



Breeding for resistance to bacterial wilt in Solanaceae crops: lessons learned and ways forward for Gboma eggplant (*Solanum macrocarpon* L.), a traditional African vegetable

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Abstract Bacterial wilt (BW) is caused by *Ralstonia solanacearum* species complex (RSSC) and can lead to severe losses in a wide range of crops, including many traditional African vegetables (TAV). Given the critical role of TAV in African food security, investigations of BW incidence, distribution, and effective breeding strategies are needed to support public and private TAV breeding programs. In this review, we address key questions related to the diversity of BW pathogens, susceptible TAV hosts, distribution, incidence, breeding strategies, sources of resistance, and gaps in the development of resistant TAV varieties in Africa. We also discuss the potential of multiomics integration to enhance our understanding of the host

plant defense system against BW in Solanaceae crops. We curated BW strain databases obtained from several online platforms, representing a total of 948 BW strains. Using a refined database, we highlighted the diversity of RSSC and TAV crops affected by RSSC in different regions of Africa. Out of 29 species documented to be affected by BW in Africa, ten are TAV, including widely consumed TAV such as Amaranths and nightshades. In addition, phylotypes I and III are reported to affect TAV, and the incidence can reach up to 72.4% in farmers' fields. An overview of the first reports revealed that the disease has become a serious threat to TAV in the past decade. Finally, this review proposes a schematic map of possible avenues for successful breeding of BW-resistant TAV using Gboma eggplant as a case study.

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Introduction

Bacterial wilt (BW) is a soil-borne disease caused by the *Ralstonia solanacearum* species complex (RSSC) that threatens agricultural productivity and food security worldwide (Janse 2004; Mamphogoro et al. 2020). RSSC pathogens are aerobic nonspore-forming and gram-negative bacteria (Munyaneza and Bizimungu 2022). They can spread through water, farm tools, infected seeds, and previously infested crop residue, leading to whole plant wilting and drying (Uwamahoro et al. 2018). In Africa, the disease was first reported in South Africa and Zimbabwe in the 1920s and has since been observed in various African countries (McClean 1930; Robertson 1998). Approximately 450 plants species worldwide, spanning 54 botanical families, are affected by BW, with up to 100% yield loss for solanaceous crops (Sharma et al. 2021). The broad host range of RSSC underscores its threat to agricultural productivity. Major vegetable crops, such as tomatoes and eggplants, and field crops, such as potatoes, which are crucial for food security and farmer income, are widely affected (N'Guessan et al. 2012; Kurabachew and Ayana 2017; Uwamahoro et al. 2018; Nikuze et al. 2020). Although there are numerous first reports of BW, little is known about its impact on traditional African vegetable (TAV) crops. TAV encompass both indigenous vegetables and introduced crops assimilated into local culinary traditions and have become part of cropping systems or agricultural landscapes (Towns and Shackleton 2018). TAV's consumption have the potential to significantly impact the promotion of healthy, well-balanced diets while also serving as a source of income for people in Africa (Ochieng et al. 2018; Sogbohossou et al. 2019). Several TAV exhibit varying levels of susceptibility to RSSC in tropical and subtropical regions including *Solanum macrocarpon*, *Amaranthus* spp. and *Ocimum* spp. in Benin, *Solanum aethiopicum* in Mali, and *Solanum nigrum* in Kenya. (Sikirou et al. 2015, 2021; Bihon et al. 2020; Mafuta et al. 2022). Disease susceptibility levels depend on plant species and genotype, pathogen phylogeny and ecotype, environmental factors, and crop

management practices (Wei et al. 2015; Mamphogoro et al. 2020). The development of cultivars resistant to bacterial wilt, either for direct production or for use as rootstocks in grafting, is the most efficient strategy for mitigating the impact of this disease (Huet 2014; Sharma et al. 2021). Fast-tracking the development of resistant TAV varieties requires prior knowledge of the diversity of RSSC strains, their effectors, and access to BW-resistant sources for breeding, either collected from the wild, from genebank collections, or mutagenesis or genetic engineering programs.

There have been tremendous advances in understanding the interactions between RSSC and Solanaceae crops (Jourda et al. 2019) and in tapping into this knowledge to breed resistant varieties (Hanson et al. 2016; Pandiyaraj et al. 2019). However, research on breeding for resistance in traditional African vegetables (TAV) is scarce. It has become imperative to leverage the success of developing bacterial-resistant global vegetable crop varieties to accelerate the development of resistant TAV varieties. The importance of such an endeavour lies in bridging the existing knowledge gaps and promoting resistance breeding for TAV, benefiting farmers and other stakeholders. In this review, we addressed key questions related to the distribution of the BW pathogen, breeding strategies for susceptible TAV hosts, and gaps in developing resistant TAV varieties in Africa based on studies conducted on common Solanaceae crops. This paper provides plant pathologists and breeders with information to speed up the development of BW-resistant TAV cultivars.

Methodology

Three data repository websites (EPPO Global Database accessed on 16/05/2023, GitHub—lowepowerlab/Ralstonia_Global_Diversity: Curated by UC Davis—Global Disease Biology Students accessed on 03/07/2023, GBIF accessed on 13/06/2023) were screened, and occurrence data (countries, regions), susceptible hosts, phylotypes and other related information such as subphylotypes, sequevars, clades, and biovar related to strains from Africa were extracted using Microsoft Excel. We cross-checked the extracted information across the databases and removed all duplicates based on strain names and references. We identified a total of 948 RSSC strains, 19

of which were sequenced by different research groups (Table S1). Among the 19 genome files, we used five genomes from Africa discovered by Sabbagh et al. (2019); these genomes are part of a worldwide database of complete genome sequences of RSSC. The five strains were used to identify common TE3 effectors between three common Solanaceae (tomato, eggplant, and potato) and black nightshade, a TAV crop. All the details on the functionally characterized RSSC T3Es of the five strains that induced susceptibility in tomato, eggplant, potato, and black nightshade are summarized in Table S3. All the analyses and graphs generated in this review were generated in R statistical software version 4.2.2 (R Core Team 2022).

History and progress of the control of BW in Africa

Diversity of the pathogen in Africa

A recent taxonomic revision of the RSSC allowed the classification of the bacterium into different phylotypes, with each phylotype corresponding to specific geographic origins such as phylotype I (Asia), phylotype II (America), phylotype III (Africa), and phylotype IV (Indonesia). In Africa, all these phylotypes (I, II, III, and IV) are present and classified into three species within the RSSC. The RSSC comprises *R. solanacearum*, which includes all phylotype II strains; *Ralstonia pseudosolanacearum*, encompassing phylotypes I and III; and *Ralstonia syzygi*, associated with phylotype IV strains (Safni et al. 2014). Nortje's 2015 study highlighted that historically, the predominant phylotypes in Africa were I and II, encompassing highly virulent IIB1 strains (Waals and Krüger 2020). Overall, the wide distribution and host range of RSSC in Africa pose significant threats to the region's food security and agricultural productivity. West and East Africa stand out as critical regions due to the extensive diversity of isolates in terms of phylotypes and sequevars. Specifically, phylotypes I, II, and III have been documented in West Africa, while all phylotypes have been observed in East Africa.

Historically, taxonomic lineages for interspecific and intraspecific classification of *Ralstonia* spp. were based only on single-gene 16S rRNA and 16-23S intergenic sequences (Kumar et al. 2013). Although

very popular, these methods have failed to accurately differentiate related strains and species in the RSSC complex. As a result, a sequevar system was developed as a phylogeny-based taxonomy for the within-species classification of RSSC. A sequevar, also called a sequence variant, is a highly conserved sequence within a sequenced genomic area (Sharma et al. 2021). The assignment of a sequevar occurs solely when two or more strains exhibit comparable sequences of the endoglucanase (*egl*) gene (Fegan and Prior 2005). The strains grouped within the same sequevar exhibit less than 1% variation in the nucleotide sequence of a 750 bp region of *egl* (Carstensen et al. 2017). Currently, 60 sequevars have been described worldwide, including approximately 30 in Africa. However, the threshold for subdividing sequevars lacks phylogenetic justification, and the correspondence between sequevars and ecotypes becomes increasingly tenuous with the growing number of available sequences. It is worth noting that sequevar classification is likely to be replaced by a "Sequence Type" (ST) classification, which aligns better with the practices of epidemiological surveillance in medical or animal microbiology (Guinard 2012).

Based on our compiled database from the literature, we observed a prevalence of sequevar 31 followed by sequevars 18 and 46 in phylotype I (Fig. 1). However, many strains for which the corresponding sequevars have not yet been studied are classified as unknown. Phylotype III consists predominantly of strains with undetermined sequevars not yet identified by sequencing. Phylotype II is categorized into two variants, A and B, with variant A exhibiting a broader range of hosts and variant B being more specific to banana species. Several phylotype II strains are also classified as unknown since any study has not determined their sequevar or has not identified them in the database. This is sometimes due to the study type often limited to the biochemical determination of strains or the strain nomenclature not being sufficiently detailed in the paper. Such information is vital since identifying sequevars enables the subclassification of strains into distinct phylotypes, thereby enhancing their classification accuracy. Moreover, some sequevars are species specific, rendering this knowledge crucial for breeding for resistance to the disease. For instance, Akarapisan et al. (2022) reported that sequevar 30 was pathogenic only to Zingiberaceae plants.



Fig. 1 Two-level relationships between phylotypes and sequevars of the studied strains in Africa; **a** geographical distribution of sequevars and **b** sequevars across crop groups

First reports and evolution of the disease

Bacterial wilt disease caused by RSSC was reported for the first time in Africa in 1924 in South Africa and affects the production of potatoes (McClellan 1930; Robertson 1998). The disease was subsequently reported in several African countries in the 1930s and 1940s (Busolo-Bulafu 1998). However, there are contradictory reports on which geographical region

where the disease was first reported. There are reports that Egypt may have been the first African country where the disease was identified in potato fields (Farag et al. 1999). Conversely, reports from southern Africa indicate that Zimbabwe and South Africa were potential locations for its initial discovery. Later, many reports were published on the disease in Africa, which began by drawing attention to its propagation and the irreversibility of the damage caused even

after applying disease control measures. Bacterial wilt caused by RSSC has been documented in several countries in Eastern and Southern Africa (Muthoni et al. 2012). More recently, several investigations were conducted in West Africa, with the first reports from 2009 to 2018 of common Solanaceae crops and later reports of TAV (Table 1). Furthermore, Madagascar was not spared, and the disease was identified in 2009 on potatoes (Ravelomanantsoa et al. 2018).

Currently, few data are available on the propagation of RSSC in Africa. Despite the important role that plant health plays in production and, consequently, in food security, it is a great concern that

until today, there are no means to control the spread of the disease in sub-Saharan Africa. However, the incidence of this disease has been well studied in America and Asia (Machmud 1986; Fortnum and Martin 1998), and statistics on losses of important crops at the farm, country, and regional levels have started to be documented (Elphinstone 2005; Liao 2005; Sarkar and Chaudhuri 2016; Jiang et al. 2017). Bacterial wilt caused by RSSC could be classified as an emerging plant disease in Africa. According to Anderson et al. (2004) and Ristaino et al. (2021), emergent plant diseases have (1) increased in incidence, dissemination, or host range (Genin 2010; de Moraes et al. 2015); (2) changed pathogenesis (Hayward 1991; Genin 2010); (3) newly evolved (Hayward 1991; Elphinstone

Table 1 First reports on bacterial wilt disease in Africa

Occurrence Year	Country	Species	Source
<i>Major crops</i>			
1924	South Africa	Groundnut (<i>Arachis hypogea</i> L.)	McClean (1930)
1926	Zimbabwe	Tobacco (<i>Nicotiana tabacum</i> L.)	Robertson (1998)
1936	Madagascar	Potato (<i>Solanum tuberosum</i> L.)	Bouriquet (1946)
1938	Uganda	Groundnut (<i>Arachis hypogea</i> L.)	Simbwa-Bunnya (1972)
1940–1950	Egypt	Potato (<i>Solanum tuberosum</i> L.)	Farag et al. (1999)
1945, 1962	Kenya	Potato (<i>Solanum tuberosum</i> L.), tomato (<i>Solanum lycopersicum</i> L.) and Pepper (<i>Capsicum annum</i> L.)	Wicker et al. (2007), Muthoni et al. (2012), Otipa et al. (2003)
1956	Ethiopia	Solanaceous crops such as tomato (<i>Solanum lycopersicum</i> L.), potato (<i>Solanum tuberosum</i> L.), pepper (<i>Capsicum annum</i> L.) and eggplant (<i>Solanum melongena</i> L.)	Kurabachew and Ayana (2017)
1984	Côte d'Ivoire	<i>Solanum melongena</i> L	N'Guessan et al. (2012)
1984	Rwanda	Potato (<i>Solanum tuberosum</i> L.)	Uwamahoro et al. (2018)
2009	Madagascar	Potato (<i>Solanum tuberosum</i> L.)	Ravelomanantsoa et al. (2018)
2012	Benin	Tomato (<i>Solanum lycopersicum</i> L.)	Sikirou et al. (2015)
2012	Ghana	Tomato (<i>Solanum lycopersicum</i> L.), pepper (<i>Capsicum annum</i>)	Subedi et al. (2014)
2018	Togo	Tomato (<i>Solanum lycopersicum</i> L.), pepper (<i>Capsicum annum</i> L.)	Kunwar et al. (2021)
2018	Republic of Guinea, Conakry	<i>Solanum melongena</i> L	Gbonamou et al. (2020)
<i>TAV</i>			
2000	Kenya	<i>Solanum scrabrum</i> Mill	Schippers (2000)
2012	Ghana	Gboma eggplant (<i>Solanum macrocarpon</i> L.)	Subedi et al. (2014)
2015	Benin	Gboma eggplant (<i>Solanum macrocarpon</i> L.)	Sikirou et al. (2015)
2017	Benin	<i>Amaranthus</i> spp.	Sikirou et al. (2021)
2018	Togo	Gboma eggplant (<i>Solanum macrocarpon</i> L.)	Kunwar et al. (2021)
2018	Madagascar	<i>Bidens pilosa</i> L., <i>Solanum nigrum</i> Mill., <i>solanum aethiopicum</i> L	Ravelomanantsoa et al. (2018)

2005); or (4) were discovered or newly recognized (Mansfield et al. 2012).

Distribution, incidence and susceptible crops in Africa

RSSC has been reported to cause bacterial wilt disease in 29 countries across all regions of Africa, with tomato being the most affected, with 35–100% losses depending on the country (Fig. 2, Table S2). In West Africa, pepper is most commonly reported after tomato, with losses ranging from 10–50% in Togo and up to 80% in Mali, but potato and eggplant are more prevalent in East Africa (Table S2). Reports on the incidence of BW on TAV are scarce, with only one reported on Gboma eggplant in southern Benin and one on a nightshade in Kenya (Schippers 2000; Sikirou et al. 2015). Different members of RSSC infect different host plants, with *R. solanacearum*

infecting tomato and potato plants, *Ralstonia pseudosolanacearum* targeting many Solanaceae crops, and *R. syzygi* infecting only potato plants (Table 2). To date, 29 host species from 9 families and 9 orders were reported among 948 strains collected and recorded in Africa. Therefore, effective disease management strategies should prioritize horizontal resistance development rather than gene-by-gene-based resistance in crops most affected by various pathotypes of the pathogen. As the pathogen is highly diverse, effective management strategies combining resistant cultivars with sanitation measures and cultural practices that prevent BW infection and spread are crucial for controlling the disease.

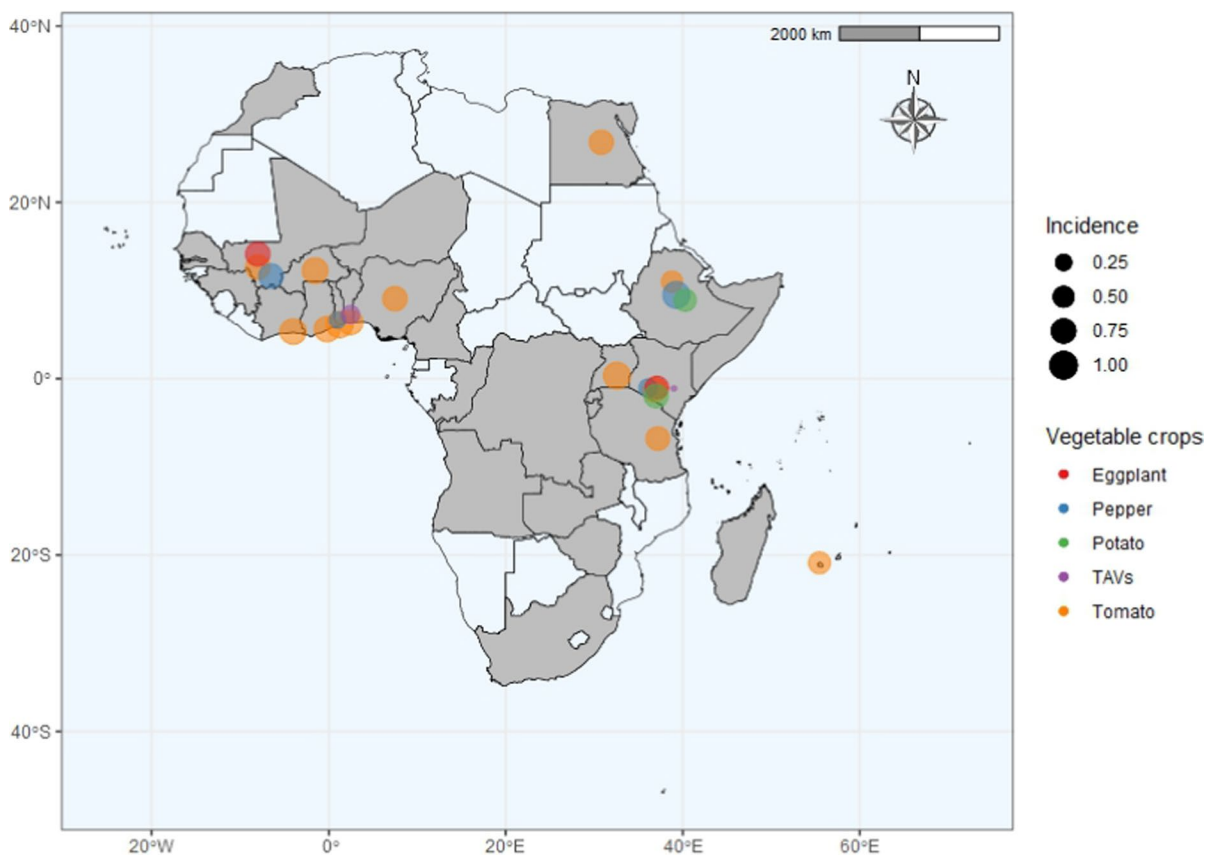


Fig. 2 Occurrence and incidence of bacterial wilt caused by RSSC in Africa

Table 2 Major families and orders of vegetable species infested by the four phylotypes of RSSC in Africa

Phylotype	Host order	Host family	Host species	TAV species	Regions
I	Caryophyllales, Fabales, Lamiales, Myrtales, Solanales, Zingiberales	Amaranthaceae (5), Asteraceae (1), Fabaceae (2), Lamiaceae (1), Musaceae (1), Myrtaceae (4), Solanaceae (500)	16	8	All regions except Northern Africa
II	Geraniales, Poales, Solanales	Geraniaceae (6), Poaceae (1), Solanaceae (217), Fabaceae (1)	11	3	All regions
III	Boraginales, Fabales	Boraginaceae (1), Fabaceae (1), Solanaceae (184), Asteraceae (4), Geraniaceae (15)	15	4	Eastern, Middle, and Western Africa
IV	Solanales	Solanaceae (4)	1	0	Eastern Africa

Number in brackets (*) indicate the number of strains recorded for the host family

Traditional vegetables susceptible to bacterial wilt disease caused by *Ralstonia* spp. in Africa

An RSSC can cause severe losses in a wide range of TAV. The following traditional vegetables, namely, *Amaranthus* spp., *Bidens pilosa*, *Ocimum basilicum*, *Solanum macrocarpon*, *Solanum nigrum*, *Solanum scabrum*, and *Vernonia amygdalina*, have been reported to be infested by *Ralstonia* spp., causing bacterial wilt disease at various levels of incidence in farmers' fields (Fig. 3). In addition, 50% of the species affected by phylotype I strains are TAV. The severity of the disease can vary depending on the host plant, with some crops such as amaranth being highly susceptible, with up to 72.4% incidence and an equivalent level of yield loss due to damage to the entire plant (Sikirou et al. 2021), while other wild or cultivated traditional vegetables such as purslane (*Portulaca olearacea*), whose leaves is consumed as vegetables in Africa (Daunay et al. 1991), is considered hosts. For instance, cowpea serves to contain the spread of wilt from diseased to healthy plants when intercropped with potatoes, whereas purslane is a symptomless host (French 1987). Previous studies revealed BW resistance in several vegetable species, including TAV such as nightshades and African eggplant (*Solanum americanum* syn *Solanum nigrum*, *Solanum aethiopicum* grp. *aculeatum*, and *Solanum scabrum*). However, recent findings provide evidence that these species are increasingly susceptible to BW (Fig. 3). Although many TAV are known for their excellent adaptation to their environment and

resilience to biotic and abiotic stresses, the processes of domestication, intensified production and genetic exchange between countries could weaken their resistance to diseases and spread new races of pathogens (MacLeod et al. 2010; Graziosi et al. 2016; Ferrero et al. 2020). The impact of RSSC on TAV can be devastating for smallholder farmers who rely on these crops for their livelihoods. In addition, this disease can lead to the loss of valuable genetic resources and traditional food cultures. Therefore, it is essential to prioritize research on BW on TAV and initiate efforts to breed BW-resistant TAV genotypes.

Breeding strategies for resistance to bacterial wilt disease

Screening methods

Various methods have been adopted to screen genetic resources for bacterial wilt resistance, including field screening/sick plot methods and artificial inoculation methods, such as the soil drenching method, leaf-clipping method, axil-puncturing method, root dipping method, and hydroponically grown seedling inoculation (Hussain et al. 2005; Hacısalihoglu et al. 2009; Artal et al. 2012; Kwon et al. 2021; Maxwell et al. 2022). These methods have strengths and limitations, and their effectiveness is influenced by the specific plant species under investigation. A quick desk review or a pre-test of a selected method and optimization if needed is critical to select the most

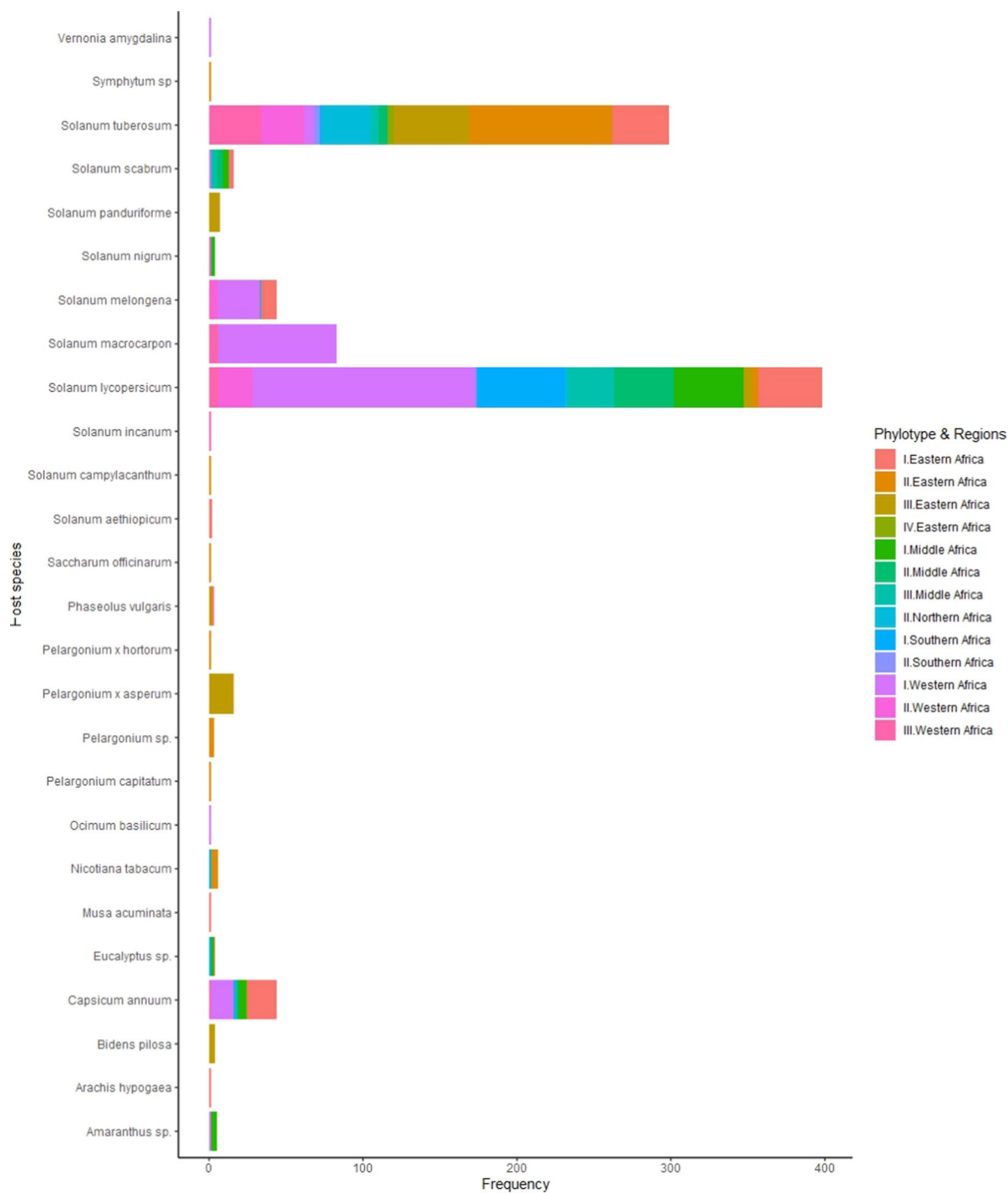


Fig. 3 Record of RSSC phylotype infestations in vegetable crops farmed across Africa

efficient method for a given crop or circumstance. Isolation, culturing, and inoculation require specialized

skills and facilities that may not be available in many research institutions.

Field screening is another effective way to identify BW-resistant lines. A field with a uniform and moderate level of infestation varying between 30 and 50% wilt incidence in the previous cropping season is needed. To account for insufficient inoculum pressure and unevenly infested plots, fields are recommended to be planted with a susceptible crop variety during previous cropping seasons. The infested plants were uniformly spread on the field and buried at harvest to homogenize and enhance soil inoculum levels. For most studies on screening for bacterial resistance in natural fields, a randomized complete block design (RCBD) with at least 3–4 replications is often used for fewer than 30 accessions or entries (Namisy et al. 2019; Zohoungbogbo et al. 2021). Other experimental designs, such as lattice or alpha designs, are recommended when experimental units consist of plots arranged in more than one row or when there are more than 30 entries, including controls (Muthoni et al. 2014; Mathai 2022). In both cases, a minimum of 3–5 plants/plot are acceptable, specifically for potatoes (Mihovilovich et al. 2017), and 10–20 plants/plot are acceptable for other vegetable crops (Sood et al. 2023; Wang et al. 1998a, b). Appropriate experimental design is necessary to avoid escape. Symptomatic plants can be quickly tested in the field using the water test to confirm whether or not the causal agent is RSSC.

Progress in traditional breeding approaches: evaluation and selection, crossbreeding, mutation breeding

A wide range of breeding strategies have been used to develop inbred lines resistant to bacterial diseases, particularly bacterial wilt. These strategies were mainly focused on crops such as tomatoes, eggplants, and potatoes and encompassed many conventional breeding techniques. These techniques involve screening large germplasm collections for bacterial resistance following crossing susceptible and resistant parents to introgress resistance into desired genotypes and subsequent backcrossing to restore the recurrent phenotype.

Traditional breeding approaches have made significant progress in selecting and developing new tomato, pepper, and eggplant varieties with improved resistance to bacterial wilt. The most promising lines or parents tested for BW resistance in West Africa

are tomato lines such as the well-known Hawaii7996, which showed consistent results across different environments. Some local landraces from Uganda, Kenya, and the West Indies were tested and suggested as additional sources of resistance to BW (Osiru et al. 2001; Kathimba et al. 2021). Other sources of resistance are conserved at the World Vegetable Center, the University of California Davis, and INRA (Institut National de Recherche Agronomique) of Guadeloupe (Table 3). Segregating populations were obtained from crosses between susceptible and resistant parents to map BW resistance loci such as Bwr-12, Bwr-6a, Bwr-c, and Bwr6-d (Bihon et al. 2022), and markers have been developed to accelerate breeding through marker-assisted selection (Hanson et al. 2016). Several eggplant species (*Solanum macrocarpon* and *Solanum melongena*) have been tested in Benin and Côte d'Ivoire and have shown some level of resistance to BW. Other TAV, namely, *Solanum scabrum*, *Solanum nigrum*, and *Solanum villosum*, have been screened for their resistance to BW in Kenya, and five accessions of *Solanum scabrum* were found to be resistant to the disease (Mafuta et al. 2022). Several sources of BW resistance and potentially resistant breeding materials for major vegetable crops, such as peppers, tomatoes, potatoes, and eggplants, evaluated in Africa are summarized in Table 3.

Crossbreeding has contributed to the development of Solanaceae crop inbred lines resistant to BW disease worldwide. The BW-resistant source Hawaii7996 is an *S. lycopersicum* inbred line with BW resistance from *S. pimpinellifolium* PI 127805A (Hanson et al. 1998). It is one of the few breeding lines with good resistance to diverse *R. solanacearum* and *R. pseudosolanacearum* strains, with the best combining ability in many crosses performed worldwide, and is a parent of most commercial wilt-resistant tomatoes (Scott et al. 2004; Lopes et al. 2022). The BW-12 and BW-6 QTLs used in tomato breeding are derived from H7996 (Wang et al. 2013). Hybridization has also been performed in tomato breeding programs to develop varieties resistant to BW in Africa. For instance, the crosses between MT55, MT74, MT15, and MT164 in Uganda allowed the development of segregating populations, and after a joint regression analysis, they revealed an additive plus dominance model for bacterial wilt resistance with no evidence of epistasis and found two genes controlling resistance. Researchers have conducted successful crossbreeding

Table 3 Breeding materials tested for their resistance to BW disease in common Solanaceae and TAV crops tested in Africa

Crops	Accessions/inbred lines/varieties	Source	Evaluation countries	References
Tomato (<i>Solanum lycopersicum</i>)	CLN3125L, CLN3078A, CLN3078C, CLN3150A-5, FMTT1733D, FMTT1733E, CLN3900D, CLN3902C, CLN3961D, CLN3961C, CLN3641F, CLN3938E, CLN4018A, CLN4018B, CLN4018C, CLN4018D, CLN3902D, CLN3961E, Hawaii7996, LA 0442, LA 0443 and LA 0376	World vegetable center	Mali	Bihon et al. (2022)
	MT55, MT74, MT15 and MT164	World vegetable center and University of California Davis	Ghana	Boakye-Mensah (2020)
	AVTO1424, AVTO1429 (FMTT1733D), and AVTO1314, Valoria FS, KK accI, NRB, KK acc II, KISII, BRNG acc II and KLF acc III	Makerere University	Uganda	Osiru et al. (2001)
	From AVTO1955-1 to AVTO1955-22, CLN1621L, Hawaii7996, CRA66, AVTO1803, Padma F1, Mongal F1	World vegetable center, local Farmers *-selection (Kenya)	Kenya	Kathimba et al. (2021), Mathai (2022)
Pepper (<i>Capsicum spp</i>)	<i>C. annuum</i> , <i>C. baccatum</i> , and <i>C. chinense</i> (PM659, PM687, PM1443, PBC631A, PBC66, and PBC384, PM702, PM1022)	World Vegetable center, INRA	Reunion	Lebeau et al. (2011)
<i>Solanum melongena</i>	EG203, AG ₉₁₋₂₅ (MM960), WCCR 112-8* MM152	World vegetable center; INRA (Gua-deloupe)	Reunion Island, Cameroon, Côte d'Ivoire	N'Guessan et al. (2012), Lebeau et al. (2013), Peeters et al. (2013a, b), Xi'ou et al. (2015), Salgon et al. (2017)
<i>Solanum macrocarpon</i>	AUB3G	National Agricultural Research Center CNRA/Ivory Coast	Benin	Oussou et al. (2020)
<i>Solanum scabrum</i>	Transnozia 4, Bongoma 7, Kakamega 2, Kakamega 3 and Kakamega 9	Collection from farmer's fields in Western Kenya	Kenya	Mafuta et al. (2022)

programs in African eggplant and obtained a commercial F1 hybrid cultivar called Kalenda from a crossing between *S. aethopicum* and *S. melongena*, which is resistant to bacterial wilt (BW) and has been introduced in French West Indies (Ano et al. 1991).

Mutation breeding involves inducing variations in coding and/or regulatory gene sequences in plant genomes to create new genetic variations. The limited access to BW-resistant genotypes suggested that mutation breeding is an alternative approach for screening biodiverse accessions to develop resistant genotypes (Jyothi and Santhosha. 2012). O’Herlihy et al. (2010) reported that bacterial wilt resistance in *S. lycopersicum* mutants improved by 10–80% compared to that in the control. In the same study, however, screening of potato mutant populations for resistance to bacterial wilt using a pathogenicity test was inconclusive. However, variations

in response were observed, suggesting the potential effects of mutagen dose rates and variety reactions (Chepkoech et al. 2020). Peiris et al. (2008) successfully developed the bacterial wilt-resistant variety ‘M 127’ using mutation breeding. However, it is crucial to address issues such as the stability of the selected resistant genotypes in hot and humid climates and their suitability for target agroecological regions.

Progress in molecular and biotechnology approaches

QTLs and molecular markers in global Solanaceae crops

Many studies have focused on the development of molecular markers for marker-assisted breeding to develop varieties resistant to bacterial wilt in

Table 4 Genes or markers identified among common QTLs for bacterial wilt resistance in major cultivated Solanaceae crops

Species	Bw markers or genes/QTLs	Phylotypes/biovar	Methods of detection	References
<i>Solanum tuberosum</i>	Rbw6-1, Rbw6-2/ PBWR-6b	I/biovar 3	QTL analysis	Habe et al. (2023)
	solcap_snp_c2_50637/ PBWR-3	I/biovar 4	QTLs analysis	Habe and Miyatake (2022)
<i>Solanum melongena</i>	ERPR6, ERPR9, ERPR3, I RE-bw, EBWR2, ER _{S1} , 2 other genes	I	Linkage map, QTLs analysis and associa- tion markers analysis	N’Guessan et al. (2012), Lebeau et al. (2013), Peeters et al. (2013a, b), Xi’ou et al. (2015), Salgon et al. (2017)
<i>Solanum lycopersicum</i>	Rs-762	–	Linkage analysis	Bi-hao et al. (2009)
	Solyc03g114600.4.1 (Asc)/Bwr3	I and II	Variant calling and Molecular marker development	Barchenger et al. (2022)
	RsR6-5 and RsR12-1/ Bwr6 and Bwr12	I and II	Sequence analysis and marker development	Abebe et al. (2020)
	SLA801053/Bwr-4, SLA781759/Bwr-12, SLA785401/Bwr-1, SLA771573/Bwr-9, SLA815542/Bwr-6	–	Genome wide associa- tion	Nguyen et al. (2021)
<i>Capsicum annum</i>	CAMS 451/Bw1	I (former race 1, biovar 4)	QTLs mapping	Mimura et al. (2009), Nar- esh et al. (2018), Sood et al. (2023)
	CA01g18650, CA01g20130, CA01g20110, CA01g20140/pBWR-1	I	Linkage Map Construc- tion, QTLs analysis and Candidate genes prediction	Chae et al. (2022)
	EcoACT+Mse CAC	–	Bulked segregant analysis	Naresh et al. (2018), Thakur et al. (2014)

Solanaceae crops (Table 4). Wang et al. (2013) identified two key quantitative trait loci (QTLs), namely, Bwr-6 on chromosome 6 and Bwr-12 on chromosome 12, associated with bacterial wilt resistance in the tomato inbred line 'Hawaii7996'. Their findings also showed that Bwr-12 was effective against phylotype I, and Bwr-6 was associated with resistance to race 1-phylotype I and race 3-phylotype II strains. However, the effectiveness of the combination of Bwr-12 and Bwr-6 on a given RSSC strain or on coinfecting strains has yet to be elucidated. A trade-off was observed between fruit size and those loci in the 1990s and was later broken in the early 2000s. To further elucidate the underlying mechanisms of Bwr-6 and Bwr-12 QTLs, a set of six cleaved amplified polymorphic site (CAPS) markers, along with derived CAPS (dCAPS) markers, were developed within the genomic region associated with resistance. Then, two markers, RsR6-5 on chromosome 6 and RsR12-1 on chromosome 12, were selected based on genotypic and phenotypic analysis to effectively distinguish resistant and susceptible cultivars (Abebe et al. 2020). In addition, Shin et al. (2020) found a total of seven QTLs associated with BW resistance to race 1-phylotype I and/or race 3-phylotype II strains located on chromosomes 6 (Bwr-6.1, 6.2, 6.3, and 6.4) and 12 (Bwr-12.1, Bwr-12.2, and Bwr-12.3). Previous studies have shown cases in which the marker–trait associations were weak due to the distance between the markers and the resistance genes, reducing their effectiveness for MAS (Perez-de-Castro et al. 2012; Nguyen et al. 2021). A genome-wide association study (GWAS) conducted on a core collection of 191 tomato accessions detected eight markers–trait associations (MTAs) for bacterial wilt resistance on chromosomes 4 and 12 corresponding to QTLs Bwr-4 and Bwr-12 (Nguyen et al. 2021). Furthermore, multilocation testing confirmed QTLs on chromosomes 1, 4, 6 and 12, with four environment-specific QTLs on chromosomes 1 and 8–10. Previously, the same QTLs were detected in Hawaii7996, with putative QTLs on chromosomes 8 and 10 (Thoquet et al. 1996). Multiple QTLs associated with BW resistance indicate that resistance is polygenic (Thoquet et al. 1996). Barchenger et al. (2022) identified candidate genes contributing to resistance beyond Bwr-6 and Bwr-12. The results revealed a sequence variant previously identified as Bwr3 on chromosome 3 that was captured by the marker Bwr3.2dCAPS, which is located in the

Asc (Soly03g114600.4.1) gene and has a significant association with resistance. However, this finding did not completely explain the resistance phenotype. In pepper, six QTLs were mapped in a double haploid population derived from the cross *Capsicum annuum* var. Yolo Wonder × *Capsicum annuum* var. PM687 and a recombinant inbred line (RIL) population from the cross Yolo Wonder × CM334 (Lafortune et al. 2005; Mahbou-Somo-Toukam 2010). This suggests that BW resistance in pepper is also polygenic.

QTLs for bacterial wilt resistance have also been identified in several resistant potato lines. Bacterial wilt resistance genes in potato are quantitative, with additive, nonadditive, or epistatic effects and environment- and pathogen strain-specific responses (Chakrabarti et al. 1994; López and Biosca 2005). The first attempt at marker identification used a combination of seven RAPD primers in which three primers amplified the markers associated with BW resistance (Sallam et al. 2013). Successive QTL analyses were performed and identified five QTLs (qBWR-1 to -5) on chromosomes 1, 3, 7, 10, and 11 using a dense linkage map comprising 4193 SNPs obtained from a bi-parental cross between the resistant diploid potato clone 10-03-30 and the susceptible diploid clone F-1-1 (Habe and Miyatake 2022; Habe et al. 2023, 2019). Subsequently, composite interval mapping was performed using resistant and susceptible parents of the potato species *Solanum phureja*, *Solanum chacoense*, and *Solanum tuberosum*, and five major and five minor resistance QTLs on chromosomes 1, 3, 5, 6, 7, 10, and 11 were identified. The major QTLs (PBWR-3 and PBWR-7) conferred stable resistance against phylotype I and IV strains, whereas PBWR-6b was strain-specific against phylotype I/biovar 3 and was more effective in cold environments. Another study compared the nucleotide sequences of one of the candidate genes located within the QTL region of PBWR-6b between the susceptible and resistant parents used for the previous QTL analysis, resulting in an allele-specific molecular marker (Rbw6-1) for PBWR-6b.

Significant effort has been made to map BW-resistance genes or QTLs in eggplant (Fukuoka et al. 2010; Nunome et al. 1998). Nunome et al. (1998) identified two QTLs associated with BW resistance in eggplant in an intraspecific F2 population of *Solanum melongena* derived from a cross between the Indian BW-resistant accession WCGR112-8 and the breeding

line EPL1. Bulk segregant analysis (BSA) was also used to develop a SCAR marker named Rs-762 (S401, 762 bp), which is linked to a single dominant BW resistance gene from the Chinese accession E31 (Bi-hao et al. 2009). Bulk segregant analysis is widely used to rapidly discover marker–trait associations for traits conferred by a single gene or a few genes. The primary benefit of using BSA compared to traditional QTL analysis is the reduced workload for genotyping within a segregating population. Instead, the approach involves grouping plants based on extreme phenotypes of a specific trait (*e.g.*, resistance and susceptibility to a disease) and extracting DNA from bulks of resistant and susceptible genotypes. This significantly reduces the workload for genotyping, as only two DNA pools are genotyped.

Genetic engineering, transcriptomics, metabolomics, and effectoromics analysis

Genetic engineering for crop improvement involves the use of gene transfer methods to insert genes of interest into a plant. These methods use vectors and agrobacterium-mediated or other methods to bring the vector into the host plant. A powerful genetic engineering tool is RNA interference (RNAi), which uses genetic transformation to stimulate the host system against specific double-stranded cellular or viral RNAs. This mechanism involves the generation of small noncoding RNAs such as microRNAs (miRNAs) and small interfering RNAs (siRNAs), which interfere with target mRNA translation and repress gene expression (Kiran and Abdin 2022).

AtEFR is a resistance gene of *Arabidopsis thaliana* that increases resistance to bacterial pathogens (Boschi et al. 2017). Specifically, AtEFR expression in tomato (*S. lycopersicum* variety Moneymaker) confers resistance to *R. solanacearum* (Lacombe et al. 2010). Specifically, for BW resistance, Kunwar et al. (2018) conducted field trials to evaluate the resistance of transgenic tomato lines expressing the EFR and Bs2 genes to bacterial wilt. Compared with those in the other lines, the expression of EFR or Bs2/EFR in the lines significantly reduced the incidence of bacterial wilt and increased the total yield under BW pressure. Furthermore, transgenic potato lines expressing AtEFR-Tu exhibited improved resistance to bacterial wilt. The transgenic expression of AtEFR-Tu in the

lines had a significant additive effect on the resistance QTLs. As a result, the authors suggested that combining the heterologous expression of AtEFR with quantitative resistance introgressed from wild relatives is a promising strategy for developing bacterial wilt resistance in potato (Bostick et al. 2004).

In contrast, overexpression of the NAC family transcription factor SmNAC reduced BW resistance in transgenic eggplant lines through reduced accumulation of salicylic acid (SA) and reduced expression of ICS1 (encoding isochorismate synthase 1, involved in SA biosynthesis), demonstrating that low SA biosynthesis plays a role in BW resistance (Na et al. 2016). The same results were obtained for transgenic potato lines expressing the AP1, Cecropin B, and Shiva genes (Jia et al. 1993; Xuping et al. 1996).

RNAi technology has also been applied to obtain transgenic lines that exhibit a high degree of resistance to bacterial wilt by targeting the RNA transcript of the PAP2 gene, which is responsible for plant wilting via the accumulation of reactive oxygen species/hypersensitive response (Lavale et al. 2022a). RNAi transgenic lines targeting the PAP2 gene showed reduced PAP2 expression, leading to increased expression of the jasmonic acid marker gene PR-4 and decreased expression of the salicylic acid marker gene PR1, resulting in resistance (Chakrabarti et al. 2019). It is worth noting that these findings are proof that genetic engineering could be used to develop BW-resistant crop varieties, but there have not been any commercialized BW-resistant varieties resulting from this technology. For instance, virus-induced gene silencing (VIGS) has been used to understand the role of the NLRs SIADR1 and SINRG1, the key nodes of effector-triggered immunity (ETI) pathways, in the resistance of Hawaii7996 to bacterial wilt (Xu et al. 2023). However, to date, no reports on CRISPR approaches for enhancing bacterial resistance in Solanaceae plants have been reported.

Understanding the molecular mechanisms of pathogen-plant interactions through omics is important to design better disease management strategies. To date, several studies, known as in planta transcriptomics, have analyzed the transcriptome of *Ralstonia* strains in plant tissues during pathogenesis. In planta transcriptomic studies revealed many pathways involved in plant infection, including genes in the scrABY cluster, which are components of the bacterial sucrose uptake and catabolism pathway. The presence of

sucrose in tomato xylem fluid and the dependence of *R. solanacearum* strains on sucrose in infected plants are important factors for virulence. In contrast, lines with low sucrose levels could generate wilt-resistant crops (Jacobs et al. 2013). A detailed investigation revealed that the overexpression of other genes, such as TSRF1, Ferredoxin-I, and Xa21, successfully improved resistance to BW in tomato plants. The transcriptome and metabolome data of eggplants after *R. solanacearum* infection revealed 2,896 DEGs and 63 metabolite differences. Further analysis revealed that the biosynthesis pathways for phytohormones, phenylpropanoids, and flavonoids were altered after inoculation. The results also revealed seven resistance genes and 24 genes involved in the jasmonic acid signaling pathway in the defense response of eggplant to bacterial wilt (Xiao et al. 2023). Transcriptome analysis of plant roots in response to *R. solanacearum* in wild potato (*S. commersonii*) using RNA-seq identified 221 and 644 DEGs in *S. commersonii* accessions resistant (F118) and susceptible (F97) to the pathogen, respectively. In pepper, gene expression analysis revealed 115 resistance-specific (R-response) and 109 susceptibility-specific (S-response) DEGs in the root system. R-responsive genes were associated with xyloglucan biosynthesis and cell wall organization, while S-responsive genes were related to stress response and cell death. Genes that play vital roles in cell wall restructuring and reinforcement were found to restrict bacterial movement in xylem vessels (Hwang et al. 2011). Dual RNA-seq technology revealed changes in the transcriptomes of the susceptible chili pepper line CM334 and the pathogen *R. solanacearum* strain Rs-SY1. The hypocotyls of pepper plants showed differentially expressed genes (PDEGs), reflecting the suppression of photosynthesis, the induction of ethylene production, the down-regulation of polysaccharide metabolism, and the weakening of cell wall defenses by *R. solanacearum* for successful infection. Pathogen-specific differentially expressed genes (RDEGs) in *Ralstonia* were also detected, showing enhanced starch and sucrose metabolism and upregulation of virulence factors (Du et al. 2022).

Recent metabolomics experiments identified 41 metabolites involved in resistance against BW in tomatoes. The metabolites of the phenylpropanoid pathway accumulate rapidly in infected roots of tobacco (Shi et al. 2022), and other metabolites,

including flavonoids, hydroxycinnamic acids, putrescine, dopamine, the auxin pathway, and tyramine derivatives, are also found in the root, stem, and leaf tissues of tomato and pepper plants (Lavale et al. 2022b; Zeiss et al. 2019). Further analyses revealed flavonoids in root tissues and hydroxycinnamic acids in leaf and stem tissues as primary metabolites from the phenylpropanoid pathway in tomato defense against bacterial wilt (Zeiss et al. 2019). The metabolic response was also reoriented to the phenylpropanoid pathway and its subbranches in tomato plants infected by bacteria after pretreatment with csp22. It elicited increased resistance to *R. solanacearum* infection (Zeiss et al. 2022). RSSC infection enriches xylem sap with 22 different metabolites, including putrescine and trehalose, which promote bacterial colonization of plant vessels (French et al. 2018; Lowe-Power 2017; Zeiss et al. 2018, 2019). However, Murti et al. (2021) recently reported that leucine and valine in leaf tissues are significantly distinguishable metabolites between the resistant cultivars Permata and Hawaii7996 and the susceptible cultivar GM2 in tomato. Identifying higher metabolite levels in Solanaceae crops after *Ralstonia* spp. infection and linking them with resistance resulted in noteworthy findings. These metabolites could create an avenue for developing new varieties with enhanced resistance to bacterial wilt through direct selection of lines with naturally higher levels of these metabolites. These lines could be crossbred with elite cultivars to transfer resistance through marker-assisted selection. However, it is paramount to characterize the identified metabolites and validate their roles and candidate genes because of their accumulation in gene expression studies, metabolic pathway analysis, and virulence validation in controlled and field experiments.

Effectoromics is a specialized omics field in which high-throughput functional screening of germplasm effectors is used to accelerate and improve the exploitation of resistance genes such as nucleotide-binding leucine-rich repeat (NLR) resistance genes (Du and Vleeshouwers 2017). It has contributed to classical resistance breeding and genetically modified approaches and has shown effectiveness; hence, it is referred to as “effector-assisted breeding” (Vleeshouwers and Oliver 2014). *Ralstonia* spp. pathogen-associated molecular patterns (PAMPs) and effector proteins are secreted into plant cells, where they activate and suppress

plant immunity, thereby affecting susceptible plants. Approximately twelve family of effectors plus one family of candidate effectors have been reported to trigger hypersensitive reactions (HRs) in common Solanaceae cultivated crops from Africa's strains (Table S3). The effector proteins of RSSC are under strong and diverse positive selection and contribute to bacterial pathogenicity and dampening plant defense responses (Peeters et al. 2013b; Deslandes and Genin 2014). The accessibility and advances of high-throughput sequencing technologies have allowed the sequencing of eleven RSSC strains spanning four existing phlotypes and enabled the identification of the bacterial effector repertoire (Peeters et al. 2013a, b). These core effectors are presumed to be ancestral and pivotal for interactions between *R. solanacearum* and its hosts. Thus, effector-assisted breeding has also been instrumental in evaluating the potential of new resistance genes for broad and long-lasting protection. This involves testing the ability of resistance genes to recognize different effector variants within a pathogen population (Vleeshouwers and Oliver 2014). Recent effectoromics studies investigated the T3E repertoires of twelve plants pathogenic *Ralstonia* strains, representing 12 strains spread throughout

all the phlotypes of the RSSC complex. This generated a pangenome repertoire to construct a comprehensive database of type III effectors (T3Es) and identified new allelic versions of specific T3Es (102 T3Es and 16 hypothetical T3Es) (Sabbagh et al. 2019). Considering the considerable genetic diversity within *Ralstonia* spp., optimizing effectomics could involve focusing on bacterial strains and plant germplasms coevolving in the same geographic region. Although the aforementioned studies tried to connect T3E diversity to the host specificity of RSSC strains and could identify some host specificity determinants, the power of such studies has usually been largely limited by the lack of exhaustive strain host range empirical data (Landry et al. 2020). In this review, we also compared T3Es among four isolated hosts (tomato, eggplant, potato, and black nightshade), as shown in Fig. 4, using curated African-sequenced strains from the worldwide database of complete genome sequences of *Ralstonia* spp. (Sabbagh et al. 2019). Ninety-four genes (86 T3Es and eight putative T3Es) were associated with virulence (Table S3), mainly in eggplant (83 genes), tomato (68 genes), black nightshade (66 genes), and potato (39 genes).

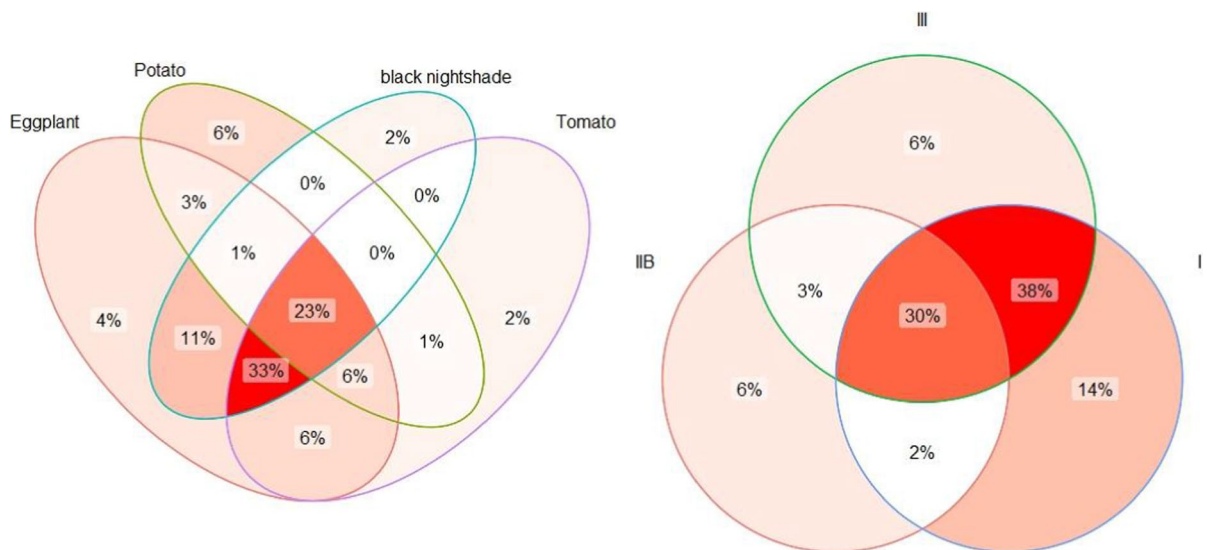


Fig. 4 Venn diagram depicting conserved T3Es among different phlotypes of five sequenced African strains (Burkina-Faso, Cote d'Ivoire, Cameroon and Egypt) and different Solanaceae hosts from which they were isolated; Comparison

of conserved T3Es between phlotypes I, III and IIB (right); Comparison of conserved T3Es between black nightshade and other widely cultivated Solanaceae crops (left). (Color figure online)

Lessons learned from BW resistance research on major solanaceous crops and perspectives for improving resistance of traditional vegetables to bacterial wilt: a case study of *Solanum macrocarpon*

The BW-borne crop system is intricate, but several observations and implications arise from studies conducted on Solanaceae crops and are conclusive for breeding BW-TAV-resistant varieties. Successful breeding for BW resistance in TAV might rely on the following points:

Germplasm and biodiversity

Germplasm conservation and increased access to biodiversity, including mostly crop wild relatives, have proven their fundamental importance in enhancing bacterial wilt resistance in solanaceous crops through screening and crossbreeding. For instance, access to wild relatives was important for finding resistant sources in tomato (*S. pimpinellifolium* PI 127805A), and several wild eggplant species have exhibited consistent and reliable resistance to BW. Moreover, several accessions of *Solanum macrocarpon* and *Solanum aethiopicum*, two largely consumed traditional vegetables in West and East Africa, have been tested under different combinations of scion and rootstock eggplant, and two of these accessions were reported to be resistant to bacterial wilt caused by RSSC (Musa et al. 2021).

The information gathered from TAV collections is provided through platforms such as Genesys (<https://www.genesys-pgr.org/welcome>), an international resource providing information on genebank collections worldwide. The World Vegetable Center is a key institution for the conservation of vegetable germplasm and holds in trust the largest public sector vegetable collection of approximately 61,000 active accessions (<https://genebank.worldveg.org/>). For instance, more than 300 accessions of *Solanum macrocarpon* from Africa are available at the World Vegetable Center and could be exploited to conduct a systematic screening with known RSSC strains

under controlled conditions to reveal BW-resistant material for research and breeding.

Understanding pathogen diversity

Insight into pathogen diversity is essential for accessing the right RSSC strains for resistance screening. A better understanding of the diversity and distribution of BW would help identify crops at risk, identify disease hotspots, and determine the most virulent strains. Evaluations of pathogens should include an assessment of their biochemical and molecular characteristics, host range, and pathogenicity under various environmental conditions.

Germplasm screening

Efficient screening of core collections could be achieved through inoculation under controlled conditions with known RSSC pathotypes using fast-tracking screening methods to identify narrow and broad resistance and enable pyramiding of R genes. A variety of screening methods have been developed for vegetables worldwide, and these methods can be used or refined, if necessary, for screening large germplasm collections. The collection of germplasms from regions where the disease is prevalent and their characterization can help to identify new sources of resistance. There is currently scarce information on BW resistance screening of TAV, although some sources of tolerance have been identified for *Solanum macrocarpon* and *Solanum nigrum* complex (Oussou et al. 2020; Mafuta 2022). Some TAV could also benefit as rootstocks for bacterial wilt resistance in common crops such as eggplant and tomato.

R gene identification and integration of omics and gene engineering

The collection of BW-resistant lines after germplasm screening can further reveal which R gene(s) are needed for our varieties based on the strains highly infecting the region. At this stage, prebreeding and backcrossing or gene pyramiding are essential activities for the creation of high-yielding BW-resistant varieties. Hence, the use of omics and gene

engineering can play an intermediary role in BW-breeding of TAV. Although limited literature is available, since 2015, approximately eight TAV have been fully sequenced, and their draft genomes are available (Kamenya et al. 2021), facilitating the development of a dense genome-wide molecular marker set. Moreover, other TAV, including *A. blitum*, *A. cruentus*, *A. tricolor*, *Basella alba*, *Brassica carinata*, *Celosia argentea*, *Corchorus olitorius*, *Crassocephalum rubens*, *Moringa oleifera*, *Solanum scabrum*, and *Talinum fruticosum*, are on the agenda of the African Orphan Crops Consortium (AOOC) (Sogbohossou 2019).

Global market-oriented breeding

TAV usually have a localized market, but through value addition, their market can be considerably

expanded. Breeding competitive TAV varieties requires an in-depth understanding of current and future clients' (seed producers, farmers, processors, consumers) needs. This information is essential for defining market segments and target product profiles to prioritize investments and guide decision-making in breeding programs. This approach is routinely used to develop global vegetable varieties. Market segmentation, along with target product profiles, can be used to attract funding to TAV breeding programs, which are currently underfunded.

The prospects of bacterial wilt resistance breeding in TAV are promising, as evidenced by the success achieved in developing resistant cultivars using traditional breeding methods and molecular tools on significant vegetable crops. However, some challenges are still associated with the use of molecular breeding techniques, such as limited genomic resources, the complex genetic architecture of bacterial wilt

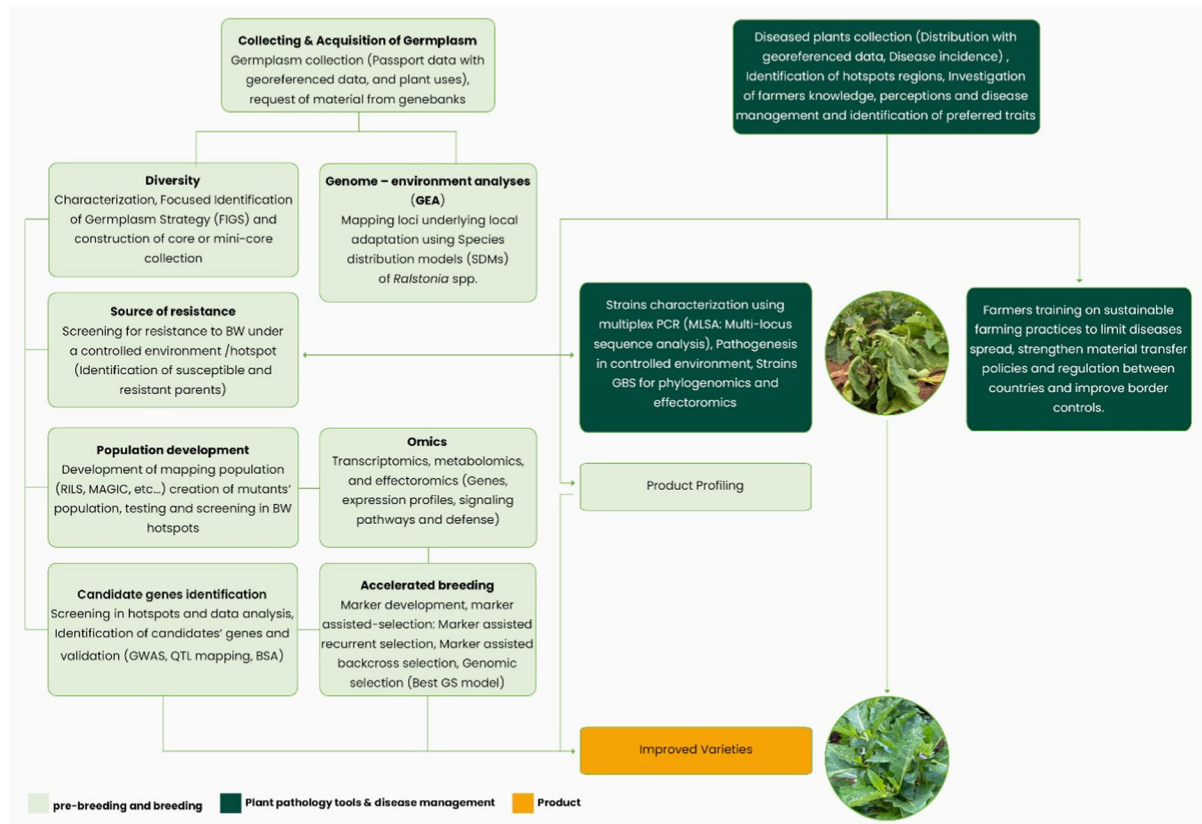


Fig. 5 Schematic map of an integrated breeding program for developing bacterial wilt-resistant varieties of Gboma eggplant (*Solanum macrocarpon* L.)

resistance, and a lack of understanding of host–interactions. To elaborate a comprehensive action plan that integrates conventional breeding strategies and quantitative genomics breeding for resistance to bacterial wilt in TAV, we used Gboma eggplant (*Solanum macrocarpon*) as a case study. Details of the action plan are illustrated in Fig. 5.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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