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VIRULENCE IN XANTHOMONAS: IMPLICATIONS FOR PATHOGEN EVOLUTION AND CELLULAR AND MOLECULAR EVIDENCES

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ABSTRACT

Molecular infection biology and evolutionary theories have yielded insights into the evolution of bacterial virulence. Virulence evolution is contingent on host interactions, environmental heterogeneity that drives evolution and co-existence of multiple clones occupying different niches, intra- and interspecies social interactions, multi environments lifecycles, and transmission. *Xanthomonas* comprises an important ubiquitous group of Gram-negative plant pathogenic bacteria causing diverse plant diseases in several crops, fruits and vegetables. Mechanisms of virulence in *Xanthomonas* are brought about through several mechanisms such as a co-ordinated network of protein secretion systems, transcription-modulating effectors, and surface polysaccharides to suppress plant immunity and colonize host tissues. Rapid adaptation through genetic mechanisms exacerbates challenges in disease management. The rise of antibiotic resistance and climate-driven shifts in pathogen distribution threatens food security. The goal of the current review is summarize the current knowledge of virulence in *Xanthomonas* along with the genetics contribution and discuss the current anti-virulence approaches in practice against this important pathogen. Given the wider significance of the pathogen in plant diseases regular updates will aid in assessing new cellular and molecular virulence factors. Also offers ample opportunities for development anti-virulence methods. In summary, the theme emerging from the current available data is that several global hotspots exists explaining the diversity and host-range. Further, genus and strain level virulence factors are deployed by the pathogen to counter the host defenses.

KEYWORDS: Microbe-Associated Molecular Patterns; Mitogen-Activated Protein Kinase (MAPK) signaling; Executor **(*E*)** genes; Transcription activator-like effectors; TonB-dependent receptors.

1. INTRODUCTION

The evolution of bacterial virulence has been investigated using a number of practical approaches. Important insights can be obtained by linking Molecular Infection Biology (MIB) and Evolutionary Theory (EvT) (Bonneaud *et al*., 2020). Genetic changes associated with virulence can be studied by epidemiologic analysis of pathogen populations or re-sequencing of clones that have evolved during pathogen–host interactions, and competition experiments allow quantifying the relative fitness of competing strains (Diard and Hardt 2017). Experimental evolution of microorganisms has identified key general mechanisms of adaptation providing important insights concerning the relation between genetic and phenotypic changes, and the repeatability of evolution. However, in order to specifically address virulence evolution, one must take into account the complexity of natural environments in which pathogens evolve (e.g. host interactions, environmental heterogeneity that drives evolution and co-existence of

multiple clones occupying different niches, intra- and interspecies social interactions, multi environments lifecycles, and transmission (Gupta 2023).

The genus *Xanthomonas* comprises an important ubiquitous group of Gram-negative plant pathogenic bacteria that belong to the Gamma subdivision of Proteobacteria (Willey et al., 2016). Members of the genus *Xanthomonas* infect approximately 124 monocotyledonous and 268 dicotyledonous plants and are of economic importance in regions with a warm and humid climate. *Xanthomonas* spp. uses numerous virulence factors for pathogenicity and fitness in plant hosts. *Xanthomonas* spp. utilizes a collection of toxins, adhesins, and protein effectors as part of their toolkit to thrive in their surroundings, and establish themselves within plant hosts. The potent virulence and systematic infection system result in rapid dissemination of the bacteria, thus posing significant challenges in management and substantial crop loss (Singh et al., 2026). In this scenario, deeper insights into the cell, molecular and signaling mechanisms of the pathogen will yield insights into the components, pathways and biochemical events. These insights will enable subsequent several investigations at the biochemical, biophysical, cellular and genetic levels. These studies will enable trace the virulence, adaptation and evolutionary trajectories. Valuable insights from these studies will enable design sustainable management methods.

This narrative review was prepared by synthesizing peer-reviewed literature on Xanthomonas virulence. Literature was identified through searches of major scientific databases including Web of Science, Scopus, PubMed Central, Google Scholar, and Science-Direct. The search covered the period from 2000 to 2026, with emphasis on recent developments. Several foundational papers and reviews necessary to define the field were included. The literature was critically evaluated for relevance, scientific quality, and contribution to the understanding virulence.

Xanthomonas species (spp.) are typically rod shaped with a single polar flagellum, are obligate aerobes and have an optimal growth temperature of 25–30 °C. The bacteria are hemibiotrophic pathogens that initially feed on living host tissue, but in later infection stages, cause the death of plant cells (Catara, *et al*., 2021). *Xanthomonas* spp multiply either locally in the intercellular space or colonize the xylem vessels and then spread systemically within the plant. Bacterial colonies are usually yellow due to the presence of the membrane-bound pigment xanthomonadin, which might protect the bacteria from photobiological damage (Candido da Silva *et al*., 2017). Members of the genus *Xanthomonas* were originally grouped into separate species on the basis of their host range, but according to the classical nomenclature, most species were later merged into the single species *Xanthomonas campestris* and subgrouped into different pathovars (Rodriguez-R *et al*., 2012). Availability of whole genome sequences for the majority of *Xanthomonas* spp. has allowed the expansion of our understanding of the overall relationships among different species beyond classically used multilocus sequence typing. Average nucleotide identity among representative strains has been used as a criterion for classifying strains into species (Konstantinidis and Tiedje 2005). Several taxonomic revisions have been proposed in a larger species complex, sp. *axonopodis*, sp. *campestris*. While species nomenclature in xanthomonads has been defined based on its host specificity, whole genome comparisons have led to redefinition of some species (An et al., 2020). The virulence mechanism covered in individual and reviews are limited to a genus, lineage of study. Although there is a wealth of research on host specialization in model *Xanthomonas* species, the current knowledge is limited in understanding of the host range evolution and genetic exchange among closely related but differentially host-specialized species. The current study aims to collate data on diverse mechanisms, the associated unique features and contributions to virulence.

The current review is aims to review/collate and briefly discuss the diverse Virulence strategies of the pathogen in the initial section and their roles in pathogen evolution and adaptation. In the next section describes the earlier and new genomics DNA analysis based methods done act across various locations globally. The results provide useful genomic insights into the evolution of the pathogen. Finally we discuss the range of current strategies employed against the pathogen.

2. Virulence strategies in *Xanthomonas* species

Common mechanisms of virulence in *Xanthomonas* is brought about through the following mechanisms synthesis of Extracellular polysaccharides (EPSs) protect bacteria against environmental stress and adhesins for adherence. Virulence-associated protein secretion systems, virulence gene expression by quorum sensing and gene expression control. In this section we cover the various mechanisms through review of literature succinctly to provide an overview of the mechanisms.

2.1. Signalling mechanisms

Cell external and internal Signaling mechanisms

Cyclic dimeric-GMP (c-di-GMP) is an intracellular signaling molecule implicated in the control of cellular properties that can influence the virulence of pathogens (Hall and Lee. 2017). The PilZ domain of certain proteins can bind c-di-GMP and thereby have a regulatory impact on c-di-GMP-mediated processes. Yang *et al*., 2015 examined PilZ domain proteins of *X. oryzae* and demonstrated two proteins, PXO_00049 and PXO_02374, with high binding affinities for c-di-GMP. Gene deletions of the proteins confirmed their increased virulence. Flagellin is the primary structural protein making up bacterial flagella, acting as one of the most critical and evolutionarily conserved MAMPs (Microbe-Associated Molecular Patterns) in nature (Zhong *et al*.,

2017). Flagella are essential for bacterial motility and host invasion. Plants rely on plasma membrane-bound pattern recognition receptors (PRRs), such as FLS2 (Flagellin Sensing 2) (Zhong *et al*., 2017). MAMPs are conserved molecular patterns essential molecular signatures found on whole classes of microorganisms. They are critical to innate immunity and act as "danger signals" that allow hosts to distinguish non-self from self and mount an appropriate immune response (Choi, *et al*., 2016). Through a comprehensive analysis of flagellin polymorphisms within the genus *Xanthomonas*, Malvino, *et al*., 2022 elucidate their potential impact on host recognition and bacterial pathogenicity. By altering conserved epitopes (such as the *flg22* or *flgII-28* regions), *Xanthomonas* spp. avoid detection by host pattern recognition receptors like FLS2 and FLS3, undermining Pattern-Triggered Immunity (PTI) and thus evading immune evasion. Discoveries of Solanaceous-specific receptors, such as flagellin sensing 3 (FLS3), and their implications for plant defense responses, and bacterial motility in host colonization and infection highlight the multifaceted relationship between flagella-mediated chemotaxis and bacterial virulence (Hind *et al*., 2016).

MAMPs present an evolutionary dilemma for *Xanthomonas*: the traits required for infection (virulence) are the exact features that sound the host's alarm system. The flagellum is essential for *Xanthomonas* survival and multiplication. However, the shedding of flagellin components during movement immediately primes the host's apoplastic defense (Mani et al., 2023). Similarly, LPS/LOS structures enable protection against plant phytoalexins and environmental stress. However, shedding fragments of LPS act as highly potent immune elicitors (Ranf et al., 2016). Specific adaption to promote virulence includes subtle amino acid variations in specific epitopes to dramatically lower plant recognition without breaking the protein's structural function referred as “molecular mimicry and diversification”. An example is the *elf18* variants in *Xanthomonas campestris* pv. *campestris* (Xcc) which trigger only 0.8% to 3.2% of the immune activity (Huang et al., 2024). *Xanthomonas* secretes a signature exopolysaccharide such as xanthan gum**s** which coat the bacterial cell, creating a physical barrier that restricts the release of internal MAMPs and physically blocks host PRRs (Dzionek et al., 2021). Another mechanism includes injection of Type III Effectors (T3Es / Xops) directly into the plant cell cytoplasm. These effectors then degrade host PRR co-receptors, blocking Mitogen-Activated Protein Kinase (MAPK) signaling cascades, and suppress cell death (Üstün et al., 2013).

Quorum-Sensing Pathways

Xanthomonas relies heavily on the Diffusible Signal Factor (DSF) system (Zhao, *et al*., 2023). The DSF pathway (governed by *rpf* genes) monitors bacterial population density and regulates vital processes such as biofilm dispersal, motility, and the production of extracellular polysaccharides (EPS) and extracellular enzymes (Wang *et al*., 2016). Multiple TCS operate to detect environmental changes (e.g., nutrient availability, low oxygen, host signals) and translate them into genetic responses. A primary example is the RpfC/RpfG system, which acts as the core of DSF signal transduction (Ryan *et al*., 2015). Several global and specific transcription factors act downstream of the signaling pathways to adjust gene expression. Transcription activator-like effectors (TALEs) are important virulence factors secreted by *Xanthomonas* with the ability to directly bind to the promoters of target genes and activate their expression, which often facilitates the proliferation of pathogens (Xue *et al*., 2021). Numerous studies have revealed the modes of action of TALEs in plant cells and plant defense strategies to overcome TALE attack. The bacteria inject TAL effectors into the plant cells via a Type III secretion system (Mondal, 2020). The effectors bind to specific sequences called Effector Binding Elements (EBE) in the promoters. In pomegranate binding of EBE up-regulates the plant's susceptibility genes, rerouting cellular resources to feed the bacteria and suppress the plant's immune system.

While TAL effectors drive targeted gene activation, the bacterium also relies heavily on non-TAL effectors (like XopC2, XopL, and XopN) to further suppress host defenses and promote unrestricted bacterial growth and water-soaked lesions (Cox, *et al*., 2017). Non-TAL (Transcription Activator-Like) effectors like XopC2, XopL, and XopN are critical virulence proteins secreted by *Xanthomonas* species to promote bacterial infection. They act as molecular disablers, collectively suppressing plant basal immunity (Pathern-Triggered Immunity or PTI) to allow the bacteria to proliferate unhindered (Liu, *et al*., 2014). The XopN is a highly conserved effector that localizes to the host plant’s plasma membrane. It acts by interacting with and sequestering host scaffold proteins and immunity-related kinases (such as TARK1). By doing so, it blocks early defense signaling cascades (Wang *et al*., 2025). It heavily suppresses reactive oxygen species (ROS) production, reduces callose (cell wall) deposition, and stunts the activation of immune-responsive genes, enabling widespread tissue colonization. The XopL is an E3 ubiquitin ligase localized at the plasma membrane. XopL manipulates the host's ubiquitin-proteasome system (Ortmann *et al*., 2023). It targets and degrades specific plant immune regulators (e.g., proteins related to PAMP receptors) while hijacking host pathways for bacterial advantage. It severely cripples the plant's ability to trigger cell death (hypersensitive response) and impairs host pathogen-associated molecular pattern (PAMP) responses (Ortmann *et al*., 2023). XopC2 is a crucial, membrane-localized effector protein it targets multiple host cell proteins, including those involved in chromosome maintenance, hormone signaling, and mRNA processing (Ai, 2024). XopC2 actively represses defense responses and prevents plant cells from mounting a robust immune attack, playing a major, sometimes redundant, role

alongside other Xop effectors in driving severe blight and tissue necrosis (Wang *et al*., 2021). The prediction of TALE binding elements (EBEs) in the promoters of up-regulated genes identified a set of TALE-targeted candidate genes in pomegranate-Xcp interaction. The predicted candidate susceptibility genes include two oxoglutarate-dependent dioxygenase, ethylene-responsive transcription factor and flavanone 3-hydroxylase-like gene (Sivaraman *et al*., 2022). *Xanthomonas* catalase was induced over six fold by superoxide generators and methyl methane sulfonate but weakly by H2O2.

2.2. Secretion Systems and Effectors

Effector-Triggered Susceptibility (ETS)

To overcome plant immune system *Xanthomonas* uses a Type III Secretion System (T3SS) to deliver virulence effectors (*Xanthomonas* outer proteins or Xops) directly into the host cytoplasm (Alvarez-Martinez, *et al*., 2021). Notably, through the Transcription Activator-Like (TAL) effectors which enter the nucleus, bind to specific host gene promoters, and hijack the plant's transcriptional machinery to upregulate host susceptibility genes. This manipulation diverts plant nutrients to feed the bacteria and suppresses defense hormones like Salicylic Acid (SA) in favor of Abscisic Acid (ABA). Resistant plant varieties possess intracellular immune receptors (often Nucleotide-Binding Leucine-Rich Repeat or NLR proteins) that detect specific bacterial effectors (Förderer and Kourelis *et al*., 2023). This recognition triggers a robust and localized programmed cell death known as the Hypersensitive Response (HR), halting the spread of the pathogen (Balint-Kurti *et al*., 2019). Key to pathogenicity of most *Xanthomonas* pathovars is a Hrp-type III secretion (T3S) system that translocates effector proteins into plant cells. The T3S system is a molecular syringe-like nanomachine that allows *Xanthomonas* species to inject virulence effector proteins directly into host plant cells (Teper *et al*., 2016). It is the primary driver of bacterial pathogenesis, enabling the pathogen to cause disease, suppress plant immunity, and obtain nutrients. By silencing PTI, *Xanthomonas* prevents the production of reactive oxygen species (ROS), stomatal closure, and cell wall strengthening, allowing uninhibited bacterial proliferation (Mishra, et al., 2026). Through ETS, effectors such as AvrBs2 the pathogen forces the plant to leak sucrose and glucose into the intercellular spaces (Wang et al., 2025). Plants try to block ETS by mutating the EBEs on their S-gene promoters. In response, *Xanthomonas* utilizes its highly repetitive TALE domains to undergo rapid recombination (Erkes, et al., 2023). Studies show that TALEs can rapidly shift their repeat sequences to regain affinity for mutated host promoters, restoring susceptibility.

2.3. Genomic mechanisms

Transcription activation

Inside the host, the transcription effectors manipulate host cellular processes to prevent the plant from mounting an effective defense (Doyle *et al*., 2013). *Xanthomonas* utilizes a highly specialized, large family of effectors known as Transcription Activator-Like (TAL) effectors (e.g., AvrBs3). These proteins enter the plant nucleus, bind directly to specific promoter sequences in the host genome, and induce the expression of plant genes that benefit the bacteria (e.g., nutrient secretion) (Scheibner *et al*., 2017). TAL effectors act as transcriptional activators in the plant cell nucleus determined by modular DNA-binding domain. Two hypervariable amino acid residues in each repeat recognize one base pair in the target DNA. However, plants have evolved Executor **(*E*)** genes as a clever trap. When the TALE binds to the promoter of an *E* gene, it inadvertently drives the expression of the *E* gene itself. This sudden activation triggers a localized HR—a form of programmed cell death—which effectively starves the pathogen and halts the spread of disease. (Ji *et al*., 2022). The coordinated expression of bacterial virulence factors is orchestrated by quorum-sensing pathways through multiple two-component systems and transcriptional regulators such as Clp, Zur, FhrR, HrpX and HpaR (Giannakara and Koumandou 2022). Furthermore, virulence gene expression is post-transcriptionally controlled by the RNA-binding protein RsmA (Liu, *et al*., 2021)

Transposon mediated Virulence

They act as "jumping genes" that introduce, rearrange, or disrupt genetic sequences, ultimately determining how aggressively the pathogen infects plants (Bhat, *et al*., 2022). Tn3-like Transposons are primary drivers of *Xanthomonas* pathogenicity acting as vehicles that carry T3SS effectors and TALEs. TALE diversity- is a replicative transposition mechanism (specifically "fork slippage") which allows the transposons to generate diversity in TALE repeats (Weis *et al*., 2021). This enables the bacteria to adapt to new host niches, shift hosts, and bypass plant immune systems. Transposon insertions in the *gum* gene cluster disrupt extracellular polysaccharide (EPS) production, which is a major virulence factor needed for the pathogen to clog plant vascular tissue and cause wilting or lesions(Lucas,, *et al*., 2021). Insertions into housekeeping and metabolic networks (e.g., purine biosynthesis genes like *purH*) severely impair bacterial fitness and result in avirulent strains (Lu, *et al*., 2009). However, when transposons insert into essential metabolic or regulatory genes, they cause a loss of virulence also. In *Xanthomonas axonopodis* (and closely related species), transposons function as critical drivers of both virulence evolution and functional genomics. Oliveira 2018 report that the passenger that the genes of the Tn*3* family transposon Tn*Xax1* are known to play a significant role in the evolution and emergence of pathogenicity in the genomes of *Xanthomonadales*. Fernandes *et al*., 2024 identify a total of 35,692 ISs and 71 transposons were identified in 270 complete genomes in several phytopathogen including *X. oryzae*. Transposons such as the *Xanthomonas campestris* effector XopJ6 adjust the expression levels of virulence factors to alter the copy

number of the gene, tuning virulence and expression levels to adapt optimally to different plant tissue environments (Lauber et al., 2024). Transposons frequently insert themselves directly into or near these avirulence genes (e.g., in *Xanthomonas oryzae*), thus altering the gene's function allowing the pathogen to bypass plant immunity while continuing to replicate (Fernandes et al., 2024).

Horizontal Gene Transfer (HGT)

HGT is a primary driver of microbial evolution. By bypassing standard parental inheritance, bacteria can rapidly acquire entirely new, complex functional traits—like antibiotic resistance or toxins—directly from other organisms, accelerating the emergence of new virulent strains through HGT (Goyal, *et al*., 2022). Conjugation, Transformation and Transduction are the mechanism effecting HGT (Burmeister, *et al*., 2015). Incoming foreign DNA can replace homologous regions or seamlessly integrate into the host's chromosome, changing the pathogen's metabolic profile or immune evasion capabilities (Rohmat, *et al*., 2025). Further, Plasmids, transposons and genomic islands act as vehicles. They frequently move around the genome, scrambling gene order, duplicating sequences, and modifying existing gene functions (Domingues, *et al*., 2012). Evidence of population shift and local adaptation is reported (Sharma, *et al*., 2022). Horizontal Gene Transfer (HGT), genome rearrangements, emergence of new virulent strains with modified or lost effectors are the mechanisms adopted by the pathogen as part of its virulence arsenal. Horizontal gene transfer plays a major role in the pathological convergence of *Xanthomonas* lineages on common bean mediated through plasmids (Chen *et al*., 2018). Huang *et al*., 2024 report unique combinations of pathogenicity and virulence factors in *Xanthomonas euvesicatoria* and *Xanthomonas perforans*. Wider horizontal gene transfer was indicated by the fact that the lipopolysaccharide cluster of one strain was most similar to that of a distantly related *Xanthomonas* pathogen of barley. HGT confers virulence and adaptation of the pathogen by enabling acquisition of specialized gene clusters via plasmids which allows specific pathovars to adapt to new crop hosts and enables shift in strain's host range (Lauber et al., 2024). Frequent gene gains and losses create a large, flexible accessory genome that equips populations to several survive such as agriculture, climate and enables shifting of the host immune barriers (Assis et al., 2026).

Role of small non-coding RNAs (sRNAs) and RNA-binding proteins (RBPs)

In the *Xanthomonas* species, small non-coding RNAs (sRNAs) and RNA-binding proteins (RBPs) form complex post-transcriptional regulatory networks that control critical functions like virulence (Quendera *et al*., 2020). Hundreds of sRNAs have been identified across *Xanthomonas* strains (e.g., X. campestris, X. oryzae, and X. vesicatoria). The antisense sRNA Xonc3711 binds to the mRNA of a DNA-binding protein, negatively regulating its expression to impact flagella biosynthesis, biofilm formation, and oxidative stress tolerance (Wu *et al*., 2021). Studies identified hundreds of sRNA candidates in Xcc, with RsmU acting as a negative regulator of virulence, cell motility, and the HR (Tang *et al*., 2020). Other sRNAs like sX12 and sX13 are essential for pathogenesis, and their deletion significantly attenuates the bacteria's virulence (Islam, *et al*., 2017). Transcriptome screens have identified intergenic and antisense sRNAs, with key expression being regulated by the master virulence regulators HrpG and HrpX (Monnens *et al*., 2024). RNA-binding proteins act as the crucial intermediaries in these pathways, mediating the interactions between regulatory sRNAs and target mRNAs to alter translation or transcript stability (Quendera *et al*., 2020). The RsmA/CsrA family of global post-transcriptional regulators has been extensively studied in *Xanthomonas* (Mo*et al*., 2024). RsmA interacts with sRNAs like RsmU (or its isoform sRX061) to integrate environmental signals with bacterial toxicity. sRNAs help *Xanthomonas* rapidly adapt to reactive oxygen species, osmotic shifts, and nutrient limitations inside the plant host environment by repressing or activating specific antioxidant and metabolic networks(Wu et al., 2021). RBPs like Hfq and specific regulatory sRNAs fine-tune the flagellar and extracellular polysaccharide biosynthesis genes thus dictating swimming/sliding motility and attachment (Abendroth et al., 2014).

2.4. Cell architecture and Nutrient acquisition

Changes to cell architecture

In *Xanthomonas*, virulence is tightly coupled to the ability to alter host cell architecture and dismantle structural barriers. Luneau et al., 2022 report the transcriptomic profile of Xcc of cauliflower hydathodes directed towards deciphering the physiological and virulence strategies deployed by Xcc during early stages of infection. The study implicates high-affinity phosphate transport is needed for bacterial fitness. XopL homologs harbor a combination of a leucine-rich-repeat (LRR) domain and an XL-box which has E3 ligase activity. Despite similar domain structure there is evidence to suggest that XopL function has diverged, exemplified by the finding that XopLs expressed in plants often display bacterial species-dependent differences in their sub-cellular localization and plant cell death reactions (Ortmann *et al*., 2023). The XopL from X. euvesicatoria (XopLXe) directly associates with plant microtubules (MTs) and causes strong cell death in agroinfection assays in *N. benthamiana* (Erickson *et al*., 2018). Localization of XopLXe homologs from three additional *Xanthomonas* species, of diverse infection strategy and plant host, revealed that the distantly related X. campestris pv. campestris harbors a XopL (XopLXcc) that fails to localize to MTs and to cause plant cell death (Huang *et al*., 2024). The study exemplifies how the study of a T3E within the context of a genus rather than a single species can shed light on how effector localization is linked to biochemical activity. Functional analyses of

XopLXe truncations and amino acid exchanges within the PRR suggest that MT-localized XopL activity is required for plant cell death reactions (Alex *et al*., 2013). *Xanthomonas* citri subsp. citri (Xcc) mobilizes cell wall sugars by hijacking a fruit-ripening program through the type III effector PthA4, which activates the ripening coordinator CsLOB1 (Phan *et al*., 2025). CsLOB1 induces several genes encoding enzymes involved in cell wall breakdown. PthA4 coordinates an advanced "feedforward loop" that links the Type III (T3SS) and Type II (T2SS) secretion systems (Chen, *et al*., 2026). The cell wall breakdown products (such as xylose) act as signals to induce T2SS-secreted xylanases, further accelerating sugar mobilization for bacterial growth (Santos *et al*., 2014). Research shows it later binds with CsLOB1 in a dose-dependent manner to exert feedback control and prevent the over-induction of certain downstream targets at the later stages of infection. *Xanthomonas* oryzae pv. oryzae (Xoo) causes bacterial blight disease in rice. As a part of its virulence repertoire, Xoo secretes a cell wall degrading exoglucanase enzyme Cellobiosidase which is a critical virulence factor and also a determinant of tissue specificity (Tayi, *et al*., 2024). The CbsA protein is made up of an N-terminal catalytic domain and a C-terminal fibronectin type III domain. As a member of the glycosyl hydrolase-6 (GH6) family, it functions by cleaving cellulose from non-reducing ends to release cellobiose (Tayi*et al*., 2024).

Utilization of Nutrients

Iron is a vital nutrient to bacteria, not only in the basal metabolism but also for virulent species in infection and pathogenicity (Cassat and Skaar 2013). TonB-dependent receptors (TBDRs) are essential outer membrane proteins in *Xanthomonas*. They enable the high-affinity uptake of ferric-siderophore complexes and carbohydrates by harvesting energy from the inner membrane through the TonB-ExbB-ExbD complex (Braun *et al*., 2024). In *Xanthomonas* virulence, TBDRs are critical for overcoming iron-depleted host environments to sustain pathogenesis. Disruption of genes required for xanthoferrin synthesis or its corresponding TBDR utilization pathways limits bacterial fitness, severely stunting the pathogen's ability to grow inside host tissues and thereby reducing overall virulence (Pandey *et al*., 2017). This highlights its importance in virulence. Iron uptake is tightly co-regulated with other virulence traits. In *Xanthomonas*, the ferric iron-binding transcription factor *XibR* coordinately regulates TBDR gene expression alongside motility and chemotaxis genes (Pandey, *et al*., 2016). It strictly controls iron homeostasis to prevent toxicity. The two-component system *VgrRS* senses iron levels, repressing the expression of specific TBDRs (e.g., *tdvA*) that would otherwise be detrimental to bacterial virulence during iron abundance (Wang *et al*., 2016). Limited availability of magnesium within host tissues, acts as a cue that further modulates bacterial physiology and virulence. *Xanthomonas* has evolved efficient strategies to scavenge and store magnesium, integrating through tightly regulated gene networks (Shah, *et al*., 2026) The madB gene encodes the malonyl-ACP decarboxylase (MadB) enzyme, which plays a critical role in fatty acid biosynthesis and bacterial virulence. MadB is an active malonyl-ACP decarboxylase with the YiiD_C protein domain (Yan *et al*., 2025). It is vital for producing branched-chain fatty acids (BCFAs) and regulating signaling factors like the DSF family it enables complete virulence. Mutation studies of the gene in *X. oryzae pv. oryzae* (Xoo, which causes bacterial leaf blight in rice) implicates large spike in branched-chain fatty acids and significantly alters DSF signaling (Jiang *et al*., 2026). In *X. campestris pv. campestris* (Xcc) mutating madB results in only minor changes in fatty acid makeup and mainly impacts straight-chain DSF signaling suggesting host specific variability in virulence (Cai *et al*., 2017).

2.5. Environmental sensing mechanisms

Xanthomonas adapts to a range of abiotic and biotic stresses, including temperature, light, osmotic changes, oxidative stress, and host immune responses (Bhandari, *et al*., 2023; Hailu *et al*., 2017). The bacteria rely on sophisticated environmental sensing mechanisms, including chemotaxis mediated by methyl-accepting chemotaxis proteins (MCPs), which help them detect host-derived chemical signals(e.g., L-malic acid, tartaric acid, amino acids, and sugars) and navigate toward infection sites. By binding to attractants (like nutrients) and repellents (like toxins), they dictate a microbe's swimming and directional movements (Salah *et al*., 2017). Beyond navigation, MCP-mediated sensing regulates complex cellular behaviors such as biofilm formation, encystment, and host colonization (Lu *et al*., 2012). In *Xanthomonas oryzae* MCP mediated sensing functions as a primary environmental sensor detecting specific chemical gradients (chemoeffectors) before initiating the infection process (Kumar *et al*., 2018). *Xanthomonas* exhibits strong positive chemotaxis toward essential xylem sap components, including methionine, xylose, and glutamine (China, *et al*., 2026). Specialized chemoreceptors (such as Mcp2**)** sense specific constituents of xylem exudate this tissue-specific sensing is vital for bacterial proliferation and colonization. In *Xanthomonas* oryzae pv. oryzicola (Xoc) studies have identified specific transmembrane MCPs with distinct ligand-binding capabilities. In rice crops Xoc receptor, RS10815**,** binds specialized organic molecules like ethanolamine and tyramine (Liu et al., 2025). The evolutionary acquisition of these specific ligand bindings directly correlates with promoted bacterial growth and enhanced virulence. Figure-1 illustrates the contributors to evolution of virulence in *Xanthomonas*. Table-1 lists few *Xanthomonas* Virulence factors and their mode of action.

3. DNA based Population and Comparative Genomics of Virulence Evolution

Phylogenomic analysis revealed the clustering of Xoo strains from India along with other Asian strains, distinct

from African and US Xo strains (Midha *et al*., 2017). The Indian Xoo population consists of a major clonal lineage and four minor but highly diverse lineages with high pathogenicity restricted to minor lineages L-II to L-V and in particularly to lineage L-III. Molecular dating revealed that the major lineage, L-I is youngest and of recent origin compared to remaining minor lineages that seems to have originated much earlier in the past. The population structure of *Xanthomonas* oryzae pv. oryzae in Guangxi Zhuang South China is reported by (Chen *et al*., 2019). The results indicate all the pathotypes were found to be incompatible with xa5 and Xa7. One pathotype was virulent to Xa14, Xa21, and Xa23, whereas another virulent to Xa21 and Xa23, but incompatible with Xa14. A dendrogram suggests the prevalence of high genetic diversity of Xoo throughout Guangxi, and no association between the molecular haplotypes and pathotypes. Similarly in another study Curland *et al*., 2018 report the genetic diversity analysis of 82 strains of *X. translucens* in wheat, barley, rye, and intermediate wheatgrass. The results through MLSA report relatedness to *X. translucens pv. undulosa* and *X. translucens pv. translucens*. Clustering of strains based on Bayesian, network, and minimum spanning trees correlated with relative virulence levels in inoculated wheat and barley. DNA probes revealed the similar genetic diversity among *X. campestris pv. phaseoli* strains from Tanzania, East Africa, and in Wisconsin, U.S. were assessed by (Mkandawire *et al*., 2004). Results implicate probe hybridized with only one or two fragments in the East African strains, but with multiple fragments in the other *X. campestris pv. phaseoli* strains. East African *X. campestris pv. phaseoli* strains were highly pathogenic on Andean beans, but were significantly less pathogenic on Middle American beans. In contrast the pathogen from new world locations is highly pathogenic on beans of both gene pools. These initial studies describe the diversity and traces of region pathogen evolution insinuation the genomic evolution contributing to the virulence. These data indicates the existence of genetically and geographically distinct *X. campestris pv. phaseoli* genotypes.

The rep-PCR fingerprints of *X. campestris pv. phaseoli var. fuscans* strains from East African and New World locations were indistinguishable, and were readily distinguished from those of *X. campestris pv. phaseoli* strains. East African and New World *X. campestris pv. phaseoli var. fuscans* strains were highly pathogenic on Andean and Middle American beans. Genetic diversity and population structure along with four *X. arboricola pv. pruni* isolates from plum and three isolates of *X. arboricola pv. juglandis* as comparison is reported by Luo, *et al*., 2022. The Genetic diversity and phylogenetic analysis revealed the profound heterogeneity between *X. arboricola pv. juglandis and X. arboricola pv.* Moderate genetic differentiation within *X. arboricola pv. Pruni* was observed and host specificity but weak geographical differentiation in *X. arboricola* population was observed. DNA polymorphism was assessed by a restriction fragment length polymorphism analysis (RFLP), using an *X. axonopodis pv. manihotis* plasmid DNA sequence (pthB) as a probe to evaluate the genetic relatedness among 189 Colombian strains (Restrepo and Verdier 1997). The sampling intensity permitted the estimation of genetic differentiation within and among ecological zones, sites, and fields and even within an individual plant. A multiple correspondence analysis indicated that the Colombian X. axonopodis pv. manihotis population showed a high degree of diversity relative to X. axonopodis pv. manihotis populations studied previously, and the entire collection was grouped into seven clusters. A general correlation was observed between the clusters and the geographical origin of the strains, as each cluster was largely composed of strains from the same ECZ. Virulence variation was observed within the Colombian collection. Strains of different aggressiveness were found in all ECZs, understanding the X. axonopodis pv. manihotis population structure in Colombia. Khojasteh *et al*., 2019 screened 65 *Xanthomonas* bacterial strains isolated from wheat, barley, and gramineous weeds in eight Iranian provinces. Multilocus sequence analysis and typing (MLSA and MLST) of four housekeeping genes (dnaK, fyuA, gyrB, and rpoD), identified 57 strains as X. translucens pv. undulosa, while eight strains were identified as X. translucens pv. translucens. High genetic diversity of the BLS pathogen in Iran was in congruence with the fact that the Iranian Plateau is considered the center of origin of cultivated wheat. Similarly a phylogenetic tree constructed using a broad set of conserved housekeeping genes in four *Xanthomonas* species is reported by kanika *et al*., 2017. The method clustered all the fruit pathovars under study in one distinct phylogenetic group. Further, the results implicate Xac, Xap, Xvt, and Xmi emerged from a common ancestor and possibly belong to same species despite being classified as different species, i.e., *X. axonopodis*, *X. axonopodis*, *X. campestris*, and *X. citri*, respectively. To support the finding of their close phylogenetic relationship, ANI analysis of these pathovars was found to be >98.8%, suggesting that these pathovars may just be specialized strains. Cumulatively, these studies highlight host specificity, and variation in virulence in the genus. The results highlight heterogeneity with a genus and the evolution of strains from a ancestor strain.

Application of modern high resolution sequencing, multilocus DNA analysis has yielded insights into variations in diseases reactions and pathogen variability. Sivaraman et al., 2026 report Illumina–Oxford Nanopore sequencing approach to characterize the transcription activator-like effector (TALE) repertoires and virulence diversity among Indian isolates, four Indian Xoo strains (IX-123, IX-188, IX-249, and IX-423) using a hybrid. Data suggest that each strain harbored 17–19 tal genes, revealing TALome variation. Further, Effector binding element (EBE) predictions identified multiple TALEs targeting promoters of clade-III OsSWEET genes. Comparative analysis showed several Indian TALEs

shared EBE similarities with known virulence effectors such as PthXo1 and AvrXa7. Genomics study of recent outbreaks of bacterial spot in Turkey. Singh *et al*., 2011 screened 19 cultivars of cruciferae including seven Brassica spp. viz., *B. campestris, B. carinata, B. juncea, B. napus, B. nigra, B. oleracea and B. rapa,* and *Raphanus sativus* screened at Indian Agricultural Research Institute, New Delhi. The results indicate that the Xcc (22 strains) and other species of *Xanthomonas* (2 strains) formed three distinct groups of pathogenic variability i.e., Group 1, 2, and 3 under 50% minimum similarity coefficient. All strains of Xcc clustered under Groupl except Xcc-C20. The strains of Xcc further clustered in 6 subgroups viz., A, B, C, D, E, and F based on diseases reaction on host. Genetic variability of 22 strains of Xcc was studied by using Rep-PCR (REP-, BOX- and ERIC-PCR) and 10 strains for hrp (hypersensitive reaction and pathogenecity) gene sequence analysis. Xcc strains comprised in cluster 1, Xac under cluster 2, while Xoo formed separate cluster 3 based on >50% similarity coefficient. Cluster 1 was further divided into 8 subgroups viz., A, B, C, D, E, F, G, and H at 75% similarity coefficient. The hrpF gene sequence analysis also showed distinctness of Xcc strains from other Xanthomonads. Kaur et al., 2026 sequenced six novel *Xanthomonas* strains and analyse the evolutionary relationships. The results indicate the six novel strains were from *X. perforans* (3), *X. euvesicatoria* (2) and *X. campestris* (1). While the *X. perforans* strains were all part of the same evolutionary lineage, this was not the case for *X. euvesicatoria*, where strains from two distinct lineages with divergent T3SE repertoires were isolated from two distinct sites.

4.0. Current management strategies

Current strategies to combat virulence utilise several methods. First plant based anti-microbials such as phenolics that effectively suppress the assembly of the T3SS preventing the bacteria from injecting disease-causing effectors into host cell (Fan, *et al*., 2017). Tea tree oil and cinnamon oil show strong anti-biofilm properties, hindering bacterial motility and EPS production (Vishakha *et al*., 2022). Advancements in this method of control include the Metallic nanoparticles (like zinc oxide or copper-based) formulation for targeted delivery and enhanced antimicrobial efficacy (Rajpal *et al*., 2024). Next, biocontrol methods include application of antagonistic strains of Bacillus and Pseudomonas which secrete lipopeptides and cell wall-degrading enzymes that inhibit *Xanthomonas* growth and attenuate its virulence factors (Markelova and Chumak 2025). Certain biocontrol bacteria trigger the host plant's immune system to actively alert its defenses against incoming pathogens (Zhao *et al*., 2023). Modern molecular tools are used to permanently disrupt bacterial attack mechanisms or fortify plant immunity. CRISPR technology edits host susceptibility (S) genes to modify or remove specific transcription activator-like effector (TALE) binding sites, which prevents the pathogen from hijacking the host's genetic machinery (Zárate-Chaves, 2023). Currently, deploying *E* gene resistance is becoming a major component in disease resistance breeding, especially for rice bacterial blight resistance (Ji *et al*., 2022). Finally, developing and cultivating resistant crop varieties remains the most durable and effective lines of defense against pathovars like *Xanthomonas oryzae* (Jiang *et al*., 2020). Simultaneous study of population biology, pathogen interactions within the microbial community, and species evolution can be used to guide design effective strategies for disease management.

4. DISCUSSION

Understanding pathogen diversity and plant−microbe interactions is crucial for developing durable management strategies for bacterial diseases. These findings are important for understanding how major crop pathogens emerge, the potential for host range expansion, and evolution in response to management practices (e.g., evolution of resistance to antimicrobials or overcoming host resistance) or changing environmental conditions (Wang *et al*., 2026). The members of the genus *Xanthomonas* as a whole are pathogenic to more than 400 plant species, and at the same time, individual species or pathovars tend to be adapted to one or a few host species, all of which makes them excellent subjects for studying plant−pathogen interactions (Shah *et al*., 2026).

Recent population and comparative genomics studies have revealed patterns of *Xanthomonas* evolution within and between species. Whole-genome analyses of genetically diverse strains and samples from disease outbreaks have led to inference of past events and improved our understanding of present-day interactions (Li, *et al*., 2021). The arsenal of the *Xanthomonas* genus includes several molecules, signaling mechanisms, anti-immunity factors. At the genetic level HGT, transposons, and transcription factors aid evolution of virulence. Progress in omics methods has provided crucial insights into the taxonomy and phylogenetic relationships within this important bacterial genus. The current genetic data of 95% average nucleotide identity criterion for delimitation of species leaves room for considerable variation in phenotype (Harrison *et al*., 2023).

Xanthomonas genomes carry heavily redundant arsenals if a single effector is recognized by the host neighboring effectors within the same strain function to actively suppress that specific ETI signal. Distantly related genetic lineages of *Xanthomonas* can acquire identical transposon-associated effector modules, allowing divergent strains to converge on the same high level of virulence against a shared host. The evolution of antibiotic and copper tolerance is attribute to the transposition activity of transposons. Transposons such as Tn*Xaj417* (in *Xanthomonas arboricola* pv. *juglandis*) carry copper-resistance passenger genes which facilitate horizontal dissemination of populations to quickly adapt to chemical treatments in orchard ecosystems (Assis et

al., 2021). The structural diversity in TALEs, allows the bacteria to target new host genetic sequences and shift hosts over time. Example is the replicative transposition of Tn3-like elements which trigger replication fork slippage, which actively drives rearrangements within the highly repetitive central regions of TALE genes (Nicolas, et al., 2026). Despite high genetic similarity (~87.5% sequence identity) madB functions differently in major species highlight divergence contributing to virulence (Yan *et al*., 2025).

With reference to host adaptation existence of multiple lineages of *Xanthomonas* in the same host plant has been reported. Differential host specialization within species shows a high degree of host diversification that has occurred within an evolutionarily short time frame, as measured by genetic variation within the core genome (Liyanapathiranage *et al*., 2022). Figure-2 is an illustration of *Xanthomonas* taxonomy in family Araceae indicating in evolution. For example the *Xanthomonas* sp. strain CPBF 424 isolated from the asymptomatic dormant buds of a diseased walnut tree with bacterial blight symptoms (Fernandes *et al*. 2018). Studies show the blight pathogen's genome encodes roughly two to seven TAL effector genes (depending on the strain), which function similarly to those found in cotton and citrus-infecting *Xanthomonas* bacteria (Shah *et al*., 2025). Distinct patterns of RNA transcript expression both spatially and temporally enable dual lifestyles and the ability to rapidly transition between lifestyles remarkably in *Xanthomonas perforans* infecting on tomato (Kaur et al., 2026). Contrary to these mechanism research insights into the pathogenicity of *Xanthomonas* axonopodis pv. punicae indicates that is highly specific to pomegranate and there are no alternate hosts to this pathogen. Thus virulence is the pathogen is contributed through combined host, pathogen, genetic and environmental factors (Patil, et al., 2026).

A central regulatory system involves diffusible signal factor (DSF)-mediated quorum sensing, which coordinates community-level behaviors such as motility, extracellular polysaccharide production, and secretion of virulence effectors is a characteristic of *Xanthomonas* (He, *et al*., 2023). Quorum sensing modulates metabolic pathways to withstand changing microenvironments within plant apoplasts or xylem. It also facilitates interaction with other phyllosphere or rhizosphere microorganisms, granting a competitive edge during epiphytic survival (Majdura et al., 2023). A common observation among studies is evidence of bursts of evolution and diversification followed by gene flow among differentially host-specialized or geographically distinct populations. Few virulence mechanisms are lineage species and few strain and host specific. The continued evolution and host adaptation of Xanthomonas has hindered the ability of researchers to reconstruct population ancestry (Timilsina, *et al*., 2024).

These observations and data from the several virulence studies have impact on the ongoing global movement of plant pathogens. Expansion of geographic ranges due to and changes due to climate will require better knowledge of the ecological niche of *Xanthomonas* pathogens and the extent to which these niches overlap and provide opportunities for genetic exchange among co-occurring strains (Denancé *et al*., 2018). Recent comparative genomic studies have addressed the important aspects of diversity and evolution of nonpathogenic, weakly pathogenic, and pathogenic strains of *Xanthomonas* (Pena *et al*. 2024), which, together with increasing knowledge of virulence.

Figures and Tables

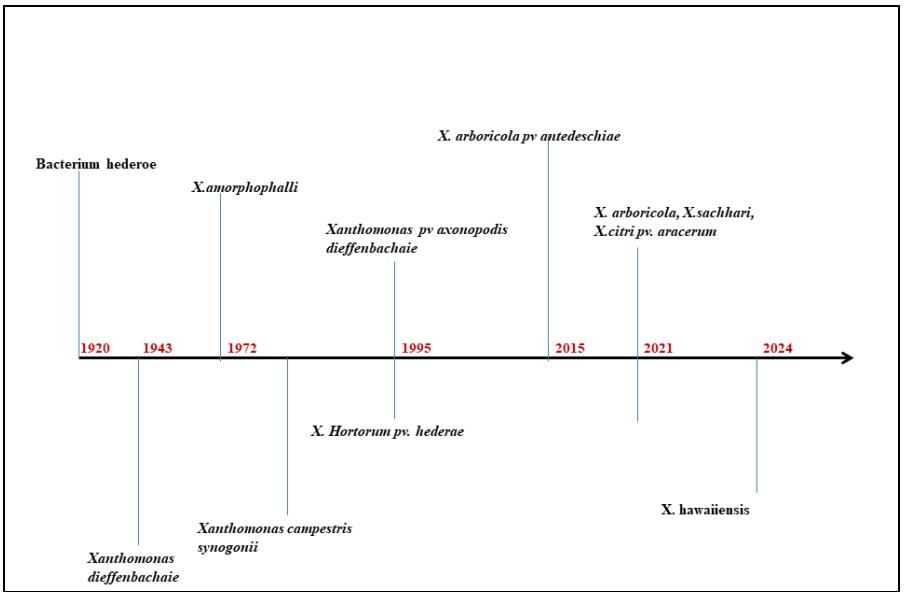


Figure 1: Illustration of changing nomenclature of Xanthomonas since 1920 to 2024 in Araceae crop. The frequent change and naming are indicative of the evolution and adaptation of the pathogen.

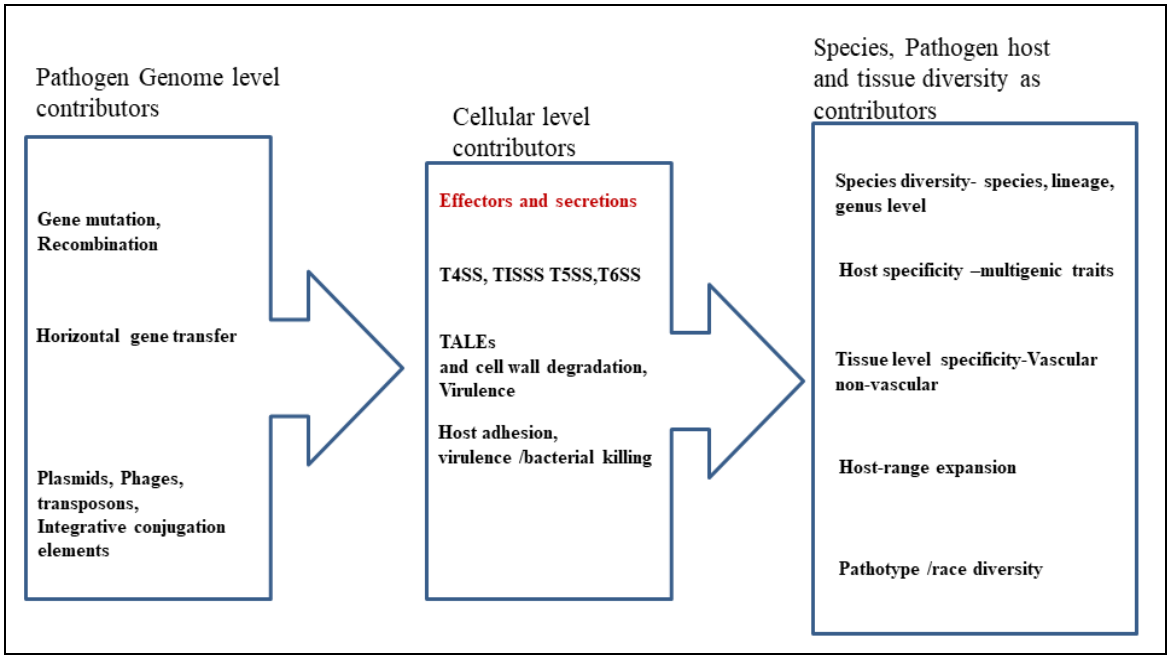


Figure 2: Contributors to pathogen evolution inXanthomonas at genome, cell and species/pathogen levels. Adapted from Timilsina et al., Phytopathology 2024.

Table 1: Virulence contributors in *Xanthomonas* and their mode of action.

Extracellular polysaccharides (EPS)	**Clog the xylem vessels and restricts water transport**	**Romaní *et al*., 2025**
Type III secretion systems	Inhibit host immune responses	Rahmatelahi *et al*., 2021
Methyl-accepting chemotaxis proteins.	Guide flagellar motility	Genova *et al*., 2026
PthA4 Type III effector	TAL effector that activates host transcription	Zou *et al*., 2021
Regulators (such as *hrpX* and *hrpG*)	Virulence effectors	*Teper et al*., 2021
Xanthan	Bacterial multiplication	Revin *et al*., 2023
Cellulases and pectinases	Plant cell walls	Xu *et al*., 2018
Xanthan gum	Protects the bacteria to survive in environmental stress	Silva *et al*., 2017
Immune-response Flagellin (FliC) Variation	Evades initial PAMP-triggered immunity (PTI)	Malvino *et al*., 2024
Trehalose	Withstand dehydration	Sharma, *et al*., 2026
copL and copB	Copper resistance genes	Krishna, *et al*., 2020
rpsL, *strA*, and *strB*	Streptomycin resistance genes	Krishna, *et al*., 2020
Transcription factor OsWRKY26	Negative regulator	Rehman 2021
DSF-family fatty acid molecules	Quorum sensing	Zhou, *et al*., 2017
Xcf and *Xcp*	Adaptation	Ruh *et al*. 2017

CONCLUSION

Emerging and re-emerging plant diseases continue to present multifarious threats to global food security. Considerable recent efforts are therefore being channeled towards understanding the nature of pathogen emergence, their spread and evolution. The genetically similar strains were present on different continents, are likely due to the international movement crops in the food supply chain. Periodic monitoring of these pathogen populations for evolution, variability is thus warranted. Effective management should involve use of judicious and conscious approaches specific to the host and pathogen. Practices such as screening for resistance in multi-environment trials to ascertain stability across environments/sites should be incorporated.

Limitations- Several studies could have been missed due to our search pipe-line. Also several databases and regional studies in English and non-english language could have been not included. The authors agree to the fact that the review is not comprehensive and it's only a narrative summary.

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