Phylogenetic and phenotypic analysis of five subgroups of Ralstonia solanacearum phylotype IIB sequevar 4 reveals that the "not pathogenic to banana (NPB)" ecotype is polyphyletic.

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Abstract

The bacterial wilt pathogens in the *Ralstonia solanacearum* species complex (RSSC) have broad but finite host ranges. Population genetic surveys of RSSC pathogens show that many sequevars (subspecies groups) are predominantly recovered from wilting solanaceous plants. In contrast, strains in the IIB-4 sequevar have been isolated from plants in over a dozen families. We characterized the natural variation in host range of nineteen IIB-4 strains to explore the molecular determinants of host range within the RSSC. We used Illumina sequencing to assemble draft genomes of 12 strains. Based on whole genome phylogenetic analysis, these IIB-4 strains cluster into five subclades. We quantified virulence of each strain on tomato cv. Moneymaker (Solanaceae), banana cv. Dwarf Cavendish (Musaceae), melon cv. Sweet Granite (Cucurbitaceae), and impatiens cv. Beacon Orange (Balsaminaceae). To enable future meta-analyses that identify genetic factors that drive host-range, the raw virulence data is included as a supplemental table. Overall, the virulence patterns correlated with phylogeny. Strains from Martinique, Dominican Republic, Brazil, as well as multiple strains imported into Florida were highly virulent on tomato, melon, and impatiens. Several strains from Peru were highly virulent on tomato and had moderate-to-low virulence on banana, melon, and impatiens. One strain from Colombia was highly virulent on all hosts. Our findings reinforce the phenotypic plasticity within the *Ralstonia solanacearum* species complex.

Introduction

The *Ralstonia solanacearum* species complex is a group of related tropical and temperate pathogens that cause plant wilt diseases after they invade and colonize the xylem [1, 2]. Collectively, the species complex has a remarkably broad host range, capable of infecting hundreds of host species in dozens of taxonomic families [3, 4]. However, the breadth in host range is not uniformly distributed across the species complex. Whereas many clades are predominantly isolated from Solanaceae family plants (tomato, potato, pepper, etc.)[4], strains in the *R. solanacearum* phylotype IIB sequevar 4 clade (IIB-4) exhibit a particularly broad host range [5, 6]. *R. solanacearum* IIB-4 strains have been isolated from 33 plant species in 19 botanical families [4, 6–14]. They are distributed throughout Central and South America, the ancestral range of phylotype II *Ralstonia*. This lineage is globally invasive as IIB-4 strains have become established in Malaysia [13] and have been imported into Florida [7].

R. solanacearum IIB-4 have caused several well-studied wilt epidemics. In the 1960s, *R. solanacearum* IIB-4 caused a high-impact Moko disease epidemic of plantains and bananas in Colombia and Peru [15, 16]. These Moko isolates were also pathogenic to solanaceous crops: tomato, pepper, and potato [15]. In the 2000s, a subgroup of *R. solanacearum* IIB-4 from Martinique were recognized as a novel “not pathogenic to banana (NPB) ecotype” with high virulence on cucurbits but low virulence to banana [6]. In 2020, a third ecotype of IIB-4 from Colombia was described [12]; these novel Colombian strains are the only IIB-4 strains that are known to be avirulent on tomato. Overall, the well-documented natural history of IIB-4 strains and the diversity of their hosts position *R. solanacearum* IIB-4 as a model clade for investigating the factors that limit and enable the breadth of host range in bacterial wilt pathogens.

Results

In this study, we quantified the natural variation in virulence of 19 *Ralstonia solanaceaurm* IIB-4 strains against four natural host species from four botanical families. The strains were isolated

59 from diverse plants and locations (see Table S1). Seven strains were isolated in Peru and
60 Colombia from 1960-1963. Of these, six were from plantain during an epidemic of Moko
61 disease, and one from *Heliconia* (Buddenhagen and Elsasser 1962; French et al. 1970). Three
62 strains were isolated on Anthurium and Heliconia during the Martinique epidemic (Wicker et al.
63 2007). Seven strains were isolated from ornamentals imported into Florida. Of these, six were
64 isolated between 1996-2012 from *Pothos*, and one from *Anthurium* in 1997 (Norman et al.
65 2009). One strain was isolated in 1999 from cucumber in Brazil (Ailloud et al. 2015), and one in
66 2017 from *Pothos* in the Dominican Republic.
67
68 To determine the diversity of these strains, we used Illumina sequencing to assemble draft
69 genomes of 12 strains. An additional four unpublished genomes were shared by Caitilyn Allen
70 and Boris Vinatzer. The draft genome assembly of P488 is lower quality than others. The P488
71 assembly is fragmented into 200 contigs with an N_{50} of ~56 kb while the other assemblies have
72 40-115 contigs with an N_{50} of 111-414 kb. Full genome assembly statistics are in Table S1. We
73 collected genomes of five additional IIB-4 strains, the closely related IIB-51 strain CFBP7014,
74 and two distantly related strains (phylotype I GMI1000 and phylotype IIC K60 [17]) from NCBI.
75
76 We constructed a phylogenetic tree using 4,317 genes comparing 369,907 intragenic SNPs (Fig
77 1). Three of the IIB-4 genomes had longer branch lengths (P488, CFBP6783, and UW179),
78 consistent with the lower-quality, more fragmented assemblies for these strains. The tree
79 separated the IIB-4 strains into five branches, which we refer to as subclades A to E. The
80 *Heliconia* isolate from 1961 (UW170) was the sole genome on subclade A. Seven *Pothos* and
81 *Anthurium* isolates from Florida, and one from the Dominican Republic all clustered in subclade
82 B. The Brazilian cucumber isolate IBSBF1503 clustered into subclade C with the three strains
83 from the Martinique epidemic. The four Peruvian strains from the 1960s Moko epidemic
84 clustered into subclade D. Subclade E contained three Colombian strains isolated from plantain

85 in the 1960s, three Colombian strains recently isolated from plantain, and one Mexican strain
86 isolated from potato.
87
88 We quantified virulence of 19 IIB-4 strains on four diverse plant species that are documented
89 natural hosts for *Ralstonia* IIB-4: tomato (*Solanum lycopersicum* cv. Moneymaker), melon
90 (*Cucumis melo* cv. Sweet Granite), impatiens (*Impatiens walleriana* cv. Beacon Orange), and
91 banana (AAA *Musa acuminata* cv. Dwarf Cavendish). Tomato, melon, and impatiens were
92 grown from seed while banana plants were purchased as tissue cultured plantlets. Plants were
93 grown in growth chambers at 28° C (tomato, melon, and impatiens) or 32° C (banana) with a 12
94 hr light cycle and 40% humidity. Tomato and melon seeds were sown into Sunshine Mix #1 to a
95 depth of 1 cm, and impatiens were sown onto the surface of Sunshine Mix and topped with 1
96 mm vermiculite. Seedlings were transplanted into 3.5" pots with approximately 60 g Sunshine
97 Mix at 7 days (melon), 14 days (tomato), 21 days post sowing (impatiens), or at the 3-leaf stage
98 (banana).
99
100 We inoculated plants at 21 days post sowing (tomato and melon), 35 days post sowing
101 (impatiens), or at the 4-leaf stage (banana). We inoculated tomato and impatiens via a standard
102 cut-petiole approach where the lowest petiole was excised, and a 2 µl droplet of bacterial
103 suspension (containing approximately 1000 CFU) was placed on the cut surface [18]. Due to
104 rapid wound responses of cucurbits [19], we inoculated melons by applying a 2 µl droplet of
105 1000 CFU onto a razor blade and excising a petiole with the infested blade. Banana plants were
106 inoculated by drenching the soil with a bacterial suspension (50 mL with $5x10^{7}$ to $1x10^{8}$ CFU/g
107 soil) after the roots were lightly wounded with a 2 cm-wide metal spatula [20]. We rated
108 symptoms daily for 14 days (Fig. 2). We rated tomato symptoms on a standard 0-4 disease
109 index (DI) where 0 = no wilt, 1 = 0.1-25% of leaflets wilted, 2 = 25.1-50% of leaflets wilted, 3 =
110 50.1-75% of leaflets wilted, and 4 = 75.1-100% of leaflets wilted [18]. We measured symptoms

111 on melon, impatiens, and banana as the percentage of leaves with wilt. Symptom
112 measurements, area under the disease progress curve (AUDPC), and incidence are displayed in
113 Table S2.
114
115 Although all strains were pathogenic to tomato, three strains had reduced virulence: UW170
116 (subclade A), UW162 (subclade D), and UW175 (subclade E). Because these strains have been
117 stored as "waterstocks" (in distilled water at room temperature) for decades, we suspect that
118 these strains acquired mutations in culture storage that reduced their virulence. The subclade A
119 strain UW170 was moderately virulent on both tomato and impatiens but caused minor wilt on
120 only a few banana or melon plants. The subclade D strain UW162 had moderate virulence on
121 tomato and mild virulence on impatiens, melon, and banana. The subclade E strain UW175 had
122 moderate virulence on tomato, mild virulence on impatiens and melon, and no virulence on
123 banana. Similarly, little is known about the IIB-4 strains isolated from Banana in Malaysia [13],
124 but we predict they could be in subclade D or a represent a novel subclade.
125
126 Virulence of strains generally correlated with their phylogenetic relationships. The subclade B
127 and C strains were avirulent on banana but highly virulent on tomato, impatiens, and melon.
128 The subclade C strains displayed slightly higher virulence on melon than the subclade B strains.
129 Three other subclade D strains were highly virulent on tomato and had low-to-moderate
130 virulence on impatiens, melon, and banana. The subclade E strains included UW70 which was
131 highly virulent on tomato, melon, and banana. UW70 was more virulent on impatiens than
132 subclade D strains, but less virulent than the subclade B and subclade C strains.
133
134 **Discussion**
135 Although many *Ralstonia* isolates only wilt plants efficiently at tropical temperatures, some
136 *Ralstonia* isolates can wilt plants at temperate temperatures. Cool-virulence is famously a trait

137 of the global pandemic lineage of *Ralstonia* (IIB-1 AKA the U.S. Select Agent-regulated "Race 3
138 Biovar 2" group)[21], but recent studies have shown that multiple lineages of *Ralstonia* can wilt
139 tomato plants at cool temperatures: IIB-27, III-48, and the focal clade of this study, IIB-4 [22,
140 23]. Although we carried out this study's virulence assays at warm, tropical temperatures,
141 several of our isolates, P673 (subclade B), CFBP6783 (subclade C), and UW163 (subclade D) can
142 wilt tomatoes at cool temperatures (18°C) [22, 23].
143
144 Early studies suggested that IIB-4 strains have binary host range profiles with either a "Moko"
145 profile with pathogenicity to banana/ tomato/ plantain or a "Not Pathogenic to Banana (NPB)"
146 profile with pathogenicity to tomato/ plantain/ anthurium/ cucurbits [5, 6, 20]. However, this
147 study shows that the virulence patterns are more complex. First, we show that banana
148 pathogenesis is rare among the strains tested. The "not pathogenic to banana" phenotype was
149 shared by the subclade C strains previously described as "not pathogenic to banana" [5] and
150 strains from subclade A and B. Our results suggest that pathogenesis on banana might be an
151 acquired trait within the subclade D/E lineage. Consistently, pathogenesis on banana is a
152 polyphyletic trait shared by distantly related lineages in phylotype IIA, IIB, and IV [24–26]. Our
153 study did not include any genomes from the recently identified IIB-4 subclade /ecotype from
154 Colombia that lacks pathogenicity to tomato [12]. If strains from this ecotype cluster
155 independently from the five subclades of the 24 IIB-4 strains in this study, we propose to name
156 the newly described ecotype as "subclade F".
157
158 One subclade E strain (UW70 also known as "CIP417") was highly virulent on all host species
159 tested. UW70 was isolated from plantain in Colombia in the 1960s and is closely related to
160 strains isolated from Plantain in Colombia in 2012 (UA-1591 and UA-1617)[12]. Interestingly,
161 UW70 was highly virulent on melons, but UA-1591 is reported to be avirulent on cucumber

[12]. Cucurbit pathogenicity has also been documented in phylotype I strains isolated in Taiwan, Thailand, China, and Japan [27–30].

Overall, our findings reinforce the phenotypic plasticity within the *Ralstonia solanacearum* species complex broadly. In addition to host range variation within sequevar IIB-4, banana-virulent strains in IIA-24 and IIA-41 clades vary in their pathogenicity on tomato [25]. A study of phylotype I *Ralstonia* from Guanxi, China showed that closely related strains shared virulence on tomato, eggplant, tobacco, and potato but varied in their pathogenicity on pepper, mulberry, ginger, and cucurbits [27]. Host range patterns in the *Ralstonia solanacearum* species complex are complicated because they are generalists with limits to their host range. The genetic and evolutionary drivers of host range in the *Ralstonia solanacearum* species complex remains and important and unsolved puzzle.

Data Availability

The raw virulence data is available in Table S2. The genome data is available on NCBI (xxxTo be added)

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Conflicts of Interest

The authors declare that there are no conflicts of interest.

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283

Figures

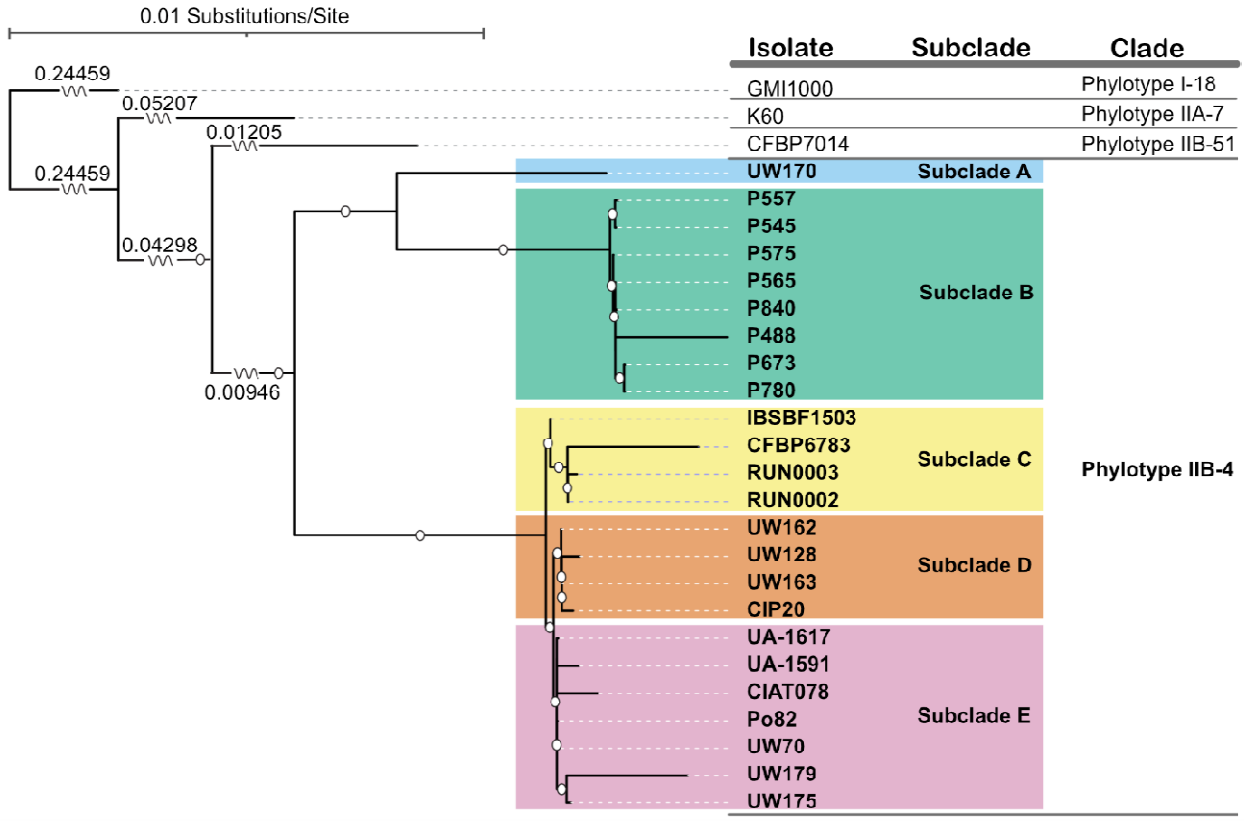


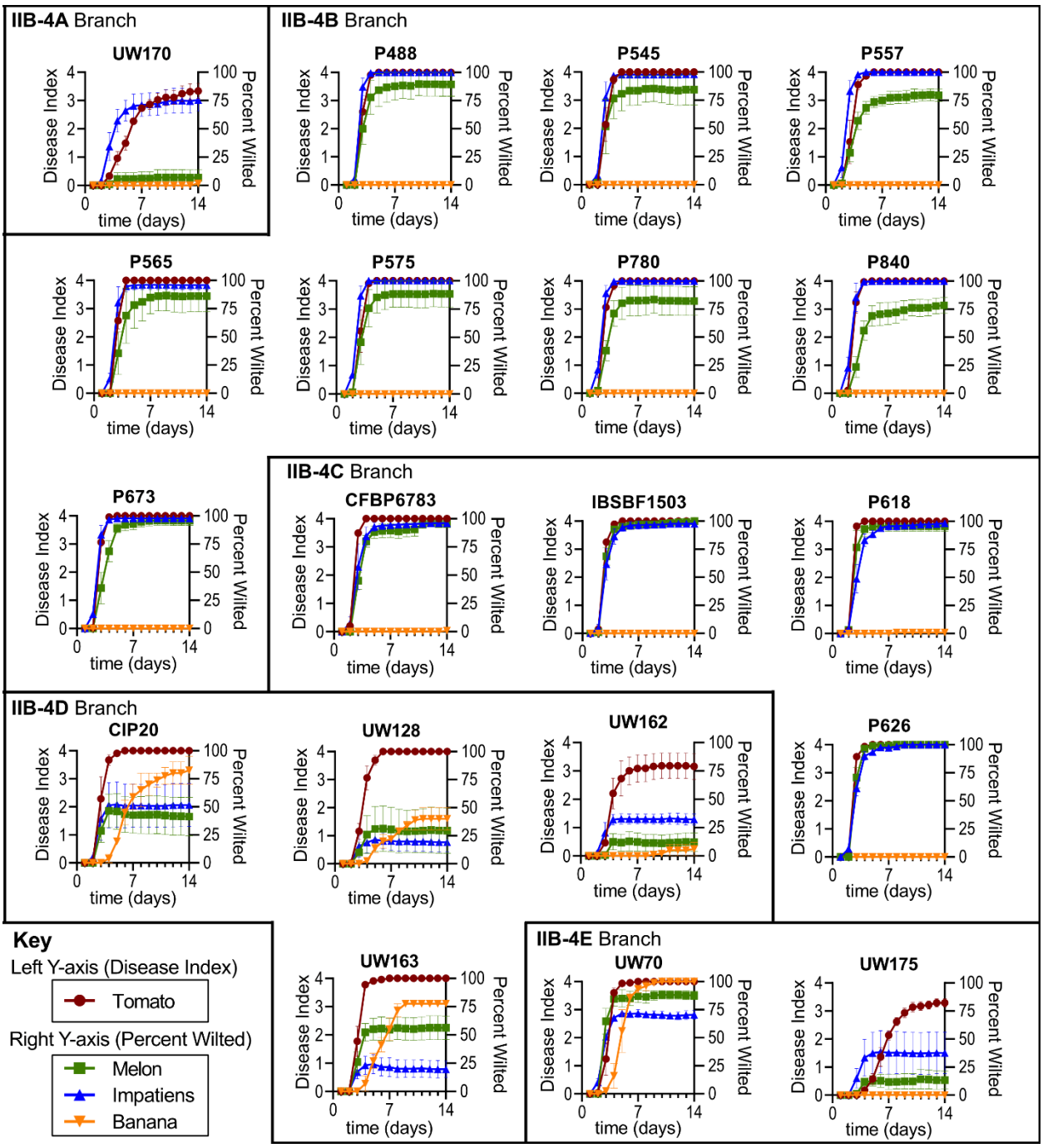
Fig 1. Maximum likelihood tree describing 27 strains of the *Ralstonia solanacearum* species complex, based on 369,907 intragenic SNPs. The tree includes 24 IIB-4 strains and three reference strains from phylotype IIB-51 (CFBP7014), IIC-7 (K60) [17], and I (GMI1000). Isolates are described as belonging to one of five IIB4 subclades (A-E). 95% bootstrap support is indicated by a white circle. Some branch lengths were condensed for clarity. SNPs were identified by grouping orthologous genes across all isolates using PIRATE v1.0.4 with default parameters and nucleotide-based clustering [31]. Orthologous gene groups identified by PIRATE were concatenated and reduced to positions present in at least 20 accessions, with at least one variable nucleotide, by a python script Reduce_alignment.py (github.com/Erysiphe-graminis/Utilities). These positions were used to generate the tree using RAxML v8.2.12 with the GTRGAMMA model, Lewis ascertainment bias correction, and 1000 bootstraps [32].

297 GMI1000 was the outgroup. Tree was visualized using ITOL v6.5.2 [33], and the figure prepared

298 using Adobe Illustrator.

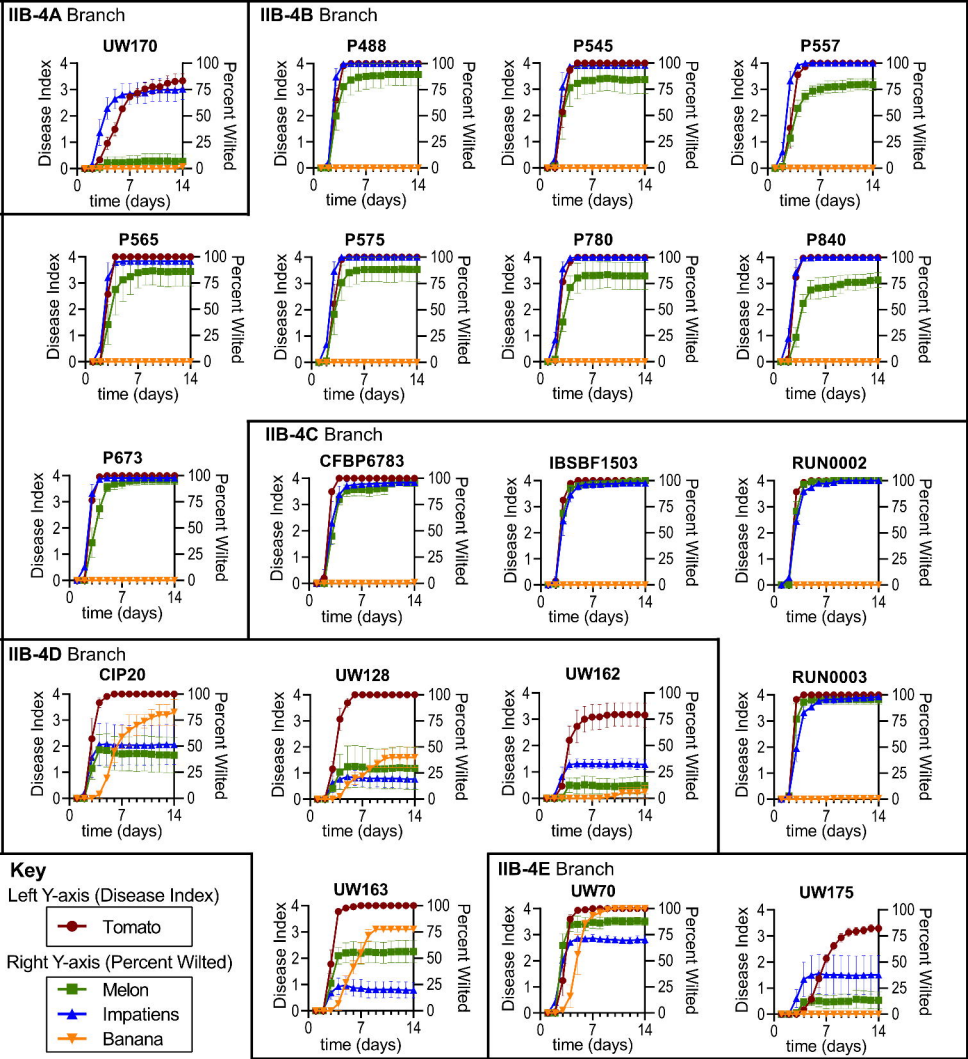
299

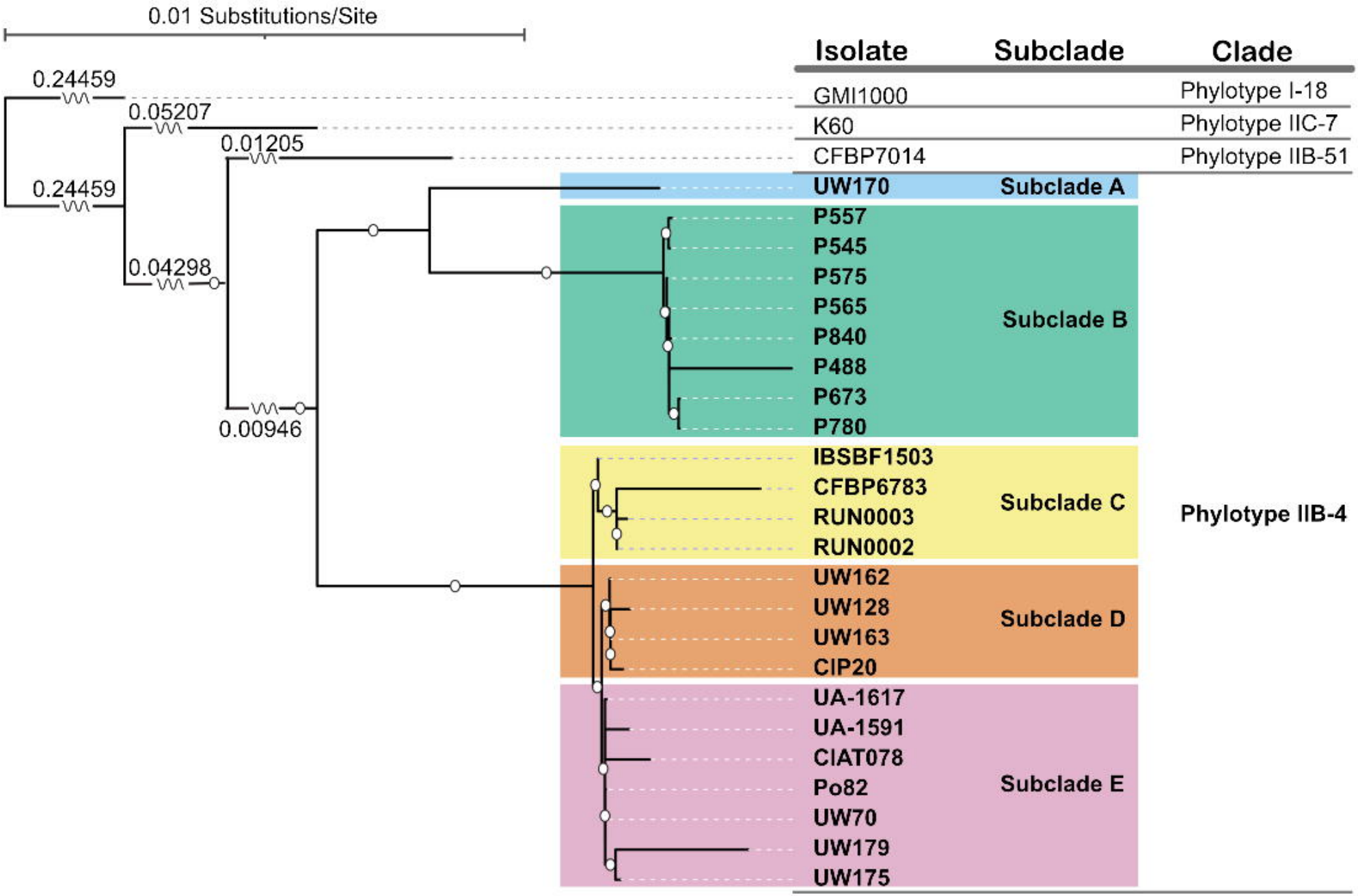
300



301

302 **Fig 2.** Disease progress of 19 *R. solanacearum* IIB-4 strains on four host species: tomato cv.
303 Moneymaker (n≥44 plants), melon cv. Sweet Granite (n≥43), impatiens cv. Beacon Orange
304 (n≥44), and Banana cv. Dwarf Cavendish (n≥19). Each graph represents one strain. Virulence on
305 tomato was quantified on 0-4 disease index (left Y-axes), and virulence on other hosts was
306 quantified as a percentage of leaves with wilt (right Y-axes). Symbols represent the mean of 2-3
307 trials and bars show standard error of the mean (SEM). Strains are grouped based on the
308 phylogeny from Fig 1. Raw virulence data is available in Table S2.
309


IIB-4A Branch
UW170
IIB-4B Branch
P488
P545
P557
P565
P575
P780
P840
P673
IIB-4C Branch
CFBP6783
IBSBF1503
RUN0002
IIB-4D Branch
CIP20
UW128
UW162
RUN0003
UW163
IIB-4E Branch
UW70
UW175
Disease Index
Percent Wilted
time (days)
Key
Left Y-axis (Disease Index)
Tomato
Right Y-axis (Percent Wilted)
Melon
Impatiens
Banana


0.01 Substitutions/Site
Isolate
Subclade
Clade
0.24459
0.05207
0.01205
0.24459
0.04298
0.00946
GMI1000
Phylotype I-18
K60
Phylotype IIC-7
CFBP7014
Phylotype IIB-51
UW170
Subclade A
P557
P545
P575
P565
P840
P488
P673
P780
Subclade B
IBSBF1503
CFBP6783
RUN0003
RUN0002
Subclade C
Phylotype IIB-4
UW162
UW128
UW163
CIP20
Subclade D
UA-1617
UA-1591
CIAT078
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UW70
UW179
UW175
Subclade E