High-Temperature, Adult-Plant Resistance to Stripe Rust of Wheat

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ABSTRACT

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Resistance to *Puccinia striiformis* in plants of winter wheat cultivars at different growth stages was studied in the greenhouse at low diurnal temperatures (2–18 C, 4–18 C, and 6–21 C), high diurnal temperatures (13–32 C, 13–34 C, and 15–36 C), and under natural conditions in the field. The cultivars were susceptible in the seedling stage at both low and high temperatures and at all stages of growth at low temperatures. At the high temperatures, cultivars Cheyenne, McCall, Gaines, Itana/PI 178383 Selection 111, Wanser, Nugaines, and Luke at the boot and later growth stages showed resistance that increased as the plants matured; cultivars Michigan Amber, Orin, Omar, Golden, Columbia, Westmont, Itana, and Itana/PI178383 Selection 110 were susceptible at all growth stages. Cultivars that were resistant at the high temperatures differed in degree of resistance, and cultivars that had the highest resistance at later stages also expressed resistance earlier than those with less resistance at later stages. High-temperature adult-plant resistance was expressed only at the high postinoculation temperatures. Flag leaves were more resistant than the lower leaves of the same plant. Cultivars that were resistant at the high postinoculation temperature became susceptible when subsequently transferred to a lower temperature. The results were similar for all races tested; there was no evidence of race-specificity. The cultivars with high-temperature adult-plant resistance were resistant in the field at the jointing and later stages of growth, and rust developed slower on them. This type of resistance has been used extensively in wheat breeding programs and has remained effective against all races of *P. striiformis* in the northwestern United States for more than 20 yr indicating that it is durable and may be nonspecific. In contrast, cultivars with high specific resistance were resistant for not more than 3 yr before new races that could circumvent the resistance became prevalent.

Stripe rust caused by *Puccinia striiformis* West. is the most economically important foliar disease of wheat in the northwestern United States. The major method of controlling the disease has been to grow resistant cultivars. Even though cultivars with high resistance have been developed, stripe rust continues to cause significant losses. Resistance to stripe rust has usually been provided by one or a few specific genes which are easily manipulated in a breeding program, but it has remained effective only until a race of the pathogen able to circumvent it becomes established (6,8). Consequently, wheat cultivars with specific resistance to stripe rust have been useful for only a few years. For this reason, interest in other types of resistance (adult plant resistance, nonspecific resistance, field resistance, and slow rusting) has increased in recent years.

Several workers (1,5,7,12) have reported that resistance of some wheat cultivars in the adult stages differed from resistance in the seedling stage. Many of the wheat cultivars grown in northwestern United States are relatively resistant to stripe rust in the field at later stages of growth, but in the greenhouse they are susceptible in the seedling stage. Little is known about the nature of this type of adult-plant resistance, and no concerted attempt has been made to determine the factors that affect its expression.

This report is on a series of experiments conducted in 1974 and 1975 to determine the effect of temperature at various stages of growth on resistance to stripe rust in selected winter wheat cultivars and to compare their resistance in controlled greenhouse environments and under ambient field conditions.

MATERIALS AND METHODS

The winter wheat cultivars used were Michigan Amber (WA 5770), Orin (CI 12687), Omar (CI 12072), Golden (CI 10063), Columbia (CI 12928), Westmont (CI 12930), Itana (CI 12933), and Itana/PI 178383 Selection 110 (MTS 110), which were considered susceptible to stripe rust in both seedling and adult stages; Cheyenne (CI 8885), McCall (CI 13842), Gaines (CI 13448), Wanser (CI 13844), Nugaines (CI 13968), and Luke (CI 14586), which were considered susceptible at the seedling stage in the greenhouse but were resistant to local races of *P. striiformis* in the field; and Itana/PI 178383 Selection 111 (MTS 111), which was reported to have resistance at high temperatures (16). All cultivars except Itana/PI 178383 Selections 110 and 111 and Michigan Amber either have been or presently are grown in the northwestern United States.

Resistance in the field was determined by planting the cultivars at Walla Walla, WA, in 1975 in three replicated randomized blocks. Each plot consisted of a 2-m row, separated by a row of Orin. All rows were 30 cm apart. Plots were irrigated with overhead sprinklers on three different dates after the plants were in the boot stage of growth. The inoculum consisted of naturally occurring race CDL-3 of *P. striiformis*. The system of identifying and classifying the races has been reported by Line et al (9).

Infection types and rust intensity were recorded at jointing, boot, heading, milk, and dough stages of growth, which are stages 3, 4, 5, 7, and 8, respectively, in the numerical scale described by Zadoks et al (20). The scale for stripe rust infection types has been described by Line (5) and Line et al (7) and is illustrated in the Wheat Compendium (18): 0 = no visible signs or symptoms; 1 = necrotic or chlorotic flecks with no sporulation; 2 = necrotic and/or chlorotic blotches or stripes with no sporulation; 3 = necrotic and/or chlorotic blotches or stripes with only a trace of sporulation; 4, 5, and 6 = necrotic and/or chlorotic blotches or stripes with light, intermediate, and moderate sporulation, respectively; and 7, 8, and 9 = abundant sporulation with necrotic and/or chlorotic blotches or stripes, chlorosis behind the sporulation area, and no chlorosis or necrosis, respectively. Blotches occur on seedlings and stripes on adult plants. On the 0–9 scale, plants with infection types 1–3 would be considered very resistant to moderately resistant, plants with infection types 4–6 would have intermediate resistance, and plants with infection types 7–9 would be moderately susceptible to very susceptible. Ranges in infection types on the same plant were designated by a dash (-). Data on rust intensity were based on the modified Cobb's scale for cereal rusts (11).

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To determine resistance at different growth stages under controlled environmental conditions, seedlings were grown in 10-cm-diameter pots (10–15 plants per pot) and adult plants were grown in 15-cm pots (four plants per pot). Plants used for the adult studies were vernalized either by placing seedlings in the two-leaf stage outside in a lath-house from mid-February to mid-April, or by placing germinated seeds at 0–5 C in an incubator for 6 wk before planting. All plants were grown before and after inoculation at diurnal temperature cycles that were programmed to change gradually from the high extreme at 1400 hours to the low extreme at 0200 hours. Plants received 16 hr of light per day consisting of natural daylight supplemented with fluorescent light.

Plants were inoculated by dusting with urediospores of races CDL-1, CDL-2, CDL-3, or CDL-5 of *P. striiformis* mixed with talc and then placed in a dark dew chamber at 10 C. After 20–24 hr of dew, the plants were placed at various temperatures depending on the experiment. Infection types were recorded 6–8 days after sporulation started (the number of days from inoculation to sporulation varied depending upon the temperature).

TABLE 1. Infection types produced by *Puccinia striiformis* on winter wheat cultivars at different stages of growth in plots at Walla Walla, WA, in 1975

Cultivars	Infection type[a]				
	Jointing	Boot	Heading	Milk	Dough
Michigan Amber	8	8	8	8	7
Orin	8	8	7	7	7
Omar	8	8	7	7	7
Golden	8	8	7	7	7
Columbia	8	8	7	7	7
Westmont	8	8	7	7	7
Itana	8	8	7	7	7
Itana/PI 178383-110	8	8	8	8	7
Itana/PI 178383-111	8	7	3–5	3–5	3–5
Cheyenne	5–8	3–5	3–5	3–5	3–5
McCall	5–8	4–7	2–4	3–4	3–5
Gaines	4–8	2–7	2–4	3–4	2–4
Wanser	3–7	3–5	2–3	2–4	2–3
Nugaines	4–7	3–5	2–3	2–3	2–4
Luke	4–6	3–5	2–3	2–3	2–3

[a] Infection type is based on a scale of 0–9 (0 = no symptom, 1–3 = very resistant to moderately resistant, 4–6 = intermediate resistance, and 7–9 = moderately susceptible to very susceptible). A dash (–) indicates a range of infection types on the same plant. Data are based on three replicates of 2-m rows.

To determine the effects of temperature and stage of plant growth, seedlings were grown before and after inoculation at diurnal cycles of 2–18 C, 6–21 C, or 13–32 C. Adult plants grown at 10–18 C were divided into two groups 10 days before inoculation. One group was placed at 6–21 C and the other at 13–33 C. The plants were inoculated at the seedling (two-leaf stage), jointing, boot, and heading stages. Postinoculation temperatures at the high range were slightly higher following inoculation at the later stages of growth (15–35 C at boot and 15–36 C at heading stages).

To determine the effect of both pre- and postinoculation temperatures, McCall, Gaines, Wanser, and Nugaines grown at 4–18 C were divided into two groups 15–20 days prior to inoculation. One group was kept at 4–18 C and the other was moved to 13–34 C. The plants were inoculated at the anthesis stage with races CDL-1, CDL-2, CDL-3, or CDL-5. After removal from the dew chamber, the plants that had been at preinoculation temperatures of 4–18 C and 13–34 C were further subdivided into two groups. One group was placed at postinoculation temperatures of 4–18 C and the other at 13–34 C.

To determine resistance on different leaves of the same plant, plants grown at 4–18 C or 13–32 C were inoculated with races CDL-1 and CDL-3 at the boot, heading, and anthesis growth stages. The infection types that developed on the flag-leaf and lower leaves were recorded.

To determine the effect of changing the postinoculation temperature, cultivars McCall, Gaines, Wanser, and Nugaines grown at 10–20 C were inoculated at the boot stage with races CDL-1 and CDL-5. After removal from the dew chamber, plants were placed at 14–40 C for 26 days, then they were moved to 4–18 C for 11 days. Infection types were recorded before and after the plants were moved to the 4–18 C temperature.

RESULTS

Field data on the infection types (Table 1) and the amount of rust (Fig. 1) at various stages of plant growth, show that Michigan Amber, Orin, Omar, Golden, Columbia, Westmont, Itana, and Itana/PI 178383 Selection 110 were susceptible throughout the growing season. However, Itana/PI 178383 Selection 111, Cheyenne, McCall, Gaines, Wanser, Nugaines, and Luke became

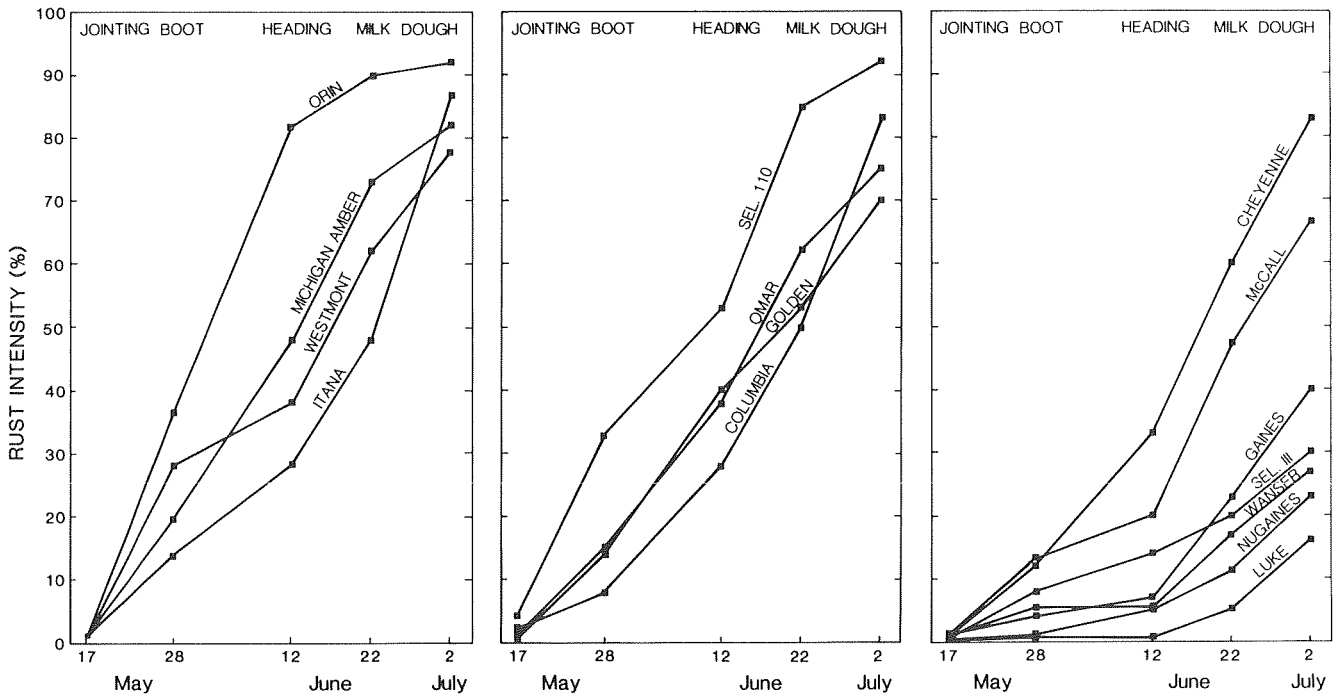

Fig. 1. Stripe rust intensity on 15 winter wheat cultivars grown adjacent to susceptible cultivar Orin at Walla Walla, WA, in 1975.

progressively more resistant as the plants became older. The cultivars are listed from least to most resistant. Rust developed more slowly on those that were most resistant as measured by infection type.

The data in Table 2 show that all cultivars were highly susceptible in the seedling stage at the low temperatures (infection types were 9 at 2–18 C and 8 at 6–21 C). However, at the high temperatures (13–32 C), seedlings of Itana/PI 178383 Selection 111 were less susceptible (infection types 5–7) than seedlings of other cultivars (infection types 7–8). Leaves of seedlings were more chlorotic and died quicker even in the absence of rust at the highest temperature, which may explain why the infection types were lower at the highest temperature.

When inoculated at later stages (jointing, boot, and heading), all cultivars were susceptible (infection type 8) at the low temperatures. However, at the high temperatures, Itana/PI 178383 Selection 111, Cheyenne, McCall, Gaines, Wanser, Nugaines, and Luke were resistant. These cultivars have high-temperature, adult-plant (HTAP) resistance. Some of these cultivars became resistant at earlier stages than others. For example, Luke, Itana/PI 178383 Selection 111, Nugaines, and Cheyenne showed some resistance even when inoculated at the jointing stage. Infection types on the susceptible cultivars were lower when inoculated at the heading stage (infection types ranged from 5 to 7 depending on the cultivars) probably because of the combined effect of high day-time temperature (36 C) and the nearly ripe condition of the plants when the data were recorded.

The infection types were affected only by postinoculation temperatures (Table 3). Both seedlings and adult plants of the HTAP resistant cultivars were susceptible (infection type 8) at the low postinoculation temperature (4–18 C), but at the high postinoculation temperature (14–34 C), adult plants were resistant (infection types 2–5 to infection types 4–6 depending on the cultivars) and seedlings were susceptible (infection type 7). The cultivars responded similarly to all four races at low and high temperatures. These results confirmed the results of the previous experiment.

At the low temperature, the flag leaves were slightly more susceptible (infection types 8 or 9) than the lower leaves (infection type 8). However, at the high temperature, the flag leaves of HTAP resistant cultivars (McCall, Gaines, Wanser, Nugaines, and Luke) were more resistant than the lower leaves (Table 4).

When the cultivars were placed at a high postinoculation temperature (14–40 C), low infection types developed on all HTAP resistant cultivars but when the cultivars were subsequently transferred to a lower temperature (4–18 C), infection types changed from low to higher types on both flag and lower leaves (Table 5).

DISCUSSION

Cultivars used in this study can be classified into two groups: those that were susceptible in all stages of growth at both low and high temperatures in the greenhouse and throughout the growing season in the field and those that were susceptible in the seedling stage but resistant in later stages of growth at high temperature and in the field. Selection 111 was different from the other HTAP resistant cultivars because it also had some resistance in the seedling stage at high temperatures. The resistance of Selection 111 is consistent with the results obtained by Sharp and associates (4,16,17) who reported that PI 178383, which is one of the parents of Selection 111, has minor recessive genes conditioning resistance at high temperatures in the seedling stage.

Flag leaves of HTAP resistant cultivars were the most resistant leaves at high temperatures, but at low temperatures flag leaves were usually more susceptible than lower leaves. The slightly higher infection types on flag leaves at the low temperatures may have been caused by the flag leaves being greener and more turgid than the lower leaves. Zadoks (19) working with stripe rust, and Johnston (3) and Newton and Johnson (10) working with leaf rust, reported that upper leaves of some cultivars were more resistant than lower leaves. In contrast, Clifford (2) observed that lower leaves of oats were more resistant to crown rust.

In the greenhouse, cultivars with the highest HTAP resistance (Luke, Nugaines, and Selection 111) showed some resistance even when inoculated as early as the jointing stage. Those with lower HTAP resistance were not resistant at the jointing stage, but were resistant when inoculated at the boot or later stages of growth. Therefore, cultivars with the highest HTAP resistance also became resistant at earlier stages. However, HTAP resistant cultivars expressed some resistance as early as the jointing stage in the field.

Sharp (14,15) reported that some cultivars were susceptible when grown at 15 C before inoculation, but were resistant when grown at 24 C before inoculation. In contrast, the HTAP resistance was only affected by high postinoculation temperatures and not by high preinoculation temperatures (Table 3). Resistance of the HTAP resistant cultivars can be changed by changing postinoculation temperature. When transferred from high to low temperatures infection types changed from low to high (Table 5). This is

TABLE 2. Effect of programmed temperatures on the infection types produced by *Puccinia striiformis* on wheat cultivars when inoculated at different stages of plant growth[a]

	Infection type[b]								
	Seedling			Jointing		Boot		Heading	
Cultivar	2–18 C	6–21 C	13–32 C	6–21 C	13–33 C	6–21 C	15–35 C	6–21 C	15–36 C
Michigan Amber	9	8	7–8	8	8	8	7	8	6–7
Orin	9	8	7–8	8	8	8	8	8	5–6
Omar	9	8	7–8	8	8	8	7	8	5
Golden	9	8	7–8	8	8	8	7	8	6
Columbia	9	8	7–8	8	7–8	8	7	8	4–5
Westmont	9	8	7–8	9	8	8	7	8	5
Itana	9	8	7–8	8	8	8	7	8	6–7
Itana/PI 178383-110	9	8	8	9	9	8	8	8	7
Itana/PI 178383-111	9	8	5–7	7–8	5–6	7–8	1–3	7	0
Cheyenne	9	8	7–8	7–8	6–7	7–8	4–5	7	2–3
McCall	9	8	7–8	8	8	8	6–7	8	3–5
Gaines	9	8	7–8	8	7–8	8	2–4	8	2–4
Wanser	9	8	7–8	8	7–8	7–8	2–5	7–8	2–3
Nugaines	9	8	7–8	8	6	8	1–5	7	1–2
Luke	9	8	7–8	8	5	8	1	7–8	1–2

[a] Temperatures were programmed to change gradually from low to high and from high to low on a diurnal cycle. Numbers indicate the extremes.
[b] Data were recorded 6–8 days after beginning of sporulation. Infection type is based on a scale of 0–9 (0 = no symptom, 1–3 = very resistant to moderately resistant, 4–5 = intermediate resistance, and 7–9 = moderately susceptible to very susceptible). A dash (–) indicates a range of infection types on the same plant. Data are based on 25 or more seedlings and 12–16 adult plants.

TABLE 3. Effect of pre- and postinoculation temperature on the infection types produced by *Puccinia striiformis* on wheat cultivars inoculated at seedling and anthesis stages of growth

Cultivar	Temperature (C)[a]		Infection type[b]	
	Pre-inoculation	Post-inoculation	Seedling stage	Anthesis stage
McCall	4–18	4–18	8	8
	13–34	4–18	8	8
	4–18	13–34	7	3–6
	13–34	13–34	7	3–6
Gaines	4–18	4–18	8	8
	13–34	4–18	8	8
	4–18	13–34	7	4–6
	13–34	13–34	7	4–6
Wanser	4–18	4–18	8	8
	13–34	4–18	8	8
	4–18	13–34	7	3–6
	13–34	13–34	7	2–6
Nugaines	4–18	4–18	8	8
	13–34	4–18	8	8
	4–18	13–34	7	3–5
	13–34	13–34	7	2–5

[a]Temperatures were programmed on a diurnal cycle. Numbers indicate the extremes.
[b]Data were recorded 6–8 days after beginning of sporulation. Infection types are based on a scale of 0–9 (0 = no symptom, 1–3 = very resistant to moderately resistant, 4–6 = intermediate resistance, and 7–9 = moderately susceptible to very susceptible). A dash (–) indicates a range of infection types on the same plants. Data are based on 24 plants (eight plants for each of the three races).

TABLE 4. Infection types produced by *Puccinia striiformis* on the flag leaf (top leaf) and lower leaves of wheat cultivars inoculated at different stages of growth and grown at 4–18 C or 13–32 C[a]

Cultivar	Leaf position	Infection type[b]					
		4–18 C			13–32 C		
		Boot	Heading	Anthesis	Boot	Heading	Anthesis
Michigan Amber	Flag	9	9	9	8	7–8	7–8
	Lower	9	9	8	8	7–8	7–8
Westmont	Flag	9	9	9	7–8	7–8	7–8
	Lower	9	8	9	7–8	7–8	7–8
McCall	Flag	9	8	9	4–6	5–6	3–5
	Lower	8	8	8	6–7	6–7	5
Gaines	Flag	8	9	9	5–6	5–6	4–5
	Lower	8	8	8	6–8	6–7	6–7
Wanser	Flag	8	9	8	4–5	4–5	2–5
	Lower	8	8	8	6–7	7	6
Nugaines	Flag	9	9	9	4	3–5	2–4
	Lower	8	8	8	6–7	7	5–6
Luke	Flag	8	9	9	1–3	1–3	1–2
	Lower	8	8	8	3–5	1–4	1–3

[a]Temperatures were programmed on a diurnal cycle. Numbers indicate the extremes.
[b]Data were recorded 6–8 days after beginning of sporulation. Infection type is based on the scale of 0–9 (0 = no symptom, 1–3 = very resistant to moderately resistant, 4–6 = intermediate resistance, and 7–9 = moderately susceptible to very susceptible). A dash (–) indicates a range of infection types on the same plant. The data are based on eight plants.

consistent with the earlier observation that infection types on Nugaines and Gaines in the field changed from low to high types following a period of cool weather (5). This type of resistance might be useful for studying the physiology of host parasite interactions because this host-pathogen interaction can be changed by changing temperatures without changing the genetics of the host or pathogen.

TABLE 5. Effect of changing postinoculation temperatures on infection types produced by *Puccinia striiformis* on wheat cultivars when inoculated at early boot stage[a]

Cultivar	Leaf position	Infection type[b]	
		After 26 days at 14–40 C	After 11 additional days at 4–18 C
McCall	Flag	2–4	2–6
	Lower	2–5	7–8
Gaines	Flag	2–5	6–8
	Lower	3–5	6–8
Wanser	Flag	2–3	2–5
	Lower	2–4	5–6
Nugaines	Flag	2–3	2–5
	Lower	2–4	7–8

[a]Temperatures were programmed on a diurnal cycle. Numbers indicate the extremes.
[b]Data were recorded 6–8 days after beginning of sporulation. Infection types are based on a scale of 0–9 (0 = no symptom, 1–3 = very resistant to moderately resistant, 4–6 = intermediate resistance, and 7–9 = moderately susceptible to very susceptible). A dash (–) indicates a range of infection types on the same plant. The data are based on eight plants.

Rust increase in the field was directly correlated with the level of HTAP resistance. Rust increased slowest on cultivars with the most resistance (the lowest infection types) (Table 1 and Fig. 1). There were also slight differences between some of the susceptible cultivars in rate of rust development that were not associated with infection types. The difference in rust development on the susceptible cultivars could be due to differences in number of infections, rate of growth of the sporulation area, or latent period. Studies of these factors in relationship to slow rusting resistance are being conducted.

There is no evidence of race specificity related to HTAP resistance. These cultivars with HTAP resistance and other HTAP resistant cultivars have been grown extensively in northwestern United States and have remained resistant for more than 20 yr. Therefore, these HTAP resistant cultivars have durable resistance. The HTAP resistance has been equally effective against all 32 races of *P. striiformis* present in the northwestern United States (13). Cultivars with HTAP resistance were also resistant to races at sites throughout western Europe in 1980 (8). In contrast, cultivars with high race-specific resistance to stripe rust, which is expressed at all stages of growth and all temperatures, have been attacked by new virulent races within 3 yr after their release (6,8). Damage to HTAP resistant cultivars caused by *P. striiformis* has been slight in most years, but when there is abundant inoculum in the early spring or when spring temperatures are unusually cool, some damage can occur, especially if the cultivar has only moderate HTAP resistance. Even in those years, however, yield losses are not as great as the losses in fields of susceptible cultivars.

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