Bacterial Wilt Resistance in Blueberry Species

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ABSTRACT
Blueberry production is expanding rapidly in the United States and globally. In 2016, bacterial wilt was discovered in Florida blueberry production. Because of the international movement of plants, this disease poses a significant risk to production. The purpose of this project was to evaluate the resistance of blueberry species and cultivars to the three genetically distinct populations of Ralstonia identified in Florida blueberry production. Nineteen cultivars/species of Vaccinium were used in this study. Plants were selected from wild, northern, southern, midbush, lowbush, and rabbiteye varieties. Plants were inoculated with three genetically distinct strains of the pathogen, and experiments were replicated three times. Varying levels of quantitative (multigenic) bacterial wilt resistance were observed among varieties tested, with rabbiteye cultivars being the most resistant. These results are similar to bacterial wilt resistance observed in other agronomic crops. We also observed a unique specific qualitative (vertical) resistance in the rabbiteye cultivar ‘Ochlockonee’. The pathogen was unable to colonize plant tissue and cause disease on this cultivar. This is the first report of qualitative resistance to Ralstonia solanacearum in blueberry. Both the multigenic and vertical resistance can be incorporated into blueberry breeding programs to mitigate potential losses to bacterial wilt.

Introduction

Bacterial wilt caused by Ralstonia spp. is common throughout the world, and Ralstonia is considered to be the second most damaging bacterial pathogen of plants in the world (Mansfield et al., 2012). For many years, this pathogen has been classified as Ralstonia solanacearum, but it was always referred to as a species complex of high genetic diversity that infects a broad host range, including economically important crops such as banana, ginger, peanut, pepper, potato, tobacco, and, tomato (Allen et al., 2005; Buddenhagen et al., 1962; Elphinstone, 2005). Populations within the species complex have been separated into four phylotypes by sequencing the Internal Transcribed Spacer (ITS) region of the bacterial DNA (Fegan and Prior, 2005; Prior and Fegan, 2005). Phylotype I contains strains originally found in Asia and Oceania, phylotype II in the Americas, phylotype III in Africa, and phylotype IV in Indonesia and Asia (Remenant et al., 2010). These four phylotypes have been recently separated into three species using genomic and proteomic methods with phylotypes I and III being placed into R. pseudosolanacearum, phylotype II R. solanacearum, and phylotype IV R. syzygii (Safni et al., 2014). Within the R. solanacearum species is a subset of phylotype II classified as IIB that contains the US Select Agent Strain sequvar 1 which has been termed R3B2 by regulatory agencies. This distinct population of Ralstonia has been highly regulated throughout the world. The R3B2 population is thought to have coevolved with wild potato species in the Andes (Poussier et al., 2000). Within the
three bacterial wilt species the endoglucanase gene sequence has successfully been used to study subpopulations within these species, termed “sequevars” (Fegan and Prior, 2005; Prior and Fegan, 2005).

Numerous introductions of Ralstonia into the United States have occurred over the past three decades (Hong et al., 2012; Norman et al., 2009; Roman-Reyna et al., 2021; Weibel et al., 2016). Most of these introductions have been linked to the importation of plant propagative material, with over 4 billion propagative cuttings being brought into the US each year (Drotleff, 2018). Screening for Ralstonia is very difficult, due to the large volume of propagative cuttings and the ability of the pathogen to remain latent within asymptomatic hosts.

The bacterial wilt population in the southern US was initially considered to be genetically homogeneous, with most strains being placed into a subset of phylotype II, now belonging exclusively to R. solanacearum. In 2016, we isolated three distinct populations of Ralstonia causing scorch, wilt symptoms, and death of blueberries in Florida (Norman et al., 2018). Two populations were classified as R. solanacearum, phylotype II sequevar 7 and 38, and the third was a R. pseudosolanacearum, phylotype I, sequevar 13. This R. pseudosolanacearum population became the predominant strain affecting blueberry production and has been linked to the distribution of young asymptomatic plants. This was not the first time a population of R. pseudosolanacearum was detected in Florida. It had been identified earlier on Mandevilla plants from Florida in 2007 (Ruhl et al., 2011). Since that first introduction, R. pseudosolanacearum strains have fully established themselves within mandevilla production in South Florida (Weibel et al., 2016). More recently, a similar population of R. pseudosolanacearum was described in Europe infecting tea rose (Bergsma-Vlami et al., 2018; Bocsanctzy et al., 2022; Tjou-Tam-Sin et al., 2017). The spread in Europe was also linked to the distribution of infected but asymptomatic propagative stock. This population is relevant because it is also pathogenic on blueberry (Bocsanctzy et al., 2022).

The genus Vaccinium includes many economically important berry species such as blueberry, bilberry, cranberry, huckleberry, and lingonberry. The worldwide wholesale value of Vaccinium berries was over 3.8 billion in 2020 [https://www.tridge.com/intelligences/billberry/export]. Within this group, the two most economically important are cranberry and blueberry. Cultivated blueberries are separated into four growth types: highbush (Vaccinium corymbosum), lowbush (V. angustifolium), hybrid midbush (cross between highbush X lowbush), and rabbiteye (V. virgatum, syn. V. ashei). Different blueberry cultivars have been developed to tolerate cold northern latitudes, hot southern extremes, and acidic to basic soil. Since numerous crosses were made to achieve this goal, blueberry cultivars are further distinguished by the description Southern or Northern before their name. Except for the wild lowbush blueberry, most cultivars are hybrids and not pure species. These taxonomic and horticultural groupings may or may not correspond with disease resistance against specific pathogens. For example, Ehlenfeldt and Polashock (2009) found that midbush and lowbush cultivars tended to be more resistant to Phomopsis twig blight (Phomopsis vaccinii) and mummy berry diseases (Monilinia vaccini-corymbosi) than other types, while no such distinctions existed for resistance to anthracnose (Colletotrichum acutatum) (Ehlenfeldt and Polashock, 2009). To our knowledge, no previous studies have examined resistance to bacterial wilt among a range of blueberry cultivars, and across the genetic groupings.

Strict sanitation and exclusion are the most common ways of protecting crops from the bacterial wilt pathogen, since varieties with strong resistance are generally not available. For many decades there have been resistance breeding programs for eggplant, pepper, tobacco, tomato, and potato and other historically affected economic hosts. In all cases, the type of resistance observed has been partial resistance, which relies on multiple genes that can be found clustered in quantitative trait loci (QTL) (Drake-Stowe et al., 2017; Du et al., 2019; Muthoni et al., 2020; Namisy et al., 2019; Norman et al., 2020; Shin et al., 2020). With continual selections, this type of multigenic resistance breeding program can produce partially resistant breeding lines that can be particularly useful in environments where Ralstonia is prevalent. There are two major shortcomings with multiple gene quantitative resistance: 1) Resistance is usually specific to Ralstonia populations found in one geographic location. Once
challenged with genetically different strains of the pathogen, resistance is broken. 2) Multigenic resistance is dependent on environmental conditions; it often breaks down at higher temperatures, or with other types of environmental stress, favoring pathogen infections.

Qualitative resistance, also termed ETI (effector-triggered immunity), confers a complete immunity to the host. It is usually specific to particular plant variety-pathogen strain combinations. Qualitative resistance is associated with monogenic responses by resistance genes to pathogen effectors. Ideally, qualitative resistance is desired by breeders; however, it also has the drawback of being overcome by the emergence of different pathogen strains. Identifying sources of resistance, and possibly qualitative resistance, in blueberry is necessary to improve blueberry production in Florida and other southern states. The purpose of this project was to evaluate the resistance of blueberry species and cultivars to the three populations of *Ralstonia* identified on blueberry in Florida.

### Materials and Methods

#### Plants Used in the Study

Nineteen *Vaccinium* varieties were selected for this study, with representatives from southern highbush, northern highbush, midbush, rabbiteye and wild species (Table 1). Tissue culture liner plugs of *V. angustifolium* x *V. corymbosum*, *V. angustifolium*, *V. arboresum*, *V. virgatum*, *V. corymbosum*, *V. darrowii*, *V. macrocarpon*, *V. pensylvanicum*, and *V. visis-idea* were acquired from AgriStarts, Apopka FL or Hartmann’s Plant Company, Grand Junction MI. The rest of the *Vaccinium* varieties that were not available via plug liners, were propagated from cuttings or seeds.

All plants were potted into 4" pots containing Jolly Gardener Potting Mix #2. Plants were allowed to establish and grow to approximately 15 cm in height. The experiment was performed three times in a greenhouse with temperatures set between 21 and 32°C and light levels ranging between 9,688 and 12,917 lm/m². Plants were hand-watered three times a week. Insecticides were applied at labeled rates as needed to keep aphids, mites, and whiteflies from interfering with plant growth and testing.

#### Experimental Design

Three genetically distinct *Ralstonia* populations were identified infecting blueberry in Florida in 2016 (Norman et al., 2018). A representative strain of each of these populations was selected for this study: phylotype II sequevar 38 (P816), phylotype II sequevar 7 (P822), and phylotype I, sequevar 13 (P824). Each of the three *Ralstonia* strains were grown on nutrient agar amended with 0.5% sucrose for 48 h at 28°C, then harvested into saline solution (8.5 g/liter NaCl), and spectrophotometrically adjusted to 1 × 10⁶ CFU/ml. Using pruning shears that had been surface sterilized in 70% ethanol, a lower lateral branch was removed close to the soil surface from 10 plants of each of the 19 varieties of *Vaccinium* (Table 1). A 10 µL aliquot of the bacterial suspension (= 1 × 10⁶ CFU) was then pipetted onto the cut surface of the wound. Saline buffer was pipetted onto the cut surface of another set of plants as a negative control. Inoculation experiments were repeated three times with each of the three *Ralstonia* strains on the 19 *Vaccinium* varieties. Accordingly, each of the three *Ralstonia* strains was used to inoculate 570 plants in total (10 plants of each Vaccinium variety per test times 19 Vaccinium varieties times 3 replicate experiments) for 1710 inoculated plants in total (excluding noninoculated control plants). Inoculated plants were monitored over 45 days. At the end of the 45-days, the number of plants with symptoms were counted and the disease incidences (expressed as a percentage of symptomatic plants) were recorded for each group. Disease incidence data from each of the three bacterial strains tested were compared using ANOVA and Tukey’s LSD procedures in Sigma Plot 13 (Systat Software Inc.). Further statistical comparisons were done between rabbiteye cultivars and the other production cultivars by grouping the blueberry varieties into two groups, with seven rabbiteye blueberries *V. virgatum* (syn. *V. ashei*) in one group, and seven other production cultivars (southern and northern highbush, northern lowbush, northern midbush) in the other group (Table 2). To
Table 1. Disease incidence expressed as the mean percentage of symptomatic plants plus standard error values per species/cultivar of Vaccinium genus when inoculated with Ralstonia strains.

| Genus Species/cultivar | Description | Mean (%)<sup>a</sup> | STDerr  | Tukey’s LSD (α = 0.05)<sup>b</sup> | Mean (%) | STDerr  | Tukey’s LSD (α = 0.05) | Mean (%) | STDerr  | Tukey’s LSD (α = 0.05) |
|------------------------|-------------|----------------------|---------|----------------------------------|----------|---------|------------------------|----------|---------|------------------------|
| Production Cultivars   |             |                      |         |                                  |          |         |                        |          |         |                        |
| Vaccinium corymbosum   |             |                      |         |                                  |          |         |                        |          |         |                        |
| 'Duke'                 | Northern    | 53.3                 | 18.6    | abcd                             | 43.3     | 28.5    | abcd                   | 33.3     | 12.0    | abc                    |
| 'Sweet Crisp'          | Northern    | 26.7                 | 12.0    | abc                              | 13.3     | 3.3     | ab                     | 20.0     | 5.8     | ab                     |
| 'Arcadia'              | Southern    | 86.7                 | 6.7     | d                                | 76.7     | 6.7     | bcd                    | 60.0     | 10.0    | bcd                    |
| 'Kestrel'              | Southern    | 6.7                  | 3.3     | ab                               | 16.7     | 11.6    | abc                    | 30.0     | 3.3     | abc                    |
| 'Brunswick'            | Northern    | 60.0                 | 20.8    | bcd                              | 83.3     | 12.0    | cd                     | 33.3     | 8.8     | abc                    |
| 'Leslie'               | Northern    | 80.0                 | 12.5    | cd                               | 66.7     | 12.0    | abc                    | 83.3     | 12.0    | cd                     |
| 'Top Hat'              | Northern    | 33.3                 | 13.3    | abcd                             | 96.7     | 3.3     | d                      | 33.3     | 23.3    | abc                    |
| Rabbiteye Cultivars    |             |                      |         |                                  |          |         |                        |          |         |                        |
| Vaccinium virgatum     |             |                      |         |                                  |          |         |                        |          |         |                        |
| 'Alapaha'              | Rabbiteye   | 26.7                 | 8.8     | abc                              | 53.3     | 20.3    | abcd                   | 46.7     | 6.7     | abcdI                   |
| 'Brightwell'           | Rabbiteye   | 76.7                 | 6.7     | cd                               | 16.7     | 3.3     | abc                    | 66.7     | 8.8     | bcd                    |
| 'Kewer'                | Rabbiteye   | 26.7                 | 12.0    | abc                              | 10.0     | 10.0    | ab                     | 36.7     | 13.3    | abc                    |
| 'Ochlockonee'          | Rabbiteye   | 0.0                  | 0.0     | a                                | 0.0      | 0.0     | a                      | 0.0      | 0.0     | a                      |
| 'Pink lemonade'        | Rabbiteye   | 0.0                  | 0.0     | a                                | 26.7     | 3.3     | abc                    | 50.0     | 11.5    | abc                    |
| 'Titan'                | Rabbiteye   | 6.7                  | 3.3     | ab                               | 0.0      | 0.0     | a                      | 33.3     | 17.6    | abc                    |
| 'Vernon'               | Rabbiteye   | 3.3                  | 3.3     | ab                               | 6.7      | 3.3     | a                      | 16.7     | 8.8     | ab                     |
| Other species          |             |                      |         |                                  |          |         |                        |          |         |                        |
| Vaccinium arboareum,   | Southern    | 13.3                 | 8.8     | ab                               | 13.3     | 3.3     | ab                     | 20.0     | 0.0     | ab                     |
| sparklberby            | Native      |                      |         |                                  |          |         |                        |          |         |                        |
| Vaccinium darrowii,    | Southern    | 80.0                 | 10      | cd                               | 60.0     | 11.5    | abcd                   | 96.7     | 3.3     | d                      |
| Florida                | Native      |                      |         |                                  |          |         |                        |          |         |                        |
| Vaccinium elliott      | Southern    | 10                   | 5.8     | ab                               | 0        | 0       | a                      | 23.3     | 8.8     | ab                     |
| Native                 |                      |         |         |                                  |          |         |                        |          |         |                        |
| Vaccinium visi-idea    | Lingonberry | 26.7                 | 12.0    | abc                              | 50.0     | 26.5    | abc                    | 43.3     | 8.8     | abc                    |
| Vaccinium macrocarpon, | Cranberry   | 73.3                 | 12      | abcd                             | 56.7     | 23.3    | abc                    | 70.0     | 10.0    | bcd                    |
| 'Stevens'              |                      |         |         |                                  |          |         |                        |          |         |                        |

<sup>a</sup> Combined mean percentage of plants (N = 30) infected with Ralstonia across the three experiments.

<sup>b</sup> Species/cultivars that do not share the same letter in individual columns are significantly different (α = 0.05).

compare the disease incidences of the two populations, an unpaired t-test was performed in Sigma Plot 13 (Systat Software Inc.).

**Confirming Pathogenicity**

To confirm pathogenicity and systemic infection, reisolations were performed from all plants that exhibited 100% wilt symptoms as it happened or at the end of the 45 days. Sampling consisted of aseptically removing a 2 cm stem section, at least 3 cm above the inoculation zone. These stem sections were dipped in a 10% bleach solution, blot dried on a clean paper towel, trimmed with a sterile scalpel,
and then diced and placed into a sterile ceramic well containing 300 µL of sterile distilled water. After soaking for 5 minutes, the suspension was dilution streaked onto TZC medium (Kelman, 1954). TZC plates were incubated at 28°C. Plates were checked at 24 hr to observe the presence of diagnostic star-shaped microcolonies of *Ralstonia*, indicating twitching motility. Forty-eight hours after plating, the cultures were scanned for the presence of mucoid red, egg-shaped colonies also characteristic of the *Ralstonia* genus.

### Table 2. Bacterial wilt resistance compared between rabbiteye cultivars and other blueberry cultivars in production.

| Blueberry cultivars          | R. solanacearum | R. pseudosolanacearum |
|------------------------------|-----------------|-----------------------|
|                              | Phylotype II, sequevar 38, Strain P816 (P = .07 *) | Phylotype II, sequevar 7, Strain P822 (P = .01) |
| Rabbiteye cultivars³         | Mean (%)        | Std Dev               | Mean (%)        | Std Dev               |
| Other production cultivars²  | 20              | 27.6                  | 16.2            | 18.9                  |
|                              | 49.5            | 29.0                  | 56.7            | 32.8                  |
|                              | 35.7            | 22.1                  | 41.9            | 21.9                  |

*Unpaired t-test at 95% confidence level. Significant difference (at α = 0.05) only observed for strain P822.

²Seven rabbiteye cultivars listed in Table 1.

³First seven production cultivars listed in Table 1, including southern and northern highbush, northern lowbush and northern midbush.

### Results and Discussion

#### Multigenic Resistance Observed

At the end of 45 days, all plants with symptoms were found to be systemically infected with *Ralstonia* and asymptomatic plants were found not to be harboring the pathogen. We observed varying degrees of bacterial wilt resistance, as is common when studying partial, multigenic resistance (Table 1). Similar results have been documented in other crops such as potato, tomato, pepper, tobacco, and eggplant (Drake-Stowe et al., 2017; Du et al., 2019; Muthoni et al., 2020; Namisy et al., 2019; Norman et al., 2020; Shin et al., 2020). This type of resistance relies on multiple genes that are often clustered in quantitative trait loci (QTL). We observed a large variation in bacterial wilt resistance within the genus *Vaccinium*. The range of responses indicates that there are likely good opportunities to identify QTLs for multige genetic resistance in blueberry.

*Vaccinium macrocarpon* (Cranberry) was highly susceptible to all strains of *Ralstonia* tested. Cranberry is native to northeastern North America, outside of the tropical-subtropical range of *Ralstonia* spp., and likely has no evolutionary history of interaction with this pathogen. However, as climatic conditions and growing regions shift, there is potential for *Ralstonia* to become a serious problem in cranberry production. Cranberry production now extends south into western North Carolina, where *R. solanacearum* is present. It would be very hard to control an outbreak of this pathogen within the bog/marsh system that is used in cranberry production.

#### Rabbiteye Blueberries are More Resistant than Other Production Cultivars

The results indicated that the rabbiteye group is significantly (α = 0.01) more resistant to bacterial wilt by the phylotype II sequevar 7 (P822) than the other production cultivars, with mean disease incidences more than three times higher than the other production cultivars (Table 2). With the phylotype II sequevar 38 (P816), the mean disease incidence was also more than twice as high among the other production cultivars as in the rabbiteye cultivars, though the difference was not significant due to high variability in plant responses between experiments. With the phylotype I (P824), the rabbiteye varieties had lower observed mean disease incidence compared to other production cultivars, but the magnitude of the difference was much smaller and not significant as evaluated in the t-test. Rabbiteye blueberries...
are native to the southeastern United States, which is also the probable center of origin of the *Ralstonia* phylotype II sequevar 7 (Wicker et al., 2012). Phylotype II sequevar 38 strains are also American in origin, currently known from French Guiana, Guyana, Martinique, Trinidad, and Florida (Deberdt et al., 2014). The isolate against which rabbiteye varieties did not show higher resistance was from Phylotype I, which originated in Asia and Oceania (Deberdt et al., 2014).

Early use of rabbiteye plants in production began in Florida in the 1890s (Williamson and Lyrene, 2004). Plants were originally collected from the wild and transported to production fields. Over time, selections were made, and cultivars were developed throughout the southeastern United States. Rabbiteye became the predominantly cultivated blueberry in the southeastern United States because of their tolerance to heat, drought, and a wide range of soil pH (Williamson and Lyrene, 2004). To incorporate these characteristics into northern highbush (*V. corymbosum*) varieties, *V. virgatum* as well as *V. darrowii* were crossed to develop southern highbush varieties (Hancock et al., 2008; Miyashita et al., 2009; Williamson and Lyrene, 2004). In recent years, southern highbush varieties have replaced rabbiteye plantings due to their availability for the early spring market. Our results, however, suggest that some of the resistance to American strains of *Ralstonia* may have been lost in the process.

**Vertical Resistance Observed**

We identified a special case of interest in this study: none of the strains of *R. solanacearum* caused any symptoms on the rabbiteye cultivar ‘Ochlockonee’. We were also unable to reisolate the pathogen from plant tissue. The cultivar showed a strong and specific qualitative (ETI) resistance to the three strains of the pathogen. This type of resistance is probably mediated by the interaction of one or more R-genes in the cultivar ‘Ochlockonee,’ and effectors in the pathogen strains tested. More research is needed to accurately describe the resistance interaction observed in this study, but the results provide the first indication that R-gene-based *Ralstonia* wilt resistance may be present in blueberries. Identification of the specific genes responsible will be of tremendous benefit to breeding programs, and the future of blueberry production in the southeastern United States.

**Disclosure statement**

No potential conflict of interest was reported by the author(s).

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