

Response of Wheat Fungal Diseases to Elevated Atmospheric CO₂ Level

S. BENCZE*, G. VIDA, K. BALLA, E. VARGA-LÁSZLÓ and O. VEISZ

Cereal Resistance Breeding Department, Agricultural Institute, Centre for Agricultural Research,
Hungarian Academy of Sciences, Brunszvik u. 2, H-2462 Martonvásár, Hungary

(Received 20 June 2012; accepted 25 October 2012;
Communicated by H. Bűrstmayr)

Infection with fungal pathogens on wheat varieties with different levels of resistance was tested at ambient (NC, 390 ppm) and elevated (EC, 750 ppm) atmospheric CO₂ levels in the phytotron. EC was found to affect many aspects of the plant–pathogen interaction. Infection with most fungal diseases was usually found to be promoted by elevated CO₂ level in susceptible varieties. Powdery mildew, leaf rust and stem rust produced more severe symptoms on plants of susceptible varieties, while resistant varieties were not infected even at EC. The penetration of *Fusarium* head blight (FHB) into the spike was delayed by EC in Mv Mambo, while it was unaffected in Mv Regiment and stimulated in Mv Emma. EC increased the propagation of FHB in Mv Mambo and Mv Emma. Enhanced resistance to the spread of *Fusarium* within the plant was only found in Mv Regiment, which has good resistance to penetration but poor resistance to the spread of FHB at NC. FHB infection was more severe at EC in two varieties, while the plants of Mv Regiment, which has the best field resistance at NC, did not exhibit a higher infection level at EC.

The above results suggest that breeding for new resistant varieties will remain a useful means of preventing more severe infection in a future with higher atmospheric CO₂ levels.

Keywords: *Triticum aestivum*, elevated CO₂, powdery mildew, leaf rust, stem rust, *Fusarium culmorum*

Introduction

The disease resistance of plants is influenced by a variety of environmental factors. Over the last 200 years, the global ecosystem has been exposed to an accelerating rate of change as a consequence of human activity. The rise in the CO₂ level is thought to play a major role in global climate change. High atmospheric CO₂ levels affect the metabolism, physiology and development of the plant; which, in turn, has an impact on pathogen invasion and disease progress. Although the impact of elevated CO₂ level on plants is well known, much less attention has been paid to the interaction between plants and diseases (Newton et al. 2011; Pangga et al. 2011).

* Corresponding author; E-mail: bencze.szilvia@agrar.mta.hu

In previous work, the following general tendencies have been reported in response to high CO₂ levels (based on reviews by Manning and von Tiedemann 1995; Chakraborty et al. 1998; Coakley et al. 1999; Chakraborty and Datta 2003; Chakraborty et al. 2008):

- (i) The change in microclimate resulting from increased leaf mass and biomass may enhance the risk of infection by most microorganisms. An increase in the root mass may affect root pathogens, parasites and symbiotic interactions in the soil. Greater plant biomass may increase the amount of residues in the soil, which could favour necrotrophic organisms and promote the over-wintering of pathogens and pests;
- (ii) The greater assimilation of carbon may result in a change in the carbon to nitrogen ratio in plant tissues, and lower N content may influence the extent of damage caused by certain plant pathogens (McElrone et al. 2005). Higher carbohydrate concentration within the host tissue promotes the development of certain biotrophic pathogens such as rusts (Gassner and Straib 1930), although increased silicon accumulation may inhibit others, such as mildews, due either to the higher proportion of conidia being arrested at the appressorial stage or to the slower development of the fungus (Hibberd et al. 1996a);
- (iii) Partial stomatal closure due to high CO₂ concentration may hinder the entry of pathogens that germinate through the stomata and enter with the air flow (Royle and Thomas 1971; Ramos and Violin 1987), while lower humidity on the leaf surface may also delay pathogen invasion (Eastburn et al. 2011);
- (iv) Infection by powdery mildew accelerated the decline in the net photosynthesis of leaves (Hibberd et al. 1996b). A faster rate of phenological development and earlier maturation might favour necrotrophic over biotrophic organisms.

Earlier research revealed increased pathogen fecundity in plant species other than cereals in the case of bacterial, viral and fungal diseases (e.g. Chakraborty and Datta 2003), but this idea is not always supported by the latest findings (Eastburn et al. 2011; Pangga et al. 2011). Disease severity is determined on the one hand by enhanced host resistance, which slows pathogen penetration and on the other by an enlarged plant canopy, which offers more infection sites and affects the microclimate. In the long run, higher pathogen fecundity, inoculum trapping by an enlarged plant canopy, and a higher number of infection cycles all interact with the effects of enhanced host resistance to determine host-pathogen adaptation (Chakraborty et al. 2008).

An increase in protective compounds at elevated CO₂ level may reduce infection success (McElrone 2005), although reduced or unchanged protection was also reported in response to CO₂ enrichment (Eastburn et al. 2011). The trichome density of *Brassica rapa* leaves increased by 57% under elevated CO₂ and the level of phenolics was also higher (Karowe and Grubb 2011). In addition, constitutive phenolic levels were positively correlated with the leaf C:N ratio. Investigations on powdery mildew in wheat proved that the host nitrogen content was lower at elevated CO₂, resulting in a lower rate of infection; however, when the tissue water content was higher, the disease was more severe

(Thompson et al. 1993). The aggressiveness of *Erysiphe cichoracearum* in *Arabidopsis* was, however, found to increase at elevated CO₂, as the pathogen induced morphological changes in later-formed leaves of the host plants, thus promoting the propagation of the disease (Lake and Wade 2009).

Increased plant growth rate may increase the progression of the pathogen in the canopy (Eastburn et al. 2011), thus affecting epidemiological and evolutionary perspectives (Pangga et al. 2011). This raises important questions regarding the sustainability of agricultural production and future challenges for breeding (Gregory et al. 2009).

Although several plant species and pathogens have been investigated in previous research, there is still a lack of information on the performance of most cereal diseases in response to high CO₂ concentration. The aim of the present work was to test the impact of atmospheric CO₂ enrichment on the resistance of winter wheat varieties to fungal pathogens in terms of the emergence of the symptoms and disease progress. Wheat varieties with different levels of disease resistance were chosen for tests on the variation in their responses.

Materials and Methods

Vernalized seedlings of three Hungarian winter wheat varieties (Mv Regiment, Mv Emma and Mv Mambo) were planted in pots (four plants in each 3L pot, eight pots per variety and per disease treatment) and grown in Conviron PGV-36 growth chambers either at ambient (NC, 390 ppm) or elevated (EC, 750 ppm) CO₂ levels. The plants were watered daily and supplied with nutrients in tap-water (3 dL/pot) twice a week, in the form of 0.33 g/L nutrient solution (Volldünger Linz Classic, Gartenhilfe GmbH., Austria) containing 3.3 mM N, 0.163 mM P, 0.736 mM K, 0.082 mM Mg and 0.033% microelements (B, Cu, Mn, Fe, Zn). The temperature regime changed weekly according to the T2-Ny2 (Spring 2–Summer 2) climatic programme (Tischner et al. 1997) beginning with a min/max of 10/12°C during the first week and increasing until it reached 16/20°C, before the period of infection. The maximum photosynthetic photon flux density also increased gradually from 280 to 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Tischner et al. 1997). To prevent powdery mildew infection, chemical control with elemental sulphur was applied three times during the period preceding the treatments. In the other group of plants, where no sulphur treatment was applied, the disease symptoms of spontaneously occurring powdery mildew (*Blumeria graminis*, PM) infection were evaluated using a 0–9 scale (Saari and Prescott 1975 cit. Stubbs et al. 1986) around weeks four and six after planting.

To test resistance to leaf rust (LR, *Puccinia triticina*), stem rust (SR, *Puccinia graminis*) and Fusarium head blight (FHB, *Fusarium culmorum*) the plants were artificially inoculated as follows:

For the rust pathogens, the washed and wiped, still damp surfaces of a single fully expanded flag-leaf on each plant were inoculated with uredospores suspended in tap water (2.7 million mL⁻¹ for LR, 0.9 million mL⁻¹ for SR) using a brush. For FHB, two kinds of tests were performed either to examine resistance to fungal spread from an inoculated spikelet (Type II resistance, Schroeder and Christensen 1963) or to test combined resistance to penetration and spread of the pathogen (Type I+II resistance, Schroeder and

Christensen 1963). In the case of single floret inoculation, one spikelet (usually the 6th–8th from the top of each spike, but the 10th in Mv Emma) was injected with a pipette at anthesis with 5 µl inoculum (50,000 conidia mL⁻¹), while in the latter type of infection a suspension of *F. culmorum* spores (50,000 conidia mL⁻¹) was spread along the entire surface of each spike using a brush. In all cases of artificial infection with either disease, the inoculated plant parts were covered with a plastic bag for 72 hours to provoke successful establishment of the pathogen.

The disease progress of LR, SR and FHB was monitored till the start of maturation and the area under the disease progress curve (AUDPC) was calculated accordingly (Campbell and Madden 1990). The results were evaluated with the Mann–Whitney test (SPSS 16.0).

Results

Powdery mildew

Powdery mildew appeared spontaneously on the susceptible varieties (Mv Mambo and Mv Emma) both of which had significantly higher levels of infection at both evaluation dates as a result of elevated CO₂ level (Table 1). In the resistant variety Mv Regiment, however, there were no infected plants even at the high CO₂ level.

Table 1. Effect of CO₂ level (normal, NC, elevated, EC) on powdery mildew severity in susceptible wheat varieties

Powdery mildew	Infected plants/total	Mean scale value	
		Evaluation 1	Evaluation 2
Mv Emma NC	17/32	0.41	0.73
Mv Emma EC	29/32	3.11	3.00
Asymp. Sig. (2-tailed)*		0.000	0.000
Mv Mambo NC	31/32	0.92	2.03
Mv Mambo EC	32/32	2.48	2.70
Asymp. Sig. (2-tailed)*		0.000	0.003

* Mann–Whitney test

Leaf rust

Elevated CO₂ concentration resulted in greatly enhanced severity of leaf rust in Mv Regiment (Table 2). Although both Mv Regiment and Mv Emma were found to be susceptible to LR in artificially inoculated field nursery tests (with 100% and 80% infection of the foliage, respectively, based on the modified Cobb's scale; Peterson et al. 1948), under the present conditions Mv Emma was not infected at ambient CO₂ and was only slightly infected at high CO₂. The difference was, however, significant. In the resistant variety, Mv Mambo, there was no change due to high CO₂, as no infection was detected at either level.

Table 2. Effect of CO₂ level (normal, NC, elevated, EC) on leaf rust severity in susceptible wheat varieties

Leaf rust	Infected plants/total	Mean number of pustules leaf ⁻¹			AUDPC**
		Day 7	Day 14	Day 21	
Mv Regiment NC	31/32	0.03	1.66	15.69	69.0
Mv Regiment EC	32/32	0.65	9.65	35.96	197.9
Asymp. Sig. (2-tailed)*		0.004	0.000	0.000	0.000
Mv Emma NC	0/32	0	0	0	–
Mv Emma EC	9/32	1.0	3.5	6.7	–
Asymp. Sig. (2-tailed)*		0.078	0.006	0.001	–

* Mann–Whitney test

** Calculated from data for days 0 (equivalent to 0) to 21 after inoculation.

Stem rust

Stem rust severity in the susceptible variety (Mv Emma, 80% in artificially inoculated field nursery tests) was also higher at elevated CO₂ (Table 3), but did not change significantly in the more resistant genotype (Mv Regiment, 10% infection). In Mv Mambo, which is resistant to SR, no disease symptoms were observed at either CO₂ level.

Table 3. Effect of CO₂ level (normal, NC, elevated, EC) on stem rust severity in susceptible wheat varieties

Stem rust	Infected plants/total	Mean number of pustules leaf ⁻¹		
		Day 7	Day 14	AUDPC**
Mv Regiment NC	20/32	0.88	2.19	13.8
Mv Regiment EC	16/31	0.29	1.87	8.6
Asymp. Sig. (2-tailed)*		0.063	0.423	0.295
Mv Emma NC	9/16	4.31	6.31	52.3
Mv Emma EC	13/16	92.81	138.00	1132.7
Asymp. Sig. (2-tailed)*		0.013	0.009	0.010

* Mann–Whitney test

** Calculated from data for days 0 (equivalent to 0) to 14 after inoculation.

Resistance to the spread of FHB along the spike

Mv Regiment was the most susceptible variety to the spread of *Fusarium* at ambient CO₂ (Fig. 1), while at elevated CO₂, FHB spread was significantly reduced from day 18 onwards following inoculation ($p = 0.002$), compared to the rate at ambient CO₂. There was no significant change in FHB severity in Mv Mambo in response to elevated CO₂. In Mv Emma, however, the establishment of *Fusarium* was significantly delayed at high CO₂ level ($p = 0.024$ and 0.060 on days 7 and 11, respectively), but later no difference could be seen in the number of infected spikelets, and the disease became even more severe at high CO₂ than at the ambient level by day 21 ($p = 0.073$). It should be noted that FHB exhibited a general tendency to become more aggressive from day 18 to 21 in all the varieties, de-

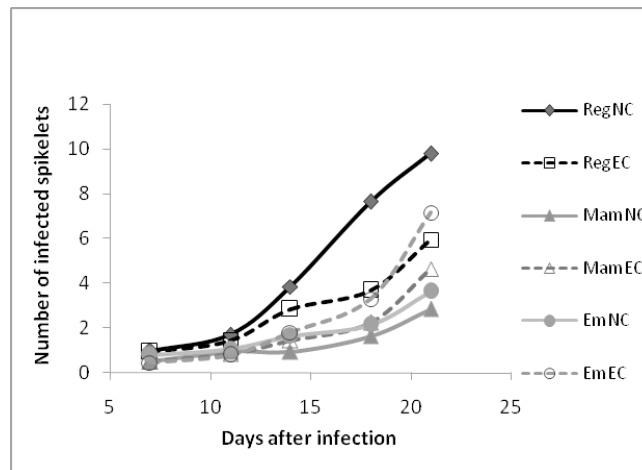


Figure 1. Fusarium head blight infection on the spikes of winter wheat varieties at normal (NC) and elevated (EC) CO₂ levels. Single floret inoculation. Reg = Mv Regiment, Mam = Mv Mambo, Em = Mv Emma

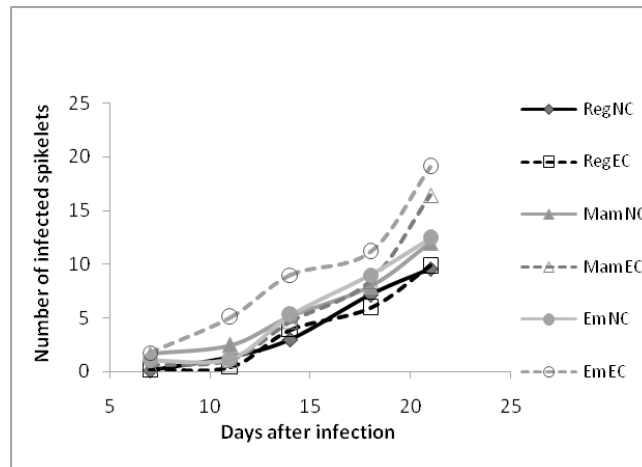


Figure 2. Fusarium head blight infection on the spikes of winter wheat varieties at normal (NC) and elevated (EC) CO₂ levels. Whole spike inoculation (For abbreviations see Fig. 1)

spite the fact that inoculation was performed on different dates in each variety (but at the same phenological stage).

Combined resistance to the penetration and spread of FHB

Fusarium inoculation of the whole spike revealed variety- and phase-specific reactions (Fig. 2). Usually several spikelets in a spike became infected at the same time. The pene-

tration of *Fusarium* was delayed in Mv Mambo at elevated CO₂; FHB severity was still lower on days 7 and 11 than at the ambient level ($p = 0.043$ and 0.015 , respectively). After successful establishment, however, the pathogen spread faster through the rachis, resulting in a higher infection rate at high CO₂ by the third week ($p = 0.053$). In Mv Emma, *Fusarium* infection was more severe at elevated CO₂ on all sampling dates (significantly on days 11 and 21). CO₂ enrichment had no influence on FHB severity in Mv Regiment at any time. This variety exhibited the lowest rate of infection when whole spike surfaces were inoculated while it was highly susceptible to fungal spread in the case of single floret inoculation.

Discussion

In the susceptible varieties, powdery mildew caused a considerably higher rate of infection in response to CO₂ enrichment, in accordance with the work of Lake and Wade (2009), who reported 40% more established colonies of another mildew species, *Erysiphe cichoracearum*, in *Arabidopsis* due to EC. Hibberd et al. (1996a) found partly similar results; if PM was successful in forming colonies on barley leaves, it spread rapidly due to the greater accumulation of carbohydrates in the host plant at high CO₂ level. It was observed, however, that although the number of conidia germinating on the leaf surface was the same at normal and doubled CO₂ level, there was a substantial decline in the number of conidia capable of forming colonies at high CO₂ level. The inhibition of the pathogen could be attributed to the intensified photosynthesis, which resulted in the accumulation of protective compounds and structures (e.g. papillae, silicon) at the site of pathogen invasion. An apparently contrasting result was also found in wheat; high CO₂ level resulted in significantly reduced tissue N contents, which caused less severe infection with PM (Thompson et al. 1993). This apparent contradiction could be due to the fact that in the latter experiment either the conidia were incapable of forming colonies at high CO₂ (as was described by Hibberd et al. 1996a) and/or the tissue nitrogen content dropped so much that it was far below the optimum required to support the spread of the fungus. McElrone et al. (2005) also reported reduced nutritive quality and increased amount of protective compounds in *Acer* leaves at EC as a possible cause for reduced disease severity. The above findings suggest that a higher level of infection can only be expected at EC when the plants have a better nutrient supply, capable of counteracting, at least to some extent, the dilution of the plant nutrient content caused by EC.

As the plants in the present study became infected spontaneously during a very early stage of development, before they were fully adapted to the elevated CO₂ level, there may have been little difference in the extent of penetration in plants at the ambient and high CO₂ levels. This hypothesis will require further investigation. It was proved, however, that the resistant variety was unaffected by high CO₂, as no PM infection was detected even at EC. These findings contradict those reported for *Arabidopsis* by Lake and Wade (2009), who suggested that resistant ecotypes may become more susceptible to infection under EC.

The present experiment also revealed increased fecundity for leaf rust and stem rust, though there were certain differences between the two susceptible wheat varieties. A higher density of leaf rust pustules was observed on the leaves of the very susceptible variety at high CO₂, while the less susceptible variety was not infected at ambient CO₂ but became slightly infected at elevated CO₂ level. Stem rust was considerably more severe in the susceptible variety in response to CO₂ enrichment, but there was no significant change in the more tolerant variety. In both rust species, the resistant variety remained resistant even at high CO₂ concentration. This suggests that breeding for new resistant varieties will remain a useful means to prevent more severe infection in a future with higher atmospheric CO₂ levels.

As little information has been published so far on the effect of elevated CO₂ level on rust species it is difficult to make a relevant comparison. In early works, high CO₂ concentration was only applied after inoculation, so these results may have limited general applicability, despite the fact that enhanced infection rates were found for various cereal species (Gassner and Straib 1930; Volk 1931). Later work reported results different from the present findings; e.g. EC was found to have no effect on rust infection in tree species (Eastburn et al. 2011). The incidence of other diseases in trees was also reduced at EC, e.g. *Phyllosticta minima* in *Acer* (McElrone et al. 2005), nor was any change reported in the uredospore production per unit lesion area or in the disease progress of *Puccinia striiformis* (stripe rust) in FACE experiments (preliminary results, Chakraborty et al. 2010).

In the present work the penetration phase of infection and the latent period were not investigated, so no data are available on whether there was any difference in these factors due to CO₂ enrichment. For *Fusarium* head blight, however, the penetration of the fungus and the progress in the rachis was studied separately by applying specific inoculation methods.

In the case of Mv Mambo, the penetration of *Fusarium* was delayed at high CO₂, but following establishment, the spread of the disease was even faster than at NC. This was very similar to the situation with PM in barley, described by Hibberd et al. (1996a). This suggests that the pathogen adapts to the circumstances in plants grown at elevated CO₂. Another feature suggesting some kind of adaptation to the host conditions was that aggressiveness increased (the spread of FHB was accelerated) by the third week after inoculation, irrespective of the CO₂ level. In the most susceptible variety, Mv Emma, no delay was observed and FHB was more severe at elevated CO₂ at all the dates. In Mv Regiment, which was the least susceptible variety, a similar rate of infection was observed at both ambient and elevated CO₂ levels. The variation found here between wheat varieties was in accordance with previous results reported by Melloy et al. (2010) on *Fusarium pseudo-graminearum*, which causes wheat crown rot. These authors found increased fungal biomass and/or increased stem browning in response to EC in some situations, which exhibited variety dependence.

When the inoculum was injected directly into the spikelet to test the spread of *Fusarium* (single floret inoculation), no difference was observed between plants grown at different CO₂ levels in Mv Mambo, while in Mv Emma, despite the initial delay in the appearance

of the disease symptoms, the disease became more severe at EC. Increased resistance was detected, however, in the third variety (Mv Regiment), which had the poorest resistance to fungal spread at ambient CO₂. This may have been due to structural changes or protective compounds, and needs further investigation.

Other research done on maize suggested that *Fusarium* ear infection might be reduced at 550 ppm CO₂, as the DON (deoxynivalenol) concentrations detected in maize kernels in one year of the experiment (2007) were significantly reduced compared to those recorded at 380 ppm CO₂ (Oldenburg et al. 2009). However, the infection was very low, so no visible differences in the symptoms could be detected between the CO₂ levels. These results contradict those found in the present work on wheat. Although elevated CO₂ level delayed the establishment of FHB in some cases, after a time the disease generally became more severe at high CO₂. In one variety, Mv Regiment, however, no visible difference in *Fusarium* infection was detected, as in the work of Oldenburg et al. (2009). The present results underline the importance of differences between varieties, originating from either their different genetic backgrounds, and/or the type of resistance or the level of susceptibility.

The present study provided practical answers to the question of how elevated atmospheric CO₂ level affects the onset and severity of several fungal diseases in wheat (for summary see Table 4). The process of pathogen invasion was studied for *Fusarium culmorum*. The results showed that elevated CO₂ level caused a delay (Mv Mambo), had no effect (Mv Regiment) or promoted (Mv Emma) the penetration of *Fusarium*. This was in accordance with previous work, where the penetration of pathogens and/or the process of the infection was found to be delayed in some but not all cases (Coakley et al. 1999; McElrone et al. 2005; Eastburn et al. 2011). In both biotrophic and necrotrophic organisms, significant changes were reported in the onset and duration of the stages in the patho-

Table 4. Summary of changes in wheat diseases in response to elevated CO₂

	Powdery mildew	Leaf rust	Stem rust	Penetration of <i>Fusarium</i>	Rate of spread of <i>Fusarium</i>	Severity of <i>Fusarium</i> infection WSI	Severity of <i>Fusarium</i> infection SFI
Ambient CO ₂							
Mv Mambo	+	0	0	++	+	++	+
Mv Emma	+	0	+	++	+	++	+
Mv Regiment	0	+	+	+	+++	+	+++
Elevated CO ₂							
Mv Mambo	++*	0	0	+	++*	+++*	+
Mv Emma	++*	+	++*	+++*	++*	+++*	++*
Mv Regiment	0	++*	+	+	++*	+	++*

WSI – whole spike inoculation

SFI – single floret inoculation

0 – no symptoms visible

+, ++, +++ – degree of relative severity of disease symptoms

* – significant difference between CO₂ levels

gen life cycle under elevated CO₂. The latent period, the time between inoculation and sporulation, was sometimes longer at high CO₂ (Chakraborty et al. 1998). The present resistance tests performed by direct inoculation of single florets also pointed to a longer latent period in one variety, Mv Emma, before *Fusarium* symptoms became visible.

Evidence was also given here that the disease severity and/or reproductive success of most wheat fungal species increased at EC; powdery mildew, leaf rust and stem rust were significantly more severe on the leaves of plants in the susceptible varieties. High CO₂ level also increased the propagation of *Fusarium* in two varieties (Mv Mambo and Mv Emma, whole spike inoculation). Only Mv Regiment had increased resistance to the spread of the fungus at EC. This variety, which had the lowest infection rate at both CO₂ levels, proved to be the most resistant of all the varieties, when the pathogen had to invade the plant tissues itself.

Although the diseases were usually more severe in susceptible varieties at elevated CO₂, resistant varieties remained resistant even under these conditions. These findings provide important evidence that resistance traits will still be useful in the future when developing new resistant varieties adapted to higher atmospheric CO₂ conditions. However, further research will be needed to achieve a better understanding of the processes taking place during penetration and in the early phase of infection.

Acknowledgements

This research was supported by the projects TÁMOP-4.2.2.b-10/1-2010-0025 and TÁMOP-4.2.2.A-11/1KONV-2012-0064 and the grant OTKA K-105949 from the National Scientific Research Fund.

References

- Campbell, C.L., Madden, L.V. 1990. Introduction to Plant Disease Epidemiology. John Wiley & Sons, New York, USA, 532 pp.
- Chakraborty, S., Murray, G.M., Magarey, P.A., Yonow, T., O'Brien, R.G., Croft, B.J., Barbetti, M.J., Sivasithamparam, K., Old, K.M., Dudzinski, M.J., Sutherst, R.W., Penrose, L.J., Archer, C., Emmett, R.W. 1998. Potential impact of climate change on plant diseases of economic significance to Australia. *Australasian Plant Pathology* **27**:15–35.
- Chakraborty, S., Datta, S. 2003. How will plant pathogens adapt to host plant resistance at elevated CO₂ under a changing climate? *New Phytology* **159**:733–742.
- Chakraborty, S., Luck, J., Hollaway, G., Freeman, A., Norton, R., Garrett, K.A., Percy, K., Hopkins, A., Davis, C., Karnosky, D.F. 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.
- Chakraborty, S., Luck, J., Hollaway, G., Fitzgerald, G., White, N. 2010. Rust-proofing wheat for changing climate. BGR Workshop, May 30–31 2010. Saint Petersburg, Russia. url: <http://www.globalrust.org/db/attachments/about/19/15/09-chakraborty%20BGR1%20talk.pdf>
- Coakley, S.M., Scherm, H., Chakraborty, S. 1999. Climate change and plant disease Management. *Annu. Rev. Phytopathol.* **37**:399–426.
- Eastburn, D.M., McElrone, A.J., Bilgin, D.D. 2011. Influence of atmospheric and climatic change on plant–pathogen interactions. *Plant Pathol.* **60**:54–69.

- Gassner, G., Straib, W. 1930. Untersuchungen über die Abhängigkeit des Infektionsverhaltens der Getreiderostpilze vom Kohlensäuregehalt der Luft (Investigations on the dependence of the delay of cereal rust infection on the CO₂ content of the air). *J. Phytopathol.* **1**:1–30. (in German)
- Gregory, P.J., Johnson, S.N., Newton, A.C., Ingram, J.S.I. 2009. Integrating pests and pathogens into the climate change/food security debate. *J. Exp. Bot.* **60**:2827–2838.
- Hibberd, J.M., Whitbread, R., Farrar, J.F. 1996a. Effect of elevated concentrations of CO₂ on infection of barley by *Erysiphe graminis*. *Physiol. of Mol. Plant Pathol.* **48**:37–53.
- Hibberd, J.M., Whitbread, R., Farrar, J.F. 1996b. Effect of 700 µmol per mol CO₂ and infection of powdery mildew on the growth and partitioning of barley. *New Phytologist* **134**:309–345.
- Karowe, D.N., Grubb, C. 2011. Elevated CO₂ increases constitutive phenolics and trichomes, but decreases inducibility of phenolics in *Brassica rapa* (Brassicaceae). *J. Chemical Ecol.* **37**:1332–1340.
- Lake, J.A., Wade, R.N. 2009. Plant–pathogen interactions and elevated CO₂: Morphological changes in favour of pathogens. *J. Exp. Bot.* **60**:3123–3131.
- Manning, W.J., 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* **8**:219–245.
- McElrone, A.J., Reid, C.D., Hoye, K.A., Hart, E., Jackson, R.B. 2005. Elevated CO₂ reduces disease incidence and severity of a red maple fungal pathogen via changes in host physiology and leaf chemistry. *Global Change Biology* **11**:1828–1836.
- Melloy, P., Hollaway, G., Luck, J., Norton, R., Aitken, E., Chakraborty, S. 2010. Production and fitness of *Fusarium pseudograminearum* inoculum at elevated carbon dioxide in FACE. *Global Change Biology* **16**:3363–3373.
- Newton, A.C., Johnson, S.N., Gregory, P.J. 2011. Implications of climate change for diseases, crop yields and food security. *Euphytica* **179**:3–18.
- Oldenburg, E., Manderscheid, R., Erbs, M., Weigel, H.J. 2009. Interaction of free air carbon dioxide enrichment (FACE) and controlled summer drought on fungal infections of maize. In: Feldmann, F., Alford, D.V., Furk, C. (eds), *Crop Plant Resistance to Biotic and Abiotic Factors*. Deutsche Phytomedizinische Gesellschaft, Braunschweig, Germany, pp. 75–83.
- Pangga, I.B., Hannan, J., Chakraborty, S. 2011. Pathogen dynamics in a crop canopy and their evolution under changing climate. *Plant Pathol.* **60**:70–81.
- Peterson, R.F., Campbell, A.B., Hannah, A.E. 1948. A diagrammatic scale for estimating rust intensity of leaves and stem of cereals. *Canadian J. of Research* **26**:496–500.
- Ramos, L.J., Violin, R.B. 1987. Role of stomatal opening and frequency on infection of *Lycopersicon* spp. by *Xanthomonas campestris* pv. *versicatoria*. *Phytopatology* **77**:1311–1317.
- Royce, D.J., Thomas, G.G. 1971. The influence of stomatal opening on the infection of hop leaves by *Pseudoperonospora humuli*. Observations with the scanning electron microscope on the early stages of hop leaf infection by *Pseudoperonospora humuli*. *Physiology of Plant Pathol.* **33**:329–343.
- Saari, E.E., Prescott, J.M. 1975. A scale for appraising the foliar intensity of wheat disease. *Plant Disease Reporter* **59**:377–380.
- Schroeder, H.W., Christensen, J.J. 1963. Factors affecting resistance of wheat to scab caused by *Gibberella zeae*. *Phytopathol.* **53**:831–838.
- Stubbs, R.W., Prescott, J.M., Saari, E.E., Dubin, H.J. 1986. *Cereal Disease Methodology Manual*. Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT), Mexico, p. 46.
- Thompson, G.B., Brown, J.K.M., Woodward, F.I. 1993. The effects of host carbon dioxide, nitrogen and water supply on the infection of wheat by powdery mildew and aphids. *Plant, Cell & Environment* **16**:687–694.
- Tischner, T., Kőszegi, B., Veisz, O. 1997. Climatic programmes used in the Martonvásár Phytotron most frequently in recent years. *Acta Agronomica Hungarica* **45**:85–104.
- Volk, A. 1931. Einflüsse des Bodens, der Luft und des Lichtes auf die Empfänglichkeit der Pflanzen für Krankheiten (Effect of soil, air and light on the susceptibility of plants to diseases). *J. of Phytopathol.* **3**:1–88. (in German)