Management of Powdery Mildew in Summer Squash with Host Resistance, Disease Threshold-based Fungicide Programs, or an Integrated Program

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ABSTRACT

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Powdery mildew resistant (PMR) yellow summer squash (*Cucurbita pepo*) hybrids PSX 2287 and HMX 1707 had significantly lower disease severities than the susceptible hybrids Goldbar and Supersett, respectively. The level of control obtained with host resistance was not as good as that obtained with fungicides (chlorothalonil applied weekly with either triadimefon or benomyl), except when fungicide resistance developed. Average disease severities on 11 September 1991 on adaxial/abaxial leaf surfaces were 3%/0.4% and 0%/0% for nontreated and fungicide-treated PSX 2287, respectively, and 22%/9% and 0%/0% for nontreated and fungicide-treated Goldbar. In 1993, the values were 4%/2%, 0%/0%, 12%/27%, and 0%/15%, respectively, on 30 September, and all *Sphaerotheca fuliginea* isolates from fungicide-treated plants were insensitive to both triadimefon and benomyl. An integrated program was best with PSX 2287: significantly more fruit were produced when fungicides were applied compared with nontreated plants because fruit weight was 40 to 51% higher during the last third of the harvest period. The fungicide-treated susceptible hybrids produced 12 to 34% more fruit than the fungicide-treated PMR hybrids, indicating an inherent difference in yielding potential. Disease severity and yield were similar for plants treated with fungicides on a preventive schedule (six to eight applications) or an IPM schedule with treatment initiated after reaching the threshold of one leaf with symptoms out of 45 old leaves examined (five applications). A disease threshold-based, mid-season fungicide program (three applications, the last one made 3 to 5 weeks before the last harvest) applied to Goldbar was effective because disease development late in the growing season was not associated with a significant reduction in yield compared with a full-season fungicide program.

Additional keywords: cucurbits, economics, integrated pest management

Powdery mildew, caused by *Sphaerotheca fuliginea* (Schlechtend.:Fr.) Pollacci, is an important disease of cucurbits in most production areas in the world. Management is required to avoid a reduction in yield or market quality for most crops. Fungicides are currently the only commercially available management practice for powdery mildew on pumpkin (*Cucurbita pepo* L. and *C. maxima* Duchesne), winter squash (*C. pepo* and *C. moschata* (Duchesne) Duchesne ex Poir.), and summer squash (*C. pepo* L. var. *melopepo* (L.) Alef.). Controlling powdery mildew in summer squash with fungicides increases yield as much as 280% (39). Where feasible, reducing fungicide inputs needed for profitable agriculture is desirable because of societal concerns about possible impacts of pesticides on the environment. A conventional calendar-based fungicide program is initiated before disease detection (preventive schedule) and continued until harvest is complete (full-season). With some diseases, yield may not be affected significantly by fungicides applied before a critical disease severity or incidence level is reached or by applications made near the end of crop development. Genetic, cultural, or biological control practices can also be useful for replacing fungicide inputs. Hybrid cultivars with resistance to powdery mildew are available for cucumber and cantaloupe. Breeders are actively pursuing the incorporation of this resistance into squash and pumpkin.

Several promising powdery mildew resistant (PMR) summer squash hybrids have recently emerged with resistance developed at Cornell University (M. M. Kyle, personal communication). Our objectives were to (i) evaluate two PMR summer squash hybrids for disease development and yield, (ii) evaluate the efficacy of fungicides applied to PMR hybrids and to susceptible hybrids, (iii) determine if powdery mildew can be controlled successfully in summer squash with a disease threshold-based fungicide program (applications initiated after disease detection under an integrated pest management [IPM] scouting program), (iv) determine if the number of fungicide applications can be reduced further without affecting yield by using a disease threshold-based, mid-season fungicide program (treatment stopped 3 to 5 weeks before the completion of harvest), and (v) assess the usefulness of a program that integrates a disease threshold-based fungicide program and host-plant resistance. An additional experiment was conducted to assess direct impacts of fungicides on yield apart from powdery mildew control. Preliminary reports of part of this work have been made (14,15,20,21,23,24,26,27,29,30).

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MATERIALS AND METHODS

Cultural practices. Experiments were conducted on Haven loam soil and Riverhead sandy loam soil at the Long Island Horticultural Research Laboratory (LIHRL) in Riverhead, NY. Fertilizer (10-10-10 or 10-20-20) was preplant broadcast, then incorporated at a rate of 1,120 kg/ha. Three- to four-week-old seedlings were transplanted into plastic mulch at 76-cm plant spacing and 173-cm row spacing. Plots consisted of 4 rows of 6 or 7 plants each. Transplanting dates were 23 July 1991, 10 June 1992, 24 July 1992, and 4 August 1993. Insect pests and weeds were managed as needed by applying pesticides, mechanically cultivating, and hand weeding (14,20,26,27). The fields were irrigated immediately after transplanting and as needed thereafter.

Hybrids. Resistant PSX 2287 and susceptible Goldbar, straightneck yellow squash from Petoseed Company, were used in 1991, 1992, and 1993. Resistant HMX 1707 and susceptible Supersett, crookneck yellow squash from Harris Moran Seed Company, were used in 1993. These PMR hybrids contain resistant material from the Cornell Department of Plant Breeding. They have not been released as yet for commercial production.

Fungicide treatments. A tank mix of triadimefon (0.14 kg a.i./ha Bayleton 50DF) and chlorothalonil (2.81 kg a.i./ha Bravo 720) was applied in alternation with a tank mix of benomyl (0.28 kg a.i./ha Benlate 50DF) and chlorothalonil on a 7-day schedule with a tractor-mounted, boom sprayer equipped with no. 3 hollow cone nozzles delivering 374 liters/ha at 469 kPa. These materials were selected because they were the primary fungicides recommended for commercial use to control powdery mildew of cucurbits in the northeastern U.S. at the time of this study (2,9). The Bayleton label specifies *Erysiphe cichoracearum* because this fungus had been found to be the causal agent of cucurbit powdery mildew in the U.S. before Bayleton was registered for this use and there was concern from experience trying to control *Sphaerotheca* spp. with sterol inhibiting fungicides in Europe (K. Noegel, personal communication). Since the label was written, efficacy against *S. fuliginea* has been demonstrated (12).

The first application under the preventive schedule was made 6 to 12 days after transplanting. The first application in the disease threshold-based fungicide programs was made after the threshold of one leaf with powdery mildew out of 45 old leaves examined was reached in each plot. This threshold is effective for pumpkin (18). Powdery mildew typically develops first on old leaves; therefore, leaves were selected for examination from the older quarter of the canopy, which included the first two to six leaves produced, depending on the overall number of leaves. After treatment was started, fungicides were applied weekly until 1 to 2 weeks before the end of the harvest period (full-season fungicide program) or until 3 to 5 weeks before harvest completion (mid-season fungicide program). In 1991, fungicides were applied eight times (31 July; 8, 16, 23, and 30 August; and 7, 16, and 22 September) for the preventive full-season fungicide program. The disease threshold-based fungicide programs were initiated on 23 August and terminated after three or five sprays on 7 or 22 September, respectively, for the mid-season and full-season programs. Two experiments were conducted in 1992. The "early summer" experiment was conducted early in the growing season when powdery mildew is traditionally less extensive. Fungicides were applied eight times (22 and 29 June; 7, 14, 21, and 30 July; and 6 and 13 August). In the "late summer" experiment in 1992, fungicides were applied six times (30 July; 6, 13, 22, and 30 August; and 5 September) for the preventive full-season fungicide program. Applications for the disease threshold-based fungicide programs were initiated on 13 August for Goldbar and on 22 August for PSX 2287, and terminated after three or five applications, respectively, for the mid-season and full-season programs. In 1993, fungicides were applied six times (16, 22, and 28 August; and 2, 9, and 20 September) for the preventive full-season fungicide program. Fungicide applications were initiated on 22 August after disease detection for the disease threshold-based fungicide programs and terminated after three or five applications, respectively, for the mid-season and full-season programs.

Disease and yield measurements. Leaves were usually examined once a week and powdery mildew colonies were counted or severity was visually estimated as percent leaf area covered by mildew on both adaxial and abaxial leaf surfaces. Initially, 45 old leaves were examined in each plot. With the exception of the early summer 1992 experiment, assessments were also made on fully expanded leaves from the middle and upper thirds of a plant; these represented mid-aged and young leaves, respectively. Eight or 10 leaves were assessed in each age class (total of 24 or 30 leaves). Only sporulating colonies visible to the unaided eye were included in the assessment. Raised chlorotic spots developed occasionally on PSX 2287. An average severity value was calculated for each leaf surface for each plot. Data from all three age classes of leaves were averaged together. Colony counts were converted to severity values by using a conversion factor of 10 colonies = 1%. This factor was derived from colony and leaf sizes measured with a leaf area meter (LI-COR Model LI-3000 portable meter plus Model LI-3050A transparent belt conveyor). Area under the disease progress curve (AUDPC) was calculated by standard iterative procedures (35) for severity from 12 August through 19 September 1991, from 13 July through 19 August 1992, from 12 August through 2 September 1992, and from 25 August through 5 October 1993.

Fruit were harvested, counted, and weighed every 2 to 5 days. All fruit of marketable size were harvested from all plants in each plot except in 1993, when yield data was obtained from 12 plants per plot. The harvest periods extended from 16 August to 30 September 1991 (46 days), from 6 July to 24 August (50 days) and from 21 August to 4 September in 1992 (15 days), and from 30 August to 8 Octo-

Table 1. Effect of using a powdery mildew resistant (PMR) hybrid (PSX 2287) and/or fungicide programs on powdery mildew severity and yield in yellow straightneck squash in 1991

		Adaxial severity[b]		Abaxial severity[b]		Fruit wt (g/plant)[c]			
Hybrid	No. fungicide applications[a]	9/11	AUDPC	9/11	AUDPC	8/16–29	9/3–13	9/16–30	8/16–9/30
PSX 2287 (R)	0	3.2	66.36	0.4	7	207	1,713	606	2,525
PSX 2287 (R)	3	0.0	0.02	0.0	0	241	1,557	1,079	2,878
PSX 2287 (R)	5	0.0	0.03	0.0	0	197	1,632	1,117	2,945
PSX 2287 (R)	8	0.0	0.00	0.0	0	398	1,671	915	2,983
Goldbar (S)	0	22.2	360.02	9.4	270	765	1,914	563	3,242
Goldbar (S)	3	0.2	2.27	0.6	12	473	1,409	952	2,834
Goldbar (S)	5	0.1	4.60	0.8	20	685	1,613	997	3,296
Goldbar (S)	8	0.0	0.02	0.0	2	664	1,673	1,001	3,338
R-0 vs S-0[d]		0.0736[e]	0.0001	0.0001	0.0001	0.0002	0.2594	0.9971	0.0492
R-0 vs S-8		0.0001	0.0005	0.0001	0.7178	0.0011	0.9667	0.0079	0.0301
S-0 vs S-8		0.0001	0.0001	0.0001	0.0001	0.3947	0.2036	0.0043	0.7891
R-0 vs R-8		0.0001	0.0005	0.0001	0.0001	0.0925	0.9570	0.0269	0.1643
S-5 vs S-8		0.0092	0.7776	0.0001	0.0140	0.9216	0.6537	0.7543	0.7050
R-5 vs R-8		0.5781	0.9986	0.4709	0.2085	0.1093	0.6867	0.2022	0.7966
S-3 vs S-5		0.7276	0.8856	0.1001	0.6914	0.3441	0.4200	0.9743	0.4775
R-3 vs R-5		0.7679	0.9993	0.7172	0.3420	0.6641	0.8750	0.8489	0.9914

[a] Fungicides (chlorothalonil at 2.81 kg a.i./ha every 7 days, triadimefon at 0.14 kg a.i./ha every 14 days, and benomyl at 0.28 kg a.i./ha every 14 days) were applied 8, 5, or 3 times in a preventive full-season fungicide program, in a disease threshold-based full-season fungicide program initiated on 23 August after powdery mildew was detected and continued until 1 week before the end of the harvest period, and in a disease threshold-based mid-season fungicide program terminated on 7 September, 3 weeks before the end of the harvest period, respectively.

[b] Exact lesion counts were made when there were less than approximately 50 lesions per leaf. Thereafter, severity was estimated using a conversion factor of 1% = 10 lesions per leaf. Data from an equal number of old, mid-aged, and young leaves were averaged together. Area under the disease progress curve (AUDPC) was calculated for severity from 12 August through 19 September. A natural log transformation was used where necessary to stabilize variance. De-transformed values are presented.

[c] Cumulative weight of marketable-sized fruit harvested every 2 to 5 days over time periods listed.

[d] Planned comparisons. R = PSX 2287. S = Goldbar. Numbers denote the number of fungicide applications.

[e] P values for the planned comparisons. These numbers are significantly different when the P value is < 0.05.

ber in 1993 (40 days). The second experiment in 1992 was terminated prematurely on 8 September because of severe damage from Phytophthora crown rot. Average cumulative yield, expressed as grams of fruit per plant, was calculated for the first third, middle, and last third of the harvest periods.

Fungicide sensitivity. Eight isolates of *Sphaerotheca fuliginea* were collected from fungicide-treated Supersett plants in four plots on 14 October 1993. Fungicide sensitivity was assessed by means of cotyledon leaf disks from fungicide-treated summer squash seedlings (cv. Seneca Prolific). Triadimefon, formulated as technical grade Bayleton 50DF (Bayer Corporation, Kansas City, MO), was used at 0, 6.25, and 50 µg/ml. Blank Bayleton 50DF formulation (Bayer Corp.) was added to these solutions so that they all contained 50 µg of inert ingredients per ml. Benomyl, formulated as Benlate 50DF, was used at 200 µg/ml. Seedlings were sprayed with fungicide solutions by means of a DeVilbiss Model 152 atomizer (DeVilbiss Health Care, Inc., Somerset, PA) operated at 138 kPa, air-dried, then 81-mm^2 disks were cut from leaves with a no. 6 cork borer. Four disks treated with the same fungicide concentration were placed together on 2% water agar in compartmentalized petri dishes with four sections per dish. Approximately three to five conidial chains (15 to 25 conidia) of each isolate were transferred to the center of each of the disks with an eyelash affixed to a disposable pipette. After incubation for 12 days, quantity (percent leaf disk covered with mycelium) and quality of fungal growth were evaluated by means of a dissecting microscope.

Statistical analysis. A randomized complete block design with four replications was used in all tests. Severity data and AUDPC values were transformed by natural log transformation to stabilize variances where necessary based on scattergrams of residuals versus fitted *Y* before subjection to analysis of variance. A square root transformation was not as effective. Because log of 0 is undefined, before transforming the data a value of 0.0022% severity, which is approximately 1 colony on 45 leaves, was assigned to plots where no symptoms had been found. Only severity data collected near the end of the experiment were analyzed. Planned comparisons were made between treatment combinations of interest by means of SuperANOVA version 1.1 for Macintosh computer. Yield data from four plots in 1991 were excluded from analysis because these plants were not as productive as others in this experiment, most likely due to soil conditions.

RESULTS

1991. Powdery mildew was suppressed by fungicides and by the resistant hybrid, PSX 2287 (Table 1 and Fig. 1A). Powdery mildew was first observed on the susceptible hybrid Goldbar on 12 August (day 224), which was 20 days after transplanting and 4 days before the first harvest, and on the PMR hybrid PSX 2287 on 21 August. Eight colonies were found on the abaxial surface of five of the 1,440 leaves examined on 12 August. Powdery mildew severity was low through 30 August (day 242), then increased rapidly in nontreated Goldbar (Fig. 1A). Disease development was suppressed substantially in the resistant hybrid compared with the nontreated susceptible hybrid. However, the level of control achieved with eight fungicide applications to Goldbar was statistically superior to that obtained with nontreated PSX 2287, based on severity ratings for both adaxial and abaxial leaf surfaces on 11 September and based on AUDPC for severity on adaxial leaf surfaces (R-0 versus S-8 in Table 1). The preventive full-season fungicide program with eight applications suppressed powdery mildew significantly ($P \leq 0.0001$) in both PSX 2287 and Goldbar; severity on 11 September was less than 0.1% on both leaf surfaces for these treatments (R-0 versus R-8 and S-0 versus S-8 in Table 1).

The disease threshold-based fungicide programs initiated on 23 August after disease detection provided good disease control. For PSX 2287, there were no significant differences in the level of control achieved with the disease threshold-based fungicide program (five applications) and with the preventive fungicide program (eight applications) (R-5 versus R-8 in Table 1). Although there was more powdery mildew on both the adaxial and abaxial leaf surfaces of Goldbar treated with the disease threshold-based fungicide program (five applications) than with the preventive program, severity was still less than 1%. The disease levels in the two disease threshold-based fungicide programs (three or five applications) were not significantly different (R-3 versus R-5 and S-3 versus S-5 in Table 1). By the end of the experiment, many old leaves had senesced because of powdery mildew on plants of the susceptible hybrid that were not treated with fungicides. In comparison, plants of the susceptible hybrid that had been sprayed with fungicides and plants of the resistant hybrid still appeared relatively healthy.

Yield was affected by genotype and by powdery mildew. Nontreated Goldbar produced significantly more fruit than nontreated PSX 2287 during the first third of the harvest period (16 to 29 August; days 228 to 241) (R-0 versus S-0 in Table 1 and Figure 2A). Goldbar began to produce fruit before PSX 2287 and yielded 270% more fruit by weight per plant early in the season. There were marketable-sized fruit in 14 of 16 plots of Goldbar on 16 August, while only seven plots of PSX 2287 had fruit of sufficient size to warrant harvesting. A hurricane on 19 August (day 231) damaged plants and affected yield for all treatments. There were no significant differences in yield among treatments during the middle of the harvest period (3 to 13 September; days 246 to 256). Powdery mildew greatly reduced yield in both hybrids during the last third of the harvest period (16 to 30 September; days 261 to 273). Yield of nontreated Goldbar began to decline on 18 September (day 261), which was more than 1 week after powdery mildew began to develop rapidly. Goldbar plants sprayed preventively produced 78% higher yield than nontreated Goldbar while PSX 2287 sprayed preventively had 51% higher yield than nontreated PSX 2287. There were no significant yield differences between the disease threshold-based and preventive fungicide programs (R-5 versus R-8 and S-5 versus S-8 in Table 1) or between the two disease threshold-based programs (R-3 versus R-5 and S-3 versus S-5 in Table 1).

1992. Powdery mildew development was suppressed substantially by the fungicide treatment and/or by the resistant hybrid in the early summer experiment (Table 2; Fig. 1B). Substantial powdery mildew developed in this experiment despite our expectations that little disease development would occur early in the season. Symptoms were observed first on 13 July, which was 33 days after transplanting and 7 days after the first harvest. Out of the 16 plots, symptoms were found on 13 July in all four nontreated plots of Goldbar and in three plots of PSX 2287. Only old leaves were examined during this experiment. Powdery mildew development was suppressed significantly in PSX 2287 compared with nontreated Goldbar (R-0 versus S-0 in Table 2). However, genetic control was not as effective as chemical control (R-0 versus S-8 in Table 2). Fungicide treatment provided exceptional disease control in both genotypes: 0 to 2 colonies were found on 45 old leaves examined in each plot throughout the experiment with the exception of one plot on 19 August, the last assessment date.

Yield was affected by genotype and by powdery mildew (Table 2; Fig. 2B). Goldbar began to produce fruit before PSX 2287 and produced more fruit per plant early in the season. There were marketable-sized fruit in all eight plots of Goldbar on 6 July, while only one plot of PSX 2287 had marketable fruit. The average cumulative weight of fruit per plant picked during the first five harvest dates was 828 g for Goldbar (6 to 15 July) and 644 g for PSX 2287 (8 to 17 July). Nontreated plants produced more fruit than fungicide-treated plants between 6 July and 3 August; this difference was statistically significant only for PSX 2287 during the middle of the harvest period (22 July to 3 August) (S-0 versus S-8 and

R-0 versus R-8 in Table 2). Yield was 645 g (17%) lower in nontreated Goldbar than in fungicide-treated Goldbar during the last third of the harvest period (5 to 24 August). Powdery mildew did not have a significant negative impact on yield for PSX 2287 (R-0 versus R-8 in Table 2).

Powdery mildew was not observed in the late summer experiment until 12 August although inoculum was present in the adjacent early summer experiment prior to the late experiment transplant date of 24 July. Fruit in the late experiment plots were up to 5 cm long on 12 August and some reached marketable size by 21 August. Symptoms were found on both hybrids on 12 August, with symptoms more severe on Goldbar. The threshold of one leaf with powdery mildew out of 45 old leaves examined was reached in each plot by 12 August for Goldbar (an average

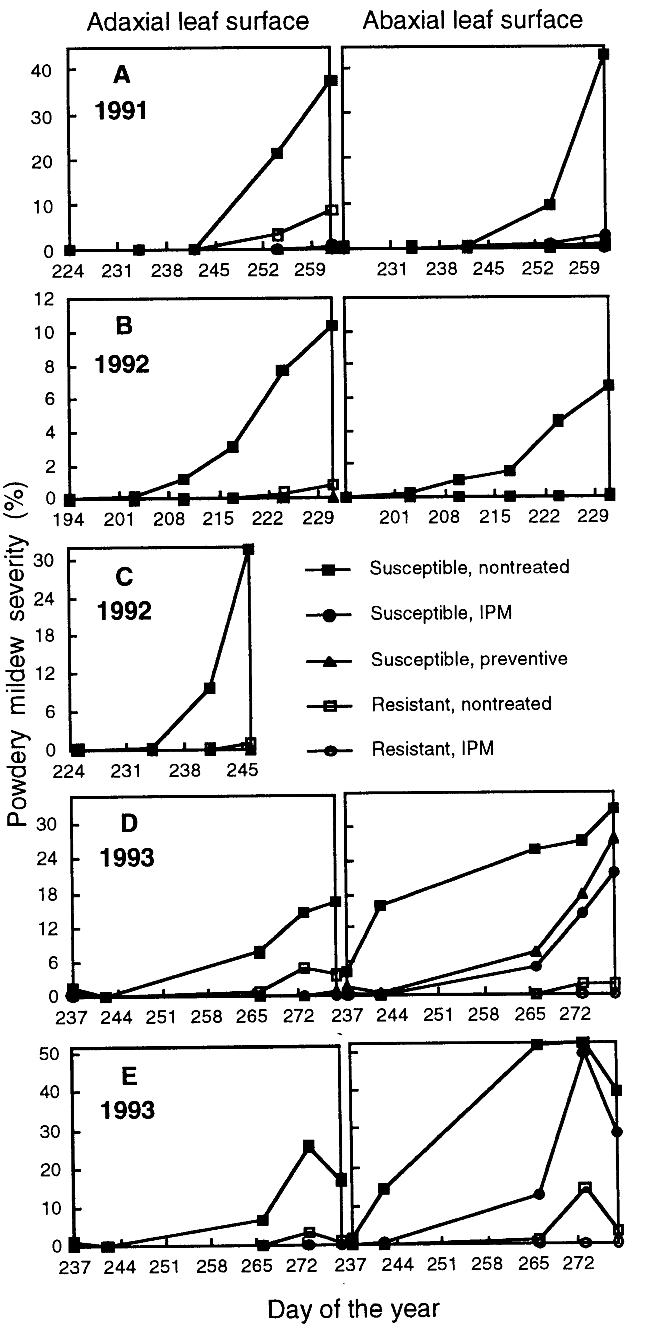

Fig. 1. Powdery mildew progress as affected by host resistance and chemical control in summer squash. The susceptible hybrid was either Goldbar (**A–D**) or Supersett (**E**) and the resistant hybrid was either PSX 2287 (**A–D**) or HMX 1707 (**E**). The fungicide chlorothalonil was applied weekly with either triadimefon or benomyl. The preventive fungicide programs were started 6 to 12 days after transplanting (5 to 8 applications). The disease threshold-based fungicide programs were begun after disease detection through scouting (2 to 5 applications). The second experiment in 1992 (**C**) ended prematurely because of Phytophthora crown rot, therefore only data from the adaxial leaf surface are presented. (**B**) A disease threshold-based fungicide program was not included in this experiment. (**E**) A preventive fungicide program was not included in this experiment.

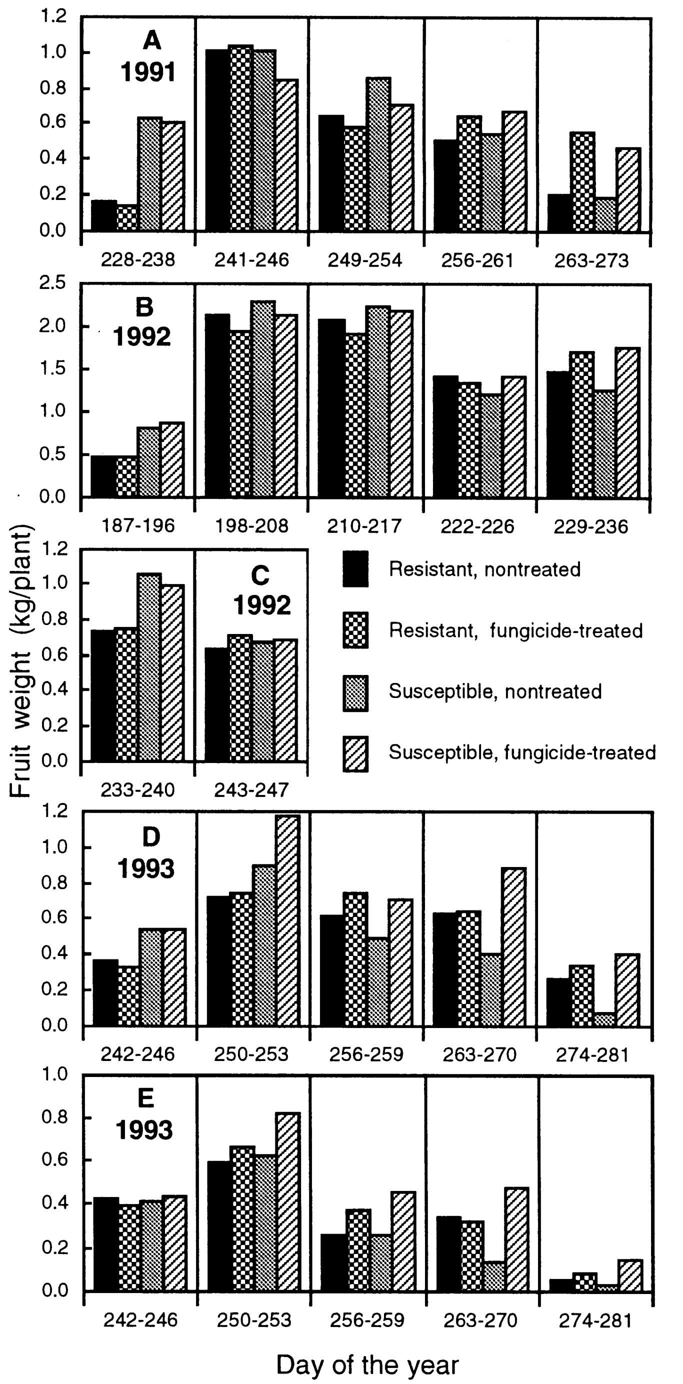

Fig. 2. Average weight per plant of all fruit harvested over each of five time periods for summer squash. The susceptible hybrid was either Goldbar (**A–D**) or Supersett (E) and the resistant hybrid was either PSX 2287 (**A–D**) or HMX 1707 (**E**). The fungicide chlorothalonil was applied weekly with either triadimefon or benomyl beginning after disease detection (2 to 5 applications) (**A, C, D**) or on a preventive schedule (8 applications) (**B**). (**C**) Experiment was terminated early because of Phytophthora crown rot.

of 2 colonies per leaf was found) and by 21 August for PSX 2287 (an average of 0.6 colonies per leaf was found). The disease threshold-based fungicide programs were initiated on 13 August for Goldbar and on 22 August for PSX 2287.

Powdery mildew development was suppressed substantially by the fungicide treatment and/or by the resistant genotype in the late summer experiment (Table 3; Fig. 1C). Disease development on both adaxial and abaxial leaf surfaces was slower in the resistant genotype than in the nontreated susceptible hybrid. However, the level of control achieved with genetic resistance alone was statistically inferior to the level of control achieved with five fungicide applications to Goldbar (based on data from adaxial leaf surfaces) and with the integrated use of genetic and chemical controls (R-0 versus S-5 and R-0 versus R-5 in Table 3). These differences do not appear to be of practical significance. However, complete evaluation of treatments was not possible because of losses from a severe epidemic of Phytophthora crown rot. The preventive fungicide program suppressed powdery mildew development on both adaxial and abaxial leaf surfaces of both genotypes. Powdery mildew generally was more severe at the end of the experiment on plants of both genotypes treated with the disease threshold-based fungicide program (two or three sprays) than on plants treated with the preventive fungicide program (five sprays excluding the application on 5 September); however, yield differences between fungicide-treated and nontreated plants were not significant (S-3 versus S-5 and R-2 versus R-5 in Table 3).

1993. Both genetic control (PSX 2287) and chemical control provided powdery mildew suppression and maintained fruit production during the last third of the harvest period (Table 4; Figs. 1D and 2D). There was less powdery mildew on both leaf surfaces in nontreated PSX 2287 than in nontreated Goldbar; however, this difference was statistically significant only for abaxial leaf surfaces (R-0 versus S-0 in Table 4). Although disease ratings were lower for PSX 2287, nontreated Goldbar produced more fruit during the first third of the harvest period. Host-plant resistance was not as effective as fungicides for powdery mildew control. Compared with fungicide-treated Goldbar, nontreated PSX 2287 had significantly more powdery mildew on adaxial but not on abaxial leaf surfaces, and significantly lower yields (R-0 versus S-6 in Table 4). The difference in yields is partially due to the greater yield potential of Goldbar early in the harvest

Table 2. Effect of using a powdery mildew resistant (PMR) hybrid (PSX 2287) and/or fungicide programs on powdery mildew severity and yield in yellow straightneck squash in early summer, 1992

		Adaxial severity[b]		Abaxial severity[b]		Fruit wt (g/plant)[c]			
Hybrid	**No. fungicide applications[a]**	**8/19**	**AUDPC**	**8/19**	**AUDPC**	**7/6–20**	**7/22–8/3**	**8/5–24**	**7/6–8/24**
PSX 2287 (R)	0	2.48	14.51	0.20	1.63	1,407	2,622	3,517	7,546
PSX 2287 (R)	8	0.00	0.00	0.00	0.03	1,316	2,417	3,662	7,395
Goldbar (S)	0	30.48	261.12	15.55	91.38	1,978	2,794	3,071	7,844
Goldbar (S)	8	0.00	0.00	0.00	0.02	1,932	2,693	3,716	8,341
R-0 vs S-0[d]		0.0001[e]	0.0001	0.0003	0.0087	0.0005	0.0605	0.0511	0.3085
R-0 vs S-8		0.0001	0.0001	0.0002	0.0045	0.0008	0.4038	0.3412	0.0181
S-0 vs S-8		0.0001	0.0001	0.0001	0.0001	0.6767	0.2363	0.0099	0.1049
R-0 vs R-8		0.0001	0.0001	0.0001	0.0050	0.4199	0.0305	0.4831	0.5979

[a] Fungicides (chlorothalonil at 2.81 kg a.i./ha every 7 days, triadimefon at 0.14 kg a.i./ha every 14 days, and benomyl at 0.28 kg a.i./ha every 14 days) were applied 8 times in a preventive full-season fungicide program between 22 June and 13 August.
[b] Exact lesion counts were made when there were less than approximately 50 lesions per leaf. Thereafter, severity was estimated using a conversion factor of 1% = 10 lesions per leaf. Area under the disease progress curve (AUDPC) was calculated for severity from 13 July through 19 August. A natural log transformation was used where necessary to stabilize variance. De-transformed values are presented.
[c] Cumulative weight of marketable-sized fruit harvested every 2 to 5 days over time periods listed.
[d] Planned comparisons. R = PSX 2287. S = Goldbar. Numbers denote the number of fungicide applications.
[e] *P* values for the planned comparisons. These numbers are significantly different when the *P* value is < 0.05.

Table 3. Effect of using a powdery mildew resistant (PMR) hybrid (PSX 2287) and/or fungicide programs on powdery mildew severity and yield in yellow straightneck squash in late summer, 1992

		Adaxial severity[b]		Abaxial severity[b]		Fruit wt (g/plant)[c]		
Hybrid	**No. fungicide applications[a]**	**9/2**	**AUDPC**	**9/2**	**AUDPC**	**8/21–28**	**8/31–9/4**	**8/21–9/4**
PSX 2287 (R)	0	0.08	0.91	0.04	0.80	738	630	1,368
PSX 2287 (R)	2	0.001	0.01	0.004	0.2	745	681	1,426
PSX 2287 (R)	5	0.00	0.00	0.00	0.0	768	678	1,446
Goldbar (S)	0	29.46	134.56	25.89	288.01	1,053	670	1,723
Goldbar (S)	3	0.012	0.04	0.35	19.0	1,055	719	1,773
Goldbar (S)	5	0.00	0.00	0.05	0.19	1,038	783	1,821
R-0 vs S-0[d]		0.0001[e]	0.0008	0.0001	0.0001	0.0015	0.4564	0.0102
R-0 vs S-5		0.0004	0.0001	0.8758	0.1632	0.0002	0.0177	0.0016
S-0 vs S-5		0.0001	0.0001	0.0001	0.0001	0.9580	0.1191	0.4477
R-0 vs R-5		0.0004	0.0001	0.0001	0.0062	0.8441	0.2548	0.5433
S-3 vs S-5		0.5334	0.0082	0.0137	0.0001	0.8391	0.1778	0.6682
R-2 vs R-5		0.4524	0.0737	0.0227	0.1143	0.7744	0.9481	0.8568

[a] Fungicides (chlorothalonil at 2.81 kg a.i./ha every 7 days, triadimefon at 0.14 kg a.i./ha every 14 days, and benomyl at 0.28 kg a.i./ha every 14 days) were applied 5 times in a preventive full-season fungicide program or 2 or 3 times in a disease threshold-based full-season fungicide program initiated after powdery mildew was detected on 13 August for Goldbar and on 22 August for PSX 2287.
[b] Exact lesion counts were made when there were less than approximately 50 lesions per /leaf. Thereafter, severity was estimated using a conversion factor of 1% = 10 lesions per leaf. Data from an equal number of old, mid-aged, and young leaves were averaged together. Area under the disease progress curve (AUDPC) was calculated for severity from 12 August through 2 September. A natural log transformation was used where necessary to stabilize variance. De-transformed values are presented.
[c] Cumulative weight of marketable-sized fruit harvested every 2 to 5 days over time periods listed.
[d] Planned comparisons. R = PSX 2287. S = Goldbar. Numbers denote the number of fungicide applications.
[e] *P* values for the planned comparisons. These numbers are significantly different when the *P* value is < 0.05.

period: nontreated Goldbar produced 33.5% more fruit by weight than nontreated PSX 2287 between 30 August and 10 September. The preventive full-season fungicide program, with six applications, and the disease threshold-based full-season fungicide program, with five applications, provided excellent control of powdery mildew on adaxial leaf surfaces of the susceptible hybrid Goldbar; however, the fungicides were much less effective on abaxial leaf surfaces. Goldbar receiving the preventive fungicide program produced significantly more fruit than nontreated Goldbar throughout the experiment (S-0 versus S-6 in Table 4). Although Goldbar receiving the disease threshold-based mid-season fungicide program (three applications between 22 August and 2 September) was more severely infected during the last third of the harvest period (27 September to 8 October) than Goldbar receiving either the preventive fungicide program (16 August to 20 September) or the disease threshold-based full-season fungicide program (22 August to 20 September), lack of disease suppression late in the growing season was not associated with a significant reduction in yield (S-3 versus S-6 in Table 4). The disease threshold-based fungicide programs were effective although powdery mildew severity at the time of the first application greatly exceeded the threshold of one out of 45 leaves with symptoms (severity was not quantified on 20 August). An integrated management program (fungicides applied to PSX 2287) provided exceptional control of powdery mildew on both leaf surfaces, with a significant yield response during the latter stage of harvest (R-0 versus R-6 in Table 4). Powdery mildew reduced yields more on the susceptible hybrid. During the last 2 weeks of the harvest period, fungicide-treated Goldbar produced 366% more yield than nontreated plants while the difference was only 40.5% for PSX 2287. The disease threshold-based mid-season fungicide program more effectively reduced powdery mildew on abaxial leaf surfaces when the resistant hybrid was used.

Powdery mildew development in yellow crookneck squash was suppressed substantially in the resistant hybrid HMX 1707 and/or by fungicides applied after disease detection (Table 5 and Fig. 1E). There was less powdery mildew on both adaxial and abaxial leaf surfaces in nontreated HMX 1707 than in nontreated susceptible Supersett. HMX 1707 also produced significantly more yield during the last third of the harvest period (R-0 versus S-0 in Table 5 and Figure 2E). Host-plant resistance compared favorably with chemical control in this test, as there was significantly less powdery mildew on abaxial leaf surfaces of nontreated HMX 1707 compared with the fungicide-treated susceptible hybrid Supersett (R-0 versus S-5 in Table 5). However, powdery mildew was more severe on adaxial surfaces of nontreated HMX 1707 and fungicide-treated Supersett produced significantly more yield than nontreated HMX 1707 (R-0 versus S-5 in Table 5). Supersett receiving the disease threshold-based fungicide program had significantly less powdery mildew and produced significantly more yield than nontreated Supersett (S-0 versus S-5 in Table 5). The fungicides were not as effective on abaxial leaf surfaces as on adaxial leaf surfaces of the susceptible plants. An integrated management program (fungicides applied to HMX 1707) provided exceptional control of powdery mildew on both leaf surfaces but did not result in a significant increase in yield. During the last 2 weeks of the harvest period, fungicide-treated Supersett produced 86% more yield than nontreated plants, whereas only a 24% yield increase was recorded when HMX 1707 was treated.

Fungicide sensitivity. All eight isolates collected at the end of the experiment in 1993 from fungicide-treated Supersett were insensitive to 50 µg of triadimefon and 200 µg of benomyl per ml, indicating development of fungicide resistance in the field plots.

DISCUSSION

The PMR summer squash hybrids evaluated in 1991 to 1993 performed well, particularly in terms of disease suppression, compared with horticulturally comparable susceptible hybrids being grown commercially in the United States. The differences in powdery mildew ratings between these PMR and susceptible hybrids were consistently much greater than the differences reported previously between the least and most susceptible, commercially available yellow crookneck cultivars evaluated in Florida (33). In the

Table 4. Effect of using a powdery mildew resistant (PMR) hybrid (PSX 2287) and/or fungicide programs on powdery mildew severity and yield in yellow straightneck squash in 1993

Hybrid	No. fungicide application[a]	Adaxial severity[b] 9/30	Adaxial severity[b] AUDPC	Abaxial severity[b] 9/30	Abaxial severity[b] AUDPC	Fruit wt (g/plant)[c] 8/30–9/10	Fruit wt (g/plant)[c] 9/13–24	Fruit wt (g/plant)[c] 9/27–10/8	Fruit wt (g/plant)[c] 8/30–10/8
PSX 2287 (R)	0	4.20	44.26	2.02	20.02	1,080	1,070	442	2,591
PSX 2287 (R)	3	0.49	6.79	0.04	1.92	1,121	1,201	628	2,950
PSX 2287 (R)	5	0.00	0.13	0.00	0.45	1,075	1,243	488	2,806
PSX 2287 (R)	6	0.00	0.01	0.00	0.01	1,132	1,209	621	2,963
Goldbar (S)	0	12.34	229.75	27.40	887.38	1,442	799	164	2,405
Goldbar (S)	3	5.13	57.00	38.60	600.22	1,781	1,420	811	4,013
Goldbar (S)	5	0.01	1.34	17.89	306.46	1,727	1,378	623	3,728
Goldbar (S)	6	0.02	0.15	14.54	221.58	1,769	1,442	764	3,975
R-0 vs S-0[d]		0.1724[e]	0.2203	0.0001	0.0001	0.0107	0.0250	0.0005	0.3585
R-0 vs S-6		0.0001	0.0003	0.0147	0.0584	0.0001	0.0033	0.0001	0.0001
S-0 vs S-6		0.0001	0.0001	0.0126	0.0001	0.0193	0.0001	0.0001	0.0001
R-0 vs R-6		0.0001	0.0001	0.6731	0.8444	0.6881	0.2293	0.0151	0.0768
S-3 vs S-6		0.0001	0.0002	0.0001	0.0011	0.7454	0.5763	0.0514	0.2293
R-3 vs R-6		0.0001	0.0001	0.9929	0.9851	0.6629	0.7649	0.0621	0.4398
S-3 vs S-5		0.0001	0.0090	0.0003	0.0082	0.6761	0.7124	0.0115	0.1676
R-3 vs R-5		0.0001	0.0059	0.9929	0.9885	0.7272	0.7087	0.0507	0.4772

[a] Fungicides (chlorothalonil at 2.81 kg a.i./ha every 7 days, triadimefon at 0.14 kg a.i./ha every 14 days, and benomyl at 0.28 kg a.i./ha every 14 days) were applied 6, 5, or 3 times in a preventive full-season fungicide program initiated on 16 August, in a disease threshold-based full-season fungicide program initiated on 22 August after powdery mildew was detected and continued until 18 days before the end of the harvest period, and in a disease threshold-based mid-season fungicide program terminated on 2 September, 5 weeks before the end of the harvest period, respectively.

[b] Exact lesion counts were made when there were less than approximately 50 lesions per leaf. Thereafter, severity was estimated using a conversion factor of 1% = 10 lesions per leaf. Data from an equal number of old, mid-aged, and young leaves were averaged together. Area under the disease progress curve (AUDPC) was calculated for severity from 25 August through 5 October. A natural log transformation was used where necessary to stabilize variance. De-transformed values are presented.

[c] Cumulative weight of marketable-sized fruit harvested every 2 to 5 days over time periods listed.

[d] Planned comparisons. R = PSX 2287. S = Goldbar. Numbers denote the number of fungicide applications.

[e] P values for the planned comparisons. These numbers are significantly different when the P value is < 0.05.

present study, important host-plant resistance was documented: significant differences were detected in ratings for both leaf surfaces between the nontreated PMR and susceptible hybrids in four of the five experiments. Previous comparisons revealed significant differences in only 1 of 3 years (33). Average powdery mildew severity remained less than 5% on both adaxial and abaxial leaf surfaces of nontreated PSX 2287 whereas severity was three to 647 times higher for nontreated susceptible Goldbar and frequently exceeded 20% at the end of each experiment.

The resistant hybrids did not produce as much fruit as the susceptible hybrids. The fungicide-treated susceptible hybrids produced more fruit than the fungicide-treated PMR hybrids in all experiments, indicating a genetic difference in yielding ability. Nontreated Goldbar produced significantly more fruit than PSX 2287 during the first third of the harvest period in all four experiments. Resistant hybrids developed subsequently by Petoseed Company have yielding ability equivalent to standard susceptible hybrids (16,17). PSX 2287 is no longer being produced. Weight of fruit obtained from nontreated HMX 1707 and from nontreated Supersett were not significantly different during the first and middle thirds of the harvest period in 1993. HMX 1707 therefore is being considered for commercial release. There are numerous examples of disease-resistant cultivars yielding less than susceptible counterparts in the absence of disease. For example, susceptible cucumber (*Cucumis sativus* var. *sativus* L.) plants flower earlier, produce longer fruits, and are higher-yielding than nearly isogenic plants resistant to bacterial wilt (37). Numbers of fruit and total fruit weight produced by susceptible cucumber plants were equal to or significantly greater than the quantity from plants selected for resistance to scab, anthracnose, downy mildew (36), and angular leaf spot (32). Yield potential also has been compromised during selection for pest resistance and for market characteristics in corn (6,7,10,11,40).

A fungicide program with triadimefon, benomyl, and chlorothalonil generally controlled powdery mildew on susceptible hybrids more effectively than host-plant resistance alone. Fungicide-treated susceptible hybrids had significantly lower powdery mildew severity on adaxial leaf surfaces and produced significantly more fruit during the last third of the harvest period than the horticulturally comparable, nontreated PMR hybrids. PMR hybrids probably would perform better than they did in this study when not grown near nontreated susceptible hybrids severely infected by powdery mildew (31). Yield of PMR genotypes could be reduced by powdery mildew because of energy expended by the host in response to infection.

Genetic control was less costly than chemical control; however, in all experiments the fungicide-treated susceptible hybrids produced enough fruit to economically justify costs of chemical inputs. The increase in seed cost for 7,581 plants/ha would be about $15/ha, based on the 1994 prices for PMR and standard squash hybrids marketed by Park Seed Company. The total cost for the five fungicide applications used in the disease threshold-based full-season fungicide program tested would be $508/ha, based on $262.65/ha for chlorothalonil (five applications), $112.11/ha for triadimefon (three applications), and $46.70/ha for benomyl (two applications), plus $17.29/ ha/application (D. D. Moyer, personal communication). The difference in yield between nontreated PSX 2287 and Goldbar receiving the disease threshold-based full-season fungicide program was 0.77, 0.40, and 1.14 kg per plant in 1991, 1992, and 1993, respectively. These yield increases are worth $4,295, $2,256, and $6,334 per ha, respectively, based on a median price for squash of $0.73/kg (D. D. Moyer, personal communication). The value was less in 1992 because the harvest period was shorter than in 1991 and 1993. The difference in yield between HMX 1707 and Supersett in 1993 was 0.68 kg per plant ($3,772/ha).

Yield differences between the nontreated PMR hybrids and the fungicide-treated susceptible hybrids near the end of the harvest period appear to be due primarily to impact of powdery mildew on the nontreated PMR hybrids. Fungicide-treated susceptible plants produced more yield than nontreated plants of the PMR hybrids (this difference was significant for PSX 2287 in 1991 and 1993). *S. fuliginea* can infect PMR genotypes before fungal growth is arrested. Resistance to *S. fuliginea* is expressed at the cellular level, resulting in smaller powdery mildew colonies with fewer conidiophores and conidia. Germination, penetration, or haustorial formation are not expected to be affected (1). The observed yield differences also may be partially due to differences in yield potential, since the fungicide-treated susceptible hybrids produced more fruit than the fungicide-treated PMR experimental lines in all experiments (these comparisons were not subjected to statistical analysis because they were not planned beforehand). The systemic fungicides probably did not have a direct effect on yield through growth-regulator activity (8), because fungicide-treated plants generally did not produce significantly more yield than corresponding nontreated plants during the first third of the harvest period except for susceptible Goldbar and Supersett in 1993, when powdery mildew was more severe and probably did have an impact on yield early in production.

Although chemical control generally was better than host-plant resistance alone in these experiments, development of fungicide resistance can interfere with fungi-

Table 5. Effect of using a powdery mildew resistant (PMR) hybrid (HMX 1707) and/or fungicide programs on powdery mildew severity and yield in yellow crookneck squash in 1993

		Adaxial severity[b]		Abaxial severity[b]		Fruit wt (g/plant)[c]			
Hybrid	No. fungicide applications[a]	9/30	AUDPC	9/30	AUDPC	8/30–9/10	9/13–24	9/27–10/8	8/30–10/8
HMX 1707 (R)	0	3.30	17.98	14.41	110.32	1,018	515	128	1,661
HMX 1707 (R)	5	0.00	0.08	0.10	1.58	1,059	610	169	1,838
Supersett (S)	0	25.60	294.12	52.03	1,395.65	1,042	376	42	1,460
Supersett (S)	5	0.00	1.81	49.26	571.90	1,267	791	279	2,338
R-0 vs S-0[d]		0.0001[e]	0.0001	0.0001	0.0001	0.7488	0.3452	0.0199	0.2448
R-0 vs S-5		0.1567	0.0001	0.0001	0.0001	0.0083	0.0785	0.0008	0.0023
S-0 vs S-5		0.0001	0.0001	0.5273	0.0001	0.0142	0.0154	0.0001	0.0004
R-0 vs R-5		0.1567	0.0001	0.0080	0.1113	0.5884	0.5137	0.2177	0.3006

[a] Fungicides (chlorothalonil at 2.81 kg a.i./ha every 7 days, triadimefon at 0.14 kg a.i./ha every 14 days, and benomyl at 0.28 kg a.i./ha every 14 days) were applied 5 times in a disease threshold-based full-season fungicide program between 22 August and 20 September.

[b] Exact lesion counts were made when there were less than approximately 50 lesions per leaf. Thereafter, severity was estimated using a conversion factor of 1% = 10 lesions per leaf. Data from an equal number of old, mid-aged, and young leaves were averaged together. Area under the disease progress curve (AUDPC) was calculated for severity from 25 August through 5 October. A natural log transformation was used where necessary to stabilize variance. De-transformed values are presented.

[c] Cumulative weight of marketable-sized fruit harvested every 2 to 5 days over time periods listed.

[d] Planned comparisons. R = HMX 1707. S = Supersett. Numbers denote the number of fungicide applications.

[e] *P* values for the planned comparisons. These numbers are significantly different when the *P* value is < 0.05.

cide efficacy. Fungicide-treated Goldbar had significantly lower powdery mildew severity than nontreated PSX 2287 on abaxial leaf surfaces in 1991 and in 1992 (early summer experiment), but not in 1993. The fungicides were not as effective on abaxial leaf surfaces of susceptible hybrids in 1993 as on adaxial leaf surfaces in 1993 and as on abaxial leaf surfaces in previous years. This is most likely due to fungicide resistance. All eight isolates collected at the end of the experiment in 1993 were resistant to triadimefon and to benomyl. Chlorothalonil was applied with these systemic materials. This broad-spectrum, contact fungicide suppresses powdery mildew development only where deposited, which is primarily on adaxial leaf surfaces (18). We have found that selection pressure during one growing season is sufficient to bring about large increases in the frequency of isolates resistant to both triadimefon and benomyl, and fungicide efficacy declines after resistance develops near the end of the crop (13,19,25). The difference in disease control between abaxial and adaxial leaf surfaces in 1993 probably is due to the protective action of chlorothalonil on adaxial surfaces. In another experiment, this broad-spectrum fungicide suppressed powdery mildew on adaxial but not abaxial surfaces of pumpkin leaves. Chlorothalonil provided full-season powdery mildew control, whereas effectiveness of triadimefon declined substantially late in the growing season (25). The fungicide program selected for the present study was perceived to be one of the best options currently available to commercial cucurbit growers in the United States because two systemic fungicides with different modes of action were applied alternately and they were applied with a protectant fungicide.

Powdery mildew development was suppressed with fungicides applied after disease detection (disease threshold-based fungicide programs) for all four hybrids in the four experiments conducted between 1991 and 1993. There is ample time for disease detection and management response with use of the threshold of one leaf with symptoms out of 45 old leaves examined, based on the fact that powdery mildew was suppressed adequately on adaxial leaf surfaces in 1993 although incidence exceeded this level when fungicide applications were initiated. Similar results have been obtained with pumpkins (28). A disease threshold-based mid-season fungicide program, with three to five applications following disease detection, resulted in yields comparable to those under the disease threshold-based full-season fungicide program (five to eight applications) although powdery mildew severity was somewhat higher at the end of the growing season.

An integrated management program utilizing host resistance and a few timely fungicide applications may be an effective antiresistance strategy. Triadimefon and benomyl applied alternately on a weekly schedule were not very effective over the long term in reducing powdery mildew on abaxial leaf surfaces of the susceptible hybrids because of development of fungicide resistance. In sharp contrast, powdery mildew severity was substantially lower on abaxial leaf surfaces of fungicide-treated PMR hybrids PSX 2287 and HMX 1707 than on abaxial leaf surfaces of nontreated plants of those hybrids. Similar results have been obtained with triadimefon and *Erysiphe graminis* f. sp. *hordei*, which causes powdery mildew in barley (4), and with metalaxyl and *Bremia lactucae* Regel, which causes downy mildew in lettuce (5). Fungicide sensitivity appears to be linked to certain pathogen virulence genes. Thus, fungicide-insensitive pathotypes are avirulent on hybrids with particular resistance genes. An integrated program may be useful for preserving both fungicide efficacy and host resistance.

Onset of powdery mildew epidemics in these experiments seemed to be influenced more by host growth stage and host condition than by availability of inoculum. Symptoms were found first after fruit had started to form (maximum fruit length was 5 cm) and 4 to 10 days before the first harvest. Although abundant powdery mildew inoculum was present in adjacent older plantings, symptoms were not found in the late summer 1992 experiment until 19 days after transplanting. This is ample time for infection and symptom development because powdery mildew conidia germinate and penetrate under a wide range of environmental conditions (3). Even under conditions of low humidity and leaf wetness, symptoms should be visible by 7 days after infection (34). Powdery mildew developed early in 1993: symptoms were observed 16 days after transplanting and 10 days before the first harvest (plants were not examined earlier). These plants appeared to be stressed because they recovered slowly from transplanting. They were not in good condition when transplanted because they were old, weather was hot, and many were affected by squash silverleaf (22). The 1993 epidemic obviously commenced several days before we noted symptoms and inoculum likely was more abundant than in previous years. Symptoms of powdery mildew also first appear in pumpkin and winter squash as fruit begin to enlarge (38, 41), even when planted late (38) and when inoculum is abundant from adjacent older plants (M. T. McGrath, unpublished). It appears that cucurbits become susceptible to powdery mildew when stressed by fruit production or by a suboptimal environment.

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