Resistance in Soft Red Winter Wheat to *Mycosphaerella graminicola*

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ABSTRACT

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Six soft red winter wheat cultivars and four breeding lines that had shown various levels of resistance to speckled leaf blotch in the field were inoculated in the greenhouse with pycnidiospores of *Mycosphaerella graminicola*. Significant differences were found in both percent leaf area affected and number of pycnidia per square millimeter of lesion among cultivars at all growth stages ranging from pseudostem erection to midmilk. More significant differences among cultivars were detected at the later growth stages. Cultivar Oasis, which derives its resistance to *M. graminicola* from cultivar Bulgaria 88, was consistently the most resistant, and cultivar Monon was the most susceptible. Several other cultivars became more resistant with age. Fewer pycnidia per unit area of lesion were produced on cultivar Caldwell even though necrotic lesions developed. This suggests that *M. graminicola* would not spread effectively in pure stands of this cultivar. Several of the resistant cultivars were derived from parents susceptible to speckled leaf blotch, suggesting that their resistance is the result of a combination of genes that individually are ineffective for resistance.

In the early 1960s, when efforts began at Purdue University to develop soft red winter wheat cultivars resistant to *Mycosphaerella graminicola* (Fuckel) Schroeter (Conidial state = *Septoria tritici* Rob. ex. Desm.), the cause of speckled leaf blotch, wheat cultivar Bulgaria 88 (PI 94407) was the main source of resistance. The high level of resistance from Bulgaria 88 was transferred to wheats that matured early, yielded well, had good soft wheat quality, and were resistant to other diseases and insects of importance in the eastern soft wheat region of the United States. The cultivars Oasis (CI 15929) and Sullivan (CI 17684) were derived from this breeding project (6,7).

Although in our breeding nurseries wheat is grown in 2–4-yr rotations with crops other than wheat, we consistently find infections of *M. graminicola* on lower wheat leaves in early spring. Whether speckled leaf blotch becomes severe as the season progresses or remains confined to lower leaves seems to depend on weather conditions rather than on the abundance of primary inoculum (10). In dry years, infections are confined to lower leaves and symptoms of the disease are difficult to distinguish from necrosis due to other causes, including the natural senescence that follows anthesis. During such years selection for resistance to *M. graminicola* based on differences in amount of necrotic leaf area is not possible. Instead, selection is based on the absence of pycnidia of *M. graminicola* within necrotic tissue. Many lines with Bulgaria 88 in their pedigree are free of pycnidia, and other lines show densities of pycnidia within necrotic tissue that are clearly lower than those seen in highly susceptible wheats (11).

In unusually wet seasons, *M. graminicola* infections spread rapidly up susceptible plants. Resistance can be clearly distinguished by a lower proportion of necrotic leaf area, as well as by fewer pycnidia within lesions. Breeding lines that have pycnidial densities intermediate between those of the Bulgaria 88 type and the fully susceptible type in years of moderate disease severity are also intermediate in degree of necrosis during wet years (11). The consistent behavior of many of these lines during years of severe speckled leaf blotch (1971, 1973, 1974) has led us to conclude that they have an intermediate level of resistance even though they have no previously known source of resistance to *M. graminicola* in their pedigrees.

We have continued to use this intermediate type of resistance in our breeding program because it provides a source of genetic diversity for resistance to *M. graminicola*. To better understand this intermediate resistance and its quantitative effects, greenhouse inoculation studies were performed on several wheat lines representing various levels of resistance. One objective was to determine whether the lower severity seen on these lines in the field was due to a reduction in pycnidial formation and secondary inoculum production and/or to a reduced frequency of infection or lesion development.

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MATERIALS AND METHODS

Ten cultivars and breeding lines of soft red winter wheat (*Triticum aestivum* L. em. Thell) were used in this study. Susceptible checks were Monon (CI 13278) and Arthur (CI 14425). The resistant check was Oasis. The other lines tested were thought to have intermediate resistance to *M. graminicola*, based upon their reaction in the field (10). These lines were cultivars Beau (CI 17420), Knox (CI 12798), and Caldwell (CI 17897) and Purdue breeding lines 6413A9-26-2-11 (P6413), 67129D1-4-35H-3-3 (P67129), 68152A4-1-14 (P68152), and 711368MC1-18 (P711368). Seedlings in the early one-leaf stage were vernalized in a dimly lit (12 hr/day) coldroom for 70 days at 3 C and then transferred to the greenhouse and transplanted to individual 10-cm plastic pots containing a standard soil-peat mix. Natural daylight was supplemented with cool white fluorescent and incandescent illumination (167 uE/m^2/sec) for 16 hr/day. Two sets of plants were raised. The first set was brought out of the coldroom 2 wk before the second set.

Three cultures of *M. graminicola*, collected in southern Indiana in commercial wheat fields during the spring of 1976, were combined for use in these experiments. Petri dishes containing potato dextrose agar were inoculated with 1 ml from nutrient broth shake cultures of the fungus that had incubated in dim light at 23 C. The plates were incubated on a laboratory bench, receiving only daylight from a north window and normal laboratory light. Within 1 wk, the agar surface was covered with a dense mat of macroconidia of *M. graminicola* morphologically indistinguishable from pycnidiospores produced on leaves.

Conidia were collected from petri dishes by washing with water and scraping the agar surface with a rubber policeman. The spore suspension was strained through two layers of cheesecloth and diluted to 10^6 spores per milliliter.

The spore suspension was atomized onto plants arranged in a randomized block design on a greenhouse bench. The block of plants was sprayed as uniformly as possible from all directions until incipient runoff to obtain a uniform distribution of inoculum. In

each experiment, five plants of each line from each set were included. Plants from the two sets were at different stages of growth, so each experiment was a factorial design (age and cultivar). Five experiments were conducted, beginning before plants jointed and continuing through the grain-filling stages.

After inoculation, plants were enclosed in a moist chamber consisting of wet muslin hung on a frame erected around the plants and covered with clear polyethylene. A quadruple layer of cheesecloth was hung 50 cm above the moist chamber to reduce solar insolation and consequent heating within the chamber. Plants were kept in the chamber for 7 days at 100% RH. During the first three nights, the leaves were kept wet by atomizing them with water. Following the 7-day wetting period, the plants were placed on an open greenhouse bench.

Percent necrotic leaf area and density of pycnidia were visually estimated 21 days after inoculation. Pycnidial density was recorded per square millimeter. The uppermost one or two leaves were rated on the main culm of every plant.

RESULTS

Percent necrotic leaf area. Severe speckled leaf blotch developed in all experiments on susceptible lines. Severities on the uppermost fully expanded leaf ranged from 0 to 100% among cultivars. Because of this range in the data, the arcsin-square root transformation of percent severity was used before statistical analysis (12). Before transformation, values of 0% were converted to 0.25% and values of 100% to 99.75%.

In all experiments, host cultivar was a highly significant source of variation (Table 1). Plant age was a significant source of variation in only one experiment (No. 4). Although the age by cultivar mean squares were small, relative to cultivar mean squares, they were significant in four experiments (No. 2–5). Therefore, separate analyses of variance and mean separations were done for cultivars within each age group (Table 2).

Oasis consistently had less necrosis than any other cultivar. In five comparisons, its mean percent necrosis was 0; inoculated plants showed only a few faint chlorotic flecks. In six comparisons, the severity on Oasis was significantly less than the severity on any other cultivar. Severity on Oasis was always significantly less than severity on Monon, Arthur, P67129, Beau, P68152, and Knox. Some necrosis developed on Oasis in later experiments, but the greatest severity observed on any plant was only 12%.

Cultivar P711368 ranked second overall in resistance based on amount of leaf necrosis. It maintained this rank fairly consistently. The severity on P711368 was significantly less than severity on Monon in eight of the 10 comparisons. The responses of the other cultivars were more variable. In some of the earlier experiments, some cultivars, eg, P6413 and Caldwell, were as severely infected as Monon, but in other experiments they were much less severely infected. Among the remaining cultivars, severity was at least half that on Monon, except for one comparison in which Beau had only 43% of the severity on Monon. Tests involving the flag leaf (F) or the leaf just below it (F-1) were more discriminatory than tests involving the lower leaves.

The error mean squares from the five factorial analyses of variance were homogeneous according to Bartlett's chi-square test (12). Therefore, a pooled error mean square was used in an overall analysis of the five experiments to test the consistency of results in repeated experiments, using a procedure given by Cochran and Cox (2). In this analysis, the appropriate denominator for the variance ratio for cultivars is the experiment by cultivar interaction because the analyses for individual experiments revealed significant age by cultivar interactions. Even using this more conservative denominator, the effect of cultivar was highly significant (Table 3). The F-value for experiment by cultivar tested against the pooled error mean square likewise was highly significant. Thus, although Oasis, P711368, Arthur, and Monon were consistently resistant or susceptible, the relative behavior of the remaining cultivars was sufficiently variable that no one experiment would clearly reveal the behavior of all cultivars.

In experiments 4 and 5 severity could be recorded on F and F-1 on all plants. A split plot analysis was used to compare severities on these leaves (Table 4). In both analyses, cultivar was the greatest source of variation. Severity on F-1 was always greater than severity on F, but the difference was significant only in experiment

TABLE 1. Mean squares for the factorial analyses of variance of arc sin-square root of percent leaf area affected by speckled leaf blotch

Source of variation	Degrees of freedom	Experiment[a]				
		1	2	3	4	5
Age	1	239.8	125.00	413.76**	1,686.83**	634.23
Cultivar	9	6,571.97**	4,652.68**	4,909.82**	2,135.74**	3,210.72**
Age × cultivar	9	127.63	717.91*	464.72*	422.56*	545.79*

[a]* and ** = significance at $\alpha = 0.05$ and 0.01, respectively.

TABLE 2. Mean arc sin-square root severity of speckled leaf blotch on the uppermost fully expanded leaf of 10 wheat cultivars[a,b]

	Experiment, growth stage, and leaf examined[c]										
	1		2		3		4		5		
Cultivar	Pseudostem erection; F-3 to F-4	1–2 nodes visible; F-2 to F-3	4–8-leaf stage; F-2 to F-3	Early boot; F-1 to F-2	Boot; F-1	Heading; F	Boot; F	Early milk; F	Anthesis; F	Midmilk; F	Mean
Oasis	3 a	3 a	3 a	4 a	7 a	3 a	12 a	10 a	8 a	14 a	7
P711368	63 bc	56 b	33 b	33 b	38 b	29 b	21 ab	19 ab	39 cde	16 ab	35
Caldwell	87 c	84 c	66 cd	33 b	60 bcd	46 c	62 de	29 bc	17 ab	17 ab	50
P6413	87 c	84 c	51 bc	67 c	69 cd	48 c	28 ab	26 bc	18 abc	27 ab	51
Knox	51 b	62 bc	51 bc	58 c	59 bcd	76 d	40 bc	35 bcd	35 bcd	52 cd	52
P68152	80 c	63 bc	55 bc	75 c	49 bc	51 c	35 bc	42 cd	45 de	49 cd	54
Beau	79 c	80 c	73 cd	64 c	69 cd	49 c	49 cd	38 cd	38 cde	35 bc	57
P67129	85 c	80 c	77 cd	62 c	70 cd	60 c	38 bc	42 cd	40 de	57 d	61
Arthur	87 c	83 c	57 bc	67 c	64 cd	80 d	77 e	48 d	59 e	52 cd	67
Monon	84 c	81 c	87 d	67 c	82 d	85 d	52 cd	41 cd	52 de	82 d	71

[a]Within each column, means followed by a letter in common are not significantly different (Duncan's new multiple range test, $\alpha = 0.05$).

[b]A value of 3 corresponds to 0% and a value of 87 corresponds to 100% necrotic leaf area because 0 and 100% were converted to 0.25 and 99.75%, respectively, before transformation.

[c]For each experiment, the range of growth stages exhibited is given, with the most frequent growth stage first. In experiments 1 and 2, the leaf examined depended on the growth stage. F = flag leaf, F-1–F-4 = leaves below flag leaf.

4 (44 vs 37%). The source of the significant age by cultivar and leaf position by cultivar interactions could not be ascribed to any specific subset of cultivars. Individual analyses of variance and mean separations of severities averaged over leaf position and within age group, or averaged over age group within leaf positions, showed that means of most cultivars were significantly different from means of certain other cultivars at one age group or leaf position and not significantly different at the other age group or leaf position. This is not to say, however, that no consistent differences existed. Oasis always had less necrosis than P67129, Beau, Knox, Arthur, and P68152.

Pycnidial density. In all five experiments, the effect of cultivar was highly significant (Table 5). The effect of plant age was highly significant when plants were inoculated before flag leaves had appeared but was nonsignificant in the later experiments. Pycnidia on the more susceptible cultivars tended to be more abundant on older plants inoculated after flag leaves had emerged (Table 6). In experiments 3–5, in which flag leaves of most plants were infected, the effect of age on pycnidial density was less pronounced. Thus, most of the effect of age was due to the leaves inoculated, ie, F and F-1 or the lower leaves, and not to the age of the inoculated plant per se.

Because pycnidial density was estimated only within necrotic tissue, it could be evaluated even on leaves not fully expanded at the time of inoculation. Consequently, we were able to record pycnidial density on two leaves of each main culm of every plant in every experiment. The effect of leaf position on pycnidial density was unambiguously significant only in experiments 3 and 5 (Table 5). In experiments 1 and 4, leaf position was significant when tested with a pooled error term, assuming a true split-plot design. However, leaf position of necessity could not be randomized within cultivar-age group main plots. When the mean squares for leaf position were tested more conservatively with the block by leaf position mean square, the variance ratio was not significant, owing to the reduction in error degrees of freedom. Under the conditions of these experiments, a large difference in environmental conditions between leaf positions 1 and 2 was not likely. In the moist chamber, the air was saturated with water vapor and therefore a humidity gradient from soil to canopy level did not exist. We suspect that the leaf position effects were due to inherent physiological differences in the leaves and not to differences in environment between the two leaf positions.

The error mean squares for the five factorial analyses of pycnidial density were more homogeneous than those for the analyses of severity. An overall analysis of pycnidial density for the five experiments was performed as described for disease severity (Table 3). Differences among cultivars averaged over experiments were highly significant. The experiment by cultivar interaction was likewise highly significant when tested with the pooled error mean square.

Just as Oasis had the least necrotic leaf area, it had the fewest pycnidia (Table 6). Oasis consistently had significantly fewer pycnidia per unit area of lesion than all cultivars except P711368, Caldwell, and P6413. These cultivars, in turn, had significantly fewer pycnidia than Monon in all cases (except for P6413 in one age group of experiment 3). Variation in pycnidial density on Knox, Beau, and Arthur among experiments probably contributed most to the experiment by cultivar interaction mean square. P67129 and P68152 consistently supported an intermediate number of pycnidia.

Pycnidial density and percent necrotic leaf area (arcsin-square root) were positively correlated (Table 6). The point for Caldwell deviated most from the regression line relating cultivar means for pycnidial density and severity (Fig. 1). It had fewer pycnidia than predicted by the regression line.

TABLE 3. Combined analysis[a] of variance of speckled leaf blotch severity and density of *Mycosphaerella graminicola* pycnidia on leaves of 10 wheat cultivars compared in five experiments

Source of variation	Severity[b]		Pycnidia per unit area (mm^2) of lesion	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Experiment	4	18050.13	4	187.698
Cultivar	9	17063.70**	9	1107.442**
Experiment × cultivar	36	4947.42**	36	33.927**
Pooled error	377	229.92	767	6.929

[a] ** = significance at $\alpha = 0.05$.
[b] Arc sin-square root transformation of percent necrotic leaf area.

TABLE 4. Split plot analysis of variance for the arcsin-square root of percent area of the flag leaf and penultimate leaf affected by speckled leaf blotch on 10 wheat cultivars

Source of variation	Degrees of freedom	Mean squares[a]	
		Experiment 4	Experiment 5
Age	1	0.17608	0.52921*
Cultivar	9	1.31005**	1.66677**
Age × cultivar	9	0.23183**	0.26434**
Leaf	1	0.30921**	0.2300
Age × leaf	1	0.14039*	0.01949
Cultivar × leaf	9	0.06017*	0.05916*
Age × cultivar × leaf	9	0.04423	0.09191**

[a] * and ** = significance at $\alpha = 0.05$ and 0.01, respectively.

DISCUSSION

Of the wheat cultivars and breeding lines investigated in this study, only Oasis was derived from a cross made specifically to incorporate speckled leaf blotch resistance into a commercially acceptable soft red winter wheat cultivar (6). We first noticed the resistance of Beau, Knox, and the Purdue breeding lines in severe natural epidemics of speckled leaf blotch when these lines were grown in yield nurseries (10). In the controlled greenhouse conditions used in the present study, the resistance of Oasis was

TABLE 5. Mean squares for *Mycosphaerella graminicola* pycnidia per square millimeter of lesion on wheat[a]

Source of variation	Degrees of freedom	Experiment[b]				
		1	2	3	4	5
Cultivar	9	103.55**	233.22**	306.99**	40.68**,NS	293.01**
Age	1	205.03**	249.09**	59.19*	1.65	1.67
Cultivar × age	9	23.64**	36.37**	66.87**	45.56**	18.35
Leaf	1	29.11**,NS	9.86	297.68**,*	40.68**,NS	119.97**,*
Cultivar × leaf	9	1.44	5.03	21.02**	8.65	9.24
Age × leaf	1	10.63	1.07	5.31	0.00	23.19*,**
Cultivar × age × leaf	9	1.50	8.82*	13.83NS,*	7.77	11.11*

[a] Experimental design is a factorial with "leaf" nested within "cultivar-age" main plots.
[b] The first indicator of significance is based on an F value calculated from a pooled error b. The indicator of significance following the comma is based on an F value calculated from the appropriate block × treatment interaction. NS = not significant; * and ** = significance at $\alpha = 0.05$ and 0.01, respectively.

consistently superior to the resistance of the other lines. Faint chlorotic flecks were the only evidence of infection on Oasis plants inoculated before heading. Even on plants inoculated at heading or later, necrosis was very limited and very few pycnidia were found within necrotic areas. In the field, sparse pycnidia of *M. graminicola* are sometimes present on Oasis leaves (11), suggesting that the monogenic resistance of Oasis, derived from Bulgaria 88 (8), might have succumbed to a new virulent strain of the fungus. Eyal et al (3) found evidence for physiologic specialization in *M. graminicola*; one isolate was described as moderately virulent on Bulgaria 88. However, we have never seen a level of infection and fructification on Oasis in the field that would indicate an erosion of its resistance. When we inoculated Oasis with *M. graminicola* cultures reported to be virulent to Bulgaria 88, Oasis was no more susceptible than it was in the present study (Shaner and Finney, *unpublished*). Indeed, in the greenhouse, following inoculations that produced nearly complete necrosis on Monon, Oasis showed less necrosis on lower leaves than it often shows in the field. We believe that the necrosis seen in the field is due mostly to infection by other fungi, most likely *Leptosphaeria nodorum* Müller and *Pyrenophora tritici-repentis* (Died.) Drechs.

The other cultivars and breeding lines that were identified in the field as having some resistance fell along a continuum of resistance between Oasis and Arthur. This difference in resistance was not seen as consistently on lower leaves as on the flag leaf, suggesting that resistance, as a restriction of necrotic lesion development, is an adult plant resistance.

Cultivars showed a greater relative range in pycnidial density than in percent necrotic leaf area. Cultivars such as P711368 and Caldwell, which had one half or two thirds as much necrosis as Monon, had less than one fifth as many pycnidia within lesions. On these cultivars, as well as on P6413 and P67129, restriction of fructification of *M. graminicola*, rather than interference with the development of necrotic lesions, is the important form of resistance. Moreover, this inhibition of fructification is expressed consistently throughout the life of the plant. Rosielle (9) rated wheats for resistance to *M. graminicola* on a scale that implied an association between lesion size (ie, percent leaf area necrotic) and pycnidial density. He noted, however, that some cultivars had extensive leaf necrosis but sparse pycnidia. Gough and Smith (5) likewise reported that some wheats in a screening nursery had sparse pycnidia despite extensive necrosis.

Although significant differences in pycnidial density among cultivars were detected in all experiments, the range was greater when plants were inoculated after flag leaves had emerged. This was due mostly to a greater density of pycnidia on flag leaves than on lower leaves of the very susceptible cultivar Monon. Brokenshire likewise observed more pycnidia on flag leaves than on seedling leaves (1).

The restriction of necrotic lesions and the inhibition of fructification would complement each other in the field to retard disease development. *M. graminicola* produced pycnidia over most of the necrotic area of leaves of Monon and Arthur. On the other cultivars, some of the necrotic tissue contained no pycnidia, so not all of the necrotic tissue indicated in Table 2 was occupied by pycnidia at the densities indicated in Table 6. Consequently, the difference in total number of pycnidia per leaf between Monon or Arthur and the remaining cultivars is greater than the data in Tables 2 and 6 imply.

Another possible aspect of resistance is size of pycnidia. Gough (4) showed that *M. graminicola* pycnidia on Oasis were smaller and produced fewer spores than pycnidia on the susceptible wheat cultivar Improved Triumph.

An interesting finding in our study is that, with the exception of

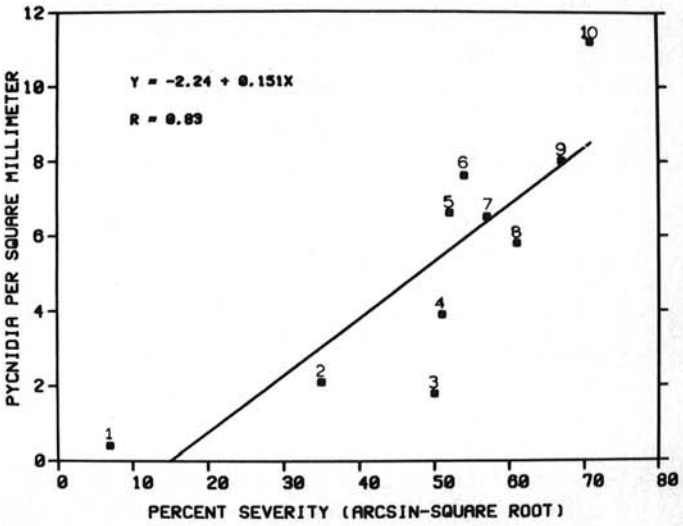

Fig. 1. Relationship between density of pycnidia of *Mycosphaerella graminicola* in lesions on leaves and percent necrotic leaf area on wheat. Values are means of all experiments reported in Tables 2 and 6. Numbers above data points refer to cultivars: 1 = Oasis, 2 = P711368, 3 = Caldwell, 4 = P6413, 5 = Knox, 6 = P68152, 7 = Beau, 8 = P67129, 9 = Arthur, 10 = Monon.

TABLE 6. Mean number of pycnidia of *Mycosphaerella graminicola* per square millimeter of lesion on the two uppermost leaves on 10 wheat cultivars[a]

	Experiment and growth stage at time of inoculation[b]										
	1		2		3		4		5		
Cultivar	Pseudo-stem erection	1–2 nodes visible	4–8-leaf stage	Early boot	Boot	Heading	Boot	Early milk	Anthesis	Mid-milk	Mean
Oasis	0 a	0 a	0.2 a	0 a	0.2 a	0 a	0 a	0.5 a	1.2 a	1.7 a	0.4
P711368	1.9 bc	2.4 ab	1.4 ab	1.6 b	1.2 ab	2.2 ab	3.7 bcd	0.7 a	4.0 bc	2.0 a	2.1
Caldwell	0.9 ab	1.5 ab	1.9 b	1.4 a	1.2 ab	4.3 bc	2.1 ab	2.8 ab	0.7 a	1.5 a	1.8
P6413	2.1 bc	3.0 bc	4.5 cd	4.9 b	10.9 e	5.5 c	2.9 abc	1.7 a	1.8 ab	1.6 a	3.9
Knox	1.8 bc	6.8 d	4.4 c	9.5 de	5.5 cd	9.4 d	5.8 cd	7.8 cd	5.9 cd	9.4 b	6.6
P68152	4.5 de	6.1 d	6.1 de	11.3 e	6.7 cd	9.4 d	6.3 d	9.3 de	9.4 e	6.9 b	7.6
Beau	2.3 bc	5.3 cd	4.9 cd	9.0 d	4.1 bc	8.1 d	9.6 e	6.8 c	7.1 de	8.2 b	6.5
P67129	4.8 de	5.3 cd	6.1 de	6.4 de	8.6 de	5.2 c	5.9 cd	4.4 b	4.4 bcd	6.7 b	5.8
Arthur	3.4 cd	9.9 e	6.9 e	7.8 cd	9.9 e	8.6 d	6.5 d	13.0 f	7.1 de	7.2 b	8.0
Monon	5.9 e	7.6 de	7.3 e	13.9 f	10.1 e	16.5 e	13.8 f	11.2 ef	14.0 f	12.1 c	11.2
Mean	2.8	4.8	4.4	6.6	5.8	6.9	5.6	5.8	5.6	5.7	5.4
r[c]	0.60	0.54	0.76	0.83	0.72	0.85	0.45	0.86	0.80	0.91	0.83
Leaf 1	4.2		5.7		7.6		6.2		6.4		
Leaf 2	3.4		5.2		5.1		5.3		4.9		

[a] Within each column, means followed by a letter in common are not significantly different (Duncan's new multiple range test, $\alpha = 0.05$).
[b] For each experiment, the range of growth stages exhibited is given, with the most frequent growth stage first.
[c] Correlation coefficient between pycnidial density and severity (Table 2).

Oasis, all lines showing resistance to *M. graminicola* were derived from parents that do not possess any noteworthy resistance. P711368 was selected from a three-way cross involving parents all as susceptible as Arthur. Caldwell is a selection from Benhur sib *2/Siete Cerros. Benhur sib has been slightly more resistant than Arthur in some field trials but equally susceptible in others. Siete Cerros has been consistently very susceptible in our spring wheat nurseries. The superior resistance of Caldwell and the other breeding lines in this study, compared to that of their parents, suggests that their resistance results from additive or complementary gene action, thus providing additional protection to that conferred by the gene from Bulgaria 88.

If speckled leaf blotch is at least moderately severe in the field, plants can be selected reliably according to the extent of necrosis on the upper four or five leaves and the density of pycnidia within necrotic tissue. The resistance of lines selected as parents can be confirmed by evaluation in the greenhouse. Movement of inoculum between rows does not seem to obscure quantitative resistance to *M. graminicola* as much as it does with the cereal rust fungi. Even within drilled rows of F_2 plants that are segregating for resistance, the more resistant plants can be recognized. Resistant 1-m rows of F_3 plants are easily recognized. Consequently we have been able to make rapid and steady progress in incorporating this quantitative resistance into much of our breeding material.

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