A CASE FOR CONSERVING PLANT PATHOGENS

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Abstract

A case is made for the counter-intuitive proposal that plant pathologists and plant pathological societies should consider the development of policies for the conservation of plant pathogens. First the report of the Royal Botanic Gardens, Kew, entitled *The State of the World's Plants and Fungi 2020,* is reviewed briefly. Next, the reasons why plant pathologists should take this report seriously are outlined and the risks to plant pathogen diversity assessed. In this section and all that follow, the paper focuses on fungal (*sensu lato*) pathogens, although it is suggested that the general principles developed apply to all plant pathogens, whatever their taxonomic status. There then follows an assessment of the significance of native plant pathogens in the functioning, stability and productivity of unmanaged and partially managed plant populations and communities. It is concluded that there is now compelling and growing evidence that very many do play such a role. Also assessed, more briefly, is the actual or potential value of plant pathogens to human activities, such as selecting for novel disease-resistance factors in evolving populations of wild crop relatives, developing novel, sustainable plant disease and weed control strategies, use in industrial processes and use as model systems for research. New and evolving genomics technologies are likely to facilitate significantly the study or selection of the benefits of plant pathogens to ecosystems or human activities. Potential strategies for the conservation of plant pathogens are outlined briefly, including in situ in unmanaged and partially managed ecosystems and centres of diversity of the progenitors of crop species, and ex situ in culture, spore, DNA, and herbarium collections. In these and many other areas of plant pathology, citizen science research groups have a potentially significant role. It is concluded that there is a strong case for plant pathologists and plant pathological societies to develop and act upon strategies for the conservation and sustainable use of plant pathogens.

1. SETTING THE SCENE: THE KEW REPORT 2020

This paper constitutes a case for the counter-intuitive proposal that we as plant pathologists should consider seriously the development of policies for the conservation of plant pathogens. It was stimulated first by the BSPP blogs of Nicola Hawkins and Fay Newberry entitled #wildplantdisease and @wildflowerhourchallenge, which rekindled memories of my presidential lecture to the 7th International Congress of Plant Pathology, 1998 (Ingram, 1999), and then by publication of *The State of the World's Plants and Fungi 2020*, a landmark conservation report from the Royal Botanic Gardens, Kew (Antonelli et al., 2020a; hereafter referred to as the Kew Report). This report was accompanied by the expert-reviewed papers in a special issue of the New Phytologist Foundation's journal *Plants, People, Planet* (https://nph.onlinelibrary.wiley.com/toc/25722611/2020/2/5) that drew on the collaboration of 210 research workers in 97 institutions across 42 countries. The report's findings may therefore be regarded as being comprehensive, rigorous and of international significance.

One of the principal conclusions of the Kew Report is arresting: c. 40% of plant species in the world are estimated to be under threat of extinction (Lugharda et al., 2020), an estimate derived by informed extrapolation from data published by the International Union for the Conservation of Nature (IUCN) in its *Red List of Threatened Species 2020-23* (www.iucnredlist.org). This list is the most trusted source for such information, with assessments for each species being based initially on the following criteria: geographic range, population size and population decline/increase. These criteria, together with threats to the individual species and to the ecosystems of which they are a part, especially from agriculture, biological resource use, natural system modification and residential and commercial development, lead to a determination of the category to which each species is assigned: 'extinct; extinct in the wild; critically endangered; endangered; vulnerable; near threatened; least concern; or data deficient'. The IUCN *Red List* is not comprehensive in terms of the entire world's flora, being based on only a c. 10% sample of the known total. However, the Kew Report estimate of the numbers of plant species thought to be under threat of extinction, having been determined by rigorous statistical analysis of the IUCN data, especially for the correction of bias, may nevertheless be regarded as sufficiently accurate to be a cause for grave concern to all plant scientists.

To put Kew's findings and conclusions into perspective, it is useful to compare them with those given in 1998 (Ingram, 1999). In that year the first ever *IUCN Red List of Threatened Plants* had just been published (Walter & Gillett, 1998). The conclusion then was that some 34 000 species, representing c. 12.5% of the world's flora, faced extinction. I noted that 34 000 species was roughly the equivalent of the then entire known flora of China and that the list included wild relatives of almost every major crop and forestry genus or group: *Brassica, Dipterocarpus, Hordeum*, *Musa, Oryza*, *Triticum* species were all included, for example, along with many others relevant to food production and the support of human societies. In essence, the only thing that has changed since 1998 is the proportion of the world's plant species estimated to be at risk, which more than tripled between then and late 2020.

It should be emphasized, as I also noted in 1998, that species are not of course the sum total of plant diversity. They are simply the most obvious and most easily measured components of biodiversity. Significant plant diversity is also found within species (Des Roches et al., 2021), as plant pathologists are well aware with regard to resistance and tolerance to plant pathogens (Wilkinson et al., 2020). The *IUCN Red List*, however, then as now, is an indicator of the genetic erosion that is most probably occurring at all levels in both wild (unmanaged) and semi-wild (partially managed) plant ecosystems (populations and communities), as well as among populations of (managed) agricultural and horticultural crops (Bélanger & Pilling, 2019). However, it is the rate, not merely the occurrence of change that is the critical factor. So, is the current rate of loss of plant genetic diversity faster than might be predicted? Rate is difficult to estimate and figures vary according to the taxonomic groupings and geographical locations of the plants assessed (Bélanger & Pilling, 2019; Antonelli, 2020; Lugharda et al., 2020), but it is clear from these publications that the current rates are sufficient to cause great concern.

2. REASONS WHY PLANT PATHOLOGISTS SHOULD TAKE PARTICULAR NOTE OF THE KEW REPORT 2020

Why, however, should we as plant pathologists, specifically, take this report seriously, apart from our duty as biologically trained citizens? Two reasons spring to mind immediately. Firstly, because invasive alien plant pathogens pose a risk to native (indigenous) plant species diversity, worldwide (Willis, 2018; Linders et al., 2019; Antonelli et al., 2020a; Lugharda et al., 2020), as was especially highlighted among the plant pathological community in 2020, the International Year of Plant Health (see also Harwood, et al., 2011; Fisher et al., 2012; Grünwald et al., 2019).

Secondly, because large-scale plant extinctions threaten food security, since many of the endangered species are the progenitors of present or future crops which plant pathologists are committed to protecting from disease, especially through the use of resistance factors derived from wild species (Savery et al., 2012; Bélanger & Pilling, 2019; Savery & Willocquet, 2020).

Often forgotten, however, is a third reason: that if a significant number of plant species and subspecies are at risk, their native pathogens, like their hosts, may be at significant risk too. The level of such risk will be proportional to their degree of specificity (not necessarily a characteristic restricted to obligate parasites; Bever et al., 2015; Wilkinson et al., 2019), and their ability to survive, with their infra-specific diversity intact, on alternative host species, including crops. Whatever the level of risk, it should be of concern for several reasons. Firstly, because indigenous (native) plant pathogens are major components of all unmanaged and partially managed plant assemblages, potentially contributing significantly to their complexity (Burdon, 1987; Ingram & Robertson, 1999; Alexander, 2010; Mordecai, 2011; Bever et al., 2015). Also, because wild progenitors of present and future crop plants co-evolve with their indigenous pathogens and this generates a diversity of disease resistance and tolerance factors that are major resources in producing new disease-resistant /tolerant cultivars, especially given recent developments in identifying such genetic variation and incorporating it rapidly and with precision into cultivars of major crop species (Bélanger &

Pilling, 2019; Kersey et al., 2020). Moreover, all plant pathogens will continue to be of actual or potential value to human societies as, for example: scientific research tools and model systems for study; biotechnologically important sources of novel, bio-sustainable human healthcare materials and strategies; enzymes for waste management or other industrial processes; disease control agents and bio-control strategies; food products; and energy sources (Antonelli et al., 2020b).

Therefore, it might reasonably be concluded that we as plant pathologists, whose traditional roles are the diagnosis and control of plant diseases in crops and ornamental plantings, counter-intuitively also have a role in helping to conserve plant pathogen diversity. In discussing this conclusion, my focus, like the Kew Report 2020 and because I am most familiar with them, will be on the Fungi, but here taken *sensu lato* to include also the fungus-like members of the Protista (Oomycota). However, the general concepts discussed and conclusions reached, I suggest, will be in a broad sense equally applicable to almost all plant pathogenic groups.

3. RISKS TO PLANT PATHOGEN DIVERSITY

The risks to plant pathogen diversity are even more difficult to estimate than for plants, not least because taking all members of the kingdom Fungi alone, whether pathogenic or not, the Kew Report 2020 reveals that although some 148 000 species have so far been identified, principally among the Basidiomycota and Ascomycota, it is estimated that c. 90% (c. 1, 332 000) of all fungal species remain to be described by science, especially because of their often cryptic natural history. Not all of these will be plant pathogens (Willis, 2018), of course, and an exact proportion is as yet impossible to determine accurately, but some sense of scale may be derived from the work of Dietzel et al. (2019), who estimated that in the United States of America, with its wide climatic range, c. 21.5 % of the total fungal community in outdoor dust samples were determined to be ‘putative pathogen’ spores.

The potential threat to plant pathogens resulting from loss of host diversity has already been discussed above. In addition, the external factors constituting risks to fungi in general, including plant pathogens, and the ecosystems of which they are a part (Antonelli et al., 2020a; Lugharda et al., 2020), include residential and commercial development, biological resource use, agriculture and aquaculture, and natural system modifications, with, not surprisingly for fungi, pollution and climate change following closely.

4. POSITIVE VALUE OF PLANT PATHOGENS IN UNMANAGED AND PARTIALLY MANAGED PLANT POPULATIONS AND COMMUNITIES

Next it is necessary to examine the validity of my claim concerning the positive value of plant pathogen diversity, beginning, arguably most importantly, with the significance of native (indigenous) plant pathogens as components of plant assemblages of various kinds and in various contexts.

4. 1. Significance of native (indigenous) plant pathogens in native plant populations and communities

Interspecific competition has long been regarded as the principal driving force in the organization of unmanaged and partially managed plant communities (Tilman, 1982). Various mechanisms have been suggested for this, including resource partitioning, variation in life histories, and the effects of animal feeders such as herbivores and seed consumers. During the last thirty years, however, increasing research interest among ecologists has focused on the possible role of plant pathogens.

The immense damage inflicted on unmanaged and partially managed native plant populations and communities by invasive alien pathogens points up the significance of the co-existence of plants and pathogens that is normally the case in un-invaded native communities. To achieve such a state, the co-evolution of plants and pathogens in such communities would, in theory, need to be regulated by a trade off between the costs of virulence to the pathogens and of resistance to the plant hosts. If the costs of both were relatively high, co-evolution might thus promote the maintenance of plant genetic variation (Sasaki, 2000), a point that I shall return to later (see discussion of the review of Bever et al., 2015).

As an observer of the natural world, both as a plant pathologist and a botanist, it has long been clear to me that native pathogens are ubiquitous among virtually all unmanaged and partially managed populations and mixed communities of plants, whatever their taxonomic level from mosses and liverworts to flowering plants and trees (see for example, Ingram & Robertson, 1999). On the balance of probability it has always seemed that populations of growth limiting organisms such as pathogens would have a positive role in the organization of plant communities (Ingram, 1999 & 2002), only fuelling imbalance when circumstances changed, such as short term weather perturbations, longer term climate changes (Helfer, 2014; Burdon & Zhan, 2020), or the introduction of alien diseases, as with *Cryphonectria parasitica*, cause of chestnut blight, *Ophiostoma novo*-ulmi, cause of Dutch elm disease and many other plant pathogens (Anagnostakis, 1987; Harwood et al., 2011; Roy et al., 2014). Despite strong evidence from the study of individual plant pathogen systems, however, definitive scientific evidence for a significant and widespread, positive ecological role for pathogens in plant communities has until recently remained elusive (Burdon, 1987; Alexander & Holt, 1998; Gilbert, 2002; Burdon et al., 2006; Alexander, 2010; Mordecai, 2011), although a clearer picture now seems to be emerging (Bever et al., 2015).

Despite the outstanding research of such authors as those listed above, and the many other authors they cite, two factors seem to have impeded progress. The first is the traditional roles of members of the disciplines of plant pathology and ecology, the former to control diseases in managed, genetically relatively uniform crop plants, and the latter to study the causes of patterns in genetically complex natural ecosystems (Tilman, 1989). With notable exceptions (see, for example, Burdon, 1987; Wolfe, 2000; Jeger et al., 2013; Burdon & Zhan, 2020) this has often resulted in a partitioning rather than a sharing of knowledge and understanding that might have contributed significantly to the missions of both.

The second factor has been the dauntingly immense diversity among the pathogens that may infect unmanaged and partially managed host populations and mixed species communities of plants, making experimentation and modelling extremely challenging. Taxonomically, this diversity embraces non-cellular Viruses, Bacteria (Prokaryota) and Fungi and Protista (Eukaryota). At the species and sub-species level such diversity becomes immense, even incalculable in the case of poorly studied host-pathogen interactions. Such taxonomic diversity (Ingram, 2002; Alexander, 2010) may be reflected in a number of aspects of pathogenicity, for example:

- trophic strategies (holobiotrophy, hemibiotrophy and necrotrophy);
- eco-physiological strategies (facultative parasitism and ecologically obligate or physiologically obligate parasitism);
- host specificity (expressed at a variety of levels, ranging from highly specific to generalist at the level of the host family, with such specificity often reversed when measured at other taxonomic levels such as *formae speciales* (Wilkinson et al., 2019);

- physical and genetic complexity of pathogen life cycles, including the role of vectors in some.

The visible effects of such pathogen diversity on the ecology of hosts may be described in relatively straightforward terms as follows (Burdon 1993; Alexander, 2010):

- rapid death of the host (especially in the case of soil borne diseases affecting seeds or seedlings, or certain rapidly developing necrotrophic infections such as root rots and some vascular wilts;
- reduced overall aerial growth or vigour, resulting in fewer nutrients being available for reproduction (foliar lesions, from biotrophy to necrotrophy, and tumours and cankers); and
- reduced seed production, which may be caused either directly by invasion and prevention of pollen or embryo production by anthers or ovules, respectively, or indirectly as a result of reduced seed development and consequent loss of seed longevity and viability, resulting from pathogen induced diversion of nutrients or physical diminution of leaf areas available for photosynthesis.

However, in all of these visual categories, the situation described is significantly more diverse when studied genetically, metabolically and ecologically at the level of individual plant-pathogen systems. This diversity becomes yet more complex when interaction with mutualistic or commensal partners such as mycorrhizal fungi, rhizosphere and phylloplane microorganisms in soils or on leaves, respectively, or endophytic microorganisms of roots and leaves are taken into account.

Given the relatively small body of research on the potential, positive role of pathogens in ecosystems carried out so far, it is not surprising that it took so long for the following statement to emerge in the ecological literature: ‘we present strong evidence that pathogens play a critical role in structuring plant communities and maintaining plant diversity’ (Bever et al., 2015). Before examining this and the other conclusions of Bever et al. (2015) in detail, it is useful to outline the recent history of the subject, as set out in comprehensive reviews by Alexander (2010); Mordecai, 2011; & Bever et al. (2015).

4.1.1 Alexander (2010)

When reviewing the situation critically in 2010, Alexander, explored in detail the diversity of native pathogens and their ecological impact in unmanaged and partially managed populations and communities by focusing on a range of levels of ecological organization. These included the effects of disease on survival and reproduction of: individual plants within a single species; numbers of plants comprising a population (‘population size’) and how this changes with time (‘population dynamics’); and the composition, stability, dynamics and productivity of mixed species communities. She also included studies made at the larger scales of meta-populations and meta-communities (many separate populations or communities, respectively, spread across wide geographic areas), and even at the level of regional and global distributions of species.

In evaluating and comparing the research, Alexander first emphasized the significance of two seminal books: *Population Biology* of *Plants* (Harper, 1977) and *Diseases and Plant Population Biology* (Burdon, 1987). These were rightly seen as landmark publications, together analyzing the effects of pathogens on unmanaged and partially managed community structure and dynamics, as well as on the ecological consequences of this. In both cases, significantly, work with crop species was also drawn on, especially relating to the gene for gene hypothesis of Flor (1956) and the epidemiological work of van der Plank (1960).

As efforts to understand the significance of plant pathogens in natural ecosystems advanced, the long term studies of two groups (see Alexander, 2010 for details) were also seminal: that of Burdon and Thrall, who studied, principally but not exclusively, the genetic variation for resistance in wild Australian flax (*Linum marginale*) to anther smut (*Melampsora lini*); and that of Antonovics and collaborators, who studied and mathematically modelled the long term spatial and temporal patterns of disease in *Silene latifolia* infected by anther smut (*Microbotryum violaceum*).

Alexander (2010) also summarized and analyzed her own research and that of many others on the possible role of a wide range of specific, and generalist host-pathogen combinations in the soils and aerial environments of unmanaged and partially managed communities, including temperate and tropical forests, grasslands and pastures with various levels of tree and shrub cover, mountains, wetlands and coastal habitats. This comprehensive review led her to conclude, firstly and unsurprisingly, that in unmanaged and partially managed populations of single plant species, native pathogens may reduce host survival and reproduction of individual plants, and that more extensive outbreaks may sometimes limit population expansion. With regard to mixed communities, she concluded, significantly, that to provide the most meaningful information, ecological studies of pathogens must proceed in tandem with genetic investigations and ‘evolutionary ecological’ research to unravel such occurrences as host switches in the specificity of a pathogen (e.g. Morris & Benoît, 2019).

Alexander (2010) further concluded that studies to date had shown that at the complexity level of a community of many plant species, diseases might in some cases lead to increases in plant diversity, and in others to decreases, so by inference clear generalizations would therefore be inappropriate. She also noted that work with relatively non-host-specific (‘generalist’) pathogens was especially significant. Examples included studies of the ecological outcomes from:

- shared pathogens (e.g. ‘spillover’ from one species to another; Mordecai, 2013);
- ‘apparent competition’ (e.g. negative, indirect interactions between different plant species that are susceptible to the same enemy species; Holt & Bonsall, 2017) ;
- the significance of host ‘phylogentic relationships’ in determining host ranges.

She also highlighted research on ‘feedback’ between different soil microbial (including plant pathogen) communities and individual plant species, because this might help to explain the balanced co-existence of complexes of species in some plant communities.

Finally, Alexander (2010) commented that then recent research had suggested that changes in temperature, greenhouse gases and nutrients could alter disease levels in communities, and that plant diseases and their effects may sometimes also alter ecosystems on a wider scale (see ‘Global change’, below).

4.1.2 Mordecai (2011)

In the context of making a plea for what she described as ‘greater conceptual unification’, Mordecai (2011) covered much of the same ground as Alexander (2010), although structured somewhat differently, as follows:

- the Janzen-Connell hypothesis (see Janzen, 1970 and Connell, 1971; that specialised natural enemies, such as plant pathogens, promote and help to maintain diversity in plant communities by reducing the survival of

conspecific seeds and seedlings close to reproductive adults, or in areas of high conspecific density);
- plant-soil feedback (a process whereby plants alter the abiotic and biotic qualities of the soil in which they grow, which then alters the ability of plants to grow in that soil subsequently);
- competition-defence trade-offs among the hosts of plant pathogens;
- escape of invasive alien plants from their native pathogen load;
- and epidemic-driven population changes.

She concluded with an outline of what she described as ‘an emerging theoretical framework’ for understanding the basis of plant species co-existence to include various pathogen impacts on communities. However, she suggested that although theoretical, observational and circumstantial evidence generate predictions about how various modes of pathogen attack might affect plant co-existence, ‘surprisingly, no study gives direct empirical evidence for effects on mutual invisibility, a key criterion for co-existence’.

4.1.3 Bever, Mangan & Alexander (2015)

Five years later a clearer picture seemed to be emerging: Bever, Mangan & Alexander (2015), in their scholarly analytical review in which particular emphasis is given to research on temperate and tropical forests, provide persuasive evidence that plant pathogens have a key role in the structuring of many unmanaged and partially managed plant communities and of maintaining plant species diversity within them.

The majority of Bever et al.’s (2015) evidence for coming to their conclusion arises, they suggest, from five earlier lines of study:

- observations and experiments in forests based on hypotheses concerning the maintenance of the diversity of trees species proposed by Janzen (1970) and Connell (1971);
- development by Bever (1994) and Bever et al. (1997) of experimental approaches to, and the theoretical framework for, plant-soil feedback;
- research arising from the above, when integrated with forest demographic studies, strongly suggesting that soil pathogens structure plant communities (Mangan et al. 2010);
- increasing credibility of the proposal that the success of invasive alien plant species is dependent on escape from their native pathogen load (‘enemy release hypothesis’; Keane & Crawley, 2002; Callaway et al., 2004), suggesting by implication that plant pathogens contribute positively to the mechanisms regulating co-existence in mixed populations of native plant species (Mitchell et al., 2006);
- research suggesting that plant pathogens play a critical role in observed correlations of increased biomass productivity and stability with increasing diversity (Maron et al., 2011; Schnitzer et al., 2011; Hendriks et al., 2013).

Later, they emphasize the immense impact of invasive alien pathogens on native plant populations and communities by reference to the effects of, for example, *Ophiostoma novo-ulmi* (Dutch elm disease), *Chryphonectria parasitica* (chestnut blight) and *Phytophthora ramorum* [and *P. kernoviae*] (sudden oak death) (Roy, 2014). By reference to Alexander (2010), they contrast this with the apparently less dramatic, but significant positive role of native pathogens in the population dynamics of many native plant communities. Comparisons such as these, they suggest, point up the significance of the balanced co-existence of plants and pathogens in un-invaded native plant communities. The co-evolution of plants and pathogens in such communities would in theory, they propose, need to be regulated by a trade-off between the costs of virulence to the pathogens and of resistance to the plant hosts. If the costs of both were high, co-evolution might promote the maintenance of plant genetic variation (Sasaki, 2000).

After carefully building on all of these themes, Bever et al. (2015) reach conclusions that I paraphrase as follows.

Theoretical analyses suggest that plant pathogens could potentially have a role in maintaining the balance among different plant species in mixed communities through: trade-offs between the inherent competitive ability of individual plant species and the cost of resistance to pathogens; or differences in the magnitude of the build-up of specific pathogens on individual plant species. Both of these theoretical proposals are strongly supported by empirical evidence, as follows.

- Experimental variation of individual host-pathogen systems provides evidence to confirm the suggestion that the maintenance of co-existence among plant species may be achieved via trade-offs between competitive ability and resistance to disease;
- Although there are relatively few direct experimental demonstrations of the part played by host specificity of pathogens in regulating co-existence in individual host-pathogen systems, there is clear evidence that build -up of host-specific pathogens has often been apparent in observations of, and experiments on, the strong negative feedback through soil communities manifest as reductions in the survival and rate of growth of seedlings near adult trees of the same species (Janzen-Connell hypothesis).

A combination of such theoretical and empirical research, Bever et al. (2015) suggest, provides the most compelling evidence so far for ‘the importance of plant pathogens in regulating the structure of plant communities.’

- Additional support for this conclusion, they propose, derives from evidence that plant species demonstrating relatively strong negative feedback occur in relatively low numbers in mixed communities, and simulations that demonstrate that this pattern only occurs when negative feedback underpins the co-existence of plant species.
- Such experiments are also supported, they propose, by the circumstantial evidence that escape of invasive alien plants from their native pathogens, and from evidence that pathogen build-up in communities with a relatively low diversity of plant species may be responsible for the positive association of productivity and diversity observed in experiments.

Finally, they propose that the evidence outlined above constitutes what they describe as ‘a promising foundation on which to build a general framework for understanding the dynamics of plant communities and the large-scale patterns of plant diversity’.

4. 2 Grasslands for livestock production: a special case?

Before leaving the issues discussed in 4.1, above, and without intentional prejudice on my part to the very compelling conclusions of Bever et al. (2015), I draw attention to an interesting paper by Jeger et al. (2013) concerning grassland ecosystems. These, which the authors suggest may account for c. 40 per cent of the earth’s land surface, range from minimally cultivated grasslands used in rotation or as semi-permanent leys for raising livestock, to largely undisturbed or deliberately conserved ecosystems. The authors point out, however, that most of the research on the impact and role of pathogens on grassland systems has been based on grasslands used for forage production or livestock grazing, and that a comprehensive review of the large body of knowledge and understanding arising from such research is long overdue. In pursuit of this goal they offer as a starting point a most valuable summary analysis of recent key research papers on the subject, after which they describe in detail studies of two plant-pathogen systems in the very long-term Park Grass Experiment at Rothamsted Research, UK: *Tragopogon pratensis-Puccinia hysterium* and *Holcus lanata-Puccinia coronata*.

The conclusions of Jeger et al. (2013) I paraphrase as follows.

- Plant death resulting from disease is not necessarily required for the regulation of plant populations [and communities] by plant pathogens.
- Soil seed banks influence both the qualitative and quantitative dynamics of natural plant populations [and communities], a factor relatively understudied in field-based research on the impact and role of disease in native plant populations.
- Responses such as adaptation and evolutionary changes in response to disease may alter the ecology and population dynamics of individual species in grasslands over longer timescales, thereby altering community composition and levels of biodiversity.
- Most approaches to the improvement of grasslands for human purposes involve the use of fertilizers. However, the effects of fertilization practices on grassland disease dynamics, host adaptive responses and species diversity remain poorly understood and merit further study.
- That in the studies of the authors, the co-existence of different plant species in natural plant communities on an evolutionary timescale does not appear to be completely explained by biological processes such as what they describe as ‘frequency dependent infection and

competition interactions’, although there is evidence that these may have an effect over ‘ecological time scales’.
- That the distinction between unmanaged, partially managed and managed plant populations and communities is an indistinct continuum rather than a stepwise progression and this needs to be kept in mind when comparing one with another.
- Finally, that studies of grassland diseases and their significance in the regulation and structuring of unmanaged and partially managed grassland communities benefit significantly from combining observational, experimental and modelling methods. Also, and in my view most significantly, on integrating plant pathological and ecological research methods. They suggest that studies of grasslands would be ideal for such integrated approaches, not least because in their management there is a continuum of a wide range of management inputs. I would simply add that for Harper (1977) and Burdon (1987) this principle seems to have applied equally to all plant communities from the outset.

4. 3 Global change

A final and most significant conclusion in the reviews of all the authors discussed in 4.1 and 4.2 above was that ecological studies of plant diseases in unmanaged and partially managed plant populations and communities should be seen as significant components of global environmental change research, especially that relating to climate change. This topic is of great significance to human health (Suk & Semenza, 2011; Lindgren et al., 2012), and has been reviewed recently with respect to plant disease by at least two authors. First, Helfer (2014), deals with the influence of global change in the widest sense on a specific group of foliar plant pathogens, the Uredinales (Rust fungi); and secondly, Burdon & Zhan (2020) consider the effects of climate change only, but in the wide sense of its effects on all plant disease diseases whether in managed, partially managed or unmanaged plant communities.

Helfer (2014) first emphasizes that the Uredinales are significant components of most unmanaged and partially managed plant communities and their functioning, and would probably be particularly vulnerable to environment change given their biotrophic association with their hosts, and their complex, weather- and often insect-dependent life cycles. Based on his own experience and the published literature, he concludes that under conditions of predicted global change scenarios, some host-rust combinations would decline, others would remain as now, while some might become more widespread. For example: some rusts of the Poaceae are negatively affected by higher temperatures and elevated levels of atmospheric carbon dioxide; rust diseases of trees are favoured by elevated atmospheric ozone levels, but not those of grasses; while the combined effects of carbon dioxide and ozone are intermediate. Significantly, however, Helfer suggested, the major world wide drivers of the geographical range of rusts and their hosts appeared to be international trade, host genetic homogenization and the regular occurrence of favourable environmental conditions, most notably moisture. Finally, Helfer noted that although rusts usually flourish in high humidity conditions, they also often survive in desert habitats, and taken as a group their environmental tolerance is significant.

Burdon & Zhan (2020), in the conclusions to their discussion paper (essentially a plea for a greater research effort) first note that the effects of climate change on the occurrence, severity and geographic range of most plant diseases is equally relevant to both managed horticultural and agricultural production and to the structure and diversity of unmanaged and partially managed (‘natural’) plant communities. Some components of the effects of climate change on the former, they say, seem to be relatively easy to forecast and mitigate. In contrast, the consequences for plant-pathogen interactions in complex, unmanaged and partially managed plant populations and communities, the results of the multiplicity of changes that might follow significant climate change, have still not been explored in detail. Gaining an understanding of the nature and drivers of such changes, they suggest, will be essential in developing appropriate and effective conservation strategies, especially for ecosystems that cross large environmental boundaries or which occur in areas where climate change is predicted to have a major impact, especially the fragile boreal zone(see, for example, Faticov et al., 2021) .

4. 4 Conclusion

The overarching conclusion of the papers discussed in 4.1-4.3 above is that native plant pathogens are significant inherent components of unmanaged and partially managed ecosystem diversity, complexity and productivity as a whole and as such should be conserved, *in situ,* just like any other group of organisms present. Whether they are significant mediators in the balanced development of unmanaged and partly managed mixed plant communities (ecosystems) in all cases studied, or only some, is beside the point. That the research on this topic is still not as wide-ranging as it could be, is itself an argument for conservation (application of the precautionary principle). And of course, plant pathogens will always have a place in unmanaged and partially managed ecosystems by inducing decay and nutrient cycling.

5. VALUE OF PLANT PATHOGENS TO OTHER HUMAN ACTIVITIES

In addition to their significance in regulating the balanced co-existence of populations and communities of plant species in unmanaged and partially managed ecosystems, plant pathogens in the widest sense are, or have the potential to become, of great practical value to human societies in a diversity of other ways. Example are reviewed briefly below.

5.1 Selecting for novel disease-resistance factors in evolving populations of wild crop relatives

Wild progenitors of present and future crop plants have co-evolved with their native pathogens over millenia and this has generated a diversity of disease resistance and disease tolerance factors in their hosts. Such genetic source material has already played a significant role in breeding for resistance to diseases, especially in the case of wheat (e.g. Dinoor, 1977; Wahl et al., 1984; Kersey et al., 2020). Now, recent advances in DNA sequencing technologies have significantly improved the ability to identify and use genetic diversity from wild crop progenitors and to speed up the breeding cycle, while the development of CRISPR/Cas9 gene editing technology has increased the ability to introduce novel genetic variants without extraneous genetic material (Kersey et al., 2020; Yu et al., 2021). Such developments strongly suggest that co-evolving wild host-pathogen systems, with carefully drafted legislation (Anon., 2021a), are set to become increasingly significant resources for plant breeders in producing new disease-resistant/tolerant cultivars of most major crops

5. 2 Development of novel disease control strategies

The study of unmanaged communities of the wild progenitors of present and future crop plants co-evolving in relative balance with their native pathogens (see Alexander, 2010) has already suggested novel strategies for the non-chemical control of disease in crops, for example the use of disease-resistant cultivar multi-lines and mixtures (e.g. Browning, 1974; Wolfe, 1985 & 2000; Zhu et al., 2000). Now, with knowledge of the co-evolution of plant pathogens with their hosts and the mechanisms of interaction between them and other associated microorganisms advancing rapidly (e.g. Bever et al., 2015), it is highly likely that further novel strategies for the non-chemical control of disease will emerge in the future.

5. 3 Weed control

Plant pathogens of all types, including fungi, have potential as sustainable weed control agents (Harding & Raizada, 2015). Indeed, researchers at the agro-research organization CABI (www.himalayanbalsam.cabi.org; last accessed 20 March 2021) have recently found that a previously unidentified rust fungus, *Puccinia komorovii* var. *glandulifera,* which is highly specific to Himalayan Balsam (*Impatiens glandulifera*) in its indigenous range in Himalayan foothills, may have potential as a biological control for this pernicious and ecologically damaging invasive alien plant species in the UK landscape. It must be borne in mind, however, that in using plant pathogens as weed control agents, there will always be the danger that the pathogen might itself adapt genetically and become an invasive alien on plant species related to the target species.

5. 4 Use in industrial processes

The kingdom Fungi represents a major resource relatively unexplored for its value to industry (Willis, 2018; Antonelli et al., 2020b, Kersey et al., 2020; Simmonds et al., 2020). Current and potential applications of either fungi or their products include: generation of bioenergy (see also Grace et al., 2020); production of pharmaceutical and other healthcare products (see also Howes et al., 2020); food and drinks manufacture (see also Ulian et al., 2020); management of waste, including the bioremediation of soil and water; and manufacture of plastics and biomaterials.

Although most of the present usage of fungal enzymes and products for such purposes comes from saprotrophic species, future explorations for sustainable use, enhanced in their precision by recent knowledge of metabolic pathways derived from genomic analysis (Kersey et al., 2020) will, I suggest, involve fungal pathogens, especially necrotrophic species.

5. 5 Value as model systems for scientific study

The role of studies of *Agrobacterium tumefaciens*, cause of crown gall disease, in the development of the techniques of plant genetic manipulation is legendary. Less well appreciated is that many other plant host-pathogen systems such as *Malus-Venturia inaequalis*, one of the first combinations in which Flor's proposals concerning the gene-for-gene relationship was demonstrated (see Bus et al., 2011), have over many years become classic models to be built upon for study of fundamental aspects of plant-pathogen interaction. Such collections are invaluable, often irreplaceable and should be added to by later researchers, yet are often at risk for reasons of funding, retirement or moving-on of the individual who assembled them, or closure of a research programme. It is I suggest, essential that such working collections, built up by plant pathologists over long periods, should be conserved and curated for future use. Although beyond the scope of the present discussion, there is an urgent need for a detailed case to be developed to support the provision of resources by funding bodies and plant pathological societies for such initiatives.

It would be invidious to say here which of the present UK collections, for example, should be earmarked for conservation. I would suggest that the 'top ten lists' of plant pathogens compiled by the journal *Molecular Plant Pathology* might provide a useful starting point for consideration of the matter:

Viruses (Scholthof et al., 2011); Bacteria (Mansfield et al., 2012); Oomycetes (Kamoun et al., 2015); and Fungi (Dean et al., 2012).

6. CONSERVATION OF PLANT PATHOGENS

Plant pathologists already and routinely conserve plant pathogen diversity in culture collections associated with particular research activities (see 5.5 above). In my view, however, the arguments in sections 1-5 constitute sufficiently valid reasons for plant pathologists to consider seriously the subject of plant pathogen conservation in a wider sense . It is, therefore, important to outline briefly what conservation strategies might be available.

6.1 In situ conservation of native plant pathogens with their hosts

The conservation of evolving plant populations and communities with their pathogens, ex situ, as in the Rothamsted Research grasslands (Jeger et al., 2013), may be important for empirical studies, but for the most part in situ conservation in fully functioning ecosystems is the only way forward since it is only by this means that the complex pathogen interactions on the phylloplane, within the plant (endophytes) and in the rhizosphere are conserved with their host plants. This means, when devising conservation strategies for plant communities, account is taken of the pathogens and their biology as well as the plants themselves (Helfer, 1993; Burdon, 1998).

Plant pathogen populations, especially at the infraspecific level, are often distributed unevenly within plant populations and communities (personal observations and see the reviews discussed in section 4). Great care must therefore be taken to ensure that areas chosen for conservation embrace as many elements as possible of pathogen diversity. This requirement presents a significant challenge, however, since knowledge and understanding of the biology, life cycles, epidemiology and ecology of pathogens of wild plants is on the whole very limited (see, for example, Helfer, 1993, regarding rusts on rare plants in the UK, and Chater et al., 2021 concerning white moulds [*Ramularia* and *Phacellium* species] in Wales). It is axiomatic, therefore, that if the conservation of plant pathogen diversity in situ is to be effective, significant progress needs to be made to increase knowledge of their biology and to develop effective ways of surveying and monitoring their presence and distribution at both the species and infraspecific levels. Increasing knowledge of native pathogen biology at a professional level will require changes to plant pathology curricula for undergraduate and post-graduate courses, and a drive to encourage more post-graduate and post-doctoral research on plant pathogens in unmanaged and partially managed plant populations and communities, especially through collaboration with member of cognate disciplines, most notably ecology.

Surveying and monitoring pathogen diversity even at the species level is particularly labour intensive and in the case of soil-borne diseases presents significant challenges. In conservation it is important to think internationally, but often to act locally. In my local (i.e. UK) experience, recruiting the assistance of local citizen science groups, including and/or in collaboration with professional plant pathologists, is especially effective for visual surveys of holobiotrophic and hemi-biotrophic pathogens. One group whose work I have followed in the UK is the Welsh Microfungi, s.l. Group (formerly the Welsh Rust Group), which has recently surveyed the occurrence and conservation status of Rusts (Uredinales), Smuts (Ustilaginales) and allied fungi, Powdery Mildews

(Erisyphales), Downy Mildews (Peronosporaceae) and White Blisters (Albuginaceae), and White Moulds across Wales (Woods et al., 2015; Woods et al., 2018; Chater and Woods, 2019; Chater et al., 2020; Chater et al., 2021). Another UK survey, at a much earlier stage of development, is the work of the Wyre Forest Study Group (Westwood et al., 2015), currently surveying foliar pathogens in the Wyre Forest of the West Midlands, England (Ingram & Winnall, 2020), which records its findings in *The Wyre Forest Study Group Annual Review.*

The value of social media in promoting the importance of plant pathogens to citizen science research groups and among other interested professionals cannot be overestimated (see, for example, the work of Nicola Hawkins, Fay Newbery and the British Society for Plant Pathology in launching, in August, 2020, #wildplantdisease and @wildflowerhour challenge.

For further information concerning the possibilities offered by citizen science see Bonney & Cooper, 2016; and Skarlatidou & Haklay, 2021).

Monitoring the occurrence of necrotrophic plant pathogens, especially those in more challenging environments such as soils or water, requires, of course, professional laboratory culture and identification techniques and expertise. At present such research is highly labour intensive, but in the relatively near future genomic science may offer more effective solutions. For example, methods for the DNA barcoding of plants as tools for use in conservation-related and environmental surveys are well advanced (Hollingsworth et al., 2016; Kress, 2017) and, although less well developed, rapid strides are currently being made in fungal DNA barcoding for similar purposes (Xu, 2016; Truong et al., 2017; Lücking et al., 2020; Kulik et al., 2020).

It is important to point out that in a period of rapidly evolving approaches to and justification for the conservation of species (see Antonelli et al., 2020a; Maxwell et al., 2020; Anon., 2021b), plant pathogens conservation should be pursued in collaboration with international and national government conservation agencies and/or respected non-governmental conservation organizations, and with due regard to national and international conservation law, including that relating to benefit sharing (Williams et al., 2020). Also, it should be pursued in such a way, if possible, as to help rather than hinder its use for legitimate scientific purposes (Williams et al., 2020). Finally, it should be noted that a danger posed by the in situ conservation of plant pathogens is that certain species, especially those exhibiting a high level of host specificity, such as some members of the Uredinales and Ustilaginales, may pose a threat to populations of an endangered host species (Helfer, 1993; Ingram, 2002; Alexander, 2010). In such cases, the pathogen conservationist must decide, in collaboration with the appropriate professional field conservationist, how best to proceed: whether to conserve the vulnerable population of the host at the expense of the pathogen, or vice versa.

6.2 In situ conservation of plant pathogens on the wild progenitors of crop plants

More problematic is the notion of conserving in situ evolving host-pathogen systems in the centres of origin and diversity of appropriate crop species to ensure a continuing supply of genes for resistance for the plant breeder or scientist (Wood & Lenné, 1997, 1999). Such an approach was first mooted for wild cereal species by Browning (1974), who proposed the name ‘living gene parks’ for the resulting reserves, and later by Dinoor & Eshed (1990), who suggested the name ‘genetic reserves’. Although the idea seems attractive at first sight, it is still not clear whether sufficient is known about the biology, epidemiology and population genetics of populations of pathogens and their hosts in agro-ecosystems and in natural ecosystems (see Alexander, 2010 and Bever et al., 2015) to manage such reserves safely. The existence of reservoirs of pathogen inoculum, inevitably close to cultivated host crops, in resource-poor regions of the world, especially those that are war zones, could have consequences for local food security and economics. The global consequences of the accidental spillover of novel, highly virulent forms of plant pathogens, particularly during a period of global environmental change, as now, has been comprehensively documented for many major crops by Bebber et al. (2014) and for Race Ug99 races of *Puccinia graminis*, a threat to world wheat production, by Singh et al. (2011).

6.3. Ex-situ conservation: culture, spore, DNA natural history and herbarium collections.

6.3.1 Culture, spore, DNA and herbarium collections

This strategy, which has already been mooted with regard to culture collections of pathogens used in specific scientific research projects (see 5.1, above), potentially offers a safer way forward for the pathogens and potential pathogens of crop plants. The World Data Centre for Microorganisms gives a good picture of microorganisms stored internationally. Despite recent progress in storage, however, problems remain (Ryan et al., 2019; Paton et al., 2020; Pearce et al., 2020). For example: only a small proportion of the world's pathogens are currently stored; the geographical distributions of pathogens in collections is poor, with the USA and Europe over represented and other continents under represented; many plant pathogen species have not been described or have been poorly studied; obligate pathogens present a particular challenge, although there has been significant progress in developing advanced cooling technology in recent years, which offers hope for the storage of such organisms or their propagules. Despite these problems, it should be noted, however, that the recently established UK Crop Microbiome Cryobank UK-CMCB is working to widen the coverage of fungi and bacteria held in culture and spore collections.

Finally, natural history collections, including fossils, and herbarium collections of pressed and preserved plants held by botanic gardens, natural history museums and universities worldwide (Harmon, Littlewood and Wood, 2019; Paton et al., 2020; Ristaino, 2020), offer unique facilities for studying the history of diseases, whether caused by animals or plants, and their changes and distribution over very long period of time.

6. CONCLUSIONS

The report of the Royal Botanic Gardens, Kew entitled the *State of the World's Plants and Fungi 2020* is a most important document that should be taken very seriously by plant pathologists, since the risks to plant pathogen diversity are considerable. This is of great concern because there is very strong and growing evidence for the positive and significant role of native plant pathogens in the functioning, stability and productivity of unmanaged and partially managed plant populations and communities. Moreover, plant pathogens or their products have major current and potential future roles in many human endeavours, including selecting for novel disease resistance and tolerance factors in evolving populations of wild crop relatives, developing novel, sustainable plant disease and weed control strategies, and use in industrial processes, such as the production of drugs and other healthcare products, waste disposal and soil and water remediation, the production of biofuels, and acting as model systems for research. There are various possible approaches to the conservation of plant pathogens, including: in situ, in unmanaged and partially managed ecosystems and centres of diversity of the progenitors of crops; and ex situ in collections such as those of plant pathogen cultures, spores, DNA and pressed and preserved plants (herbaria). The developing technologies of plant genomics are likely to be important in all of the studies and applications discussed, as will citizen science research groups, especially in carrying out surveys of the distribution and conservation status of native plant pathogens. It is concluded, on the basis of the evidence presented, that there is a compelling case for plant pathological societies to develop policies for the conservation and sustainable use of plant pathogens of all kinds. It is strongly recommended that such strategies should be undertaken in close collaboration with: other plant-based societies and groups, especially those concerned with ecology; citizen science groups; and appropriate, reputable international, national and local governmental and non-governmental organizations for the conservation and sustainable use of species and ecosystems.

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