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Susceptibility of Weeds from Potato Production Systems to Potato-Aggressive Isolates of *Verticillium dahliae*

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INTRODUCTION

Verticillium wilt, caused by the soil-borne fungus *Verticillium dahliae*, is an important disease of potato in North America (Pegg and Brady 2002; Mace, Bell, and Beckman 1981). Verticillium wilt of potato has been reported to cause yield loss of up to 50% but yield loss can vary by environment, host susceptibility, and cultural conditions (Powelson and Rowe 1993). A resting structure called a microsclerotium enables *V. dahliae* to survive in soil for up to 14 years (Wilhelm 1955), as well as to survive fluctuations in temperature and moisture (Mace, Bell, and Beckman 1981). Microsclerotia are often located in the top 4 to 12 inches of field soil (Jordon 1971; Taylor et al. 2005). Microsclerotia are generally distributed where infected plants decompose or where infested soil is moved by farm equipment (Mace, Bell, and Beckman 1981).

Certain *V. dahliae* isolates are considered more aggressive than other isolates when increasingly severe symptoms or greater numbers of microsclerotia are produced within one plant host compared to other hosts (Douhan and Johnson 2001). Individual *V. dahliae* isolates that are aggressive to a plant host are called host-adapted pathotypes (Dung et al. 2013; Pegg and Brady 2002), or pathotypes.

Weeds present in the field are competitors for water, nutrients, sunlight, and space (Baker 1974). Hairy nightshade (*Solanum physalifolium*) at a density of one or three plants per 3-ft row of potato can reduce U.S. No. 1 yield of potato cultivars Russet Norkotah and Russet Burbank by up to 27% and 10%, respectively (Hutchinson et al. 2011). One barnyard grass (*Echinochloa crus-galli*) plant per m² of potato reduced marketable tuber yield by 19% if the barnyard grass emerges prior to the adjacent potato plants and remained throughout the season (Vangessel and Renner 1990).

Weeds can support pathogens and pests (Linde et al. 2016) and return inoculum to the soil when plant residue decomposes at the end of the season (Woolliams 1966). Aggressive pathotypes of *V. dahliae* may infect a weed and persist in the environment while possibly maintaining aggressiveness until a crop host is infected again. A similar observation was made with another fungal pathogen called *Rhynchosporium commune* in that aggressiveness to barley was maintained from barley grass (*Hordeum* spp.) to barley (*Hordeum vulgare*) (Linde et al. 2016). Management of disease where aggressiveness can be maintained from a weed to a crop requires documentation of fungal aggressiveness transferring between hosts and ultimately managing the aggressive fungus on both the weed and crop.

Black nightshade (*Solanum nigrum*) and hairy nightshade are important to potato production in the Pacific Northwest because of their ability to directly compete for resources and serve as a host for potato disease-causing organisms (Hutchinson et al. 2011; Woolliams 1966). The interaction of *V. dahliae* pathotypes with weeds has not been explored. Complete understanding of the interaction of aggressive isolates of *V. dahliae* with weeds is important to successful long-term management of Verticillium wilt of

potato because locations where *Verticillium*-susceptible weeds are prevalent in the potato field could pose greater inoculum pressure from *V. dahliae* isolates aggressive to potato in subsequent years. The objective of this study was to: identify the susceptibility of 16 weeds from the Columbia Basin to eight *V. dahliae* isolates and identify weeds where the potato or mint pathotype of *V. dahliae* produce greater numbers of microsclerotia compared to the other *V. dahliae* isolates.

MATERIALS AND METHODS

Quantification of *V. dahliae* microsclerotia in weeds and crops.

Verticillium dahliae isolates were previously characterized for aggressiveness to various hosts by Dung et al. (2013) (Table 1). A total of eight *V. dahliae* isolates was used in all four trials (Table 1), with one non-inoculated control treatment. Comparisons in aggressiveness of *V. dahliae* isolates to 16 weeds and two crops hosts (Table 1) were made in four trials in a greenhouse from 2014 to 2016. A broad range of weeds was evaluated for *V. dahliae* susceptibility in the first two trials. The third and fourth trial focused on nightshades to further explore the interaction of the potato-aggressive pathotype of *V. dahliae* and nightshades.

A *V. dahliae* isolate was deemed aggressive to a weed if either increasingly severe symptoms or greater numbers of microsclerotia are produced by one isolate compared to other isolates. The observation of one isolate's aggressiveness to a weed must be consistent across multiple trials for the purposes of repeatability to demonstrate results were not spurious.

Susceptibility of weeds to *V. dahliae* was determined by weekly visual assessment of *Verticillium* wilt symptoms such as marginal or unilateral chlorosis, stunting, wilting, and premature senescence (early dying). Susceptibility to *V. dahliae* was also determined by observing microsclerotia in dried plant matter from weeds.

Seedlings no greater than 10 cm in length were inoculated by submerging the hypocotyl and primary root in an agitated conidial suspension of one *V. dahliae* isolate. Inoculated plants were grown for four months before being dried for four weeks to facilitate the formation of *V. dahliae* microsclerotia. The number of *V. dahliae* microsclerotia from collected stems and roots was evaluated in a total of one gram per dry, ground plant matter (particle size <4 mm²) on a semiselective medium for *V. dahliae*. The number of microsclerotia was enumerated under a dissecting microscope after incubating for 10 days.

Differences in the number of observed *V. dahliae* microsclerotia for each *V. dahliae* isolate from an inoculated plant host was determined using an analysis of variance with distance matrices from both within and among assigned groups called PERMANOVA (Primer-E Ltd, v7, Devon, UK). Conducting many pairwise comparisons simultaneously in PERMANOVA increases the risk of type I errors (false positives). The risk of a false positive was controlled using a false discovery rate (FDR) to adjust the *P*-value for significance to less than 0.05 for each trial to ascertain truly significant differences from false positives.

RESULTS

Quantification of *V. dahliae* CFU in weeds and crops. All weed and crop hosts evaluated were infected by at least one isolate of *V. dahliae* as evident by microsclerotia observed in the hosts (Tables 2-5). Infections of weeds by *V. dahliae* often yielded small numbers of observed microsclerotia (<5 microsclerotia per gram of plant, Tables 2-5). Differences in *V. dahliae* microsclerotia production by *V. dahliae* isolate existed for some, but not all weeds (Tables 2-5).

Table 1. Weed and crop hosts, number of trials, and isolate characteristics of *Verticillium dahliae* used to determine microsclerotia production when potential host plants were inoculated with *V. dahliae* host-adapted isolates in four trials in 2014-2016.

Common Name	Latin Binomial	No. of Trials
Annual Bluegrass	<i>Poa annua</i>	2
Annual Sowthistle	<i>Sonchus oleraceus</i>	2
Barnyard Grass	<i>Echinochloa crusgalli</i>	2
Bittersweet Nightshade	<i>Solanum dulcamara</i>	2
Black Nightshade	<i>Solanum nigrum</i>	4
Common Lambsquarters	<i>Chenopodium album</i>	2
Downy Brome	<i>Bromus tectorum</i>	2
Eastern Black Nightshade	<i>Solanum ptycanthum</i>	2
Eggplant (cv. 'Night Shadow')	<i>Solanum melongena</i>	3
Green Foxtail	<i>Setaria viridis</i>	2
Hairy Nightshade	<i>Solanum physalifolium</i>	2
Large Crabgrass	<i>Digitaria sanguinalis</i>	2
Litchi Tomato	<i>Solanum sisymbriifolium</i>	2
Pigweed Powell	<i>Amaranthus powellii</i>	2
Pigweed Tumble	<i>Amaranthus albus</i>	1
Potato (cv. 'Russet Norkotah')	<i>Solanum tuberosum</i>	2
Rattail Fescue	<i>Vulpia myuros</i>	2
Wild Oat	<i>Avena fatua</i>	3

<i>V. dahliae</i> Isolate	Pathotype	Original Host ^a
111	Mint	Mint
155	Mint	Mint
381	-	Watermelon
461	-	Tomato
625	-	Sugar Beet
653	Potato	Potato
SF	-	Sunflower
Vmd-4	-	Tomato

^aHost of origin for the *V. dahliae* isolate. Isolates originating from potato or mint are the potato or mint pathotypes, respectively.

The *V. dahliae* potato pathotype (isolate 653) produced more microsclerotia than other *V. dahliae* isolates within black nightshade in three of four trials (Fig. 1). The *V. dahliae* isolate from tomato (isolate 461) produced more microsclerotia than other *V. dahliae* isolates within wild oats in two of three trials (Fig. 1). That same *V. dahliae* isolate from tomato (isolate 461) caused infections with significantly greater numbers of *V. dahliae* microsclerotia than other *V. dahliae* isolates in pigweed tumble (first trial), large crabgrass (second trial), and henbit (third trial) (Fig. 1) but only in one trial each.

The FDR-adjusted *P*-value for significance was set at $P \leq 0.0149$ for the first trial. The *V. dahliae* potato pathotype (isolate 653, Table 1) produced more microsclerotia within litchi tomato than the other *V. dahliae* isolates ($P \leq 0.0149$, Table 2) except for isolate 461 ($P = 0.0473$). One *V. dahliae* isolate was not expected to produce greater numbers of microsclerotia than every isolate evaluated because multiple isolates came from the same host or were from the same pathotype, and would theoretically produce similar numbers

of microsclerotia within the same type of weeds. A *V. dahliae* isolate from tomato (isolate 461) caused infections in pigweed tumble resulting in greater numbers of *V. dahliae* microsclerotia than other *V. dahliae* isolates ($P \leq 0.0149$, Table 2) except for isolate 461 ($P = 0.1539$). No *V. dahliae* isolate produced more microsclerotia than the other isolates in any of the other weeds evaluated in trial one. Symptoms of Verticillium wilt were not observed in any of the weeds evaluated within this trial (Data not shown).

The FDR-adjusted P -value for significance was set at $P \leq 0.0158$ for the second trial. The *V. dahliae* potato pathotype (isolate 653, Table 1) produced more microsclerotia within black nightshade than other *V. dahliae* isolates ($P \leq 0.0158$, Table 3). The *V. dahliae* potato pathotype (isolate 653) produced more microsclerotia within eggplant than other *V. dahliae* isolates ($P \leq 0.0158$) except the isolate SF ($P = 0.1572$). Inoculation of large crabgrass with a *V. dahliae* isolate from tomato (isolate 461) caused infections with significantly greater numbers of *V. dahliae* microsclerotia than other *V. dahliae* isolates ($P \leq 0.0158$, Table 3) except for isolate SF ($P = 0.3766$). Similarly, a *V. dahliae* isolate from tomato (isolate 461) caused infections wild oat with significantly greater numbers of *V. dahliae* microsclerotia than other *V. dahliae* isolates ($P \leq 0.0158$, Table 3) except isolate 381 ($P = 0.0655$). No *V. dahliae* isolate produced more microsclerotia than the other isolates in any of the other weeds evaluated in trial two. Symptoms of Verticillium wilt were not observed in any of the weeds evaluated within this trial (Data not shown).

The FDR-adjusted P -value for significance was set at $P \leq 0.0264$ for the third trial. The *V. dahliae* potato pathotype (isolate 653, Table 1) produced more microsclerotia within black nightshade than other *V. dahliae* isolates ($P \leq 0.0264$, Table 4). The *V. dahliae* potato pathotype also produced more microsclerotia within potato than other *V. dahliae* isolates ($P \leq 0.0264$, Table 4). A *V. dahliae* isolate from tomato (isolate 461) caused infections in henbit with significantly greater numbers of *V. dahliae* microsclerotia than other *V. dahliae* isolates ($P \leq 0.0264$, Table 4). A *V. dahliae* isolate from tomato (isolate 461, Table 1) caused infections in wild oat with significantly greater numbers of *V. dahliae* microsclerotia than the other *V. dahliae* isolates ($P \leq 0.0264$, Table 4). No *V. dahliae* isolate produced more microsclerotia than the other isolates in any of the other weeds evaluated in trial three. Symptoms of Verticillium wilt were not observed in any of the weeds evaluated within this trial (Data not shown).

The FDR-adjusted P -value for significance was set at $P \leq 0.0193$ for the fourth trial. The *V. dahliae* potato pathotype (isolate 653) produced more microsclerotia within black nightshade than the other *V. dahliae* isolates ($P \leq 0.0193$, Table 5). The *V. dahliae* potato pathotype produced more microsclerotia within potato than the other *V. dahliae* isolates ($P \leq 0.0193$, Table 5). No *V. dahliae* isolate produced more microsclerotia than the other isolates in any of the other weeds evaluated in trial four. Symptoms of Verticillium wilt were not observed in any of the weeds evaluated within this trial (Data not shown).

DISCUSSION

The sixteen weeds tested in this study were confirmed or re-confirmed as susceptible hosts for *V. dahliae* as indicated by the recovery of *V. dahliae* from plants grown in greenhouse settings. Symptoms of Verticillium wilt such as chlorosis, stunting, and premature senescence (Mace, Bell, and Beckman 1981) were not observed in any of the weeds evaluated within any of the four trials despite the presence of microsclerotia in infected stems. The *V. dahliae* infections without symptoms have been previously described as asymptomatic infections (Malcolm et al. 2013; Wheeler and Johnson 2016). Asymptomatic *V. dahliae* infections have been noted in *V. dahliae* isolations from susceptible weeds (Woolliams 1966), some crops rotated with potato in the Columbia Basin (Wheeler and Johnson 2016), and monocot hosts such as barley (Mol et al. 1995).

Between 5 to 30 *V. dahliae* microsclerotia per gram of soil are needed to infect potato (Powelson and Rowe 1993). Some weeds, such as bittersweet nightshade for example, did not produce more than five microsclerotia per gram of infected dry plant matter with some of these *V. dahliae* isolates, nor was the potato pathotype of *V. dahliae* more aggressive than the other isolates on bittersweet nightshade. Bittersweet nightshade will likely not pose the risk of increasing the number of microsclerotia of potato-aggressive isolates in the field.

Eastern black nightshade and hairy nightshade were susceptible to infection by almost all the *V. dahliae* isolates used, produced more than 30 microsclerotia per gram of plant when infected, and no one isolate produced more microsclerotia than the seven other isolates. However, both hairy and eastern black nightshade were susceptible to infection by the *V. dahliae* potato pathotype (isolate 653), as evident by numerous microsclerotia recovered from their dried tissues. Hairy and eastern black nightshade possibly pose the risk of increasing the number of microsclerotia of potato-aggressive isolates in the field. These isolates can then persist and increase the number of microsclerotia in soil through infecting weeds between potato rotations provided no Verticillium wilt management practice eliminates the overwintering microsclerotia.

The consistent observation of black nightshade being susceptible to the potato pathotype of *V. dahliae* is important in managing Verticillium wilt of potato. This is because fields and locations within fields where black nightshade is prevalent may have greater inoculum pressure from *V. dahliae* aggressive to potato in subsequent years. Linde et al. (2016) highlighted that management of disease where pathogen aggressiveness can be maintained from a crop to a weed and then back to the original crop must include an understanding of two important factors: (i) the maintenance of pathogen aggressiveness and (ii) ultimately control of the weed host. These trials highlighted how black nightshade could be an important source of microsclerotia of the potato pathotype of *V. dahliae*, which is the first factor Linde et al. (2016) described. This information can be used by potato producers to note fields and field locations of weeds (such as black nightshade) and identify the likely distribution of *V. dahliae* microsclerotia in soil where these infected residues decompose. These areas could be at greater risk of having isolates of the potato pathotype of *V. dahliae* present in soil and may need to be the focus of more intense Verticillium wilt management.

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Table 2. Mean and standard error for the number of microsclerotia from eight isolates obtained from 13 weeds in the greenhouse when inoculated with *Verticillium dahliae* in the first trial.

Host	Isolate								
	111 ^a	155 ^a	381	461	625	653 ^b	SF	Vmd-4	Control ^c
Annual bluegrass	0.5 ± 0.3	6.0 ± 3.2	0.2 ± 0.2	19.2 ± 5.4	5.8 ± 2.3	3.0 ± 1.1	15.3 ± 11.6	1.5 ± 0.9	0.0 ± 0.0
Annual sowthistle	23.7 ± 16.2	3.3 ± 2	2.8 ± 0.7	2.0 ± 1.3	11.5 ± 9.3	2.3 ± 1.1	11.5 ± 10.3	0.0 ± 0.0	0.3 ± 0.2
Barnyard grass	0.7 ± 0.4	5.5 ± 3.3	0.3 ± 0.2	0.3 ± 0.3	0.3 ± 0.3	0.2 ± 0.2	5.0 ± 1.8	0.7 ± 0.4	0.0 ± 0.0
Black nightshade	3.5 ± 0.5	9.8 ± 1.2	8.0 ± 2.0	6.8 ± 3.5	5.8 ± 1.5	16.5 ± 4.2	8.2 ± 2.0	12.8 ± 6.8	0.0 ± 0.0
Common lambsquarters	1.0 ± 1.0	6.5 ± 2.2	12.8 ± 9.2	44.0 ± 20.8	16.3 ± 8.8	0.3 ± 0.3	7.0 ± 0.9	5.7 ± 1.3	0.2 ± 0.2
Downy brome	2.7 ± 1.3	0.5 ± 0.5	100.2 ± 62.7	22.5 ± 14.0	7.3 ± 4.2	48.3 ± 26.0	34.3 ± 30.4	26.8 ± 13.2	0.0 ± 0.0
Green foxtail	6.5 ± 3.8	0.0 ± 0.0	0.0 ± 0.0	13.7 ± 9.2	21.5 ± 13.9	1.2 ± 0.7	9.3 ± 4.4	2.7 ± 1.5	0.0 ± 0.0
Large crabgrass	0.2 ± 0.2	2 ± 0.9	1.2 ± 0.7	15.5 ± 11.1	10.2 ± 4.8	0.8 ± 0.7	2.8 ± 1.2	0.0 ± 0.0	0.0 ± 0.0
Litchi tomato	0.5 ± 0.3	0.2 ± 0.2	2.3 ± 1.7	6.8 ± 2	1.3 ± 0.8	5.8 ± 0.9*	2.3 ± 0.6	1.3 ± 0.7	0.0 ± 0.0
Pigweed powell	1.0 ± 0.6	0.3 ± 0.2	1.3 ± 0.6	1.8 ± 0.2	3.8 ± 2.5	23.5 ± 19.9	9.3 ± 2.0	1.7 ± 1.1	0.0 ± 0.0
Pigweed tumble	5.2 ± 1.3	2.8 ± 2.8	0.0 ± 0.0	12.3 ± 1.8*	1.2 ± 0.5	29 ± 24.3	2.2 ± 0.2	0.2 ± 0.2	0.0 ± 0.0
Rattail Fescue	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	4.7 ± 3.0	0.0 ± 0.0	2.3 ± 0.7	0.0 ± 0.0	3.2 ± 2.5	0.0 ± 0.0
Wild Oat	48.7 ± 41.5	0.0 ± 0.0	113.7 ± 47.2	38.2 ± 14.8	2.8 ± 1.8	33.2 ± 13.2	6.5 ± 3.4	70 ± 19.9	0.0 ± 0.0

^a Mint pathotype of *V. dahliae*

^b Potato pathotype of *V. dahliae*

^c Non-inoculated control

Bold* Indicates *V. dahliae* pathotype or isolate with greatest microsclerotia counts. Pairwise comparisons were considered significant at corrected $P \leq 0.0149$.

Table 3. Mean and standard error for the number of microsclerotia from eight isolates obtained from 12 weeds and one crop in the greenhouse when inoculated with *Verticillium dahliae* in the second trial.

Host	Isolate								
	111 ^a	155 ^a	381	461	625	653 ^b	SF	Vmd-4	Control ^c
Annual bluegrass	0.2 ± 0.2	0.0 ± 0.0	0.7 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.2	29.5 ± 9.9	8.8 ± 5.0	0.0 ± 0.0
Annual sowthistle	0.2 ± 0.2	0.8 ± 0.4	12.0 ± 6.8	0.0 ± 0.0	4.2 ± 1.0	2.2 ± 0.6	3.5 ± 1.6	1.0 ± 0.4	0.0 ± 0.0
Barnyard grass	1.3 ± 0.2	0.0 ± 0.0	0.7 ± 0.2	1.7 ± 0.3	0.0 ± 0.0	17.2 ± 13.3	3.2 ± 0.8	0.0 ± 0.0	0.0 ± 0.0
Black nightshade	3.2 ± 1.4	2.0 ± 0.3	0.5 ± 0.2	3.0 ± 2.0	0.3 ± 0.2	25.0 ± 13.6*	3.3 ± 1.2	5.7 ± 0.7	0.0 ± 0.0
Common lambsquarters	10.7 ± 3.1	7.8 ± 5.1	1.8 ± 0.9	25.8 ± 15.4	9 ± 1.9	0.7 ± 0.3	18.0 ± 8.7	2.8 ± 0.8	0.0 ± 0.0
Downy brome	5.0 ± 2.0	0.0 ± 0.0	1.3 ± 0.7	22.5 ± 11.8	0.0 ± 0.0	2.8 ± 1.3	74.0 ± 33.4	0.8 ± 0.5	0.0 ± 0.0
Eggplant	0.0 ± 0.0	8.0 ± 0.9	2.8 ± 0.8	6.2 ± 2.5	4.3 ± 1.5	15.0 ± 1.2*	29.5 ± 16.8	2.2 ± 1.1	0.0 ± 0.0
Green foxtail	0.2 ± 0.2	5.2 ± 5.2	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	26.8 ± 17.2	2.7 ± 0.3	0.0 ± 0.0
Large crabgrass	0.0 ± 0.0	0.7 ± 0.4	0.8 ± 0.8	6.3 ± 2.2*	0.0 ± 0.0	1.0 ± 0.5	25.7 ± 20.2	0.3 ± 0.2	0.0 ± 0.0
Litchi tomato	2.7 ± 0.7	3.5 ± 2.4	3.0 ± 0.8	0.0 ± 0.0	8.2 ± 2.8	10.7 ± 2.6	5.8 ± 2.9	5.2 ± 3.1	0.0 ± 0.0
Pigweed powell	2.0 ± 0.6	0.0 ± 0.0	2.2 ± 1.0	2.0 ± 1.5	0.3 ± 0.3	0.0 ± 0.0	1.5 ± 0.3	0.7 ± 0.4	0.0 ± 0.0
Rattail fescue	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Wild oat	5.2 ± 1.7	1.0 ± 0.6	68.2 ± 46.7	101.5 ± 22.5*	6.3 ± 2.2	58.5 ± 3.2	2.7 ± 1.4	0.5 ± 0.3	0.0 ± 0.0

^a Mint pathotype of *V. dahliae*

^b Potato pathotype of *V. dahliae*

^c Non-inoculated control

Bold* Indicates *V. dahliae* pathotype or isolate with greatest microsclerotia counts. Pairwise comparisons were considered significant at corrected $P \leq 0.0158$.

Table 4. Mean and standard error for the number of microsclerotia from eight isolates obtained from seven weeds and two crop in the greenhouse when inoculated with *Verticillium dahliae* in the third trial.

Host	Isolate								
	111 ^a	155 ^a	381	461	625	653 ^b	SF	Vmd-4	Control ^c
Black nightshade	10.3 ± 1.1	7.2 ± 0.2	7.1 ± 0.6	9.8 ± 1.8	5.1 ± 0.7	14.0 ± 0.7*	7.0 ± 0.5	3.3 ± 0.3	0.0 ± 0.0
Bittersweet nightshade	2.1 ± 0.3	5.3 ± 0.6	1.3 ± 0.2	3.6 ± 0.5	6.0 ± 0.8	1.7 ± 0.2	3.6 ± 0.6	2.6 ± 0.3	0.0 ± 0.0
Eastern black nightshade	74.0 ± 10.2	28.4 ± 5.4	75.7 ± 8.2	63.6 ± 6.5	5.1 ± 0.6	53.8 ± 1.8	40.7 ± 8.8	8.3 ± 1.6	0.0 ± 0.0
Eggplant	1.4 ± 0.2	2.9 ± 0.4	5.2 ± 1.0	37.5 ± 1.7 *	17.2 ± 2.3	10.1 ± 0.5	11.0 ± 1.7	2.1 ± 0.5	0.0 ± 0.0
Hairy nightshade	183.6 ± 24.5	15.1 ± 1.1	27.9 ± 7.6	210.3 ± 14.8	169.0 ± 10.6	102.9 ± 10.1	38.5 ± 2.6	0.0 ± 0.0	0.0 ± 0.0
Henbit	66.5 ± 10.5	7.4 ± 0.8	65.1 ± 8.7	101.4 ± 4.2 *	3.4 ± 1.7	3.4 ± 0.8	49.4 ± 5.8	11.7 ± 1.7	0.0 ± 0.0
Litchi tomato	2.0 ± 0.2	1.3 ± 0.1	2.9 ± 0.4	6.3 ± 0.4	4.1 ± 0.4	9.5 ± 1.3	2.0 ± 0.2	1.9 ± 4.2	0.0 ± 0.0
Potato	8.5 ± 1.5	17.4 ± 3.2	2.3 ± 0.7	8.2 ± 1.5	42.5 ± 5.9	212.8 ± 26.9 *	51.4 ± 6.2	7.5 ± 0.7	0.0 ± 0.0
Wild oat	1.7 ± 0.9	2.0 ± 0.4	0.8 ± 0.4	185.5 ± 19.7 *	2.4 ± 0.3	2.7 ± 0.3	2.1 ± 0.4	10.7 ± 2.7	0.0 ± 0.0

^a Mint pathotype of *V. dahliae*

^b Potato pathotype of *V. dahliae*

^c Non-inoculated control

Bold* Indicates *V. dahliae* pathotype or isolate with greatest microsclerotia counts. Pairwise comparisons were considered significant at corrected $P \leq 0.0264$.

Table 5. Mean and standard error for the number of microsclerotia from eight isolates obtained from 12 weeds and one crop in the greenhouse when inoculated with *Verticillium dahliae* in the fourth trial.

Host	Isolate								
	111 ^a	155 ^a	381	461	625	653 ^b	SF	Vmd-4	Control ^c
Black nightshade	5.7 ± 1.7	2.3 ± 0.8	7.3 ± 2.0	17.3 ± 0.5	9.7 ± 2.9	52.0 ± 1.2 *	8.3 ± 0.2	3.7 ± 1.6	0.0 ± 0.0
Bittersweet nightshade	3.7 ± 1.3	1.0 ± 0.3	6.7 ± 0.4	0.0 ± 0.0	4.0 ± 2.0	10.0 ± 3.0	10.3 ± 0.5	12.7 ± 5.2	0.0 ± 0.0
Eastern black nightshade	51.0 ± 25.5	10.3 ± 5.0	0.0 ± 0.0	43.3 ± 3.6	10.0 ± 4.9	24.7 ± 2.5	0.0 ± 0.0	13.0 ± 5.2	0.0 ± 0.0
Eggplant	5.3 ± 2	18.0 ± 5.8	14.6 ± 4.7	39.0 ± 6.5	31.7 ± 10.5	17.3 ± 6.5	32.0 ± 6.8	1.0 ± 0.5	0.0 ± 0.0
Hairy nightshade	153.3 ± 55.6	20.3 ± 1.0	44.0 ± 13.4	294.3 ± 35.7	149.3 ± 25.4	55.7 ± 11.8	36.0 ± 13.0	37.3 ± 5.6	0.0 ± 0.0
Henbit	14.0 ± 6.9	4.3 ± 1.3	75.7 ± 33.4	67.0 ± 30.1	0.0 ± 0.0	5.3 ± 2.1	2.7 ± 1.5	7.0 ± 0.6	0.0 ± 0.0
Litchi tomato	1.3 ± 0.4	2.7 ± 0.5	2.3 ± 0.5	7.3 ± 2.5	5.0 ± 1.7	15.0 ± 1.5	2.3 ± 0.2	3.0 ± 0.3	0.0 ± 0.0
Potato	42.7 ± 6.2	14.0 ± 0.3	21.7 ± 5.6	50.3 ± 9.9	70.7 ± 5.3	160.1 ± 15.8 *	34.3 ± 1.1	35.7 ± 9.6	0.0 ± 0.0

^a Mint pathotype of *V. dahliae*

^b Potato pathotype of *V. dahliae*

^c Non-inoculated control

Bold* Indicates *V. dahliae* pathotype or isolate with greatest microsclerotia counts. Pairwise comparisons were considered significant at corrected $P \leq 0.0193$.

Fig. 1

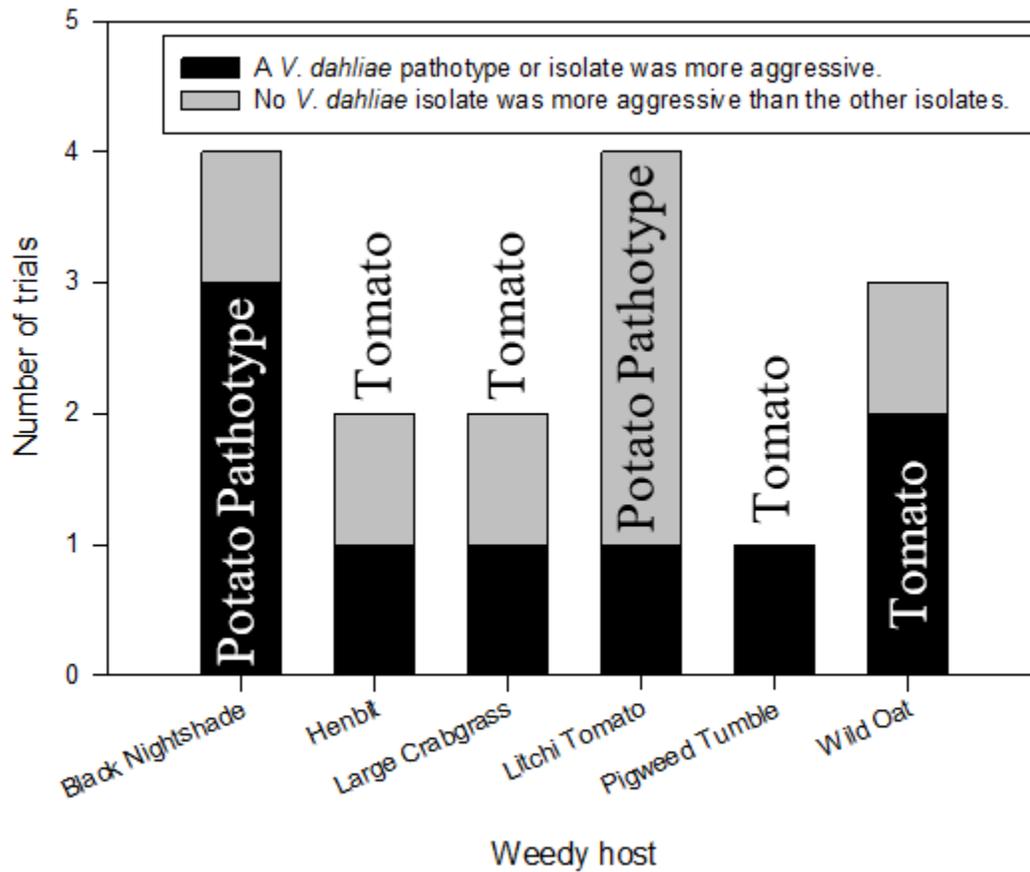


Fig. 1. Summary of the number of trials where a *V. dahliae* pathotype or isolate was more aggressive than the other isolates. Aggressiveness (Differential effect of pathotype) was determined by a greater number of microsclerotia were produced from one isolate than the other isolates for a specific weed. The host of origin or the pathotype of the *V. dahliae* isolate is written within or above each bar, and the weedy plant is along the horizontal axis.