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Molecular insight, pathogenesis and resistance management of bacterial wilt (*Ralstonia solanacearum*) disease

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ABSTRACT

Bacterial wilt disease (BWD), caused by the pathogenic microorganism *Ralstonia solanacearum*, is recognized as one of the most destructive afflictions that impacts numerous economically significant crops globally. The disease constitutes a substantial economic decline, particularly among small-scale farmers. This review presents comprehensive information on the causative agent of BWD, *R. solanacearum*, by elucidating its associated disease symptoms, host range variability, crops affected, and geographical distribution, with emphasis on Asian regions, as well as the different management strategies. Using a comprehensive meta-synthesis approach with qualitative orientation, 90 documents published between 1991 and 2023 were reviewed. The findings offer important insight regarding significant obstacles in the realm of agricultural products, including diminished crop yields and the economic ramifications resulting from pathogen-induced infections. Potential research areas that can effectively support agricultural production, facilitate rapid disease detection, and mitigate the spread of crop infections were gleaned from the review findings. Overall, molecular insights into pathogenesis and resistance mechanisms are vital for the development of effective management strategies. By combining genetic advancements and sustainable agricultural practices, conservation efforts can be advanced to alleviate the impact of this alarming disease on crop production and global food availability.

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Introduction

Ralstonia solanacearum, a deadly soilborne pathogen, is known to cause bacterial wilt disease (BWD) in numerous plants. BWD is among the most important bacterial diseases worldwide, infecting more than 450 plant species in at least 54 plant families (Ayana & Kurabachew, 2016; Chachar et al., 2025; Lebeau et al., 2011). It ranks among the top 10 bacterial pathogens in terms of scientific and economic importance in plant diseases. Major crops commonly infected by *R. solanacearum* are tomato, potato, tobacco, banana, and eggplant (Elphinstone, 2005; Phiri et al., 2024). One of the major drawbacks of planting these crops is their susceptibility to BWD, which has affected their growth and harvest, causing significant yield loss to farmers. Such economic losses are more experienced by farmers who rely on these crops as their primary source of income.

In order to develop effective management strategies for plant disease control, it is crucial to understand the molecular mechanism of the pathogen and plant interactions (Genin, 2010; Vailleau & Genin, 2023). As a result, several molecular studies ranging from genomics to transcriptomics, proteomics and metabolomics have explored the interactions between pathogens and plants (Chachar et al., 2025; de Pedro-Jové et al., 2021; Gao et al., 2019; 2020; Qi et al., 2024).

Further evidence suggesting the extensive research on *R. solanacearum* was reflected in recently published data on complete genomic analyses of many strains of *Ralstonia pseudosolanacearum* on tobacco

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in China (Liu et al., 2013). Likewise, Gao et al. (2019) investigated the comparative transcriptional gene expression of tomato and tobacco in response to *Ralstonia pseudosolanacearum*, revealing the amelioration in two groups of gene ontology terms with respect to glutathione and flavonoid metabolism in resistant tobacco cultivars. Proteomic and transcriptomic analyses also demonstrated the fundamental role of the gamma-aminobutyric acid (GABA) biosynthetic pathway and methionine cycle (MTC) in the interaction between *R. solanacearum* and tomato varieties (Wang et al., 2019).

While the aforementioned findings are promising in terms of management strategies, genetic studies of agricultural crops revealed the involvement of multiple genes in conferring resistance (Salgon et al., 2018). Thus, more time and effort are required for breeding success given the remarkable challenge when resistant traits are inherited. Further complications arise as these crops eventually lose their resistance against pathogens, leading to reduced yields in previously resistant cultivars (Qian et al., 2013). Nevertheless, advancements in the development of molecular markers linked to resistant genes in tomatoes (Abebe et al., 2020), potatoes (Habe et al., 2023), (Tiwari et al., 2022), eggplant (Gaccione et al., 2023) offer great potential for future breeding of resistant cultivars.

Further insights revealed that 40 candidate genes were responsible for the pathogenicity comprising 67% G+C content than the average G+C content in the strain GMI1000, suggesting that these genes attained horizontal gene transfer (Salanoubat et al., 2002). Flanking regions of the virulence-related genes may have co-evolved with the core genes of *R. solanacearum*, including hemagglutinin-related genes and Type 3 secretion systems (Hu et al., 2025; Prior et al., 2016; Safni et al., 2014; Sharma et al., 2022).

R. solanacearum was initially classified traditionally into races and biovars based on their capability to cause BWD, various host plants and biochemical properties (Muthoni, Shimelis, & Melis, 2012; Sikirou et al., 2017). The racial pattern system consists of five races; Race 1 (wide host range on various members from the solanaceous plants), Race 2 (strictly virulent to musaceous species); Race 3 (infects mainly potato); Race 4 (ginger) and Race 5 (mulberry) (Chandrashekara et al., 2012; Sikirou et al., 2017). The bacterium is also classified as a biovar based on its ability to oxidize three sugar alcohols (dulcitol, mannitol, and sorbitol) and three disaccharides (cellobiose, lactose, and maltose). Biovar 1 strains oxidize neither of the carbohydrates; Biovar 2 strains oxidize only disaccharides; Biovar 3 strains oxidize all of them; Biovar 4 strains oxidize only sugar alcohols; Biovar 5 strains oxidize all of them except dulcitol and sorbitol (Muthoni et al., 2012). However, these classifications were later revised to four major phylotypes according to different geographical distributions. The reclassification was performed as the former groupings were poorly defined and not phylogenetically useful. Thus, all four phylotypes were named after their originating regions, based on sequence analysis from the *Internal Transcribed Spacer* (ITS) region, *hrpB*, and *egl* genes. Phylotype I represents Asia, Phylotype II represents America, and Phylotype III represents Africa and countries bordering the Indian Ocean. Lastly, Phylotype IV indicates either Japan, Indonesia, or Australia (Fegan & Prior, 2005).

In 2014, the classification of the *R. solanacearum* bacterium was revised following a few phylogenetic approaches (Safni et al., 2014). Since then, the bacterium was further divided into three species: *R. solanacearum*, *Ralstonia syzygii*, and *Ralstonia pseudosolanacearum* (Safni et al., 2014). This division was introduced as it correlates with the previous phylotype classification whereby the first and second species correspond to phylotypes II and IV, respectively, while the third species corresponds to phylotypes I and III (Prior et al., 2016). Currently, the most common classification approach for *Ralstonia* species requires sequencing analysis of the *egl* gene, which groups the *Ralstonia* strains into sequevars, a cluster of isolates with highly conserved regions within the *egl* gene (Fegan & Prior, 2005).

Methodology

This study aimed to review epidemiological data on BWD caused by *R. solanacearum*, including the disease symptoms, host range, crops affected, geographical distribution within Asia, and available control and preventive measures. We employed a comprehensive meta-synthesis approach with qualitative orientation by searching the Scopus and Google Scholar databases for relevant studies written in English and published between 1991 and 2023. Both databases were selected as they offer a robust review background to support interdisciplinary studies on the topic.

Search terms and keywords were identified based on the proposed review topic, objectives, and articles obtained from manual search. The search strings used in the Scopus database was 'Bacterial wilt disease' OR '*Ralstonia solanacearum*' AND 'disease symptoms' OR 'Epidemiology' OR 'Mechanism' OR 'Virulence' OR 'Host range' OR 'Geographical distribution' OR 'prevalence' OR 'incidence' OR 'occurrence' OR 'control' OR 'prevent' OR 'Treatment'. Meanwhile, the same keywords without Boolean operators (i.e. OR/AND) were used in searching the the Google Scholar database.

The inclusion criteria were original articles or conference proceedings reporting any epidemiological data on *Ralstonia solanacearum*, whereas Book chapters, full books, theses, and review articles, newspaper articles, and non-academic sources were excluded. Data were then retrieved from the two search engines and saved as CSV files via the export function.

Overall, all the retrieved articles were filtered based on the eligibility criteria and duplicates were removed. Irrelevant articles based on abstract and title screening, as well as unavailable articles were also removed from the database. Finally, 90 articles covering a wide range of studies on *R. solanacearum* were shortlisted for full-text review. A quality assessment was not performed since this is an integrative rather than a systematic review.

Relevant data from the studies were synthesised qualitatively using a comprehensive meta-synthesis approach. This approach enabled key themes and recurring patterns to be identified within the literature. All the articles were reviewed by the first author. However, when necessary, a discussion was held with other co-authors to reach a consensus regarding whether to include a study, the specific themes synthesised, and their placement in the review content. As a result, pertinent research gaps and potential areas for further exploration on the topic were identified. Five main themes were derived from the qualitative review and synthesis: (1) Disease cycle and symptoms, (2) Distribution of BWD in Asia, (3) Molecular mechanisms, (4) Management measures of BWD, and (5) Implications for conservation.

Disease cycle and symptoms

While general symptoms such as wilting and yellowing of younger leaves can be observed in infected host plants, the symptoms of BWD can vary among various ranges of hosts. For instance, in tobacco and tomato, the first symptom is the wilting of younger leaves, followed by yellow discolouration. As the disease develops, scorch-like symptoms are observed, leading to total death of the plant (Denny, 2007). Meanwhile, the first symptom of the disease in potatoes may appear when the leaves from the tip of the branches depict wilting and chlorosis (Denny, 2007). Once the plant tissues are infected, high cell densities of pathogen cells, consisting of a white bacterial ooze, are presented on the surfaces of rhizomes, tubers, or freshly cut stems. The field 'stem-streaming' analysis can be performed to detect the disease, particularly under certain circumstances whereby the cell population is minimal and the ooze is not produced instantly (Denny, 2007; García et al., 2019).

R. solanacearum can survive in water for long periods depending on environmental factors. However, extreme temperature, pH, and the presence of salts or other pollutants effectively decrease its survival rate (Caruso et al., 2005; Phiri et al., 2024). Host penetration ensues once the bacterium passes its survival period. Like any other pathogenic bacteria, *R. solanacearum* gains entry into the host via a natural opening or wound, directly exposing the internal tissues. Improper agricultural practices such as contaminated machinery and equipment, contaminated water supply, and infested soil or weeds that repeatedly injure the plants may also directly allow the pathogen to enter and invade the host plants (Denny, 2007). Unlike several other pathogenic bacteria, *R. solanacearum* possibly needs only one opening passage to initiate a systemic infection, resulting in bacterial wilt. Upon infection, virulent bacteria spread rapidly through the vascular system, where they multiply and spread (Choudhary et al., 2018; Denny, 2007). Once these events occur, there are hardly any physical barriers to prevent the pathogen from systemically infecting the rest of the plant cells.

For *R. solanacearum* to successfully infect and proliferate in plant hosts, the pathogen has to either disrupt or evade the host's immune responses (Chachar et al., 2025). As a result, the pathogen has developed a complex innate immune system, which are involved in pattern-triggered immunity (PTI) (i.e. facilitated by pathogen-associated molecular patterns [PAMPs]) and effector triggered immunity (ETI) (Wu et al., 2014).

Both ETI and PTI elicit similar defense responses, including the rapid synthesis of high levels of reactive oxygen species (also known as ROS burst), induction of defense genes, activation of mitogen-activated protein kinases (MAPKs) and hormonal alterations. Studies have also demonstrated a substantial overlap in the transcriptional regulation during ETI and PTI (Shi et al., 2023). Surprisingly, recent studies revealed a strong linkage between PRR-mediated PTI and NLR-mediated ETI (An & Zhang, 2024).

Nevertheless, the main difference between ETI and PTI is the triggering factor, whereby the former is initiated by the host's recognition of conserved pathogen-associated molecular patterns (PAMPs). On the other hand, the pathogen effectors have to be recognised by the host before ETI can be activated—a process that typically ensues after PTI is suppressed by the pathogen's effectors (An & Zhang, 2024; Shi et al., 2023).

PTI activates several signaling pathways in the host cells, such as the influx of extracellular Ca^{2+} into the cytosol (Nguyen et al., 2021; Ranf et al., 2011), accompanied by activating mitogen-activated protein kinases (Zhang et al., 2012), ROS signalling, and other signalling molecules (Chinchilla et al., 2007). Pathogens deploy various effector proteins in order to mitigate PTI responses, and following their recognition by specific plant receptors such as resistance (R) proteins, the ETI (i.e. a second layer of plant immune responses) is activated (Alhoraibi et al., 2019; Peng et al., 2018). Overall, the ETI response is triggered less rapidly but has a stronger effect, leading to additional responses such as localised necrosis mediated by a hypersensitive response and involving specific nucleotide-binding leucine-rich repeat (NLR) receptor proteins (Shi et al., 2023).

Upon evading the immune responses, *R. solanacearum* usually disrupts and ruptures the functional vessels of the infected plants, thereby leaving nothing to prevent the bacteria from moving upwards in the plant unless tyloses are formed. However, tylose development is either too rare or too slow in susceptible plants such as tomatoes, hence vascular dysfunction occurs as pathogen movement cannot be prevented (Shi et al., 2023; Vailleau & Genin, 2023). At this point, water cannot reach the leaves, and a high density of bacteria accumulates in the xylem, causing wilting to develop (Figure 1).

Further understanding of tylose formation and its role in mitigating *R. solanacearum* invasion has been demonstrated in several plant models, particularly tomato (Caldwell et al., 2017; Kashyap et al., 2021; Planas-Marquès et al., 2019). As a structural defense system, tyloses can confine *R. solanacearum*

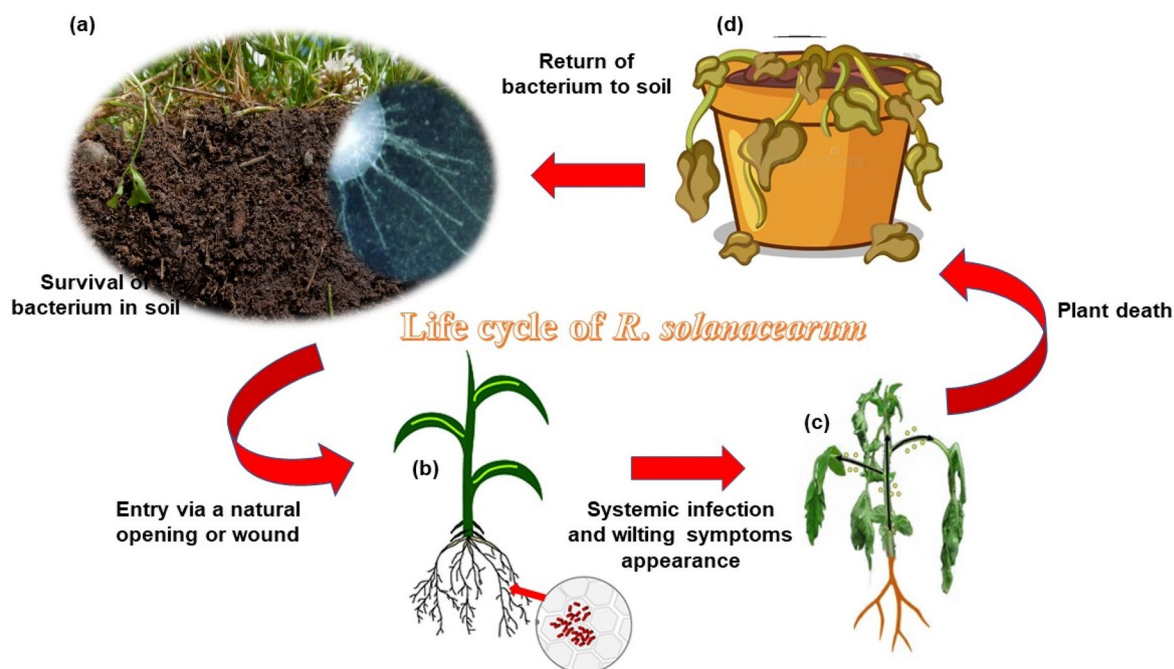


Figure 1. The development of *R. solanacearum* upon invading the host plant. (a) The bacterium is able to survive in soil and/or water; (b) The bacterium attaches itself to the plant roots and colonizes the xylem; (c) The infection spreads rapidly through the vascular system, resulting in plant wilting; (d) Upon plant's death, the bacterium is secreted in the living environment. The diagram was adapted from Genin (2010).

within the infected vessel, preventing the further dissemination of the pathogen (Kashyap et al., 2021; Planas-Marquès et al., 2019). Researchers have reported the presence of tylose formation at infected sites in tomato and potato varieties that are resistant to *R. solanacearum* (Ferreira et al., 2017; Grimault et al., 1994).

Effector proteins are secreted following the infestation of plants with *R. solanacearum*, thereby inhibiting the production of related hormones (Landry et al., 2020). Subsequently, alterations in hormone levels can either inhibit or induce tyloses formation. Effector proteins of *R. solanacearum*, such as RipAL, RipAY, RipG1, RipG3 and RipR, can inhibit the signaling of salicylic acid and induce the production of jasmonic acid (Nakano et al., 2021; Sang et al., 2018). Jasmonic acid has been found to trigger tylose formation by interacting synergistically with ethylene, while 1-aminocyclopropane-1-carboxylic acid (ACC) and salicylic acid have both inhibitory and synergistic effects on Jasmonic acid-induced tyloses (de Nicolai & Rodrigues, 2022). Despite the underlying mechanisms by which tyloses are regulated by phytohormones remain unclear, tyloses play pivotal defensive roles for plants to build a resistance against *R. solanacearum*.

Distribution of BWD in Asia

Bacterial wilt is a deadly vascular disease infecting many important crops worldwide (Hayward, 1991). The disease was first discovered in the United States following an attack on potato tubers (Burrill, 1891). Details of the incidence were later described by Smith (Smith, 1896). Among all economically important crops, the Solanaceae, Zingiberaceae, and Musaceae families are greatly affected by bacterial wilt, causing severe economic losses.

In China, the first outbreak of BWD was observed in groundnut in the 1930s; however, the disease was only reported later in 1956 (Ma & Gao, 1956). As one of the most important crops in the country at the time, the disease outbreak resulted in significant economic losses for local farmers. In past decades, *R. solanacearum* has infected more than 90 host plants in China, including potatoes, tobacco, ginger, and tomato (Liu et al., 2013; She et al., 2013), causing an alarming increase in local breeders. New host plants infected by the disease are still being discovered to date, including roselle and chard in Taiwan (Lin et al., 2015; Wu, Cheng, Lin, & Chen, 2013), and fig in Fujian (Jiang et al., 2016). In addition, approximately 20 host plants infected by *R. solanacearum* have been reported in China but no other countries. Among the host plants are *Typhonium*, *Gynura*, *Glossy nightshade*, and *Okinawan spinach* (Jiang et al., 2017).

Besides China, Japan has also reported the incidence of BWD, with an increasing number of reports in the last two decades. To date, more than 40 hosts have been discovered, with new hosts progressively being reported yearly (Horita & Tsuchiya, 2012). Potatoes and ginger are commonly affected by this disease among all economically important crops in Japan. For example, potato wilt is a widespread, severe, and destructive disease (Mitsuo Horita et al., 2010; Suga et al., 2013; Mitsuo Horita et al., 2014). Suga et al. (2013) discovered a highly virulent strain, Phylotype IV, from *Solanum tuberosum*. This strain demonstrated varying levels of pathogenicity not only in the potato but also in groundnut and tobacco. Recently, ginger was also reportedly infected by *R. solanacearum*. The first bacterial wilt infecting Zingiberaceae plants was reported in *Curcuma alismatifolia* planting fields back in 1995 before spreading to ginger, mioga, and siam tulip (*Curcuma*) planting fields in 1997, 1999, and 2005, respectively (Tsuchiya et al., 2005; Yano, Kawada, Tsuchiya, & Horita, 2005).

BWD has also been frequently reported in India. Among the earliest incidence were observed in various economically important crops, such as ginger, tomato, potato, and chili. A major outbreak of tomato and potato wilt disease was recently reported in a few states in India, causing more than 50% yield losses to farmers (Balamurugan et al., 2018; Kumar et al., 2014; Mamphogoro, Babalola, & Aiyegoro, 2020). The spread of the disease infecting these crops throughout the year created a distressing situation for local farmers, discouraging them from planting more crops, thereby reducing their food sources (Hayward, 2000).

In Malaysia, the first outbreak of BWD was reported in early 2007, affecting a banana plantation in Johor aftermath of a major flood (Hussin & William, 2010; Zulperi et al., 2014). The disease attacked almost the whole banana plantation, consisting of different varieties at that time, causing a depressing scenario and economic loss to local farmers. While the disease was initially known as Moko disease,

Table 1. Biovars and phylotype Sub-division of *R. solanacearum*, including host range, geographical distribution and race characteristics.

Race	Host range	Geographical distribution (biovar)	RFLP division	Phylotype	New proposal for phylotypes
1	Wide	Asia (3), America (1), Australia (4) and Africa (1)	I, II, III	I, III	<i>R. pseudosolanacearum</i> Phylotype I, III
2	Banana and other species	Indonesia (1), The Philippines (1), Caribbean (1), and Brazil (1)	II	II, IV	<i>R. solanacearum</i> Phylotype II
3	Potato	Global (2)	II	II	<i>R. syzygii</i> Phylotype IV
4	Ginger	Asia (3, 4)	I	I	<i>R. syzygii</i> Phylotype IV
5	Mulberry	China (5)	I	I	<i>R. syzygii</i> Phylotype IV

several bioassay findings confirmed that the infection was caused by a Blood disease bacterium (BDB). Blood disease exhibited a similar manifestation to BWD, which was originally discovered in Indonesia in 1921 (Remenant et al., 2011). However, none of the outbreaks has been properly reported since its first discovery in Malaysia. Table 1 presents the host range and geographical distributions of various biovars of *R. solanacearum*, including the existing and recently proposed phylotypes.

Molecular mechanisms

The development of molecular techniques in elucidating the interaction between *R. solanacearum* and its host range started a decade ago. Fegen and Prior (2005) were the first to propose a classification of *R. solanacearum* based on the analysis of Internal transcribed spacer (ITS), hypersensitive response and pathogenesis B (*hrp B*) and endoglucanase (*egl*) genes. The researchers analyzed 140 strains of *R. solanacearum* worldwide and subdivided them into four phylotypes, which were then linked to the geographic range. This classification was further confirmed by a comparative analysis of 140 strains that represent the microarray hybridization of strain GMI1000 genome (Guidot et al., 2007). GMI1000 was identified as the most divergent strain reflecting 68% to 69% hybridization with the GMI1000 oligonucleotide. Studies by Remenant and colleagues also confirmed the classification of nine new strains of *R. solanacearum* (Remenant et al., 2011, 2012).

The ability of *R. solanacearum* strains to use various sugar and alcohol carbohydrates was also initially used in dividing the population into biovars—also known as a phenotype-based structure (Chen et al., 2014). Historically, this bivar classification was utilised in differentiating strains of *R. solanacearum* species complex (RSSC). The current classification uses phylotypes—a modern approach based on DNA sequence analyses of 16S and 23S rRNA intergenic transcribed spacer regions (ITS). As a result, strains with similar DNA sequences are grouped into monophyletic clusters, which is often associated with geographic origin; (1) Phylotype I: Asia (2) Phylotype II: Americas (3) Phylotype III: Africa and (4) Phylotype IV: Australia and a few Asian countries.

The classifications of biovars and phylotypes are often inconsistent, thereby not corresponding always to phylogenetically coherent groups. For instance, the strains of Race 3 biovar 2 (R3Bv2) are frequently reported in America—leading to their classification under phylotype II. However, the most accurate and hierarchical system for distinguishing and understanding the RSSC's diversity is phylotype classification rather than the outdated biovar system. Presently, the partial sequencing of the *egl* gene coding for the endoglucanase enzyme (i.e. vital for the invasion of plant roots and colonisation of stems) is the most widely characterisation technique for *Ralstonia* populations. Based on this molecular characterisation, strains are assigned sequevars according to their phylogenetic relationships. A 1% variation in the *egl* gene's nucleotide sequence is further used in subdividing phylotypes into various additive number of sequevars. Most RSSC strains have been successfully characterised given the robust phylogenies obtained from the *egl* gene.

In terms of host-specific ranges of *R. solanacearum*, the event remains unclear given the species's diversity and unusually extensive host range (Elphinstone, 2005). Pathogenicity tests confirmed the host specificity in different strains, revealing the virulence of Moko strains of banana to tomatoes and

potatoes (Cellier et al., 2012). Several studies have also identified the targeted genes associated with the host specificity, using hundreds of pathogenic comparative genes to identify the microarray hybridization of *R. solanacearum* genes (Cellier et al., 2012; Guidot et al., 2007). However, upon testing these genes on tomato and banana pathogenic strains, the gene associated with the pathogenicity could not be identified.

Tan et al. (2022) also studied the pathogenic strain on legume plants in order to elucidate the virulence mechanism. The researchers screened more than 100 peanut cultivars and only two phylogenetically closed strains were identified, but their virulence profile was incredibly different. Furthermore, genomic analyses were performed to observe the major differences in these strains. A virulence mechanism was observed in several candidate genes, including regulatory genes that contribute to motility and adhesion. Nevertheless, more advanced quantification techniques are now used in genomic and transcriptomic comparison studies. For instance, Yang et al. (2021) conducted a comparative study on the metabolic content of tobacco xylem sap during *R. solanacearum* infection in susceptible and resistant cultivars of tobacco. Few of the metabolites are differentially concentrated in the significantly induced susceptible cultivars, thereby unlocking several future explorations of pathogen and how it induces such metabolic reprogramming in its host.

Likewise, tobacco-resistant gene expression was measured in two varieties; highly resistant 4411-3 and moderately resistant K326, in basal conditions after *R. solanacearum* inoculation (Pan et al., 2021). Resultantly, many genes were induced by the pathogen. It is predicted that more than 100 type 3 effectors (T3Es) are present in different *R. solanacearum* strains, with an average of about 70 T3Es in each strain. Thirty-two core TEs are conserved among them but highly variable repertoires of T3Es are responsible for the host range in different *R. solanacearum* strains. Lei et al. (2020) also observed genes-deletion mutant from the strain OEI-1 in 42 T3 effectors, particularly those virulent on both tobacco and eggplant plants. The mutant unveiled meaningfully reduced colonization and virulence in both tobacco and eggplant plants, representing the core genes (T3Es) for the OEI-1 strain's virulence towards the host plant, enabling the primary function of individual T3Es in the host cell. These comprehensive investigations reflect that this devastating pathogen can be controlled by developing sustainable management strategies.

Management measures of BWD

Several management measures have been studied and introduced since the outbreak of BWD. Unfortunately, no effective control measure has yet been developed to eradicate the disease despite infecting several important economic crops in the field. A comprehensive review by Elphinstone (2005) revealed extensive research on the management strategies of BWD. Albeit we reviewed the same topic here, by reviewing recent findings from studies published from 2010 onwards. For a robust review, we divided the management measures into cultural, chemical, biological, and integrated approaches commonly practised to control BWD.

Cultural control

Traditional breeding approaches such as crop rotation and the application of bactericides have been effectively practised as a cultural control method for BWD. However, only a few trials using these methods have been successful (Prameela & Suseela Bhai, 2020). While developing disease-resistant breeds is considered the most efficient and economic strategy to prevent the disease, obtaining a suitable variety with stable resistance remains a significant challenge (Allen et al., 2005).

Given the severe damages caused by *R. solanacearum*, farmers undertake different cultural practices in managing the disease. For example, local farmers from the African region chose traditional practices, including smoking bones, tyres, and burning porcupine bodies, to curb the spread of BWD (Geberewold, 2019). However, these farmers posit that destroying all infected plants or practising periodic crop rotation are the only treatment options. For other areas that are relatively free from the disease, farmers practice control measures such as keeping all healthy plants away from contaminated fields and handling tools (Geberewold, 2019). While keeping away the tools from those infected plants could prevent

the disease from spreading, sanitation constitutes the most important control measure as evidenced by several reviews (Geberewold, 2019). Examples of the effective strategies highlighted include generating disease-free plant materials, burying the infected plants far away from the plantation area, and thoroughly cleaning the handling tools exposed to infected plants (Brandt, 1997).

Chemical control

The application of various natural or synthetic chemicals such as pesticides for pests and disease control in plants exceeded 4.1 million tonnes in 2018 globally (FAOSTAT, 2019). Different types of chemicals have been applied to control BWD for several years but to no avail, which is mainly attributed to the pathogen's ability to survive in the soil for prolonged periods (Manda et al., 2020). Examples of the common chemicals used to control the disease spread include benomyl, carbendazim, and propiconazole, whereas the common fumigants are chloropicrin and dazomet (Wu et al., 2013). Among these chemicals, chloropicrin is the only fumigant formulation that provides efficient control in curbing BWD regardless of season (Karim & Hossain, 2018).

By producing systemic resistance on the host, specific pesticides such as fumigants (metamsodium, 1,3-dichloropropene, and chloropicrin), algicides (3-[3-indolyl] butanoic acid), and plant activators have been successfully used in controlling BWD. Microorganisms have also been effectively destroyed by using bactericides including streptomycin sulfate (400 mg kg⁻¹ of soil) (Lin et al., 2010), triazolothiadiazine (0.5–12 mM in solution) (Khanum et al., 2005), sterilisers such as bleaching powders, and weak acidic electrolysed water (40 ppm of chlorine in a neutral solution) (Yamasaki et al., 2006).

Studies have shown that acibenzolar-S-methyl induces systemic resistance (38, 100), and its combination with thymol reduced disease incidence and increased tomato's yield significantly compared to using each pesticide individually (Hong et al., 2011). A similar mechanism was also observed following the application of chitosan and silicon (Kurabachew & Wydra, 2013), leading to a marked reduction in BWD incidence. An increased population of micro-organisms in the soil and enhanced enzyme activity (acid phosphatase and urease) was associated with Si-mediated resistance (Wang et al., 2013). In tomato, an earlier study found increased seedling vigour and tolerance to *R. solanacearum* upon soaking of seeds in a low solution of sodium chloride (Nakaune et al., 2012). Antibacterial activity and induced systemic resistance are thus proposed as the various mechanisms via which non-pesticide chemicals suppress BWD.

However, excessive fumigant pesticides are prohibited in some countries as they could harm human health and reduce soil quality over time. Other chemicals, such as antibiotics, are also not effective management approaches given the bacterium's ability to move systemically within the plant, causing wilt symptoms (Sangoyomi et al., 2011). While using chemicals to control plant diseases can temporarily remove most pathogens, some pathogens resistant to chemicals may not be easy to eradicate. Such chemicals end up killing non-targeted plants instead of the original targeted plant (Dasgupta et al., 2005). Poor knowledge coupled with long-term extensive application of chemicals, such as pesticides, could contaminate the soil and groundwater. These events raise concerns about potential environmental pollution and serious health issues for humans (Hoai et al., 2011). Based on these possible devastating effects, the application of chemicals to eradicate plant pathogens has received strong deliberation, particularly on whether such chemicals should be introduced into the environment or not. Therefore, finding other alternatives to controlling BWD is necessary. For example, several studies have reported the use of microorganisms, with accumulated evidence suggesting their effectiveness in controlling the disease without harming the environment.

Biological control

Biological control entails using an organism to arrest the growth or kill another living organism (Nion & Toyota, 2015). Utilizing biological control agents in managing plant diseases or pests has become the method of choice for farmers as it offers several advantages. Apart from being relatively cheap, the approach is environmentally safe compared to chemical control methods. In countries where pesticides such as chloropicrin are banned or when the pesticides gradually lose their effectiveness, the biocontrol approach using bacterial inoculant is useful in eradicating the disease transmission. Since it is a soil-borne

disease, most studies have focused on applying antagonistic bacteria found in the root-associated zone (Le et al., 2022; Suresh et al., 2022).

For instance, antagonistic rhizobacteria such as *Pseudomonas putida*, *Pseudomonas fluorescens*, *Bacillus cereus*, and *Bacillus subtilis* were utilized as biocontrol agents to reduce *R. solanacearum* in laboratory and greenhouse settings (Kheirandish & Harighi, 2015; Wu et al., 2016). However, the underlying mechanisms of these antagonistic strains against *R. solanacearum* remain poorly understood, especially in the field.

As shown in Table 1, numerous biological control agents (BCAs), especially bacteria and fungi, have been explored to address the development of BWD in the last decade. The main source of these beneficial microbes are healthy plants' rhizosphere, and their biocontrol activities stem via interactions by competing with hosts for nutrients and space, parasitism, antibiosis or triggering plant resistance (Sharma et al., 2022). The effects of several bacterial strains on *R. solanacearum* have been investigated for their antibiosis activities via in vitro and in vivo studies, with most research reflecting their role in mitigating clinical disease, which are often associated with growth-promotion effect (Sharma et al., 2022). According to Chandrasekaran et al. (2016), *Bacillus* spp. (mainly *Bacillus cereus*, *Bacillus subtilis*, and *Bacillus amyloliquefaciens*) and *Pseudomonas* spp. (mainly *Pseudomonas fluorescens* and *Pseudomonas putida*) are the most effective microbes for BWD control given their ability to antagonise and reduce the pathogen's multiplication by producing a broad spectrum of antimicrobial compounds, niche competition and induced systemic resistance (Suresh et al., 2022).

Suresh et al. (2022) explored the induction of systemic resistance by a quantitative analysis of defense associated proteins, which enabled the detection of peroxidase and polyphenol oxidase isoform patterns upon treating tomato plants infected artificially with *R. solanacearum*. The study involved in vitro and in vivo screening with 8 strains of *Pseudomonas* to elucidate the effects of BCA genotypes. Resultantly, the strain *Pseudomonas protegens* demonstrated the strongest efficacy with protection dependent on the pathogen strain evaluated in vivo (Clough et al., 2022). Meanwhile, *B. amyloliquefaciens* elicits various complimentary effects to facilitate BWD control, such as the secretion of EPS, hydrolytic enzymes and antimicrobial compounds, as well as modifying rhizosphere's bacteria microbiome, thereby reducing the population of *R. solanacearum* population (Ahmed et al., 2022).

Upon evaluating the antagonistic characteristics of *Bacillus amyloliquefaciens* ZM9, Wu et al. (2016) found that the strain has an effective inhibitory property against *R. solanacearum* in tobacco. Wang and Liang (2014) also isolated *Bacillus amyloliquefaciens* BZ6-1 endophytic bacteria from healthy peanuts, and when tested on peanut bacterial wilt, disease occurrence was observed to subside drastically.

Another bacteria genus that is well-known for its biocontrol property is streptomyces—a Gram-positive filamentous bacteria (Olanrewaju & Babalola, 2019). Le et al. (2022) reported the role of AN090126- a strain of *Streptomyces* in producing secondary antimicrobial and volatile compounds, resulting in broad-spectrum antimicrobial properties. In an experimental study, tomato seedlings were protected against the pathogen when inoculated with two strains of bacteria (Y30 and E36) isolated from *Streptomyces virginiae* (Tan et al., 2011). Both strains developed significant protection against *R. solanacearum* in greenhouse conditions (Hu et al., 2010). Likewise, the inoculation of capsicum with bacterial endophyte *Bacillus amyloliquefaciens* Bg-C31 isolated from a mangrove strain drastically reduced wilt disease symptoms by up to 80% in both post and field trials (Ownley & Windham, 2007). A protein substance produced by this strain, identified as LCI, indicated antimicrobial activity in *Ralstonia solanacearum* (Ownley & Windham, 2007).

Despite the results from the aforementioned trials, biological control is still considered less effective compared to chemical control when applied to field conditions. This inefficiency stems from several biotic and environmental factors, such as improper agricultural application practices and mutational events in biological control agents (Yuan et al., 2014). In addition, applying biological control agents in plant production has also raised alarming concerns such as the adverse effects on different non-target microorganisms, including bacteria, fungi, and protozoa. The introduction of a new species to an environment could disrupt microbial growth, which is crucial in the soil ecosystem. Extensive studies have also explored the effectiveness of biofertilizers in combating BWD. Many of these reports depicted that the application of biofertilizers is effective in mitigating disease transmission while catalyzing the growth of tobacco (Yuan et al., 2014), banana (Fu et al., 2017), chilli (Yanti et al., 2017), and tomato (Liu et al., 2013).

Farmers are becoming more aware of the promising outcomes associated with controlling BWD, such as increased crop output and substantial economic return, thereby prompting them to practice and invest in biological control treatments. While further studies are required to confirm the efficiency of biofertilizers, findings from previous studies strongly reflect that biological control agents are reliable, effective, and alternative management approaches against BWD infecting many crops.

Engineered nanoparticles

Recent advances have shown that metal-based nanoparticles (NPs) such as silver, copper oxide, iron oxide, zinc oxide, and magnesium oxide, are promising candidates for BWD control (Elmer & White, 2018; Tortella et al., 2021). While these biocontrol agents were previously derived from physical and chemical methods, their development has been shaped by the extensive search for eco-friendly alternatives (Tortella et al., 2021). For instance, silica NPs were observed to permeate tomato leaves via stomatal pores before accumulating mainly in tomato shoots, leading to antagonistic activity against BWD in a dose-dependent manner (Wang et al., 2019). A similar study found that numerous metal oxide NPs (i.e. ZnO, CuO, and FeO) are protective against *R. solanacearum* and impacting the soil bacterial communities (Jiang et al., 2021). Besides, other researchers reported the positive effects of NP treatments in promoting plant growth (Jiang et al., 2021; Khan et al., 2021). Nevertheless, further research is required to ascertain the environmental impact of these compounds since most studies only focused on outcomes that are either host or dose dependent (Elmer & White, 2018).

The NPs derived from chitosan have been equally tested in reaction to several pathogens, including BWD causing bacteria. According to Vailleau and Genin (2023), these biopolymers are non-toxic, constituting a potential alternative for biocontrol measures, as depicted in recent studies involving the effect of chitosan extracted from black soldier fly (i.e. pupa stage) on bacterial wilt disease (Kemboi et al., 2022).

Integrated approach

Among all the control measures discussed above, the integrated approach has long been considered the most complicated yet effective strategy to control BWD. As a soil- or water-borne pathogen with a diverse host range, it is difficult to prevent bacterial wilt disease infection with a single treatment strategy. Therefore, utilizing integrated disease management (IDM) approaches by combining various methods such as cultural, chemical, and biological is recommended to prevent the spreading of *R. solanacearum*.

Among the management strategies discussed above, the combined application of antagonistic microorganisms and organic mixtures from agricultural or industrial wastes has become one of the preferred choices for farmers. This approach is considered cost-effective and environmentally friendly. Anith et al. (2004) reported effectively suppressing bacterial wilt incidence in tomatoes using formulated soil containing agricultural and industrial wastes integrated with plant growth-promoting rhizobacteria. Similarly, the combined application of different soil components and bacterial suspension on brinjal plants demonstrated greater efficiency in minimizing yield losses caused by the disease (Gargi, 2012). The use of silicon fertilizer and sugarcane bagasse as soil amendment resulted in increased fruit yield and significantly reduced bacterial wilt incidence in tomatoes (Ayana et al., 2011).

While using biological control agents to control the BWD is quite promising, the field trial results have not been validated (Salgon, Raynal, Lebon, Baptiste, Daunay, Dintinger & Jourda., 2018). Crop rotation, which is practised in several regions globally, is another alternative that involves rotating a few crops on the same farm at different periods (Ajilogba & Babalola, 2013). Rotating main crops with low-value crops such as wheat, maize, and carrot for a few years could reduce the incidence of BWD by 90% (Mao et al., 2017; Mamphogoro et al., 2020). However, continuous rotation of similar crops may eventually result in the presence of some infectious agents and damage to the soil atmosphere.

In past decades, developing resistant germplasms possessing wilt resistance has proven to be the most practical strategy for BWD control. Apart from confirming the resistance against the disease in each generation, the cultivars must also demonstrate improved agronomic traits, and the progress so far has

been encouraging. For example, several studies have identified the resistant cultivars of *Capsicum*; however, the number of successful cultivars resistant against bacterial wilt is still lacking. This research gap could be due to insufficient information on the pathogen's characteristics and inappropriate detection techniques (Thakur et al., 2021). With the continuous advancement of the pathogen, some of the resistant breeds developed were reportedly unstable in many crops, such as potato, tomato, pepper, and eggplant (Lebeau et al., 2011). To date, integrated management approaches have depicted limited effectiveness in combating BWD, as the disease incidence continues to affect major economic sectors in crop production worldwide (Phiri et al., 2024).

Implications for conservation and conclusion

R. solanacearum, the pathogen responsible for BWD, has become a serious threat affecting many important crops and causing huge losses to farmers worldwide. Hence, the present and future demand an environmentally friendly yet effective management approach to curb these economic losses. BWD control is challenging given the pathogen's ability to survive for prolonged periods in complex environments, as well as its high variability and wide host range (Denny, 2007). The rising earth's temperature due to global warming, which is likely to worsen, is expected to pose a threat to the survival of many hosts and non-hosts worldwide. For example, the hot and warm climates in Asian countries heighten crops' susceptibility to pathogen infection.

Using chemical pesticides to combat BWD has been among the preferred choices of farmers. Nevertheless, the disadvantages of pesticide application have become more distinct relative to their benefits. Apart from being relatively expensive, pesticides tend to become less efficient and pose serious risks to humans and the environment (Mamphogoro et al., 2020). Other management approaches, such as developing disease-resistant breeds, practising crop rotation, and applying biological control, are less effective in suppressing the disease (Ajilogba & Babalola, 2013). Thus, these events highlight an urgent need to develop effective strategies to manage BWD. Collaboration between experts from various backgrounds, ranging from soil and chemical scientists to microbiologists and plant pathologists, is strongly recommended to facilitate a better control approach and make environmental conditions less conducive for pathogens. Although various attempts to use microbial antagonists as biocontrol have been conducted to test their efficiency against the pathogen, the outcomes were not satisfactory, especially in field trials. In the future, thorough research on pathogen virulence mechanisms will be needed to provide insight into various host plant resistance.

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Data availability statement

Data sharing is not applicable to this article as no data were created or analysed in this study.

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