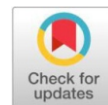


Review Article

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Ralstonia solanacearum: an overview on distribution, variability, bio-management and host plant resistance approaches



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ABSTRACT

Ralstonia solanacearum, a highly destructive soil-borne bacterium, is responsible for bacterial wilt disease in over 200 plant species belonging to over 50 different botanical families, including important solanaceous crops viz., potato, tomato and eggplant. This is the world's second most damaging bacterial plant pathogen threatening global food security due to its rapid spread, genetic adaptability and ability to persist in diverse environments. *R. solanacearum* (phylo type II) originated in Central and South America and has spread globally through contaminated agricultural materials. Infected potato facilitated its establishment in Africa, Asia, Europe and Oceania, while international trade of ornamental plants like *Pelargonium* introduced the pathogen into greenhouse systems in Europe and the United States of America. Its adaptability to varied climatic conditions has enabled the colonization in wide regions including tropical, subtropical and temperate, posing a persistent threat to crop production. The pathogen exhibits extensive genetic diversity and is classified into three species within the *Ralstonia solanacearum* species complex (RSSC) i.e. *R. solanacearum*, *R. pseudosolanacearum* and *R. syzygii*. Horizontal gene transfer drives the development of diverse strains, resulting in rapid evolution and enabling the acquisition of virulence traits. These further help in the adaptation of bacterium to new hosts and environments. This variability generated across genetic, environmental, ecological and pathogenic aspects, complicates disease management and necessitates region-specific management approaches. The conventional management approaches for bacterial wilt disease remains challenging due to pathogen's genetic heterogeneity and environmental adaptability. Hence, these limitations reduce the efficacy of traditional control measures. In line to these limitations, sustainable control of *R. solanacearum* relies on biocontrol agents (BCAs) and integrated approaches that harness ecological interactions to suppress pathogen populations. Bacteria make up the majority of BCAs at 90%, with fungi accounting for the remaining 10%. Key bacterial BCAs exploited for the control of *R. solanacearum* include *Pseudomonas*, *Bacillus* and *Streptomyces* which suppress soil pathogen populations and enhance plant immunity. Additionally, lytic bacteriophages have shown significant efficacy in controlling *R. solanacearum*. Various studies concluded that cultivation of resistant varieties, application of biocontrol measures and microbiome engineering can offer long-term sustainable management of *R. solanacearum* across diverse cropping systems. This review synthesizes worldwide distribution, variability of *Ralstonia solanacearum* along with current research in host resistance and biological management, offering insights that contribute to sustainable plant disease management.

Keywords: *Ralstonia solanacearum*, bacterial wilt, soil-borne pathogen, geographical distribution, variability, races, biovars, phylotypes, sequevars, bio-management, BCAs, organic approaches and host plant resistance.

1. Introduction

Ralstonia solanacearum (formerly called *Pseudomonas solanacearum*) [1], is a soil-borne, motile (polar flagellum), rod shaped (0.5-1.5 µm), β-proteobacteria causing enormous crop losses worldwide [2,3]. It is the second most damaging plant pathogen [4], causing bacterial wilt in wide range of plants. This pathogen is widely studied due to its worldwide distribution, extensive host range, destructive nature and lack of effective management practices. The *Ralstonia solanacearum* species complex (RSSC) [5], causing bacterial wilt is considered one of the most obliterative plant pathogenic bacteria. Thomas Jonathan Burrill was a pioneer in describing bacterial wilt disease on potatoes in 1890.

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Erwin Frink Smith also described bacterial wilt disease in brinjal, potato and tomato in 1896 and later in tobacco in 1908 [6,7]. E.F. Smith further classified the causal organism of this disease under the genus *Bacillus* as *Bacillus solanacearum* [6]. With advancements in technology, the nomenclature and taxonomy of the bacterial wilt pathogen have evolved. Initially placed in the genus *Bacillus*, it was subsequently transferred to the genus *Bacterium* [8], and later transferred to *Pseudomonas* based on Migula's description in 1914 [9,10]. It was then classified under *Phytomonas* [11], followed by *Xanthomonas* [12], and was subsequently reassigned to *Pseudomonas* [11, 13, 14, 15, 16]. Later on, it was transferred to genus *Burkholderia* [17, 18, 19], on the basis of DNA-DNA homology and phylogenetic studies. Finally, in 1995 it was placed in its current genus *Ralstonia* [1]; it was named in honour of bacteriologist Erica Ralston.

R. solanacearum is mostly found in tropical, sub-tropical conditions and has even adapted to temperate regions worldwide.

Strains of *R. solanacearum* adapted to temperate conditions were found in Western Europe, infecting potato tubers [20]. This plant pathogenic bacterium is known to affect more than 200 plant species belonging to over 50 different botanical families [21,22], including some high value crops like pepper, potato, tobacco, tomato etc. The disease caused by *R. solanacearum* is commonly referred to as bacterial wilt. However, other diseases like brown rot of potato, Moko disease in banana, Granville wilt of tobacco and southern wilt in geranium are also caused by *R. solanacearum*.

Ralstonia can thrive in wet soil or water for years [23,24], in the absence of a host plant and when this pathogen comes in contact with a susceptible host plant, it enters the plant system through root wounds or at the site of secondary root emergence. The bacterium thereafter colonizes the root cortex, invades the xylem vessels and ultimately spreads rapidly to aerial plant parts through the vascular system [22]. The bacterium secretes exopolysaccharide (EPS) which blocks xylem, the water conducting tissue, leading to the characteristic symptom of wilting in plants [25,26,27]. There are various virulence factors triggered by *Ralstonia* for disease development viz., EPS, T₃ secretion system and cell wall degrading enzymes [28, 29, 30]. The wilt is often restricted to one side of the plant. The field diagnosis of this disease is the ooze test (milky white ooze from fresh cut stems, rhizomes or tubers), representing high cell density in infected tissues [22].

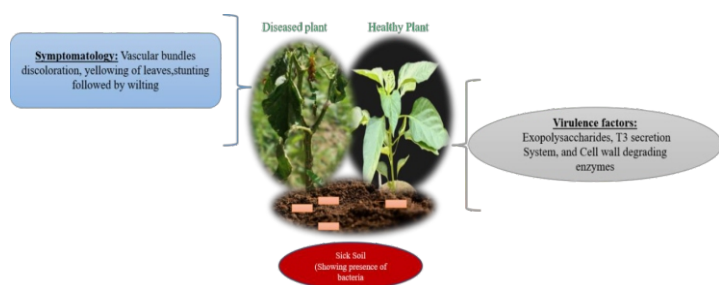


Figure 1. Pathogenesis of *R. solanacearum*

The signs, symptoms and development of bacterial wilt disease can vary, depending on the susceptibility of host plant and aggressiveness of pathogenic strain. However, general characteristic symptoms of the disease include wilting, stunting and yellowing of young plants [16, 31, 32]. Some of the other symptoms associated with this pathogen are leaf epinasty (leaves bending downwards), adventitious roots arising in stem, dark narrow stripes corresponding to the infected vascular bundles [16, 31].

Across the globe, this pathogen can lead to crop losses from 20-100% and 75-81% in India depending on crop growth stages and environmental conditions [33, 34, 35]. In potato, *R. solanacearum* is the second most important disease, resulting in 45 to 80% losses, after late blight disease. It is also reported that the bacterial wilt pathogen affects 1.6 million hectares (MH) of potato in around seventy-eight (78) countries causing an annual loss of \$848 million [36]. The pathogen is reported to affect tomato crops in Uganda, leading to yield losses of up to 88%,

while in Ethiopia, it has resulted in 100% disease incidence in pepper crop [34]. On average, yield losses caused by *Ralstonia solanacearum* range from 33-90% in potatoes, 0-91% in tomatoes, 10-30% in tobacco, 20% in groundnuts and up to 80-100% in bananas [38].

Given its significant economic impact, widespread distribution, considerable diversity coupled with the challenges in effective management, studying this pathogen is essential. Hence, this review will shed light on different aspects of *Ralstonia solanacearum* corresponding to distribution, variability and bio management.

2. Distribution

Ralstonia solanacearum (RSSC phylotype II) has originated from Central and South America, where its immense genetic diversity is found [38,39,40]. This bacterial pathogen, responsible for bacterial wilt (BW) disease, is globally distributed [37], with a huge host range and wide genetic diversity. Some strains of *Ralstonia* have spread across the globe through the commerce of infected, asymptomatic, vegetatively propagated crops like potato tubers, banana/plantain sucker [39, 40].

This pathogen is a pervasive soil inhabitant, spanning the globe, including various islands within tropical latitudes [32]. These regions receive an average annual rainfall exceeding 100 cm, have a mean summer temperature surpassing 21°C, winter temperatures above 10°C, an average yearly temperature below 23°C and a favorable growing season for more than six months [22, 41]. Moraes and his colleagues (1947) primarily described the presence of bacterial strains adapted to infect the potato crop in temperate regions ($\leq 24^\circ\text{C}$) [42]. These pathogenic strains were identified as race 3 biovar 2 (phylotype IIB; sequevar 1) and are called “potato race” [42]. *Ralstonia solanacearum* phylotype IIB; sequevar 1 is considered a quarantine pathogen and is cataloged as a federal select agent under USDA Agricultural Bioterrorism Protection Act, 2002 [32]. The table 1 below is adapted from data provided by the European and Mediterranean Plant Protection Organization [39,40], highlighting the world distribution of *Ralstonia solanacearum* species complex (RALSSO). Initially, the rainforests of Costa Rica and the Caribbean were considered the site of emergence for strains causing Moko disease. However, due to the widespread nature of the pathogen, it is now found in multiple Latin American countries. Sequevar PIIB-3 has been identified as a causal agent of bugtok and Moko diseases, affecting dessert bananas (AAA group) and plantain (saba and cardaba, ABB group) in the Philippines [43]. Similarly, PIIB-4 has been reported to cause Moko disease in dessert bananas in Malaysia [44]. Geographically originating in South America and being widespread in that region, the sequevar PIIB-1 has spread across the potato growing areas of Africa, Asia, Europe and Oceania. Moreover, this strain has spread through global trade of infected *Pelargonium* cuttings and has become established in protected horticultural systems in Europe and the USA, as reviewed in table 2 [45, 46].

Table 1. Global distribution of *Ralstonia solanacearum* across different crops

Continent	Pathogen status	Major crops affected across the continents
Africa	Present	Tomato, eggplant, potato, huckleberry, pelargonium, <i>Solanum nigrum</i> , <i>Physalis angulata</i> , chilli pepper
America	Present	Tomato, potato, banana, plantain, eucalyptus, bell pepper, eggplant, heliconia, cucumber, pelargonium, <i>Plectranthus amboinicus</i> , tobacco, coffee weed, <i>Solanum americanum</i> , dollar weed, Pennsylvania smart weed, hydrangea, blueberries
Asia	Present	Potato, eggplant, horsetail, beefwood, sweet potato, hibiscus, balsam pear, ramie, eggplant, eucalyptus, mulberry, olive tree, sweet pepper, peanut, nightshade plant, sesame, tobacco, tomato, ginger, chilli, bird of paradise, dawana, coleus, banana, <i>Rosa</i> spp., groundnut, bitter gourd, anthurium, turmeric, <i>Croton hirtus</i> , <i>Hyptis suaveolens</i> , siam tulip, marigold
Europe	Present	Potato, rose, tomato, pepper, aubergine, <i>Rosa</i> spp., <i>Curcuma longa</i> , anthurium, ginger, Pelargonium x hortorum, <i>Solanum dulcamara</i>
Oceania (Australia)	Present	Heliconia, potato, tomato, ginger, eggplant, tobacco, peanut, chilli, sweet pepper, <i>Casuarina equisetifolia</i>

Table 2. Summary of *Ralstonia solanacearum* races: distribution, host range and biovar

Race	Geographical distribution	Host range	Biovar
1	Asia, Africa, Australia, North America and South America	Wide	1,3,4
2	Caribbean, Asia, Central America, South America and Hawaii	Banana & other <i>Musa</i> spp.	1
3	Worldwide (except Canada and United States)	Geranium, potato and some other solanaceous crops	2
4	Australia, Asia and Hawaii	Ginger	3,4
5	China	Mulberry	5

The geographical area of India is divided into 15 agro-climatic zones recognized by the Indian Council of agricultural research (ICAR) and planning commission of India, which are further divided into 72 homogenous sub-zones. Table 3 below drafts the distribution of the bacterial wilt pathogen across the agro-climatic zones of India.

Table 3. Distribution of *R. solanacearum* in India (data adapted from EPPO 2025)

Agro-climatic zones	Pathogen status	Major crops affected	References
Western Himalayan Region	Present	Tomato, brinjal, potato, bird of paradise, ginger, chilli, capsicum, davana, coleus, groundnut, fennel, cumin, ajwain, cotton, jute and broad bean	[50], [51], [52], [53], [54]
Eastern Himalayan Region	Present	Potato, sweet pepper, chilli, tomato, brinjal and wild <i>Datura metel</i>	[50], [52], [54], [55]
Lower Gangetic Plains Region	Present	Potato, tomato, brinjal, marigold, chilli, tobacco, elephant footyam, bottle gourd, water melon, banana, jute, ginger, large cardamom, <i>Cestrum nocternum</i> , <i>Bougainvillea</i> sp., (weed hosts- <i>Martynia annua</i> , <i>Cleome viscosa</i> , <i>Physalis minima</i> , <i>Cestrum diurnum</i> , <i>Amaranthus spinosus</i> , <i>Costus speciosus</i> , <i>Croton sparsiflorus</i> , wild <i>Datura metel</i> , <i>Solanum indicum</i> and <i>Solanum sisymbriifolium</i>)	[50], [52], [53], [56], [57]
Middle Gangetic Plains Region	Present	Potato, tomato, brinjal, chillies and wild <i>Datura metel</i>	[50], [52], [53]
Upper Gangetic Plains Region	Present	Potato, tomato, brinjal, chillies and wild <i>Datura metel</i>	[50], [52]
Trans-Gangetic Plains Region	Not endemic	-	[50]
Eastern Plateau and Hills Region	Present	Tomato, brinjal, potato, bird of paradise, ginger, chilli, capsicum, davana and coleus; <i>Heliconia</i> spp.	[51], [53], [58]
Central Plateau and Hills Region	Present	Eggplant, potato tomato, chilli, brinjal and wild <i>Datura metel</i>	[50], [52], [53], [59]
Western Plateau and Hills Region	Present	Tomato, brinjal, potato, bird of paradise, ginger, chilli, capsicum, davana and coleus; <i>Heliconia</i> spp.	[51], [52], [53], [58], [59]
Southern Plateau and Hills Region	Present	Tomato, brinjal, potato, bird of paradise, banana, ginger, chilli, capsicum, davana and coleus	[51], [53], [54], [58], [60], [61], [62], [63], [64]
East Coast Plains and Hills Region	Present	Banana, tomato, brinjal, potato, bird of paradise, ginger, chilli, capsicum, davana and coleus	[51], [60], [61], [63], [64]
West Coast Plains and Ghat Region	Present	Tomato, brinjal, potato, bird of paradise, ginger, chilli, capsicum, davana and coleus; <i>Heliconia</i> spp.	[51], [53], [54], [58], [62]
Gujarat Plains and Hills Region	Present	Potato	[52]
Western Dry Region	Not endemic	-	[50]
The Islands Region	Present	Eggplant, tomato, chilli	[53], [65]

In 1978, Shekhawat and his co-workers conducted a study on distribution, races and biotypes of the bacterial wilt pathogen in India. They found the prevalence of race 3 and biotype II in hilly regions. Meanwhile, in the eastern plains and Deccan and central plateau race 1 and biotype III were preeminent [66]. In Chhattisgarh, bacterial wilt is endemic in major brinjal growing areas, causing significant yield losses of 40-80%. The isolates responsible for the disease belonged to race 1 and biovar III, with race 1 (53.84%) being predominant, followed by race 3 (38.46%) and race 2 (7.69%) [67]. Sagar and his colleagues were the first to report the presence of the phylotype IV sequevar 8 (bv2T) strain of *Ralstonia solanacearum*, in the mid-hill regions of Meghalaya, India, responsible for potato bacterial wilt. *R. solanacearum* isolates of potato collected from Himachal Pradesh, Uttar Pradesh and Madhya Pradesh were identified as phylotype IIB-1 (biovar 2 race 3) [52]. Isolates of *R. solanacearum* collected from Andhra Pradesh, Karnataka, Kerala, Maharashtra, Orissa and Tamil Nadu were characterized as race 1 biovar 3 (and 3B) [51]. Intraspecific identification of *R. solanacearum* strains isolated from solanaceous vegetables in Andaman Islands, India revealed the presence of race 1 biovar 3 and race 1 biovar 4. Both biovars exhibited analogous virulent approach in wilting plants. All isolated strains were classified as phylotype I and multilocus sequence typing implied that they belong to a small number of clonal complexes, that encompass strains from mainland India, particularly West Bengal and Kerala [65].

In Himachal Pradesh (H.P.), India *R. pseudosolanacearum* (Phylotype I) was identified as the causal agent of bacterial wilt of tomato. Sequevars I-44, I-46, I-47, I-57, I-70 and I-71 were reported for the first time in H.P., India by partial *egl* gene sequencing [68]. The rampant distribution of *R. solanacearum* across diverse geographical zones of India has led to considerable genetic, phenotypic and pathogenic variability within the pathogen population. This variability is evident in the diverse races, biovars and sequevars identified across different regions.

Variability

The heterogeneous nature of RSSC is because of natural transformation [69], and recombination [70], thus, evolving and adapting over time. Classically, the RSSC pathogens are divided into five races based on their host range [71], and six biovars on the basis of biochemical properties [72]. A new classification system based on phylogenetic analysis was proposed by Fegan and Prior in 2005 characterized RSSC strains into four phylotypes as per their geographic origin [38]. The phylotypes are further differentiated into sequevars on the basis of nucleotide variation in partial sequencing of *egl* gene (endoglucanase). Lately, the RSSC is divided into three species, *R. pseudosolanacearum*, *R. solanacearum*, *R. syzygii* [73]. These strains are characterized into four phylotypes:

phylotype I - originating from Asia includes *R. pseudosolanacearum*,
phylotype II - from America includes *R. solanacearum*,

phylotype III - originating from Africa and the Indian Ocean includes *R. pseudosolanacearum* and phylotype IV from Australia, Japan and Indonesia classified as *R. syzygii* [38, 73, 74].

Polymorphism created by mutations gets redistributed among bacterial strains by recombination and horizontal gene transfer (HGT) [75]. Conjugation, transduction and transformation are three mechanisms of HGT. In conjugation, DNA is directly transferred from a donor bacterial cell to recipient cell while in transduction the transfer of DNA is facilitated by bacteriophages. However, Transformation involves the uptake of DNA by a competent bacterial cell from its surroundings [76]. Furthermore, HGT is considered as the main mechanism of bacterial genome evolution [77]. In *Ralstonia solanacearum*, evolutionary ecology by recombination has been studied by Wicker and his colleagues [70]. This study analyzed prototypical strains of *R. solanacearum* by multi-locus sequence analysis (MLSA) with 9 loci and concluded that recombination played a major role in the genome evolution of *R. solanacearum*. Genomic analysis of nine strains of *R. solanacearum* unveiled multitudinous genomic islands, mostly surrounded by mobile elements, such as bacteriophages or insertion sequences (ISs), implying horizontal gene transfer (HGT) [78, 79, 80]. Moreover, laboratory experiments have demonstrated that horizontal gene transfer (HGT) occurs among strains from the four phylotypes of *R. solanacearum*, with an 80% probability of being naturally transferred by plasmid or genomic DNA [69, 76]. The role of HGT has also been demonstrated in enhancing the virulence of *R. solanacearum* on the tomato crop [81].

The ability of *R. solanacearum* to naturally develop the physiological state of competence needed to exchange the genetic material by transformation under *in vitro* and *in planta* conditions, demonstrated the underlying role of HGT in its genomic evolution [82, 83]. The premise of HGT *in planta* has been reinforced by the observation of mixed infections of *R. solanacearum* strains from two phylotypes in tomato crop [76]. Alternative Codon Usage Regions (ACURs) are the non-coding sequences with known proteins which were present in GMI1000 strain of *Ralstonia* [84]. These sequences were observed in 93 distinctive sequence regions with major variations in base compositions [85].

Prior accounts of genetic variability amongst American *R. solanacearum* strains [86, 87, 88] implied that high level of pathogenic diversity subsist in countries like French Guyana, Colombia and Brazil [89].

Recombination and HGT plays imperative role in governing the evolution of plant pathogenic bacteria. Meanwhile, phylotype and sequevar categorization of *R. solanacearum* are used to conclude the amount and distribution of phenetic and phylogenetic variability of pathogen [80].

In 2022, Ghorai and his co-workers, studied the genetic diversity of *R. solanacearum* under different agro-climatic regions of India. They were the first to report the occurrence of sequevar I-48 in bottle gourd inciting bacterial wilt disease in India. Their findings revealed that genetic variation across agro-climatic zones was relatively low (18.9%), whereas variation within individual zones was significantly higher (81.1%), suggesting extensive gene flow between populations across different zones [90]. Furthermore, the most varied gene attributing to the evolution of RSSC globally, was observed to be *egl* (endoglucanase).

Table 4. Distribution of *R. solanacearum* sequevars in India

State	Sequevar	Reference
Goa	I-17, I-14, I-48	[53], [90]
Karnataka	I-17, I-47	
Kerala	I-17, I-47	
Andaman & Nicobar Islands	I-14, I-47, I-48	
Maharashtra	I-48	
West Bengal	I-47, I-48, IIB-1	
Himachal Pradesh	I-45, I-30	
Uttar Pradesh	IIB-1	
Madhya Pradesh	IIB-1	
Meghalaya	IIB-1	

Variability in bacteria can also play a key role in their pathogenic ability. As two novel type III effectors were believed to be acquired through HGT in HA4-1 strain of *R. solanacearum*, associated with host specificity and pathogen evolution [91]. Reports have shown that the transfer of DNA polymerase gene *i.e. imuABC* from *Cupriavidus taiwanensis* could enhance the acclimatization of *R. solanacearum* to new hosts [92]. Summative adjacent is that variability plays a significant role in evolution, pathogenicity and adaptation of the RSSC.

Bio-management

Integrated disease management (IDM) for plant pathogenic bacteria includes the use of chemicals, physical practices, biological approaches, host resistance and cultural practices like crop rotation, sanitation. However, the global effort to breed resistant plant lines has faced setbacks due to the highly variable nature of this bacterial pathogen (figure 2). Moreover, the ability of bacteria to develop resistance, survival for long durations in the environment and wide host range restricts the efficiency of IDM measures [93]. Antibiotics such as streptomycin, ampicillin, tetracycline and penicillin showed meager effect on *R. solanacearum* while the application of streptomycin escalated the occurrence of bacterial wilt in Egypt [94]. Thus, the management of *R. solanacearum* poses a significant challenge. Regardless of other respective IDM measures, effective management tactics with eco-friendly effects aim to decrease or eliminate disease incidence and severity by incorporating biological control agents, organic amendments and resistant crop varieties with desirable level of effectiveness, while minimizing chemical inputs to preserve environmental health. Employing bio management tactics involves the use of living microorganisms or plant or animal-based products for plant disease management. The advantages of bio-control measures include their ability to multiply and spread after initial implementation [95]. BCAs combat diseases by competing for food and space, exhibiting parasitism, producing antimicrobial substances (antibiosis) and triggering systemic resistance in plants [96]. The ultimate aim of biological approaches is to reduce the use of chemicals while managing plant diseases. Bacterial bio-agents constitute the majority of BCAs [97], with key studies demonstrating the effectiveness of *Pseudomonas* spp., *Bacillus* spp. and *Streptomyces* spp. in combating the bacterial wilt pathogen [95, 98, 99]. Additionally, fungi and bacteriophages are also extensively examined and employed against *R. solanacearum*. Biocontrol effectiveness is influenced by inoculation techniques for biocontrol agents, such as soil drenching, root dipping and seed coatings [95]. Hence, here we discussed and analyzed information related to bio management of *R. solanacearum* for its effective management.

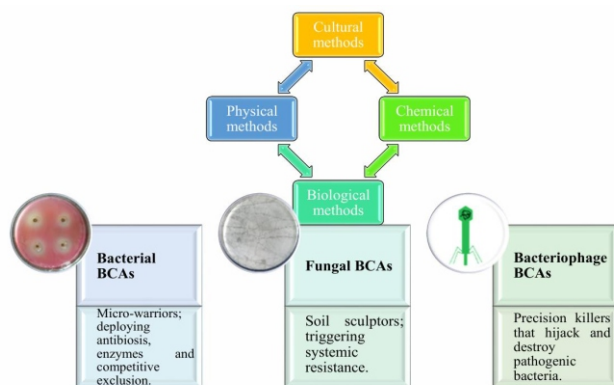


Figure 2. Management tactics employed against *Ralstonia solanacearum*

1. Bacteria- as Biocontrol agents (BCAs)

Bacteria make up the majority of BCAs at 90%, with fungi accounting for the remaining 10% [34]. Bacterial BCAs helps in managing bacterial wilt disease by producing anti-microbial compounds, improving soil health and by competing for space and nutrients. Overall, BCAs enhances plant immunity by stimulating defense responses [96, 100]. Xue and his colleagues were first to report *Acinetobacter* sp. strain as a BCA against *Ralstonia* wilt of tomato [101]. *Burkholderia pyrrocinia*, *B. nodosa*, *B. tericola*, *B. sacchari*, *Chryseobacterium daecheongense* [102], are some of the peculiar bacterial BCA which are reported for managing bacterial wilt disease. A substantial reduction in bacterial wilt disease of chilli (86%) was also achieved by the application of endophytic bacteria *Bacillus subtilis* [103]. *Paenibacillus polymyxa*, a BCA is known to suppress bacterial wilt disease up to 80% in potato field. Meanwhile, *Enterobacter cloacae*, an endophytic bacterial isolate from potato crop, showed 26.5% of disease suppression. Numerous studies have reported that endophytic and rhizobacteria effective against bacterial wilt disease as BCAs are *Bacillus*, *Serratia* spp., *Paenibacillus* and *Pseudomonas* [34]. *Pseudomonas aeruginosa* and *P. syringae* also showed effectiveness in managing bacterial wilt disease via host resistance and antibiosis. Agarwal and his colleagues isolated forty endophytic bacterial isolates from *Gnetum gnemon* plant and tested their efficacy against bacterial wilt disease in the tomato crop [105]. Among 40 bacterial isolates, two endophytic bacterial species viz., *Bacillus velezensis* and *Staphylococcus warneri* demonstrated antibiosis activity against *R. solanacearum*. *Bacillus licheniformis* was found to be amply effective against this disease (67%) through soil drenching and seed priming application methods. *In planta* evaluation of this BCA during artificial pathogenic inoculation showed 71% disease reduction. Furthermore, field evaluation involving soil solarization and application of *B. licheniformis* notably reduced the *R. pseudosolanacearum* population managing ginger bacterial wilt. This bacterium is being advertised as a potential remedy for bacterial wilt of ginger and the product is termed as “Bacillich” [106].

Mode of action of bacterial bio-agents

Bacterial bio-agents can either be endophytic or plant growth promoting rhizobacteria (PGPR) that protects the crop plants from diseases via different action mechanisms. Endophytic bacteria are those which reside inside the plant system without causing any harm and can trigger induced systemic resistance (ISR) in order to the suppress plant diseases. ISR involves the production of reactive oxygen species, phytoalexins, phenolic compounds or pathogenesis-related (PR) proteins, or the formation of physical barriers like modifications of cell walls

and cuticles [107]. Safdarpour and Khodakaramian reported *Pseudomonas mossellii* and *P. fluorescence* as potential endophytic BCAs against bacterial wilt of tomato [108]. *In vitro* investigations by Das and his co-workers identified five genera viz. *Curtobacterium*, *Pantoea*, *Pseudomonas*, *Microbacterium* and *Paracoccus* as promising endophytic bacterial biocontrol agents against bacterial wilt of tomato [109]. Meanwhile, PGPR are free-living bacteria in the rhizosphere of plants that promote plant growth and suppress plant diseases via antibiosis, competition for space and food, hyperparasitism, or ISR. Antibiosis refers to the mode of action involving the secretion of low molecular weight secondary metabolites that inhibit pathogen growth [110]. Hyperparasitism is competitive interaction between one living organism and a parasite. *Bdellovibrio bacteriovorus* is a predatory bacterium known for its competitive interaction with plant pathogenic bacteria [111]. *Ralstonia pickettii* and *Priestia megaterium* were found as promising rhizospheric bacterial isolates against *Ralstonia solanacearum* [109].

2. Fungi- as BCAs

Some antagonistic fungal strains are also reported as BCAs for *R. solanacearum*. Greenhouse studies revealed a decrease in the population of *R. solanacearum* on the root surface and xylem tissue by 26.7, 79.3 and 81.7% post *Glomus vesiforme* Berch. treatment on tomato. Treated plants had high amounts of soluble phenols and cell-wall-bound phenols in root tissues. Increase in cell-wall-bound phenol content was because of *R. solanacearum* and *G. vesiforme* preferably boosted the soluble phenol content [112]. *In vitro* and greenhouse studies showed *Trichoderma viridae* as an effective bio-agent against *R. pseudosolanacearum*. By the production of secondary metabolites, *Trichoderma* spp. inhibited the growth of *R. solanacearum in vitro* [113]. *Pythium oligandrum* was also found to have biocontrol potential for suppressing bacterial wilt disease by regulating the signaling pathway for ethylene [114]. Furthermore, *Parmotrema tinctorum*, a lichen fungus [115], and three other fungi viz., *Scutellospora* sp., *Glomus margarita* and *G. mosseae* were also recognized as biocontrol fungi against bacterial wilt disease [49]. A reduction in *R. solanacearum* population on the root surface and xylem of tomato plant was observed following the inoculation of *Glomus vesiforme*. The colonization of *Glomus vesiforme* and *R. solanacearum* resulted in a higher concentration of root phenols, thus inducing host resistance [34].

Mode of action of fungal bio-agents

ISR, antibiosis, hyperparasitism and competition for food and space are action mechanisms for delimiting and killing the pathogens causing disease in crop plants. *Trichoderma asperellum* suppresses *Fusarium* wilt through iron competition, mediated by the production of iron-chelating siderophores [116]. *Trichoderma* spp. and *Clonostachys* (earlier, *Glilocladium*) were found to produce antimicrobial compounds like 6-PAP, gliovirin, gliotoxin and viridin [117]. *Trichoderma* and *Clonostachys* are the most studied mycoparasites, having varied and wide host range. These fungal antagonists produce attachment and infection structures, and kill their hosts by the release of cell wall degrading enzyme (CWDE) and antimicrobial secondary metabolites [118, 119, 120, 121, 122].

3. Bacteriophages- as a BCAs

Bacteriophages are the viruses that infect and kill bacteria, which are gaining attention as effective biocontrol agents in agriculture and food production. Ramírez and his co-workers isolated eight lytic bacteriophages which were evaluated against 65 strains of *Ralstonia solanacearum* [123]. Two of the isolated bacteriophages showed 100% protection against Moko disease when inoculated with two two-phage cocktail solution. Wafula and his colleagues isolated SN1 and WT1 phages which exhibited high lytic activity, high thermotolerance and acid tolerance [94]. Thus, showed great potential in managing bacterial wilt disease in a variety of conditions. They also concluded that bacteriophages offer great potential in managing bacterial wilt pathogen. Lytic bacteriophages isolated from banana cultivated soil were found to have efficacy in managing *R. solanacearum* pathogen [123]. In 2019 Alvàrez and his co-workers isolated waterborne phages, three of which belonged to *Podoviridae*, were found to be effective in managing *R. solanacearum* [124]. This was the first report on the management of *R. solanacearum* via single or combined application of bacteriophages through irrigation water. Biosca and others studied genomic analysis of the phage having depolymerase activity.

The genomic analysis contributes to recognizing the abilities of the phages to damage host cells, thus, improving biological control of *R. solanacearum* [125]. Bacteriophages isolated from ginger growing soils were tested for their host specificity and antagonistic activity against *R. pseudosolanacearum*. They found that isolated bacteriophages were effective against the pathogenic bacteria of the same geographical area from which it is isolated [126].

Mode of action of bacteriophages

Bacteriophages are bacteria infecting viruses that have lytic or lysogenic life cycle. In the lytic cycle, bacteriophage hijacks the host machinery and eventually lyses the host cell with the release of new virus particles. Lysogenic phages integrate their DNA in host bacterium genome and replicate passively until triggered to enter the lytic phase. Bacteriophages have bactericidal, target specific clinical action with the ability to clear biofilm [127]. Hasanien and his co-workers (isolated and characterized phages ϕ RS1 (Myoviridae family), ϕ RS2 (Myoviridae), and ϕ RS3 (Podoviridae) and observed 91.3, 95.6 and 95.6 % reversal of bacterial wilt disease symptoms [128]. Phage SN1 and WT1 also exhibited lytic activity, thus showed promising results against bacterial wilt disease amidst varying conditions [94].

Table 5. Effective BCAs against bacterial wilt disease

BCA	Mode of action	Crop	Reference
Bacterial BCAs			
Genus - <i>Bacillus</i>			[99]
a.) <i>B. thuringiensis</i>	Acyl homoserine lactone lactonase	Tomato	
b.) <i>B. amyloliquefaciens</i>	-		[129]
c.) <i>B. subtilis</i>	-	Potato	[129]
d.) <i>B. cereus</i>	Antibiosis (lactic acid and hexanoic acid)	Potato	[130]
	Difficidin and oxydifficidin production	Potato	
e.) <i>B. methylotrophicus</i>		Tomato	[131]
Genus - <i>Pseudomonas</i>			
a.) <i>P. aeruginosa</i>		Tomato	[104]
b.) <i>P. syringae</i>	Host resistance and antibiosis Host resistance and antibiosis	Tomato	[104]
c.) <i>P. fluorescens</i>	Lipase, protease and α -amylase enzymes production	Tomato	[104]
d.) <i>P. putida</i>	-	-	[132]
<i>Myroides</i> sp.	-	Ginger	[133]
<i>Stenotrophomonas</i> sp.	-	Ginger	[133]
<i>Chryseobacterium daecheongense</i>	-	Tomato	[134]
<i>Paenibacillus polymyxa</i>	Lipopeptide production	Eggplant	[135]
<i>Bradyrhizobium japonicum</i>	Abscisic acid production	Tomato	[136]
Fungal BCAs			
<i>Gigaspora margarita</i>	-	Tomato	[49]
<i>Glomus mosseae</i>	-	Tomato	[49]
<i>Scutellospora</i> sp.	-	Tomato	[49]
<i>Glomus versiforme</i>	Induces systemic resistance	Tomato	[112]
<i>Pythium oligandrum</i>	Ethylene-dependent signalling system	Tomato	[114]
<i>Trichoderma harzianum</i>	Metabolites	Tomato	[131]
Bacteriophages			
Bacteriophages	Lytic activity	Banana	[123]
Bacteriophages (PE226)	Lytic activity	Pepper, tomato, tobacco	[137]
Bacteriophages (TM227)	Lytic activity	Pepper, tomato, tobacco	[137]
Bacteriophages	Lytic activity	Tomato	[138]

Host Resistance

Most effective, cost-efficient and environment-friendly approach in managing bacterial wilt pathogen is highly resistant cultivars [139]. A wide range of investigations led to the development of bacterial wilt resistant germplasm. Major vegetable and field crops are being bred for resistance against bacterial wilt disease. Electrical fusion of mesophyll protoplasts between *Solanum melongena* and two varieties of *Solanum aethiopicum* resulted in somatic hybrid that possess resistance to *R. solanacearum*. CF6, a potato genotype reduced the bacterial wilt severity by 90-100% in Phureja, South America [34]. Resistant genotypes invaded by *R. solanacearum* do not exhibit any wilt symptoms. Limited pathogen movement has been reported from protoxylem to other xylem tissues, hence preventing bacterial multiplication in the stems of resistant tomato plants [34]. Introgression of *NPR1* gene from *Arabidopsis* to a tomato variety showed a substantial reduction in bacterial wilt disease by inducing systemic acquired resistance (SAR) and induced systemic resistance (ISR) [140]. Studies from the Southern United States, South Korea and Japan showed grafting resistant stock to susceptible scions as an effective method of disease management [141, 142, 143]. McAvoy and his colleagues grafted scions of the susceptible BHN 602 tomato line onto the rootstocks of various resistant tomato lines [141]. They concluded that the grafted hybrids had low disease incidence and high fruit yield as compared to non-grafted plants. Identification and characterization of genetic bases responsible for specific and non-specific resistance can serve as a foundation for resistance breeding. Heaps of studies in tomato identified quantitative trait loci (QTLs) on chromosomes 1,2,3,4,5,6,7,8,10 and 11 against bacterial wilt disease [150, 151, 152]. Albeit a slew of QTLs has been identified and studied, only Solyc03g114600.4.1 on chromosome 3 [153] and Solyc12g009690 [154] and Solyc12g009770 on chromosome 12 are identified to impart resistance against tomato bacterial wilt [155]. Xiao and his colleagues observed non-synonymous mutation in the exonic region of SMEL4_05g015980.1 and a variant in the promoter region of SMEL4_05g016110.1 in brinjal [156].

Table 6. Resistant accessions/germplasm for resistance to bacterial wilt disease

Accession/ Germplasm	Host crop	Level of resistance	Reference
IT 201664	Tomato	Resistant (R)	[143]
IT 201662	Tomato	Resistant (R)	[143]
IT 201659	Tomato	Resistant (R)	[143]
IT 173773	Tomato	Resistant (R)	[143]
AG91-25	Eggplant	Resistance (R)	[144]
CIP 394895.7	Potato	Resistant (R)	[145]
Skyline-II	Chilli	Highly resistant (HR)	[146]
Hifly	Chilli	Highly resistant (HR)	[146]
UK Local-2	Tomato	Highly resistant (HR)	[147]
RIL-118	Tomato	Highly resistant (HR)	[148]
Indam-1004	Tomato	Highly resistant (HR)	[148]
Arka Samrat	Tomato	Highly resistant (HR)	[148]
PKM-1	Tomato	Highly resistant (HR)	[148]
PED	Tomato	Highly resistant (HR)	[148]
EC-802390	Tomato	Highly resistant (HR)	[148]
EC-816105	Tomato	Highly resistant (HR)	[148]
IT236738	<i>Capsicum chinense</i>	Highly resistant (HR)	[149]
IT283498	<i>Capsicum chinense</i>	Highly resistant (HR)	[149]

Table 7. R gene / QTL identified against bacterial wilt disease

R gene / QTL	Chromosome No.	Host crop	Reference
ERs1 (R dominant gene)	9	Brinjal	[144], [157]
Solyc03g114600.4.1	3	Tomato	[153]
Solyc12g009690	12	Tomato	[154]
Solyc12g009770	12	Tomato	[155]
SMEL4_05g016110.1	5	Brinjal	[156]
SMEL4_05g015980.1	5	Brinjal	[156]
qBWR-1	LG1	Peanut	[158]
qBWR-1	1	Potato	[159]
qBWR-2	3	Potato	[159]
qBWR-3	7	Potato	[159]
qBWR-4	10	Potato	[159]
qBWR-5	11	Potato	[159]
Bwr6w-5.1	5	Chilli pepper	[161]
Bwr6w-6.1	6	Chilli pepper	[161]
Bwr6w-7.1	7	Chilli pepper	[161]
Bwr6w-7.2	7	Chilli pepper	[161]
Bwr6w-8.1	8	Chilli pepper	[161]
Bwr6w-9.1	9	Chilli pepper	[161]
Bwr6w-9.2	9	Chilli pepper	[161]
Bwr6w-10.1	10	Chilli pepper	[161]

Organic approaches

Organic matter, including plant residues and animal waste, can suppress bacterial wilt by improving soil properties and enhancing microbial activity. The use of organic matter is directly proportional to crop productivity and management of *R. solanacearum* by enhancing soil chemical, physical and biological properties which favours plant growth [162, 163]. Plant residues contributing 80% followed by animal waste (10%) and simpler organic matter (OM) (10%) were found to have an oppressive effect on bacterial wilt disease. Numerous studies showed that organic matter could efficiently tackle bacterial wilt disease in field and greenhouse conditions. Cardoso and his colleagues used fresh parts of crotalaria and pigeon pea in greenhouse conditions and found 100% suppression in bacterial wilt disease of tomato [164]. Animal waste was also used to suppress bacterial wilt disease in various studies. Pig slurry, poultry and farmyard manure (FYM) were found to be efficient in suppressing bacterial wilt disease by increasing the count of antagonist BCAs [165]. Additionally, methyl gallate (MG), an antioxidant phenolic compound found in various plant species such as *Meliaceae* species showed potential bactericidal effects on *R. solanacearum* [166].

Mode of action: Organic matter degradation in soil can release natural inhibitory chemical substances which can affect the survival and viability of pathogens [162]. Incorporation of organic matter enhances soil health, aeration, water retention and nutrient cycling. Henceforth, organic amendments to soil can increase soil microbial activity, augment activities of ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase, thereby imparting resistance against the bacterial wilt pathogen [167, 168].

Table 8. Organic approaches to manage bacterial wilt disease

Organic matter used	Mechanism of action	Host crop	Reference
Compost (cattle manure, chicken manure, brassica and rice husk at a ratio of 3:1:1:1)	Increases enzymes ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase and glutathione reductase,	Potato	[168]
<i>Tagetes patula</i> L.	Antibacterial substances; 5-(3-buten-1-ynyl)-2, 2'-bithienyl and 5 (4-acetoxy-1-butynyl)-2, 2'-bithienyl	<i>Invitro</i>	[169]
<i>Cryptomeria japonica</i>	Sandaracopimaranol and ferruginol	<i>Invitro</i>	[170]
<i>Cyphomandra betacea</i> (Cav.) Sendtn.	Glycosidase inhibitory protein	<i>Invitro</i>	[171]
Lemon guava	-	<i>Invitro</i>	[172]
Benin pepper	-	<i>Invitro</i>	[172]
Olive waste compost	Combined effects (presence of antagonistic microorganisms	<i>Invitro</i>	[173]
<i>Clausena lansium</i>	Lansiumamide B	Tobacco	[174]
Lantana	-	Hot pepper	[175]
China berry	-	Hot pepper	[175]

Conclusion

Ralstonia solanacearum is a globally distributed pathogen, prevalent in tropical and subtropical regions, affecting over 200 plant species. The genetic variability of *R. solanacearum* is influenced by geographical isolation and spatial distance, leading to four phylotypes and distinct sequevars. This variability impacts the bacterium's aggressiveness and host range, making it a significant threat to diverse agricultural systems. Biological control methods, such as antagonistic microorganisms and integrated disease management approaches are crucial for managing *R. solanacearum*.

Future Scope

Given the global impact of *R. solanacearum*, international collaboration is necessary to share knowledge, develop consistent management strategies and prevent the spread of the pathogen across borders. Combining biological control, plant breeding and microbiota engineering to create robust and sustainable management strategies can help in the potential management of plant diseases. Understanding the evolutionary dynamics of *R. solanacearum* will help predict its adaptation to new environments and hosts. This knowledge can inform strategies to stay ahead of emerging strains. Meanwhile, leveraging biotechnological techniques to develop novel antimicrobial compounds or to engineer biocontrol agents with enhanced efficacy may serve as a viable approach for bacterial wilt management.

Conflict of interest

The authors declare they have no conflict of interest.

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