

Commentary

Climate change and plant pathosystems – future disease prevention starts here

The concentration of carbon dioxide (CO₂) in the atmosphere is increasing (Keeling *et al.*, 1989) and may double during this century (Bolin, 1986). The opportunities available for those interested in the study of plant diseases within the emerging field of global change science were noted over a decade ago (Bruck & Shafer, 1991). However, the manner in which increasing levels of atmospheric CO₂ will affect crop diseases remains virtually unstudied. One group which has taken up this challenge and has begun to address the effects of climate change and elevated atmospheric CO₂ on plant diseases is Sukumar Chakraborty and colleagues in Queensland, Australia. In this issue of *New Phytologist* (pp. 733–742), Chakraborty & Datta present results from an indepth investigation of the effects of elevated atmospheric CO₂ on a crop, *Stylosanthes scabra*, to one of its major diseases (anthracnose, caused by the fungus *Colletotrichum gloeosporioides*).

'Climate change will directly impact crops, as well as their interactions with microbial pests'

A glance at the past

Humans have been plagued by the effects of plant diseases since they first adopted an agrarian lifestyle, with the first causes ascertained and proven by early scientists such as Tillet, Prevost, and de Bary (Ainsworth, 1981; Agrios, 1988). We now know that numerous types of microorganisms (primarily fungi, bacteria, nematodes, and viruses) are the causal agents of diseases of both humans and plants. And we have seen how plant disease has drastically altered history (e.g. emigration from Ireland in the mid 1800s resulting from the potato famine, due to the fungus *Phytophthora*

infestans, the causal agent of late blight of potato). We have also seen disease alter the ecological landscape of a country (e.g. chestnut blight, caused by the fungus *Cryphonectria (Endothia) parasitica*). History tells us that we can expect plant disease to have devastating effects in the future.

Plant diseases continue to destroy crops and reduce agromonic productivity – each year billions of dollars in yield are lost to diseases and millions more are spent managing these pests (Agrios, 1988). However, we now understand many of the underlying principles surrounding plant diseases, their epidemiology, and management (Fry, 1982). We know that differing disease-causing organisms require differing environmental conditions for pathogenesis. We have mapped the minimum, maximum, and optimum temperatures and moisture conditions for many pathogenic microbes. We have also devised a variety of means for managing these organisms to reduce their impacts, including integration of cultural, chemical and biological control strategies. We have observed for many years that some plants remain disease-free, while their neighbors become infected or die. These early observations have led to strategies for breeding crops which are resistant to infection and, with new advances in biotechnological methodologies (Bent, 2003), host plant genetics remains a primary weapon in our arsenal against plant disease.

Changing climate, changing research priorities

We cannot continue to rely on what we know now, as our current global environment is changing. Increases in atmospheric concentrations of greenhouse gases has brought about concern for rising temperatures, altered precipitation patterns, as well as numerous other potential changes in our global climate (Norby *et al.*, 2001; Paul, 2001). Climate change will directly impact crops, as well as their interactions with microbial pests (Rosenzweig *et al.*, 2000). While we can use current knowledge to predict how climatic changes might affect crop productivity and interactions of crop plants with disease-causing organisms, few data are available to validate such speculations. This fact remains as true for the known increase in atmospheric CO₂ concentration as it does for potential increases in temperature or altered precipitation patterns.

It is well established that elevated CO₂ increases growth and yield of most plant species (Kimball, 1983) and that this increase is generally caused by increased rates of photosynthesis (Amthor, 1995) and/or increased water use efficiency (Rogers & Dahlgren, 1993). CO₂-induced changes in plant morphology, physiology, and biochemistry have the potential to effect the major diseases of the world's food and fiber crops. Further, as with aspects of climate change, it has been

suggested that generalities regarding effects of CO₂ on host–pathogen interactions can be theorized using knowledge of plant responses to elevated CO₂ and of ecophysiological differences among pathosystems (Runion *et al.*, 1994). However, the manner in which increasing levels of atmospheric CO₂ will affect crop diseases is only just beginning to be investigated.

What effects can elevated CO₂ have on pathosystems?

In this issue, Chakraborty & Datta present results from a study on the regionally important pasture legume *Stylosanthes scabra*. They investigated the effects of ambient and twice-ambient levels of atmospheric CO₂ on changes in aggressiveness, fecundity, and genotype of the fungal pathogen *Colletotrichum gloeosporioides* when grown for 25 successive infection cycles on host plant cultivars varying in genetic resistance to the disease. The findings are relevant not only to the genetics of an important host–pathogen interaction, but also to the epidemiology of this pathosystem. First, they demonstrate (using pathogen isolates collected from the field over the past 22 years) that, under field conditions, aggressiveness has increased towards the resistant, but not the susceptible, cultivar. It is interesting to note that the authors' use of the term aggressiveness – which they define as a property of the fungus reflecting the relative amount of damage caused to the host without regard to resistance genes – is synonymous with disease severity. Nonetheless, it seems logical that aggressiveness would not be altered on the susceptible cultivar as it can be readily infected, placing little or no pressure on the pathogen for adaptation to survive and reproduce. However, disease severity (and presumably inoculum production) was substantially lower on the resistant cultivar, 'forcing' the fungus to adapt by selecting for races which can infect this resistant host. The proportion of the overall population comprised by these races likely increased over time and resulted in increased severity.

The authors noted that aggressiveness increased over the course of the infection cycles on both cultivars when grown under ambient CO₂. They also note that this study is the first to document a change in pathogen aggressiveness when inoculated onto host plants and grown under elevated CO₂ – overall aggressiveness of both isolates was reduced on both resistant and susceptible cultivars. This suggests that host plants may benefit from future, higher atmospheric CO₂ concentrations through a reduction in damage from this pathogen. However, the overall reduction in pathogen aggressiveness resulted from an initial lag phase of 10 infection cycles, after which aggressiveness increased on both cultivars. Presumably, during this initial period the pathogen was adapting to whatever CO₂-induced changes in the host led to the initial decrease in aggressiveness, after which aggressiveness increased in a manner similar to that which occurred on plants grown under ambient CO₂. It has been suggested that an increase in production of defensive

compounds and/or other changes in host physiology, morphology, or anatomy under elevated CO₂ could lead to reductions in incidence or severity, at least for some pathosystems (Runion *et al.*, 1994; Hibberd *et al.*, 1996; Chakraborty *et al.*, 2000; Hartley *et al.*, 2000). By carrying this pathosystem through numerous infection cycles, the authors correctly note that enhanced resistance at elevated CO₂ may not result in reduced host damage in the long term.

Perhaps one of the most important observations reported in this study, nevertheless following an earlier, similar finding using the same pathosystem (Chakraborty *et al.*, 2000), was an increase in fecundity (spores produced/lesion area) under elevated CO₂. This increase was noted for both isolates but was more consistent and pronounced for the more aggressive of the two. Spore production has critical implications for the epidemiology of any disease – an increase in spore numbers implies increased inoculum pressure for subsequent infection cycles and, generally, an increase in the spread and severity of disease. Although, through the inoculation methods used, the authors ignored the effects of fecundity on aggressiveness and suggest the increased fecundity was a result of a better canopy microclimate from larger plants under high CO₂, they nonetheless note that the high reproductive fitness of the more aggressive isolate is an important component of its high level of aggressiveness. They further note that increased fecundity under elevated CO₂ could have important implications in the functional duration of resistance in crop plants.

Interestingly, while genotypic alterations occurred in both *C. gloeosporioides* isolates on the susceptible cultivar at twice-ambient CO₂, they were not related to increased aggressiveness of the fungus. The authors duly note that: there are known mechanisms of genetic variation in this pathogen (i.e. hyper-variable chromosomes and retrotransposons, in addition to mutation and parasexual recombination); that aggressiveness groups can arise from differing genetic lineages, can be influenced by the physical environment, and may arise more frequently under weather conditions favorable for pathogen growth; and therefore aggressiveness should not necessarily be related to genetic alterations in the fungus. Still, it is curious that growth in elevated CO₂ resulted in genetic alterations in both pathogen isolates only on the susceptible cultivar, while this occurred only in ambient CO₂ for the more aggressive isolate on the resistant cultivar. While the authors note that growth in elevated CO₂ can result in numerous changes in host morphology, anatomy, and physiology, speculation on possible factors driving the more frequently noted alterations in genotype under high CO₂ would have been of interest. It is possible that an increase in host photosynthate production, providing a better substrate for fungal growth, resulted in an increase in spore production under elevated CO₂ (i.e. the increase in fecundity noted), which resulted in a more variable genetic composition of the fungus. However, as the fecundity of the

more aggressive isolate increased on the more resistant cultivar under twice-ambient CO₂ (which did not exhibit any genetic alterations), this explanation appears not to fit the results obtained in this study.

A look into the future

Will disease incidence or severity increase, decrease, or remain essentially unchanged under future projected climate and atmospheric composition conditions? This is a question of utmost importance to the future stability and security of food and fiber production. Undoubtedly, rising temperatures, altered precipitation patterns, and increases in atmospheric CO₂ concentration will elicit complex changes in plant pathosystems – these changes will vary depending on host responses, the pathosystem of interest, and with the specific environmental conditions in which they are grown. Although we can theorize that host–pathogen interactions might respond in somewhat predictable ways, our current lack of knowledge precludes having any real confidence in these predictions. Further, research on interacting effects of climatic variables with CO₂ have generally indicated that plant responses are complex, highly variable, and rarely follow predictable patterns.

Nonetheless, we must begin somewhere as the CO₂ concentration in the atmosphere rises, will probably continue to do so into the foreseeable future, and will likely elicit changes in the global climate. No definitive answers are forthcoming from the current study, nor should they have been expected – the question is too broad and variable to address in a single study. However, the study does provide evidence suggesting that: elevated atmospheric CO₂ can impact important crop pathosystems; pathogen aggressiveness/disease severity might be decreased under rising CO₂, which suggests there may be plant responses which can be taken advantage of within breeding programs; this decrease in pathogen aggressiveness may not hold in the long term; fecundity may increase, which implies farmers will likely need to alter disease management strategies; and pathogen evolution might be accelerated under a high CO₂ environment. There are many more questions than there are answers.

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Key words: climate change, plant pathogen, *Stylosanthes scabra*, anthracnose, *Colletotrichum gloeosporioides*.

Volcanic deserts and primary succession – when and how do mycorrhizal fungi participate?

Is it not fascinating how barren land, such as a newly exposed glacial moraine or a cooled volcanic lava flow, is recolonized by living organisms and new communities assemble and develop? The characteristic 'first' sign of life is the appearance of green plants, and theories of primary succession worked out by plant ecologists define, essentially, a process involving the colonization and establishment of such vegetation on newly exposed substrates (e.g. Begon *et al.*, 1990). Indeed, until a few decades ago, the emphasis on community assembly of the autotrophic plants had dominated successional ecology. However, with increasing awareness of the importance of heterotrophic communities and their interactions, more and more studies focussed on these ecosystem components. It has recently been proposed that primary community assembly by autotrophs is preceded by a heterotrophic phase established from allochthonous deposited dead and living organic material (Hodkinson *et al.*, 2002). These authors suggested that the deposition of invertebrates and organic detritus in microsites of barren land might provide the initial inputs of energy and nutrients. This would allow the development of heterotrophic communities, which in turn might be instrumental in facilitating the establishment of green plants by conserving nutrients, particularly nitrogen. Now, Nara and colleagues are providing answers to some of the most fundamental questions involving ectomycorrhizal fungi in these situations through detailed research in a volcanic desert on Mount Fuji, Japan (Nara *et al.*, 2003b, also see pp. 743–756 in this issue).

Role of mycorrhizal associations

It is well known that symbiotic associations of plants with nitrogen fixing bacteria or mycorrhizal fungi can greatly enhance nutrient as well as water availability for the plant hosts (Smith & Read, 1997). These symbioses may therefore play a crucial role in harsh environments such as primary succession sites, where nutrients are usually limited. Studies on the effects of mycorrhizal fungi on vegetation succession have mainly been conducted on herbaceous species and their associated vesicular–arbuscular mycorrhizal fungi (VAM). Essentially these studies showed that non- or facultatively mycotrophic plants were the first invaders, followed by mycotrophic plants after VAM populations had established in the soil (Allen & Allen, 1990). Since VAM had been shown to mediate competitive interactions between plants

and to influence the resultant community structure (van der Heijden *et al.*, 1998), patterns of VAM distribution across early successional sites were thought to regulate and drive plant community assembly (Allen & Allen, 1990).

Primary succession of ectomycorrhizal fungi in a volcanic desert

In volcanic areas or on deglaciated land, the invasion of ectomycorrhizal (ECM) host plants has been observed after 5–20 yr of substrate exposure (Allen *et al.*, 1992; Jumpponen *et al.*, 2002). The associated ECM fungal community and its development over time in such primary succession sites have been reported in a handful of studies (Allen *et al.*, 1992; Helm *et al.*, 1996; Jumpponen *et al.*, 2002). Since vegetative structures (e.g. mycelium and mycorrhiza) are hidden in the soil, assessing the extent of the ECM community poses problems – the presence of ECM fungi has therefore usually been assessed by above-ground sporocarp surveys. However, because fruiting of ECM fungi occurs unpredictably and only sporadically, such surveys have to be intensive (e.g. weekly) and carried out ideally over several years. The usually difficult access to primary succession sites, such as glacier forefronts and volcanic areas, has prevented fungal ecologists from utilizing these sites in their studies. However, an exhaustive investigation has now been performed by Nara and colleagues in a volcanic desert on Mount Fuji, Japan (Nara *et al.*, 2003). These authors counted and mapped ECM sporocarp production weekly for 2 yr in vegetation patches recovering from the eruption of 1707. In the study site, vegetation coverage made up *c.* 5% of the land area. Sporocarp abundance was related to the exclusively dominant ECM host, *Salix reinii*, in these patches. To study fungal succession, the coverage area of individual *S. reinii* patches was taken as an indicator of the age after first colonization. These ranged from a several-year-old seedling of 0.016 m² to large bushes of over 50 m². Based on these sporocarp surveys, one or two of three so-called first-stage fungi (two *Laccaria* and one *Inocybe* species) were the first colonizers and were joined by additional species with host development, resulting in an increase of species richness. Their data confirmed earlier models of fungal succession, which postulate that few ruderal species are able to colonize young root systems effectively by spore, and with time, they are joined and sometimes replaced by additional, more competitive species. The appearance of these so-called late-stage fungi was attributed to host age and with it the quality and quantity of carbon supply, as well as changes in soil conditions (Last *et al.*, 1984). Because the vegetation patches were sparsely distributed on the volcanic desert, individual associations between host and ECM sporocarps could be clearly identified and spatially correlated. This allowed Nara *et al.* not only to describe the fungal succession

with increasing host development, but also to evaluate possible reasons for successional patterns. That is, they could show that many species (e.g. *Hebeloma* spp., *Cortinarius* spp., *Russula* spp.), which appeared later in the succession, were always situated inside the vegetation patches. This was clearly related to changes in soil conditions, since organic material accumulated in these locations. Other species (e.g. *Scleroderma bovista*) appearing later in the succession were mainly situated in the surrounding bare ground which therefore might be attributed to the increased host age.

Where did the inoculum of these colonizing fungal species come from? Since the existing vegetation was completely destroyed by the volcanic eruption and covered with scoria, the inoculum must have been brought in from far outside the area by wind dispersal. In a primary succession system in a glacier forefront, Jumpponen (2003) detected some mycorrhizal taxa by rDNA analysis of soil samples even in the youngest substrate near the glacier terminus, although no plant hosts were present in this area. They attributed this to an aerially deposited, dormant spore bank, which might grow out when conditions are favourable. Once established, short-distance dispersal probably occurs from these fungi, as detected for the host species *S. reinii* (Lian *et al.*, 2003). Exceptionally large sporocarp production was in fact observed by Nara *et al.* in their study site. This large sporocarp production might be indispensable to improve ectomycorrhiza formation on existing and new *S. reinii* hosts by supplying a huge number of spores on-site.

Sporocarp production and host vitality

A very interesting observation was the fact that sporocarp biomass production was positively correlated with the photosynthetic rate of associated hosts, which varied greatly between nine patches of mid-sized hosts (Nara *et al.*, 2003). In addition, the photosynthetic rate increased linearly with N- and P-status in leaves. This implies that the bidirectional interaction could determine the activity of both symbionts in these ECM associations since nutrient supply from ECM fungi is essential for plant photosynthetic activity, which in turn will determine the amount of photosynthetate delivered to the associated fungi. ECM fungi may therefore play a very important role in carbon and nutrient cycling during primary succession.

In addition to the much lower sporocarp biomass production in patches of less healthy hosts (based on photosynthetic rate, leaf biomass and one-year shoot length), Nara *et al.* also observed a change in the ECM fungal species composition associated with these plants. *Scleroderma bovista*, for example, which was one of the most abundant species in the study site, was hardly encountered with less healthy hosts, whereas a *Hebeloma* species was relatively frequent in these patches. Overall ECM species richness seemed to be reduced with less healthy hosts. The question

is, do these above-ground observations really reflect below-ground abundances at the root level? Is *S. bovista*, for example, in fact less abundant on the root system or does this species only produce fewer sporocarps because less carbon is supplied from the plant?

A below-ground view

In the present issue, Nara *et al.* provide answers to the above-mentioned questions by looking below ground. Using a carefully considered sampling design and well elaborated molecular techniques, the authors determined the ECM species composition on the root system of *S. reinii* of three different size classes. In addition, they provided data on the spatial distribution of the ECM community on the root system of individual large hosts (outside, on the periphery, and inside host coverage) and compared the below-ground ECM community between hosts with different levels of health.

This study reveals several interesting results: first, unlike the situation in older forests and secondary succession sites in which most above- and below-ground comparisons were performed previously (Gardes & Bruns, 1996; Peter *et al.*, 2001), the below-ground species composition corresponds well with the one above ground, in particular at the earlier successional stages. The study confirms the observed chronosequence, abundances and spatial patterns of the fungal species observed by the sporocarp inventories. This overlap might be explained by the much simpler community structure of ECM species in primary succession sites, as well as the intensive sporocarp production in both years of survey. This could have been due to the favourable environmental conditions for fruiting (Nara *et al.*, 2003), but may also be related to the life strategies of the fungal species in primary succession sites being considered to be those of ruderal species, with consequent large reproductive effort (Begon *et al.*, 1990). The overlap was less pronounced in larger hosts, in particular inside the coverage area, as well as in the ECM community associated with less healthy hosts. The main reason for this mismatch is that at these locations, a high percentage of the mycorrhizas (up to 25%) are formed by species which produce no (*Cenococcum geophilum*) or inconspicuous, easily overlooked (*Sebacina* sp., species belonging to *Thelophoraceae*) sporocarps. These species are usually very abundant (> 50%) in older forests (e.g. Gardes & Bruns, 1996; Peter *et al.*, 2001), and are mainly responsible for the discrepancy between the above- and below-ground abundances of ECM species in these sites.

Finally, the study by Nara *et al.* in this issue reveals that the ECM communities on the root system of more or less healthy *S. reinii* are significantly different. It shows not only that the sporocarp production is reduced or ceases in some species (e.g. *Scleroderma bovista*), but also that these species are unable to colonize or sustain growth with the amount of carbon supplied from the host. Nevertheless, the coloniza-

tion of species forming inconspicuous, resupinate sporocarps was supported under these conditions. These species may be able to use carbon sources other than the photosynthates provided by the host. Under stressed conditions, they might ensure the beneficial effects of the mycorrhizal symbiosis for the plant. The ECM community therefore may influence the growth and survival of *S. reinii* in the volcanic area on Mount Fuji.

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Key words: primary succession, mycorrhizas, ectomycorrhizas, ecosystem change, volcanic desert.

Letters

Ergosterol and mycorrhizal fungi – the way forward

Ergosterol and fatty acids for biomass estimation of mycorrhizal fungi are discussed in a *New Phytologist* article by Olsson *et al.* (2003). The findings indicate that arbuscular mycorrhizal fungi (AMF) do not contain ergosterol and thus cannot be assessed using an ergosterol assay. This speaks directly to a recent study in which we used ergosterol

analysis to estimate living AMF biomass in the root and soil (Hart & Reader, 2002a,b).

The results of Olsson *et al.* suggest that our results do not reflect AMF colonization but rather colonization by nonglomerular fungi. We feel that our results do reflect AMF activity for the following reasons. First, our ergosterol measurements were extremely low in nonAMF treatments, thus it is unlikely that there was a high degree of contamination solely in AMF treatments. Second, our ergosterol measurements were almost perfectly correlated with measures of per cent root length colonization (using uniquely AMF structures) and soil hyphal length (Hart & Reader, 2002b). Finally,

because our results showed high ergosterol in roots for the Glomaceae and high ergosterol in soil for the Gigasporaceae, the results of Olsson *et al.* would suggest that contamination in our study mirrored the pattern of AMF colonization. If this were the case, and contaminating fungi were so closely associated with AMF, then ergosterol would still provide a good, if indirect, estimate of AMF activity.

Olsson *et al.* have shown that, *in vitro*, two AMF isolates contain little ergosterol. In the future, it will be important to examine more isolates and more species. It remains to be seen how ergosterol production is affected by edaphic conditions because monoxenic cultures do not reflect the way in which AMF behave under natural conditions. More work needs to be done to discover the true origin of ergosterol in such studies. Is the ergosterol contaminant in origin and, if so, how is it so closely linked to AMF colonization? Or do AMF in soil behave very differently to monoxenic cultures?

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Key words: ergosterol, fatty acids, biomass estimation, mycorrhiza, colonization.

Nutrients and sink activity drive plant CO₂ responses – caution with literature-based analysis

I was excited to see a recent meta-analysis dealing with plant reproduction under conditions of elevated CO₂ (Jablonski

et al., 2002). A highly needed assessment. Literature-based syntheses of this type have the potential to contribute more to our understanding and the development of theory than often costly individual experiments. However, I was disappointed to find that this assessment will be of much less help than I had hoped because the analysis did not strictly stratify data based on the fertility of the growth conditions. A meta-analysis on CO₂ responses provides a rather limited advance unless we have a completely clear picture of the resource status of the test plants.

With adequate moisture, treatment variables other than nutrition are of almost negligible interest. For instance, CO₂ enrichment technology does not usually emerge as a major driver of responses. Pot size may matter, but it is not only the pot or its absolute size, but the pot size/plant size ratio and the amount of nutrients flushed through which are critical. Small pots (with a soft substrate) may become functionally large pots if highly fertilized, and species may show contrasting responses (McConnaughay *et al.*, 1996). So, selecting pot vs nonpot data misses the key issue, nutrition.

Furthermore, the analysis is based on 75% crop data and 25% wild species data. Because half of the wild species were grown like crops, and since a selection criterion was for species which completed a full life cycle (or most of it) under CO₂ enrichment, the results are, at a level of up to 88%, based on short-lived plants grown under nonnutrient limited conditions. Therefore the statistical power was insufficient to allow any conclusions to be drawn regarding non-fertilized, perennial wild plants.

The authors are not to blame for this bias in the experimental work available. However, it would have been better if the paper had made it obvious that this problem exists and that we have very little data from which to draw valid conclusions about reproductive efforts under elevated CO₂ for plants tested where they grow with no amendments other than CO₂ availability included (Thürig *et al.*, 2003).

I hope that it becomes more widely acknowledged that meta-analysis on aspects of ecological CO₂ research must account for the resource status of the test plants – otherwise I see little advance in our understanding. This was also a shortcoming of earlier attempts (Curtis & Wang, 1998; Wand *et al.*, 1999; Kerstiens, 2001).

The next most important criterion by which data should be grouped is plant age. I suggest a shift in emphasis in data treatment from technology-oriented or taxonomy-oriented criteria to those which control sink activity of plants – nutrition, moisture, developmental stage (Körner, 2001). As an example, the legume vs nonlegume separation of CO₂ responses does not often lead to differentiation in cases where plants are grown on substrates with natural (poor) P supply. The 'legume CO₂ effect' is an agricultural phenomenon at best rarely seen in nature, unless P is added or is naturally high – not a very common situation

in late successional plant communities (Stöcklin & Körner, 1999).

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