Partial Resistance to Powdery Mildew in Soft Red Winter Wheat

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ABSTRACT

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Powdery mildew (caused by *Erysiphe graminis* f. sp. *tritici*) is a disease that can cause significant yield loss in soft red winter wheat (*Triticum aestivum*). In selecting for resistance, one strategy is to incorporate partial resistance into breeding populations. The objectives of this study were to (i) estimate heritability of partial resistance to powdery mildew, (ii) determine which growth stage is optimal for measuring powdery mildew in terms of predicting yield loss, and (iii) measure yield loss associated with powdery mildew. In 1991, we evaluated 94 F_3 lines from a single-cross population believed to be segregating for partial resistance in a replicated experiment near Lexington, KY. The bulked F_5 progeny were evaluated in a replicated experiment in 1993. Plants were rated according to leaf infected (LI), an index of powdery mildew on the flag leaf and the subtending two leaves at Feekes growth stages (GS) 9 and 10.5. Severity of infection was assessed only on the uppermost leaf on which powdery mildew was present. Broad sense heritability estimates ranged from 0.31 (LI, 1991) to 0.65 (severity, 1991). Heritability of severity of infection was considerably higher at GS 9 than at GS 10.5 (0.57 versus 0.34). Severity of infection at GS 9 also had the strongest correlation with yield (r = –0.55; P < 0.01) of any powdery mildew rating. We observed an average yield loss of 20% associated with powdery mildew over the 2 years of the study. Our data indicate that GS 9 is better than GS 10.5 for evaluating powdery mildew in terms of likely yield loss and heritability.

In the areas of the United States where soft red winter wheat (*Triticum aestivum* L. em. Thell) is grown, powdery mildew (caused by *Erysiphe graminis* DC. f. sp. *tritici* Ém. Marchal) is considered one of the major leaf diseases, with yield losses ranging up to 34% (7).

It is now commonplace in Kentucky to rely on fungicides, e.g., propiconazole (Tilt), for control of powdery mildew and other wheat diseases (D. A. Van Sanford and D. E. Hershman, *unpublished*). Complete dependence on fungicides for disease control carries risks for the producer, in that accurate coverage and distribution of fungicides on the wheat leaves can be very difficult to achieve (8), and there are potential problems with correct timing of applications. Furthermore, increasing concern for the environment will likely mean greater regulation of pesticide usage.

Use of cultivars with powdery mildew resistance can improve yield while reducing economic inputs. However, there is a need to improve powdery mildew resistance in wheat cultivars through the introgression of new resistance genes (2). Typically, wheat breeders have relied on single gene resistance. Leath and Heun (13) found that of 17 powdery mildew resistance genes available to breeders in 1990, only three were represented in the 22 cultivars they tested. An alternate strategy in breeding for powdery mildew resistance is to select for partial resistance. If plants are scored prior to anthesis, this approach allows the breeder to intermate selected individuals in attempting to accumulate genes for partial resistance. Therefore, it would be useful for breeders to have estimates of heritability of partial resistance (6). Such estimates are scarce, because most studies have been conducted with cultivars rather than genetic reference populations and have been unsuitable for estimating genetic variance and heritability (3,13).

We were also interested in determining the optimal growth stage for rating powdery mildew in a wheat breeding program. Rating before anthesis would facilitate phenotypic recurrent selection, but it is also important that ratings are made at a stage that most accurately reflects potential yield loss. Previous research had shown Feekes growth stage (GS) 10.5 (spikes completely emerged) to be optimal for rating breeding populations for powdery mildew (8), which would preclude preanthesis selection of resistant types. However, other studies that have focused on fungicide timing indicate that control of powdery mildew prior to flag leaf emergence can reduce yield loss (12,14).

Our objectives were to (i) estimate heritability of partial resistance to powdery mildew in this population, (ii) determine whether GS 9 or 10.5 is better for measuring powdery mildew in terms of predicting yield loss, and (iii) measure yield loss associated with powdery mildew in soft red winter wheat grown in Kentucky.

MATERIALS AND METHODS

This study was carried out from 1990 to 1993 at the Spindletop research farm near Lexington, KY. In 1990, single wheat plants were evaluated for powdery mildew in the F_2 population KY83-27/Cardinal at GS 6 (first node detectable), 9 (flag leaf sheath extending), and 10.5 (all of heads emerged) (10). This population was chosen because it was believed to be segregating for only partial resistance. After the study was underway, the parents were inoculated with a combination of isolates of *E. graminis*. No resistance genes were detected in Cardinal, but KY83-27 carries *Pm3a* and *Pm6,* which are ineffective against the virulence genes in isolates of *E. graminis* from Kentucky (S. Leath, *personal communication*). Powdery mildew ratings consisted of two parts: (i) presence of the disease on the flag leaf and the subtending two leaves (F-1 and F-2 leaves), and (ii) an estimate of the severity of the disease, recorded as the percentage of the uppermost leaf covered by powdery mildew. Presence of powdery mildew on the flag, F-1, and F-2 leaves was assigned respective values of 1.0, 0.75, and 0.50. In other words, if powdery mildew was present on the flag, F-1, and F-2 leaves of a given culm, that culm received a value of 1.0 + 0.75 + 0.5 = 2.25. A culm that had powdery mildew only on the F-2 leaf was assigned a value of 0.5. The mean value of three (1990 to 1991) or 10 (1992 to 1993) culms per experimental unit was recorded. This trait is hereafter referred to as "leaf infected" (LI), rather than incidence, since powdery mildew was observed on every culm that was evaluated, giving an incidence of 100%. Because powdery mildew spreads from the lower to the upper part of the plant canopy, severity ratings were made on the highest leaf to which the disease had progressed. The reason for assessing severity on this leaf only was that most assimilate is de-

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rived from flag leaf photosynthesis (4). Other traits measured were individual plant yield, height, and heading date.

On 2 November 1990, two groups of 93 random $F_{2:3}$ headrows were planted in separate blocks. There was enough seed from each F_2 plant for three replications of each $F_{2:3}$ row. The experimental units were single rows 0.5 m in length, with 30 cm between rows. A four-row pass of the cultivar Becker, which is highly susceptible to powdery mildew, was planted between the four-row passes in which the headrows were planted to assure an even spread of powdery mildew inoculum.

All rows were fertilized with ammonium nitrate at the rate of 136 kg ha^{-1} of actual N in a split application of 68 kg ha^{-1} per application on 8 March (GS 3) and 28 March 1991 (GS 5). This rate of N fertilizer is higher than recommended, but it was chosen to promote greater leaf area and greater development of powdery mildew (11). All rows were sprayed with Harmony Extra (thifensulfuron plus tribenuron) at 20.8 g ha^{-1} a.i. to provide weed control.

To estimate yield loss due to powdery mildew, one block of $F_{2:3}$ lines was treated weekly with mancozeb (Dithane M-45) at 1.8 kg ha^{-1} a.i., which allowed powdery mildew to develop but controlled other leaf diseases such as Septoria blotch (*Septoria tritici* Roberge in Desmaz.) and leaf rust (*Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici*). The second block was treated weekly with mancozeb at 1.8 kg ha^{-1} a.i., plus triadimefon (Bayleton) at 208 g ha^{-1} a.i., which provided complete protection against all fungal leaf diseases. The block treated with mancozeb only was rated for powdery mildew at GS 6, 9, and 10.5. LI and severity of mildew infection on the uppermost leaf were measured as described earlier. In each row three plants were rated and the mean was recorded. Other traits measured in 1991 were yield (g m^{-2}), plant height (cm), and heading date. The rows were harvested individually and threshed in a stationary thresher. Grain was dried to approximately 10% moisture and then weighed to the nearest gram.

Severe winter kill in 1991 to 1992 made it impossible to collect data. Seed was harvested from 74 $F_{2:4}$ lines that survived. On 12 October 1992, $F_{2:5}$ seed was planted in plots (3.4 m^2) in two blocks with four sets per block and two replications per set. Becker was planted in the alleys between replications as a solid six-row pass to assure an even spread of powdery mildew inoculum throughout the entire experiment.

Nitrogen, herbicide, and fungicide applications were identical to those used in 1991. The block treated only with mancozeb was rated for powdery mildew at GS 9 and 10.5. Powdery mildew ratings at GS 6 were omitted from the study due to the very low incidence of infection and the excessive variability of ratings at this growth stage. Ten plants per plot were rated for LI and severity at GS 9 (5 to 7 May) and 10.5 (20 to 21 May). Plot means were used for statistical analysis. Plant height at maturity and heading date also were measured. Plots were harvested on 2 to 3 July with a Hege 125B plot combine. Grain samples were dried to approximately 10% moisture and weighed to the nearest gram. Test weight was measured on all genotypes in the first replication of each set in both blocks.

Analysis of variance was performed on LI and severity at GS 9 and 10.5, grain yield, plant height, and heading date, with untreated and treated blocks analyzed separately. All effects in the model were considered random. Broad sense heritability (h^2) and 90% confidence intervals also were estimated for each trait (9). For individual year analyses h^2 was estimated as the ratio of the genotype variance component to the error mean square. In the combined analysis over years, h^2 was estimated as the ratio of the genotype variance component to the genotype × year mean square. In order to generate an exact confidence interval for the h^2 estimates, the variance components were expressed as a function of mean squares, (e.g., genotype and genotype × year), the ratio of which is distributed as an F statistic (9). Correlation coefficients were estimated for all traits measured, with genotype means. Comparisons were made between the unprotected block and the protected block with regard to yield and test weight to estimate the effect of powdery mildew on these traits.

RESULTS AND DISCUSSION

Means and standard errors for LI, severity, and other traits are presented in Table 1. GS 9 ratings were made on the F-2, F-1, and flag leaves, while ratings at GS 10.5 were made on the F-1 and flag leaves. In 1991, mean LI was higher at GS 10.5

Table 1. Means and standard errors (SE) of powdery mildew resistance traits measured on F3 and F5 wheat lines at growth stages (GS) 9 and 10.5 in 1991 and 1993

	1991		1993		1991 to 1993	
Trait	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
LI[a]						
GS 9	0.77	0.008	0.59	0.005	0.70	0.005
GS 10.5	0.98	0.006	0.65	0.008	0.85	0.006
Severity[b]						
GS 9	13.0	0. 7	4.0	0. 1	9.0	0.4
GS 10.5	8.0	0. 5	4.0	0. 2	6.0	0.3
Yield (g m^{-2})	177.6	6.3	563.7	6.3	332.4	4.8

[a] Leaf infected: an index of infection of the flag leaf and the two leaves below (GS 9) or the flag leaf and the first leaf below (GS 10.5).
[b] Percentage of the uppermost leaf infected.

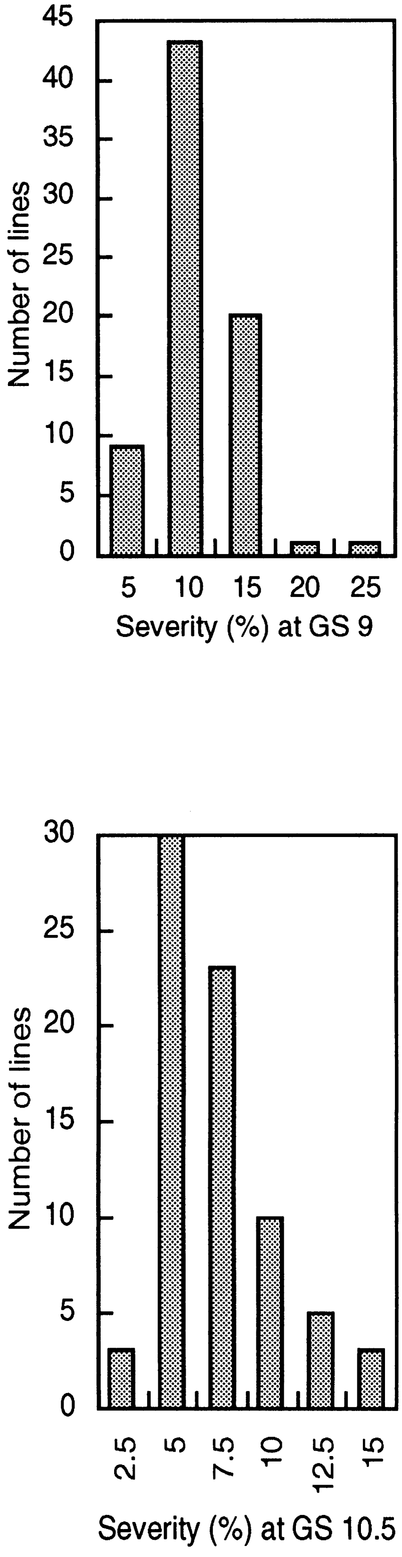

Fig. 1. Frequency distributions of 74 F_3 wheat lines and their bulk F_5 progeny for severity of powdery mildew infection at growth stages (GS) 9 and 10.5, 1991 and 1993.

(0.98) than at GS 9 (0.77). This result was not surprising, since powdery mildew spreads from the lower to the upper part of the canopy. Severity of infection was 8% at GS 10.5 and at 13% at GS 9. The highest severities recorded for individual plots were 30% at GS 9 and 22% at GS 10.5. The higher severity at GS 9 could be attributed to two factors: (i) a more favorable environment for powdery mildew infection (cooler, more humid) existed at GS 9 than at GS 10.5, or (ii) our rating system had the potential to underestimate severity at GS 10.5, in that severity was measured only on the uppermost leaf to which the disease had progressed. For example, at GS 9, powdery mildew could be severe on the F-1 leaf with no symptoms present on the flag leaf. By GS 10.5, powdery mildew severity could be even higher on the F-1 leaf, but with some infection on the flag leaf. In this case, the severity on the flag leaf would have been recorded, and it might have been less than the severity on the F-1 leaf recorded at GS 9.

Frequency distributions of severity at GS 9 and 10.5, averaged across years, are presented in Figure 1. The severity values for Cardinal, KY83-27, and Becker were 15, 20, and 25%, respectively, at GS 9 and 12, 15, and 30%, respectively, at GS 10.5.

In 1993, LI ratings at GS 9 and 10.5 were similar: 0.59 and 0.65, respectively. Mean severity was identical (4%) at both growth stages. Mean yield was 563.7 g m^{-2}, more than 3 times the yield recorded in 1991 (Table 1). The low yields in 1991 were attributable to head scab (caused by a *Fusarium* sp.), which reduced yields throughout the state (16).

In 1991, mean yield of the treated block was 257.1 g m^{-2} while mean yield of the untreated block was 177.6 g m^{-2}, representing a 30% yield loss due to powdery mildew infection. In 1993, we observed a 14% yield loss when comparing treated versus untreated blocks. In the combined analysis over years, a yield loss of 20% could be attributed to powdery mildew infection. This yield loss was apparently due to fewer seeds per unit area, since the mean seed weight between the two blocks differed by only 0.05 g (data not shown). Everts and Leath (5) observed that number of tillers and number of kernels per spike were both affected by powdery mildew infection.

Averaged over the 2 years of the study, severity at GS 9 was the trait with the strongest negative correlation to grain yield (Table 2). Our results agree reasonably well with the negative correlation of $r = -0.78$ between yield and powdery mildew infection reported by Johnson et al. (7). LI at GS 9 was significantly correlated only with LI at GS 10.5. LI at GS 10.5 was not correlated with severity at GS 10.5, but was significantly negatively correlated with yield. Severity at GS 10.5 was negatively correlated with yield.

The correlations indicate a stronger relationship between grain yield and powdery mildew severity at GS 9 than at GS 10.5. The regression of yield on severity at GS 9 produced a regression coefficient of $\beta_1 = -6.4 \pm 1.1$ g m^{-2} with $R^2 = 0.31$. Regressing yield on severity at GS 10.5 provided a regression coefficient of $\beta_1 = -5.0 \pm 1.6$ g m^{-2} with $R^2 = 0.12$. Regression analysis of yield and severity thus indicates that a severe powdery mildew infection at GS 9 had a greater effect on yield than an infection that did not reach a similar level of severity until GS 10.5. In a breeding program, therefore, GS 9 would be a better growth stage than GS 10.5 for assessing yield loss due to powdery mildew.

To our knowledge, estimates of heritability of adult plant resistance to powdery mildew in the field are rare. Abdalla et al. (1) carried out two cycles of recurrent selection for powdery mildew resistance in two broad-based wheat populations. The authors did not present heritability estimates, but gains of up to 53% were realized from selection for seedling resistance in the greenhouse. Das and Griffey (3) recently reported on adult plant resistance to powdery mildew in a diallel series of crosses among diverse wheat cultivars. They estimated effects, rather than variances or heritability, due to the nature of the parents. In their study, general combining ability effects were predominant.

There is a semantic difficulty in discussing heritability of severity of a disease, since, in the case of partial resistance, the breeder is clearly interested in the *reduced* severity of the disease. However, heritability of severity, for example, should be equal to heritability of partial resistance by the following argument. Let severity = S and partial resistance = 1 − S. Let the variance of severity VAR(S) = σ^2. Then the variance of resistance, VAR(1 − S) = σ^2 since VAR(1) = 0.

Broad sense heritability estimates (h^2) with 90% confidence intervals are presented for all traits of interest in Table 3. The heritability of LI in 1991 was higher at GS 10.5 than at GS 9. Heritability of severity in 1991 was also slightly higher at GS 10.5 than at GS 9. Similarly, in 1993, heritability was higher at GS 10.5 than at GS 9 for LI. However, severity of infection had a higher heritability value at GS 9 than at GS 10.5.

In the combined analysis, because genotype × year interaction is accounted for, heritability estimates should be less biased than single-year estimates. Heritability of LI was identical at both growth stages. Thus, there would be no advantage in waiting to rate incidence of powdery mildew infection until GS 10.5 instead of rating at GS 9. Beyond this fact, we ob-

Table 2. Simple correlation coefficients among LI[a] and severity of powdery mildew at growth stages (GS) 9 and 10.5 and yield in 74 wheat lines, 1991 to 1993

	LI		Severity[b]		
Trait	**GS 9**	**GS 10.5**	**GS 9**	**GS 10.5**	**Yield**
LI					
GS 9	1.0	0.53**[c]	0.02	0.19	0.09
GS 10.5		1.0	0.29	0.17	−0.22*
Severity					
GS 9			1.0	0.62**	−0.55**
GS 10.5				1.0	−0.34**
Yield					1.0

[a] Leaf infected: an index of infection of the flag leaf and the two leaves below (GS 9) or the flag leaf and the first leaf below (GS 10.5).
[b] Percentage of the uppermost leaf infected.
[c] *,** = $P < 0.05$, 0.01, respectively.

Table 3. Heritability estimates with 90% confidence intervals for LI[a] and severity of powdery mildew at growth stages (GS) 9 and 10.5, plant height, heading date, and yield in 74 wheat lines in 1991 and 1993

Trait	**1990 to 1991**	**1992 to 1993**	**Combined analysis**
LI			
GS 9	0.05 < 0.31 < 0.50	0.10 < 0.39 < 0.58	0.35 < 0.52 < 0.64
GS 10.5	0.30 < 0.49 < 0.63	0.42 < 0.61 < 0.74	0.48 < 0.53 < 0.61
Severity[b]			
GS 9	0.43 < 0.59 < 0.70	0.40 < 0.59 < 0.72	0.23 < 0.57 < 0.58
GS 10.5	0.53 < 0.65 < 0.75	0.07 < 0.37 < 0.57	0.11 < 0.34 < 0.51
Height	0.63 < 0.73 < 0.80	0.81 < 0.87 < 0.91	0.70 < 0.77 < 0.83
Heading date	0.65 < 0.74 < 0.81	0.78 < 0.85 < 0.90	0.59 < 0.70 < 0.77
Yield	0.35 < 0.52 < 0.66	0.52 < 0.67 < 0.78	−0.07 < 0.20 < 0.41

[a] Leaf infected: an index of infection of the flag leaf and the two leaves below (GS 9) or the flag leaf and the first leaf below (GS 10.5).
[b] Percentage of the uppermost leaf infected.

served that heritability of severity was much higher at GS 9 than at GS 10.5. Furthermore, the strongest association between any mildew rating and grain yield was the negative correlation between severity at GS 9 and yield. Severity ratings at GS 9 would give the breeder a more accurate assessment of susceptibility, and would allow selection and intermating of genotypes with low ratings in the same growing season.

The results from this study do not indicate whether the resistance we observed is due to minor genes rather than residual effects of defeated major genes (15). Recurrent selection studies currently underway may shed some light on that question. In any case, it should be possible to select for partial resistance to powdery mildew in soft red winter wheat. Heritability of severity at GS 9, the trait most strongly associated with yield reduction, was considerably higher than heritability of yield itself. In our environment, it is important that powdery mildew infection is assessed at GS 9. It appears that ratings at GS 10.5 or later may overestimate the seriousness of infection in terms of reducing yield. This could cause the breeder to discard plants or families that show little or no actual yield reduction in response to powdery mildew infection.

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