A Meta-analysis of the known Global Distribution and Host Range of the *Ralstonia* Species Complex

Tiffany Lowe-Power*, Jason Avalos, Yali Bai, Maria Charco Munoz, Kyle Chipman, Cloe E. Tom, and Darrielle Williams

University of California Davis

Abstract

The *Ralstonia* species complex is a group of genetically diverse plant wilt pathogens. Our goal is to create a database that contains the reported global distribution and host range of *Ralstonia* clades (e.g. phylotypes and sequevars). In this fourth release, we have cataloged information from 197 sources that report one or more *Ralstonia* strains isolated from 105 geographic regions. Metadata for nearly 8,000 strains are available as a supplemental table. The aggregated data suggest that the pandemic brown rot lineage (IIB-1) is the most widely dispersed lineage, and the phylotype I and IIB-4 lineages have the broadest natural host range. Although Phylotype III is largely restricted to Africa, several studies report that these strains have been introduced into the Americas (the Caribbean and South America). Similarly, although Phylotype IV is mostly found in East and Southeast Asia, phylotype IV strains are reported to be present in Eastern Africa.

Additionally, we have created an open science resource for phylogenomics of the RSSC. We associated strain metadata (host of isolation, location of isolation, and clade) with over 250 genomes in a public KBase Narrative. Our colleagues can use this narrative to identify the phylogenetic position of newly sequenced strains.

* Corresponding author: tlowepower@ucdavis.edu

Introduction

Bacterial pathogens in the *Ralstonia* species complex are xylem pathogens that infect a broad range of agricultural and natural plant hosts. *Ralstonia* strains clog plant xylem vessels, leading plant hosts to wilt [1]. Historically, *Ralstonia* strains were classified based on carbon utilization patterns ("Biovar") and host range ("Race"). However, DNA sequence-based taxonomies more accurately reflect the evolutionary trajectories of *Ralstonia* lineages.

Currently, the *Ralstonia solanacearum* species complex (RSSC) is classified into three species: *R. solanacearum*, *R. pseudosolanacearum*, and *R. syzygii*. The separation of *Ralstonia* into three species was first proposed by Remenant *et al.* 2010 [2], formalized by Safni *et al.* 2014 [3], and reinforced by Prior *et al.* 2016 [4]. Strains are also classified into a phylotype system, which overlaps with the species boundaries. All *R. solanacearum* strains are within phylotype II, but phylotype II is divided into IIA, IIB, and IIC groups. *R. pseudosolanacearum* strains are either in phylotype I or phylotype III. *R. syzygii* strains are in phylotype IV. Strains are further sub-classified into sequence variants, or "sequevars", based on the DNA sequence of the conserved *egl* endoglucanase gene (Fig 1). Because *Ralstonia* are known to be naturally competent, we hypothesized that horizontal gene transfer of *egl* could confound sequevar-based phylogenies. We recently use whole genome phylogenetic trees to interrogate the robustness of *egl*-based trees [5]. We found that *egl* trees work well for phylotype II, but *egl* trees are highly inaccurate for phylotype I. Although only a small number of phylotype III and IV genomes were analyzed, the longer branch lengths in phylotype III and IV suggests that sequevars/*egl*-based trees may provide effective estimation of these strains' phylogenetic position. Since the phylotype-sequevar system was first developed and described by Prior and Fegan in 2005 [6], hundreds of papers have used this system to describe the genetic diversity of *Ralstonia* isolates around the world. However, there has not been any public database that aggregates this population genetics information.

The *Ralstonia* community typically states that *Ralstonia* strains infect over 250 plant species in over 50 botanical families. Is that an under-estimation? Our goal is to perform a meta-analysis that documents the known host range and global distribution of each sequevar in the *Ralstonia* species complex. We intend to update this preprint and the associated GitHub repository at regular intervals as we populate the database. In version 4 of the database (this update), we also establish a user-friendly KBase narrative[7] that allows users to place new *Ralstonia* genomes within the phylogenomic context of public genome sequences.

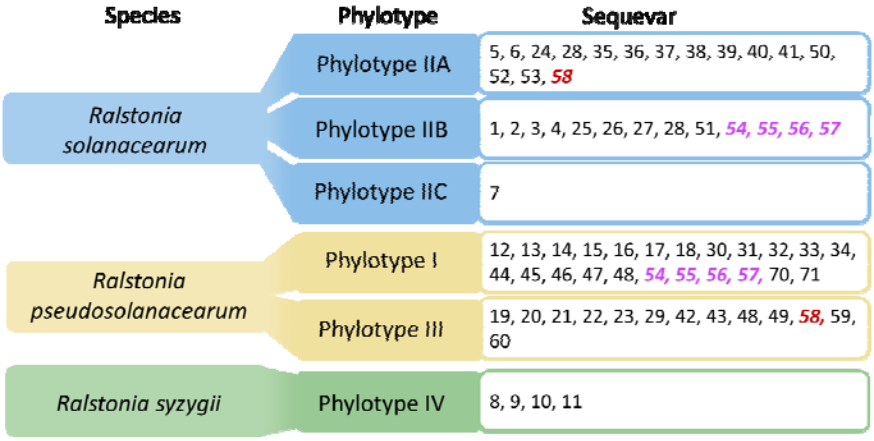

Fig 1. Taxonomic classification of the *Ralstonia* species complex at the species, phylotype and sequevar levels. Sequevars highlighted in red or purple italics are assigned to strains in conflicting phylotypes. As a note, many of the phylotype I sequevars are polyphyletic (See Sharma et al 2022 for details [5]), so the *Ralstonia* community needs to identify a cost-effective alternative for describing diversity of these strains. The clonal lineage that cause Blood Disease of Banana (BDB) are nested within phyl. IV-10 with non BDB phyl. IV strains.

Methods

Article Selection Criteria and Search Strategy:

We prioritized articles that used the phylotype and/or phylotype-sequevar system to characterize strains. We identified these articles by using Google Scholar to find the papers and theses that cite "How complex is the *Ralstonia solanacearum* species complex?" by Fegan and Prior 2005 [6]. We did not include the Race or Biovar information in the database. Although host range is an important trait of strains, measuring multi-host virulence is labor and time-intensive, and has rarely been performed. Therefore "race" assignments are usually listed solely based off of the host-of-isolation, which does not accurately predict the strains' host range. We also excluded biovar data because the carbon utilization patterns are not predictive of phylogeny or the most important phenotypes for *Ralstonia*.

To get a better estimate of the diversity of potential hosts for Ralstonia, we did a search of the literature using search terms like "weeds", "host range", and older names for the pathogen (*Pseudomonas solanacearum*, *Burkholderia solanacearum*).

Table 2: List of Papers in this Study

Year Published	References
1971	[8,9]
1976	[10]
1978	[11]
1980	[12]
1984	[13]
1986	[14–24]
1993	[25–37]
1995	[38]
1998	[39–48]
1999	[49–51]
2001	[52–55]
2003	[56–58]
2004	[59]
2006	[60,61]
2007	[62–71]
2008	[72–76]
2009	[77–84]
2010	[85–90]
2011	[91–99]
2012	[100–103]
2013	[104–113]
2014	[3,35,114–124]
2015	[125–139]
2016	[4,140–143]
2017	[144–155]
2018	[156–166]
2019	[167–171]
2020	[83,172–188]

2021	[189–193]
2022	[194–198]

Converting strain metadata into a structured format for data science:

We focused on cataloging information that is relevant to the epidemiology of the *Ralstonia* strains: Phylogenetic position, host of isolation, and geographic location where isolated. Additionally, when listed, we include any NCBI accessions for the genome, *egl* marker genes, or other genes.

For **phylogeny**, we record the phylotype (I-IV), sub-phylotype (for phylotype II, this is the IIA, IIB, or IIC subdivision), and sequevar (1-71). Several sequevars have been subdivided based on phylogeny and/or ecologically important traits, so we created a "sub-sequevar" column to denote these. This includes multiple subdivisions of sequevar IIB-4 and IV-10 sequevar which includes the "*R. syzygii* subspecies celebensis" (causes Blood disease of banana) and a clade of the paraphyletic "*R. syzygii* subspecies indonesiensis".

For **host**, we created several columns to annotate the host at multiple taxonomic scales (order to species). We attempted to systematize all common names and species to a unified label. For example, all potato isolates are listed as "Solanum tuberosum (Potato)". The systematic structure will make it easier to use R, python Pandas, or Excel equations to summarize and visualize the contents of the database.

For **location**, we record the most precise location information available (e.g. city, province, or country). We also have columns that describe the location at the country (or territory if the land region is geographically separated from the governing body), subcontinent, and continent levels.

Database:

The full dataset is available as a supplementary table on this preprint.

Table 2: Summary of the database

Database Release Date	# Papers	Paper published range	# Strains	# Sequevars[b]	# Countries or Territories	# Host plants
2020/07/03	35	2017-2020	1625	57	50	56
2021/03/23	73	2012-2020	3395	over 64[a]	86	124
2021/11/03	93	2007-2020	4924	Over 71	86	139
2022/08/30	197	1971-2022	7794	68[b]	105	392

[a] *As of this release, we have not investigated the sequevar assignment of strains classified into "unknown" or "new" sequevars.*

[B] *Note that sequevar is an imperfect phylogenetic system. See Sharma et al. 2022 for details* [189]

Extracting metadata for genomes available on NCBI.

Genomes on NCBI do not always have a corresponding Genome Announcement or other publication, but most of these genomes are deposited with ecological metadata on the corresponding "BioSample" page. The NCBI taxonomy is disorganized because of taxonomic revisions in this group. Many genomes for "*Ralstonia pseudosolanacearum*" (taxonomy ID: 1310165) and "*Ralstonia syzygii*" (taxonomy ID: 28097) were deposited as the "*Ralstonia solanacearum*" (taxonomy ID: 305), primarily because they were deposited prior to the renaming in 2014. Moreover, several genomes of the blood disease pathogen (*Ralstonia syzygii* subsp. *celebensis*) were deposited with their own taxonomy ID due to a peculiar taxonomic rule: these strains could not be formally named because the type strain was not viable in culture collections.

In July 2022, we extracted metadata for all RSSC genomes that we could identify in relevant "taxonomy IDs". For each genome, we listed the "RefSeq Assembly Accession" when possible (GCF_xxx). Some assemblies have been excluded from RefSeq due to problems like "too many frameshifted

proteins" or "highly fragmented genome". In this case, we list the GenBank Assembly Accession (GCA_xxx).

Importing genomes into the "RSSC Phylogenomics" narrative on KBase .

KBase is a user-friendly graphical user interface for biological informatics that is developed and maintained with significant investment from the US Department of Energy [194]. Because RSSC genomes are dispersed across several (often inaccurate) taxid pages, we developed a KBase Narrative that can help us and other scientists identify the phylogenetic identity of new RSSC genomes.

We used the structured data on our spreadsheet to assign a systematic name to each genome, such as: "IIB-4D_UW128_Plantain-Musaceae_SouthAmerica.genome". The systematic name lists:

1. Phylogenetic information (phylotype, sequevar, subsequevar)
2. Strain name (spaces and parentheses removed. Colons, underscores, and hyphens were often removed)
3. Host of isolation (common name and family)
4. Location (subcontinent)

Initially, there were genomes that lacked precise phylogenetic information. To identify the phylogenetic identity of these genomes, we used the KBase App "Batch Create GenomeSet v1.2.0" to create a GenomeSet object that included all genomes ending in ".genome". Then we used the "Insert Set of Genomes into SpeciesTree v2.2.0" to create a low-resolution phylogenetic tree. This app uses FastTree2 [199] with the -fastest setting to construct a tree based on an MSA of 49 core, universal bacterial genes. We inspected the tree, and we were able to assign many genomes to phylotypes and sequevars.

Results and Discussion

We compiled 7,794 strains from almost 200 sources. These strains represent over 68 sequevars isolated from 105 countries or territories (Table 2). Most of the reported strains are phylotype I or II strains (Fig. 2). The full dataset is included as Table S1, which should be accessible on this pre-print. For each strain, we recorded taxonomy (phylotype and sequevar), host (specific name and the host plant's taxonomic Family and Order), isolation year, isolation location, NCBI accessions (genome or partial sequences of *egl, mutS* and/or *rplB* market genes genes) and the citation.

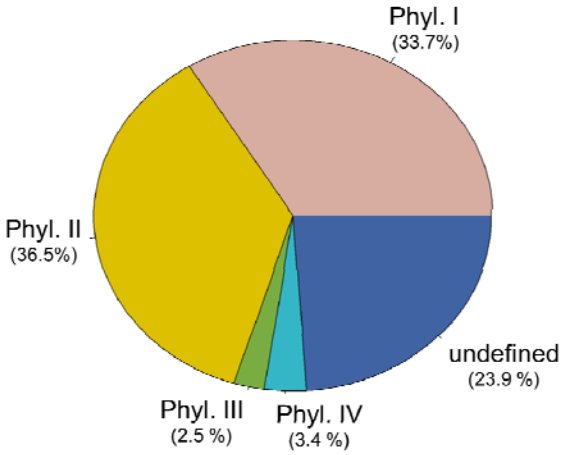

Fig 2. Phylotype assignments for strains in the Global Ralstonia Diversity database

We analyzed some of the host range and biogeographic distributions of the RSSC and phylotypes. You can find the full details in Table S1.

Host Range:

Tables 3-5 summarize information about host range in the RSSC and the phylotypes. Table 6 attempts to look at host range within more narrow clades.

Table 3: The number of unique plant hosts (reported at various taxonomic levels)

	Species	Genera	Family	Order
All RSSC	392	246	78	35
Phyl. I	95	79	46	28
Phyl. II	63	45	33	25
Phyl. III	16	8	7	7
Phyl. IV	7	5	3	3

Table 4: The top 21 most common host species to be listed in the database, sorted by frequency

Host Species	Frequency Reported	% of the total hosts reported
Solanum tuberosum	2295	32.0%
Solanum lycopersicum	1532	21.4%
Solanum melongena	448	6.2%
Capsicum annuum	437	6.1%
Musa acuminata	373	5.2%
Nicotiana tabacum	339	4.7%
Zingiber officinale	181	2.5%
Eucalyptus pellita	118	1.6%
Arachis hypogaea	92	1.3%
Solanum macrocarpon	84	1.2%
Musa paradisiaca	76	1.1%
Solanum dulcamara	54	0.8%
Epipremnum aureum	52	0.7%
Anthurium andraenum	40	0.6%
Syzygium aromaticum	39	0.5%
Cucurbita maxima	28	0.4%
Solanum nigrum	27	0.4%
Casuarina equisetifolia	26	0.4%
Vaccinium sect. Cyanococcus	24	0.3%
Morus alba	24	0.3%
Ipomoea batatas	22	0.3%

Table 5: Heatmap that attempts to answer the question: "If I have a wilted [plant species], what phylotype is most likely the culprit?

Host Species (Common name)	I	II	III	IV
Solanum tuberosum (Potato)	358	1390	91	147
Solanum lycopersicum (Tomato)	695	432	48	25
Solanum melongena (Eggplant)	323	26	7	0
Capsicum annuum (Pepper)	300	21	4	2
Musa acuminata (Banana)	3	217	0	53
Nicotiana tabacum (Tobacco)	240	33	5	1
Zingiber officinale (Ginger)	134	5	0	0
Eucalyptus pellita (Eucalyptus)	43	74	0	0
Arachis hypogaea (Peanut)	54	4	0	0
Solanum macrocarpon (Gboma/African eggplant)	77	0	6	0
Musa paradisiaca (Plantain)	0	67	0	0
Solanum dulcamara (Bittersweet nightshade)	0	52	0	0
Epipremnum aureum (Pothos)	0	17	0	0
Pelargonium sp. (Geranium)	10	20	9	0
Anthurium sp.	3	45	0	0
Anthurium andreanum (Flamingo flower/laceleaf)	5	35	0	0
Syzygium aromaticum (Clove)	1	2	0	33
Cucurbita maxima	26	0	0	0
Pelargonium sp. (Geranium)	10	20	9	0
Casuarina equisetifolia (Ironwood tree)	10	3	0	0
Vaccinium sect. Cyanococcus (Blueberry)	1	3	0	0
Morus alba (Mulberry)	19	0	0	0
Ipomoea batatas (Sweet Potato)	15	1	0	0

We investigated which clades of *Ralstonia* have been isolated from the most plant species. In previous versions of the database, we considered individual sequevars to be equally diverse clades. After working more extensively with RSSC diversity, we have realized that phylotype I is about as diverse as some phyl II, III, and IV sequevars (at the ANI level). Therefore, we analyzed the host range of all phylotype I strains collectively. Results are in Table 6.

As a significant caveat, *Ralstonia* host range can vary between strains that are closely related (i.e. in the same sequevar) [64,190,195,200]. Nevertheless, host range patterns often correlate with phylogeny [195,200]. Collectively, Phylotype I has a wide host range (123 plant species in 43 botanical families). Phylotype IIB-4 has the next broadest host range (48 species in 21 botanical families). Phylotype IIB-1 has been isolated from 20 plant species in 7 botanical families. However, IIB-1 is also the most widely dispersed lineage, so it has appeared in more population survey studies than other lineages. The IIB-1 lineage is most commonly isolated from Solanaceae and Geranium family plants.

Table 6: RSSC clades whose members have been isolated off of the most diverse plants. (Note, this was determined using the "Host species (Common Name)" column while Table 3 was determined using the "Host species" column, which lacks any plants that were only identified to the genus level.

Clade	plant species
phyl. I	123
phyl. IIB-4	48
phyl. IIB-1	20
phyl. III-48	11
phyl. IIB-3	9

Biogeography

Ralstonia strains have been isolated from over 100 countries (Fig. 3). Tables 7-8 summarize information about biogeography of the RSSC and the phylotypes. Table 9 attempts to look at distribution of more narrow clades.

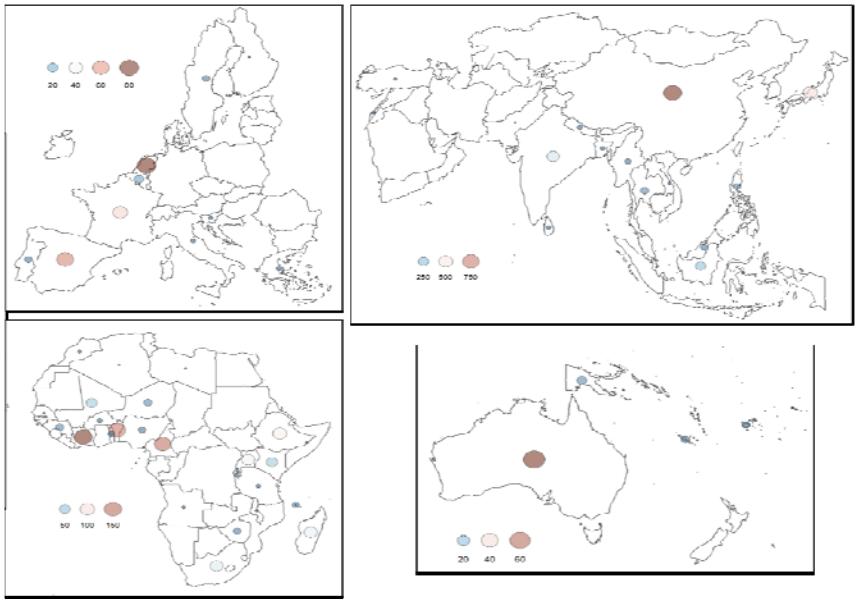

Fig. 3. Locations of strains included in the Global Ralstonia Database. Proportional circles in each country reflect the number of strains reported in the Global Ralstonia database, relative to other countries in the same continental group. The next update of the Global *Ralstonia* database will normalize the size of the circles across all countries and will show the abundance of *Ralstonia* in the Americas.

Table 7: Relative distribution of the RSSC and each phylotype, based on the number of unique countries where the strain has been isolated

		Unique Countries
	All RSSC	105
I	Phyl. I	51
II	Phyl. II	76
III	Phyl. III	19
IV	Phyl. IV	11

Table 8: Distribution of each phylotype level on different subcontinents. Red boxes indicate distributions that were unexpected.

	I	II	III	IV
Northern America		x		
Central America	x	x		
Southern America	x	x	x	
Caribbean	x	x	x	
Western Europe	x	x		
Southern Europe		x		
Northern Africa	x	x		
Western Africa	x	x	x	
Middle Africa	x	x	x	
Eastern Africa	x	x	x	x
Southern Africa	x	x		
Western Asia		x		
Southern Asia	x	x		x
Eastern Asia	x	x		x
South-Eastern Asia	x	x		x
Micronesia				
Melanesia	x			
Australia and New Zealand	x	x		x
Polynesia	x	x		

Pandemic Clades

We investigated which clades of *Ralstonia* have been isolated from the most countries. In previous versions of the database, we considered individual sequevars to be equally diverse clades. After working more extensively with RSSC diversity, we have realized that phylotype I is about as diverse as some phyl II, III, and IV sequevars (at the ANI level). Therefore, we analyzed the distribution of all phylotype I strains collectively. Results are in Table 9 and Table S1. Although phylotype I has a wide distribution (51 countries), the pandemic brown rot lineage (IIB-1) has been reported in more countries (58 countries). The next most widely dispersed clades are IIB-4, IIC-7, IIA-6, IIA-35, and IIB-3. Many of the widely dispersed clades are known to cause epidemics on crops (potato, banana, ginger) or ornamentals that are propagated vegetatively.

Table 9: Distribution of clades of *Ralstonia*

Clade	# countries
phyl. IIB-1	58
phyl. I	51
phyl. IIB-4	14
phyl. IIC-7	10
phyl. IIA-6	9
phyl. IIA-35	8
phyl. IIB-3	8
phyl. III-48	6
phyl. IIA-38	5
phyl. IIA-39	4
phyl. IIA-41	4

RSSC Phylogenomics narrative on KBase

We created two open KBase narratives that have 275 or 340 decent-to-high quality genomes labeled with a structured name that indicates their phylogenetic identity, strain name, host of isolation, subcontinent of isolation, and an NCBI accession number:

- Narrative 1 has the maximum diversity of available Ralstonia genomes (n=275), but only has 5 of the clonal IIB-1 genomes (a pandemic lineage). This narrative has some suggestions for how to navigate KBase https://narrative.KBase .us/narrative/123807
- Narrative 2 has all genomes with a RefSeq quality assembly available (n=340). https://narrative.KBase .us/narrative/124825 . Figure 4 shows the 340 strain tree.

Anyone can create a copy of these narratives, upload their own assembly to KBase, annotate the genes, and re-build the 49 gene phylogenetic tree to identify the position of new genomes. We will continue to update the narrative as we add genomes, so our colleagues should create a copy of the latest version of the narrative to assess new genomes. Narrative 1 is better suited for this purpose—removing 65 clonal genomes will allow the KBase applications to run faster.

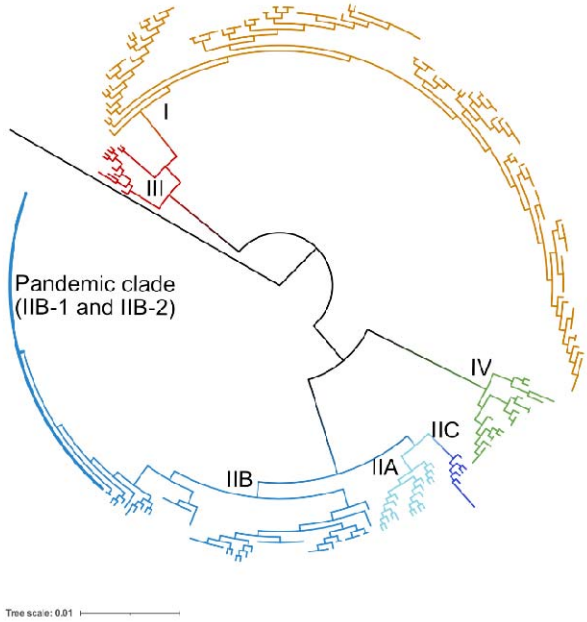

Fig 4. A phylogenetic tree of 340 RSSC strains. The outgroup is an *R. mannitolytica* genome. To create the stylized tree, the Newick format tree was downloaded from Narrative 2, stylized in iTol [201], and annotated in Affinity Designer. A high resolution version (PDF, PNG, or Newick format) can be downloaded from the KBase narrative.

We used the tree to curate the phylogenetic assignments of strains:

- One genome clustered in an unexpected position in the tree. Strain CRMRs218 was labeled a phylotype I strain in the original genome announcement [144], however, it clearly clusters with IIA strains. A search of Google Scholar indicates that many prior studies have drawn the same conclusion. We re-labeled this genome as a IIA strain.
- There was one strain (CIP120) that was called a "IIA-38" or a "IIA-50" sequevar strain in different references, but the whole-genome tree revealed that this strain is not closely related with three other IIA-38 strains (P597, RS489, and P816). So we assigned this strain to IIA-50.
- We assigned 21 genomes to phylotype I: B17_UW800, FJ1003, FJAT1303.F1, FJAT1452.F1, FJAT-1458, FJAT1463.F1, FJAT15244.F1, FJAT15252.F1, FJAT15304.F1, FJAT15340.F1, FJAT15353.F1, FJAT442.F1, FJAT445.F1, FJAT448.F1, FJAT454.F1, FJAT-91, KACC10709, MAFF241647, MAFF241648, MAFF311693, and P380. These genomes had all been deposited to the *R. pseudosolanacearum* taxid, which can correspond to phyl I or III strains.

- We assigned 1 genome to phylotype III: LMG9673. This genome had been deposited to the *R. pseudosolanacearum* taxid, which can correspond to phyl I or III strains.

- We assigned 1 genome to phylotype IIA: RS489. RS489 is closely related to the IIA-38 genomes P597 and P816, so we assigned it to sequevar 38.

- We assigned 3 genomes to phylotype IIB: NCPPB3985, RS488, RsT01. Of these, RsT01 is closely related to the IIB-4 genomes in the C/E subclades, so we assigned it to IIB-4 (C or E).

- We assigned 1 genome to phylotype IV (*R. syzygii* subsp. *syzygii*): LMG10661.

- We assigned 2 genomes to phylotype IV (*R. syzygii* subsp. *indonesiensis*): KACC10722, T12.

Assessing quality of genomes for downstream analyses

Not all genome assemblies are equal. Assemblies can suffer from many flaws. We did not import genomes that NCBI flagged as "many frameshifted proteins" (often due to being a Nanopore-only assembly), "fragmented assembly" (4700+ contigs, which suggests that the user uploaded only the coding sequences instead of the actual assembly)

For the assemblies imported into the KBase narrative, we used CheckM to assess their quality. CheckM yields estimates of the genomes' completeness (are all of the expected genes present in the genome assembly?) and contamination (are there multiple homologs of genes that should be present in a single copy, suggesting that an unrelated genome has contaminated the assembly?). For completeness, we set a cut-off of requiring genomes to have no more than 4 missing "single copy genes". This generally corresponds to a 99% complete cut-off. For contamination, we set a cut-off of 1%.

CheckM ran an error when processing eight genomes, so these could not be assessed. Based on the cut-offs, we classified 39 genomes as low-quality (24 genomes for low completeness and 15 genomes for high contamination). All of the draft genomes from Ailloud et al. 2015 have low completeness, likely because they were assembled from very short Illumina reads (2×50-nt paired). These genomes are estimated at 96-98% complete, which means the assemblies could be missing upwards of 200 genes. Two additional genomes have very low completeness: phyl. IIA-38 genome P816 was 81% complete and phyl. I genome VT0801 is 91% complete. After filtering for quality, there are only four phylotype IIA high quality genomes available, making this the least represented major branch of *Ralstonia* diversity.

Conclusion

Bacterial wilt pathogens in the *Ralstonia* species complex are high impact global pathogens. We created a strain database that we will regularly update to document the distribution and host range of *Ralstonia*.

Acknowledgements

We thank all of our colleagues who have carried out diversity surveys for *Ralstonia*. We thank Darrell Sparks for his contributions to the database.

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