

Review

CLIMATE CHANGE AND PLANT DISEASES

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ABSTRACT: Human activities are altering greenhouse gas concentrations in the atmosphere and causing global climate change. In the near future, there will certainly be changes in the Brazilian phytosanitary scenario attributed to global climate change. The impacts of climate change can be positive, negative or neutral, since these changes can decrease, increase or have no impact on diseases, depending on each region or period. These impacts will also be observed on plants and other organisms as well as on other agroecosystem components. However, these impacts are not easily determined, and consequently, specialists from several areas must go beyond their disciplinary boundaries and placing the climate change impacts in a broader context. This review focuses on the discussion of different aspects related to the effects of climate change on plant diseases. On the geographical and temporal distribution of diseases, a historical context is presented and recent studies using data of forecast models of future climate associated with disease simulation models are discussed in order to predict the distribution in future climate scenarios. Predicted future disease scenarios for some crops in Brazil are shown. On the effects of increasing concentrations of atmospheric CO₂ and other gases, important aspects are discussed of how diseases change under altered atmospheric gases conditions in the future. The consequences of these changes on the chemical and biological control of plant diseases are also discussed.

Key words: CO₂, global climate change, global warming, spatial analysis, control

MUDANÇAS CLIMÁTICAS E DOENÇAS DE PLANTAS

RESUMO: As atividades antrópicas estão alterando as concentrações de gases de efeito estufa da atmosfera e causando mudanças no clima do planeta. Certamente, num futuro próximo, devido às mudanças climáticas globais, ocorrerão modificações no cenário fitossanitário brasileiro. Os impactos podem ser positivos, negativos ou neutros, pois as mudanças podem diminuir, aumentar ou não ter efeito sobre as doenças, em cada região ou época. Esses impactos também serão observados sobre as plantas e outros organismos, além de outros componentes do agroecossistema. Porém, esses impactos não são facilmente determinados e, desta forma, os especialistas das diferentes áreas precisam ir além de suas disciplinas e abordar os impactos das mudanças climáticas em um contexto mais amplo. Nessa revisão são discutidos os aspectos relacionados com os efeitos das mudanças climáticas sobre as doenças de plantas. Na distribuição geográfica e temporal das doenças, um contexto histórico é apresentado, incluindo estudos recentes utilizando dados de modelos de previsão do clima futuro associados com modelos de simulação da doença a fim de prever a distribuição nos cenários climáticos futuros. Também são apresentados os cenários futuros de previsão de doenças de algumas culturas no Brasil. Sobre os efeitos do aumento da concentração de CO₂ atmosférico e outros gases são discutidos importantes aspectos do comportamento das doenças sujeitas às condições alteradas de gases atmosféricos no futuro. As consequências dessas alterações sobre o controle químico e biológico das doenças de plantas também são discutidas.

Palavras-chave: CO₂, mudanças climáticas globais, aquecimento global, análise espacial, controle

INTRODUCTION

Greenhouse gas concentrations in the atmosphere are being altered by Human activities, thus causing global climate change. These activities, intensified after the Industrial Revolution at the end of the eigh-

teenth century result from the use of natural resources such as fossil fuel burning, deforestation and other land use changes. The atmospheric concentration of carbon dioxide (CO₂) has reached levels significantly higher than in the last 650 thousand years (Siegenthaler et al., 2005). Since 2000, the growth rate in CO₂ con-

centration is increasing more rapidly than in the previous decades (Canadell et al., 2007). Similar trends have been observed for methane (CH₄), nitrous oxide (N₂O), and other greenhouse gases (Spahni et al., 2005; IPCC, 2007).

Consequently, several changes in the climate have been registered. The average global surface temperature has increased by 0.2°C per decade in the past 30 years (Hansen et al., 2006). Eleven of the twelve warmest years ever registered by instruments since 1850 occurred between 1995 and 2006 - with the exception of 1996. Alterations in the water cycle have also been observed. Changes will probably continue to happen even if greenhouse gas concentrations stabilize, due to the system's thermal inertia and to the long period necessary for returning to a lower equilibrium (IPCC, 2007).

The importance of the environment on the development of plant diseases has been known for over two thousand years. Theophrastus (370-286 B.C.) observed that cereals cultivated in higher altitude regions exposed to the wind had lower disease incidence than cereals cultivated in lower altitude areas. During the eighteenth century and the beginning of the nineteenth century, the effects of factors such as nutrition, air humidity and wind on plant disease occurrence started to be studied (Colhoun, 1973). Nowadays, the environment can influence host plant growth and susceptibility; pathogen reproduction, dispersal, survival and activity; as well as host-pathogen interaction.

The classic disease triangle establishes the conditions for disease development, i.e. the interaction of a susceptible host, a virulent pathogen and a favorable environment. This relationship is evidenced in the definition of plant disease itself. A plant disease is a dynamic process in which a host and a pathogen intimately related to the environment are mutually influenced, resulting in morphological and physiological changes (Gaumann, 1950).

Diseases are responsible for losses of at least 10% of global food production, representing a threat to food security (Strange & Scott, 2005). Agrios (2004) estimated that annual losses by disease cost US\$ 220 billion. Besides direct losses, the methods for disease control - especially the chemical methods - can result in environmental contamination and in residual chemicals in food, in addition to social and economic problems. The close relationship between the environment and diseases suggests that climate change will cause modifications in the current phytosanitary scenario. The impacts can be positive, negative or neutral, since there can be a decrease, an increase or no effect on the different pathosystems, in each region. The analysis of the potential impacts of climate change on plant diseases is essential for the adoption of adap-

tation measures, as well as for the development of resistant cultivars, new control methods or adapted techniques, in order to avoid more serious losses (Chakraborty & Pangga, 2004; Ghini, 2005).

Plant pathogens are ubiquitous in natural and managed systems, being among the first to demonstrate the effects of climate change due to the numerous populations, ease of reproduction and dispersal, and short time between generations. Therefore, they constitute a fundamental group of biological indicators that needs to be evaluated regarding climate change impacts, besides being responsible for production losses, and potentially threat to agroecosystem sustainability.

Despite the threat posed by climate change to plant protection in the near future, there are few reports about this subject (Garrett et al., 2006). This review aims to report and discuss the impacts of climate change on the spatial and temporal distribution of plant diseases, the effects of increased concentration of atmospheric CO₂ and the consequences for disease control. The impacts on abiotic diseases associated with the occurrence of extreme values of environmental variables will not be discussed, in spite of an expected increase in their incidence (Rosenzweig et al., 2001; Boland et al., 2004).

GEOGRAPHICAL AND TEMPORAL DISTRIBUTION

Once environment and diseases are closely related, climate change will probably alter the geographical and temporal distribution of phytosanitary problems. The host plant agroclimatic zoning for coffee will be altered, as showed by Assad et al. (2004); likewise, pathogens and other microorganisms related to the disease process will be affected. Therefore, new diseases may arise in certain regions, and other diseases may cease to be economically important, especially if the host plant migrates into new areas (Coakley et al., 1999). According to these authors, pathogens tend to follow the host plant in its geographical distribution, but the rate at which pathogens become established in the new environment is a function of the mechanism of pathogen dispersal, suitability of the environment for dispersal, survival between seasons, and physiological and ecological changes in the host plant. According to Chakraborty et al. (2000a), more aggressive strains of pathogen with broad host range, such as *Rhizoctonia*, *Sclerotinia*, *Sclerotium* and other necrotrophic pathogens can migrate from agroecosystems to natural vegetation, and less aggressive pathogens from natural plant communities can start causing damage in monocultures of nearby regions. Regarding unspecialized necrotrophs, the range of hosts can be extended due to crop migration.

Disease simulation models frequently used for forecasting can be utilized in simulation studies of spatial and temporal distribution in future climate scenarios. For vector-transmitted pathogens the risk analysis may include the effects of climate change on the vector population, as discussed by Harrington (2002) for the barley yellow dwarf disease.

One of the first studies about this subject was conducted by Luo et al. (1995). These authors carried out a risk analysis of rice blast epidemics and plant growth associated with climate change in several Asian countries due to the importance of this crop and to the losses related to this disease, caused by *Magnaporthe grisea*. Simulations were made to study the risk of blast epidemics under the effects of temperature change and enhanced UV-B radiation. The results demonstrated that changes in the amount of rainfall do not affect the occurrence of the epidemics since they have little effect on the leaf wetting period. In cool subtropical zones, higher temperatures caused increases in disease severity and in the area below the disease progress curve, because higher risk of epidemics occurs under higher temperatures. In humid tropical and humid warm subtropical zones, such as Southern China, Philippines and Thailand, the opposite effect was observed. Lower temperatures increased the risk of rice blast epidemics since the current temperatures in these regions are above favorable values for the occurrence of this disease. However, a larger area below the disease progress curve does not always result in lower rice yield, since the effect in plant growth also takes place. The effects of the increase in UV-B radiation were highly significant for the occurrence of epidemics.

Using mathematical models, Carter et al. (1996) simulated climate change in Finland and concluded that warming will expand the cropping area for cereals by 2050 (100 to 150 linear km per Celsius degree increase in mean annual temperature); furthermore, higher yields are expected with higher CO₂ concentration. In this scenario, potato cropping will also be benefited with an estimated 20 to 30% increase in yield. However, a new distribution of the potato cyst nematode (*Globodera rostochiensis*) is also predicted, with northward expansion in the country and a higher number of generations per year. In this context, the risk of potato blight (caused by *Phytophthora infestans*) is significantly higher in all regions of Finland. The losses caused by an increase in the incidence of these important phytopathogens were not estimated.

Boag et al. (1991) obtained similar results for the plant-parasitic nematodes *Xiphinema* and *Longidorus*. The geographical distribution of these virus-vector nematodes in Great Britain and Continental

Europe (samples collected in 10 km² and 50 km² grids, respectively) were associated to July soil surface temperature isotherms. Since the nematodes geographical distribution is directly related to temperature, there could be more problems with these microorganisms in northern Europe, caused by the increase in existing populations and to the dissemination of these species from the southern region.

A similar scenario was predicted by Brasier & Scott (1994) and Brasier (1996), for the occurrence of *Phytophthora cinnamomi* in oak (*Quercus* spp.) in the European continent. Under conditions of global warming the survival and degree of root disease seems likely to be enhanced, while the host range of the organisms might also be increased. The model simulated three scenarios: increases of 1.5 and 3°C of the mean annual minimum and maximum temperatures, and a 3°C increase of the mean annual minimum and maximum temperatures with a 20% increase in summer precipitation. In all situations, the results showed that there could be a significant rise in pathogenic activity in contaminated areas. Nevertheless, there will probably be a lower pathogen dissemination in regions with a rigorous winter, such as Scandinavia, Russia and the central Danube. Among the factors responsible for the increased importance of this disease, the authors mention the possibility of its dissemination to new areas, a longer favorable period for inoculum production and infection, higher dissemination and survival rates in roots and the soil, besides an increased plant predisposition. A similar study was conducted by Booth et al. (2000), who performed a risk analysis for the occurrence of *Cylindrocladium quinqueseptatum* in eucalyptus in the various production regions in the world.

All of these pioneering studies assumed constant increments in temperature, precipitation, or other climate variables. However, the development and availability of global climate models (General Circulation Models, GCM) enabled the application of these spatial increments in the risk evaluation of disease occurrence. One of the most important accomplishments of the Intergovernmental Panel on Climate Change (IPCC) was the presentation of a group of greenhouse gas emission scenarios known as SRES (Special Report on Emissions Scenarios), which take into account driving forces such as population, economy, technology, energy, agriculture (land-use), as well as their interactions. Thus, four scenario families were defined: A1, A2, B1 and B2, which constitute references related to future greenhouse gas emissions (IPCC, 2001). The IPCC Data Distribution Centre (DDC) was established to facilitate the dissemination of these scenarios, as well as of related environmental and socio-economic factors, for climate impact evaluations. The GCM

quantify the behavior of climate compartments (atmosphere, oceans, vegetation, soils, etc.) and their interactions, allowing the estimation of climate variables (mean, maximum and minimum temperatures, precipitation, etc.) for the various greenhouse gas emission scenarios established by the IPCC (2001).

Marengo (2006) presented a detailed characterization of the variability and regional climate trends for Brazil during the twentieth century and future climate scenarios for South America, using data provided by the IPCC (2001). Rainfall and temperature maps of the country were produced for the climatological normal from 1961-1990, considered a reference period, and for future projections using five GCM.

Comparing methodologies of plant disease spatial distribution maps associated to climate change effects in Brazil, Hamada et al. (2006) used the coffee leaf miner (*Leucoptera coffeella*), as a biological model. For future climate conditions, constant increments in temperature for the country were used in a first method, and spatially variable increments (provided by the GCM) were used in a second method. Both methods were centered in the 2080 decade (simulation of the period from 2071 to 2100), for the A2 scenario. Future increases in the probable number of generations of the coffee leaf miner were observed in both methods of map elaboration. However, the use of constant increments in mean temperature led to an underestimation of the number of generations in the future as compared to the use of spatially variable temperature increments. In addition to a seasonal difference, a regional difference was observed in the occurrence of the probable number of generations of the coffee leaf miner.

Bergot et al. (2004) have used a GCM to simulate the potential impacts of climate change on the expansion of *Phytophthora cinnamomi* in oak, by modeling phloem temperature of infected trees to evaluate overwintering probabilities. For the downy mildew of grape, caused by *Plasmopara viticola*, Salinari et al. (2006) used GCM to evaluate disease pressure, defined as the number of fungicide sprays necessary to control the disease. Using temperature and rainfall data from a regionalized climate model based on a GCM, Hadley Climate Model 3 (HadCM3), from the Hadley Centre for Climate Prediction and Research, UK, Evans et al. (2008) estimated the severity of phoma stem canker epidemics on oilseed rape across the UK, under high- and low-carbon emissions for the 2020s and 2050s.

The climate change risk analysis for the Blacksigatoka of banana (caused by *Mycosphaerella fijiensis*) was studied by Ghini et al. (2007), elaborating disease distribution maps assembled from scenarios and GCM

data provided by the IPCC (2001). The maps revealed that there will be a reduction in the favorable area for the disease in Brazil. This reduction will be gradual for the 2020, 2050 and 2080 decades, and will be more pronounced in the A2 scenario than in the B2. In spite of this, extensive areas will still remain favorable for the occurrence of this disease, especially in the period of November through April. The same climate database was used by Ghini et al. (2008) in order to evaluate the potential climate change impacts on the spatial distribution of nematodes (*Meloidogyne incognita* races) and leaf miner (*Leucoptera coffeella*) for the coffee crop. Maps obtained considering the A2 scenario indicated that there could be an increase in infestation of both the nematode and the pest, due to the higher number of generations per month when compared to the climatological normal from 1961-1990. For the B2 scenario, the number of generations will also be higher as compared to the current scenario, but it will be lower than for the A2 scenario for both.

The use of GCM presents some problems since their outputs have low spatial and temporal resolution, in spite of the advances achieved from 1990 until recently (IPCC, 2007). These characteristics on which the evaluations are based make it difficult to match the predicted scenarios with the models of biological responses such as plant or disease growth, which require daily or even hourly input data. One of the great challenges is to adapt the requirements of biological process models to what is provided by the GCM, with long term approaches (Schermer & Brugger, 1994; Scherm & Coakley, 2003; Scherm, 2004).

The high degree of uncertainty of the anomalies among the models of some climate variables is another important aspect. For example, precipitation predictions of the GCMs are generally more uncertain than temperature predictions. Therefore, precipitation does not follow the same pattern of behavior in the various models, unlike the temperature increase predicted in all models. One way to deal with this issue is to calculate the arithmetic mean of the results of the various models in order to smooth out the differences, though this option is quite work-intensive. Despite the limitations, these scenarios continue to serve as a basis for impact evaluation of global climate change (Vuuren & O'Neill, 2006). These authors discussed the consistency of the IPCC scenarios, comparing projections to recently-obtained actual data on population, economy, energy use, and gas emissions.

Models can simulate global climate change scenarios and different levels of disease severity, with the aim to estimate yields, establish control tactics and strategies, aiding the decision making process. More efforts must be dedicated to this type of study, which

can result in significant time and resource savings. Therefore, Ghini & Hamada (2008) edited a book to discuss the impacts of climate change on diseases of the main crops in Brazil. For example, Lopes et al. (2008) considered that if the predictions about a rise in global temperature actually take place, rainy season potato crops will be more stricken with disease than winter crops, and cropping will not be feasible in low altitude regions due to the increase of biotic and abiotic diseases. Gioria et al. (2008) showed a prediction for the main tomato diseases and argued that climate change will not be favorable for the occurrence of late blight (*Phytophthora infestans*), verticillium wilt (*Verticillium albo-atrum*), and white mold (*Sclerotinia sclerotiorum*); and will not alter the importance of the tomato mosaic caused by the tomato mosaic virus (ToMV) and the septoria leaf spot (*Septoria lycopersici*). In contrast to those diseases, the authors considered that the importance of powdery mildew (*Leveillula taurica*) will increase in all tomato production regions across the country, just as the importance of early blight (*Alternaria solani*), fusarium wilt (*Fusarium oxysporum* f.sp. *lycopersici*), bacterial wilt (*Ralstonia solanacearum*), tomato spotted wilt virus - TSWV, tomato chlorotic spot virus - TCSV, groundnut ring spot virus - GRSV, Chrysanthemum stem necrosis virus - CSNV and yellow leaf curl virus (Geminivirus).

ATMOSPHERIC CARBON DIOXIDE

There is a relatively large number of studies on the beneficial effect of increased concentration of atmospheric CO₂ on plant growth. In the last few years, approximately 3,000 reports have been published on the subject (Jones & Curtis, 2000; Loladze, 2002). High CO₂ concentration results in benefits for plant growth, although there might be differences among species. Several authors reached the same conclusions with different crops, natural ecosystems and forest species.

CO₂ enrichment promotes changes in plant metabolism, growth and physiological processes. There is a significant increase in the photosynthetic rate and a decrease in the transpiration rate per unit leaf area, while total plant transpiration sometimes increases, due to the larger leaf area (Jwa & Walling, 2001; Li et al., 2003). The alterations also include higher efficiency in the use of water and nitrogen by the plant (Thompson & Drake, 1994). The stimulus on photosynthesis is due to the reduction in competition between the atmospheric CO₂ and O₂ being fixed by the ribulose 1,5-bisphosphate carboxylase-oxygenase (RUBISCO) enzyme. The atmospheric concentration of O₂ normally inhibits CO₂ absorption by plants, and triggers photorespiration. With a rise in CO₂ concentration, the inhi-

bition of photosynthesis by O₂ tends to decrease due to an increase in the CO₂:O₂ ratio.

Despite evidence of beneficial effects of CO₂ on the host plant, it is not well known if these effects will still take place in the presence of pathogens or other limiting factors, particularly in tropical countries. Few studies were conducted in controlled conditions, which might not reflect plant responses in the field, where there are variations and interactions among temperature, precipitation, and other factors.

In a review about the effects of the increase in CO₂ concentration on plant diseases covering the period of 1930 to 1993, Manning & Tiedemann (1995) observed an upward trend in diseases. The authors analyzed the potential effects of higher CO₂ concentration on plant diseases, based on the plant responses to this new environment. The increase in plant biomass production, i.e., the increase in production of shoots, leaves, flowers and fruit, represents more tissue that can be infected by pathogens. Increased carbohydrate contents can stimulate the development of sugar-dependent pathogens, such as rusts and powdery mildews. Increases in canopy density and plant size can promote higher growth, sporulation and spread of leaf infecting fungi, which require high air humidity, but not rain, as rusts, powdery mildews and leaf necrotrophs. The increase in crop residues can represent better survival conditions for necrotrophic pathogens. The reduction in stomatal opening can inhibit stomata-invading pathogens, such as rusts, downy mildews and some necrotrophs. The shortened growth period and accelerated ripening and senescence can reduce the infection period for biotrophic pathogens, and increase the necrotrophic pathogen populations. The increase in root biomass increases the amount of tissue that could be infected by mycorrhiza or soil-borne pathogens, but can compensate the losses inflicted by the pathogens. Higher root exudation can stimulate both pathogens and antagonistic microbiota in the rhizosphere (plant growth promoters). In a more recent review on the subject, Chakraborty & Pangga (2004) concluded that of the 26 diseases studied to date most of them increased in severity when in CO₂-enriched environments.

The effects of increased CO₂ atmospheric concentration are often observed in the host plant, resulting in alterations in the host-pathogen relationship. According to Braga et al. (2006), the exposure to CO₂-enriched atmospheres can change inducible defensive responses in plants against pathogens. These changes occurred in individual metabolites and were dependent on cultivar resistance patterns. Pangga et al. (2004) stress the importance of induced resistance studies, besides canopy size, in the evaluation of CO₂ effects.

The reduction in incidence and severity of the red maple fungal pathogen (*Phyllosticta minima*) in *Acer rubrum* in a CO₂-enriched atmosphere was a consequence of stomatal conductance reduction providing smaller openings for infecting germ tubes (McElrone et al., 2005). The reduction in silicon content in rice leaves due to a reduction in respiration rates was the explanation for an increase in rice blast severity in a FACE (Free Air Carbon Dioxide Enrichment) experiment (Kobayashi et al., 2006).

The impact of increased CO₂ concentrations can be observed in several stages of the pathogen-host relationship cycle. Hibberd et al. (1996a,b) conducted detailed studies of these effects on the powdery mildew (*Erysiphe graminis*) cycle for barley. Chakraborty et al. (2000b), studying the effects of elevated CO₂ concentration on the epidemiological components of anthracnose caused by *Colletotrichum gloeosporioides* in *Stylosanthes scabra* demonstrated that the gas influences both the pathogen and the host, with differences in the expression of the disease resistance under these conditions, however varying with the cultivar. In a controlled environment, the increase in CO₂ concentration promoted higher plant growth, but did not compensate for reduced growth due to anthracnose in the most resistant cultivar. For the more susceptible cultivar, though, there was a compensation effect. Thus, Hibberd et al. (1996a,b) concluded that the benefits of CO₂ fertilization on growth depend on the nature of plant resistance. Delayed growth of the pathogen germ tube and appressorium reduced the germination percentage of conidia on leaves and extended the incubation period in a controlled environment with high CO₂ concentration. Consequently, there was a reduction in disease severity. Furthermore, pathogen penetration takes place through the stomata, and the increase in CO₂ reduces leaf stomatal density. On the other hand, the latent period was not altered and spore production was significantly higher.

Regarding the pathogen, important alterations can occur as a consequence of an increase in CO₂ concentration. To better understand the aggressiveness evolution process of *Colletotrichum gloeosporioides* in *Stylosanthes scabra*, Chakraborty & Datta (2003) inoculated two isolates in two cultivars with different resistance levels during 25 sequential infection cycles, in environments with 350 ppm and 700 ppm of CO₂. The aggressiveness increased for the resistant cultivar, but not for the susceptible cultivar, and there was an increase in isolate fecundity in the environment with higher CO₂ concentration. These results are extremely important for the epidemiology of the disease demonstrating that the pathogen can adapt to a new environment.

The effects of increased atmospheric CO₂ concentration can interact with the effects caused by other factors, such as nitrogen fertilization and irrigation. Thompson et al. (1993) studied these interactions for the powdery mildew on wheat, caused by *Erysiphe graminis*, in England. Thompson & Drake (1994) evaluated C₃ and C₄ plants regarding infestation by insects and fungal disease severity as a function of water and N contents. In a factorial FACE experiment, Mitchell et al. (2003) assessed the effects of increased CO₂ concentration, nitrogen input and ecosystem species diversity on the occurrence of foliar fungal diseases in C₃ and C₄ plants.

Besides N and irrigation, the effects of elevated CO₂ concentration can be affected by other gases that are also changing. The increase in the ozone (O₃) concentration was studied by Tiedemann & Firsching (2000) in combination with CO₂ increase, for spring wheat plants infected or not with leaf rust disease (*Puccinia recondita* f. sp. *tritici*). These authors observed that the leaf rust disease was strongly inhibited by O₃, but unaffected by elevated CO₂. They also observed that elevated CO₂ largely equalized the negative effects of O₃ on the photosynthetic rate, growth and yield parameters, but was not capable of compensating for the detrimental effects of fungal infection. Percy et al. (2002) investigated in a FACE experiment the impacts of elevated CO₂ and O₃ on poplar leaf rust (*Melampsora medusae*) in natural disease outbreaks. In this study, CO₂ alone did not alter the rust occurrence, rust infection increased fourfold under enhanced O₃, and co-exposure did not completely offset the negative effects of O₃, as infection remained almost threefold higher as compared to the control leaves. Karnosky et al. (2002) also observed that the effects of O₃ on leaf surface properties resulted in increased incidence of this rust. Osswald et al. (2006) investigated whether elevation of CO₂ (400 up to 700 ppm) and/or ozone (ambient or two-fold ambient) resulted in a change in susceptibility of potato plants infected with *Phytophthora infestans*. The main result was that a rise in CO₂ caused a significantly enhanced resistance of the susceptible potato cultivar 'Indira' towards *P. infestans*, whereas ozone had no significant effect. These authors investigated the effect of N-fertilization in combination with CO₂-treatment on the resistance of potato to *P. infestans*, because CO₂ induced an increase in resistance correlated with an increased C/N-ratio in potato leaves. They observed that a lower C/N-ratio, due to higher N-concentrations, decreased resistance to *P. infestans*.

There have been few studies to verify the effect of soil air CO₂ on disease incidence. The order of magnitude of this concentration is naturally many

times higher than the concentration in the atmosphere. Runion et al. (1994) conducted one of the few studies with soil-borne pathogens, in a FACE experiment. The authors observed an increased incidence of “damping-off” caused by *Rhizoctonia solani* for cotton plants cultivated with elevated atmospheric CO₂. More recently, Jwa & Walling (2001) studied the effects of elevated CO₂ concentration on the development of root rot in tomato, caused by *Phytophthora parasitica*. They observed that the pathogen incidence in the roots was significantly lower for plants grown under 700 ppm than under 350 ppm CO₂, but *P. parasitica* hyphal growth rates *in vitro* were similar for both concentrations.

Osozawa et al. (1994) evaluated the effects of CO₂ in the gaseous phase of two soils, one suppressive and the other conducive in relation to the clubroot disease caused by *Plasmodiophora brassicae* on cabbage. They concluded that the increase in the CO₂ concentration promoted the occurrence of the disease in the conducive soils at high soil moisture levels. The promotive effect of high CO₂ concentration on the occurrence of the disease is ascribed to the fact that the decrease of the soil water pH by CO₂ accumulation may activate the germination of resting spores and impair the activity of crucifer roots. On the other hand, in the suppressive soil, the alterations were not significant since other physical and chemical mechanisms contribute to induce the suppressiveness.

To study the effect of increased atmospheric CO₂ concentration on plant viroses, Malmström & Field (1997) observed that the CO₂ enrichment stimulated the growth of oats infected with the barley yellow dwarf virus (BYDV), attenuating the dwarfing symptom. The CO₂ enrichment stimulated photosynthesis in infected plants by a greater amount than in healthy plants. Sixty days after the beginning of the treatments, the healthy plants had a 12% increase in total biomass as compared to plants grown in the lower CO₂ concentration, while diseased plants had a 36% increase. The growth stimulation is probably due both to direct effects of CO₂ on carbohydrate production, and to indirect effects on plant water relations, allowing the diseased plants to take up more carbon and perhaps to distribute it better. With these results, Malmström & Field (1997) analyzed the epidemiological consequences of the alterations triggered by the atmospheric CO₂ enrichment. The epidemiology of the barley yellow dwarf virus depends upon the pathogen inoculum reservoir, which consists of infected plants, and upon the rates at which vectors acquire and transmit the virus, since aphids are the only vectors and there is no transmission by seeds. The results obtained by these authors demonstrate that CO₂ enrichment may

enhance the virus reservoir in the agroecosystem, by increasing the size and persistence of the infected plants. This effect can be noticed, for example, due to the increase in root biomass and to the water-use efficiency by diseased plants which can reduce losses of infected plants by drought, the main cause of death. Furthermore, CO₂ enrichment may enable diseased plants to compete better with healthy neighbors. Thus, while the effects on virus epidemiology will also depend strongly on the vector response, these plant responses would tend to increase the prevalence of the disease, but decreasing its severity.

DISEASE CONTROL

Disease management strategies depend on climate conditions. Climate change will cause alterations in the disease geographical and temporal distributions and consequently the control methods will have to be adapted to this new reality. There are few discussions on how chemical control will be affected by climate change, despite the importance of this subject. Changes in temperature and precipitation can alter fungicide residue dynamics in the foliage, and the degradation of products can be modified. Alterations in plant morphology or physiology, resulting from growth in a CO₂-enriched atmosphere or from different temperature and precipitation conditions, can affect the penetration, translocation and mode of action of systemic fungicides. Besides, that changes in plant growth can alter the period of higher susceptibility to pathogens which can determine a new fungicide application calendar (Coakley et al., 1999; Chakraborty & Pangga, 2004; Pritchard & Amthor, 2005).

The fungicide market will certainly change. Chen & McCarl (2001) performed a regression analysis between pesticide usage (provided by the USDA – United States Department of Agriculture) and climate variations in several US locations, with climate data provided by NOAA - the National Oceanic Atmospheric Administration. The per acre pesticide usage average cost for corn, cotton, potatoes, soybeans and wheat were found to increase as precipitation increases. Similarly, the pesticide usage average cost for corn, cotton, soybean and potatoes also increase as temperature increases, while the pesticide usage cost for wheat decreases.

However, the main impact of climate change on chemical control will be in the cultural realm. The fact that the entire humanity is suffering the consequences of anthropogenic activity in the process of exploiting the resources of the planet will raise an awareness that this activity must be conducted in a sustainable way. Society will certainly exert pressure for the use of non-chemical methods to control plant diseases.

One of the direct consequences of climate change in the pathogen-host relationship is the genetic resistance of plants to diseases. Many changes in plant physiology can alter the resistance mechanisms of cultivars obtained by both traditional and genetic engineering methods. Several studies provide evidences of these alterations, such as significant increases in photosynthetic rates, papillae production, silicon accumulation in appressorial penetration sites, higher carbohydrate accumulation in leaves, more wax, additional epidermal cell layers, increased fiber content, reduction in nutrient concentration and alteration in the production of resistance-related enzymes (Hibberd et al., 1996b; Chakraborty et al., 2000a; Osswald et al., 2006).

Paoletti & Lonardo (2001) conducted one of the few studies to verify the effects of increased CO₂ concentration on disease control by using resistant cultivars. The authors reported that *Cupressus sempervirens*, a cypress clone resistant to canker caused by *Seiridium cardinale*, maintained the genetic resistance when cultivated in a high CO₂ content environment. There is a larger number of studies regarding the effects of temperature and other climate variables, as reported by Huang et al. 2006.

Some types of resistance can be more affected than others. Many changes in host physiology can potentially enhance plant resistance. Nonetheless, the greatest threat to genetic resistance is the acceleration of pathogen cycles, which can be affected during all life cycle by increased CO₂ concentrations. Some studies revealed that in spite of a delay in the initial development and a reduction in host penetration, the established colonies develop faster. The increased fecundity of the pathogen, associated to a favorable microclimate within enlarged canopies favors the occurrence of epidemics (Hibberd et al., 1996b; Chakraborty et al., 2000a).

There is practically no information on the impacts of climate change on plant disease biological control. The few results obtained focus on climate change impacts on the composition and dynamics of the microbial community of the phyllosphere and the soil, which can be very important for plant health.

Key soil aspects for microbial activity will be modified, such as soil nutrient availability, soil temperature, and soil water content. In addition, the amount of nitrogen introduced into natural and agricultural systems through fertilizers and pollutants can cause significant impacts on the microbiota (Nosengo, 2003). Grüter et al. (2006) concluded that exposition to an environment with a 600 ppm CO₂ concentration did not quantitatively alter the soil bacterial community. However, these same authors concluded that one of the potential effects of climate change is on plant di-

versity, which results in changes in the soil bacterial composition (types of bacteria and frequency of occurrence). Using a FACE experiment to evaluate the effects on saprophyte fungi, Rezácová et al. (2005) observed that *Chlonostachys rosea*, an important biological control agent of *Botrytis* and other pathogens, and *Metarrhizium anisopliae*, one of the most important entomopathogens for insect pest control, were strongly associated with the cover crop in a high CO₂ concentration environment. The authors suggest the abundance of these fungi species can indicate an increase in the soil suppressiveness to phytopathogenic fungi and other pests.

Warwick (2001) conducted one of the few detailed studies on the effect of climate conditions on biological control efficiency, demonstrating the effects of the rainfall regime and time of application of *Acremonium vittelinum* and *A. persicinum* for the control of the tar spot of coconut caused by *Catacauma torrendiella* and *C. palmicola*. However, there is no information on most antagonists. Studies on this subject will be important for maintaining the efficiency of biological control. Additionally, it is necessary to know the responses of the diseases to these changes. These answers will allow conclusions on what might happen to biocontrol, both natural and through the introduction of bioagents.

The prediction of the effects of climate change on plant disease biological control is complex and currently based on indirect observations. Nevertheless, the vulnerability of biocontrol agents will surely be higher with climate change, since this is one of the problems when applying antagonists (Garrett et al., 2006).

The adaptability of some agricultural systems can help to minimize the negative impacts of climate change with the adoption of new cultivars and other practices. Developing countries, though, will have more difficulties in adapting to climate change, due to the lower technological development and to the scarce resources available for the adoption of measures.

Ghini & Bettiol (2008) argued that in general the climate change will be beneficial for biological control, both natural and introduced, since the awareness of the society towards environmental problems will demand measures that minimize pollutant emissions. Therefore, the biological equilibrium of agricultural systems will be benefited, leading to an increase in the complexity of the system, and consequently, to biological control. To achieve this, specialists from different agriculture-related areas need to go beyond disciplinary boundaries and position the global climate change impacts in a broader context, including the whole agroecosystem.

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