

Components of Variation for Quantitative Adult-Plant Resistance to Powdery Mildew in Winter Rye

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ABSTRACT

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The genetics of quantitative resistance to powdery mildew (*Erysiphe graminis* f. sp. *secalis*) in winter rye (*Secale cereale*) was investigated by testing four sets of factorial crosses along with their parental inbred lines (53 crosses, 28 inbred lines in total) at two locations during 1988 and 1989. Genotypes were scored on a 0-9 scale for the percentage of infected leaf area at booting and heading stages on the upper three leaves of 10 randomly chosen main stems per plot. Estimates of heritability were high in all materials at both assessment stages ($h^2 = 0.65-0.95$). High correlations were found among leaves ($r = 0.75-0.97$; $P = 0.01$) for all sets and between booting and heading pooled over leaves for three out of four sets ($r = 0.89-0.98$; $P = 0.01$). Significant quantitative variation

was observed among crosses and lines. General combining ability (GCA) variances were significant for the males in all sets and for the females in three sets; specific combining ability (SCA) was negligible throughout. Strong GCA-environment interactions were found. Moderate ($r = 0.68$; $P = 0.05$) to strong ($r = 0.77-0.87$; $P = 0.01$) correlations existed between line and GCA effects. The resistance levels of lines and crosses were similar in two sets, whereas in the third set the inbred lines and in the fourth set the crosses were slightly more resistant. We concluded from the data that considerable progress can be expected from selection for quantitative resistance to powdery mildew in current hybrid rye breeding programs.

Additional keywords: *Blumeria graminis*, partial resistance.

Powdery mildew (*Erysiphe graminis* DC. f. sp. *secalis* Én. Marchal, syn. *Blumeria graminis* (DC.) E.O. Speer f. sp. *secalis* Én. Marchal) may cause considerable damage in winter rye (*Secale cereale* L.) under favorable environmental conditions (2). Resistance of rye to powdery mildew can vary qualitatively and

quantitatively (10,17,18,22). Until recently, varieties of the obligate allogamous rye consisted exclusively of genetically heterogeneous populations. Thus, major gene resistance has not been used in practical breeding and has been described only occasionally (2,12,18,22). No differential host lines are available to date. In the University of Hohenheim rye inbred line collection (Stuttgart, Germany), resistance to powdery mildew ranges continuously from completely disease free to highly susceptible under laboratory conditions (17). Most of these lines display a quantitative type of resistance *sensu* Parlevliet (25), i.e., a reduced number of

colonies without hypersensitive or completely disease-free host reaction. Koch et al (20) found that in powdery mildew of rye, additive gene action was responsible for such resistances. Using a quantitative genetic approach, Koch (19) estimated that powdery mildew resistance in rye was conditioned by a low to moderate number of effective resistance factors. Laboratory experiments (8,30) indicated that this resistance may be highly durable.

In the study presented here, a greater sample of rye single-crosses and their parent lines were investigated for quantitative powdery mildew resistance under field conditions to estimate 1) the correlation of adult-plant resistance between different assessment stages (booting and heading), 2) the relative importance of the components of variation (i.e., genotype, environment, and their interaction), 3) the partitioning of general and specific combining ability (GCA and SCA, respectively), and 4) the correlation between the resistance of lines and their GCA effects.

MATERIALS AND METHODS

Genotypes tested. Twenty-eight self-fertile inbred lines derived from the Petkus and Carsten gene pools, the two major heterotic groups currently used in hybrid rye breeding (7), were used as parents. Four sets of factorial single-crosses were established, using three or four female and male lines each per set (Table 1). One line (L304-P) was included in two sets as a female parent. The parents represent a genetically unrelated sample of elite inbreds and are nearly homozygous ($>S_5$ [selfing generation 5]). They were developed directly from populations or from crosses among second-cycle material by subsequent selfing and selection for agronomic characters, such as vitality, plant height, lodging resistance, seed set, and kernel size (7) but not for powdery mildew resistance. However, lines with extreme powdery mildew susceptibility were eliminated during inbreeding. None of the lines used for this experiment showed complete powdery mildew resistance, hypersensitive reactions, or carried one of the few major genes that are known. The crosses were produced during 1987 by means of cytoplasmic male sterility (CMS), in plots isolated by polyethylene walls, using lines of the Petkus gene pool in the CMS-inducing Pampa cytoplasm (11) as females and lines of the Carsten gene pool with restorer genes as males. To our knowledge, no effect of cytoplasm on powdery mildew resistance

exists (19).

Field testing. During 1988 and 1989, the 28 parents and 53 single-crosses were planted at two test sites: Grabau near Hamburg in northern Germany (40 m above sea level, 8 C mean annual temperature, 853 mm mean annual precipitation) and Sirnau in the Neckar Valley near Stuttgart in southern Germany (250 m above sea level, 10 C mean annual temperature, 641 mm mean annual precipitation). Winter rye is commonly infected by powdery mildew at these two locations. During 1988 and 1989, autumn and winter temperatures were unusually high, supporting an early start of the epidemic.

At Grabau, lines and single-crosses were drilled in three-row microplots. Rows were 1.5 m long with 0.21 m spacing between the rows (plot size 0.945 m²). During both years, seeds were sown at the end of September at a density of 250 seeds m⁻² for the single-crosses and 350 seeds m⁻² for the inbreds to compensate for their reduced seedling vigor. Because of stand establishment problems at Sirnau, plants were transplanted to the field at the three- to four-leaf stage during October. Each plot at Sirnau consisted of 30 plants grown in three rows with 0.15 m spacing within and 0.2 m spacing between rows.

The four sets of materials were grown in four blocks in the field. Within these blocks, the lines were tested in randomized complete-block designs with six replicates and the crosses in 7- × 8-lattice designs with three replicates. Three single-crosses were added twice to complete the lattice. Two replicates of the lines and one replicate of the crosses alternated with each other within the four field blocks. In the alleys (1.5 m width), a rye population selected at the University of Hohenheim over several cycles of recurrent selection for increased powdery mildew susceptibility (MSS = mildew susceptible synthetic) was sown as a disease spreader. To decrease interplot interference, the rye plots were separated from each other by three rows of a nonhost, *Triticale* (× *Triticosecale* cv. Lasko).

Inoculum and inoculation. A powdery mildew population composed of wild-type samples from heterogeneous rye populations grown in 16 German locations was used for inoculation to avoid any specific interaction between host and pathogen. MSS seedlings were artificially inoculated in the greenhouse and transplanted clumpwise during October and March into the spreader rows. The spreader rows, including the clumps, were removed at jointing (EC₃₁ on the Zadoks [33] scale) when all genotypes of the experiment were visibly infected.

Disease assessment. Disease development was assessed at booting (EC₃₇) and midheading (EC₅₅) at the respective developmental stage of the genotypes. Ten main stems randomly chosen from the center row of each plot were marked and evaluated for powdery mildew on each of the upper three leaves with a nonlinear rating scale (27): 0 = completely mildew free, 1 = 1-3%, 2 = 4-8%, 3 = 9-15%, 4 = 16-24%, 5 = 25-35%, 6 = 36-48%, 7 = 49-63%, 8 = 64-80%, 9 = 81-100% leaf area affected, respectively. At booting, the flag leaf (F) was not fully expanded. Therefore, the upper first, second, and third leaves below the flag leaf were rated (F-1, F-2, and F-3, respectively). At heading, the F, F-1, and F-2 leaves were rated. Senescence of the F-3 leaf prevented its inclusion at this stage.

Statistical analyses. Analyses of variance were based on single-plot data, i.e., on the mean powdery mildew rating of an entry over 10 stems and three leaves at each assessment stage, separately. The four location-year combinations were analyzed as four environments. For the crosses, lattice-adjusted means were used for combined analysis over environments (6). As essential prerequisites for this combined analysis (6), no significant deviation from normality of individual environments and no heterogeneity of plot errors were detected in any of the sets. Estimates of GCA and SCA variances were obtained by established procedures (32). Repeatability estimates for one-environment analyses and heritability estimates for the multi-environment analysis were based on entry means (1). All statistical analyses were computed with the PLABSTAT computer program (29), assuming the effects of the genotypes, environments, and replicates as random variables.

TABLE 1. Mean powdery mildew ratings of 28 rye inbred lines and their crosses from four sets of factorial matings at booting and their standard errors (SE) averaged over three leaves and four environments

Set	Female			Male		
	Parent	Line	Crosses ^a	Parent	Line	Crosses
I	L185-P	1.3 ^b	1.7	L59-F	3.1	2.6
	L301-P	2.1	2.2	L271-F	2.4	2.1
	L304-P	3.3	3.0	L283-R	3.3	2.7
	L7171-P	2.9	2.1	L288-R	2.1	1.7
	Mean	2.4	2.3		2.7	2.3
II	L306-P	2.1	2.3	L286-R	2.0	2.2
	L307-P	2.9	2.7	L287-R	3.4	3.0
	L311-P	2.7	3.0	L289-R	3.1	2.7
	Mean	2.6	2.7		2.8	2.6
III	L5-P	1.9	3.0	L7365-R	1.3	2.8
	L201-P	2.7	2.5	L7372-R	2.9	3.3
	L304-P	4.1	3.8	L7504-R	1.9	2.6
	L7170-P	2.2	2.7	L7505-R	3.6	3.4
	Mean	2.7	3.0		2.4	3.0
IV	L2003-P	3.9	2.9	L7131-R	4.6	2.8
	L2010-P	3.8	2.5	L7134-R	5.3	4.2
	L2016-P	3.9	3.6	L7136-R	2.5	2.4
	L2036-P	3.5	3.5			
	Mean	3.8	3.1		4.1	3.1
SE		0.4	0.2		0.4	0.2

^aCross performance of a female was averaged over all crosses with the males of the same set and vice versa.

^bBased on a 0 (mildew free) to 9 (81-100% leaf area affected) scale.

RESULTS

In all environments, a moderate infection level was observed (Fig. 1). Slight, though significant, differences occurred between environments. The mean powdery mildew ratings of the inbred lines and their single-crosses were in the same order at both assessment stages. At booting and heading, significant ($P = 0.05$) differences between leaves existed with the youngest leaf having the lowest powdery mildew rating and the oldest leaf the highest rating (Fig. 1). During 1988, the disease progressed from booting to heading, whereas during 1989 an early summer drought stopped the epidemic. The difference in powdery mildew rating between

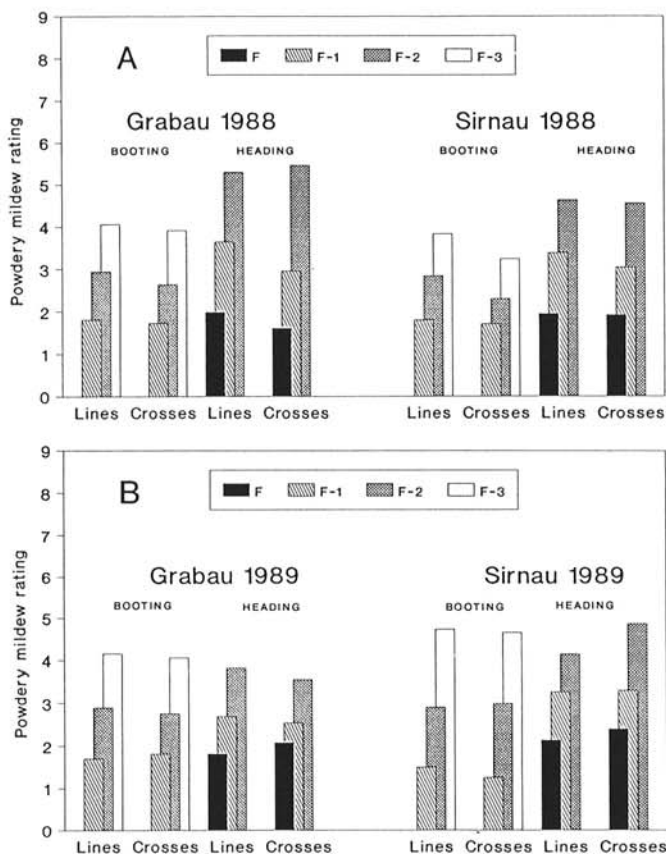


Fig. 1. Mean powdery mildew ratings (0-9 scale: 0 = mildew free, 9 = 81-100% leaf area affected) at Grabau and Sirnau, Germany, on the upper three, fully expanded leaves at booting and heading stages averaged across 28 rye inbred lines and 53 single-crosses. A, 1988 data; B, 1989 data.

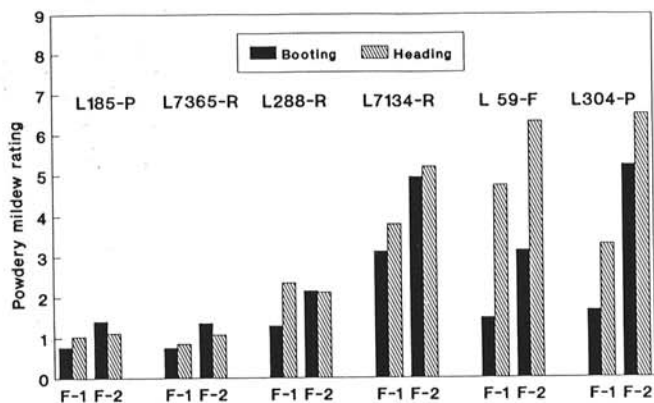


Fig. 2. Mean powdery mildew ratings (0-9 scale: 0 = mildew free, 9 = 81-100% leaf area affected) of three selected, partially resistant (L185-P, L7365-R, and L288-R) and three susceptible (L7134-R, L59-F, and L304-P) inbred lines on two leaves (F-1 and F-2) at booting and heading stages averaged across four environments.

booting and heading was associated for most lines with their resistance level (Fig. 2). The disease progressed considerably between both assessment stages on susceptible lines (i.e., L59-F and L304-P) and stagnated at a low infection level on the more resistant lines (i.e., L185-P, L7365-R, and L288-R); L7134-R showed an intermediate reaction.

The powdery mildew ratings on the upper three leaves were highly correlated in all groups of material at booting as well as at heading (Table 2). At heading, the coefficients of phenotypic correlation were slightly lower due to premature senescence of the older leaves in set II and to the occurrence of leaf rust, both reducing the precision of rating. A high agreement also existed between the two assessment stages ($r = 0.89-0.98$; $P = 0.01$) averaged over leaves in all genetic materials except for the inbred lines in set II ($r = 0.64$). Because of this close association between booting and heading, only data for booting are shown.

Significant genotypic variation was observed for the powdery mildew ratings of inbred lines and crosses in all four sets (Table 3). The environment variances were only occasionally significant. In the individual environments, moderate to high repeatabilities were obtained ranging from 0.50 to 0.98 for the inbred lines and from 0.44 to 0.90 for the crosses. For the combined analysis, estimates of heritability were medium to high in all sets for lines and crosses (Table 3). The inbred-environment interaction variances were significant and important throughout. GCA variances were significant for the males in all sets and for the females in three sets. SCA variances though significant in set I were negligible throughout. Variation due to GCA-environment

TABLE 2. Coefficients of phenotypic correlation for powdery mildew ratings of 28 inbred lines and their 53 single-crosses between each of the three leaves assessed at booting (F-1, F-2, and F-3) and heading (F, F-1, and F-2) pooled over four sets of factorial crosses and four environments^a

Assessment stage	Leaves correlated	Inbreds	Crosses
Booting	F-1:F-2	0.94**	0.95**
	F-2:F-3	0.96**	0.97**
	F-1:F-3	0.82*	0.94**
Heading	F:F-1	0.81*	0.86**
	F-1:F-2	0.84*	0.93**
	F:F-2	0.84*	0.75**

* and ** are significant at $P = 0.05$ and 0.01 , respectively.

TABLE 3. Estimates of variance components (VC; $\times 10^3$) and heritabilities of powdery mildew ratings of four sets of 28 inbred lines and their 53 single-crosses at booting averaged over three leaves and four environments^a

Source of variation	Set I		Set II		Set III		Set IV	
	df	VC	df	VC	df	VC	df	VC
Inbred lines								
Environment (E)	3	15	3	13*	3	98	3	10
Inbreds (I)	7	37**	5	25**	7	56**	6	60*
E \times I	21	56**	15	19**	21	33**	18	85**
Pooled error	140	34	100	35	140	16	120	56
Heritability	0.71		0.80		0.90		0.65	
Single-crosses								
Environment (E)	3	17*	3	11	3	44	3	57
GCA males	3	19**	2	11*	3	12*	2	83**
GCA females	3	28**	2	8	3	26**	3	22**
SCA	9	4*	4	1	9	0	6	4
GCA males \times E	9	9**	6	3	9	8*	6	10**
GCA females \times E	9	4*	6	12*	9	9**	9	16**
SCA \times E	27	8	12	14	27	16	18	9
Pooled error	21	5	12	6	21	5	13	11
Heritability	0.95		0.71		0.81		0.89	

^adf = degrees of freedom, GCA = general combining ability, SCA = specific combining ability. * and ** are significant at $P = 0.05$ and 0.01 , respectively.

interaction was significant for all lines except for the males in set II. In general, GCA-environment interaction was more important than SCA. The pooled error variances compared to the genetic variances were considerably lower for the single-crosses than for the inbred lines. At heading, variance proportions were similar to those at booting (data not shown).

The variation in resistance between lines was different in the four sets of material (Table 1). In set III, the resistance level ranged from high to low (1.3–4.1), whereas in each of sets I and II lines with high quantitative resistance (1.3–3.3, 2.0–3.4, respectively) and in set IV lines with only medium to low resistance (2.5–5.3) occurred. The differences between genotypes were small but significant in most instances. The resistance level of the lines averaged over females and males was similar to that of the crosses in sets I and II, whereas in set III the lines and in set IV the crosses were slightly more resistant (Table 1).

The powdery mildew ratings of the lines were significantly correlated with the corresponding GCA effects in sets I, II, and III at booting ($r = 0.83, 0.81, \text{ and } 0.78$, respectively; $P = 0.05$). In set IV, the correlation coefficient was 0.55, not reaching the 5% level of significance. The coefficients of genotypic correlation ranged from 0.6 to 1.0, exceeded the corresponding phenotypic values in all instances, and were greater than twice their standard error. Accordingly, medium ($r = 0.68$; $P = 0.05$) to strong ($r = 0.77\text{--}0.87$; $P = 0.01$) relationships existed between cross and midparent values.

DISCUSSION

The experimental design used in this study was well suited for assessing quantitative differences in resistance to powdery mildew (Table 3). An early onset of the epidemic was supported by mild winter temperatures in both years. This is an important prerequisite for a good differentiation among genotypes (31). The highly diseased spreader rows provided a high level of initial inoculum for all genotypes. The high estimates of heritability in all sets clearly demonstrate the adequacy of the experimental approach, in particular the usefulness of microplots for quantitative disease assessment. Two crucial points have to be fulfilled to use microplots in quantitative powdery mildew studies: 1) an early removal of the disease spreader to assure that subsequent cycles of the epidemic are mainly caused by autoinfection and 2) the use of border plots of a nonhost to reduce alloinfection among neighboring plots. According to Parlevliet and van Ommeren (26), the autoinfection rate for powdery mildew is more important than it is for leaf rust.

The disease stagnated from booting to heading on plants with high resistance levels (Fig. 2). In former growth-chamber studies (17), such genotypes reduced spore production and infection efficiency and caused a prolonged latent period of the mildew fungus. All three resistance components may have contributed to the stagnation of the epidemic on the most resistant genotypes. Similar results were obtained for adult-plant resistances of wheat (14) and oats (15) to powdery mildew.

The infection level was moderate to high, as judged from the highly diseased spreader rows and from the highly susceptible lines L59-F and L304-P that showed a powdery mildew rating of 6.5 on F-2 at heading according to the 0–9 scale (Fig. 2). The average powdery mildew rating across all genotypes, in contrast, was moderate because of the high proportion of quantitative resistant inbreds in the material (Table 1) that reduced the epidemic within plots effectively, as exemplified by the inbreds L185-P and L7365-R (Fig. 2). An intermediate level of disease severity secures a good differentiation among quantitative resistant genotypes. Actually, despite the relatively small differences in powdery mildew ratings (Table 1), highly significant genotypic variances were found among the lines and crosses for all sets (Table 3).

Quantitative powdery mildew resistance in adult plants did not depend on the assessment stage nor on the leaf position as long as early senescence did not blur the disease symptoms. Thus, reliable resistance data can be obtained at a single assessment

stage and by scoring just one leaf. However, for this approach to be valid, the epidemic should have progressed far enough to let differences in quantitative resistance become clearly visible. Broers (5) arrived at similar conclusions when studying the resistance of wheat to leaf rust. Visually scoring disease severity at a single stage was as effective as determining the area under the disease progress curve or measuring individual components of resistance, such as latent period and infection frequency. Taking into consideration the great amount of labor and time required for the latter two methods, visual scoring clearly is the best approach when a large number of entries has to be tested, as in the case of breeding programs.

All sets of genotypes revealed significant GCA variances. On average, GCA variance explained more than 85% of the whole genotypic variation. This indicates a strong preponderance of additive gene action in quantitative resistance of rye to powdery mildew. The same conclusion can be drawn from the tight correlations between GCA and line effects or between cross and midparent values. Similar results were obtained in many other plant pathosystems with both self- and cross-pollinated hosts (9).

Interestingly, the type of gene action did not change from booting to heading. Koch (19) and Seitz et al (28), using similar rye materials, studied the inheritance of quantitative resistance to powdery mildew in an early, nonvernalized seedling stage under growth-chamber conditions and in the adult-plant stage under field conditions. They observed an increase in the importance of nonadditive gene action during plant development. In the experiments reported here, the time interval between the two assessment stages was only 2–3 wk and, therefore, possibly too short to reveal any trend in gene action. However, Jones et al (16) also found dominant gene action more marked at the heading stage than at the booting stage for the resistance of barley to powdery mildew.

Heterosis, defined as the deviation of a cross from its midparent value was absent in sets I and II and was of opposite sign in sets III and IV. In set III the inbreds and in set IV the crosses were slightly more resistant. In general, these differences were small though significant. Thus, heterosis does not seem to be an important phenomenon in the inheritance of quantitative powdery mildew resistance in rye. Similar results were obtained by Kast and Geiger (17) for the same pathosystem with different genetic materials for mildew of barley (13), leaf rust of wheat (3,4,21) and stripe rust of wheat (23,24).

The use of parent lines from two gene pools and test environments in both northern and southern Germany warrants sound genetic inferences for the rye breeder. Ample, significant GCA variance and high heritability offer good prospects for rapid progress from recurrent selection. Close agreement between line and GCA effects allows selection among lines without prior testcrossing. Because no important heterosis for resistance was found, selection for resistance is necessary in both the seed- and the pollinator-line gene pools. Disease rating at a single assessment stage between booting and heading and on one leaf will suffice after a medium infection level, i.e., a powdery mildew rating of 3–4, is reached and before senescence or leaf rust interferes with the powdery mildew rating. Strong genotype-environment interactions in all sets (Table 3), however, require testing in different environments (sites or years).

Improving rye for quantitative resistance is recommended, although some sources of complete monogenic resistance exist (2,12,18,22,28). Geiger and Dölz (8) and Welz et al (30) performed growth-chamber experiments to study the ability of genetically heterogeneous mildew populations to overcome the resistances of inbreds, hybrids, and populations. Only entries with quantitative resistance proved durable in these tests. Line L185-P, a parent of a widely grown hybrid cultivar in Germany included in set I of this study, is a good example of a genotype with a high level of stable quantitative resistance.

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