# Characterization of Resistance of Spinach to White Rust (*Albugo occidentalis*) and Downy Mildew (*Peronospora farinosa* f. sp. *spinaciae*)

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## ABSTRACT

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Resistance of spinach to white rust (*Albugo occidentalis*) and races 3 and 4 of downy mildew (*Peronospora farinosa* f. sp. *spinaciae*) was quantified on several cultivars and breeding lines in separate field inoculation experiments. Several cultivars and breeding lines from the Arkansas breeding program had undergone repeated field selections for white rust resistance (Fall Green, Ozarka II, FA88-310, FA88-354, and FA86-70) while others had not (Grandstand, St. Helens, and Hybrid 424). Resistance to both diseases was quantified by measuring disease incidence and severity at regular intervals 7–32 days after inoculation. The latent periods and the area under the disease progress curve (AUDPC) also were compared. Overall, the cultivars and breeding lines that had undergone selection for white rust resistance had significantly higher levels of field resistance to both white rust and races 3 and 4 of downy mildew relative to the other cultivars tested. Two cultivars (Fall Green and Ozarka II) and three breeding lines (FA88-354 and FA88-310 or FA86-70) had significantly lower disease incidences and severity ratings to white rust and race 4 of downy mildew on most sampling dates than did St. Helens, Hybrid 424, and Grandstand. The AUDPC for Fall Green, Ozarka II, FA88-354, and FA88-310 or FA86-70 also was significantly lower than that of St. Helens, Hybrid 424, and Grandstand for white rust and race 4 of downy mildew. Fall Green, Ozarka II, and FA88-354 had significantly lower disease incidences and severity ratings than did Grandstand in the race 3 downy mildew tests. The AUDPC for Fall Green, Ozarka II, and FA88-354 also was significantly lower than that of Grandstand in the race 3 downy mildew tests. The estimated latent periods were generally 1–4 days longer for Fall Green, Ozarka II, FA88-354, and FA88-310 or FA86-70 in the white rust and race 3 tests compared with the other cultivars tested. The latent periods for the race 4 tests could not be accurately estimated. Several of the cultivars and breeding lines have measurable levels of field resistance to both white rust and races 3 and 4 of downy mildew and can be used to help manage these economically important diseases of spinach.

Downy mildew and white rust of spinach (*Spinacea oleraceae* L.), caused by the obligate fungal pathogens *Peronospora farinosa* (Fr.:Fr.) Fr. f. sp. *spinaciae* Byford (5) and *Albugo occidentalis* G. W. Wils., respectively, are economically important diseases of spinach in the United States (6,8,18,25). Both diseases can cause substantial yield losses and reduce quality of both fresh and processed spinach (11,32).

*A. occidentalis* was first described on *Chenopodium capitatum* (L.) Aschers. in Colorado in 1907 (33) and on commercial spinach from Virginia in 1910 (30). Currently, white rust is an economically important spinach disease in southern and eastern states including Arkansas, Maryland, New Jersey, Oklahoma, Tennessee, Texas, and Virginia (11,14,30,32; J. Van Derwerken, *personal communication*). The development of spinach cultivars with resistance to white rust was initiated in 1960 through the cooperative efforts of the U.S. Department of Agriculture and Texas A&M University (31). The cultivars Wintergarden, Jewel, and Crystal were jointly released in 1975 by the department and the university. The resistance in these cultivars resulted in a reduction in white rust disease incidence and development compared with susceptible cultivars (31). On the basis of disease observations of $F_1$ progeny from a cross between white rust-resistant breeding lines and susceptible cultivars, Bowers (1) hypothesized that white rust resistance in spinach was under polygenic control.

A spinach breeding program was initiated in Arkansas in 1972 that utilized material from the U.S. Department of Agriculture and others. A field selection process was used to further develop field resistance to white rust as well as to select for resistance to other diseases. A modified recurrent selection breeding method was employed (2). This method involved making field selections of individual plants with the highest levels of white rust resistance and mass-crossing these individuals. Progeny from these crosses were then replanted into the breeding nursery. The process was repeated each year.

Downy mildew has periodically been a serious problem in commercial spinach in the United States and Europe since the late 1800s (6). Four races of the downy mildew pathogen have been reported (6). Race 2 of *P. f. spinaciae* was first reported in California in 1958 (34). Race 3 was reported in California in 1978 (16) and in Texas in 1982 (18). Race 4 was reported in both California and Texas in 1991 (6).

Historically, the control of downy mildew of spinach has been achieved with cultivars utilizing single-gene resistance to a particular race of *P. f. spinaciae* (18,26,27). Typically, single-gene resistance is qualitative. It can readily be screened for in a greenhouse inoculation test and can be quickly incorporated into commercial cultivars. In contrast, horizontal resistance is quantitative. It is usually more difficult to screen for in a greenhouse inoculation test and is difficult to rapidly incorporate into commercial cultivars (21,29). Horizontal resistance has been effectively utilized in many breeding programs because of its putative field durability and race nonspecific interaction (20,28). Numerous components have been used to quantify horizontal resistance, including disease incidence and severity, latent period, and degree of sporulation (17,23).

Field observations of selected spinach cultivars and breeding lines indicated that they may have resistance to both white rust and downy mildew (15). The objective of the current study was to quantify several resistance parameters to both white rust and races 3 and 4 of downy mildew in selected spinach cultivars and breeding lines in separate field inoculation tests. A preliminary report has been published (4).

## MATERIALS AND METHODS

**Fungal isolates.** The isolate of *A. occidentalis* used in the field inoculation tests was collected from spinach at Uvalde, Texas, in 1990 and maintained on the spinach cultivar St. Helens. Isolates of races 3 and 4 of *P. f. spinaciae* were obtained in 1989 from the state of Washington and California, respectively (6). The race 3 isolate was maintained on the spinach cultivar Grandstand, and the race 4 isolate was maintained on St. Helens. Isolates of *P. f. spinaciae* and *A. occidentalis* were periodically stored by freezing leaf material that had sporulating lesions.

**Cultivars.** Five cultivars (Fall Green, Ozarka II, St. Helens, Hybrid 424, and Grandstand) and three Arkansas breeding lines (FA88-354, FA88-310, and FA86-70) were examined (Table 1). The cultivar St. Helens has resistance to races 1, 2, and 3 of downy mildew (18); Hybrid 424, Grandstand, and Ozarka II have resistance to races 1 and 2 (6,22,27). All cultivars and breeding lines used were susceptible to race 4 (6). Because of the unavailability of seed, FA88-354 was not used in all of the tests. FA88-310 was substituted for FA88-354 in the first white rust inoculation test, and FA86-70 was used in the first white rust test under natural epidemic conditions.

The cultivars Fall Green and Ozarka and the breeding lines FA88-354, FA88-310, and FA86-70 were developed over a period of 8–12 yrs with the modified recurrent selection process described earlier. Ozarka and Fall Green were released in 1980 and 1988, respectively (2,15). Ozarka II is a selection from Ozarka (J. Schafer, *personal communication*).

**Transplants and plot design.** Transplants were grown in peatlite growing medium (Fissons Sunshine Mix 1, Vancouver, British Columbia) and 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 grown in the greenhouse at temperatures of 15–30 C for 21–28 days and then transferred to an unheated cold frame for 7–14 days prior to transplanting in the field.

Field plots were fertilized prior to transplanting with 10-20-10 at a rate of 34 kg/ha. Transplants were planted 31 cm apart on 107-cm bed centers to facilitate inoculation and data collection. The plants were watered once after transplanting with a dilute nutrient solution of Peters 20-20-20 at a rate of 500 ppm N-P-K. Following transplanting, supplemental overhead irrigation was used to maintain optimum soil moisture.

**Experimental design.** The experiment was conducted as a randomized complete block design with five replicates. Each replicate consisted of 10 plants per cultivar or breeding line. The white rust experiment was conducted in May 1990 and again in May 1991 at Fayetteville, Arkansas. The race 3 field experiments were conducted in November 1990 and again in May 1991 at Fayetteville and the race 4 experiments in November 1991 and April 1992 at Mt. Vernon, Washington. The race 4 experiments were conducted in Washington because race 4 had not been observed in the field in Arkansas.

**Inoculation procedures.** To collect inoculum of both pathogens, symptomatic leaves with evidence of sporulation were placed in 2-L flasks each containing 1 L of chilled (4 C) distilled water. The containers were sealed and vigorously shaken for approximately 2 min. The suspensions were then poured through two layers of cheesecloth. The spore concentrations were determined with a hemacytometer and adjusted to 2.2–5.0 $\times 10^5$ spores per milliliter for *A. occidentalis* or 0.4–1.5 $\times 10^5$ spores per milliliter for *P. f. spinaciae* (Table 1).

Plants were inoculated at dusk on two consecutive nights. Approximately 6 ml of inoculum was uniformly applied to each plant with a 1-L capacity hand pump sprayer (Spray Pal Household Sprayer #610100, Delta Industries, Ft. Wayne, IN). Leaf wetness was maintained by a mist system during the first 48 h following the initial inoculation. The mist system had 60 mist nozzles on three mist lines (Flora-Mist 300B-8.5 GPH, A. H. Hummert, St. Louis, MO) distributed throughout the plot. Temperature and humidity changes were further buffered in the 1990 white rust test and the 1990 race 3 downy mildew tests by shading the entire field plot with 40% shade cloth suspended 1 m above the soil surface for the duration of the experiments. Temperature, relative humidity, and leaf wetness were monitored with a Campbell micrologger (Campbell Scientific Instruments Co., Logan, UT), and temperature and relative humidity were monitored from a local weather observation station located within five miles of the test site.

**Disease assessment.** Plants were rated for disease at regular intervals 7–32 days after inoculation for the six field inoculation experiments. All leaves of five randomly selected plants per replicate were rated for disease. A rubber band was placed around the newly emerging leaves so that only leaves that were present at the time of inoculation were rated. Disease incidence was recorded as the proportion of total leaves examined that exhibited a disease severity rating of $\geq 1.0$.

Disease severity was assessed on the basis of the percentage of the leaf area covered with sporulating lesions. Downy mildew lesions were considered to be sporulating if the blue gray conidiophores were visible to the unaided eye. White rust lesions were considered to be sporulating if the white sori were visible to the unaided eye. A severity scale of 0–4, where 0 = 0% of the leaf covered with sporulating lesions; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; and 4 = 76–100%, was used in the spring of 1990 for the initial white rust experiment. After the initial experiment, it was determined that this scale was not refined enough to reflect the observable differences in disease severity. Therefore, the scale was modified to 0–6, where 0 = 0% of the leaf covered with sporulating lesions; 1 = 1–10%; 2 = 11–25%; 3 = 26–50%; 4 = 51–75%; 5 = 76–90%; and 6 = 91–100%.

The latent period, typically defined as the time from infection until symptom development or sporulation, is difficult to quantify under field inoculation conditions because of plant-to-plant varia-

TABLE 1. Parameters and conditions for the *Albugo occidentalis* and *Peronospora farinosa* f. sp. *spinaciae* field inoculation experiments

| Experiment | Cultivar tested[z] | Test period | Concentration ($\times 10^5$ spores/ml) | Temperature | | |
|---|---|---|---|---|---|---|
| | | | | Average | Average maximum | Average minimum |
| *A. occidentalis* | | | | | | |
| 1990 | SH, GS, 424, FG, OZ, 310 | 16 April–15 May | 2.5–5.0 | 15.6 | 21.6 | 10.9 |
| 1991 | SH, GS, 424, FG, OZ, 354 | 15 April–10 May | 2.2–3.0 | 16.7 | 22.9 | 11.1 |
| *P. f. spinaciae* | | | | | | |
| Race 3, 1990 | SH, GS, 424, FG, OZ, 354 | 20 November–18 December | 0.4–1.2 | 9.7 | 14.4 | 5.4 |
| Race 3, 1991 | SH, GS, 424, FG, OZ, 354 | 28 March–17 April | 0.4–0.8 | 14.5 | 20.2 | 9.3 |
| Race 4, 1991 | SH, GS, 424, FG, OZ, 354 | 24 October–27 November | 1.1 | 6.8 | 10.6 | 4.3 |
| Race 4, 1992 | SH, GS, 424, FG, OZ, 354 | 15 April–13 May | 1.0–1.3 | 12.4 | 17.7 | 6.3 |

[z]SH = St. Helens; GS = Grandstand; 424 = Hybrid 424; FG = Fall Green; OZ = Ozarka II; 310 = FA88-310; and 354 = FA88-354.

bility. Thus, a modified latent period ($LP_{50}$) was defined as the length of time from inoculation until a cultivar reached 50% of the observed maximum disease incidence for a given experiment. A relatively accurate estimate of the latent period could be obtained by this method because the epidemic typically encompassed a single infection cycle. Linear interpolation was used to calculate latent periods that fell between data points.

The area under the disease progress curve (AUDPC) was determined as described by Campbell and Madden (7). AUDPC per day was determined by dividing the AUDPC by the number of days from inoculation to the last sample date (12).

**Natural epidemics.** White rust disease incidence and severity under natural epidemics were measured on spinach at a breeding nursery near Kibler, Arkansas, in the fall 1990 and spring 1992 growing seasons. The fall 1990 and overwinter 1992 crops were planted 8 September and 12 November, respectively. Ten leaf samples were randomly collected on two or three sample dates for both growing seasons. The sample dates in the 1990 season were 4 and 20 December, and the sample dates in the 1992 season were 13 and 25 March and 3 April. A randomized complete block design with four replicates was used.

**Analysis of data.** Data from each sample day of each experiment were analyzed with analyses of variance, and the means were separated with least significant difference tests where the cultivar effect was significant (24).

## RESULTS

**White rust disease incidence.** Disease incidence of white rust on Fall Green, Ozarka II, and FA88-310 was significantly lower than that on St. Helens, Hybrid 424, and Grandstand for all sample dates in the 1990 inoculation test (Fig. 1A). Disease incidence ratings for Fall Green, Ozarka II, and FA88-310 increased from 0.3, 0.2, and 0.2, respectively, 15 days after inoculation to 0.7, 0.6, and 0.6 after 18 days. Disease incidence ratings for St. Helens, Hybrid 424, and Grandstand increased from 0.7 at 15 days after inoculation to 0.9, 0.8, and 0.9, respectively, after 18 days. In 1991, disease incidence ratings for Fall Green, Ozarka II, and FA88-354 were significantly lower for the first three sample days (13, 15, and 17 days after inoculation) when compared with the other three cultivars (Fig. 1B). Disease incidence ratings for Fall Green, Ozarka II, and FA88-354 increased from 0.1 at 13 days after inoculation to 1.0 after 26 days. After 26 days, disease incidence was 1.0 for all entries.

**White rust disease severity, AUDPC per day, and $LP_{50}$.** Disease severity ratings also were significantly lower for Fall Green, Ozarka II, and FA88-310 or FA88-354 than for St. Helens, Hybrid 424, and Grandstand for all sample dates in the 1990 and 1991 tests (Fig. 1C and D).

In both 1990 and 1991, Fall Green, Ozarka II, and FA88-310 or FA88-354 had significantly lower AUDPC per day when compared with St. Helens, Grandstand, and Hybrid 424 (Table 2).

The $LP_{50}$s for Fall Green, Ozarka II, and FA88-310 or FA88-354 were longer than the $LP_{50}$s for St. Helens, Hybrid 424, and Grandstand. In 1990, Fall Green, Ozarka II, and FA88-310 had an estimated $LP_{50}$ of 15.5 days, while St. Helens, Hybrid 424, and Grandstand had an estimated $LP_{50}$ of $\leq$14.5 days. In 1991, Fall Green, Ozarka II, and FA88-354 had an $LP_{50}$ of 14.0 days, while St. Helens, Hybrid 424, and Grandstand had an $LP_{50}$ of $\leq$12.5 days (sample day 22 was used as the disease incidence maximum to calculate the $LP_{50}$s, because it was apparent that

TABLE 2. Area under the disease progress curve per day for the *Albugo occidentalis* and *Peronospora farinosa* f. sp. *spinaciae* field inoculation tests

| | | | *P. f. spinaciae* | | | |
|---|---|---|---|---|---|---|
| | *A. occidentalis* | | Race 3 | | Race 4 | |
| Cultivar | 1990 | 1991 | 1990 | 1991 | 1991 | 1992 |
| Grandstand | 0.3 b[z] | 2.2 a | 1.5 a | 0.6 a | 0.3 b | 0.3 a |
| St. Helens | 0.4 a | 2.3 a | 0.0 c | 0.0 d | 0.4 b | 0.4 b |
| Hybrid 424 | 0.4 a | 2.3 a | 0.2 b | 0.1 b | 0.5 a | 0.3 a |
| Fall Green | 0.1 c | 1.2 b | <0.1 c | <0.1 bcd | 0.1 c | 0.2 b |
| Ozarka II | 0.1 c | 1.2 b | 0.1 c | 0.1 b | 0.1 c | 0.2 b |
| FA88-310 | 0.1 c | ... | ... | ... | ... | ... |
| FA88-354 | ... | 1.1 b | <0.1 c | <1.1 cd | 0.1 c | 0.1 b |

[z] Numbers followed by the same letter within a column are not significantly different according to a least significant difference test ($P = 0.05$).

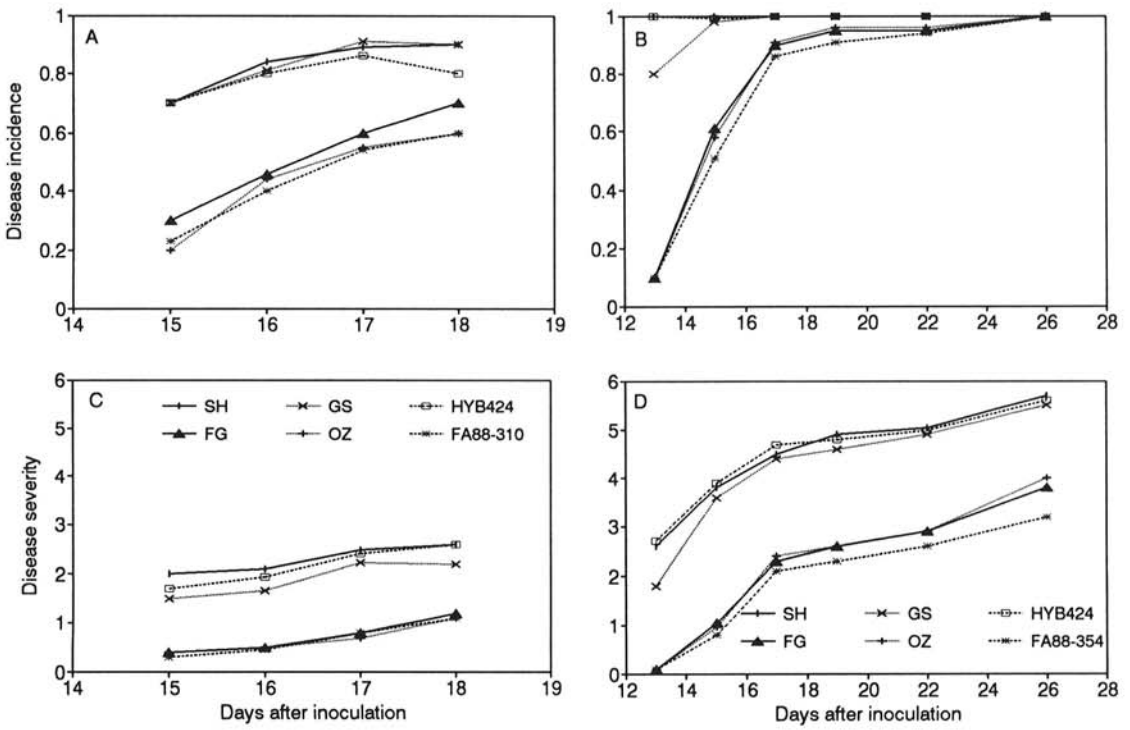


**Fig. 1.** Disease incidence of white rust on spinach cultivars in field inoculation experiments for **A,** 1990 and **B,** 1991 and disease severity for **C,** 1990 and **D,** 1991. SH = St. Helens; GS = Grandstand; HYB 424 = Hybrid 424; FG = Fall Green; and OZ = Ozarka II.

disease incidence on day 26 was likely caused by secondary infections).

Disease incidence and severity were considerably higher in 1991 when compared with the 1990 tests (Fig. 1). For example, in 1990 disease severity ratings for St. Helens, Hybrid 424, and Grandstand were 2.0, 1.7, and 1.5, respectively, 15 days after inoculation and increased to 2.6, 2.6, and 2.2, respectively, after 18 days. In 1991, disease severity ratings for St. Helens, Hybrid 424, and Grandstand were 2.6, 2.7, and 1.8, respectively, 13 days after inoculation and increased to 5.7, 5.6, and 5.5, respectively, on day 17.

**White rust under natural epidemics.** In general, relative disease measurements under natural epidemic conditions were similar to those observed in the inoculation tests. Under natural epidemics, disease incidence was significantly lower for Fall Green, Ozarka II, and FA88-354 or FA86-70 when compared with St. Helens, Hybrid 424, and Grandstand on sample days 1 and 16 in 1990 and on days 12 and 21 in 1992 (Fig. 2A and B). Disease severity for Fall Green, Ozarka II, and FA86-70 or FA88-354 also was significantly lower than that of St. Helens, Hybrid 424, and Grandstand on day 1 in 1990–1991 and on days 12 and 21 in 1992 (Fig. 2C and D).

**Race 3 disease incidence.** In the race 3 downy mildew tests in 1990 and 1991, Fall Green, Ozarka II, and FA88-354 had a significantly lower disease incidence than did Grandstand for all sample dates (Fig. 3A and B). Disease incidence for Grandstand was consistently high for all sample dates in 1990 (Fig. 3A). In 1991, plants were sampled closer to the inoculation date; consequently, a rapid increase in disease incidence was observed on Grandstand between days 10 and 12. A second rapid increase in disease incidence was observed on Grandstand between days 23 and 27 (Fig. 3B); this was probably due to new infections from secondary inoculum. For Fall Green, Ozarka II, and FA88-354, disease incidence ratings increased from 0.01, 0.03, and 0.01, respectively, 13 days after inoculation to only 0.1, 0.2, and 0.1, respectively, after 28 days in 1990 and from 0.0 at 10 days after inoculation to 0.1, 0.3, and 0.1, respectively, after 27 days in 1991. Disease incidence for Hybrid 424 was similar to that for Ozarka II on most sample days in 1990 and on all sample days in 1991 and was not significantly higher than that for Fall Green for day 20 in 1990 and for most sample dates in 1991 (Fig. 3A and B). Disease incidence for Hybrid 424 was significantly higher than that for FA88-354 for all sample dates in both years except sample days 10, 12, and 21 in 1991. No downy mildew was observed on St. Helens in the race 3 inoculation tests. St. Helens has single-gene resistance to race 3 (18).

**Race 3 disease severity, AUDPC per day, and $LP_{50}$.** In both 1990 and 1991, disease severity was significantly lower on Fall Green, Ozarka II, FA88-354, and Hybrid 424 than on Grandstand on all sample dates (Fig. 3C and D). Also, the AUDPC per day for these four cultivars was significantly lower than for Grandstand in both years (Table 2).

For Fall Green, Ozarka II, FA88-354, and Hybrid 424, $LP_{50}$s also were longer than for Grandstand in both years. Grandstand had estimated $LP_{50}$s of $\leq$12.5 days in 1990 and 10.5 days in 1991 (day 16 was used as the disease incidence maximum in 1991 because day 27 likely represented secondary infections). Fall Green, Ozarka II, and FA88-354 had $LP_{50}$s of approximately 15 days in 1990 and 15, 14, and 12.5 days, respectively, in 1991. Hybrid 424 had $LP_{50}$s of 12.3 days in 1990 and 12.5 days in 1991.

**Race 4 disease incidence.** In 1991, St. Helens, Grandstand, and Hybrid 424 also exhibited similar disease incidence curves. Of the cultivars tested, Grandstand exhibited the most rapid increase in disease incidence between days 14 and 32 (Fig. 4A). The disease incidence ratings for Fall Green, Ozarka II, and FA88-354 increased from 0.01, 0.0, and 0.0, respectively, on day 12 to 0.4 on day 32. Disease incidence ratings for Fall Green, Ozarka II, and FA88-354 were significantly lower on all sample days except days 12 and 14 (Fig. 4A). In 1992, disease incidence ratings increased from 0.3, 0.3, and 0.2 on day 15 for Fall Green, Ozarka II, and FA88-354, respectively, to 0.5, 0.6, and 0.4 on day 28 (Fig 4B). St. Helens, Grandstand, and Hybrid 424 had disease incidence ratings on day 15 of 0.6, 0.5, and 0.5, respectively, that increased to 0.9, 0.7, and 0.8 on day 28. Again, disease incidence ratings for Fall Green, Ozarka II, and FA88-354 were significantly lower on all sample days.

**Race 4 disease severity, AUDPC per day, and $LP_{50}$.** Disease severity ratings for Fall Green, Ozarka II, and FA88-354 were significantly lower than those for St. Helens, Hybrid 424, and

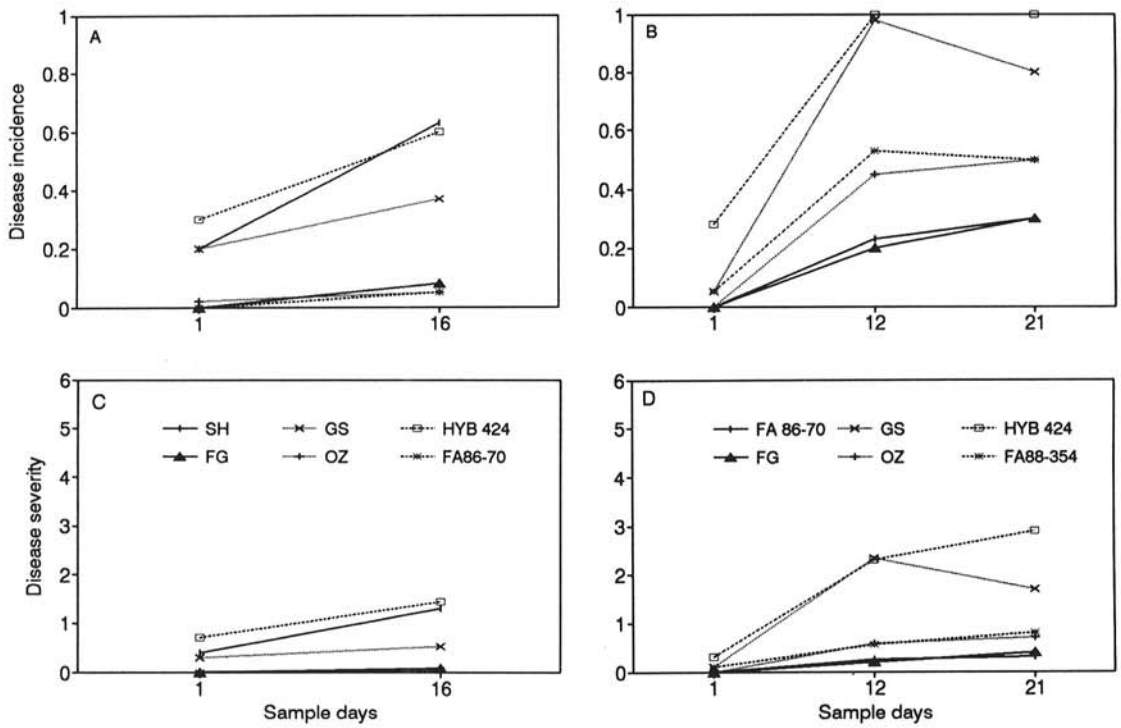


**Fig. 2.** Disease incidence of white rust on spinach cultivars during natural epidemics for **A,** the 1990–1991 and **B,** the 1992 growing seasons and disease severity for **C,** the 1990–1991 and **D,** the 1992 growing seasons. SH = St. Helens; GS = Grandstand; HYB 424 = Hybrid 424; FG = Fall Green; and OZ = Ozarka II.

Grandstand for all sample days except days 12 and 14 in 1991 and day 21 in 1992 (Fig. 4C and D). Also, AUDPC per day for Fall Green, Ozarka II, and FA88-354 was significantly lower than for St. Helens, Hybrid 424, and Grandstand in both years (Table 2).

The $LP_{50}$s could not be accurately estimated in the 1991 or the 1992 race 4 inoculation tests because of the continued increase in disease incidence for all sample dates. Environmental conditions may have favored continuous infections from background inoculum.

## DISCUSSION

Various parameters have been used to quantify horizontal resistance to plant diseases, including disease incidence and severity,

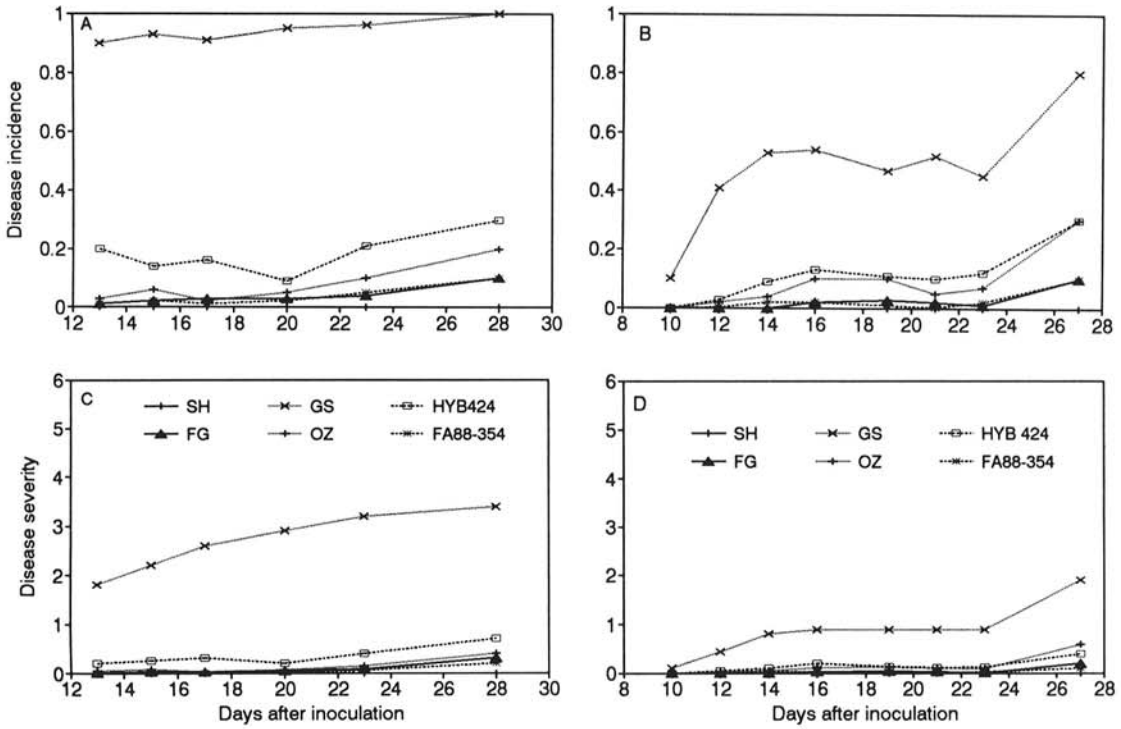


**Fig. 3.** Disease incidence of race 3 of downy mildew on spinach cultivars in field inoculation experiments for **A,** 1990 and **B,** 1991 and disease severity for **C,** 1990 and **D,** 1991. SH = St. Helens; GS = Grandstand; HYB 424 = Hybrid 424; FG = Fall Green; and OZ = Ozarka II.

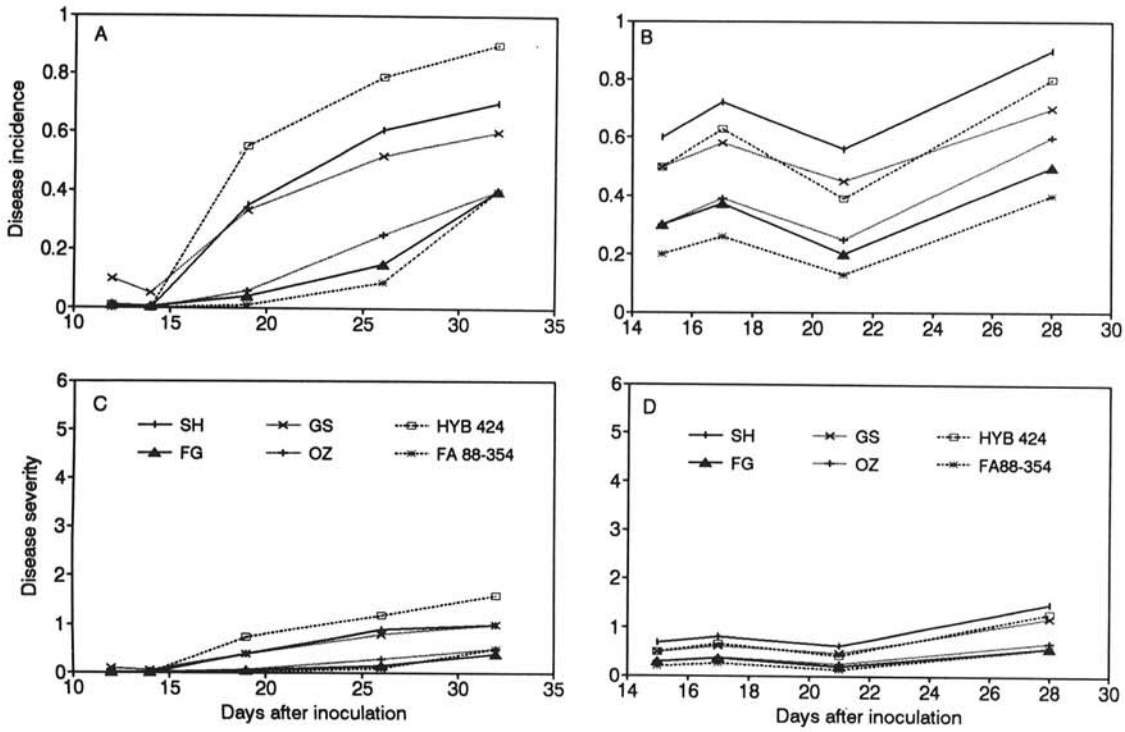


**Fig. 4.** Disease incidence of race 4 of downy mildew on spinach cultivars in field inoculation tests for **A,** 1991 and **B,** 1992 and disease severity for **C,** 1991 and **D,** 1992. SH = St. Helens; GS = Grandstand; HYB 424 = Hybrid 424; FG = Fall Green; and OZ = Ozarka II.

AUDPC, and latent period (13,17). Overall, measurements of disease incidence and severity and AUDPC per day were significantly lower for Fall Green, Ozarka II, FA88-354, and FA88-310 or FA86-70 than for St. Helens, Hybrid 424, and Grandstand in the white rust and races 3 and 4 downy mildew inoculation experiments for most sample dates. Also, estimates of the latent periods were generally 1–4 days longer for the resistant lines for both diseases. Disease assessments on the various cultivars and breeding lines in the white rust field inoculation experiments were similar to those recorded during the natural white rust epidemics in the breeding nursery.

White rust disease incidence, severity, and AUDPC per day were considerably higher in 1991, and the $LP_{50}$ was generally shorter than in 1990. Because quantitative resistance is influenced by environmental conditions, several factors, including higher temperatures during the 1991 test, may have influenced the results obtained (Table 1). White rust developed more quickly at 25 C than at 15 or 20 C in greenhouse inoculation tests (3). In production areas that favor white rust disease development, an integrated approach, including the use of cultivars with quantitative resistance, crop rotation, and preplant fungicide use, has been a very effective disease management strategy (10,19). Because single-gene resistance to white rust is not available for spinach and only a few commercially available cultivars have quantitative resistance to white rust, the development of spinach cultivars with increased levels of white rust resistance will continue to make this type of resistance an effective management tool.

Resistance to white rust and races 3 and 4 of downy mildew in Fall Green, Ozarka II, and FA88-354 was developed primarily from selections of spinach breeding lines that were subjected to repeated white rust epidemics only. The apparent development of resistance to downy mildew was inadvertent. One hypothesis for the simultaneous development of resistance to these two pathogens is that they are closely related, both belonging to the Peronosporales, and similar resistance mechanisms may be operative. In contrast, there may be a link between resistance genes for white rust and those for downy mildew. However, when the probable multigenic nature of horizontal resistance is considered, this seems unlikely. A third hypothesis is that the resistance observed may be more general in nature and effective on multiple diseases. Although the resistance has not been quantified, several of these spinach cultivars have been reported to have resistance to several other soilborne and foliar pathogens (15).

Hybrid 424, which does not have single-gene resistance to race 3 (22,27), showed a somewhat unexpected level of field resistance to race 3 in the field inoculation experiments that was comparable to the resistance measured in Fall Green, Ozarka II, and FA88-354. One possibility for this measurable level of resistance may be the fact that Hybrid 424 and the Arkansas lines have common genetic backgrounds. All were derived from similar U.S. Department of Agriculture parental lines (2,22).

For downy mildew control, it is unlikely that spinach growers would choose cultivars with horizontal resistance over cultivars with single-gene resistance to a particular race. However, cultivars with single-gene resistance are not readily available when new races of downy mildew appear. Furthermore, the spinach downy mildew host-pathogen system is relatively simple; only four races have been reported (6), and thus, it is currently relatively easy to deploy cultivars with single-gene resistance to each of the four races. This may become more difficult as more races of the spinach downy mildew pathogen appear. The deployment of cultivars with single-gene resistance will most likely put selection pressure on the pathogen population, resulting in the development of additional races. A similar scenario has been observed in the lettuce downy mildew host-pathogen system (9).

If commercially acceptable levels of horizontal resistance to downy mildew could be incorporated into commercial cultivars, not only would these cultivars be useful in the 2- to 5-yr time period between the development of a new race and the release of a commercial cultivar with single-gene resistance to the race (as recently occurred in California with race 4), but they could possibly reduce the selection pressure on the downy mildew pathogen population on a regionwide basis. Such a management strategy may also reduce the rate at which new races of this pathogen appear.

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