# An integrative approach to understanding the pest and disease threats to agricultural biosecurity under future climates

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## Abstract

*Despite increasing knowledge of the predicted impacts of climate change, potential threats from pests and diseases to agriculture remain uncertain. In this study, we developed models to understand better the likely responses of pest and disease threats to the changing Australian climate. By coupling host-plant physiology, virus and vector population growth and climatic data with projected climate change scenarios, we are able to project individual species responses and shifts to historic geographic ranges. Strengthened by empirical data, these models can be incorporated into plant biosecurity management and contingency planning, forming the basis of integrated scenario-based decision support systems for emergency plant pest management. Current work focuses on developing an innovative spatial modelling environment using the bird cherry-oat aphid (Rhopalosiphum padi) which vectors barley yellow dwarf virus (BYDV). The effect of climate change on aphid feeding behaviour, flight time and synchrony with the crop, virus acquisition and transmission rates, wheat phenology changes and physiological responses are being incorporated. Experiments in the Australian Grains Free Air Carbon Dioxide Enrichment research facility have enabled field based investigations of the effects of elevated (e)$CO_2$ on wheat pathosystems. Wheat stripe rust (Puccinia striiformis) and crown rot (Fusarium pseudograminearum) severity, latent period, fecundity and host resistance were assessed under ambient and 550ppm $CO_2$. This paper presents preliminary results from e$CO_2$ and wheat disease studies and describes the approach used to construct a model to project the effects of climate change on the future yields of wheat infected with BYDV.*

**Keywords** *biosecurity, climate change, $CO_2$, wheat, model, crop disease*

## Introduction

Pest and disease outbreaks occur when changes in climatic conditions such as temperature and soil moisture, and biotic factors such as host condition and natural enemy abundance are most favourable for growth, survival and dissemination. A change in climatic conditions can cause a pest or disease to expand its normal range into a new environment, extending agricultural losses and affecting natural plant communities (Rosenzweig et al., 2001). A poleward shift in the geographical range of some pests and pathogens has been observed during the last century. For example, the northerly spread of sudden death syndrome caused by *Fusarium solani* f. sp. *glycines* is a major threat to the U.S.A. soybean production (Roy et al. 1997). Rising temperatures associated with climate change are predicted to be associated with the future poleward movement of other insects and pathogens (Coakley 1999, Rosenzweig, 2001).

While future spatial distribution of a species can be predicted under climate change scenarios using models, there appears to be limited knowledge of how climate change will influence the biology of a pathogen or insect and the interaction with their host.

The effect of climate change on plant pathogen and insect biology may be variable (Coakley et al. 1999; Fuhrer 2003, Chakraborty et al., 2008). For example, climatic factors such as storm severity, rainfall, humidity, temperature, and $CO_2$, affect the life cycle of the plant, pest/pathogen, vectors and their dispersal, by changing the rate of infection or infestation (Anderson, 2004; Berry, 2002; Cannon, 1998; Chakraborty, 2000; Pimentel, 2000; Pimentel, 2001). There may also be a change in cropping patterns leading to novel plant pathogen or pest interactions (Cannon, 1998; Coakley 1999; Parker and Gilbert, 2004) through: eg.

1. the movement of a new pest/pathogen into an existing crop, which then infects a previously unaffected indigenous (native and non-native) host;

2. the introduction of a new host through changes in cropping practices, which an indigenous pest/pathogen infects; and

3. the introduction of both new host and new pest/pathogen which interact with each other.

Conversely, climate change may restrict the prevalence of a pest/pathogen or a crop, subsequently restricting the occurrence of disease or infestation.

We explore two methods of testing whether climate change will increase the risk of damage to crops by pest and diseases, through (i) field and controlled environment-based experiments examining increased atmospheric $CO_2$ and (ii) modelling. This paper will outline both approaches in focussing on the effects of climate change on three diseases of wheat.

## The interactions of increased atmospheric $CO_2$ and plant pests and diseases

Studies from controlled environments and Free Air $CO_2$ Enrichment (FACE) experiments have shown that changes in plant anatomy, morphology and phenology under elevated $CO_2$ can potentially influence disease epidemiology (Chakraborty et al., 2008; Manning and von Tiedemann, 1995). Of particular concern are changes to pathogen life-cycle and host-pathogen interactions that may reduce the efficacy of current control measures or accelerate the evolution of new pathogen races.

Increases in $CO_2$ can affect herbivore consumption rates, growth rates, fecundity and population density of insect pests (Awmack et al., 1997; Cannon, 1998; Fuhrer, 2003; Heagle et al., 2002; Jones et al., 1998; Whittaker, 1999). These effects are often associated with altered plant physiology and composition (including increased carbon:nitrogen ratio), altered concentrations of non-structural carbohydrates, starch and fibre content and other plant chemicals, but may also be associated with changes in the geographical range of native and cultivated host plant species (Cannon, 1998; Lincoln et al., 1993).

Elevated $CO_2$ may modify pathogen virulence and/or host susceptibility affecting the initial establishment of the pathogen on the host (Coakley et al. 1999; Matros et al. 2006; Plessl et al., 2005). In most examples, host resistance increased, possibly due to changes in host morphology, physiology and composition. However, an increase in plant canopy size (especially in combination with humidity), and an increase in host abundance can increase pathogen load (Chakraborty and Datta, 2003; Manning and von Tiedemann, 1995; Mitchell 2003; Pangga et al*.,* 2004). Studies of BYDV infections in oats grown at $eCO_2$ led to an increased plant biomass compared to uninfected plants under $eCO_2$. Potentially this could increase the virus reservoir due to improved winter survival of infected plants (Malmstrom and Field, 1997).

### Wheat Diseases and increasing atmospheric $CO_2$

In 2007, the Australian Grains FACE (AGFACE) facility at Horsham in Victoria (Fig. 1) was established (Mollah et al., 2009) to study changes in wheat agronomy at $CO_2$ concentrations projected under the IPCC emission scenario A1B. With eight 12 m diameter stainless steel rings dispersing $CO_2$ at a concentration of 550 ppm, the main trial was a factorial design of two $CO_2$ levels, two wheat varieties, two times of sowing and two levels of water supply in four replicates. Small areas of this trial have been used to study pathogen biology and host-pathogen interaction for the biotrophic pathogen, stripe rust (*Puccinia striiformis*), necrotrophic pathogen, crown rot (*Fusarium pseudograminearum*) and BYDV (Barley yellow dwarf virus).

Figure 1. Australian Grains Free Air $CO_2$ Enrichment (AG FACE) experiment site, Horsham, Australia

### eCO$_2$ and wheat stripe rust (*P. striiformis*)

A susceptible (H45) and a partially resistant (Janz) cultivar of wheat were planted in the AGFACE rings to determine whether wheat was more or less susceptible to stripe rust under increased atmospheric $CO_2$. The wheat was inoculated with spores of *P. striiformis* and the area under disease progress curve was recorded for infected wheat grown under ambient and eCO$_2$. Components of pathogen life-cycle including incubation period, latent period and fecundity were also recorded over two seasons (2007 and 2008).

For the fecundity assessment, segments from 3 infected leaves of the same age group were destructively sampled from each subplot, shaken for 1hr in water with 0.01% Tween 20. Urediniospore concentration was determined using a haemocytometer and expressed as pustule per unit area. Leaf segments were blotted dry, scanned and the area covered by pustules calculated and analyzed using image analysis software (Fig. 2). There was no difference in the pathogen fecundity levels between the $CO_2$ treatments in either season. However, these results need further examination because the expected difference in fecundity between the wheat varieties was not evident either. Assessments of fecundity and latent period of *P.striiformis* needs a high level of precision and may be best studied in controlled environment chambers. Similarly, there was no significant effect of eCO$_2$ on disease progress or latent period.
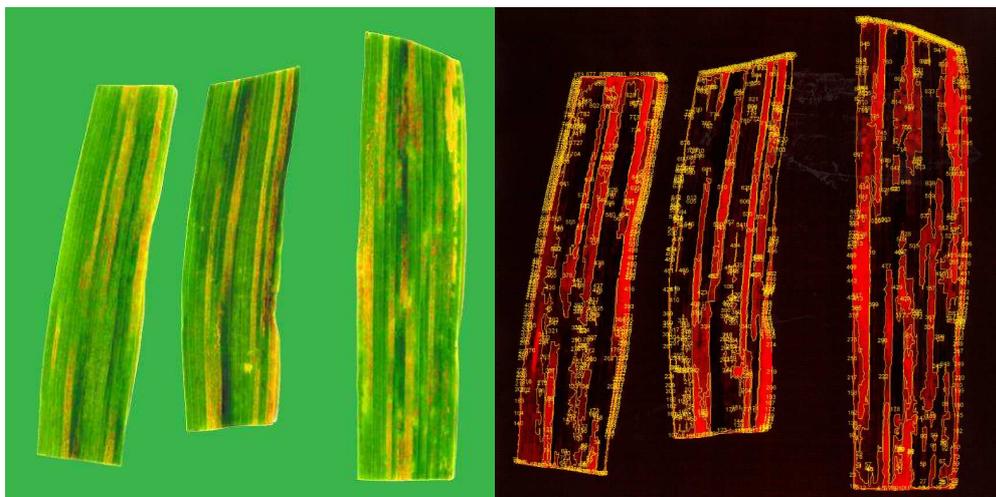


Figure 2. Wheat leaves unprocessed (left) and processed (right) using image analysis software to determine the area covered by stripe rust pustules.

### eCO$_2$ and crown rot (*Fusarium pseudograminearum*)

To determine if eCO$_2$ influenced the severity of crown rot infections in wheat, seeds from a bread wheat breeding line with partial resistance (2-49) and susceptible durum wheat (Tamaroi) were artificially inoculated with *F. pseudograminearum.* The seeds were sown into a plot under the FACE rings and the plants were monitored for disease severity and pathogen life cycle traits. Stubble and soil samples were collected to monitor pathogen survival and fitness. Fungal biomass had significantly increased in the wheat stems grown under eCO$_2$ when compared to infected wheat grown at ambient CO$_2$ in a relative comparison of fungal DNA to wheat DNA using RT quantitative PCR (Melloy et al., 2010).

### eCO$_2$, cereal yellow dwarf virus and *Rhopalosiphum padi* interactions

To determine the movement and concentration of virus particles under eCO$_2$, viruliferous and non-viruliferous colonies of *R. padi* have been established in glasshouse and growth rooms using the *Cereal yellow dwarf virus* (CYDV) RPV isolate as a model system. The aphids were transferred to the AGFACE rings to inoculate wheat plants (Yitpi variety) to determine whether eCO$_2$ changes the virus titre and rate of spread throughout the host plant. Parallel studies in closed environment chambers will complement the field studies

In conjunction with the virus studies, yellow sticky traps have been deployed in the AGFACE rings to determine if there are any changes in the vector population seasonal abundance, activity and flight times in an eCO$_2$ atmosphere compared to ambient CO$_2$. Further, understanding possible changes in transmission and acquisition efficiency of of phloem restricted CYDV by *R. padi* to plants gowned under ambient and eCO$_2$ is critical to predict disease occurrence and severity under future climate.

To investigate this, an electrical penetration graph (EPG), commonly used to study feeding behaviour of aphids and other sap-sucking insect is being used. It provides, in real time, information on aphid feeding behaviour as EPG waveforms, which can be correlated to specific feeding patterns and feeding locations (Tjallingii,1988). Measuring the time required by the aphid to reach phloem tissue and the period spent salivating in the phloem and ingesting sap will clearly indicate the potential impact of eCO$_2$ on virus transmission and acquisition. Data recorded from *R. padi* exposed to plants grown under eCO$_2$ and connected to the EPG electrode (Fig. 3) will reveal any modifications to feeding behaviour and subsequent CYDV transmission.



Figure 3. *Rhopalosiphum padi* connencted to an EPG feeding on wheat tissue.

The results generated from the AGFACE and closed environment chambers studies will be used in conjunction with other biological data to support the BYDV-*R.padi*-wheat integrated model to acurately capture the interacting effects of climate change on a crop yield. This research will assist in determining if diseases like yellow dwarf viruses, crown rot and wheat stripe rust will become an increased threat in future climates or whether they will reach

thresholds beyond which their life-cycle is limited.  This knowledge is important in assisting crop planting dates, varietal selection, disease surveillance protocols and control options.

## Modelling the impacts of climate change on plant biosecurity

Predictions of future climatic trends indicate that the nature, extent and intensity of climatic changes will vary strongly both spatially and temporally.  The response of plants, insects and pathogens to these changes is expected to be species specific and made more complex due by the degree of interaction and interdependence existing between these organisms.

A number of different modelling approaches have been described in the literature to investigate the potential distribution of plants as a result of changes in climatic conditions or their introduction outside of their native geographical range. Bioclimatic modelling approaches have been widely applied to study the potential distribution of invasive species (Baker et al., 2000; Kriticos & Randall 2001). Most of these programs use regression-based approaches to match current climatic parameters to species distribution in order to determine its climatic envelope. Because pest risk assessment and climate change applications demand that these models operate in an extrapolation mode, their performance in these applications is unlikely to yield robust reliable results.  Other approaches (e.g. CLIMEX and NAPPFAST) use a more mechanistic approach to model the species growth and survival responses to various climatic factors, and are likely to provide more reliable projections of species geographic risk. However, despite the demonstrated usefulness of climate mapping to determine species maximum limits of establishment this approach does not typically take into consideration elements such as the timing of development of organisms, specific life stages, or the size of populations, which can be important factors to estimate the threat presented by an organism to an ecosystem or agricultural industry. Furthermore they do not capture species interactions, or dispersal mechanisms, host availability and synchrony with host

Phenological models, incorporating multiple life stages and detailed life history characteristics of both insects and plants have also been widely used. However, as with climate mapping, many phenological approaches have focused on modelling one organism at a time, assuming permanent food or host availability (Steinbauer et al 2004; Gray, 2004; Yonow et al., 2004). The structure of phenological models tend to be much more complex than that of climate mapping models and their design requires availability of species-specific data such as emergence, development and death rates. This is the case for models developed in complex programming languages such as Java used by Parry et al. (2006) and FORTRAN or C++. The use of modular modelling software packages such as DYMEX, used by Yonow et al. (2004) or STELLA, used by Costanza and Voinov (2001) can help simplify model building and modification and make them more easily understood.

To determine if climate change would increase the risk of a pest threat to the Australian citrus industry, Aurambout et al., (2009) modelled factors influencing Asian citrus psyllid (*Diaphorina citri)* population variation in relation to increasing temperature, using an insect-host linked model developed in STELLA 9.01 in combination with a spatial modelling environment (SME: Maxwell, et al., 2002). In other work, the construction of multitrophic process-based population models (Stuart et al 2002; Kriticos et al., 2010) has been made feasible with the development of DYMEX.

### Modelling the interactions of *barley yellow dwarf virus*, its aphid vector, *R. padi* and wheat

There are few crop models with integrated pest and disease epidemiology modules that explore the interactions of environmental factors, let alone the spatial behaviour across regions (see Newman et al., 2003).  Such models, however, are needed to develop robust biosecurity adaptation and mitigation strategies.  In this study we focus on wheat (*Triticum aestivum*) and the bird cherry-oat aphid (*R. padi*) the vector of BYDV, an economically important cereal disease.

We are constructing a spatially explicit model that couples aphid dispersal, host-plant physiology, virus and vector population dynamics and projected climate change conditions to predict the impact on wheat yield production. Model functions are supported by empirical data of the influence of BYDV infected plants on aphid feeding behaviour, virus acquisition and transmission rates and plant physiology and growth using both growth chambers and the AGFACE resources.

*Construction of a Wheat -BYDV sub-model*

We compiled a model simulating the phenology, growth and yield of wheat based on a simplification of the O'Leary transpiration driven wheat model (O'Leary and Connor 1996; O'Leary *et al.* 1985). We incorporated O'Leary's equations into a preliminary model developed in the STELLA (Costanza and Voinov, 2001) modelling software, that allowed for the visualisation of interactions between variables. The model was then translated into the DYMEX (Maywald et al 2007) environment to allow the integration of this model with an aphid vector dispersal model and enable the evaluation of the impacts of BYDV on wheat at the landscape scale.

The model, running on a daily time-step comprised three modules: (1) soil water module, (2) wheat phenology and (3) wheat biomass-yield.. The soil water module was a one layer simplification of the O'Leary 10 layer model and considered evaporation, transpiration and drainage. The wheat phenology model made use of a direct translation of the O'Leary equations to model the wheat phenostages; emergence, stem elongation, booting, anthesis, and maturity as a function of thermal and photothermal time. The biomass module simulated daily net biomass increment and partitioning between shoot and roots, and grain as a direct function of plant transpiration The model reads daily meterological data and $CO_2$ functions were taken from CropSyst (http://bsyse.wsu.edu/cropsyst/). The crop model was validated using experimental data gathered at AGFACE Horsham site in 2007.

In order to account for the effect of BYDV on wheat growth, we developed an "infected wheat" life-cycle component, with identical phenology and soil water modules to the healthy wheat model but for which biomass accumulation was modified to simulate known and hypothesised BYDV influences on wheat growth. The transition between uninfected wheat and healthy wheat components was triggered by the presence of infected ahpids, obtained from the aphid life-cycle described below.

*Construction of the virus vector (*Rhopalosiphum padi*) lifecycle sub-model*

The model is initiated by populations of aphids building up in irrigated pastures, often some distance from wheat fields illustrated by a simplified model diagram, Figure 4. These populations begin as apterous (wingless) aphids when temperatures are cool enough to sustain a population (temperatures above 30 °C cause high mortality of *R. padi*). When densities are high enough alate (winged) nymphs form. When these alates become adults they may migrate if conditions are favourable (particularly local temperature, wind speed, physiological age and relative humidity). A spatial model that incorporates the effects of wind speed and direction is used to simulate the aphid movement across the landscape each day.

Alate exules (migrants) arrive from irrigated grassland into wheat fields at the start of the season. Once a population establishes in the wheat field the lifecycle begins, with the production of apterous nymphs. These become adults, and as the population density increases the proportion of nymphs that are alate increases. Mortality affects the population largely by the impact of high temperatures. When alate nymphs become adults they mainly 'flit' between plants or, if conditions are optimal, eg. wind speed, aphid physiological age, temperature and relative humidity, the aphid may migrate longer distances, using the same spatial modelling as the alate exule migration for the irrigated pasture to initiate the wheat population (as above).
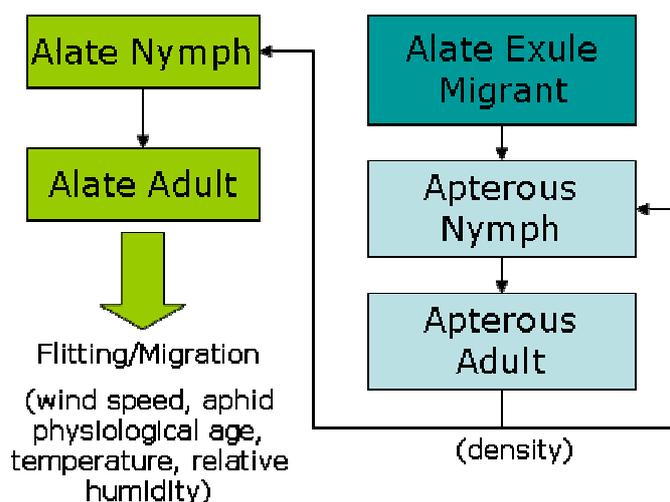
**Figure 4. Simplified conceptual diagram of the within-field aphid model**

*The integrated wheat-aphid-virus model*

The integrated wheat-aphid-virus model is being constructed in DYMEX (Maywald et al 2007). The DYMEX model was modified to better support dispersal modelling and the incorporation of spatial and spatio-temporal variables and processes.

This model operates at a regional extent, focusing on wheat growing areas of Western Australia, South Australia and Victoria initially. The model scale is a 5km grid, with the area of wheat and irrigated grassland contained within each grid cell assigned as a value to the grid cell. An estimated area of roadside grassland will also be assigned to each cell, as this can harbour aphids, acting as a 'green bridge' for migrants from the irrigated pasture at the start of the season.

The integrated model consisted of two main components: an aphid life-cycle and a wheat life-cycle, which run as a set of parallel lifecycles, one per model gridcell. The lifecycles only interact through dispersal, and life processes (growth, development and reproduction and user-defined processes) are all driven by either global variables (e.g., $[CO_2]$, or spatially- or spatio-temporally-explicit variables. For example, the aphids can respond to the availability of environmental variables that allow them to persist in favourable habitats such as irrigated perennial ryegrass pastures over summer. As temperatures fall, they respond to cues to start producing alate nymphs. The resulting alate adults then fly on prevailing winds when they are suitable for dispersal.

A set of planting rules was used to cue the initialisation of the wheat lifecycle. If the aphids arrive in a cell and wheat plants are present, then the wheat is colonised, and if the aphids are infected with the virus, they can transmit the virus to the wheat plants. The impact of the virus on wheat yield then depends upon the phenostage at which it is infected, and the time course of growing conditions, and the $[CO_2]$ value. The subsequent results of the modelled impact of BYDV on wheat yield under future climates will be published separate to this paper.

Due to the number and diversity of plants, insects and pathogens it is difficult to empirically evaluate the true extent of each species' response in a generic construct. Each pathogen or insect's response is not only inexplicably tied to its host but it is also modulated by evolutionary processes where adaptation to changes in the host and changes its environment will occur. Nonetheless the continued improvement of computer models, based on theoretically, or empirically established rules will improve our understanding of these processes and assist in measuring general trends for future plant biosecurity planning. Most importantly there is a critical need to continue to monitor biological changes to crops and their pest and pathogen species in order to develop these models.

# References

Anderson, PK, Cunningham, AA, Patel, NG, Morales, FJ, Epstein, PR and Daszak, P. (2004) Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *TRENDS in Ecology and Evolution* 19, 535-544.

Aurambout, J-P., Finlay, K, Luck, J, Beattie, A. (2009) A concept model to estimate the potential distribution of the Asiatic citrus psyllid (*Diaphorina citri* Kuwayama) in Australia under climate change-A means for assessing biosecurity risk *Ecological modelling*220, 2512–2524

Awmack, CS, Harrington, R and Leather, SR. (1997) Host plant effects on the performance of the aphid Aulacorthum solani (Kalt.) (Homoptera: Aphididae) at ambient and elevated $CO_2$. *Global Change Biology* 3, 545-549.

Baker, R.H.A., Sansford, C.E., Jarvis, C.H., Cannon, R.J.C., MacLeod, A., Walters, K.F.A. (2000). The role of climatic mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. *Agric.Ecosyst. Environ*. 82, 57–71.

Berry, PM, Dawson, TP, Harrison, PA and Pearson, RG. (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography* 11, 453-462.

Cannon, RJC. (1998) The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology* 4, 785-796.

Chakraborty, S and Datta, S. (2003) How will plant pathogens adapt to host plant resistance at elevated $CO_2$ under changing climate? *New Pathologist* 159, 733-742.

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,** No 54, 15 pp.

Chakraborty, S, Tiedemann, AV and Teng, PS. (2000) Climate change: potential impact on plant diseases. *Environmental Pollution* 108, 317-326.

Coakley, SM, Scherm, H and Chakraborty, S. (1999) Climate change and plant disease management. *Annual Review of Phytopathology* 37, 399-426.

Costanza, R. and Voinov, A., (2001). Modeling ecological and economic systems with STELLA: part III. *Ecol. Model.* 143, 1–7.

Fuhrer, J. (2003) Agroecosystem response to combinations of elevated $CO_2$, ozone, and global climate change. *Agricultural, Ecosystems and Environment* 97, 1-20.

Gray, D.R., 2004. The gypsy moth life stage model: landscape-wide estimates of gypsy moth establishment using a multi-generational phenology model. Ecol. Model. 176, 155–171.

Hannon, B and Ruth, M. (1997). *Modeling Dynamic Biological Systems*, New York.

Heagle, AS, Burns, JC, Fisher, DS and Miller, JE. (2002) Effects of carbon dioxide enrichment on leaf chemistry and reproduction by twospotted spider mites (Acari: Tetrachynidae) on white clover. *Environmental Entomology* 31, 394-601.

Jones, TH, Bezemer, TM, Knight, KJ, Newington, JE and Thompson, LJ. (1998) The effect of elevated atmospheric carbon dioxide on aphids and Collembola: an Ecotron experiment. In: *Brighton Crop Protection Conference: Pests and Diseases* 973-978. British Crop Protection Council,Farnham, UK, Brighton, UK.

Kriticos, DJ & Randall, RP. (2001). A comparison of systems to analyse potential weed distributions. In: *Weed Risk Assessment* (eds RH Groves, FD Panetta & JG Virtue) 61-79. CSIRO Publishing, Melbourne, Australia.

Kriticos, DJ, Brown, JR and Maywald, GF (2003) SPAnDX: a process-based population dynamics model to explore management and climate change impacts on an invasive alien plant, *Acacia nilotica*. *Ecological Modelling* **163**, 187-208.

Lincoln, DE, Fajer, ED and Johnson, RH. (1993) Plant insect herbivore interactions in elevated $CO_2$ environments. *Trends in Ecology and Evolution* 8, 64-68.

Malmstrom, CM and Field, CB. (1997) Virus-induced differences in the response of oat plants to elevated carbon dioxide. *Plant, Cell and Environment* 20, 178-188.

Manning, W and von Tiedemann, A. (1995) Climate change: potential effects of increased atmospheric carbon dioxide (CO2), ozone (O3), and ultraviolet-B (UV-B) radiation on plant diseases. *Environmental Pollution* 88, 219-245.

Matros, A, Amme, S, Kettig, B, Buck-Sorlin, GH, Sonnewald, U and Mock, HP. (2006) Growth at elevated $CO_2$ concentrations leads to modified profiles of secondary metabolites in tobacco cv. SamsunNN and to increased resistance against infection with potato virus Y. *Plant, Cell and Environment* 29, 126-137.

Maxwell, T, Villa, F and Costanza, R. (2002) The Spatial Modeling Environment. International Institute for Ecological Economics, Center for Environmental Science, University of Maryland System, Solomons, MD.

Maywald, GF, Kriticos, DJ, Sutherst, RW & Bottomley, W. (2007) *Dymex Model Builder Version 3: User's Guide*, Hearne Publishing, Melbourne.

Melloy P, Hollaway GJ, Luck J, Norton R, Aitken E, Chakraborty S (2010) Production and fitness of *Fusarium pseudograminearum* inoculum at elevated $CO_2$ in FACE. *Global Change Biology* doi: 10.1111/j.1365-2486.2010.02178.x

Mollah M, RM Norton, JE Huzzey (2009) National Free-Air $CO_2$ Enrichment facility at Horsham Australia for grain crops: design and performance *Crop and Pasture Science*, 60 (8), 697-707.

Mitchell, CE, Reich, PB, Tilman, D and Groth, JV. (2003) Effects of elevated $CO_2$, nitrogen deposition, and decreased species diversity on foliar fungal plant disease. *Global Change Biology* 9, 438-451.

Newman, JA, Gibson, DJ, Parsons, AJ & Thornley, JHM. (2003) How predictable are aphid population responses to elevated $CO_2$. *Journal of Animal Ecology* 72, 556-566.

O'Leary, GJ, Connor, DJ and White DH (1985) A simulation model of the development, growth and yield of the wheat crop. *Agricultural Systems* 17, 1-26.

O'Leary, GJ and Connor, DJ. (1996) A simulation model of the wheat crop in response to water and nitrogen supply: II Model validation. *Agricultural Systems* 52, 31-55.

Pangga, IB, Chakraborty, S and Yates, D. (2004) Canopy size and induced resistance in Stylosanthes scabra determine anthracnose severity at high CO2. *Phytopathology* 94, 221-227.

Parker, IM and Gilbert, GS. (2004) The evolutionary ecology of novel plant-pathogen interactions. *Annual Review of Ecology, Evolution, and Systematics* 35, 675-700.

Parry, H.R., Evans, A., Morgan, D., (2006). Aphid population response to agricultural landscape change: a spatially explicit, individual-based model. *Ecol. Model.* 199, 425–463.

Pimentel, D, Lach, L, Zuniga, R and Morrison, D. (2000) Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50, 53-65.

Pimentel, D, McNair, S, Janecka, J, et al. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment* 84, 1-20.

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

Rosenzweig, C, Iglesias, A, Yang, XB, Epstein, PR and Chivian, E. (2001). Climate change and US agriculture: the impact of warming and extreme weather events on productivity, plant diseases, and pests.  pp.46. Center for health and the global environment. Harvard Medical School, Boston, MA.

Roy, KW, Rupe, JC, Hershman, DE and Abney, TS. (1997) Sudden death syndrome of soybean. *Plant Disease* 81, 1100-1111.

Steinbauer, MJ, Kriticos, DJ, Lukacs, Z & Clarke, AR. (2004) Increased voltinism can promote outbreaks of endemic species in resource abundant systems. *Forest Ecology and Management* 198, 117-131.

Stuart, RM, Kriticos, DJ & Ash, JE. (2002). Modelling the biological control of bitou bush (*Chrysanthemoides monilifera*: Asteraceae) by Mesoclanis polana.  (eds H Spafford-Jacobs, J Dodd & JH Moore) 591-594. Plant Protection Society of WA.

Kriticos, DJ, Watt, MS, Withers, TM, Leriche, A & Watson, M. (2010) A process-based population dynamics model to explore target and non-target impacts of a biological control agent. *Ecological Modelling* 220.

Tjallingii WF. (1988). Electrical recording of stylet penetration activities. In: Aphids: their biology, natural enemies and control. Ed. by A K Minks and P Harrewijn, Elsevier, 95-108.

Whittaker, J. (1999) Impacts and responses at population level of herbivorous insects to elevated $CO_2$. *European Journal of Entomology* 96, 149-156.

Yonow, T., Zalucki, M.P., Sutherst, R.W., Dominiak, B.C., Maywald, G.F., Maelzer, D.A.,Kriticos, D.J., (2004). Modelling the population dynamics of the Queensland fruit fly, *Bactrocera (Dacus) tryoni*: a cohort-based approach incorporating the effects of weather. *Ecol. Model.* 173, 9–30.