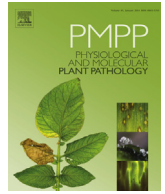




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Mini review

When plants brace for the emerging pathogens

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ABSTRACT

Emerging phytopathogens ranging from viruses, bacteria, oomycetes, and fungi to nematodes have seriously threatened global crop productivity and food security, mostly owing to changing demographic dynamics and geographical movements of crops brought by human beings. An understanding of these new pathogens would allow timely intervention in biological control, phytosanitation, and biosecurity of crops and plants. With the flooding of information in the genomic era and with ensuing advances in other related 'omics', technologies would pave the path to improvement of plants to protect against the pathogens. We introduce the recently reported, emerging repertoire of phytopathogens, from diverse taxa such as fungi, oomycetes, bacteria, viruses, and nematodes, to the re-emerging ones and the cross-kingdom host jumping pathogens.

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1. Introduction

Plants are constantly exposed to and challenged by a realm of biotic factors, many of which many are beneficial while a plethora are pathogens. Plant pathogens belong to viruses, bacteria, fungi, nematodes, protozoa, and insects. In addition, the would-be pathogens are lurking in their immediate environment which, in spite of the presence of a solid innate immunity, fail to provide resistance to the newly faced microbes. Over the course of evolution and agricultural history, pathogens are armored with tools to move and colonize new hosts in the agricultural phase of human civilization, thus changing the plant disease landscape globally. Human population boom, global trade, and co-evolution of both host and pathogens have led to the incremental instances of catastrophic outbreaks from plant pathogens. These exotic pathogens have grown to epidemic proportions. Thanks to the migration, divergence, speciation, recombination events, the intricate interplay of pathogens, newer host availability, susceptibility and abundance, expansion of parasitism protein families within their genomes, and suitability of changing climate conditions, these recent groups of pathogens have evolved to kill in a very efficient manner. Pathogens

secrete proteins among other molecules to modulate plant defense machinery and facilitate colonization of plant tissue, collectively known as 'effectors' [1]. These effectors form a huge part of secretome whose roles are starting to be understood in host-defense modulation, e.g. proteins, toxins and hormones. Of the two major kinds of effectors, apoplastic effectors are released into the extracellular space, while the cytoplasmic effectors are translocated inside the plant cell, thus targeting numerous subcellular compartments [2]. These evolving pathogens show up in a new host species and evolve adaptation to a new host range, owing to mutations leading to increased virulence, or owing to geographic migrations that are mostly human mediated. The behavior of pathogens and their patterns are intriguing. Since the last few decades, these virulent infections have affected both natural populations [3], forests, and managed landscapes, which are subjected to growing systems affected by local practices and economies. This happened in unprecedented proportions, leading to extinction of wild species, loss of biodiversity [4], and affecting crop productivity. Understanding these intensifying disease emergence scenarios is critical to their imminent prevention in a timely fashion, thus the recently known, emergent pathogens are the focus of this commentary.

Historical records for the emerging pathogens are scanty and not available for the majority of the pathogens and possibly many more which have not come under the scanner or stay latent until a catastrophic outbreak. In case of more worrisome emerging

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zoonotic viruses, bats are believed to be the reservoirs of such viruses as Hendra, Nipah, SARS and Ebola, in addition to a plethora of unknown viral sequences in their mammalian genomes. This is attributed to their ancient evolutionary origins, while the spread is explained by their flying nature [5]. Although soils and natural resources are also understandably reservoirs for them, by drawing parallels it could be speculated that for plants, similar natural reservoirs are existing in nature in the form of wild species, insect carriers, endophytes, parasites, etc. Both natural and man-made landscapes with cultivated plants represent considerably different habitats for pathogens. A top 10 list of fungal pathogens in terms of their scientific/economic importance was generated that includes *Magnaporthe oryzae*, *Botrytis cinerea*, *Puccinia* spp., *Fusarium graminearum*, *Fusarium oxysporum*, *Blumeria graminis*, *Mycosphaerella graminicola*, *Colletotrichum* spp., *Ustilago maydis*, *Melampsora lini* [6], while a similar list for emerging plant pathogens is imminent. The emerging infectious diseases of plants have been the point of interest of several important reviews here [7], and more recently, here [8].

2. Bacterial pathogens

Plants are host to bacterial communities on the phyllosphere and rhizosphere which are best characterized with species chiefly belonging to *Actinobacteria*, *Bacteroidetes*, *Firmicutes*, and *Proteobacteria* [9]. The *Proteobacteria*, *Burkholderia glumae* was recently recognized as an emerging pathogen of rice [10]. *Dickeya* species cause diseases in numerous crops and ornamental plants worldwide. First reported in potato in the Netherlands in the 1970s, the diseases have spread to other European countries. However, since 2004–05 a new pathogen named '*Dickeya solani*' is spreading across Europe, leading to economic losses in potato tuber trade [11]. Bacterial pathosystems underscore a large repertoire of constantly evolving bacterial communities which catch the host defense system off-guard and lead to new colonization events.

Horizontal gene transfer among bacteria has facilitated not only genome adaptation in bacteria by the transfer of pathogenicity islands (i.e., regions of localized enrichment of pathogenicity-related genes), but the cross-kingdom horizontal gene transfer events that have also helped increase the pathogenicity in the pathogens by using plant host's genes against themselves [8]. Interestingly, analysis of 37 bacterial plant-pathogen genomes revealed 5169 genes of phage origin with approx. 50% with unknown function or relevance to phage biology, suggesting an association between plant diseases and prophage transcriptional modulation in bacteria for these phage lineages [12]. For bacteria such as *Pectobacterium*, *Pseudomonas*, *Ralstonia*, and *Streptomyces*, the prophage is involved in disease symptoms, while in *Xylella* and *Xanthomonas* the prophage activity is associated with genome rearrangements and strain differentiation [12]. A deeper understanding of the shared genes and their encoded proteins among the genomes of these pathogens would provide immense insights into the common evolutionary strategies employed to colonize new hosts. These newer insights into phage-mediated regulation of bacterial pathogenesis holds tremendous potential in understanding of the emergence of these bacterial species.

3. Oomycetes in action

The most notorious oomycete known to affect food security in human history is *Phytophthora infestans* that caused the Irish potato famine. A recently emerged plant pathogen, *Phytophthora ramorum* is the causative agent of the sudden oak death epidemic [13]. Invasion of *P. ramorum* and emergence of the sudden oak death disease in forests has caused a severe decline of tanoak (*Notholithocarpus*

densiflorus) population in Californian coastal forests [4]. *Phytophthora alni*, a heteroploid hybrid oomycete pathogen, was discovered in 1993 in southern England to be causing lethal root and collar rot in alders and was reported in many European countries. First observed in North America associated with mortality of tanoak (*Lithocarpus densiflorus*) and coast live oak (*Quercus agrifolia*) in coastal forests of California during the mid-1990s, it now has a host range of over 40 plant genera, thus exemplifying the undesirable linkages between horticultural practices and natural forest ecosystems [14]. Hybrid plant pathogens such as *Phytophthora andina*, an increasingly common pathogen in Andean crops such as *Solanum betaceum*, *Solanum muricatum*, *Solanum quitoense*, and several wild *Solanum* spp., has emerged via hybridization between *P. infestans* and a unknown *Phytophthora* species [15]. The secretome of *P. infestans* was recently unraveled [16], while genome sequencing projects on *Phytophthora parasitica* [17] have advanced our understanding of this menacing oomycete. Recently, the analysis of evolutionary dynamics of 10 Stramenophiles yielding 18,459 gene trees constituting the phylome indicated that the genomes of pathogenic oomycetes have constantly gained and lost genes [18]. In particular, *Phytophthora* genus was identified as a major transition point characterized by increased frequency of duplication events that has driven the speciation within the genus. The oomycete specific features of genome evolution include repeat-driven expansions, deletions, gene fusions, and horizontal gene transfer in a landscape organized into gene-dense and gene-sparse sectors and influenced by transposable elements, in addition to gene expression profiles that are highly dynamic throughout the oomycete life cycles that demonstrate striking variation in genome size and content, a plastic set of genes related to pathogenesis, and adaptations associated with obligate biotrophy [19]. Comparing the secretomes of two *Saprolegnialean* oomycetes with that of eight other oomycetes using *de novo* genome and transcriptome sequencing showed novel horizontal gene transfers to the oomycete secretome from bacterial and fungal donor lineages and changes in oomycete secretomes associated with shifts from free-living to pathogenic taxa [20]. The importance of horizontal gene transfers on the emergence of phytopathogens has been shown to be significant for oomycetes and across the bacterial and fungal kingdoms [8]. Comparative genomics and *de novo* genome sequencing of *Hypochytrium catenoides*, a free-living sister of the oomycetes, indicated that horizontal gene transfers largely converge within the radiation of oomycetes that colonize plant tissues where these transferred genes are implicated in resisting plant defense mechanisms and effector proteins for attacking plant cells [21]. Thanks to the continuing genome sequencing efforts [22–25] and pathogenomics research endeavors in oomycetes, our understanding of plant parasitic oomycete effector repertoire ('effectoromics') function and plant host responses have significantly increased [26]. With several oomycetes species undergoing genome sequencing and annotation, a genome-wide cataloguing of oomycete effectors sounds more realistic [2].

4. Fungal invaders

A large number of species of fungi, specifically belonging to ascomycetes, are plant pathogens of great notoriety and economic importance. Gene transfers since 1940s have created a pathogen population with significantly enhanced virulence, thus leading to the emergence of new damaging disease of wheat [27]. Another ascomycete fungus *Ramularia collo-cygni* has elevated itself to an important pathogen of barley in Northern Europe and New Zealand [28]. Similarly, other hybrid plant pathogens include the poplar rust *Melampsora columbiana*, the crucifer pathogen *Verticillium longisporum*, the onion pathogen *Botrytis allii*, and *Heterobasidion* forest pathogens. Furthermore, hybridization and

introgression were hypothesized to be the principal causes behind the continued epidemic of Dutch elm disease in Europe [15]. Another ascomycete fungus, *Stagonospora nodorum*, (teleomorph: *Phaeosphaeria nodorum*), is the causative organism of wheat *S. nodorum* blotch [29]. An ascomycete, *Hymenoscyphus pseudoalbidus*, has spread all over the Europe within recent years, causing devastating destruction on European common ash trees (*Fraxinus excelsior*) and associated plant communities, thus demonstrating the additive genetic variation in susceptibility of natural *F. excelsior* populations to the newly invasive pathogen [30]. The ascomycete *F. graminearum* (teleomorph: *Gibberella zeae*), a highly destructive pathogen, co-infects with other *Fusarium* species, thus affecting major cereal-growing regions worldwide and thus are indicative of re-emergence of *Fusarium* epidemics [31]. In fact, it was shown that the lineage-specific (LS) genomic regions in *F. oxysporum* comprising four entire chromosomes, are rich in transposons and genes related to pathogenicity, indicated their horizontal acquisition. Furthermore, it was demonstrated that the transfer of two LS chromosomes between strains of *F. oxysporum*, converted a non-pathogenic strain into a pathogen, thus providing a very strong evidence towards emergence of new pathogenic lineages in *F. oxysporum* [32]. Although, not many genomes of the emergent phytopathogens have been sequenced, certainly the efforts will continue to stride forward with renewed vigor. *Chalara fraxinea* (teleomorph- *H. pseudoalbidus*) is an emerging pathogen that affects ash stands all over the Europe in devastating proportions in addition to being an invasive spread in the last decade, although was known to have been present long before the recent epidemic outbreak [33]. *Zymoseptoria pseudotrifici*, a fungal phytopathogen of various grass species in the Middle East, i.e., Iran, has possibly emerged after a hybridization event as genome sequences suggested two distinct haplotypes, indicating two distinct parents, which further evidenced that hybridization of distinct species can beget phytopathogen emergence [34]. Similarly, the emergence of wheat blast caused by *M. oryzae* in wheat (*Triticum aestivum*) has now spread to rice (*Oryza sativa*) in Brazil and has led to genome sequencing efforts [35].

In addition, it has been recently stressed that although genome sizes of pathogens have reduced over time, the genomes of lineages of several filamentous plant pathogens were shaped by repeat-driven expansions. Interestingly, the polymorphic genes encoding proteins involved in phytopathogen interactions were established to reside within these repeat-rich regions [36]. The pathogen's specialization in carbon utilization that possibly avoids plant responses, the genome expansion by repeated elements, and protein family expansion with desirable functions have aided in faster emergence of adaptation in these phytopathogens.

5. Pathogens of diverse origin

Viral emergence is associated with ecological changes and agronomical practices, bringing together reservoirs and crop species. A recent review paints the emergence of plant RNA viruses into the framework of evolution, stressing that viral emergence begins with the transmission of a preexisting viral strain into a new host species, followed by adaptation to the new host [37]. For instance, the maize streak virus, one of the most serious viral crop diseases of Africa, is obligately transmitted by leafhoppers and affects maize and another 80 species in the Family Poaceae to cause economically significant streak disease in maize, at instances showing up to 100% infection rates and complete yield loss [38]. Pepino mosaic virus that was originally isolated from pepino (*S. muricatum*), was identified in natural infections of the wild tomato species *Solanum chilense*, *Solanum chmielewskii*,

Solanum parviflorum, and *Solanum peruvianum*, thus compounding the problems in the cultivation of the glasshouse tomato *Solanum lycopersicum* [39]. Interestingly, a unicellular eukaryote belonging to the group *Phytophyxa* (protists), *Plasmodiophora brassicae*, is another emerging pathogen of the Canadian canola (*Brassica napus*) and causes the club root disease of epidemic proportions [40]. Ranging from viruses to protists and nematodes, the emerging pathogens encompass the breadth and width of the living world. But with the recent acquisitions of high-throughput molecular data in addition to the increasingly available omics-scale data would aid in systematic study of plant-microbe interactions from a systems biology perspective.

A pinewood nematode, *Bursaphelenchus xylophilus*, responsible for the devastating epidemic of pine wilt disease in Asia and Europe, underscored the importance of the independent origin of plant parasitism in nematodes, as it is both ecologically and taxonomically distinct from other nematodes [41]. Introduced at the start of 20th century into Japan from North America, the genome of this nematode boasts a diverse array of unique advantages conferred by parasitism genes such as RNA interference effectors, peptidergic neurotransmitters, contracted set of chemosensory receptors, a huge repertoire of digestive proteases, lysosome pathway gene expansions, and lack of proteins homologous to effectors from other plant parasitic nematodes, thus confirming the distinctive molecular basis of plant parasitism in the *Bursaphelenchus* lineage.

6. Cross-kingdom host jumps by emerging pathogens

Many of these pathogens are known to have resulted from cross-kingdom jumps within plants to humans. *Exserohilum rostratum*, *Burkholderia cepacia*, and *Pseudomonas aeruginosa* cause cystic fibrosis, *Cryptococcus gattii* from forest trees to animals and humans, and fungal plant pathogens such as *Alternaria alternata*, *Aspergillus flavus*, *F. oxysporum*, *Microascus cinereus*, and *Rhizopus arrhizus* cause invasive fungal infections, while *Aspergillus* spp. cause aspergillosis and aspergilloma, *Fusarium* spp. (primarily *Fusarium solani*) causing fusariosis, while *Coccidioides* sp. causes valley fever or coccidiomycosis [42]. Plant organs, such as roots and inner tissues are natural reservoirs of emerging opportunistic pathogens belonging to *Burkholderia*, *Enterobacter*, *Herbaspirillum*, *Ochrobactrum*, *Pseudomonas*, *Ralstonia*, *Staphylococcus*, and *Stenotrophomonas* that contain plant-associated strains which can encounter dual interactions with both plant and human hosts [43], mostly because the mechanisms responsible for the colonization of plant and human tissues are comparable [43]. Thus, not only do they pose a serious threat to the plant population and thus, economy, but also to human health at a global scale.

7. Re-emerging pathogens

Potato late blight is now considered a re-emerging disease as several of the *P. infestans* introduction events took place in the 19th and 20th centuries outgoing from Latin America to Europe [44]. Recently, *Pseudomonas syringae* pv. *Actinidiae*, the causative agent of bacterial canker of green-fleshed kiwifruit (*Actinidia deliciosa*) and yellow-fleshed kiwifruit (*Actinidia chinensis*) have demonstrated a re-emerging wave of this disease, thus affecting kiwifruit production globally at pandemic proportions [45]. In fact, the current kiwifruit canker epidemic is the fourth outbreak of the disease caused by *P. syringae* in last 50 years, with each such outbreak attributed to a unique genetic line of the bacterium [46]. As this mini-review was being compiled, an excellent treatise on the re-emerging *P. infestans* has appeared elsewhere [47], where the authors clearly stress that devastation caused by the pathogen

Table 1

List of phytopathogen categories representing cross-kingdom host jumping pathogens, fungi, re-emerging pathogens, virus, nematodes, bacteria, oomycetes, and others addressed in this mini-review.

Cross-kingdom host jumping Pathogens	Fungi	Re-emerging pathogens
<i>Exserohilum</i>	<i>Ramularia</i>	<i>Phytophthora</i>
<i>Burkholderia</i>	<i>Verticillium</i>	<i>Pseudomonas</i>
<i>Pseudomonas</i>	<i>Melampsora</i>	<i>Puccinia</i>
<i>Cryptococcus</i>	<i>Botrytis</i>	<i>Fusarium</i>
<i>Coccidioides</i>	<i>Heterobasidion</i>	Virus
<i>Enterobacter</i>	<i>Stagonospora</i>	Pepino mosaic
<i>Herbaspirillum</i>	<i>Hymenoscyphus</i>	Nematode
<i>Ochrobactrum</i>	<i>Fusarium</i>	<i>Bursaphelenchus</i>
<i>Ralstonia</i>	<i>Zymoseptoria</i>	Bacteria
<i>Staphylococcus</i>	<i>Magnaporthe</i>	<i>Burkholderia</i>
<i>Stenotrophomonas</i>		<i>Dickeya</i>
<i>Alternaria</i>		Plasmodiophora
<i>Aspergillus</i>		<i>Plasmodiophora</i>
<i>Fusarium</i>		Oomycetes
<i>Microascus</i>		<i>Phytophthora</i>
<i>Rhizopus</i>		

continues to appear in surprising new locations and/or with surprising new intensity, the populations of *P. infestans* worldwide are in flux, and that the genomics revolution has enabled investigators to make tremendous progress in terms of understanding its pathogenicity. The ascomycete *F. graminearum* is a leading and destructive pathogen that is indicative of the re-emergence of *Fusarium* epidemics [31]. For instance, changes in watermelon production practices via reduction in fumigation with methyl bromide, increasing human flux which affects rotational land availability, and the spread of more virulent forms of *F. oxysporum* f. sp. *niveum*, have led to a resurgence in *Fusarium* wilt [48]. Using a “field pathogenomics” strategy to the wheat yellow (stripe) rust pathogen *Puccinia striiformis* f. sp. *tritici* using transcriptome sequencing of infected wheat leaves uncovered a dramatic shift in the *P. striiformis* f. sp. *tritici* population in the UK and supported the hypothesis that recent introduction of a diverse set of lineages possibly have displaced the previous *P. striiformis* f. sp. *tritici* populations [49].

8. Conclusions

Over the past few decades, agriculture across the world has been affected by a succession of devastating epidemics caused by new pathogens that spilled over from reservoir species or by new variants of classic pathogens that acquired new virulence factors or changed their epidemiological patterns. Although the plant–host interactions are biochemically complex and represent challenging scenarios, metabolomic approaches [50] are equipped to understand the underlying mechanisms of the process at the ultimate level of post-genomic analysis. Nonetheless, the cataloguing of the chemical inter-kingdom signaling that encompasses both phytochemicals interacting with bacterial regulatory proteins and bacterial quorum-sensing signals inducing a diverse array of functional responses in plants would hold the key in understanding the finer regulation of new host–pathogen interaction systems. In addition, the plant genome sequencing efforts underway at a rapid-scale world-wide would allow understanding of the suppression of plant defense mechanism when challenged with these emergent pathogens. Undoubtedly, the genetic, cellular and physiological complexity of these recently evolved pathosystems (Table 1) pose a challenge to understanding their biology and hence efficient development of control mechanisms. Efforts are also constrained in phenological observations, molecular marker tools for their identification, systematic understanding of the life-cycle, and virulence mechanisms of these pathogens. Nonetheless access to population

genetic data, cheaper sequencing, parallel computing, and ‘omics’ approaches have created ample opportunity to apply these advancements to address the evolution of emerging pathogens and uncertainties in the predictions of these events. Moreover, to successfully manage the infectious diseases, greater efforts are required in international policy and partnerships and forums to facilitate communication among experts in wildlife and disease systems, including veterinary and plant pathologists, ecologists, epidemiologists, wildlife managers, academic and government researchers, and others [51]. In addition, these progresses would help unravel the drivers of emergence, fast and changing distribution, etiology, patterns of spread, and transmission dynamics amidst heightened calls to tighten biosecurity worldwide.

Competing interests

The authors declare that they have no competing interests.

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