Relative Resistance of 47 Strawberry Cultivars to Powdery Mildew in California Greenhouse and Field Environments

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ABSTRACT

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Forty-seven strawberry cultivars were screened for relative powdery mildew resistance in greenhouse, fruit production field, and propagation nursery trials. Genetic differences contributed a large fraction of the phenotypic variance among cultivars for powdery mildew severity in all three screening environments (plot-mean $H^2 = 0.89 - 0.93$). Powdery mildew reactions were expressed similarly, but not completely, in all three test environments, and greenhouse screening may provide a valuable first step in identifying field-resistant genotypes. Because this trait is highly heritable, considerable potential exists for developing new cultivars with enhanced resistance, and reducing reliance on chemical fungicides for strawberry powdery mildew control.

Powdery mildew of strawberry (*Fragaria* × *ananassa* Duchesne) is caused by the obligate parasite *Sphaerotheca macularis* (Wallr. ex Fr.) Jacz. f. sp. *fragariae* Peries. The pathogen infects all aboveground host organs including leaves, flowers, fruit, and their supporting stems. Powdery mildew–induced yield losses of up to 60% have been reported in the U.S. (10). In California, the marketable fruit yield of Selva, which makes up approximately one-third of the state's strawberry acreage (1), was reduced 35% when the disease was left uncontrolled for the entire fruit production season (M. D. Nelson, unpublished).

Powdery mildew occurs annually in all California fruit production regions. Currently, all commercially grown cultivars are susceptible to infection, although field observations indicate that some are more susceptible than others. In order to minimize infection and associated fruit yield losses, growers use alternating foliar applications of sulfur and myclobutanil (Rally, Rohm and Haas, Philadelphia, PA) as needed throughout the season.

One alternative strategy for control of powdery mildew that has yet to be fully utilized is the identification and incorporation of host resistance genes into commercial cultivars. Differences in varietal susceptibility were first reported by Berkeley almost 150 years ago (3). Since then, other researchers have identified extensive genetic variation for powdery mildew resistance in several strawberry populations (2,5,6,14,16–18). While most of the resistance screening work has been conducted in fruit production field trials, Darrow et al. (5) evaluated varietal reactions in both screenhouse and production field tests. They observed somewhat similar results in the two screening environments, although the relationship between screenhouse and production field observations was not analyzed statistically. Several reports also document the inheritance of powdery mildew resistance in *F.* × *ananassa* (7,9,11–13,15,19). Despite these advances, many of the cultivars grown today both in California and abroad are quite susceptible to the disease and many probably could not be grown commercially without chemical fungicides.

The first objective of this study was to screen 47 strawberry cultivars maintained within the University of California germ plasm collection for relative resistance to powdery mildew infection. If found, highly resistant cultivars could subsequently be incorporated into ongoing disease resistance breeding work. A second objective was to investigate the genetic relationship between resistance expressed in greenhouse-grown versus field-grown plants. The precision of field evaluations of genetic resistance is adversely affected by environmental variation and heterogeneous levels of natural inoculum. More controlled greenhouse screening trials may increase the efficiency of identifying potentially useful parents for use in resistance breeding, but only when relative resistance in the different test environments is conferred by the same sets of genes. A complementary study based on segregating seedling populations demonstrated the importance of both genetic variation for resistance and of inoculum level in obtaining correspondence in test outcomes (15). The study reported herein was conducted to supplement the seedling-based evaluations by extending the analysis to a typical strawberry nursery site and by comparing current and historically important cultivars from the University of California program with a small sample of those adapted to other regions in North America.

MATERIALS AND METHODS

Forty-seven strawberry cultivars were screened for relative resistance to powdery mildew infection at three locations in California: a Davis greenhouse, a Santa Maria fruit production field, and a Winters propagation nursery field. Forty of these cultivars (including two unnamed selections) originated within the University of California strawberry improvement program, whereas seven were developed at other programs in Maryland (Earliglow, Lateglow, Redchief, and Tribute), Washington State (Rainier), and Canada (Glooscap and Totem). Cultural descriptions are given below for each of the three screening trials.

Davis greenhouse test. Dormant runner plants were transplanted 15 February 1994 to 14-cm-diameter plastic pots where they were maintained for the duration of this test. The cultivars were randomized on each of four greenhouse benches, all within one large greenhouse. Each cultivar was represented by eight potted plants, distributed among four benches, treated as replicates, of two plants each. Potted runner plants were watered as needed and fertilized weekly with 250 ml of a 2.4 gm per liter solution of soluble 20-20-20. Plants were inoculated mid-March 1994 at the two- to four-leaf stage with dry *S. macularis* f. sp. *fragariae* conidia of a mass isolate collected in Watsonville, CA. Inocula were first raised in a separate greenhouse on Sunset plants by gently touching infected field-collected leaves to abaxial surfaces of healthy Sunset leaves. Four weeks later, completely and uniformly infected Sunset leaves were used in like manner to inoculate the 47 test cultivars. Each leaf of every test cultivar was

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inoculated using one uniformly infected Sunset leaflet. The test plants were maintained in the greenhouse for nearly 2 months to allow for extensive disease development. Cultivars were evaluated for relative powdery mildew resistance 5 May 1994 by rating the abaxial surfaces of 12 randomly selected leaflets per plant for percent leaflet area infected by *S. macularis* f. sp. *fragariae*.

Santa Maria fruit production field test. Dormant runner plants were transplanted to the field 8 March 1993 at the University of California Cooperative Extension Strawberry Research Facility in Santa Maria, CA. Each cultivar was represented by twelve plants, distributed among three replicates on raised beds, with four plants per replicate. Each bed measured 30.5 cm high and 1.63 m wide, comprised four plant rows, and was covered with clear polyethylene mulch. Cultivars were randomized within each replicate bed and plants were spaced 35 cm down the rows. Plants were grown following standard commercial practices (20) and became naturally infected by indigenous *S. macularis* f. sp. *fragariae* inocula during the course of the season. Cultivars were evaluated for relative powdery mildew resistance 11 June 1993 by rating the abaxial surface of one randomly selected leaflet per plant for percent infection by the pathogen.

Winters propagation nursery field test. An additional five dormant runner plants per cultivar were transplanted within each of two replicate nursery field plots 28 May 1992 at the University of California Wolfskill Experimental Orchard in Winters, CA. The plants were transplanted into single plant rows spaced 1.3 m apart on flat ground, with plants spaced 0.35 cm down the rows. Plants were grown and propagated per standard commercial nursery practices and became naturally infected by indigenous *S. macularis* f. sp. *fragariae* inocula. Cultivars were evaluated for relative powdery mildew resistance 14 November 1992 by rating the abaxial surface of one randomly selected leaflet from each of six randomly selected daughter plants per replicate plot for percent infection by the pathogen.

Powdery mildew severity data from each trial site were subjected to analyses of variance to test the significance of cultivar variances, using expectations of mean squares (Table 1). For the purpose of this study, powdery mildew severity is defined as the mean percent infection of abaxial leaflet surfaces by *S. macularis* f. sp. *fragariae*. The distribution of this original variable from all three test sites was significantly skewed and leptokurtic. Because these distributional features will violate several statistical assumptions of our model, data from each site were treated with a LOGIT transformation prior to performing statistical analyses.

Table 1. Form and expected mean squares for analysis of variance of powdery mildew severity data from 47 strawberry cultivars screened for relative resistance in a greenhouse (Davis, CA), fruit production field (Santa Maria, CA), and propagation nursery (Winters, CA)

Source of variation	Degrees of freedom			Expected mean squares[1]
	Davis	Santa Maria	Winters	
Replications	3	2	1	$\sigma^2_e + 47\ \sigma^2_r$
Cultivar	46	46	46	$\sigma^2_e + k_1\ \sigma^2_v$
Error	138	140	93	σ^2_e

[a] Coefficients for Davis, Santa Maria, and Winters trials, respectively, are k_1 = 4.0, 3.0, and 2.0; σ^2_r, σ^2_v, and σ^2_e are variances due to replications, cultivars, and experimental error, respectively.

Table 2. Powdery mildew severity (percent leaflet area infected, abaxial surface) means and standard deviations from 47 strawberry cultivars screened for relative resistance in a greenhouse (Davis, CA), fruit production field (Santa Maria, CA), and propagation nursery (Winters, CA)

Cultivar	Greenhouse (Davis)[a]		Fruit production field (Santa Maria)[b]		Propagation nursery (Winters)[c]	
	Mean	SD	Mean	SD	Mean	SD
Aiko	13.3	3.7	19.2	5.2	34.6	14.7
Aliso	16.9	3.6	31.7	17.0	6.7	1.2
Aptos	34.0	7.0	35.2	4.3	7.5	2.4
Brighton	55.2	23.3	50.9	14.8	45.8	17.7
Capitola	46.9	13.0	65.0	4.3	43.8	20.6
Carlsbad	30.2	7.3	67.8	8.2	64.6	6.5
Chandler	28.1	7.2	38.8	11.3	35.9	15.3
Cruz	4.6	2.5	12.9	3.2	5.4	0.6
Cuesta	54.2	12.9	50.4	10.7	30.5	5.3
Donner	35.3	15.4	72.1	3.1	42.1	13.6
Douglas	41.3	7.7	30.6	10.0	18.0	1.8
Earliglow	22.0	1.3	34.3	4.8	8.3	3.5
Fern	15.7	10.1	23.8	13.1	5.8	3.5
Fresno	45.6	4.2	63.2	5.4	60.0	7.1
Glooscap	14.8	10.4	25.2	11.8	1.8	1.4
Irvine	16.3	11.5	33.5	11.8	33.0	12.4
Lassen	51.3	10.4	76.0	4.2	52.1	0.6
Lateglow	12.0	3.8	33.3	18.4	20.5	8.8
Mrak	45.4	7.0	83.5	13.2	75.0	2.4
Muir	33.5	14.9	30.6	13.6	56.7	18.9
Oso Grande	7.1	4.4	26.3	7.0	53.4	11.8
Pajaro	36.2	21.1	27.1	8.4	68.4	8.3
Parker	27.2	15.4	31.3	23.4	19.2	14.1
Rainier	44.5	16.5	43.8	20.1	12.9	0.6
Redchief	28.6	10.3	22.9	6.1	3.9	4.4
Salinas	74.6	7.9	76.3	3.8	70.0	4.7
Scott	41.1	8.7	64.2	14.0	4.3	4.9
Seascape	49.3	17.6	43.3	3.8	34.2	5.9
Selva	53.5	4.4	70.8	5.2	62.5	8.2
Sequoia	18.6	5.2	50.7	4.9	15.0	10.6
Shasta	48.4	13.9	89.0	7.7	50.0	1.1
Sierra	42.3	5.0	79.0	8.9	30.5	12.4
Solana	30.1	9.7	24.2	6.3	52.1	3.0
Soquel	7.2	3.7	19.0	5.9	31.7	7.1
Sunset	76.3	16.1	76.1	10.9	71.7	10.6
Tahoe	50.9	15.6	45.4	18.0	61.7	17.7
Tioga	40.4	6.9	46.1	13.4	46.7	16.5
Torrey	57.4	13.1	68.3	16.1	80.9	12.9
Totem	47.7	16.5	47.1	13.4	5.4	4.1
Tribute	11.3	6.0	24.2	15.9	2.5	2.4
Tufts	22.8	6.8	39.6	10.0	45.4	3.0
Tustin	24.9	4.2	58.2	1.9	5.4	4.1
Vista	31.1	15.8	57.0	18.9	45.4	17.1
Wiltguard	7.5	3.3	8.8	3.8	1.3	0.6
Yolo	66.9	11.0	65.6	15.8	59.2	12.9
71.98-605	41.3	8.0	57.9	7.9	75.5	5.3
87.153-2	33.4	11.5	57.5	5.4	38.8	15.9
LSD (P = 0.05)	14.6	...	18.2	...	18.3	...
Means	34.8	20.2	46.8	22.6	36.1	25.3
n	376	376	564	564	564	564

[a] Means calculated from 12 randomly selected leaflets per plant, two plants per replicate, four replicates per cultivar.

[b] Means calculated from one randomly selected leaflet per plant, four plants per replicate, three replicates per cultivar.

[c] Means calculated from one randomly selected leaflet from each of six randomly selected daughter plants per replicate plot, two replicate plots per cultivar.

Table 3. Results from the analysis of variance of LOGIT transformed powdery mildew severity data (percent leaflet area infected, abaxial surface) from 47 strawberry cultivars screened for relative resistance in a greenhouse (Davis, CA), fruit production field (Santa Maria, CA), and propagation nursery (Winters, CA), together with heritability estimates

Source	Greenhouse ratings[a]	Field ratings: Santa Maria[a]	Field ratings: Winters[a]
Replications	1.47**	0.05	4.96**
Cultivar	4.00**	3.17**	5.12**
Error	0.30	0.36	0.34
H^2	0.93	0.89	0.93

[a] Mean squares. ** = statistical significance at the 0.01 probability level.

Plot-mean heritabilities were estimated according to Falconer (8), with $H2 = \sigma^2_g / (\sigma^2_g + \sigma^2_e/n)$, where σ^2_g and σ^2_e are variances due to genotype and error while n is the number of replications. Genotypic correlations between powdery mildew severity ratings evaluated at the three test sites were calculated as in Burdon (4): $r_g(xy) = rp/(\sqrt{H^2_x \cdot H^2_y})$, where r_g is the phenotypic correlation of powdery mildew severity scores based on cultivar means and H^2_x and H^2_y are plot-mean heritabilities for the two different test sites x and y, respectively.

RESULTS AND DISCUSSION

Powdery mildew severity means and standard deviations for each of the 47 cultivars evaluated at the three test sites are summarized in Table 2. Cultivar components of variance were highly significant ($P \leq 0.01$) in all three trials, indicating that extensive genetic variation for powdery mildew resistance was present within the sample of cultivars tested (Table 3). In addition, relatively high heritabilities were obtained from each trial, demonstrating the genetic basis for this trait (Table 3). Because this trait is highly heritable (15), considerable potential exists for developing new commercial cultivars with enhanced resistance and reducing reliance on chemical fungicides for strawberry powdery mildew control.

The extensive variation for powdery mildew resistance observed within the University of California germ plasm corresponds well with wide genetic variation reported for this trait in other strawberry cultivar subpopulations. Further, when comparing the powdery mildew reactions of the reference University of California genotypes with those of strawberry cultivars and selections developed and screened in other North American locations (2,5,6,14,16–18), it is apparent that average susceptibilities do not differ substantially, and that premier California genotypes are comparable with those developed elsewhere.

Table 4. Genotypic correlation (r_g) matrix for powdery mildew severity data (percent leaflet area infected, abaxial surface) from 47 strawberry cultivars screened for relative resistance in a greenhouse (Davis, CA), fruit production field (Santa Maria, CA), and propagation nursery (Winters, CA)

Trial location	r_g: Greenhouse	r_g: Fruit production field
Fruit production field	0.84**[a]	. . .
Propagation nursery	0.65**	0.64**

[a] ** = statistical significance at the 0.01 probability level.

The genotypic correlations (r_g) between resistance traits evaluated in different environments ranged from 0.64 to 0.84 (Table 4), and all correlations were highly significant. These results show that genetic differences in resistance were expressed similarly, but not completely, in all three test environments. Furthermore, approximately half of the genetic variation for resistance detected in the greenhouse environment was common with that detected in the fruit production field and propagation field environments. Consequently, greenhouse screening trials may provide a valuable first step in identifying the most resistant genotypes within a population. These results correspond well with those obtained from University of California strawberry progenies evaluated in greenhouse and fruit production field environments under uniformly high infection levels (15). Although the genetic correlations obtained herein were not complete, greenhouse tests require less time and expense to perform, and they may prove useful to strawberry breeding efforts aimed at early screening or parental selection.

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