Susceptibility of Strawberry Genotypes to Infection and Colonization by Races of *Phytophthora fragariae* and the Growth Responses of Inoculated Genotypes

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ABSTRACT

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Nineteen strawberry cultivars maintained in the North Carolina strawberry certification program and Cambridge Favourite, a cultivar widely grown in Europe, were evaluated for susceptibility to infection and colonization by seven races of *Phytophthora fragariae*. Darrow, Delite, Earliglow, and Midway were susceptible to infection and colonization by only one of the seven races tested. Partial resistance (i.e., incompletely effective) was detected for 12 strawberry cultivars in response to five races of *P. fragariae* and appeared to be race-dependent. In controlled environment chambers, the susceptible cvs. Tennessee Beauty, Atlas, and Earlibelle had fewer crowns per plant, lower foliar and root dry weights, and higher percent root necrosis when inoculated with isolates NC-1 and NC-2 of race Pf-2 than noninoculated controls. However, no significant reduction in the number of crowns per plant, foliar and root dry weights, or percent root necrosis was observed for the susceptible cultivar Sunrise when plants were inoculated with isolate NC-2 of *P. fragariae*. Inoculated plants of Cardinal, a cultivar with a low disease severity index (an experimental measure of infection and colonization) to race Pf-2, had reduced foliar and root dry weights and a four- to sixfold increase in percent root necrosis relative to the noninoculated controls. Growth characteristics of resistant Earliglow plants inoculated with *P. fragariae* were not reduced relative to noninoculated controls. Some of the mechanisms that could be responsible for partial resistance in the cultivars Sunrise and Cambridge Favourite are discussed.

Red stele disease of strawberry (*Fragaria* × *ananassa* Duchesne), caused by *Phytophthora fragariae* C. J. Hickman, is a major factor limiting fruit production in North Carolina and in cooler regions around the world (11,12,19). Breeding strawberry plants for resistance to *P. fragariae* has been complicated by the existence of at least seven races of the fungus (3,16–18). Races can be separated by their ability to infect and produce oospores in roots of differential strawberry cultivars (17). Similarly, the level of host susceptibility to a given race is quantified by the number of oospores produced in infected roots (17).

The evaluation of plant genotypes for resistance to individual pathogens has played a major role in the development of control strategies for many cultivated crops. Resistance in plants can vary from complete resistance (no pathogen growth) to partial or quantitative resistance (21). Selecting plants for resistance to disease can be achieved by measuring the growth and development of the pathogen in the host or by evaluating the pathogen's effects on the host (21). The purpose of the present study was to determine the level of susceptibility of strawberry genotypes to infection and colonization by seven races of *P. fragariae* and to determine the effects of *P. fragariae* on certain growth parameters of selected genotypes in controlled-environment chambers.

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MATERIALS AND METHODS

Susceptibility of strawberry genotypes to infection and colonization. Strawberry cultivars grown in the North Carolina strawberry certification program (Albritton, Allstar, Apollo, Atlas, Cardinal, Catskill, Darrow, Delite, Earlibelle, Earliglow, Guardian, Marlate, Midway, Pocahontas, Prelude, Rosanne, Sentinel, Sunrise, and Titan) and Cambridge Favourite, a cultivar widely grown in Europe and suspected of possessing a degree of partial resistance to *P. fragariae*, were used in these studies. Primary runner plants were removed from stock plants in the greenhouse and placed into 5-cm-diameter clay pots containing Metromix-220 (W. R. Grace & Co., Memphis, TN), sand, and soil (1:1:1, v/v/v). Pots were placed under intermittent mist for 10–17 days to allow roots to develop. Four plants of each genotype were removed from soil and rinsed thoroughly with tap water to remove all soil from the roots, and then were placed on saturated paper towels and spray-inoculated with a suspension of nonmotile (encysted) zoospores (2×10^4 zoospores per milliliter) of each of the isolates A-1, NC-1, A-4, A-6, A-8, A-9, and A-10, representing races Pf-1, Pf-2, Pf-3, Pf-4, Pf-5, Pf-6, and Pf-7 of *P. fragariae*, respectively (17), as previously reported (6). The paper towels and plants were placed inside clear plastic bags, closed, and placed in the dark at 15 C for 48 hr. Plants were removed and planted into round plastic containers (25 cm diameter wide × 9 cm deep) filled to a depth of 8 cm with Metromix-220 that had been moistened with 1,750 ml of cool tap water. Each container was placed inside a plastic bag, sealed, and placed under a 12-hr photoperiod at 15 C in a walk-in growth chamber for 14 days. Root systems were thoroughly rinsed with tap water and then five or 10 root tip segments (10 mm in length) were excised, mounted onto glass slides, and examined microscopically (×100) for oospores of *P. fragariae*.

Analysis of variance was performed on data for oospores per root segment and percent roots containing oospores for cultivars inoculated with the seven races of *P. fragariae*. To stabilize experimental variance, square root transformations were performed on data for the number of oospores per root segment, and arcsine transformations were performed on data for percent root segments with oospores before analyses. A disease severity index (DSI), determined by multiplying the mean number of oospores per root segment by the percent roots with oospores and dividing by 100, was used to determine host genotype susceptibility to infection and colonization (17). Each race by cultivar inoculation was repeated at least two times.

Effects of *P. fragariae* on selected strawberry genotypes in controlled environmental chambers. Primary runner plants of the cvs. Tennessee Beauty, Sun-

rise, Atlas, Cardinal, and Earliglow were removed from stock plants in the greenhouse and rooted as detailed above. These cultivars were selected because they exhibited a range of susceptibility to North Carolina isolates NC-1 and NC-2 of *P. fragariae* race Pf-2 in previous (17) and preliminary tests. For the second run of the study, primary runner plants of Atlas were not available, so runner plants of Earlibelle, a cultivar with susceptibility to isolate NC-1 of race Pf-2 similar to Atlas (DSI = 60 for Earlibelle and 66 for Atlas), were used. The cv. Surecrop, with a previously determined DSIs of 15 and 6 to isolates NC-1 and NC-2, respectively (17), also was included. Roots of each cultivar were spray-inoculated with a suspension of nonmotile zoospores of either NC-1 or NC-2 (2×10^4 zoospores per milliliter). Roots of control plants were sprayed with deionized water. Inoculated and control plants were placed into clear plastic bags, closed, and placed in the dark at 15 C for 48 hr. Plants were removed from bags, and one plant of each cultivar was transplanted into a 15.2-cm-diameter plastic pot containing Metromix-220, sand, and soil (1:1:1, v/v/v), and thoroughly watered with tap water.

Plants were arranged in a randomized complete block experimental design, six replicate plants per treatment, in a growth chamber in the Southeastern Plant Environmental Laboratories at North Carolina State University at 22 C during the day and 18 C at night. To promote flowering, plants were exposed to a 9-hr photoperiod (598 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR) for 20 days and then to a 9-hr photoperiod with a dark period interrupted from 2300 to 0200 hours with low level incandescent radiation (44 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR) for the remainder of the study (5) (E. Durner, *personal communication*). Plants were kept moist by daily watering with an automatic drip irrigation system that delivered major and minor nutrients (4). Plants were drench-inoculated after 2 wk in the environmental chamber by pouring 50 ml of a suspension of nonmotile zoospores of isolate NC-1 or NC-2 of *P. fragariae* (2×10^4 zoospores per milliliter) over the surface of the medium in each pot. Zoospores were encysted by rapidly stirring 100-ml aliquots of the zoospore suspension in a 600-ml beaker on a stir plate for 85 sec. Control plants were drenched with 50 ml of deionized water. Plants were reinoculated monthly using this procedure to promote infection of emerging primary and lateral roots by *P. fragariae*.

The number of branch crowns and flower trusses, each correlated with yield in previous studies (10,15), and foliar and root dry weights were determined for each replicate plant 3–4 mo after the experiment was initiated. Before determining root dry weight, root systems of each plant were thoroughly rinsed in tap water and rated for percent root necrosis, and then five to 10 discolored or necrotic root tips (10 mm in length) from each replicate plant were excised, mounted onto glass slides, and observed microscopically (×100) for oospores of *P. fragariae*. Data were analyzed by analysis of variance for a randomized complete block design. Log transformations were performed on data of foliar and root dry weights before analyses to stabilize ex-

Table 1. Development of oospores of *Phytophthora fragariae* per root segment[w] of selected strawberry hosts 2 wk after inoculation at 15 C

Cultivar	Pf-1	Pf-2	Pf-3	Pf-4	Pf-5	Pf-6	Pf-7	Mean[x]
Albritton	46 b[y]	51 cd	67 c–e	134 b	118 bc	180 a	6 f–h	86 bc
Allstar	0 f	10 ef	0 h	0 f	207 a	0 e	0 h	22 jk
Apollo	2 ef	108 ab	66 d–f	103 b–d	151 ab	58 bc	2 gh	73 ef
Atlas	65 a	74 a–c	121 a–c	106 b–d	91 b–d	173 a	5 f–h	92 ab
Cardinal	12 de	15 de	91 a	122 bc	53 d–f	105 ab	26 b–d	60 fg
Cambridge Favourite	10 d	75 a–c	192 a	213 ab	62 c–e	124 a	14 d–f	99 a
Catskill	0 f	42 cd	19 fg	38 de	20 fg	162 a	34 bc	45 h
Darrow	0 f	0 f	0 h	1 f	250 a	0 e	0 h	38 j
Delite	0 f	18 de	0 h	0 f	5 g	1 e	0 h	3 l
Earlibelle	0 f	70 bc	167 ab	152 ab	37 d–f	119 a	32 ab	82 cd
Earliglow	0 f	0 f	0 h	1 f	82 b–d	0 e	0 h	12 k
Guardian	0 f	57 bc	0 h	0 f	2 g	6 de	0 h	9 k
Marlate	12 de	75 a–c	115 b–d	201 ab	66 c–e	46 c	19 c–e	76 de
Midway	0 f	0 f	...	33 e	...	...	0 h	9 k
Pocahontas	25 cd	56 bc	100 b–d	167 ab	75 b–e	104 ab	37 a	81 bc
Prelude	...	15 cd	34 e–g	106 b–d	4 g	126 a	9 d–f	59 g
Rosanne	2 ef	133 a	13 gh	50 c–e	32 e–g	35 cd	1 h	40 h
Sentinel	7 de	45 cd	123 a–c	310 a	51 c–f	126 a	10 e–g	97 c
Sunrise	0 f	74 a–c	0 h	1 f	216 a	0 e	1 h	44 i
Titan	28 bc	80 a–c	159 ab	177 ab	77 c–e	138 a	32 ab	99 a
Mean[z]	11 d	52 c	67 c	96 a	84 a	79 b	11 d	...

[w] Data are means of 12 plants (five or 10 10-mm root tip segments per plant). Square root transformations of the data were analyzed; however, means of untransformed data are presented.

[x] Cultivar means followed by a common letter in a column are not significantly different ($P = 0.05$) by Waller-Duncan k-ratio t test. $k = 100$, df = 1,198.

[y] Means for isolate × cultivar treatment followed by a common letter in a column are not different ($P = 0.05$) by Waller-Duncan k-ratio t test. $k = 100$, df = 30 for Pf-1; 34 for Pf-5; 36 for Pf-3 and Pf-6; and 38 for Pf-2, Pf-4, and Pf-7.

[z] Isolate means followed by a common letter across the row are not significantly different ($P = 0.05$) by Waller-Duncan k-ratio t test. $k = 100$, df = 1,198.

Table 2. Percent root segments of selected strawberry cultivars containing oospores of *Phytophthora fragariae* 2 wk after inoculation at 15 C[w]

Cultivar	Pf-1	Pf-2	Pf-3	Pf-4	Pf-5	Pf-6	Pf-7	Mean[x]
Albritton	65 a[y]	81 a–d	78 c	98 a	79 a–e	93 ab	8 e–g	72 bc
Allstar	0 d	61 d–f	0 e	2 f	90 ab	7 e	0 g	19 h
Apollo	5 d	88 ab	75 c	83 b–d	80 a–f	85 a–c	10 e–g	64 e
Atlas	72 a	89 a–c	97 a	88 a–d	75 b–f	93 a–c	7 e–g	75 ab
Cardinal	32 bc	47 f	94 ab	100 a	71 c–f	88 a–c	30 c–e	66 de
Cambridge Favourite	15 cd	89 a–c	100 a	91 a–d	87 a–c	100 a	25 d–g	72 ab
Catskill	0 d	83 a–c	50 d	78 de	25 h	96 a	25 d–g	51 f
Darrow	0 d	2 g	2 e	12 f	93 a	0 e	0 g	16 h
Delite	0 d	57 ef	0 e	0 f	10 h	5 e	0 g	10 j
Earlibelle	0 d	85 a–c	97 a	99 a	67 ef	98 a	52 b	71 bc
Earliglow	0 d	0 g	0 e	12 f	63 ef	0 e	0 g	11 ij
Guardian	0 d	81 a–c	0 e	2 f	10 h	32 e	0 g	18 h
Marlate	15 cd	95 a	83 bc	97 ab	85 a–d	77 b–d	35 b–d	69 b–d
Midway	0 d	0 g	...	60 e	...	...	0 g	16 hi
Pocahontas	37 b	83 a–d	88 ab	96 ab	67 d–f	97 a	87 a	79 a
Prelude	...	70 b–e	71 c	92 a–d	27 gh	93 ab	40 b–d	68 c–e
Rosanne	7 cd	71 c–e	38 d	80 cd	52 e–g	57 d	13 e–g	47 f
Sentinel	18 b–d	76 c–e	92 ab	92 a–c	82 a–f	73 cd	25 d–f	65 e
Sunrise	0 d	88 a–c	3 e	5 f	93 a	0 e	3 fg	29 g
Titan	35 bc	93 ab	97 a	90 a–d	57 fg	87 a–c	47 bc	72 b–d
Mean[z]	16 d	67 ab	56 c	64 a	64 a	62 ab	20 d	...

[w] Data are means of 12 plants (five or 10 10-mm root tip segments per plant). Square root transformations of the data were analyzed; however, means of untransformed data are presented.

[x] Cultivar means followed by a common letter in a column are not significantly different ($P = 0.05$) by Waller-Duncan k-ratio t test. $k = 100$, df = 1,198.

[y] Means for isolate × cultivar treatment followed by a common letter in a column are not different ($P = 0.05$) by Waller-Duncan k-ratio t test. $k = 100$, df = 30 for Pf-1; 34 for Pf-5; 36 for Pf-3 and Pf-6; and 38 for Pf-2, Pf-4, and Pf-7.

[z] Isolate means followed by a common letter across the row are not significantly different ($P = 0.05$) by Waller-Duncan k-ratio t test. $k = 100$, df = 1,198.

perimental variance. The experiment was repeated once over time.

RESULTS

Susceptibility of strawberry genotypes to infection and colonization. A significant isolate × genotype interaction ($P \geq 0.001$) was detected for the number of oospores per root segment and percent roots containing oospores (Tables 1 and 2). The overall mean number of oospores per root segment for isolates across the 20 cultivars tested was highest for Pf-4 and Pf-5 (96 and 84, respectively, Table 1) and lowest for Pf-1 and Pf-7 (11, Table 1). The overall mean for percent root segments with oospores was highest for Pf-2, Pf-4, Pf-5, and Pf-6 (67, 64, 64, and 62, respectively, Table 2) and lowest for Pf-1 and Pf-7 (16 and 20, respectively, Table 2).

Isolates of races Pf-2 and Pf-5 were pathogenic to the greatest number of cultivars, whereas isolates of Pf-1 and Pf-7 were pathogenic to the least number of cultivars. The isolates of Pf-2 and Pf-5 infected and colonized 17 of 20 cultivars tested, with a mean DSI of 43 and 68, respectively (Table 3). Pf-2 did not produce oospores in Earliglow, Midway, or Darrow, whereas Delite and Guardian were completely resistant to race Pf-5. Isolate Pf-4 infected and colonized 14 of 20 cultivars with a mean DSI of 88 (Table 3). Isolates Pf-1 and Pf-7 infected eight of 20 and nine of 20 cultivars, respectively, and both races had a mean DSI of 5 (Table 3).

Darrow and Earliglow were resistant to infection and colonization by all races except Pf-5 (Table 3). Delite was resistant to infection and colonization by all races except Pf-2. Cardinal, Cambridge Favourite, Marlate, Pocahontas, Sentinel, and Titan were infected by isolates of all races. However, the DSIs for individual susceptible cultivars varied greatly among isolates (Table 3), suggesting that these cultivars may possess differential levels of partial resistance to races of *P. fragariae*.

To test whether susceptible strawberry cultivars possessed specificity in partial resistance to the races of *P. fragariae*, a set of transformed data of oospores per root segment and percent roots containing oospores for 12 cultivars and five races of *P. fragariae* were analyzed. Isolates of races Pf-1 and Pf-7 were omitted from the analysis because many of the 20 cultivars tested appeared to possess race-specific or major gene resistance to these races (Tables 1 and 2). The cvs. Allstar, Darrow, Delite, Earliglow, Guardian, Midway, Prelude, and Sunrise were omitted from the data set because they appeared to possess major gene resistance to races Pf-2, Pf-3, Pf-4, Pf-5, or Pf-6. Data were analyzed as a randomized complete block with replicates as blocks and plants as subsamples. The cultivar × race interactions were highly significant ($P \leq 0.0001$) for both oospores per root and percent roots with oospores and indicate specificity in partial resistance of cultivars to the *P. fragariae* races tested (Table 4).

Effects of *P. fragariae* on selected strawberry genotypes. Growth response data were analyzed separately by experimental run, however, trends and variance components were similar between runs, so data from both runs of the experiment were combined for analyses. Significant interaction ($P \geq 0.001$) among cultivars and isolates was detected for crowns per plant, foliar and root dry weights, and percent necrotic roots per plant over the cultivars tested. No significant interaction ($P \geq 0.623$) was detected among cultivars and isolates for the number of flower trusses per plant, so these data were not considered further in describing growth responses of strawberry cultivars to isolates of *P. fragariae*.

There was a reduction ($P \geq 0.05$) in the number of crowns per plant and in foliar and root dry weights relative to the noninoculated control when the highly susceptible cultivar Tennessee Beauty was inoculated with isolates NC-1 and NC-2 of *P. fragariae* (Fig. 1A–C). Percent root necrosis was greater ($P \geq 0.05$) for the inoculated Tennessee Beauty plants than for the control plants (Fig. 1D). A similar trend was noted for the susceptible cvs. Atlas and Earlibelle (Fig. 1). All of the roots examined from inoculated plants of these cultivars contained oospores typical of *P. fragariae* (11). Sunrise, a cultivar susceptible to infection and colonization by isolate NC-1 of race Pf-2 (DSI = 65, Table 3) was not greatly affected by inoculations with *P. fragariae* under the conditions of our study. The number of crowns per plant and percent root necrosis were similar for inoculated and noninoculated treatments (Fig. 1A and D). Foliar and root dry weights were similar for Sunrise plants inoculated with NC-2 and noninoculated controls; however, foliar and root dry weights were lower for plants

Table 3. Disease severity index (DSI)[y] of strawberry cultivars to different races of *Phytophthora fragariae*

Cultivar	Pf-1	Pf-2	Pf-3	Pf-4	Pf-5	Pf-6	Pf-7	Mean
Albritton	30[z]	41	53	132	93	168	0	74
Allstar	0	6	0	0	196	0	0	227
Apollo	0	95	49	85	121	49	0	57
Atlas	47	66	117	93	68	161	0	79
Cardinal	4	7	86	122	38	92	8	51
Cambridge Favourite	1	67	192	194	55	124	4	91
Catskill	0	35	9	30	5	156	9	35
Darrow	0	0	0	0	233	0	0	33
Delite	0	10	0	0	0	0	0	1
Earlibelle	0	60	161	151	24	117	17	76
Earliglow	0	0	0	0	52	0	0	7
Guardian	0	46	0	0	0	2	0	7
Marlate	2	71	96	194	56	35	7	66
Midway	0	0	...	20	...	...	0	5
Pocahontas	9	47	88	160	50	101	32	70
Prelude	...	40	24	98	1	118	4	47
Rosanne	0	94	5	40	16	20	0	25
Sentinel	1	34	113	284	42	93	2	81
Sunrise	0	65	0	0	201	0	0	38
Titan	10	75	154	160	44	120	15	82
Mean	5	43	60	88	68	71	5	...

[y] Disease severity index determined by multiplying the mean number of oospores per root segment times percent roots with oospores and dividing by 100. Reaction type classified as susceptible when DSI > 1.0 and resistant when DSI < 1.0.
[z] Data are means of 12 plants per five or 10 10-mm root segments per plant, 2 wk after inoculation at 15 C.

Table 4. Analyses of variance for oospores per root and percent roots with oospores for 12 strawberry cultivars and five races of *Phytophthora fragariae*

		No. of oospores per root[x]		Roots with oospores[y] (%)	
Source of variation	df	Mean square	*F* value	Mean square	*F* value
Runs (R)	2	13.96	0.49 NS[z]	1.08	4.55*
Isolates (I)	4	389.22	13.76***	4.27	18.08***
Cultivar (CV)	11	146.09	5.17***	1.66	7.03***
I × CV	44	68.24	2.41***	0.63	2.69***
R × I × CV	118	28.28	4.20***	0.24	1.85***

[x] Data for oospores per root segment transformed by the square root transformation before analysis.
[y] Data for percent roots with oospores transformed by the arcsine transformation before analysis.
[z] NS, *, and *** = not significant and significant at $P = 0.05$ and 0.0001, respectively.

inoculated with NC-1. Foliar dry weights of inoculated Surecrop plants (DSI = 15) were significantly less than the noninoculated controls. Oospores were observed in 27 and 14% of the inoculated plants of Sunrise and Surecrop, respectively. Cardinal, a cultivar with low susceptibility to infection and colonization by race Pf-2 of *P. fragariae* (DSI = 7 for isolate NC-1) was greatly affected by inoculations with isolates of race Pf-2 under the conditions of this study. There was a significant reduction ($P \geq 0.05$) in the foliar and root dry weights of inoculated treatments relative to the noninoculated controls (Fig. 1B and C) and a four- to sixfold increase in percent root necrosis in inoculated treatments (Fig. 1D). Oospores were observed in 92% of the inoculated replicate plants of Cardinal. Inoculated plants of the resistant cultivar Earliglow (DSI = 0) had significantly more crowns per plant and greater foliar and root dry weights than noninoculated control treatments (Fig. 1A–C). The percent root necrosis for Earliglow was low for both inoculated and noninoculated treatments (Fig. 1D). No oospores were observed in roots of inoculated plants of Earliglow.

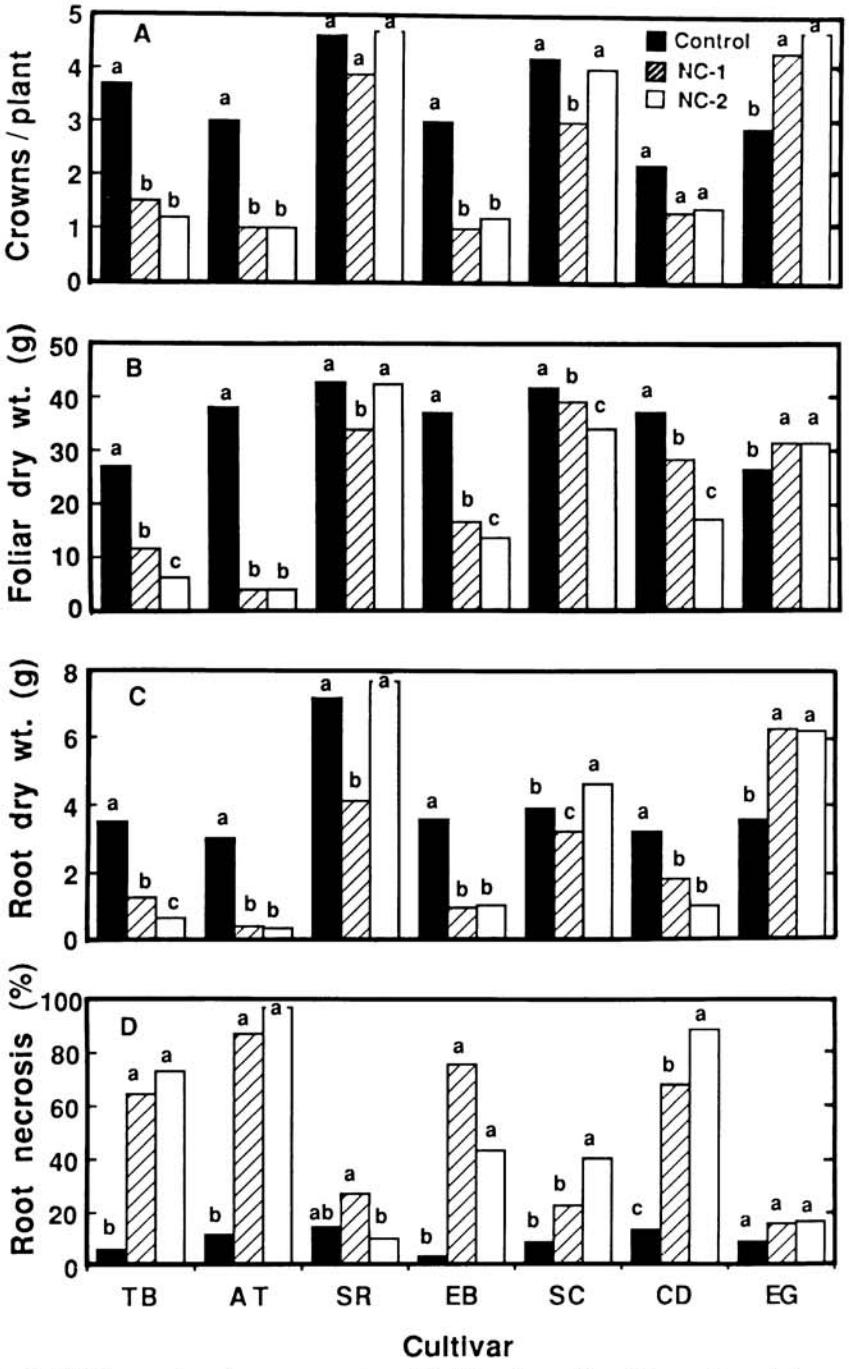

Fig. 1. (A) The number of crowns per plant, **(B)** foliar dry weight, **(C)** root dry weight, and **(D)** percent root necrosis for strawberry cultivars infected with two isolates (NC-1 and NC-2) of race Pf-2 of *Phytophthora fragariae* in a controlled-environment chamber. Strawberry cultivars were Tennessee Beauty (TB), Atlas (AT), Sunrise (SR), Earlibelle (EB), Surecrop (SC), Cardinal (CD), and Earliglow (EG), with a disease severity index (DSI) for isolate NC-1 of 172, 66, 65, 60, 15, 7, and 0, respectively. Bars with the same letter are not significantly different by Bonferroni's multiple comparison *t* test. $P = 0.05$, df = 152, number of samples = 13.

DISCUSSION

Nineteen strawberry cultivars maintained in the North Carolina certification program and Cambridge Favourite were variable in susceptibility to infection and colonization by seven races of *P. fragariae*. This information supplements previous results on the infection and colonization of 12 additional strawberry genotypes (17). To date, only race Pf-2 of *P. fragariae* has been found in North Carolina. In our study, the cultivars Earliglow, Darrow, and Midway possessed complete resistance to infection and colonization by the isolate of race Pf-2 used in this study (DSI = 0). The North Carolina cultivars (Albritton, Atlas, Apollo, Earlibelle, Rosanne, and Titan) are highly susceptible to infection and colonization by the North Carolina isolates of race Pf-2 of *P. fragariae* (DSI from 41 to 95), and are severely affected when planted in fields infested with race Pf-2 (R. D. Milholland, *unpublished*). These observations indicate a good correlation between the levels of infection and colonization of the North Carolina cultivars in our tests and disease development when these cultivars are planted in fields naturally infested with the red stele pathogen.

Levels of susceptibility of some other cultivars to race Pf-2 were low (DSI = 6 and 7 for Allstar and Cardinal, respectively). We also observed low levels of infection and colonization among some cultivars inoculated with isolates of the other races of *P. fragariae*. Goode (7) reported that encystment and penetration of root epidermal cells by zoospores of *P. fragariae* was similar in the resistant and susceptible strawberry cultivar she tested. However, no further development of the fungus occurred in the resistant cultivar, whereas mycelium grew and oospores formed in the roots of the susceptible cultivar. Goode's test included only strawberry cultivars with complete resistance or high susceptibility. It is possible that *P. fragariae* may colonize only to a limited scale cultivars with partial resistance to the pathogen. One of the principal effects of partial resistance can be to limit spore production (20).

Our analysis of susceptible cultivars having variable DSIs indicated that partial resistance to *P. fragariae* is present in some strawberry cultivars. Because only a single isolate of each race was used in this study, it is not clear if the partial resistance displayed was either race- or isolate-specific. Although partial resistance or tolerance has been characterized as race-nonspecific with other *Phytophthora* species (22), evidence of pathogen

specificity in tolerance of soybean cultivars to races of *P. megasperma* Drechs. f. sp. *glycinea* T. Kuan & D. C. Erwin has been reported (23).

In our controlled-environment studies, growth responses of the highly susceptible cultivars Tennessee Beauty, Atlas, and Earlibelle (DSI = 172, 66, 60, respectively), the moderately resistant cultivar Surecrop (DSI = 15), and the resistant cultivar Earliglow (DSI = 0) appeared to be correlated with levels of susceptibility to infection and colonization observed in the first part of our study. However, growth responses of two strawberry cultivars tested in the controlled-environment chambers did not correlate with levels of susceptibility to infection and colonization found in the earlier test. Although Sunrise was highly susceptible to infection and colonization by race Pf-2 (DSI = 65), there was no significant reduction in plant weight or number of crowns produced when plants of the cultivar Sunrise were inoculated every 2 wk over a 3-mo period. Sunrise appears to grow well in North Carolina soils infested with race Pf-2 of *P. fragariae* (R. D. Milholland, *unpublished*).

Under the conditions of our study, root systems of inoculated Sunrise plants were large relative to the other cultivars tested, with few diseased roots, even though oospores of *P. fragariae* were present in some replicate plants. Partial (nonspecific) resistance in several hosts has been related to agronomic characters such as increased root vigor (2). Kellam and Coffey (14) observed that an avocado rootstock considered resistant to *P. cinnamomi* Rands sustained a relatively high amount of root infection yet showed no significant reduction in root weight compared with the noninfected controls. Root proliferation is an important factor in resistance to *P. parasitica* Dastur in tomato (1). Waldo (24) noted that some strawberry selections susceptible to *P. fragariae* grew vigorously under field conditions. He noted that root systems of these selections, not entirely killed by red stele, produced new roots rapidly in the spring after temperatures became favorable for growth. Gooding (8) also concluded that resistance of some strawberry cultivars to *P. fragariae* was attributable to their capacity for producing large numbers of roots. Resistance in tobacco to *P. parasitica* var. *nicotianae* (Breda de Haan) Tucker may be attributable to the delay or inhibition of colonization arising from initial infection (13). It is possible that although Sunrise is susceptible to infection by *P. fragariae*, either necrotic areas on roots do not expand or this cultivar has the ability to compensate for infections by regenerating extensive root systems in a short period of time.

Although we did not test the growth response of Cambridge Favourite to *P. fragariae*, Gooding (9) reported that Cambridge Favourite grows and survives in fields infested with races of *P. fragariae* in Europe even though it lacks major gene resistance to *P. fragariae*. In our studies, Cambridge Favourite was susceptible to infection and colonization by all seven races of *P. fragariae* (DSI = 1–194). However, it is possible that Cambridge Favourite may possess the ability to generate a large root system to provide partial or field resistance to *P. fragariae*.

Cardinal, a cultivar with apparently moderate resistance to infection and colonization by isolate NC1 of *P. fragariae* (DSI = 7) was highly sensitive to this pathogen under controlled environmental conditions. There was a four- to sixfold increase in the percent root necrosis for inoculated treatments relative to the controls, and foliar and root dry weight and number of crowns were significantly lower than controls. The reason for the poor correlation between the disease severity index and growth response of the cultivars Sunrise and Cardinal in environmental growth chambers is not known.

Strawberry cultivars are known to vary greatly in susceptibility to races of *P. fragariae* based on root necrosis and the number of oospores per root (17). The procedure used by Milholland et al (17) is extremely reliable in determining levels of susceptibility to infection and colonization (oospore production) among strawberry genotypes and for the separation of isolates into different pathogenic races. However, the system does not allow plant genotypes with partial (field) resistance to be identified and characterized. Additional studies are needed to identify genetic and epidemiological mechanisms responsible for partial resistance to *P. fragariae* in strawberry cultivars. There appear to be several mechanisms that could be responsible for partial or field resistance in Sunrise and Cambridge Favourite that allows them to grow and yield well despite being susceptible to infection and colonization by *P. fragariae*. It could be attributable to extensive vigor or proliferation of roots or the ability to limit fungal growth and lesion development after initial infection and colonization. Breeders should be aware of the possibility of these types of resistance and develop screening procedures that allow for their selection. In addition, because partial resistance to *P. fragariae* does exhibit some degree of isolate specificity, selection should be against a mixture of isolates that are representative of the pathogen population in a given location.

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LITERATURE CITED

1. Blaker, N. S., and Hewitt, J. D. 1987. A comparison of resistance to *Phytophthora parasitica* in tomato. Phytopathology 77:1113-1116.
2. Bruehl, G. W. 1983. Nonspecific genetic resistance to soilborne fungi. Phytopathology 73:948-951.
3. Converse, R. H., and Scott, D. H. 1962. Physiologic specialization in *Phytophthora fragariae*. Phytopathology 52:802-807.
4. Downs, R. J., and Thomas, J. F. 1983. Phytotron procedural manual for controlled environment research at the Southeastern Plant Environment Laboratory. N.C. Agric. Res. Serv. Tech. Bull. 244. 44 pp.
5. Durner, E. F., and Poling, B. E. 1988. Strawberry developmental responses to photoperiod and temperature: A review. Adv. Strawberry Prod. 7:6-15.
6. George, S. W., and Milholland, R. D. 1986. Inoculation and evaluation of strawberry plants with *Phytophthora fragariae*. Plant Dis. 70:371-375.
7. Goode, P. M. 1956. Infection of strawberry roots by zoospores of *Phytophthora fragariae*. Trans. Br. Mycol. Soc. 39:367-377.
8. Gooding, H. J. 1972. Studies in field resistance of strawberry varieties to *Phytophthora fragariae*. Euphytica 21:63-70.
9. Gooding, H. J. 1973. Methods of evaluating strawberry plants as sources of field resistance to *Phytophthora fragariae* Hickman. Euphytica 22:141-149.
10. Guttridge, C. G., and Anderson, H. M. 1981. Assessing fruit yield characteristics and potential in strawberry. Hortic. Res. 21:83-98.
11. Hickman, C. J. 1940. The red core root disease of the strawberry caused by *Phytophthora fragariae* n.sp. J. Pomol. Hortic. Sci. 18:89-118.
12. Hickman, C. J., and English, M. P. 1951. Factors influencing the development of red core in strawberries. Trans. Br. Mycol. Soc. 34:223-236.
13. Jones, K. J. 1990. Components of resistance in *Nicotiana tabacum* to *Phytophthora parasitica* var. *nicotianae*. Ph.D. thesis. North Carolina State University, Raleigh, NC. 79 pp.
14. Kellam, M. K., and Coffey, M. D. 1985. Quantitative comparison of the resistance to Phytophthora root rot in three avocado rootstocks. Phytopathology 75:230-234.
15. Mason, D. T., and Rath, N. 1980. The relative importance of some yield components in East of Scotland plantations. Ann. Appl. Biol. 95:399-408.
16. McKeen, W. E. 1958. Races of and resistance to *Phytophthora fragariae*. Plant Dis. Rep. 42:768-771.
17. Milholland, R. D., Cline, W. O., and Daykin, M. E. 1989. Criteria for identifying pathogenic races of *Phytophthora fragariae* on selected strawberry genotypes. Phytopathology 79:535-538.
18. Montgomerie, I. G. 1966. Pathogenicity of British isolates of *Phytophthora fragariae* and their relationship with American and Canadian races. Trans. Br. Mycol. Soc. 50:57-67.
19. Montgomerie, I. G. 1977. Red Core Disease of Strawberry. Hortic. Rev. 5, Commonwealth Agricultural Bureau, Farnham Royal. 47 pp.
20. Parlevliet, J. E. 1981. Race-non-specific disease resistance. Pages 47-54 in: Strategies for the Control of Cereal Disease. J. F. Jenkyn and R. T. Plumb, eds. Blackwell Scientific Publications, London.
21. Parlevliet, J. E. 1989. Identification and evaluation of quantitative resistance. Pages 215-248 in: Plant Disease Epidemiology, Genetics, Resistance, and Management. Vol 2. K. J. Leonard and E. Fry, eds. McGraw-Hill, New York.
22. Schmitthenner, A. F. 1985. Problems and progress in control of Phytophthora root rot of soybean. Plant Dis. 69:362-368.
23. Thomison, P. R., Thomas, C. A., Kenworthy, W. J., and McIntosh, M. S. 1988. Evidence of pathogen specificity in tolerance of soybean cultivars to Phytophthora rot. Crop. Sci. 28:714-715.
24. Waldo, G. F. 1953. Sources of red stele root disease resistance in breeding strawberries in Oregon. Plant Dis. Rep. 37:236-242.