

Phytopathogen emergence in the genomics era

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Phytopathogens are a global threat to plant agriculture and biodiversity. The genomics era has led to an exponential rise in comparative gene and genome studies of both economically significant and insignificant microorganisms. In this review we highlight some recent comparisons and discuss how they identify shared genes or genomic regions associated with host virulence. The two major mechanisms of rapid genome adaptation – horizontal gene transfer and hybridisation – are reviewed and we consider how intra-specific pan-genome sequences encode alternative host specificity. We also discuss the power that access to expansive gene databases provides in aiding the study of phytopathogen emergence. These databases can rapidly enable the identification of an unknown pathogen and its origin, as well as genomic adaptations required for emergence.

The study of phytopathogen emergence has never been easier

Emerging plant pathogens represent a serious threat to agricultural industries, food security, and to the conservation of plant species across the world. Accordingly, the ability to quickly identify a new phytopathogen and understand how it has emerged is vitally important. A fascinating complex of events surround the emergence of a phytopathogen and the impact that humans have had in facilitating phytopathogen emergence (see [Glossary](#)) has been studied in detail; for example, through trade, farming practices, and climate change [1,2]. However, the exponential rise in abundance of genomic data has meant that, for the first time, researchers are now in a position to begin to understand the true extent of the genetic events involved in pathogen emergence, both recent and ancient. Sequenced genes and genomes for both pathogenic and non-pathogenic organisms have become ubiquitous, which allows in-depth comparative analyses to be performed ([Figure 1](#)). In this review we will address two specific genome adaptations relevant to phytopathogenicity that have been observed with comparative sequence analyses. Additionally, we describe how increased sequencing of both pathogenic and non-pathogenic microorganisms, and from

whole genomes to single loci, has not only imbued greater clarity to the study of phytopathogens and their emergence but has also opened our eyes as to the limitations of reference genomes. Unprecedented levels of access to genetic data have enabled rapid genomic comparisons. This means that a new phytopathogen can be quickly identified, its relationship to other microorganisms assessed, and an informed prediction of the mechanism of emergence and location of origin can be made.

To demonstrate how the genomics era has assisted the study of phytopathogen emergence we provide two specific examples whose study has been greatly aided by genome sequences and the ability to share genetic data (i.e., genetic markers or genes). Initially we discuss *Pseudomonas syringae* and the emergence of ‘kiwifruit canker’ ([Box 1](#)). We also touch upon the devastating emerging disease, *Magnaporthe oryzae* ‘wheat blast’ ([Box 2](#)), whose study would be greatly aided by genome sequencing. We finally discuss how sharing of genetic data has assisted the study of *Hymenoscyphus pseudoalbidus* and the emergence of ‘ash dieback’ ([Box 3](#)).

Glossary

Comparative genomics: studies performed to compare and contrast genes or genomes of multiple individuals. These studies allow comparisons of host specificity, virulence, or other phenotypes that can be associated with functional genome elements.

Effector genes: genes that produce proteins or metabolites produced by a microorganism that enable successful infection and disease in a plant host. Avirulence genes, commonly referred to in agricultural pests, are a subclass of effectors.

Horizontal gene transfer (HGT): a genome adaptation event whereby DNA is transferred between organisms (potentially from different species or kingdoms) in a manner different from common reproduction (i.e., sex).

Interspecific hybridisation: the process of forming viable offspring between two genetically distinct species. For example, this can be achieved through sharing of alleles by distinct species via sexual reproduction or by the formation of a polyploid organism by transfer of whole-genome sequences.

Intraspecific genomic plasticity: describes the dynamic nature of the genomes of some microorganism in which large regions (up to whole chromosomes) can be lost, gained, duplicated, or translocated to/from other isolates within the same species.

Pan genome: refers to all possible genomic sequences that can belong to an organism or organisms within a pre-defined phylogenetic clade.

Phytopathogen emergence: a process by which a microorganism is observed with increasing regularity to infect and cause disease in a new or previously unreported plant host. Phytopathogen emergence can be preceded by an adaptation event allowing a microorganism to infect a plant, or alternatively can be a result of pathogen movement into a naïve host population. For the purposes of this review we will refer to adaptation events as those that have altered the genome of a microorganism to facilitate infection on a new host; for example, the gain of a virulence gene.

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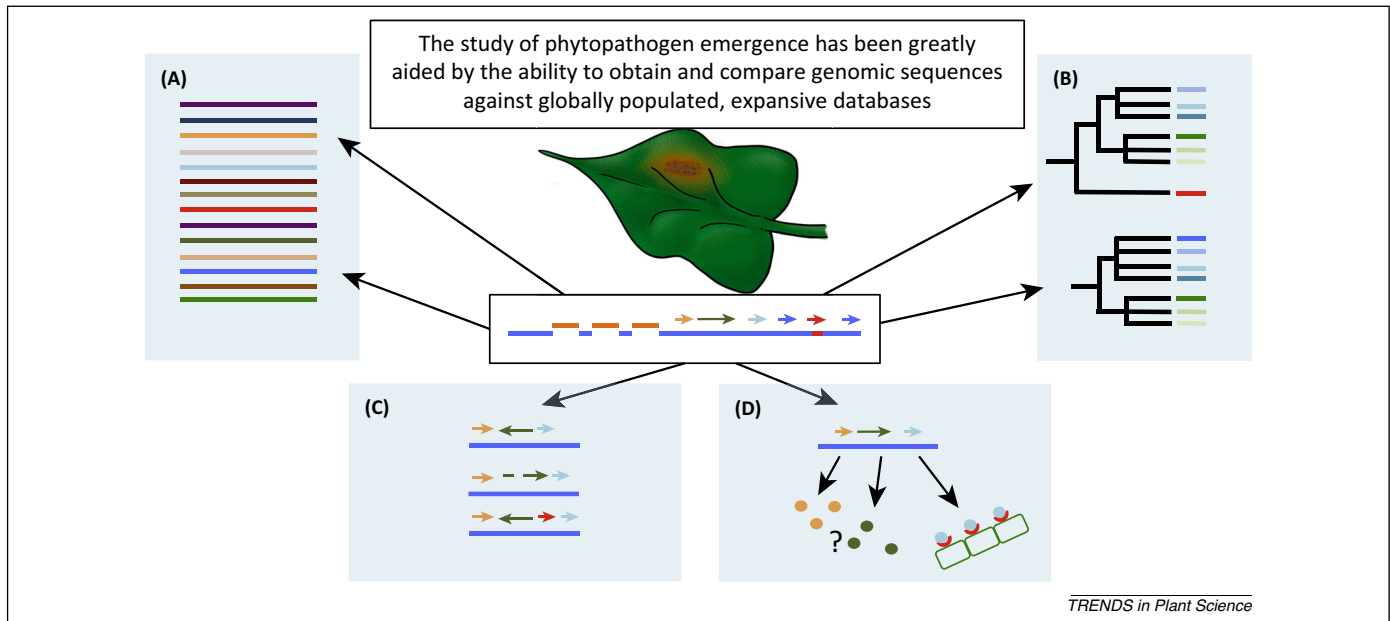


Figure 1. Understanding phytopathogen emergence in the genomics era. The ability to obtain the genomic sequence of a microorganism with relative ease has greatly improved our understanding of phytopathogen emergence. **(A)** A globally populated sequence database from all kingdoms of life. The true power of using genome analyses to study phytopathogen emergence comes from the ability to compare data against other sequences, thereby enabling rapid and accurate identification of a phytopathogen. Many studies in recent years have utilized genetic loci markers to resolve the boundaries of microorganism species, which in turn have populated databases with informative data. These data can be exploited for diagnostic purposes and for putative prediction of the centre of origin (**Box 2**). Similarly, the parental lineages of novel hybrid phytopathogen can be predicted using these resources. For an example of using genome sequences to observe a hybridisation event, see [35]. **(B)** Horizontal gene transfer (HGT) events can be predicted by comparisons to expansive sequence databases and tests of phylogenetic congruence. Access to large gene datasets for comparisons is therefore required because the standard method of HGT prediction is phylogenetic incongruence. For example, the true phylogeny for our emergent phytopathogen is shown (below) to be incongruent with the phylogenetic tree for the horizontally transferred gene (above). For an example of a pipeline for HGT prediction in phytopathogens, see [32]. **(C)** Re-sequencing within pathogenic species reveals novel genetic information within the pan-genome. Often studies that sequence more than one isolate from a single species discover novel genetic data that determine host-specific virulence. Here three genome sequences of the same species show a novel insertion (or deletion) of a genome segment that contains genes. For an example of the identification of isolate specific genome regions that confer isolate-specific virulence genes see [50]. **(D)** Increasing levels of functional data assigned to gene sequences in public databases. Newly annotated genomes can be compared with functionally characterised genes. Here we depict the light-blue gene from bacteria and its homologue in plants known to interact with a receptor on in plant cells. For an example involving previously characterised plant expansins found within bacterial genomes see [18].

Observations of genomic adaptation and its impact upon phytopathogenicity

For the purposes of this review we will not focus on the specific mechanisms of host resistance and susceptibility to phytopathogen effectors because this topic has been comprehensively reviewed [3]. Similarly, we will not focus on the beneficial outcomes of genome assemblies for important plants that are now available, especially complex genomes such as the hexaploid wheat genome (*Triticum aestivum*) [4]. Instead we will assess the impact that the ability to readily obtain genome sequences for a phytopathogen has had on improving our understanding of both the mechanisms of accelerated genome adaptation and the subsequent affect on the ability of a microorganism to cause plant disease. We will address two defined mechanisms of accelerated genome adaptation relevant to phytopathogenicity: horizontal gene transfer and inter-specific hybridisation.

Horizontal gene transfer: sharing of phytopathogenicity-related genes between species and kingdoms

One of the most publicized and sensationalistic mechanisms of accelerated genome adaptation studied has been horizontal gene transfer (HGT) [5,6]. Previously, the mechanisms of HGT, although well understood in prokaryotes [7], were hard to prove in eukaryotic organisms. One of the

primary reasons for the inability to accurately identify a HGT event was the lack of eukaryotic gene sequences available for comparison [5,8]. In more recent years this inability to successfully identify HGT has receded, and the breadth of HGT, intra and inter-kingdoms, has been explored; largely due to the ability to compare gene sequences against expansive, publicly-available databases [9–22]. The importance of HGT on the emergence of phytopathogens has been shown to be significant for oomycetes and across the bacterial and fungal kingdoms.

In bacteria, the relationship between horizontal transfer and genome adaptation has become well recognised. For example, the transfer of pathogenicity islands (PAIs) (regions of localised pathogenicity-related genes) between bacteria is well known [23,24], and recent genomic studies have reaffirmed this phenomenon and its impact on plant–pathogen interactions [25,26]. However, more recent wide-scale comparative analyses have revealed the horizontal transfer of specific pathogenicity genes not only between phytopathogens but also from plant hosts. Cross-kingdom HGT events were identified by searching public databases with a plant expansin homologue found in *Bacillus subtilis*, EXLX1 [18,27]. Subsequent phylogenetic analysis revealed the transfer of plant expansins into multiple microorganisms, including species of bacteria and fungi [18]. In plants, expansins are proteins involved in loosening cell walls [28]. It is speculated that these expansin homologues

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