Criteria for Identifying Pathogenic Races of *Phytophthora fragariae* on Selected Strawberry Genotypes

R. D. Milholland, W. O. Cline, and M. E. Daykin

Professor, research and extension specialist, and research technician, respectively, Department of Plant Pathology, North Carolina State University, Raleigh 27695-7616.

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ABSTRACT

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The pathogenicity of 12 isolates of *Phytophthora fragariae* was evaluated on 13 strawberry genotypes and then separated into seven distinct pathogenic races by their ability to infect and produce oospores in the roots of a set of differential strawberry hosts. The cultivars Aberdeen, Climax, Stelemaster, Surecrop, and Tennessee Beauty, MD683 selection, and the *Fragaria chiloensis* clone Del Norte are proposed as a new set of differential genotypes for identifying races of *Phytophthora fragariae*. A disease severity index based on the number of oospores in the root stele and the percentage of roots infected with *P. fragariae* is used to determine genotype susceptibility.

The red stele disease of strawberry (*Fragaria* × *annanassa*) caused by *Phytophthora fragariae* Hickman was first observed in 1921 (18) and the causal agent described in 1940 (6). Pathogenic races of *P. fragariae* were reported first by Scott et al (16) in 1950, and later by Hickman and English (7) and Montgomerie (10) in 1951. During the past 30 yr, additional races of *P. fragariae* have been reported by investigators in the United States (2–4,16), United Kingdom (11), Canada (9,14), and Japan (13). Attempts to differentiate races of *P. fragariae* by other physiological characters (8) have been unsuccessful; therefore, the use of differential hosts still provides the best means of separating isolates into pathogenic races.

A disease rating system based on root necrosis and extent of reddened steles has been used almost exclusively to evaluate strawberry genotypes for susceptibilty to *P. fragariae* (4,9,11,15). However, visual disease assessment procedures for red stele are generally subjective and frequently inconsistent. Scott et al (17) reported extremely variable ratings among individual plants to race A-1 of *P. fragariae* with scores ranging from 2 (highly susceptible) to 9 (highly resistant). In addition, disease escapes have been reported (11). A more reliable rating system would be of value in the initial screening of large numbers of seedlings and selections in breeding programs. Bain and Demaree (1) stated that the most dependable proof of infection is the production of oospores of *P. fragariae* in diseased strawberry roots. The method of disease evaluation proposed by George and Milholland (5) provides a reliable and quantitative method of disease evaluation and is particularly useful in race determination.

The present studies were conducted to evaluate the susceptibility of nine selected strawberry cultivars, one selection of *F. annanassa*, and three clones of *F. chiloensis* to the 10 American races of *P. fragariae* and three additional isolates obtained from North Carolina soils. The isolates were then separated into distinct pathogenic races based on the number of oospores in the root stele and the percentage of roots infected with *P. fragariae*. A disease severity index based on the above criteria is proposed for the basis of determining genotype susceptibility.

MATERIALS AND METHODS

Isolates of *P. fragariae*. Cultures of *P. fragariae* were obtained from three sources. Five isolates representing American races A-1, A-2, A-3, A-8, and A-10 were obtained from the American Type Culture Collection as ATCC 13973, 13974, 13977, 16678, and 18638, respectively. Isolates of races A-4, A-5, A-6, A-7, and A-9 were supplied by J. L. Maas, Beltsville, MD, and three isolates designated as NC-1, NC-2, and NC-3 were obtained from infested strawberry fields in Wake, Rockingham, and Perquimans counties, NC, by baiting with the susceptible cultivar, Tennessee Beauty. Stock cultures were maintained in the dark on oatmeal agar (OMA) at 20 C.

Plant sources. Stock plants of the strawberry genotypes used in these studies were obtained from three sources. Tennessee Beauty, Surecrop, and Sparkle were obtained from a registered planting located at the Sandhills Research Station, Jackson Springs, NC. *F. chiloensis* clones Yaquina B and Del Norte, and the selection MD683 were supplied by O. C. Broome, USDA, Fruit Lab, Beltsville, MD. The cultivars Climax, Red Gauntlet, Perle de Prague, Aberdeen, Siletz, and clone Yaquina A of *F. chiloensis* were obtained from the National Clonal Germplasm Repository, Corvallis, OR.

Young runner plants were removed from stock plants in the greenhouse and were placed in 5-cm-diameter clay pots filled with Metro-mix 220 (W. R. Grace & Co., Cambridge, MA) sand and soil 1:1:1 by volume. Plants were placed under intermittent mist at 25–30 C for 8–10 days (unless otherwise noted) to allow for the formation of roots. Plants were removed from the pots, and the roots were carefully and thoroughly rinsed in cool tap water.

Inoculation procedures. Zoospore inoculum of *P. fragariae* was obtained as previously described (5). Roots of all inoculated plants were sprayed with a suspension of nonmotile (encysted) zoospores at $1.2–2.0 \times 10^4$ zoospores per milliliter unless otherwise noted. Nonmotile zoospores were obtained by placing 20 ml of a motile zoospore suspension in a 2.3-cm-diameter test tube, then vibrating the suspension for 1.25 min on a Vortex Jr. mixer (model K-500-J). Plants were placed on a paper towel saturated with tap water, and the encysted zoospores were sprayed over the root system with a DeVilbiss atomizer (about 1.5 ml of inoculum applied to each plant). The paper towels and plants were then placed inside clear plastic bags, closed, and placed in the dark at 15 C for 48 hr. Plants were removed and planted in round, clear-plastic containers (25×9 cm) filled to a depth of 7.5 cm with Metro-mix 220 that had been saturated with tap water and the excess drained off. Each container was placed inside a plastic bag, sealed, then placed under 12 hr fluorescent lights (80 $\mu E \cdot sec^{-1} \cdot m^{-2}$) at 15 C in a walk-in growth chamber (Nussman Refrigeration Co., St. Louis, MO).

Roots were examined for oospore development after 2 wk. Ten root tip segments (6–8 mm long) per plant were evaluated for oospore development as reported previously (5). A disease severity index (DSI) was used to determine genotype susceptibility (DSI = number of oospores per root segment × percent root segments infected ÷ 100). Genotypes with a DSI greater than one were considered to be susceptible, and those with a DSI less than one were resistant.

Inoculum density. The effect of different concentrations of encysted zoospores on disease development was evaluated by spraying the roots of Tennessee Beauty plants that had developed under intermittent mist in the greenhouse for 10 days. Roots were sprayed with a suspension of encysted zoospores at the following concentrations: 2, 4, 8, 16, 20, and 30×10^3/ml. Two plants were inoculated with each zoospore concentration. Equal mixtures of races A-2, A-4, and A-6 were used as the source of inoculum. Ten root tip segments per plant (6–8 mm long) were evaluated for oospore development 2 wk after inoculation. The test was repeated with three concentrations (10, 20, 40×10^3 zoospores per milliliter) of inoculum of race A-6. Four plants of Tennessee Beauty were inoculated with each concentration.

Genotype susceptibility. Nine strawberry cultivars and one selection of *F. annanassa*, and three clones of *F. chloensis* that have been used by different investigators in differentiating races of *P. fragariae* were inoculated with isolates of nine known races of *P. fragariae* and three unidentified isolates designated as NC-1, NC-2, and NC-3. Numerous attempts to produce zoospores of race A-5 were unsuccessful. Four plants of each genotype were inoculated with each of the 12 isolates tested. Ten root segments per plant (6–8 mm long) were removed and observed microscopically for oospores 2 wk after inoculation. The experiment was repeated once.

RESULTS

Inoculum density. The formation of oospores by *P. fragariae* in roots of susceptible strawberry plants increased as the concentration increased from 2 to 30×10^3 zoospores per milliliter. The mean number of oospores per root segment at 2, 4, 8, 16, 20, and 30×10^3 zoospores per milliliter was 0, 9, 64, 70, 68, and 82, respectively. The percent of root segments infected for these same concentrations was 0, 40, 80, 100, 100, and 100, respectively. In the second test, the mean number of oospores/root segment at 10, 20, and 40×10^3 zoospores per milliliter was 109, 117, and 31, respectively. The percent root segments infected for the same concentrations was 87, 100, and 93, respectively.

Genotype susceptibility. Analysis of variance indicated significant differences among isolates of *P. fragariae* and among the strawberry genotypes tested (Tables 1 and 2). Significant interaction among isolates and genotypes ($P > F = 0.0001$) was

TABLE 1. Development of oospores of *Phytophthora fragariae* in roots of selected strawberry hosts 2 wk after inoculation at 15 C

	Root segments with oospores (%)[w]												
	Isolates												
Cultivar	A-1	A-2	A-3	A-4	A-6	A-7	A-8	A-9	A-10	NC-1	NC-2	NC-3	Mean[x]
Tennessee Beauty	49 ab[y]	91 a	83 a	59 c	93 a	90 b	79 a	99 a	85 a	98 a	100 a	100 a	85 a
Del Norte	43 b	54 c	33 c	91 a	80 b	75 c	1 b	84 a	89 a	68 b	88 a	54 c	63 b
Aberdeen	0 c	75 ab	1 d	73 b	54 bcd	100 a	90 a	59 b	0 c	90 a	61 b	68 bc	56 c
Climax	43 b	9 d	84 a	4 d	99 a	0 d	100 a	0 d	0 c	0 c	0 c	0 d	28 e
Perle de Prague	71 ab	0 d	48 c	0 d	81 ab	0 d	91 a	0 d	0 c	1 c	0 c	0 d	24 f
Red Gauntlet	80 a	8 d	80 ab	0 d	73 c	0 d	99 a	3 d	0 c	5 c	0 c	1 d	29 e
Sparkle	43 b	0 d	54 bc	0 d	84 ab	0 d	80 a	0 d	0 c	0 c	0 c	1 d	22 f
MD683	1 c	61 bc	0 d	9 d	41 cd	100 a	98 a	79 ab	11 b	95 a	94 a	88 ab	56 c
Siletz	0 c	0 d	5 d	0 d	30 d	0 d	100 a	0 d	0 c	3 c	0 c	0 d	12 g
Stelemaster	1 c	4 d	0 d	0 d	28 de	1 d	89 a	3 d	3 c	0 c	0 c	0 d	11 g
Surecrop	0 c	56 bc	0 d	0 d	0 e	100 a	72 b	25 c	3 c	63 b	49 b	49 c	35 d
Yaquina B	0 c	0 d	0 d	0 d	1 e	···	0 b	···	0 c	4 c	···	···	0.6 h
Yaquina A	···	···	···	···	···	1 d	0 b	1 d	0 c	0 c	4 c	6 d	3.1 ih
Mean[z]	28 g	30 fg	32 ef	20 h	55 b	39 c	75 a	29 fg	16 i	35 c	32 de	31 ef	

[w] Data are means of eight plants (10 root segments/plant).
[x] Means for cultivar with same letter down columns are not different ($P = 0.05$) by Waller-Duncan k-ratio t-test. $k = 100$, df = 864, $n = 96$.
[y] Means for isolate × cultivar with same letter down columns are not different ($P = 0.05$) by Waller-Duncan k-ratio t-test. $k = 100$, df = 11, $n = 8$.
[z] Means for isolate with same letter across columns are not different ($P = 0.05$) by Waller-Duncan k-ratio t-test. $k = 100$, df = 864, $n = 96$.

TABLE 2. Development of oospores of *Phytophthora fragariae* in roots of selected strawberry hosts 2 wk after inoculation at 15 C

	Oospores/root segment[w]												
	Isolates												
Cultivar	A-1	A-2	A-3	A-4	A-6	A-7	A-8	A-9	A-10	NC-1	NC-2	NC-3	Mean[x]
Tennessee Beauty	26 abc[y]	48 a	49 a	23 b	71 bc	110 a	107 abc	89 a	52 a	176 a	230 a	136 a	93 a
Del Norte	16 c	34 b	6 cd	50 a	76 b	25 b	0.2 c	27 b	49 a	52 c	60 b	69 b	39 b
Aberdeen	0 d	14 c	0 d	8 c	6 cd	111 a	84 abc	7 b	0 b	59 c	14 bc	19 c	27 d
Climax	30 ab	1 d	30 ab	0.7 c	170 a	0 b	212 a	0 b	0 b	0 e	0 c	0 c	37 bc
Perle de Prague	44 a	0 d	16 cd	0 c	150 a	0 b	176 ab	0 b	0 b	0.5 e	0 c	0 c	32 c
Red Gauntlet	35 ab	3 d	18 bcd	0 c	51 bcd	0 b	100 abc	0.3 b	0 b	1 e	0 c	0.1 c	17 ef
Sparkle	28 ab	0 d	24 bc	0 c	51 bcd	0 b	56 bc	0 b	0 b	0 e	0 c	0 c	13 fg
MD683	0.2 c	27 b	0 d	1 c	16 bcd	114 a	118 abc	12 b	4 b	96 b	26 bc	35 bc	37 b
Siletz	0 c	0 d	0.4 d	0 c	6 cd	0 b	223 a	0 b	0 b	0.1 e	0 c	0 c	19 e
Stelemaster	0.2 c	0.2 d	0 d	0 c	6 cd	0 b	131 abc	0 b	0.4 b	0 e	0 c	0 c	11 g
Surecrop	0 c	13 c	0 d	0 c	0 d	89 a	57 bc	2 b	0.1 b	24 d	13 c	9 c	17 ef
Yaquina B	0 c	0 d	0 d	0 c	0.7 d	···	0 c	···	0 b	0.4 e	···	···	0.1 h
Yaquina A	···	···	···	···	···	0 b	0 c	0.1 b	0 b	0 e	0.4 c	0.4 c	0.2 hi
Mean[z]	15 f	12 fg	12 fg	7 h	50 b	37 c	105 a	11 fgh	9 gh	34 c	29 d	27 e	

[w] Data are means of eight plants (10, 6–8-mm root segments/plant).
[x] Means for cultivar with same letter down columns are not different ($P = 0.05$) by Waller-Duncan k-ratio t-test. $k = 100$, df = 864, $n = 96$.
[y] Means for isolate × cultivar with same letter down columns are not different ($P = 0.05$) by Waller-Duncan k-ratio t-test. $k = 100$, df = 11, $n = 8$.
[z] Means for isolate with same letter across columns are not different ($P = 0.05$) by Waller-Duncan k-ratio t-test. $k = 100$, df = 864, $n = 96$.

detected for number of oospores per root segment, and percent roots containing oospores. The overall mean number of oospores per root segment across the 12 isolates tested was highest [93] for the cultivar Tennessee Beauty, and lowest [0.2 and 0.1] for the two clones Yaquina A and B of *F. chiloensis*. Percent root segments of Tennessee Beauty containing oospores ranged from 49 for isolate A-1 to 100 for NC-1 and NC-2 isolates.

The cultivars Climax, Perle de Prague, Red Gauntlet, and Sparkle were similar in response to the isolates tested. Although there were differences in the degree of susceptibility to the individual isolates (number of spores/root segment), the reaction types (susceptible or resistant) to the individual isolates were the same (Table 3). Number of oospores per root segment and percentage of roots with oospores were also very similar in the cultivars Siletz and Stelemaster. Surecrop was different from Stelemaster and Siletz in its response to isolates A-2, A-7, A-8 NC-1, NC-2, and NC-3.

The highest number of oospores per root segment [230] developed in the cultivar Tennessee Beauty when inoculated with isolate NC-2 (Table 2). Isolates A-6 and A-8 were highly pathogenic, infecting 10 of the genotypes tested, whereas isolates A-4 and A-10 were pathogenic on just two to three of the genotypes. Isolate A-8 was the most virulent isolate tested, with an overall mean of 105 oospores per root segment and 75% of the roots with oospores (Tables 1 and 2). Isolates A-4 and A-10 were the least virulent with a mean of seven and nine oospores per root segment, respectively. Isolates A-1 and A-3 were similar in their ability to infect and produce oospores in the roots of the same genotypes. This is evident from their DSI (Table 3) and reaction types (Table 4) and are designated as race Pf-1. Isolates A-2, A-7, NC-1, NC-2, and NC-3 reacted similarly and are designated as race Pf-2. All other isolates tested were different in their ability to infect and produce oospores in the roots of the selected strawberry genotypes, thus isolates A-4, A-6, A-8, A-9, and A-10 would be designated Pf-3, Pf-4, Pf-5, Pf-6, and Pf-7, respectively (Table 4).

DISCUSSION

During the past 30 yr, a great deal of variability has existed within and between experiments when evaluating strawberry plants for resistance to *P. fragariae*. Montgomerie (11) tested the American races (A-1 through A-6) on 16 strawberry cultivars, seedlings, and *Fragaria* spp. and determined that A-1, A-2, A-3, and A-5 were distinct races, but was unable to differentiate A-4 from A-2 or A-6 from A-5. In her test, Del Norte was susceptible to races A-3 and A-6. Converse (4) reported Del Norte to be susceptible to races A-2, A-4, and A-6. In addition, Scott et al (17) reported that MD683 was resistant to race A-2, whereas Converse (2) reported MD683 was susceptible to race A-2. Based on this new system of evaluating genotype susceptibility and using the previous differential genotypes MD683, Del Norte, Aberdeen, Stelemaster, and Yaquina A, our results indicate that A-2, A-7, and the NC isolates are the same, and represent a new race of *P. fragariae*. Attempts to produce zoospores of isolate A-5 were unsuccessful and, therefore, the isolate was not tested. However, isolate A-8 (designated as race Pf-5) was virulent on the same differential genotypes as race A-5 reported by Converse (4). Therefore, if A-5 reacted the same as in previous tests (3,4), its new race designation would be Pf-5. Previously described race A-10 (ATCC 18638) was not pathogenic on Yaquina A and would therefore be classed under the previous system as race A-4. Isolate A-9 was pathogenic on Tennessee Beauty, Del Norte, Aberdeen, and MD683, but not Yaquina A as previously reported (4). A review on the different races and their identification by researchers in the United States, Canada, Great Britain, and Japan is given by Scott et al (15).

The need for more controlled screening procedures for identifying races of *P. fragariae* is well documented (12). Our results indicate there are four major criteria that should be used in

TABLE 3. Disease severity index (DSI) of strawberry cultivars, selection, and clones to different isolates of *Phytophthora fragariae*[x,y,z]

	Isolates												
Cultivar	A-1	A-2	A-3	A-4	A-6	A-7	A-8	A-9	A-10	NC-1	NC-2	NC-3	Mean[y]
Tennessee Beauty	13	44	41	14	65	99	84	88	44	172	230	136	86
Del Norte	7	19	2	46	61	19	0	23	44	35	53	37	29
Aberdeen	0	10	0	6	3	110	76	4	0	53	9	13	23
Climax	13	0	26	0	168	0	212	0	0	0	0	0	35
Perle de Prague	32	0	8	0	122	0	161	0	0	0	0	0	27
Red Gauntlet	28	0	15	0	37	0	99	0	0	0	0	0	15
Sparkle	12	0	13	0	42	0	45	0	0	0	0	0	9
MD683	0	17	0	0	7	114	115	9	0	91	24	31	34
Siletz	0	0	0	0	2	0	223	0	0	0	0	0	19
Stelemaster	0	0	0	0	2	0	116	0	0	0	0	0	10
Surecrop	0	7	0	0	0	89	41	0	0	15	6	4	14
Yaquina B	0	0	0	0	0	...	0	...	0	0	...	...	0
Yaquina A	...	...	...	...	0	0	0	0	0	0	0	0	0
Mean	7	8	7	6	42	36	98	10	7	31	27	18	

[x] Disease severity index (DSI) determined by multiplying the mean number of oospores per root segment times the percent roots with oospores and dividing by 100.
[y] Reaction type classified as susceptible when DSI > 1.0 and resistant when DSI < 1.0.
[z] Data are means of eight plants/10, 6–8-mm root segments/plant, 2 wk after inoculation at 15 C.

TABLE 4. Reaction of seven pathogenic races of *Phytophthora fragariae* on a standard set of strawberry differentials[x]

	Pf-1		Pf-2					Pf-3	Pf-4	Pf-5	Pf-6	Pf-5
Genotypes	A-1	A-3	A-2	A-7	NC-1	NC-2	NC-3	A-4	A-6	A-8	A-9	A-10
Tennessee Beauty	S	S	S	S	S	S	S	S	S	S	S	S
Del Norte	S	S	S	S	S	S	S	S	S	R	S	S
Aberdeen	R	R	S	S	S	S	S	S	S	S	S	R
Climax	S	S	R	R	R	R	R	R	S	S	R	R
MD683	R	R	S	S	S	S	S	R	S	S	S	R
Stelemaster	R	R	R	R	R	R	R	R	S	S	R	R
Surecrop	R	R	S	S	S	S	S	R	R	S	R	R

[x] A genotype was considered to be susceptible when the disease severity index (DSI) (no. oospores per root segment times percent root segments with oospores divided by 100) was > 1.0 and resistant when < 1.0.

inoculating and evaluating strawberry genotypes and separating isolates of *P. fragariae* into distinct pathogenic races. These include the use of young strawberry roots, spraying these roots with a defined number of encysted zoospores, incubating the inoculated plants in a controlled environmental growth chamber, and determining genotype susceptibility by means of a disease severity index.

The age of strawberry roots has a definite influence on disease development by *P. fragariae*. Roots of the susceptible cultivar Tennessee Beauty inoculated with 3×10^4 encysted zoospores per milliliter of isolate A-6, 3 and 12 wk after rooting under intermittent mist differed dramatically in severity of disease. The mean number of oospores produced per root segment for 3 and 12 wk was 22.4 and 0.8, respectively, and the mean percent of roots with oospores was 88 and 0.05, respectively (Milholland, *unpublished*). Results from the tests reported in this paper indicate that inoculated strawberry roots, developed under intermittent mist after 10 days and 2 wk, responded consistently to both virulent and avirulent isolates of *P. fragariae*. Therefore, the age of strawberry roots inoculated with encysted zoospores should be within the range of 10–21 days.

Previous studies with a susceptible cultivar (5) indicated that infection increased as the inoculum was increased from 10 to 100×10^3 zoospores per milliliter, but, with a resistant cultivar, resistance was still evident even at the highest inoculum concentration tested. Wynn (19) found that infection in roots of the susceptible cultivar Blakemore was not influenced by concentrations of motile zoospores within a range of $1–10 \times 10^3$ per milliliter, but infection was erratic at concentrations of $25–50 \times 10^3$ zoospores per milliliter. Our results show that infection in roots of the susceptible cultivar Tennessee Beauty sprayed with encysted zoospores is influenced by inoculum density. Both the number of oospores per root segment and the percent of root segments infected were affected by zoospore concentrations below 10×10^3 per milliliter. No differences in infection were noted within the range of $10–30 \times 10^3$ zoospores per milliliter. Based on our results, inoculation of strawberry roots with encysted zoospores should be in the range of $10–30 \times 10^3$ per milliliter.

The use of controlled environmental chambers to provide optimum moisture and temperature requirements for infection and disease development is essential. Experiments conducted in the greenhouse where temperatures vary and moisture regimes are difficult to maintain have been a major reason for the variability in screening progeny for resistance. In addition to maintaining a temperature of 15 C and the required moisture conditions over the test period, growth chambers allow testing and evaluations throughout the year. Procedures reported previously (5) and used in our present studies in conjunction with the use of plant growth chambers also permit the evaluation of inoculated plants every 2 wk instead of 3–4 mo, when evaluations are made in greenhouse benches.

The development of a disease severity index (DSI) to evaluate susceptibility of strawberry to *P. fragariae* proved to be very effective and reliable. A few oospores frequently developed in highly resistant genotypes such as Stelemaster and Yaquina B, but the percentage of roots with oospores was extremely low. Genotypes such as Siletz, Stelemaster, Surecrop, and the two Yaquina clones that have been reported to be highly resistant in previous tests (2–4,15) usually had a DSI of 0 to most isolates tested, indicating a highly resistant reaction. Tennessee Beauty was susceptible to all isolates of *P. fragariae* tested with a DSI ranging from 13 for isolate A-1 to 230 for NC-2. The lowest DSI reading [2], indicative of a susceptible reaction was recorded for Siletz and Stelemaster inoculated with isolate A-6. The highly virulent isolate A-8 had a mean DSI of 96.7 across the 13 strawberry hosts inoculated. Isolate A-4 was the least virulent with an average DSI of 5.5.

Based on the DSI and subsequent reaction type for the different genotypes to the 12 isolates of *P. fragariae*, a set of seven strawberry hosts were established to differentiate the isolates into seven pathogenic races. We propose that the following strawberry genotypes be adopted as the standard host differentials for identifying races of *P. fragariae*: Tennessee Beauty (Blakemore or Huxley could be used as susceptible controls), Del Norte, Aberdeen, Climax, Stelemaster (Siletz could be substituted for Stelemaster), MD683, and Surecrop. Supplemental differentials may be required after all isolates of *P. fragariae* (11 British, six Canadian, and six Japanese races) have been tested, and as new cultivars of strawberry resistant to *P. fragariae* are developed that will distinguish more clearly between isolates that may be only slightly different on the standard differentials.

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