Review Paper:

Plant-Multi-Pathogen Interactions: A Growing Trend

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Abstract

Pathogen- host interactions involve competition, synergistic or cooperation and coexistence interactions. Host plant can also regulate niche battle among pathogens by defense response which target one or more pathogens either actively or passively. However, in general, virulent pathogens overcome the host defense strategies to infect it. Plant-pathogen interactions are mainly focused on single host-single disease model of infection.

However, microbes occur in complex communities in nature and plant infections generally include more than one genotypes and show complexities which cannot be explained by single host-single disease model. Here, we discuss recent understandings about the host-multi-pathogen interactions and their effects on host resistance as well as susceptibility. Here we highlight the recent insights on co-infection systems and identify their future implications in plant disease epidemiology and management.

Keywords: Plant-multi pathogen infections, pathogen competition, pathogen synergism, pathogen co-existence.

Introduction

In natural ecosystems, plants interact with various pathogen species and genotypes, resulting in complex co-infections that influence disease progression and the plant's immune response[17,53]. Co-infection represents a multifaceted relationship that can lead to altered disease severity and impact the host's immune system. Tollenaere et al[54] conducted a recent study in plant epidemiology focusing on the expression severity of multi-pathogen infections in hosts. Co-infected plants exhibit three primary types of interactions: host-pathogen, pathogen-pathogen and host-multiple-pathogen complexes[51,52]. While host-pathogen interactions are well-studied, the investigations on pathogen-pathogen and host-multiple-pathogen interactions (Figure. 1) are relatively limited but generally detrimental to the plant, resulting in reduced fitness[3].

These interactions can lead to various outcomes such as antagonism, synergism, cohabitation, mutualism, or collaboration, ultimately influencing the extent of disease damage in plants. In numerous instances, an individual microbial infection might not give rise to significant disease symptoms. However, when there is a co-infection involving another microbial species, it can lead to the development of severe diseases due to synergistic interactions.

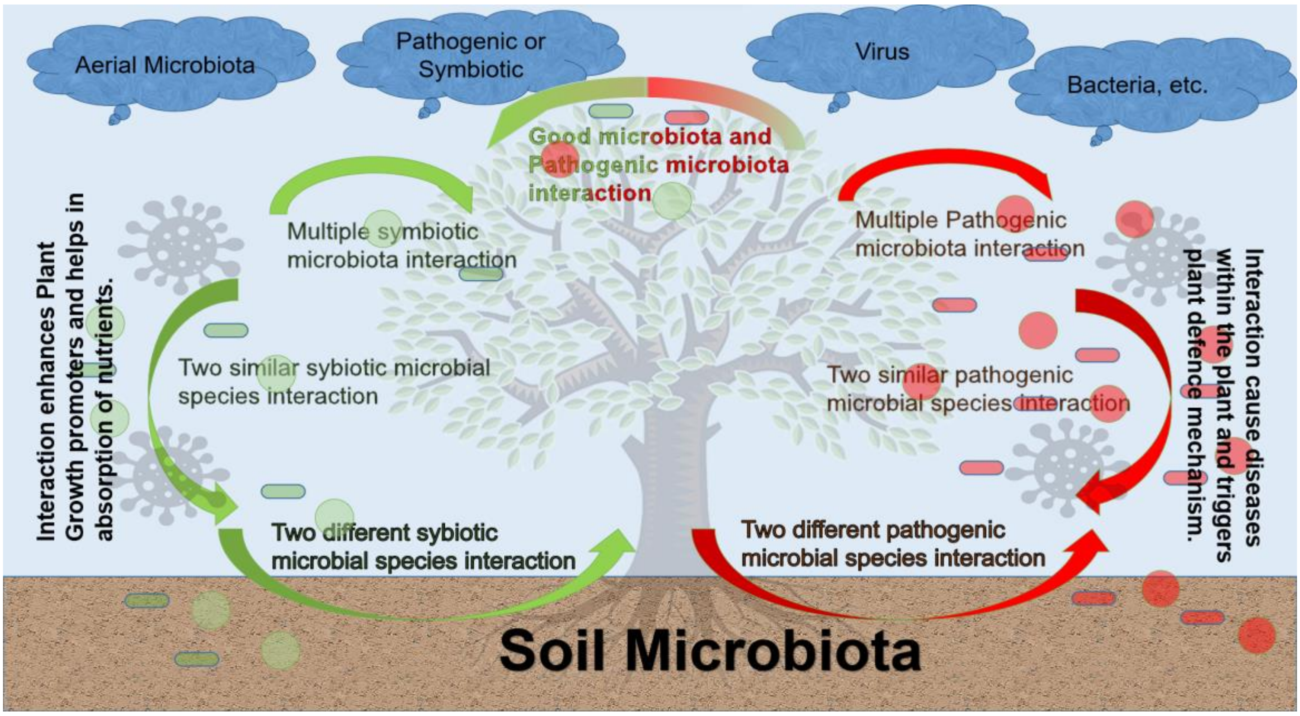


Figure 1: Plant- microbe interaction

Moreover, certain substances produced during these interactions can be phytotoxic, exacerbating disease-related damage[29,30]. Additionally, some diseases such as *Blumeria graminis* f. sp. *tritici* and the necrotroph *Zymoseptoria tritici* of wheat, do not directly interact to harm the host[37]. Instead, one pathogen may restrict the growth of another, leading to suppression. In some cases, this suppression can be so significant that the plant actively promotes the development of pathogens that suppress the primary disease[45]. Thus, understanding how hosts respond to co-infection and how pathogens interact and coexist is crucial for comprehending the overall virulence of diseases beyond infection heterogeneity.

Recent advancements in genomic and molecular technologies have provided novel insights into host-pathogen dynamics. Tollenaere et al[53] and Petrosino et al[41] have described the potential of metagenomics and microbial tag sequencing in investigating the diverse spectrum of diseases associated with a single host. These methodologies have revealed the frequency of multiple infections in the field and recent studies suggest that co-infection can have a significant magnitude in specific pathosystems[27,50]. Furthermore, Perefarres et al[40] highlighted how the presence of one pathogen population can modulate the host environment, influencing the outcomes of other infections and altering the frequency and persistence of those pathogens within the population.

Consequently, understanding the intricate host-multipathogen relationship is crucial for predicting the long-term dynamics of various disease outcomes. In this review, we are discussing recent studies regarding the diversity and dynamics of diseases occurring within a host. Our focus is on understanding interactions among bacterial, viral and fungal pathogens within plants, providing a current overview of this research area.

Bacteria-Bacteria Interaction: Interactions among plant bacteria hold a central role in the dynamics of plant health and disease (Figure 2). These interactions involve intricate relationships between different bacterial species infecting the same plant, significantly impacting plant growth and disease progression. Recent scientific inquiries have significantly advanced our understanding of the mechanisms and implications of these interactions. For instance, Liu et al[23] investigated the interaction between two bacterial pathogens, *Xanthomonas oryzae* pv. oryzae (Xoo) and *Ralstonia solanacearum*, in rice plants. Their findings revealed that the presence of *R. solanacearum* heightened the virulence of Xoo, leading to more severe disease symptoms. This study underscores the pivotal role of comprehending bacteria-bacteria interactions in the context of plant diseases.

Moreover, these interactions can profoundly affect the fitness and survival of bacterial pathogens. Loper et al[24] explored competitive interactions between *Pseudomonas fluorescens* and *Pseudomonas corrugata*, two bacterial pathogens infecting tomato plants. Their research demonstrated that co-infection intensified competition between the pathogens, resulting in reduced population sizes for both species. Similarly, Li et al[22] delved into the interplay between *Pseudomonas syringae* and *Xanthomonas campestris* in soybean plants. Co-infection led to enhanced disease severity and facilitated genetic exchange between the pathogens, giving rise to novel virulent strains.

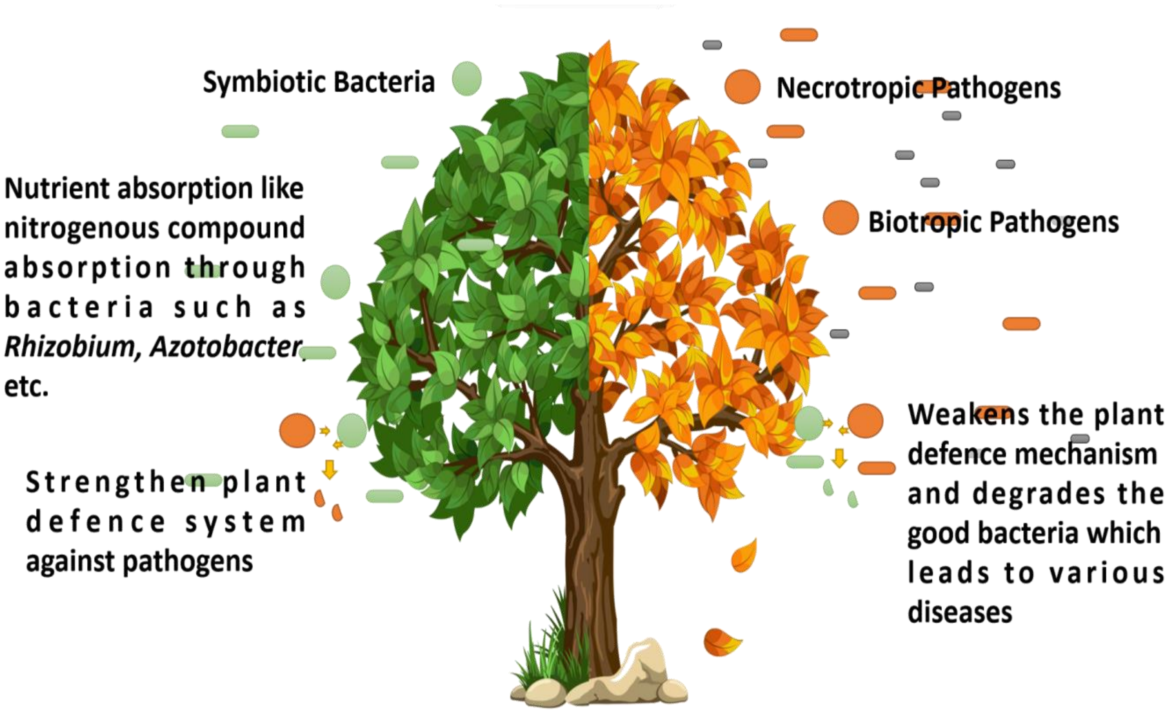


Figure 2: Multiple bacterial species interaction with plants

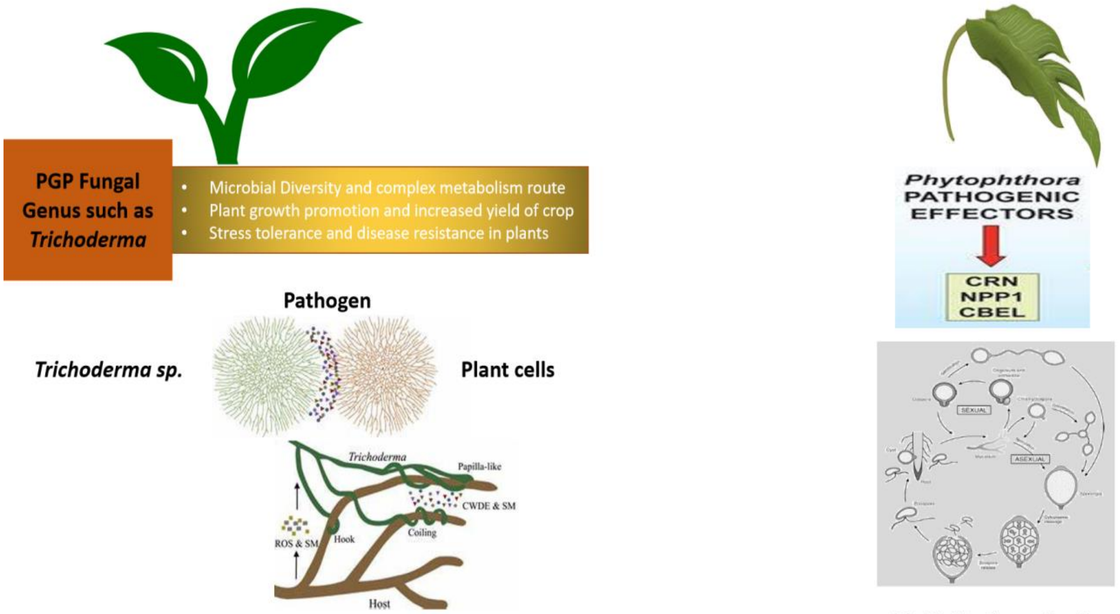
These interactions highlight the potential for accelerated evolution and increased pathogenicity through such pathogen-pathogen interactions. These findings indicate that bacteria-bacteria interactions shape the composition and dynamics of bacterial populations within plants, thereby influencing disease development and management. A comprehensive understanding of these interactions is vital for developing effective strategies to manage plant diseases. Recent research has also focused on leveraging these interactions for disease control. Wei et al[61] investigated the antagonistic interaction between *Bacillus velezensis*, a beneficial bacterium and the bacterial pathogen *Xylella fastidiosa* in grapevines. Their study revealed that *Bacillus velezensis* suppressed the growth and colonization of *X. fastidiosa*, presenting a potential biocontrol strategy against Pierce's disease.

Similarly, the antagonistic interaction between the bacterial pathogen *Pectobacterium carotovorum* and the beneficial bacterium *Bacillus velezensis* in apple trees was studied. *Bacillus velezensis* inhibited the growth and virulence of *P. carotovorum*, suggesting a promising biocontrol strategy against soft rot disease. These studies highlight the potential for exploiting bacteria-bacteria interactions in the development of sustainable and environmentally friendly biological control methods, emphasizing their significance in disease management.

Fungus-fungus Interactions: Fungi have the ability to establish diverse associations with plants including both pathogenic and symbiotic relationships (Figure 3). Changes in micro- and macro-climates can significantly alter these interactions between fungi and plants, leading to positive or negative outcomes[42,49]. Furthermore, fungi can engage in synergistic or antagonistic interactions with other fungal species within a host, profoundly influencing disease outcomes[26]. For instance, a study conducted by Spoel et al[47] investigated the co-infection of *Fusarium oxysporum* and *Pseudomonas fluorescens* in tomato plants. Their findings revealed a synergistic interaction between these fungal pathogens, where the presence of *Pseudomonas fluorescens* intensified the severity of *Fusarium oxysporum* symptoms. Similarly, in Arabidopsis, co-infection of *Pseudomonas syringae* and *Alternaria brassicicola* resulted in increased disease severity due to their synergistic relationship[39].

Many instances of coexistence among fungal pathogens on crops have also been reported. The black spot disease complex in peas was initially attributed to three fungal pathogens according to the study by Le et al[20]. However, recent research has identified four additional pathogens associated with this disease: *Phoma koolunga* [7], *Phoma herbarum*[21], *Boerema exigua* var. exigua and *Phoma glomerata*[55]. These newly discovered pathogens share common traits, being necrotrophic, generalist and polyphagous species. These characteristics enhance their ability to colonize diverse environments. In wheat a disease complex affecting wheat leaves, referred to as septoria leaf blotches, is caused by the presence of *Septoria tritici* and *Stagonospora nodorum*.

Additionally, wheat stems can be affected by *Oculimacula yallundae* and O. *acuformis,* while phoma stem canker on oilseed rape is induced by *Leptosphaeria biglobosa* and *L. maculans*. Another complex disease observed in wheat is foot and crown rot, caused by various Fusarium species. Specifically, *Fusarium graminearum, F. culmorum, F. poae* and *F. sporotrichioides* have been identified as the key pathogens associated with this condition[19].



Trichoderma and it's supporting defence mechanism with plant cells

Multiplicative cycle of fungal pathogens with genus *Phytophthora*

Figure 3: Fungal beneficial verses pathogenic interaction

It is considered that these pathogens employ synergistic interactions as a strategy to infect host plants. There are reports of antagonistic interactions such as the co-infection of *Fusarium oxysporum* and *Pseudomonas fluorescens* in wheat, where their interaction demonstrated antagonistic effects [35]. In tomato, co-infection with different strains of *Fusarium oxysporum* (Fo47 and Fol8) exhibited an antagonistic interaction between the pathogens [2]. Likewise, the co-infection of *Pseudomonas putida* and *Botrytis cinerea* in beans, *Fusarium verticillioides* and *Ustilago maydis* in maize, *Fusarium graminearum* and *Phoma sp.* in finger millet[32,36] and *Zymoseptoria tritici* and *Blumeria graminis tritici* in wheat[37] led to antagonistic interactions between the fungal pathogens.

Virus-Virus Interactions: Synergistic interactions between two or more plant pathogenic viruses, intensifying the severity of symptoms, have been observed across various crop species (Figure. 4). Notably, mutualistic cooperation among pathogens holds significant epidemiological implications and certain plant pathogens exhibit destructive effects exclusively when they collaborate with other independent pathogens[11,33,44]. For instance, an obligatory mutualism between *maize dwarf mosaic virus* and *wheat streak mosaic virus* results in lethal maize necrosis. Neither of these pathogens, when acting alone, is known to cause lethal necrosis[57]. Similarly, the co-infection of *tobacco mosaic virus* and *potato virus* induces defoliation streak and high mortality rates in young tomato leaves.

Cooperative interactions can enhance pathogen persistence by supporting higher reproduction rates, thereby increasing the likelihood of the host serving as a source of inoculum in subsequent seasons. In the case of *Nicotiana benthamiana* plants, co-infection with two strains of *cassava mosaic virus* resulted in symptoms covering all leaves, while single-strain infections led to partial coverage, with some leaves remaining asymptomatic[10].

Mixed (Fungi-bacteria-virus) Interactions: There are reports of plant disease complexes involving the association of multiple pathogenic microbial groups. An example is the root rot disease complex observed in *Panax notoginseng*. This complex involves a diverse array of plant pathogenic fungi including *Alternaria panax*, *Alternaria tenuis*, *Cylindrocarpon destructans*, *Cylindrocarpon didynum*, *Fusarium solani*, *Fusarium oxysporum*, *Phytophthora cactorum*, *Phoma herbarum and Rhizoctonia solani*. Interactions leading to communication and synergism among pathogens have been observed and documented in various instances. For example, bacteria such as *Pseudomonas sp.* and *Ralstonia sp.* have been identified in disease complexes, demonstrating mutualistic pathogenic effects[25,31].

Interactions among plant pathogens play a pivotal role in shaping the dynamics of plant diseases, influencing both the severity and spread of these diseases. Recent studies have yielded valuable insights into these interactions and their implications. For instance, Rodríguez-Romero et al[43] explored the co-infection of tomato yellow leaf curl virus (TYLCV) and the fungal pathogen *Fusarium oxysporum* in tomato plants. Their findings revealed a synergistic interaction between TYLCV and *Fusarium oxysporum* where the presence of TYLCV heightened the severity of Fusarium wilt symptoms.

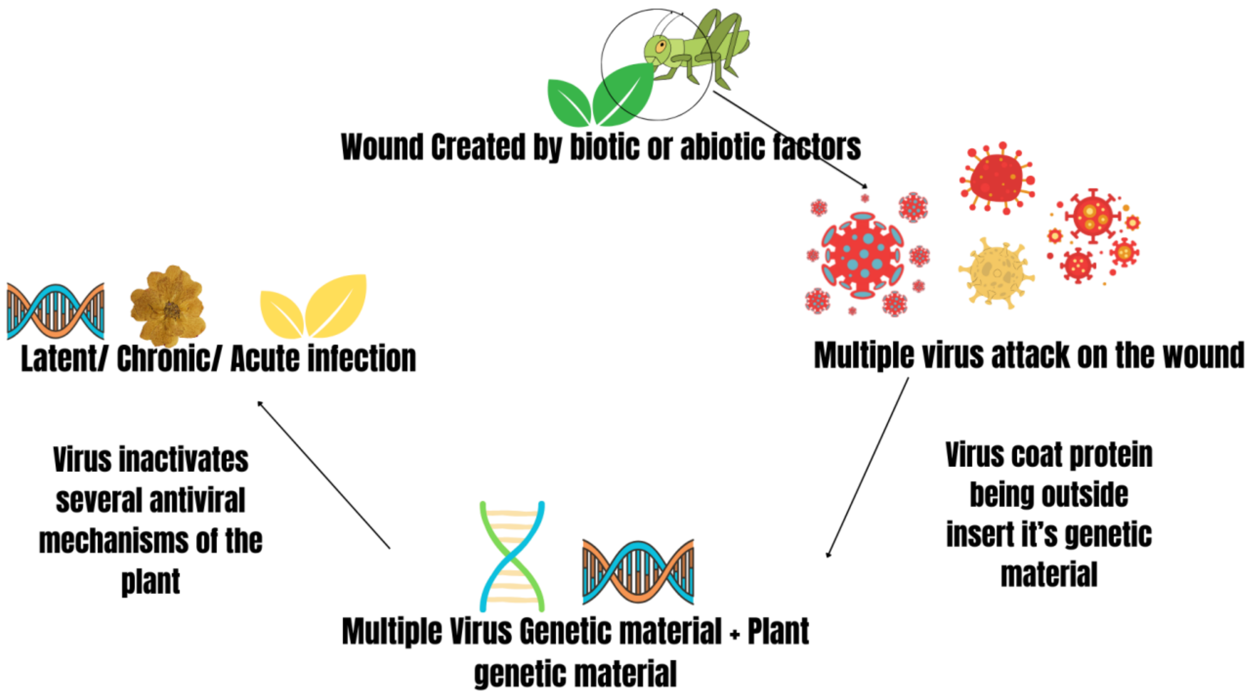


Figure 4: Multiple Virus infection leading to lethal or sub-lethal effect on plant

Additionally, research was conducted on the co-infection of the necrotrophic fungus *Botrytis cinerea* and the bacterial pathogen *Pseudomonas syringae* in *Arabidopsis thaliana*. This study uncovered a complex interaction scenario where the presence of *P. syringae* facilitated enhanced colonization of *B. cinerea,* leading to increased disease severity. These studies underscore the intricate nature of pathogen-pathogen interactions and their significant impact on plant diseases.

In another case, *Didymella bryoniae* fungal hyphae was found to transport four co-infecting bacterial species in Styrian oil pumpkin. Field samples confirmed the mutualistic pathogenic effects of these interactions[13]. A complex biochemical association was uncovered in the interaction between *Rhizopus microsporus* and *Burkholderia sp*. Initially, *R. microsporus,* a zygomycetous fungus causing blight in rice seedlings, was believed to produce the phytotoxin rhizoxin However, genome analysis did not identify standard polyketide synthesis genes in the fungus. Further investigation revealed that rhizoxin is secreted by endosymbiotic bacteria within *R. microsporus,* specifically belonging to the Burkholderia genus. Consequently, the pathogenicity of *R. microsporus* is attributed to its endosymbiotic bacteria [39].

Biochemical symbiosis between fungi and bacteria thrives through a recognition system and molecular dialogue binding them. For example, fusaric acid, secreted by specific *F. oxysporum* fungus isolates, triggers growth in the bacterial pathogen *Pseudomonas fluorescens* within tomato plants[9,15]. Endophytes, which colonize plant internal tissues without causing visible disease, play a crucial role. They produce antimicrobial compounds that enhance overall plant fitness and directly or indirectly influence pathogen interactions[38]. For instance, *F. oxysporum*, residing in plant roots, produces antimicrobial compounds that enhance plant resistance against pathogenic *F. oxysporum*[2]. In another mixed species infection study, Carrara et al[4] studied the interconnected responses among plants, fungi and bacteria and its pivotal role in shaping enzyme activity responses to nitrogen fertilization.

Plant responses during encounters with pathogens: In the context of plant-pathogen interactions, extensive research has typically focused on single plant-pathogen systems. However, plants in natural conditions frequently face challenges from multiple pathogens, each employing distinct strategies to exploit their hosts. Consequently, plants have evolved a robust defense system, featuring resistance (R) genes orchestrating responses to various pathogenic assaults. Plant genomes house a diverse array of these R-genes, enabling the recognition of pathogens and rapid activation of defense mechanisms[6].

Plant defense resource allocation is a dynamic process, where priorities shift based on the invading pathogens' modes of action[14]. This leads to strategic investments in defense metabolites tailored to combat specific pathogen threats, raising a fundamental question: Can the infection by one pathogen influence the host's response to subsequent infections?

Certain pathogenic infections can weaken the plant's defense systems, making it susceptible to secondary infections. For example, when Arabidopsis is infected by the foliar bacterium *Pseudomonas syringae,* it becomes more vulnerable to invasion by the necrotrophic ascomycete *Alternaria brassicicola*[47]. Similarly, infection by the biotrophic oomycete *Albugo candida* suppresses Arabidopsis defenses, enabling otherwise avirulent pathogens to thrive[5].

On the contrary, some pathogenic infections enhance the host's defenses, enabling it to resist subsequent attacks. For instance, infection by the foliar bacterium *P. fluorescens* initially suppresses specific defenses in Arabidopsis but triggers a defense signaling cascade that confers resistance to subsequent challenges[58]. Certain root infections establish rhizosphere networks transmitting induced resistance to neighboring plants[46]. Similarly, non-pathogenic *F. oxysporum* primes tomato plants, allowing them to respond more effectively to pathogenic *F. oxysporum* in a vaccine-like manner[2]. Recent research has explored hormonal aspects of plant defense responses during co-infection scenarios. Comparative analyses have focused on gene expression responsive to jasmonic acid (JA), ethylene (Et) and salicylic acid (SA).

JA and Et pathways typically defend against necrotrophic pathogens and SA against biotrophic pathogens. Antagonistic crosstalk between these pathways allows tailored defenses. Pathogens exploit this antagonism by secreting phytotoxins or effectors disrupting hormonal signaling, making the host susceptible to further infections[8,16]. The study of plant defense responses to co-infections reveals a complex interplay shaped by molecular signaling, resource allocation and evolving strategies of both parties, offering critical insights into plant immunity with wide agricultural implications. Plant-microbe interactions' complexity underscores the need for further research to uncover the mechanisms driving these intricate relationships.

Next-generation sequencing techniques for Studying Plant disease complex: The initial comprehensive analysis which accurately identifies the causal agent(s) of a disease, constitutes the fundamental step in plant disease management[1,28]. Following this identification, appropriate disease management tools such as antimicrobial compounds, can be deployed, tailored to the specific plant type and the affected part. While the application of chemical substances holds significance, a sustainable approach to disease management necessitates the formulation of long-term strategies. Consequently, gaining a profound understanding of pathogen-pathogen synergies in the context of complex plant diseases is crucial. For instance, many existing antimicrobial strategies in agriculture are designed to target specific microbial pathogens.

However, these targeted chemical control methods prove limited when multiple pathogenic agents contribute to a disease. In such cases, the application of a specific substance may not guarantee successful disease management. Hence, investigating plant disease complexes, understanding synergistic interactions among pathogens and unraveling the underlying mechanisms are essential. These efforts can help to identify critical connections that could be manipulated to uphold the health of crops. This endeavor presents challenges due to the influence of disease complexes by environmental factors, cultural practices and geographical variations[62]. Therefore, it is imperative to meticulously devise experimental approaches that facilitate the identification of pathogenic consortia in the context of crop production systems.

Presently, advancements in scientific knowledge and methodologies offer an unprecedented opportunity to enhance our comprehension of the diverse microbial species implicated in plant diseases, as well as the underlying mechanisms governing these interactions. Consequently, research on complex diseases necessitates embracing culture-independent analyses, exemplified by high-throughput sequencing techniques. This innovative approach stands in stark contrast to the traditional culture-based methods, effectively circumventing the limitations associated with their time-consuming and costly nature[34].

In the contemporary landscape of biodiversity surveillance, State-of-the-Art methodologies like next-generation sequencing (NGS) have revolutionized the analysis of intricate microbial populations, as comprehensively reviewed by van Dijk and colleagues[59]. This technological advancement has provided crucial insights: microbial diversity, when assessed using conventional cultivation-based techniques, is significantly underestimated, as highlighted by Gilbert and Dupont[12]. Over the past decade, the integration of metagenomic projects with NGS technologies has ushered in a new era in microbial ecology studies, dramatically accelerating the pace of research in this field[56,60].

In the realm of plant pathology and particularly in the study of plant disease complexes, leveraging Next-Generation Sequencing (NGS) and metagenomic techniques holds significant promise. Current scientific literature underscores a multitude of applications for these advanced technologies. Several studies have employed these methods to diagnose novel pathogens, as evidenced by research conducted by Adams and colleagues[1]. For instance, employing high-throughput parallel sequencing enabled the identification of three previously unknown viruses in sweet potato plants infected with well-known pathogenic viruses, albeit at remarkably low levels[18]. These groundbreaking technologies thus serve as potent tools for unraveling the involvement of multiple microbes and their collective contribution to the occurrence of plant diseases. The utilization of novel OMICs methods in studying microbial consortia and plant diseases comes with certain limitations.

While these techniques contribute to a better understanding of complex diseases, they may not definitively pinpoint the dominant microorganism responsible for the disease process. Identifying nucleic acid sequences derived from infection sites does not provide unequivocal evidence that a particular microorganism is the causal agent of the disease. For instance, Adams and colleagues[1] determined the complete genome sequence of a pathogenic virus through metagenomic analysis.

Although this data strongly suggested a link between the presence of the new Cucumovirus full genome and a transmissible infection with virus-like symptoms, Koch's postulates were not fully satisfied. Notably, viral particles were not observed and the disease was not re-established in the original host, indicating that metagenomic sequence analysis can only confirm the presence of the virus.

Consequently, metagenomics introduces a new challenge in understanding the taxonomy and role of phytopathogens in diseases[48]. Additionally, distinguishing pathogens from saprotrophic microorganisms becomes a complex task, particularly in cases of mixed infections.

Conclusion and future perspectives

In summary, delving into interactions among plant pathogens yields invaluable insights into the dynamics, evolution and strategies for disease control. Recent scientific inquiries underscore the pivotal role of comprehending diverse pathogen interactions for effective disease management. These findings emphasize the necessity of a holistic understanding of plant diseases, considering the intricate web of multiple pathogen interactions. Deciphering the mechanisms and repercussions of these interactions stands as a linchpin in disease management and control strategies. Research on multiple pathogens within plants illuminates the potential for accelerated evolution and heightened pathogenicity, all orchestrated through complex pathogen-pathogen interactions.

The exploration of these interactions for disease management promises sustainable and environmentally friendly approaches. The study of synergistic interactions underscores the intricate nature of pathogen-pathogen dynamics and their profound impact on plant diseases. Moreover, investigations into antagonistic interactions unveil the potential for harnessing these relationships in the development of biological control methods. Thus, gaining a deep understanding of the biology and molecular intricacies of these inter-microbial processes becomes crucial in identifying novel targets and strategies for effective disease control.

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