Influence of Plant Age on the Expression of Slow-Mildewing Resistance in Wheat

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ABSTRACT

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Wheat cultivars Monon and Knox and Purdue breeding lines P6217, P65104, P6693A7, and P6693A12 were inoculated in the greenhouse with *Erysiphe graminis* f. sp. *tritici* at 12 growth stages. In one set of experiments, disease severity was assessed on the upper three leaves. The sporulation index, a measure of the average spore-producing capacity of a population of colonies, was calculated for the upper two leaves. In a second set of experiments, disease severity, sporulation index, and colony density per square millimeter of leaf were determined on the penultimate leaf (F-1). For a given cultivar or breeding line, the average colony size was nearly constant at all growth stages; however, disease severity and sporulation index varied with growth stage at time of inoculation and with the leaf inoculated. Resistant and susceptible cultivars could be distinguished by colony size when plants were inoculated at any growth stage after GS 37 (flag leaf just visible). However, on the basis of disease severity or sporulation index, resistant and susceptible cultivars were most easily distinguished when plants were inoculated between GS 43 (boot just beginning to swell) and GS 64 (anthesis half-completed) on F-1 or between GS 40 (flag leaf collar just visible) and GS 58 (inflorescence completely emerged) on F-2, the leaf below F-1. Resistant and susceptible cultivars could not be distinguished by disease severity on flag leaves.

Additional key words: general resistance, powdery mildew, *Triticum aestivum.*

Because of the ephemeral nature of race-specific disease resistance, there is an increased interest in forms of resistance that may be more stable. In wheat, powdery mildew resistance that retards infection and also growth and reproduction of the pathogen (*Erysiphe graminis* DC. f. sp. *tritici* em. Marchal) in adult plants but not in seedlings has been termed "slow-mildewing" or "adult plant resistance" (9,13–15). Adult plant resistance to powdery mildew has also been observed in oats (4,5) and barley (10).

Some authors have suggested that the adult plant resistance of some cereal cultivars is general (horizontal) because it is equally effective against all races of the pathogen (6,9,16). Other cultivars with adult plant resistance do not respond in the same way to all races of the pathogen (2,10). Adult plant resistance can be race specific and controlled by a single gene (11). Slow-mildewing in our breeding material appears to be a race nonspecific form of adult plant resistance.

Selection for the slow-mildewing trait depends on the detection of small differences in disease severity among plants. In field nurseries, variations in the environment and inoculum level around individual plants necessitates the use of large replicated plots to accurately evaluate breeding lines for slow-mildewing resistance. Greenhouse testing under a standard set of screening conditions may provide a more efficient and accurate means of assessing and

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comparing levels of slow-mildewing in selections from field nurseries.

Our investigation of the influence of plant age on the expression of slow-mildewing resistance on the upper three leaves of adult winter wheat plants should assist in the identification of optimum conditions for screening wheat genotypes in the greenhouse for slow-mildewing resistance.

MATERIALS AND METHODS

Greenhouse cycle 1 (GC1). Seeds of *Triticum aestivum* L. em. Thell 'Monon' (CI 13278) and 'Knox' (CI 12798) and Purdue breeding lines (hereafter referred to as cultivars): P6693A7-1-21-9-11 (P6693A7); 65104B1-4-2-23-13-2 (P65104); and 6217C1-6-1-25-1-1 (P6217) were planted in flats over a 5-wk period and vernalized at 2.5 C for 69–76 days. Seedlings were transplanted into individual 10-cm-diameter plastic pots in the greenhouse at 3–4 day intervals over a 5-wk period. Planting dates were staggered in order to have plants of all cultivars in a similar growth stage at one time. Based on a soil test showing total N at 470 μg/g of soil, PO_4 at 0.20 μg/g and K at 50 μg/g seedlings were fertilized with 18-46-0 (N-P-K) fertilizer 10 days after being transplanted. Fluorescent lighting (2×10^4 ergs·cm^{-2}·sec^{-1}) supplemented natural daylight and extended the photoperiod to 16 hr. Volatilized sulfur was used to keep plants free of natural powdery mildew infections before test inoculations.

A field culture of *E. graminis* f. sp. *tritici* was used for inoculations. The culture was propagated on Riley 67 wheat seedlings in a Sherer growth chamber maintained at 21 C with 50–70% relative humidity and a 16-hr photoperiod. Conidia used to inoculate the experimental material were collected from infected seedlings that had been shaken vigorously 8 to 12 hr earlier.

For inoculation, plants of all cultivars at a single stage of development were placed in a randomized block design with four replications in a settling tower similar to that described by Kirby and Frick (7). Uniformity and density of deposition of conidia were monitored by placing microscope slides at pot height several places in the tower. All cultivars were inoculated at 12 growth stages (Table 1).

After inoculation, plants were taken to a greenhouse without volatilized sulfur. Fluorescent lighting (2×10^4 ergs·cm^{-2}·sec^{-1}) was used to extend the photoperiod to 15 hr. The temperature in the greenhouse ranged between 21 and 27 C while the relative humidity varied from 30 to 80%.

Disease severity on the upper three leaves of each main stem was noted when colonies were fully developed, usually 10 days after inoculation. Disease severity was rated by visually estimating the percentage of leaf surface covered by *E. graminis* colonies with the aid of a standard drawing. Severity of disease on each leaf was estimated for each of four subunits of equal area. The average severity for each leaf was the datum analyzed.

A sporulation index (14) was determined for the upper two leaves of each main stem by examining 25 *E. graminis* colonies per leaf under a dissecting microscope and rating the colonies on a 0–3 conidial chain density scale (12). On some leaves, fewer than 25 *E. graminis* colonies were found. In these cases, a sporulation index was calculated only if 10 or more colonies were present.

Greenhouse cycle 2 (GC2). The wheat cultivars Monon, Knox, P6693A7, P6217, and 6693A12-1-21-1-1 (P6693A12) were used in these experiments. Procedures were the same as in GC1 with the following exceptions. Only the leaf below the flag leaf (F-1) on the main stem of each plant was inoculated. Plants were arranged in a randomized block with four replications in a different settling tower (3) than the one used in GC1. F-1 was taped at its apex to the base of the tower so that only its adaxial surface was exposed. An apparatus similar to that described by Aust and Kranz (1) was inserted through a small hole in the upper cylinder of the settling tower and used to inoculate the leaves with approximately 35 mg of 8- to 12-hr-old conidia of *E. graminis*. Conidia were collected from Riley 67 seedlings heavily infected with an *E. graminis* culture (P721-1) derived from a single colony. Some of the 12 growth stages at which all cultivars were inoculated were different from those used in GC1 (Table 1). Postinoculation greenhouse temperatures in GC2 were usually between 21 and 32 C; however, daytime temperatures occasionally reached as high as 38 C. Relative humidity varied from 30 to 100%.

Sporulation index and disease severity on the F-1 leaf were determined 9 days after inoculation when colonies were fully developed. Disease severity was rated by making a single visual estimate of the percentage of leaf area covered by *E. graminis* colonies for the entire leaf. The sporulation index was determined as described above.

Colony density on each inoculated leaf was evaluated 5–6 days after inoculation when colonies were just becoming visible. The number of colonies in 10 equidistant holes (31 mm^2 each) of a template placed over the leaf surface was determined with a ×10 hand lens.

RESULTS

Disease severity. Disease severity on the penultimate leaf (F-1) of most cultivars was statistically indistinguishable from severity on F-1 of the susceptible cultivar Monon when plants were inoculated at growth stage 37 (GS 37) or GS 40 in greenhouse cycle 1 (GC1) or GC2 (Tables 2 and 3). However, from GS 43 to GS 84, levels of infection on F-1 were significantly greater on Monon than on P6217, P6693A7, P6693A12, and Knox (except for P6217 at GS 45 and GS 68 in GC1).

At many growth stages, it was difficult to statistically distinguish

TABLE 1. Descriptions of growth stages at which wheat plants were inoculated with *Erysiphe graminis*

Growth stage[a]	When used[b]	Description[a]
37	1, 2	Flag leaf just visible
40	1, 2	Flag leaf collar just visible
43	1, 2	Boots just visibly swollen
45	1, 2	Boots swollen
47	1	Flag leaf sheath opening
49	2	First awns visible
54	1, 2	Inflorescence half-emerged
58	1, 2	Inflorescence completely emerged
64	1, 2	Anthesis half-completed
68	1, 2	Anthesis completed
74	1, 2	Early to medium milk
78	1, 2	Late milk
82	1	Early dough
84	2	Early to soft dough

[a] From Zadoks et al (17).
[b] 1 = Greenhouse cycle 1 (September–December), 2 = greenhouse cycle 2 (January–April).

TABLE 2. Percentage of penultimate leaf (F-1) surface covered by *Erysiphe graminis* for five wheat cultivars inoculated at various growth stages (GC1 experiments)

Growth stage[a]	Cultivar				
	Monon	P6217	P65104	Knox	P6693A7
37	20 A[b]	19 A	25 A	20 A	2 B
40	11 A	8 A	6 AB	6 AB	0 B
43	18 A	8 BC	10 B	6 CD	4 D
45	24 A	22 AB	17 B	17 B	7 C
47	34 A	12 B	8 C	7 C	3 D
54	35 A	21 B	7 C	23 B	4 C
58	37 A	17 B	15 B	14 B	2 C
64	24 B	12 C	30 A	11 C	2 D
68	34 AB	33 B	40 A	18 C	2 D
74	44 B	...[c]	54 A	17 C	2 D
78	42 A	...	...	18 B	1 C
82	44 A	...	...	20 B	0 C

[a] From Zadoks et al (17).
[b] Within a growth stage, means followed by a common letter do not differ at $P = 0.05$ (Duncan's multiple range test).
[c] The leaf became senescent before severity was determined.

cultivars with intermediate levels of resistance from each other and from the most highly resistant cultivar (P6693A7) on the basis of disease severity. Disease severity on F-1 of Knox and P6217 was statistically indistinguishable at most growth stages in both GC1 and GC2. Levels of infection on P65104 (GC1 only) were usually similar to those on Knox or P6217 when inoculated between GS 37 and GS 58; however, after GS 58, P65104 was more severely infected than Monon. Disease severities on F-1 of P6693A7 and P6693A12 (GC2 only) were similar at five of the growth stages tested. However, P6693A7 usually exhibited a significantly lower level of infection than Knox, P6217, and P65104. On F-1, differences among disease severity means of cultivars were most clearly distinguished at GS 43, GS 47, GS 64, and GS 68 in GC1 and at GS 43, GS 45, and GS 58 in GC2.

Disease severity on F-2 of Monon was statistically indistinguishable from severity on F-2 of all other cultivars when inoculated at GS 37 (Table 4). From GS 40 to GS 58, levels of infection were significantly greater on Monon than on Knox, P6217, P6693A7, and P65104; however, P65104 was more severely infected than Monon when inoculated after GS 58. At many of the growth stages tested, disease severity on F-2 was significantly lower on P6693A7 than on any other cultivar. As on F-1, it was difficult at many growth stages to statistically differentiate among cultivars with intermediate levels of slow-mildewing resistance on the basis of disease severity. Differences among cultivars in mean disease severity on F-2 were most clearly distinguished when plants were inoculated at GS 40, GS 43, GS 45, GS 54, or GS 58.

On flag leaves, differences in disease severity among cultivars were not significant at any growth stage. Disease severity on flag leaves of all cultivars never exceeded 12% (*unpublished*). In general, disease severity on a particular cultivar tended to increase with descending leaf position at all growth stages except GS 37 (GC1 data). However, differences in disease severity among successively lower leaves were not always significant (*unpublished*) especially on the cultivars P6693A7, which had a low level of infection on all of its upper three leaves at most growth stages, and on Monon, which had nearly equal levels of infection on F-1 and F-2 when inoculated after GS 58.

Sporulation index: On flag leaves, sporulation indices were not calculated at any growth stage for P6693A7 or at GS 43, GS 45, and GS 47 for Knox, P6217, and P65104 because there were too few colonies for reliable estimation. Knox had a significantly lower sporulation index than P6217, P65104, and Monon at most growth stages where comparisons could be made. The sporulation indices of Monon and P65104 were statistically indistinguishable at most growth stages and were usually significantly lower or no different from the sporulation index of P6217 (*unpublished*).

In GC1, the sporulation indices of all cultivars except P6693A7 were lowest at GS 43 and remained fairly constant after GS 45 (Table 5). The sporulation indices of Monon, P65104, and P6217 were statistically indistinguishable at most growth stages. Knox usually had a significantly lower sporulation index than Monon and a significantly greater sporulation index than P6693A7. On F-1 in GC1, differences in sporulation index among cultivars were most clearly distinguished at GS 45 and GS 68.

In GC2, the sporulation indices of all cultivars were statistically indistinguishable at GS 37. After GS 37, P6693A12, P6693A7, and Knox usually had significantly lower sporulation indices than Monon. Differences between the sporulation indices of Knox and P6217 were not significant at any growth stage. At most growth stages the sporulation index of P6693A12 was statistically indistinguishable from that of Knox, but was significantly greater than that of P6693A7. As in GC1, all cultivars had a comparatively low sporulation index at GS 43. However, at later growth stages, there was more variability in the sporulation index of a given cultivar in GC2 than in GC1. On F-1 in GC2, differences in sporulation index among cultivars were most clearly distinguished at GS 45 (Table 6).

Colony density. The relationship between disease severity and colonies per square millimeter of F-1 was determined by linear regression for each cultivar used in GC2 (*unpublished*). The correlation coefficient for each cultivar was high (no less than 0.95)

TABLE 3. Percentage of penultimate leaf (F-1) surface covered by *Erysiphe graminis* for five wheat cultivars inoculated at various growth stages (GC2 experiments)

Growth stage[a]	Cultivar				
	Monon	P6693A12	P6217	Knox	P6693A7
37	23 A[b]	24 A	28 A	27 A	26 A
40	15 A	6 BC	14 A	9 AB	2 C
43	22 A	3 CD	10 B	8 BC	2 D
45	37 A	12 C	23 B	16 BC	3 D
49	54 A	4 C	13 B	14 B	12 B
54	61 A	11 B	24 B	23 B	17 B
58	60 A	29 B	11 CD	21 BC	9 D
64	35 A	18 B	5 C	8 BC	2 C
68	50 A	9 C	17 BC	26 B	5 C
74	59 A	10 C	41 B	35 B	...
78	–[c]	44 A	45 A	28 B	4 C
84	63 A	...	...	...	4 B

[a] From Zadoks et al (17).
[b] Within a growth stage, means followed by a common letter do not differ at $P = 0.05$ (Duncan's multiple range test).
[c] The leaf became senescent before severity was determined.

TABLE 4. Percentage of F-2[a] leaf surface covered by *Erysiphe graminis* for five wheat cultivars inoculated at various growth stages (GC1 experiments).

Growth stage[b]	Cultivar				
	Monon	P6217	P65104	Knox	P6693A7
37	14 AB[c]	4 B	20 A	17 A	8 B
40	33 A	10 C	26 B	15 C	1 D
43	43 A	15 C	31 B	8 D	8 D
45	43 A	32 B	21 C	12 D	10 D
47	45 A	22 B	25 B	22 B	5 C
54	45 A	31 B	12 C	16 C	2 D
58	48 A	19 C	25 B	16 C	3 D
64	24 C	...	50 A	30 B	3 D
68	38 B	...[d]	52 A	32 C	7 D
74	45 B	...	53 A	28 C	1 D
78	42 A	...	...	31 B	2 C
82	47 A	...	...	...	1 B

[a] F-2 = the leaf below the penultimate leaf.
[b] From Zadoks et al (17).
[c] Within a growth stage, means followed by a common letter do not differ at $P = 0.05$ (Duncan's multiple range test).
[d] The leaf became senescent before severity was determined.

TABLE 5. Sporulation index[a] of *Erysiphe graminis* on penultimate leaves (F-1) of plants of five wheat cultivars inoculated at various growth stages (GC1 experiments)

Growth stage[b]	Cultivar				
	Monon	P6217	P65104	Knox	P6693A7
37	90 AB[c]	85 B	94 A	85 B	41 C
40	82 A	78 A	76 A	82 A	...[d]
43	70 A	62 A	61 A	41 B	37 B
45	75 AB	70 B	80 A	61 C	26 D
47	86 A	80 A	82 A	76 A	35 B
54	87 A	77 B	83 AB	77 B	42 C
58	85 A	85 A	84 A	68 B	27 C
64	88 A	87 A	81 AB	72 B	13 C
68	92 A	84 B	85 B	74 C	18 D
74	89 A	86 AB	95 A	73 B	22 C
78	85 AB	82 B	93 A	82 B	23 C
82	91 A	81 AB	93 A	77 B	...

[a] Sporulation index = $0P_0 + 0.075P_1 + 0.223P_2 + P_3$ where P_0, P_1, P_2, and P_3 are the percent of colonies in conidial chain density classes 0, 1, 2 and 3, respectively (14).
[b] From Zadoks et al (17).
[c] Within a growth stage, means followed by a common letter do not differ at $P = 0.05$ (Duncan's multiple range test).
[d] Fewer than 10 colonies per leaf were observed.

and indicated that the average colony size for a given cultivar was nearly constant at all growth stages. As the slope of the regression line increased, the visual estimate of disease severity associated with a constant number of colonies per square millimeter also increased. We concluded that the colony size of a cultivar increased as the slope of its regression line increased and that the slope of the regression line was an estimate of average colony size. Based on regression lines, the arrangement of cultivars in order of decreasing colony size was: Monon (b (slope) = 0.72 square millimeters per colony), P6217 (b = 0.67), P6693A12 (b = 0.59), and Knox and P6693A7 (b = 0.54).

DISCUSSION

In our breeding material, slow-mildewing appears to be a race nonspecific form of adult plant resistance. Slow development of powdery mildew on wheat can also be caused by *px*/*Pmx* interactions that result in reduced host-parasite compatibility (8). The cultivars used in these experiments contain no known *Pm* genes and we therefore have no reason to believe that the resistance that we observed resulted from *px*/*Pmx* interactions.

Slow-mildewing resistance in adult wheat plants can be correlated with disease severity (13), sporulation index (14), and colony size (14). Susceptible and resistant cultivars can be distinguished on the basis of average colony size regardless of plant stage at the time of inoculation. However, large-scale screening of cultivars for slow-mildewing resistance based on colony size is impractical due to the prohibitive amount of time required to measure enough colonies to detect significant differences.

Disease severity is superior to sporulation index for evaluating cultivars for slow-mildewing resistance because it is easier to estimate and results in greater distinctions among cultivars. However, when cultivars are inoculated at certain growth stages, disease severity ratings may not accurately reflect true levels of slow-mildewing resistance. Our results indicate that highly resistant (P6693A7) and highly susceptible (Monon) cultivars are readily differentiated on the basis of disease severity when the penultimate leaf (F-1) or the leaf below the penultimate leaf (F-2) is inoculated on or after GS 40 (flag leaf collar just visible). However, at many growth stages it is difficult to distinguish cultivars with intermediate levels of resistance from each other and from highly resistant or highly susceptible cultivars. This difficulty can be minimized by inoculating cultivars at a growth stage which enhances the statistical separation of disease severity means. Such growth stages are GS 43 (boot just beginning to swell), GS 45 (boot swollen), GS 47 (flag leaf sheath opening), GS 54 (inflorescence half-emerged), and GS 64 (anthesis half-completed) on F-1 and GS 40, GS 43, GS 45, GS 54, and GS 58 (inflorescence completely emerged) on F-2. There were no significant differences among the cultivars in mean disease severity on flag leaves. Therefore, disease severity on flag leaves cannot be used to distinguish resistant and susceptible lines.

In these experiments, disease severity on the four replications of a given cultivar within a growth stage sometimes varied by as much as 30% even though conidia were uniformly distributed (S.E. = two spores per square millimeter) within the inoculation chamber at all growth stages in GC1 and GC2. Screening for slow-mildewing in the greenhouse based on single plant inoculations would, therefore, not be reliable unless more stringent control of environmental conditions or a more accurate means of characterizing resistance can decrease the error associated with the screening procedure.

In conclusion, disease severity is superior to colony size or sporulation index for evaluating cultivars for slow-mildewing resistance on a large-scale basis. Determination of disease severity on F-1 or F-2 in replicated greenhouse tests enables differentiation between highly resistant, moderately resistant, and susceptible cultivars when plants are inoculated at particular growth stages. Identification of these growth stages should be helpful in establishing a standard set of conditions to be used when screening wheat plants for slow-mildewing resistance in the greenhouse.

TABLE 6. Sporulation index of *Erysiphe graminis* on penultimate leaves (F-1) of five wheat cultivars inoculated at various growth stages (GC2 experiments)

Growth stage[a]	Cultivar				
	Monon	P6693A12	P6217	Knox	P6693A7
37	93 A[b]	94 A	98 A	96 A	98 A
40	94 A	82 B	95 A	92 AB	81 C
43	81 A	47 B	50 B	49 B	30 C
45	83 A	66 C	72 AB	68 BC	25 D
49	89 A	40 C	60 AB	57 BC	44 BC
54	92 A	60 B	61 B	69 B	62 B
58	89 A	61 B	66 B	70 B	19 C
64	79 A	65 AB	61 AB	46 B	9 C
68	91 A	47 B	67 B	68 B	23 C
74	89 A	57 C	82 AB	65 BC	...
78	...[c]	59 B	79 A	65 AB	22 C
84	90 A	64 B	31 C	...	10 D

[a] From Zadoks et al (17).
[b] Within a growth stage, means followed by a common letter do not differ at $P = 0.05$ (Duncan's multiple range test).
[c] The leaf became senescent before severity was determined.

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