Identification of and Cultivar Reactions to a New Race (Race 4) of *Peronospora farinosa* f. sp. *spinaciae* on Spinach in the United States

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ABSTRACT

Brandenberger, L. P., Correll, J. C., and Morelock, T. E. 1991. Identification of and cultivar reactions to a new race (race 4) of *Peronospora farinosa* f. sp. *spinaciae* on spinach in the United States. Plant Dis. 75:630-634.

Race 4 of *Peronospora farinosa* f. sp. *spinaciae* was identified on spinach in California and Texas. Differential cultivars used for race identification included Viroflay (susceptible to races 1, 2, and 3), Nores (resistant to races 1 and 2), Califlay (resistant to races 1 and 3), and Polka and St. Helens (resistant to races 1, 2, and 3). All five differentials were susceptible to race 4. All five isolates recovered from spinach in California were identified as race 4. A sugar beet isolate from California did not infect any of the spinach differentials. Of the five isolates recovered from spinach in Texas, two were identified as race 4 and three were identified as race 3. Inoculation tests on 29 commercial cultivars and five Arkansas breeding lines were conducted in controlled environmental chambers with an isolate of race 4 from California and an isolate of race 3 from Washington. Of the 29 cultivars tested, 18 have demonstrated or reported resistance to races 1, 2, and 3; seven have reported resistance to races 1 and 2; and two have reported resistance to races 1 and 3. All 19 cultivars resistant to race 3 tested were resistant to race 3 in our inoculation tests. Arkansas cultivars and breeding lines with reported polygenic resistance to race 3 had susceptible reactions on cotyledons and intermediate reactions on true leaves in race 3 inoculation tests. All cultivars and breeding lines tested were susceptible to race 4.

Spinach (*Spinacia oleracea* L.) is an economically important vegetable crop in many countries with more than 8,000 ha (20,000 acres) grown in the United States annually (9,18). Spinach is grown for both fresh and processing markets in many states, and in Arkansas, Texas, and California accounts for $97–102 million of revenue annually (2). There has been some confusion in recent literature over the nomenclature of the downy mildew pathogen on spinach. The correct name and authorities for this pathogen, according to our interpretation of the rules of the Botanical Code, is *Peronospora farinosa* (Fr.) Fr. f. sp. *spinaciae* Byford (*P. effusa* (Grev.) Ces.) (5).

Downy mildew of spinach is a destructive disease worldwide. In the United States, downy mildew has been reported in all spinach-growing areas (15,17,25, 27,28). When environmental conditions are favorable, epidemics can progress very rapidly and an entire crop may be lost in a short period. In addition to direct yield losses, downy mildew can reduce the quality of both processed and fresh market spinach (21).

Downy mildew on spinach has periodically been a serious problem in commercial plantings in the United States and Europe since before 1900 (14,27). A second physiologic race (race 2) of *P. farinosa* was reported in the Santa Clara Valley, the Salinas Valley, and the Oxnard Plain of California by Zink and Smith in 1958 (28) and in the Netherlands and northwestern Europe by Smith in 1958 (25). A third race was reported by Eenick in the Netherlands in 1976 (11) and was noted as occurring on all cultivars resistant to races 1 and 2 in Europe in 1977 (10). In 1978, Greathead (13) reported a downy mildew epidemic in the Gonzales area of California on a cultivar that was resistant to races 1 and 2. During the fall of 1979, spinach growers throughout California observed the spread of this new race (13). Race 3 of downy mildew was reported in 1982 on spinach in the Uvalde area of Texas (18).

Historically, the control of downy mildew on spinach has been achieved with cultivars with single-gene resistance to a given race of downy mildew (18,24). Many of the cultivars in use today have single-gene resistance to races 1, 2, and 3 of downy mildew combined in hybrids (1,10,18,23,24).

Recently, it was suspected that a new race of *P. f. spinaciae* was observed in production areas of California and Texas on cultivars with known resistance to races 1, 2, and 3. The objectives of this study were to verify that a new race (race 4) of the downy mildew pathogen on spinach was occurring on commercial spinach plantings in the United States and to evaluate spinach cultivars and breeding lines for resistance to this new race. Preliminary reports of this work have been published (3,7).

Accepted for publication 21 December 1990 (submitted for electronic processing).

MATERIALS AND METHODS

Seed preparation and planting. Pregerminated seeds were soaked in distilled water for 48 hr at 8 C, drained, rinsed with distilled water, and placed in a petri dish containing filter paper to absorb excess moisture. The seeds were incubated at 8 C for 48–72 hr, at which time the radicle reached a length of 3–5 mm.

Pregerminated seeds were planted either in 7.5 × 7.5 cm 18-cell flats for producing inoculum or in 31 × 23 × 11 cm polystyrene containers for inoculation tests. The polystyrene containers were modified to allow for bottom drainage by supporting hardware cloth 2 cm above the bottom of the container. A 5-cm layer of peatlite growing medium (Fissurs Sunshine Mix 1, Vancouver, B.C.) was applied to the top of the hardware cloth. Twenty pregerminated seeds were planted per row with five rows per container. Approximately 60 pregerminated seeds were planted per 18-cell flat. Seeds were covered with a thin layer of commercial planting mix (Metro-Mix 200, W. R. Grace & Co., Cambridge, MA). All plants were grown in the greenhouse at temperatures ranging from 15 to 25 C. Plants were watered daily with a dilute nutrient solution consisting of Peters 20-20-20 fertilizer with trace elements at a rate of 120 ppm N-P-K. Plants were inoculated when the first set of true leaves were approximately 2 cm in length (10–24 days after planting).

Experimental design. The inoculation tests for race identification and cultivar screening were set up as a completely randomized block experiment with three replications where each box served as a block. Each box for screening isolates contained five differential test cultivars with one cultivar per row. For screening cultivars to known isolates of races 3 and 4, each box contained four test cultivars and a known susceptible cultivar. Grandstand was used as the susceptible cultivar in race 3 inoculation tests, and St. Helens was used as the susceptible cultivar in race 4 inoculation tests.

Isolates. All isolates were collected by selecting leaves exhibiting symptoms and sporulation of downy mildew. Leaves were placed in plastic bags and stored at 4 C until processed. Several samples

were transported by next-day air service to Fayetteville, AR. The sources of the isolates of *P. f. spinaciae* used are listed in Table 1. One isolate was recovered from spinach in a grocery store in Fayetteville, AR, and one isolate was collected from a commercial sugar beet field in Salinas, CA. A known race 3 isolate and a known race 2 isolate were obtained from other researchers.

The initial inoculations with spores from field isolates were made on Grandstand seedlings. After the fungus had completed one growth cycle, the resulting spores were sprayed on differential cultivars.

A verified race 3 isolate from Washington (designated MV/3) and a verified race 4 isolate from the Oxnard area of California (designated OX/4) were used to inoculate all 34 cultivars and breeding lines in one to nine separate inoculation tests.

Inoculum preparation. MV/3 was grown for a minimum of three growth cycles on cv. Grandstand and was maintained on Grandstand for inoculum production. OX/4 was grown for a minimum of three growth cycles on cv. St. Helens and was maintained on St. Helens for inoculum production. Spores from field isolates were collected by placing symptomatic leaves with evidence of sporulation in a 250-ml widemouth container containing 30 ml of chilled (4 C) distilled water. The closed container was vigorously shaken for approximately 1 min. The suspension was then poured through two layers of cheesecloth. The spore concentration was determined with a hemacytometer and adjusted to between 2.0 and 3.5×10^5 spores per milliliter.

Inoculation. Plants were inoculated by applying 10–15 milliliters of the spore suspension onto a flat or polystyrene container of seedlings. The spore suspension was applied from four directions with a Sigma model S 3257 spray unit (Sigma, St. Louis, MO) at 4.6 kg/cm (65 psi). For each inoculation test, spores were sprayed on petri dishes containing 2% water agar to determine the percentage of spore germination. Inoculated plants were then moved into an unlighted dew chamber and incubated at 15 C. Plants were reinoculated with the same spore suspension, stored at 4 C, after 12–15 hr. Plants were given a total dew period of 24–36 hr. After the dew period, plants were moved to a growth chamber and incubated for 4–6 days at 15–22 C with a 12-hr light, 12-hr dark cycle. Plants were watered daily with the nutrient solution previously described. The incubation period was dependent on the onset of disease symptoms. Initial symptoms appeared either as small (approximately 0.5 cm in diameter), diffuse, yellow-green chlorotic lesions or as a general chlorosis of cotyledons and leaves. After symptoms were observed (5–8 days after the first inoculation), plants were returned to the dew chamber and incubated at 15 C as previously described for 12–24 hr to induce sporulation.

The differential cultivars used for race identification were Viroflay (susceptible to races 1, 2, and 3 of *P. farinosa*) (23), Nores (resistant to races 1 and 2) (22), Califlay (resistant to races 1 and 3) (22,26), and St. Helens and Polka (resistant to races 1, 2, and 3) (1,18).

Of the 34 cultivars and breeding lines inoculated with MV/3 and OX/4, 22 were F_1 hybrids and 12 were open-pollinated (Table 2). One cultivar, Viroflay, had no reported resistance to downy mildew, seven cultivars had reported resistance to races 1 and 2, two cultivars had reported resistance to races 1 and 3, and 18 cultivars had reported resistance to races 1, 2, and 3. Six cultivars and breeding lines from Arkansas are reported to have polygenic resistance to race 3 (12).

Disease rating. After sporulation was induced, test seedlings were rated by examining both the cotyledons and the first set of true leaves of each plant. Disease incidence was recorded as both the mean percentage of plants with at least one cotyledon exhibiting evidence of sporulation and the mean percentage of plants with at least one true leaf exhibiting evidence of sporulation. A cultivar was arbitrarily considered susceptible if the mean disease incidence on the cotyledons was >90% and on true leaves was >85%. A cultivar was considered resistant if the mean disease incidence on the cotyledons and true leaves was <10 and <15%, respectively.

RESULTS

Race identification. Three races (races 2, 3, and 4) of *P. f. spinaciae* were distinguished on the set of differential spinach cultivars used (Table 1). We were unable to obtain a race 1 isolate for testing. Of the five differential cultivars used, Viroflay was susceptible to all three races of *P. f. spinaciae* tested, Nores was susceptible to race 3 isolates but not to race 2 isolates, and Califlay was susceptible to race 2 isolates but not to race 3 isolates. St. Helens and Polka were susceptible only to the recently collected isolates designated race 4. Viroflay, Nores, and Califlay were also susceptible to race 4. Although St. Helens has reported resistance to race 2, in our race 2 inoculation tests, cotyledons did not exhibit a resistant reaction (Table 1).

Eight of the 16 isolates tested on the set of differentials were identified as a new race (race 4) of spinach downy mildew. Five of these eight isolates were from California, two were from Texas, and the remaining one was recovered from spinach in a grocery store in Arkansas (Table 1). Five of the 16 isolates tested were identified as race 3. Three of these isolates were from Texas, and the remaining two were from Arkansas and Tennessee. Of the two isolates received from other researchers, one was verified on our set of differential spinach cultivars as race 2 and the other was verified as race 3. One isolate collected in California from sugar beet did not infect any of the differential spinach cultivars and, therefore, was presumed to be *P. f.* f. sp. *betae* Byford.

Disease incidence on cotyledons. In race 4 inoculation tests, all cultivars and

Table 1. Reaction of differential cultivars to isolates of *Peronospora farinosa* f. sp. *spinaciae*

Isolate/ race ID	Origin		Cultivar reaction[x]				
	State, location	Host	Polka	St. Helens	Nores	Viroflay	Califlay
TF/2	ID, Twin Falls	Unknown	R	R?[y]	R	S	S
BV/3	TX, Batesville	DM9	R	R	S	S	R
LP/3	TX, La Prior	Fall Green	R	R	S	S	R
PS/3	TX, Pearsall	Ozarka	R	R	S	S	R
KB/3	AR, Kibler	Avon	R	R	S	S	R
MV/3	WA, Mt. Vernon	Grandstand	R	R	S	S	R
MP/3	TN, Memphis	Hybrid 7	R	R	S	S	R
OX/4	CA, Oxnard	Jade	S	S	S	S	S
PA/4	CA, Patterson	Polka	S	S	S	S	S
PV/4	CA, Porterville	424	S	S	S	S	S
SA/4	CA, Salinas	St. Helen	S	S	S	S	S
SM/4	CA, Santa Maria	Polka	S	S	S	S	S
FW/4	TX, Farwell	Cascade	S	S	S	S	S
UV/4	TX, Uvalde	Polka	S	S	S	S	S
HP/4	AR, Fayetteville[z]	Unknown	S	S	S	S	S
SB/BEET	CA, Salinas	Sugar beet	R	R	R	R	R

[x] S = >90% incidence on cotyledons and >85% incidence on the true leaves. R = <10% incidence on cotyledons and <15% incidence on the true leaves. Each reaction is the mean of three replications with 20 seedlings per replication.

[y] Disease incidence on cotyledons and true leaves of St. Helens in race 2 inoculation tests was 40 and 2%, respectively (data are the mean of two inoculation tests).

[z] Isolate was recovered from spinach in a grocery store and not from a commercial spinach field.

breeding lines tested were susceptible as indicated by the mean disease incidence on cotyledons. The mean disease incidence on the cotyledons for 11 of the 34 cultivars was 100%, and for the remaining 23 it varied from 93 to 99% (Table 2).

There was a clear distinction between resistant and susceptible cultivars in the race 3 inoculation tests based on the mean disease incidence on cotyledons. Of the 13 susceptible cultivars tested, seven had a mean disease incidence on cotyledons of 100%, whereas the other six had a mean disease incidence of 92–99%. The remaining 19 resistant cultivars had a mean disease incidence on cotyledons below 12% (Table 2).

Disease incidence on true leaves. The mean disease incidence on the true leaves for 31 of the 33 cultivars tested in race 4 inoculation tests was >85%. One cultivar (99x95) and one breeding line (88-380) had a mean disease incidence on true leaves of 85 and 84%, respectively.

There was a demarcation between susceptible and resistant cultivars and breeding lines in the race 3 inoculation tests based on mean disease incidence on the true leaves. Four susceptible cultivars (Grandstand, Indian Summer, Nores, and Viroflay) had a mean disease incidence on true leaves of >88%. Of the 19 cultivars tested resistant to race 3, eight had a mean disease incidence on the true leaves of 0%, whereas the remaining 11 had a mean disease incidence of <8%.

All Arkansas cultivars and breeding lines exhibited a unique reaction to race 3 in our inoculation tests. Although the cotyledons of this material had a mean disease incidence of 90–100% in race 3 inoculation tests and therefore were considered susceptible based on cotyledons, the mean disease incidence on true leaves was well below 85% (Table 2). For example, the cvs. Ozarka II, Ozarka, and Fall Green had a mean disease incidence on the true leaves of 0, 15, and 45%, respectively. The five Arkansas breeding lines (88-380, 88-310, 88-354, 88-117, and 86-70) had a mean disease incidence on true leaves of 0, 18, 24, 33, and 53%, respectively. Thus, these eight lines were considered susceptible to race 3 based on reactions on the cotyledons but were considered intermediate in resistance to race 3 based on reactions on the true leaves (Table 2).

To examine the differential disease reaction on cotyledons and true leaves in race 3 inoculation tests statistically, an Arkansas cultivar (Fall Green) and two Arkansas breeding lines (86-70 and 88-117) were compared with two cultivars known to be susceptible to race 3 (Grandstand and Indian Summer). All five cultivars were included in each of three inoculation boxes, and each inoculation test was repeated three times (Table 3). The mean disease incidence on the cotyledons for all five lines tested was 100% for all three tests. The mean disease incidence on the true leaves for Grandstand and Indian Summer in all three tests was >95%. The mean disease incidence on true leaves of the Arkansas material varied from test to test, but the mean across all three tests for 88-117, Fall Green, and 86-70 was 33, 45, and 53%, respectively. When averaged across all three tests, the mean disease incidence on the true leaves for these three lines was significantly ($P = 0.05$) lower than susceptible cvs. Grandstand and Indian Summer.

DISCUSSION

Our studies verified the occurrence of

Table 2. Reaction of spinach cultivars and breeding lines to an isolate of race 3 and an isolate of race 4 of *Peronospora farinosa* f. sp. *spinaciae*

Cultivar	Reported race resistance[x]	Type[y]	Race 3 Inoculation tests[z] (no.)	Race 3 Infection (%) Cotyledons	Race 3 Infection (%) True leaves	Race 4 Inoculation tests[z] (no.)	Race 4 Infection (%) Cotyledons	Race 4 Infection (%) True leaves
Attica	1, 2, 3	H	0	...	...	2	100	95
Baker	1, 2, 3	H	1	10	4	1	98	100
Carambole	1, 2, 3	H	1	3	2	1	98	95
Cascade	1, 2, 3	H	2	4	1	2	96	93
Chinook II	1, 2, 3	H	2	5	0	1	100	98
Coho	1, 2, 3	H	3	7	5	1	97	88
Crystal Savoy	1, 2, 3	H	1	0	0	4	99	99
CX5044	1, 2, 3	H	1	3	0	2	97	90
Gladiator	1, 2, 3	H	2	4	5	0	...	...
Jade	1, 2, 3	H	2	5	5	1	97	96
Nordic	1, 2, 3	H	1	0	0	2	95	99
Pacifica	1, 2, 3	H	2	0	0	1	98	98
Polka	1, 2, 3	H	3	2	0	1	100	100
Rainier	1, 2, 3	H	2	7	4	2	93	91
Skookum	1, 2, 3	H	2	10	5	3	99	96
St. Helen	1, 2, 3	H	6	0	0	17	99	99
Triangle	1, 2, 3	H	3	0	0	2	98	96
Wolter	1, 2, 3	H	2	0	0	2	99	98
Califlay	1,3	OP	4	5	4	2	99	96
Tyee	1,3	H	2	12	8	3	99	98
Grandstand	1,2	H	12	99	93	10	99	98
Green Valley	1,2	OP	2	99	38	1	100	98
Indian Summer	1,2	H	3	100	98	3	99	99
Nores	1,2	H	2	100	88	2	100	98
99x95	1,2	OP	0	...	...	1	97	85
Ozarka	1,2	OP	3	94	15	1	100	96
Ozarka II	1,2	OP	1	100	0	1	100	100
Fall Green	NPR	OP	3	100	45	5	98	96
86-70	NPR	OP	3	100	53	2	100	99
88-117	NPR	OP	3	100	33	2	100	96
88-310	NPR	OP	2	92	18	2	99	95
88-354	NPR	OP	2	98	24	3	100	99
88-380	NPR	OP	1	100	0	1	94	81
Viroflay		OP	2	98	99	1	100	97

[x] NPR = Not previously reported.
[y] H = Hybrid, OP = open pollinated.
[z] Each test consisted of three replications with 20 seedlings per replication.

a new race (race 4) of *P. f. spinaciae* on spinach in California and Texas. Race 4 appears to be widespread in spinach production areas of California as indicated by the fact that all field isolates collected from areas near Oxnard, Salinas, Santa Maria, Porterville, and Patterson were identified as race 4. The origin of this new race in the United States is not known, but it has been demonstrated that downy mildew of spinach can be seed transmitted (6,16,19). There have been unpublished reports of a new race of downy mildew occurring on spinach in Japan (J. Schafer, *personal communication*). Another possible origin for this new race could be the mutation of an existing race of downy mildew and the subsequent selection of it through the use of single-gene resistance. Race 4 is currently and will probably continue to be a problem in production areas of California because there are currently no commercial cultivars with single-gene resistance to this race. Cultural practices that include year-round production will also provide a continual source of inoculum for future epidemics. The emergency registration of fosetyl-Al (Aliette) in California under Section 18 of the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) has, however, helped to reduce the overall impact of this new race when disease pressure is low and environmental conditions are only moderately favorable for infection.

Race 4 of downy mildew on spinach appears to be less prevalent in the spinach production areas of Texas. This could possibly be attributed to the break in the production cycle where spinach is not grown from April through September and/or climatic conditions that are less favorable for disease development. In addition, the frequent use of the fungicide Ridomil 5G (metalaxyl) as a preplant treatment may have helped to reduce the buildup and spread of this pathogen (8). How race 4 became established in Texas is also not known, but it could have been introduced on seed or on fresh spinach shipped into Texas from other production areas. For example, although race 4 has not been recovered from commercial spinach fields in Arkansas, it has been recovered from spinach in a grocery store in Arkansas.

All of the cultivars and breeding lines tested were considered susceptible to race 4 of downy mildew with none of the cultivars or breeding lines exhibiting single-gene resistance in race 4 inoculation tests. The cultivars tested represented a major portion of those used for commercial spinach production in the United States, including cultivars used for fresh, frozen, and canned spinach. Single-gene resistance in spinach to downy mildew has been used since 1956 for the control of this disease (17,26) and is known to be race specific (1,18,22,23). When race 2 of downy mildew on spinach appeared in the United States in 1958, the resistance gene in Early Hybrid 7 was found to confer resistance to both races 1 and 2, whereas the resistance gene in Califlay did not; both of these genes came from PI 140467 (17,24). In 1976, Eenink determined that the dominant genes for downy mildew resistance against races 1 and 2 were closely linked, as are the dominant genes for downy mildew resistance to races 1 and 3 (10). The linked resistance gene from PI 140467 that conferred resistance to race 2 was useful for resistance to downy mildew until 1979, when race 3 of downy mildew on spinach appeared in the United States (13). The linked gene for race 3 resistance was used in spinach cultivars as early as 1982 (18) and provided resistance to downy mildew on spinach in the United States until 1989, when race 4 apparently became established in California. We are not aware of any commercially available spinach cultivars with single-gene resistance to race 4 of downy mildew at this time.

The spinach breeding program in Arkansas has employed an alternative type of breeding method based on polygenic resistance for disease control. Polygenic resistance is generally considered to be race nonspecific (12,20). The selection process for polygenic resistance is different from that used for single-gene resistance. Selection is for quantitative traits measured under field conditions, such as longer latent periods and/or reduced sporulation. These factors help to reduce overall disease severity. We chose to measure disease incidence on true leaves as well as cotyledons in our inoculation tests to determine if disease incidence on true leaves could be used as a possible measure of polygenic or field resistance.

The data indicate that disease incidence on the true leaves of Arkansas cultivars and breeding lines is much lower than comparable cultivars that are susceptible to race 3 in race 3 inoculation tests. The mean disease incidence on the true leaves in the three inoculation tests indicated a difference between the two susceptible cultivars and the Arkansas material when all three tests were compared. These differences were not quite as apparent in the individual tests. If the resistance expressed in the Arkansas material on the true leaves in race 3 inoculation tests is attributable to polygenic resistance, it may be highly dependent on such variables as incubation temperature, inoculum concentration, and plant nutritional status. This may explain, in part, the variability observed from test to test. This inherent variability may also explain why this differential reaction on the cotyledons and true leaves was not apparent in race 4 inoculation tests.

Because this is the first use of scoring true leaves in resistance screening tests with downy mildew on spinach, this technique needs to be refined by examining individual variables with each of the races. In addition, data on disease reactions on true leaves in controlled environments must be correlated with field studies on polygenic resistance. Some of these studies are currently underway (4).

ACKNOWLEDGMENTS

We thank J. Atkin of the Asgrow Seed Co., M. C. Black of Texas A&M University, S. T. Koike of the University of California, M. Savage of the Alf Christianson Seed Co., and Bill White of the Bill White Seed Co. for providing several of the isolates used in this study.

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Table 3. Differential reaction of cotyledons and true leaves among five spinach cultivars to race 3 of *Peronospora farinosa* f. sp. *spinaceae*

	Disease incidence[w] (%)							
	Test 1		Test 2		Test 3		Mean	
Cultivar	C[x]	TL[y]	C[x]	TL[y]	C[x]	TL[y]	C[x]	TL[y]
Grandstand	100	96 a[z]	100	100 a	100	100 a	100	99 a
Indian Summer	100	95 a	100	100 a	100	100 a	100	98 a
86-70	100	40 b	100	66 b	100	54 bc	100	53 b
Fall Green	100	13 b	100	45 b	100	77 b	100	45 bc
88-117	100	28 b	100	29 b	100	40 c	100	33 c

[w] Each test consisted of three replications with 20 seedlings per replication.
[x] C = Cotyledons.
[y] TL = True leaves.
[z] Numbers followed by the same letter within a column are not significantly different at $P = 0.05$ as determined by a Duncan's multiple range test. Data were analyzed after arcsine transformation.

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