter the dynamics and epidemiology of rusts. Changing proximity and relationships of wheat crops to refuge and alternate hosts will influence the complex temporal interrelationship between hosts, pathogens and the environments (Eversmeyer and Kramer 2000). For instance, in Australia survival of all three wheat rust pathogens is critical during the non-cropping phase in the warm to hot summer period in Australia (Wellings 2007). Increased summer rainfall events associated with a changing climate will increase the growth of volunteer wheat during the non-cropping part of the season and thus increase the opportunity for rust to survive the summer and increase the likelihood of earlier and more severe rust epidemics in the winter crop. In parts of Canada overwintering and/or earlier starts to rust epidemics will be the main issue (Boland et al. 2004). Implications of altered pathogen biology and epidemiology on rust management and ways to improve management must be a central theme of future research in a farming systems context. Linking rust development models with those predicting changes in wheat production zones and climate will assist in forecasting the likely changes in rust severity in the future. New tools in gene expression profiling can also be used to address epidemiological questions (Leakey et al. 2009).

**Acknowledgements** Technical and other assistance from Matthew Weinert, Paul Melloy, Rosanna Powell, Ross Perrott, Graham Exell, Johathan Bretag, Mark McLean, Russel Argall and Mahabubur Mollah is gratefully acknowledged. Co-investment from the Cooperative Research Centre for National Plant Biosecurity, CSIRO Plant Industry and Victorian Department of Primary Industry in this research is gratefully acknowledged. The continuing AGFACE experiment is supported by the Grains Research and Development Corporation, the Victorian Department of Primary Industries, the University of Melbourne and the Australian Government Department of Climate Change.

### **References**

- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytol* 165:351-372
- Akin DE, Kimball BA, Windham WR, Pinter PJ, Wall GW, Garcia RL, LaMorte RL, Morrison WH (1995) Effect of free-air CO<sub>2</sub> enrichment (FACE) on forage quality of wheat. *Animal Feed Science Tech* 53:29-43
- Bariana HS, Brown GN, Bansal UK, Miah H, Standen GE, Lu M (2007) Breeding triple rust resistant wheat cultivars for Australia using conventional and marker-assisted selection technologies. *Austr J Agric Res* 58:576-587
- Bergot M, Cloppet E, Rarnaudw VP, De Que Z M, Benoi TM, Ai S, De Sprez-Loustau M (2004) Simulation of potential range expansion of oak disease caused by *Phytophthora cinnamomi* under climate change. *Global Change Biol* 10:1539-1552
- Boland G, Melzer M, Hopkin A, Higgins V, Nassuth A (2004) Climate change and plant diseases in Ontario. *Can J Plant Pathol* 26:335-350

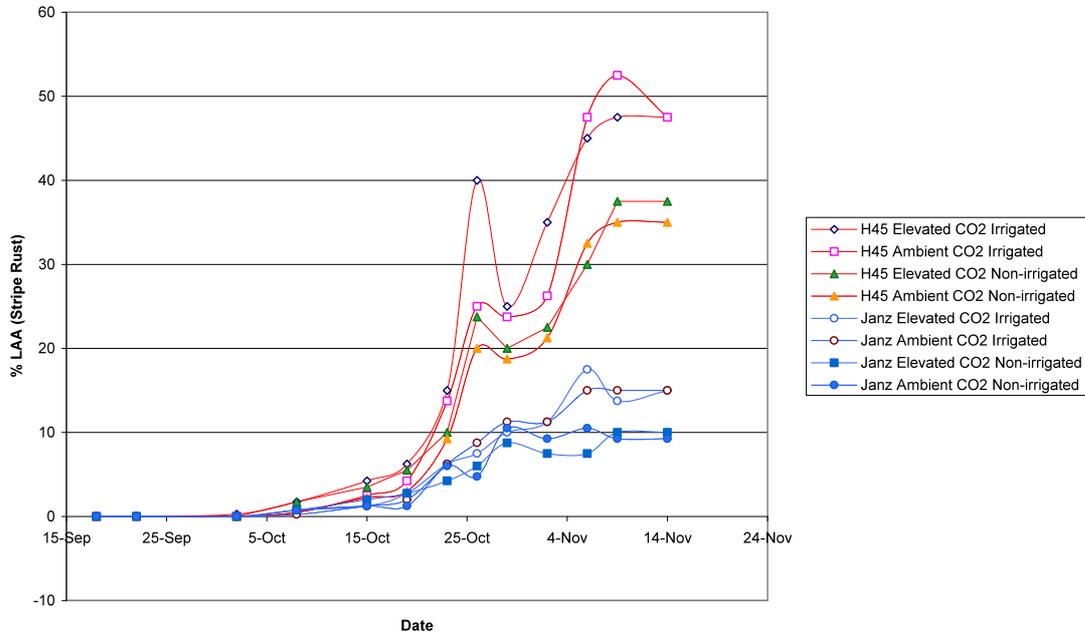
- Bolton MD, Kolmer JA, Garvin DF (2008) wheat leaf rust caused by *Puccinia triticina*. *Mol Plant Pathol* 9:563-575
- Braga MR, Aidar MPM, Marabes MA, de Godoy RL (2006) Effects of elevated CO<sub>2</sub> on the phytoalexin production of two soybean cultivars differing in the resistance to stem canker disease. *Environ Exptl Bot* 58:85-92
- Braun H-J, Rajaram S, van Ginkel M (1996) CIMMYT's approach to breeding for wide adaptation. *Euphytica* 92:175-183
- Chakraborty S, Datta S (2003) How will plant pathogens adapt to host plant resistance at elevated CO<sub>2</sub> under a changing climate? *New Phytol* 159:733-742
- Chakraborty S, Pangga IB, Lupton J, Hart L, Room PM, Yates D (2000) Production and dispersal of *Colletotrichum gloeosporioides* spores on *Stylosanthes scabra* under elevated CO<sub>2</sub>. *Environ Pollut* 108:381-387
- Chakraborty S, Murray G, White N (2002) Impact of Climate change on important plant diseases in Australia. Rural Industries Research and Development Corporation. RIRDC Publication No W02/010, RIRDC Project No CST-4A, available at <http://www.rirdc.gov.au/reports/AFT/02-010.pdf>
- Chakraborty S, Luck J, Hollaway G, Freeman A, Norton R, Garrett KA, Percy K, Hopkins A, Davis C Karnosky DF (2008) Impacts of global change on diseases of agricultural crops and forest trees. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* 3:1-15
- Chen XM (2005) Epidemiology and control of stripe rust (*Puccinia striiformis* f. sp. *tritici*) on wheat. *Can J Plant Pathol* 27:314-337
- Clifford BC, Harris RG (1981) Controlled environment studies of the epidemic potential of *Puccinia recondita* f.sp. *tritici* on wheat in Britain. *Trans Brit Mycol Soc* 77:351-358
- Coakley SM (1979) Climate variability in the Pacific Northwest and its effect on stripe rust disease of winter wheat. *Climatic Change* 2:33-51
- CSIRO (1996) Climate change scenarios for the Australian region. <http://www.dar.csiro.au/publications/scenarios.htm>. November 1996.
- Datta D, Nayar SK, Prashar M, Bhardwaj SC (2009) Inheritance of temperature-sensitive leaf rust resistance and adult plant stripe rust resistance in common wheat cultivar PBW343. *Euphytica* 166:277-282
- Dennis JI (1987) Effect of high temperatures on survival and development of *Puccinia striiformis* on wheat. *Trans Brit Mycol Soc* 88:91-96
- Duveiller E, Singh, RP, Nicol JM (2007) The challenges of maintaining wheat productivity: pests, diseases, and potential epidemics. *Euphytica* 157:417-430
- Eastburn DM, Degennaro MM, Delucia EH, Dermody O, McElrone A (2010) Elevated atmospheric carbon dioxide and ozone alter soybean diseases at SoyFACE. *Global Change Biol* 16:320-330
- Ellis JG, Mago R, Kota R, Dodds PN, McFadden H, Lawrence G, Spielmeier W, Lagudah E (2007) Wheat rust resistance research at CSIRO. *Austr J Agric Res* 58:507-511
- Eversmeyer MG, Kramer CL (2000) Epidemiology of wheat leaf and stem rust in the central great plains of the USA. *Annu Rev Phytopathol* 38:491-513
- Evans N, Baierl A, Semenov MA, Gladders P, Fitt BDL (2008) Range and severity of a plant disease increased by global warming. *J Roy Soc Int* 5:525-531
- Ghini R, Hamada E, Gonçalves RRV, Gasparotto L, Pereira JCR (2008) Risk analysis of climate change on black sigatoka in Brazil. *Proc 9<sup>th</sup> Int Cong Plant Pathol*; Turin, Italy. *J. Plant Pathol* 90:S2.105
- Gregory PJ, Johnson SN, Newton AC, Ingram JSI (2009) Integrating pests and pathogens into the climate change/food security debate. *J Exp Bot* 60:2827-2838
- Gruber BR, Davies LRR, Kruger EL, McManus PS (2009) Effects of copper-based fungicides on foliar gas exchange in tart cherry. *Plant Dis* 93:512-518

- Hannukkala AO, Kaukoranta T, Lehtinen A, Rahkonen A (2007) Late-blight epidemics on potato in Finland, 1933–2002; increased and earlier occurrence of epidemics associated with climate change and lack of rotation. *Plant Pathol* 56:167-176
- Hassan IA, Bell JNB, Marshall FM (2008) Effects of ozone-protectant chemicals on physiology and growth of Egyptian clover grown in open-top chambers and at a rural site in Egypt. Abstr, Int Cong Plant Pathol, Turin, Italy. *J. Plant Pathol* 90:S2.105
- Hibberd JM, Whitbread R, Farrar JF (1996a) Effect of elevated concentrations of CO<sub>2</sub> on infection of barley by *Erysiphe graminis*. *Physiol Mol Plant Pathol* 48:37-53
- Hibberd JM, Whitbread R, Farrar JF (1996b) Effect of 700 μmol mol<sup>-1</sup> CO<sub>2</sub> and infection with powdery mildew on the growth and carbon partitioning of barley. *New Phytol* 134:309-315
- Högy P, Wieser H, Köhler P, Schwadorf K, Breuer J, Franzaring J, Muntiferung R, Fangmeier A (2009) Effects of elevated CO<sub>2</sub> on grain yield and quality of wheat: results from a 3-year free-air CO<sub>2</sub> enrichment experiment. *Plant Biol* 11:60-69
- Howden M and Jones RN (2004) Risk assessment of climate change impacts on Australia's wheat industry. In: Fischer T et al. (eds) *New directions for a diverse planet*. Proc 4<sup>th</sup> Int Crop Sci Cong, Brisbane, Australia, 26 Sept-1 Oct. The Regional Institute, Gosford, NSW, Australia
- Intergovernmental Panel on Climate Change. Summary for policymakers. In: Solomon S et al. (eds) *Climate change 2007: The physical science basis*. Contribution of working Group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, New York, USA
- Jin Y, Szabo LJ, Carson M (2010) Century-old mystery of *Puccinia striiformis* life history solved with the identification of *Berberis* as an alternate host. *Phytopathology* 100:432-435
- Karnosky DF, Percy KE, Xiang B, Callan B, Noormets A, Mankovska B, Hopkin A, Sober J, Jones W, Dickson RE, Isebrands JG (2002) Interacting elevated CO<sub>2</sub> and trophospheric O<sub>3</sub> predisposes aspen (*Populus tremuloides* Michx.) to infection by rust (*Melampsora medusae* f.sp. *tremuloidae*). *Global Change Biol* 8:329-338
- Kimball BA, Morris CF, Pinter PJ Jr, Wall GW, Hunsaker DJ, Adamsen FJ, LaMorte L, Leavitt SW, Thompson L, Matthias AD, Brooks J (2000) Elevated CO<sub>2</sub>, drought and soil nitrogen effects on wheat grain quality. *New Phytol* 150:295-303
- Kimball BA, Pinter Jr. PJ, Garcia RL, LaMorte RL, Wall GW, Hunsaker DJ, Wechsung G, Wechsung F, Kartschall Th. (1995) Productivity and water use of wheat under free-air CO<sub>2</sub> enrichment. *Global Change Biol* 1:429-442
- Kobayashi T, Ishiguro K, Nakajima T, Kim HY, Okada M, Kobayashi K (2006) Effects of elevated atmospheric CO<sub>2</sub> concentration on the infection of rice blast and sheath blight. *Phytopathology* 96:425-431
- Kolmer JA (1996) Genetics of resistance to wheat leaf rust. *Ann. Rev. Phytopathol.* 34:43-455
- Lake J, Wade R (2009) Plant–pathogen interactions and elevated CO<sub>2</sub>: morphological changes in favour of pathogens. *J Exp Bot* 60:3123-3131
- Leach JE, Vera Cruz CM, Bai J, Leung H (2001) Pathogen fitness penalty as a predictor of durability of disease resistance genes. *Annu Rev Phytopathol* 39:187-224
- Leakey ADB, Ainsworth EA, Bernard SM, Markelz RJC, Ort DR, Placella SA, Rogers A, Smith MD, Sudderth EA, Weston DJ, Wullschlegel SD, Yuan S (2009) Gene expression profiling: opening the black box of plant ecosystem responses to global change. *Global Change Biol* 15:1201-1213
- Leonard KJ, Czochoz RJ (1980) Theory of genetic interactions among populations of plants and their pathogens. *Annu Rev Phytopathol* 18:237-258
- Leonard KJ, Szabo LJ (2005) Stem rust of small grains and grasses caused by *Puccinia graminis*. *Mol Plant Pathol* 6:99-111
- Line RF (2002) Stripe rust of wheat and barley in North America: A retrospective historical review. *Annu Rev Phytopathol* 40:75-118

- Luig NH (1979) Mutation studies in *Puccinia graminis tritici*. In: Ramanujam S (ed) Proc 5<sup>th</sup> Int Wheat Genet Symp, Indian Society of Genetics and plant Breeding, IARI, New DEelhi, India, pp533-539
- Mahmuti M, West JS, Watts J, Gladders P, Fitt BDL (2009) Controlling crop disease contributes to both food security and climate change mitigation. *Earthscan* 2009:1473-5903
- Markell SG, Milus EA (2008) Emergence of a novel population of *Puccinia striiformis* f. sp. *tritici* in Eastern United States. *Phytopathology* 98:632-639
- Matros A, Amme S, Kettig B, Buck-Sorlin GH, Sonnewald U, Mock HP (2006) Growth at elevated CO<sub>2</sub> concentrations leads to modified profiles of secondary metabolites in tobacco cv. SamsunNN and to increased resistance against infection with potato virus Y. *Plant Cell Environ* 29:126-137
- Maywald GF, Sutherst RW, Zalucki M (2000) DYMEX. Exploring population dynamics. CSIRO Entomology <http://www.ento.csiro.au/research/pestmgmt/dymex/dymexfr.htm>
- McElrone AJ, Reid CD, Hoyer KA, Hart E, Jackson RB (2005) Elevated CO<sub>2</sub> reduces disease incidence and severity of a red maple fungal pathogen via changes in host physiology and leaf chemistry. *Global Change Biol* 11:1828-1836.
- McIntosh RA, Brown GN (1997) Anticipatory breeding for resistance to rust diseases in wheat. *Annu Rev Phytopathol* 35:311-326
- Melloy P, Hollaway G, Luck J, Norton R, Aitken E, Chakraborty S (2010) Production and fitness of *Fusarium pseudograminearum* inoculum at elevated CO<sub>2</sub> in FACE. *Global Change Biol* DOI: 10.1111/j.1365-2486.2010.02178.x
- Milus EA, Seyran E, McNew R (2006) Aggressiveness of *Puccinia striiformis* f. sp. *tritici* isolates in south-central United States. *Plant Dis* 90:847-852
- Milus EA, Kristensen K, Hovmøller MS (2009) Evidence for increased aggressiveness in a recent widespread strain of *Puccinia striiformis* f.sp. *tritici* causing stripe rust of wheat. *Phytopathology* 99:89-94
- Miyazaki S, Fredricksen M, Hollis KC, Poroyko V, Shepley D, Galbraith DW, Long SP, Bohnert HJ (2004) Transcript expression profiles of *Arabidopsis thaliana* grown under controlled conditions and open-air elevated concentrations of CO<sub>2</sub> and of O<sub>3</sub>. *Field Crops Res* 90:47-59
- Mollah M, Norton R, Huzzey J (2009) Australian grains free-air carbon dioxide enrichment (AGFACE) facility: design and performance. *Crop Pasture Sci* 60:697-707
- Norton R, Fitzgerald G, Korte C (2008) The effect of elevated carbon dioxide on the growth and yield of wheat in the Australian Grains Free Air Carbon Dioxide Enrichment (AGFACE) experiment. In: Unkovich MJ (ed) Proc 14<sup>th</sup> Austr Agron Conf, Austr Soc Agron, Adelaide, Horsham pp 1-5
- O'Leary GJ, Connor DJ (1996) A simulation model of the wheat crop in response to water and nitrogen supply: I. Model construction. *Agric Syst* 52:1-29
- O'Leary AL, Jones AL (1987) Factors influencing the uptake of fenarimol and flusilazol by apple leaves. *Phytopathology* 77:1564-1568
- Ortiz R, Sayre KD, Govaerts B, Gupta R, Subbarao GV, Ban T, Hodson D, Dixon JM, Iván Ortiz-Monasterio J, Reynolds M (2008) Climate change: Can wheat beat the heat? *Agric Ecosyst Environ* 126:46-58
- Park RF (2007) Stem rust of wheat in Australia. *Austr J Agric Res* 58:558-566
- Park RF, Gavin JA, Rees RG (1992) Effects of temperature on the response of some Australian wheat cultivars to *Puccinia striiformis* f. sp. *tritici*. *Mycol Res* 96:166-170
- Pfleeger TG, da Luz MA, Mundt CC (1999) Lack of a synergistic interaction between ozone and wheat leaf rust in wheat swards. *Environ Exptl Bot* 41:195-207
- Pinter PJ, Kimball BA, Wall GW, LaMorte RL, Hunsaker DJ, Adamsen FJ, Frumau KFA, Vugts HF, Hendrey GR, Lewin KF, Nagy J, Johnson HB, Wechsung F, Leavitt SW, Thompson TL, Matthias AD, Brooks TJ (2000) Free-air CO<sub>2</sub> enrichment (FACE): blower effects on wheat canopy microclimate and plant development. *Agric For Met* 103:319-333

- Pretorius ZA, Singh RP, Wagiore WW (2000) Detection of virulence to wheat stem rust resistance gene *Sr31* in *Puccinia graminis* f. sp. *tritici* in Uganda. *Plant Dis* 84:203
- Roelfs AP (1988) Genetic control of phenotypes in wheat stem rust. *Annu Rev Phytopathol* 26:351-367
- Rogers GS, Gras PW, Batey IL, Milham PJ, Payne L, Conroy JP (1998) The influence of atmospheric CO<sub>2</sub> concentration on the protein, starch and mixing properties of wheat flour. *Austr J Plant Physiol* 25:387-393
- Salinari F, Giosuè S, Tubiello FN, Rettori A, Rossi V, Spanna F, Rosenzweig C, Gullino ML (2007) Downy mildew (*Plasmopara viticola*) epidemics on grapevine under climate change. *Global Change Biol* 12:1299-1307
- Schafer JF, Roelfs AP (1985) Estimated relation between numbers of urediniospores of *Puccinia graminis* f.sp. *tritici* and rates of occurrence of virulence. *Phytopathology* 75:749-750.
- Scherm H, Yang XB (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
- Scherm H, Yang XB (1998) Atmospheric teleconnection patterns associated with wheat stripe rust disease in North China. *Intl J Biomet* 42:28-33
- Shaw MW, Bearchell SJ, Fitt BDL, Fraaije BA (2008) Long-term relationships between environment and abundance in wheat of *Phaeosphaeria nodorum* and *Mycosphaerella graminicola*. *New Phytol* 177:229-238
- Singh RP, Nelson JC, Sorrells ME (2000) Mapping *Yr28* and other genes for resistance to stripe rust in wheat. *Crop Sci* 40:1148-1155
- Singh RP, Huerta-Espino J, Roelfs AP (2002) The wheat rusts. In: Curtis BC, Rajaram S, Macpherson HG (eds) Bread wheat. FAO Plant production and protection series No. 30, Rome, Italy <http://www.fao.org/docrep/006/y4011e/y4011e0g.htm#bm16>
- Sinha PG, Kapoor R, Uprety DC, Bhatnagar AK (2009) Impact of elevated CO<sub>2</sub> concentration on ultrastructure of pericarp and composition of grain in three *Triticum* species of different ploidy levels. *Environ Exptl Bot* 66:451-456
- Steele KA, Wellings CR, Dickinson MJ (2001) Support for a stepwise mutation model for pathogen evolution in Australasian *Puccinia striiformis* f.sp. *tritici* by use of molecular markers. *Plant Pathol* 50:174-180
- Stern N (2007) The economics of climate change: the Stern review. Cambridge University Press Cambridge, UK
- Tiedemann A, Firsching KH (2000) Interactive effects of elevated ozone and carbon dioxide on growth and yield of leaf rust-infected versus non-infected wheat. *Environ Pollut* 108:357-363
- Wanyera R, Kinyua MG, Jin Y, Singh RP (2006) The spread of stem rust caused by *Puccinia graminis* f. sp. *tritici*, with virulence on *Sr31* in wheat in Eastern Africa. *Plant Dis* 90:113
- Wellings CR (2007) *Puccinia striiformis* in Australia: a review of the incursion, evolution, and adaptation of stripe rust in the period 1979-2006. *Austr J Agric Res* 58:567-575
- Wiik L, Ewaldz T (2009) Impact of temperature and precipitation on yield and plant diseases of winter wheat in southern Sweden 1983-2007. *Crop Prot* 28:952-962
- Wittwer SH (1995) Food, climate and carbon dioxide - The global environment and world food production. CRC Press, Boca Raton, USA
- Wright RG, Lennard JH (1980) Origin of a new race of *Puccinia striiformis*. *Trans Brit Mycol Soc* 74:283-287
- Woods A, Coates DK, Hamann A (2005) Is an unprecedented Dothistroma needle blight epidemic related to climate change? *Bioscience* 55:761-769
- Yirgou D, Caldwell R (1968) Stomatal penetration of wheat seedlings by stem and leaf rusts in relation to effects of carbon dioxide, light, and stomatal aperture. *Phytopathology* 58:500-507
- Ziska LH (2008) Three-year field evaluation of early and late 20th century spring wheat cultivars to projected increases in atmospheric carbon dioxide. *Field Crops Res* 108:54-59
- Zou X, Shen QJ, Neuman D (2007) An ABA inducible WRKY gene integrates responses of creosote bush (*Larrea tridentata*) to elevated CO<sub>2</sub> and abiotic stresses. *Plant Sci* 172:997-1004

**Fig. 1** Stripe rust severity (% leaf area affected) visually assessed on 13 occasions on susceptible H45 and resistant Janz wheat varieties grown at ambient and elevated CO<sub>2</sub> concentrations, with and without additional irrigation within the AGFACE facility at Horsham, Victoria, 2007



**Fig. 2** Diseased leaf areas relative to present conditions (white bars) under climate change scenarios for 2030 (black) and 2070 (grey) for wheat variety ‘Meering’ at selected locations in NSW and Victoria, Australia. The effects of climate change on the growth of the host and the pathogen are combined

