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Emerging oomycete threats to plants and animals

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Oomycetes, or water moulds, are fungal-like organisms phylogenetically related to algae. They cause devastating diseases in both plants and animals. Here, we describe seven oomycete species that are emerging or re-emerging threats to agriculture, horticulture, aquaculture and natural ecosystems. They include the plant pathogens *Phytophthora infestans*, *Phytophthora palmivora*, *Phytophthora ramorum*, *Plasmopara obducens*, and the animal pathogens *Aphanomyces invadans*, *Saprolegnia parasitica* and *Halioticida noduliformans*. For each species, we describe its pathology, importance and impact, discuss why it is an emerging threat and briefly review current research activities.

This article is part of the themed issue 'Tackling emerging fungal threats to animal health, food security and ecosystem resilience'.

1. Introduction

Oomycetes, or water moulds, are fungal-like eukaryotes classified as stramenopiles, and are phylogenetically grouped with diatoms and brown algae [1–4]. They are among the most problematic group of disease-causing organisms in both agriculture and aquaculture, and represent a recurrent threat for global food security. Oomycetes cause some of the most devastating plant diseases affecting crops, ornamental plants and trees. They result in major economic losses and serious damage to natural ecosystems [5,6]. The most notorious species are members of the genus *Phytophthora*, such as the late blight pathogen *Phytopthora infestans*, known for triggering the Irish potato famine [7,8]. Other notable species include *Phytophthora palmivora* [9], causing cocoa black pod, and the sudden oak death pathogen *Phytophthora ramorum*, which emerged in more recent epidemics threatening native tree species [10]. Additional important oomycete plant pathogens include members of the *Pythium* genus and downy mildews [11,12].

In contrast with their terrestrial counterparts, aquatic oomycetes remain understudied [3,4]. This applies particularly to animal pathogenic oomycetes, such as *Saprolegnia* and *Aphanomyces* spp. [13]. Aquaculture has become one of the world's fastest growing food sectors, where freshwater fish dominate global aquaculture production [14]. Fish farming and fisheries provide livelihood and income for an estimated 54.8 million people, with employment in these sectors growing rapidly [15]. Diseases such as epizootic ulcerative syndrome and saprolegniosis, caused by oomycetes, are a significant threat to the aquaculture industry [16].

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2. Why are oomycetes so successful?

The key to pathogenic oomycetes' success resides in their capacity to adapt to overcome host resistance and occasionally jump to new hosts. Various features of oomycete biology can explain their high evolutionary potential. One major driving force for their success is encompassed by their flexible mating system. Oomycetes can reproduce sexually (either homothallic or heterothallic), asexually or through interspecific hybridization [17] enabling them to gain both allelic diversity (sexual and interspecific hybridization) and to rapidly proliferate, resulting in large population sizes (asexual/clonal populations) [18]. Large population sizes compensates for the lack of sexual recombination and increase the occurrence of spontaneous mutants with enhanced fitness [18].

Genome sequencing of oomycetes has provided additional insights into their capacity to adapt to hosts. Oomycete genomes harbour large repertoires of genes encoding virulence effectors, which modulate host processes [19,20]. These effector genes are typically associated with fast evolving regions of the genome, particularly in areas enriched in repeats and transposable elements, promoting genome duplication, shuffling, increased rates of mutagenesis and gene silencing [21]. This bipartite genome organization, differentiated by slow and fast evolving regions, has led to the 'two-speed' genome model, where gene-sparse repeat-rich compartments serve as a cradle for adaptive evolution, underpinning infection success by enabling the pathogen to rapidly overcome host resistance, evolve new virulence determinants and even jump to new host species [22]. Another interesting aspect about oomycete genomes is that they exhibit variations in ploidy and can exist as either triploids or polyploids [23–25]. The relevance of this feature is currently not fully understood, however, polyploidy has been shown to enhance vigour and buffer mutational changes by masking deleterious alleles [26], and is therefore believed to play a vital role in pathogen success. In fact, many successful *P. infestans* clonal lineages are made up of triploid genotypes [26].

Here, we discuss seven oomycetes that are emerging or re-emerging threats to world agriculture, horticulture, aquaculture and natural ecosystems. They were selected based on their impact on economy and society, and include both well-known and understudied pathogens of both plants and animals. For each pathogen, we describe its pathology, importance and impact, discuss why it is an emerging threat and briefly review research activities that underpin effective disease management strategies. Table 1 summarizes our current knowledge of the genome and secreted proteins of the examined species and highlights why they are (re-)emerging threats.

3. *Phytophthora infestans*: the Irish potato famine pathogen

Phytophthora infestans infects potato and tomato plants, causing late blight disease. It is infamous for triggering the Irish potato famine in the mid-nineteenth century. Today, it is still a significant threat to global food security, causing severe yield losses in these crops, and economic losses of more than USD 6 billion annually [30,31]. In addition to destroying the foliage, *P. infestans* can infect tubers, which facilitates migration of the pathogen via the global seed tuber trade [32]. Current disease management strategies include chemical control and/or deployment of resistant cultivars. Resistance to agrochemicals, however, is common in epidemic-causing isolates [33], and due to the pathogen's adaptability, disease resistance genes are also quickly broken down and rendered ineffective [34].

Disease outbreaks are typically caused by asexually reproducing clonal lineages [24,32,35,36]. These aggressive lineages dramatically reshape the population structure and become dominant over a short period of time [36,37]. For example, in Great Britain, genotype *13_A2*, first detected in July 2005, surged to more than 75% of the *P. infestans* population by 2008 (figure 1) [35]. Subsequently, *13_A2* was displaced by another genotype, *6_A1*, which increased in occurrence from 20% in 2010 to 80% in 2011 (http://www.fwi.co.uk/academy/lesson/potatoes-understanding-blight1). In addition, some *P. infestans* clonal lineages have become pandemic. *13_A2* was detected for the first time in South India in 2008, where it caused severe late blight epidemics in tomato, often resulting in 100% crop loss [38]. The emergence of this genotype in the Indian subcontinent has led to an increase in late blight incidence on tomato and potato, with epidemics reported in subsequent years following its introduction.

The *P. infestans* genome was sequenced in 2009 [8], which established this species as a model system, pioneering studies of oomycete effectors and evolution [8,40]. Notably, the study of *P. infestans* effectors have significantly moved forward our understanding of host processes targeted by the pathogen, forming strong foundations for plant–microbe interaction studies [19,41]. Furthermore, effectors have emerged as powerful tools to rapidly identify new resistances in potato germplasms.

4. *Phytophthora palmivora*: the pathogen of tropical plants

The *P. palmivora* is a plant pathogen that infects more than 200 plant species in the tropics, including dicots and monocots [7]. Economically important hosts include cocoa, coconut, pineapple, rubber tree, durian, citrus, papaya and oil palm. Disease outbreaks in these crops impact the livelihood and nutrition of millions of people globally. Annual losses due to diseases caused by *P. palmivora*, such as oil palm bud rot and cocoa black pod, range from USD 250 million to over USD 1 billion, respectively [9].

Rainy season and high humidity favour pathogen sporulation leading to rapid disease progression and production of oospores. Disease spread from the soil into the canopy is often initiated through rain splash. Once the roots, leaves and fruits in the lower canopy are infected, the pathogen quickly spreads to the upper canopy by insects, wind and through wind-driven aerosols [7,42]. Additionally, transport of infected nursery plants, improper disposal of infected material, irrigation with zoospore-contaminated water, changing temperatures and global trade all contribute to the spread of *P. palmivora*. This makes it a serious threat to the economy of many developing countries, where cultivation of highly productive perennial crops is intensifying.

The broad host range of *P. palmivora* has enabled research using model plants such as *Medicago truncatula* [43], *Hordeum vulgare* (barley) [44] and *Nicotiana benthamiana* [45], moving forward the characterization of the molecular mechanisms involved in *P. palmivora* colonization. Notably, the process of root colonization by this pathogen is used to study similarities and differences between pathogenicity

Table 1. Features of oomycete pathogens highlighted in this paper, including the primary host, genome size, repetitive DNA content (as a percentage of genome size), number of protein coding genes, percentage of predicted secreted proteins and a summary of why the pathogen is a (re-)emerging threat. n.d., no data.

pathogen	important hosts (P, plant; A, animal)	common disease name (host)	why is it a (re-)emerging threat?	genome size (Mb) (% repetitive)	protein coding genes (% secreted)[a]	references
Phytophthora infestans	P—potato, tomato	late blight	new aggressive genotypes emerged in the UK (2008 and 2011) and India (2008)	240 (7.4)	18 155 (8.7)	[8]
Phytophthora palmivora	P—cocoa, coconut, pineapple, rubber tree, papaya, oil palm	bud rot (oil palm), black pod (cocoa), fruit rot (papaya)	outbreaks regularly destroy oil palm and cocoa plantations worldwide	n.d. (n.d.)	n.d. (n.d.)	—
Phytophthora ramorum	P—oak, tanoaks, rhododendron, beech, larch	sudden oak death (oak)	outbreaks destroyed forests in North America and Europe during the last 20 years	65 (17)	14 451 (10.5)	[27]
Plasmopara obducens	P—*Impatiens* species	*Impatiens* downy mildew	outbreaks occurred in nurseries worldwide within the last decade	70 (n.d.)	n.d. (n.d.)	[28]
Aphanomyces invadans	A—carp, perch, tilapia, snakeheads, salmonids, estuarine	epizootic ulcerative syndrome	regularly kills farmed and wild fish worldwide, threatening food safety in Asia and Africa	71 (n.d.)	15 248 (n.d.)	[b]
Saprolegnia parasitica	A—fish (salmon), amphibians, crustaceans, aquatic insects	saprolegniosis	threatens fish farming in Europe, America and Asia, as well as endangered amphibian species worldwide	63 (17)	17 065 (5.7)	[29]
Halioticida noduliformans	A—abalone, mantis shrimp	abalone tubercle mycosis (abalone)	severe outbreaks occurred in South Africa and Japan between 2004 and 2006	n.d. (n.d.)	n.d. (n.d.)	—

[a]Including putative effectors.
[b]See http://www.ebi.ac.uk/ena/data/view/GCA_000520115.

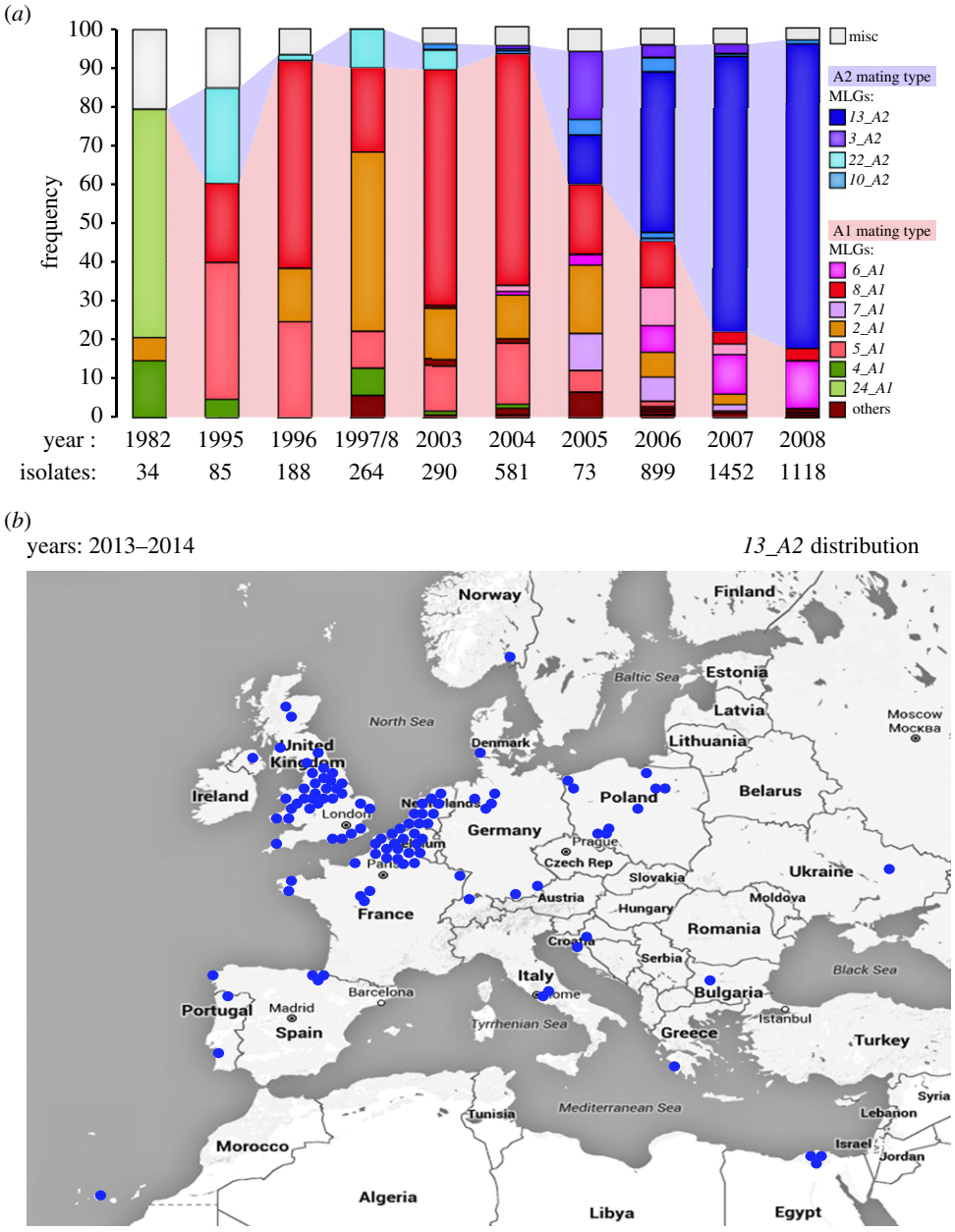

Figure 1. An emerging clonal lineage reshaped *P. infestans* populations in Great Britain. (*a*) Multilocus genotyping of *P. infestans* isolates from 4000 late blight infection sites over 11 years. This survey revealed that the late blight epidemic that started in 2006 was due to the aggressive *13_A2* isolate that became dominant in only 3 years. The number of surveyed isolates and dominant genotypes of each mating type are indicated. Genotypes with low frequency are grouped as 'misc'. The shading between bars indicates mating types. (Figure and legend are adapted from Cooke *et al.* [35].) (*b*) The *13_A2* isolate has rapidly spread to other continents and caused devastating economic losses especially in developing countries such as India and Egypt [38]. Dots represent an approximate of sampling sites for years 2013 and 2014 according to EuroBlight data and recent reports [39].

and symbiosis at the molecular level [46]. Publically available genomic resources are currently limited, which impairs research progress.

5. *Phytophthora ramorum*: the sudden oak death pathogen

Phytophthora ramorum is a devastating oomycete pathogen that causes sudden oak death disease [47]. It has a wide host range, affecting more than 100 plant species from 40 different genera. These include environmentally and economically important tree species such as oaks, tanoaks, rhododendron, European beech, Japanese larch and many woody ornamental plants [47–49]. Disease symptoms are host specific, but can vary from necrotic lesions in leaves, to shoot dieback and bleeding cankers on the stem [10,50].

In Europe, *P. ramorum* is mainly present in ornamental nurseries or gardens, however, in the UK this pathogen has caused significant tree losses and landscape-scale epidemics [48]. Despite the known reports of *P. ramorum* in Europe [51] and North America [52–55], predictive models suggest that the pathogen might be adapted to larger areas in Africa, Australasia and South America. Therefore, potential of invasion and further spread of the pathogen is possible [56]. In addition, given that diagnosis is primarily based on visual inspection, disease symptoms can be masked by agrochemicals, increasing the likelihood of pathogen intrusion into susceptible areas by the ornamental plant trade market [57].

Phytophthora ramorum occurs as four clonal lineages [58] that have resulted in the emergence of new diseases in forest

ecosystems within Europe and the USA [51,53,59]. The *P. ramorum* genome was sequenced in 2006, a few years after the pathogen was first detected, providing novel insights into its biology [60]. Recent genome sequencing of additional isolates provided further genetic information to track the spread of the pathogen [61]. However, our understanding of its emergence and adaptation remains relatively limited [62].

6. *Plasmopara obducens*: the downy mildew of *Impatiens* species

Plasmopara obducens is an obligate biotrophic pathogen of horticultural plants from the *Impatiens* genus. It causes the *Impatiens* downy mildew foliar disease, which results in wilted and defoliated plants that die within weeks of disease onset [63]. Commercially grown varieties of *Impatiens walleriana* are susceptible to *P. obducens*, making *P. obducens* a clear and present threat to the cultivation of *Impatiens* spp. worldwide [64].

Within the past decade, outbreaks have been reported in North America [65,66], the Hawaiian Islands [67], Europe [68–70], Asia [63] and Australia [71]. Such epidemics were associated with important economic losses [67]. In the USA, the spread of *P. obducens* caused great concern and resulted in the establishment of a research consortium [72]. Cultural practices and chemical applications limit the spread of the disease, however, they are not permanent solutions, as mefenoxam-insensitive *P. obducens* isolates have already been identified [72]. Additionally, *P. obducens* is a persistent pathogen; its ability to spread by wind and survive in soil means disease eradication will be difficult.

The lack of information on the genetics and the structure of *P. obducens* populations, as well as on the factors that led to the establishment of global epidemics, impair the development of effective mitigation strategies. To fill this knowledge gap, Salgado-Salazar *et al.* [28] recently released a draft genome sequence of *P. obducens*, along with a set of genetic markers. These molecular resources may help in determining both the population structure and genetic factors that control infection processes.

7. *Aphanomyces invadans*: the fish epizootic ulcerative syndrome pathogen

Aphanomyces invadans causes epizootic ulcerative syndrome, a fish disease listed on the World Organisation for Animal Health website (http://www.oie.int/en). *Aphanomyces invadans* is pathogenic on several economically important fish, including carp, perch, tilapia, snakeheads, salmonids and estuarine fish species [73–75]. It was first reported from farmed ayu, *Plecoglossus altivelis*, in 1971 in Japan [76]. Since then it has spread rapidly throughout Asia and into some areas of Africa.

Aphanomyces invadans has been responsible for large-scale mortalities of farmed and wild fish in more than 20 countries across four continents [77]. In Asia and Africa, the disease has negatively impacted the livelihood of fish farmers and fishermen and, in some cases, threatened the sustainable food supply for local populations, who depend on fish as a relatively affordable source of animal protein [74]. Experimental infection studies have demonstrated that *A. invadans* can produce severe pathological changes in several European salmonid and catfish species [78]. Hence, it is possible that it could cause serious problems in European tilapia, salmon and trout aquaculture industries and in numerous native and wild fish species.

Despite its economic and social importance, little is known about the biology of the *A. invadans* pathogen. In an effort to address this gap in knowledge, the first draft genome sequence has been completed at the Broad Institute (http://www.ebi.ac.uk/ena/data/view/GCA_000520115). These sequences will enable studies on the biology, evolution, biodiversity, genetics, virulence/pathogenicity and biochemistry of *A. invadan*.

8. *Saprolegnia parasitica*: the saprolegniosis water mould

Saprolegnia parasitica causes saprolegniosis on various fish species. In addition to fish, species of amphibians [79], crustaceans [80] and aquatic insects [81] are also highly susceptible to saprolegniosis. There is conclusive evidence that *Saprolegnia* species are major killers of populations of amphibians globally, threatening some already highly endangered species [82–84]. *Saprolegnia parasitica* is a major problem in the fish farming industry in Europe, Chile, Canada and Asia. At least 10% of all hatched salmon [13] and over 10% of all eggs succumb to *Saprolegnia* infections according to estimates [4,13].

Until 2002, *S. parasitica* was kept under control with applications of malachite green. However, the use of malachite green has been banned worldwide due to its toxicity [85–87], resulting in a dramatic resurgence of *Saprolegnia* infections in salmon aquaculture. At present, fish farmers are struggling to control this pathogen. Current control methods involve treatments with formalin-based products, which are also expected to be banned in the EU in the very near future [88–90]. Therefore, sustainable prevention and control measures are desperately needed.

Recent studies have elucidated an induced native immune response and a suppressed adaptive immune response in fish infected by *S. parasitica* [91]. In addition to distinct biochemical pathways that were described during fish–*Saprolegnia* interaction to establish infection [92], the genome sequence of *S. parasitica* [29,93] has also shed light on the molecular mechanisms of infection, broadening our understanding of infection mechanisms.

9. *Halioticida noduliformans*: the abalone tubercle mycosis pathogen

Halioticida noduliformans is a marine pathogen of abalone (*Haliotis* sp.), on which it causes abalone tubercle mycosis, and mantis shrimp (*Oratosquilla oratoria*). It is a member of the Haliphthorales, an early diverged lineage in the Oomycota phylum [94]. *Halioticida noduliformans* was first discovered in 2004 in South Africa [95,96] and is a threat for abalone in commercial aquaculture, which constitutes more than 93% of the global abalone market [97].

Between 2004 and 2006, several outbreaks in commercial aquaculture farms in South Africa and Japan caused up to 90% mortality among spat and up to 30% mortality among older animals [96,98]. Pathogen control is challenging [96]. Indeed, single *H. noduliformans* isolates can infect at least three abalone species from South Africa, Mexico and Japan [96].

Researchers from Japan and South Africa have provided insights into the distribution of *H. noduliformans* outbreaks and the molecular phylogeny of *Halioticida* species [95,96,98,99]. Additionally, Greeff *et al*. [100] have established a rapid and sensitive qPCR assay for species-specific detection and quantification of *H. noduliformans* in abalone tissue. However, important resources like genome sequences and gene expression data are lacking. Identification of natural hosts and determining whether these hosts act as reservoirs for *H. noduliformans* will be vital to successfully control this disease.

10. Five ways to tackle emerging or re-emerging oomycete threats

Outbreaks caused by oomycete diseases are a clear and present threat to food security and to natural ecosystems. Although there is a general awareness about these outbreaks, there are gaps in the community capacity to deliver effective short- and long-term response plans. Research showed that oomycetes evolved the ability to infect plants and animals independently of other eukaryotic microbes, and therefore, likely developed unique mechanisms of pathogenicity [101]. The last few decades have seen significant progress in understanding the biology and molecular basis of host infection by oomycete pathogens. Notably, genomic studies have revealed fundamental concepts that link genome architecture, pathogenicity-related proteins and evolution, key factors that drive disease emergence and pathogen success [22]. Here, we highlight five main research areas that need to be sustained or reinforced to help us tackle emerging and re-emerging oomycete threats:

— *Genomic resources*. Sequencing of plant oomycetes has pioneered our understanding of pathogenicity and has provided downstream tools that are essential for mechanistic research. In addition, as more genomes are sequenced, comparative genomic studies will help elucidate infection mechanisms across multiple isolates and species, providing critical information on conserved infection strategies. Oomycete pathogenomics have greatly impacted our approach to plant disease resistance breeding. Indeed, effector proteins have turned out to be useful tools for probing plant germplasm for new resistance traits, and can be used in pathogen-informed resistance breeding programmes. For animal pathogen oomycetes, limited genomic resources are available at the moment (table 1). More efforts are needed for identifying pathogen proteins that manipulate host immune systems, as these will allow for the selection and testing of suitable antigens, which may result in the development of vaccines [102].

— *Genetic manipulation of hosts and pathogens*. Host genetic improvement can be accomplished by precise genome editing techniques, such as the CRISPR/Cas-9 technology [103]. CRISPR/Cas-9 was successfully implemented in tomato to enhance resistance against an oomycete pathogen [104]. To date, mechanistic studies dissecting oomycete–host interactions have been limited to genetic manipulation of the host species due to the lack of efficient gene replacement methods in oomycetes. Recently, Fang & Tyler [105] implemented the CRISPR/Cas9 system in oomycetes and were able to rapidly and efficiently edit the *Phytophthora sojae* genome. Further implementation of reverse genetic tools in other oomycete species is now needed.

— *Surveillance*. Surveillance consists of the assessment of disease incidence and virulence characterization (via pathotype surveys). In agriculture, pathogen surveillance is crucial to establish national and international policies, government investment and strategies in plant protection, plant breeding, seed distribution and pathology. Surveillance remains a critical aspect of disease control, since understanding the pathogen population allows rapid deployment of control methods. In addition to managed agricultural ecosystems, pathogen surveillance should also include natural habitats and potential reservoirs, as these areas generate new inoculum for re-infection.

We have entered a new era in incursion reporting, where social media provide an efficient and rapid platform for data dissemination and collaborative efforts to tackle new disease emergence and spread. By communicating disease significance to the public and building up awareness of these destructive diseases, a community effort for surveillance can be achieved. This was successfully demonstrated in Australia, after the incursion of myrtle rust [106] and in the recent actions surrounding the outbreak of wheat blast in Bangladesh [107]. Websites such as http://rusttracker.cimmyt.org and http://euroblight.net are great examples of successful first steps to coordinating global disease surveillance efforts.

— *Field pathogenomics*. In addition to tracking movement and variation of pathogens (surveillance), tackling emerging diseases will not be successful without concurrently understanding the genetics of host resistance. Field pathogenomics adds highly informative data to surveillance surveys by enabling the rapid evaluation of pathogen population structure and host genotype [108]. This has already been successfully implemented with oomycete and fungal pathogens of potato and wheat crops, and will be applicable to other pathogens as more genomic information is generated [35,109].

— *Databases*. Committing to long-term data recording, linkage between databases, free flow of information and faster exchange of information are necessary for updating epidemiological data. Data should be made rapidly and publically available to maximize the combined and coordinated efforts of the scientific community. For instance, scientists recently released websites to share sequencing data generated as an immediate response to outbreaks such as ash dieback (https://geefu.oadb.tsl.ac.uk/) and wheat yellow rust in the UK (http://yellowrust.com/) and wheat blast in Bangladesh (http://wheatblast.net). Additionally, social media websites, such as Plant Village (https://www.plantvillage.org), allow for free sharing of crop disease information in real time. These websites not only become platforms for scientists to interact, establish collaborations and coordinate among themselves, but also provide information for the general public and farmers to directly follow and participate in research efforts. They allow the world to connect, share and collectively find solutions to emerging oomycete threats.

Fighting agriculturally important pathogens is a long-term ongoing battle. Just like the constantly morphing flu virus, oomycete pathogens continuously evolve new races to evade host resistance. Agricultural scientists, veterinarians,

breeders and farmers need to remain vigilant and work together in reporting and tackling oomycete pathogens to achieve successful control.

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