Generation Mean Analysis of Inheritance of Resistance to Barley Yellow Dwarf in Crosses Involving Bates Spring Oats

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ABSTRACT

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The spring oat cultivar Bates, resistant to barley yellow dwarf disease (BYD), was crossed with Allen, a cultivar susceptible to BYD, and with Mo.06234, an advanced line resistant to BYD. Parental, F_1, F_2, and both backcross generations were grown for each cross in randomized complete block designs with three replicates. At the three-leaf stage, the plants were infested with viruliferous *Rhopalosiphum padi*. Data on tiller number, plant height, seed yield, and percent leaf reddening were recorded on individual plants. When a genetic model with additive and dominance effects was fitted to the generation means, only percent leaf reddening in the Bates × Allen cross showed an acceptable fit. A genetic model including epistatic effects was then used. From the significance of the epistatic effects in both crosses, we conclude that inheritance of resistance to BYD is more complex in the Bates × Mo.06234 cross than the Bates × Allen cross.

Barley yellow dwarf (BYD) is a viral disease of the Poaceae. BYD is worldwide in distribution and can cause severe reductions in small-grain yields (3,8). Because the aphid vectors are mobile with no economic means of control, the only feasible method of reducing yield losses from BYD is the development of resistant cultivars (1).

In barley (*Hordeum vulgare* L.), major genes inherited in a simple, Mendelian fashion and imparting resistance to BYD have been identified (7,9). In oats (*Avena sativa* L.) and wheat (*Triticum aestivum* L.), however, inheritance of resistance appears more complex. Cisar et al (2) found significant general and specific combining abilities for BYD reaction and grain yield loss in a 12-line diallel of winter wheat. With general combining abilities accounting for 22 and 65% of the entry sums of squares for yield loss and disease reaction, respectively, they concluded that additive effects of genes were most important in determining disease resistance. Landry et al (5), using generation mean analysis, found larger additive than dominance genetic effects for a visual rating of foliar BYD symptoms in crosses of Lamar oats with seven *A. sterilis* lines. Because they did not use backcross generations, epistatic effects could not be calculated.

The purpose of this research was to investigate the inheritance of resistance to BYD in spring oats using the cultivar Bates, a source of BYD resistance from the University of Missouri spring oats breeding program.

MATERIALS AND METHODS

Two generation mean analyses (GMA) were used to assess the inheritance of BYD resistance in spring oats. The analyses involved crosses of Bates with Allen and Mo.06234. Bates is a cultivar developed at the University of Missouri and is relatively resistant to BYD compared with cultivars grown in Missouri. Because it is a high-yielding cultivar, it is used extensively in our breeding program as a source of resistance. Allen is a cultivar susceptible to BYD. Mo.06234 is a BYD-resistant experimental line with different parentage and possibly different genes for BYD resistance than Bates. In each GMA, the

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parental, F_1, F_2, F_1 × parent 1 (BC1), and F_1 × parent 2 (BC2) generations were grown. The experimental design for each analysis was a randomized complete block with three replicates. Each replicate consisted of six plots corresponding to the six generations. Two rows of Grundy, a susceptible cultivar, were seeded between plots to test for effectiveness of inoculation.

On 13 April 1980, we seeded the two experiments at the Agronomy Research Center, Columbia, MO, in a Mexico silt loam (fine, montmorillic, mesic, Udollic Ochraqualfs). Rows were 15 cm apart and 1.5 m long, and plants within a row were seeded at 15-cm intervals. The number of rows per plot differed for the generations and ranged from two for the backcross generations to nine for the parent and F_2 generations. On 5 May, when the seedlings were in the three-leaf stage, all plants were infested with greenhouse-reared, viruliferous oat-bird cherry aphids (*Rhopalosiphum padi* L.). About 10 aphids were placed on each plant. After 3 days, the aphids were destroyed with malathion.

Tiller number, plant height, seed yield, and percent leaf reddening were recorded on individual plants. Data for percent leaf reddening were taken on 11 June and transformed using the transformation: arc sine $\sqrt{x/100}$, where x represented the estimated percent leaf reddening per plant.

The genetic analysis procedure we used is outlined by Mather and Jinks (6). Because the number of individuals varied in each generation, we used weighted generation means. A three-parameter model was fitted and tested for goodness of fit by a chi-square test with three degrees of freedom. When a significant chi-square value was obtained, a six-parameter model was fitted as outlined by Gamble (4). Estimates of the generation means used in the analysis were obtained after averaging over the replicates. Standard errors of genetic estimates were obtained from variances of individual plant data after removal of replicate effects. Significance of the genetic estimates was determined by comparing the estimated values with their standard errors. If the absolute value of an estimate exceeded twice its standard error, the estimate was considered significantly different from zero. The definition of the six genetic parameters are: m = the midparent value or F_2 mean for the three- and six-parameter models, a = the amount of variation among the means resulting from the additive effect of the genes, d = the amount of variation among the means resulting from the dominance effects of the genes, aa = the amount of variation among the means due to the additive × additive epistasis, ad = the amount of variation among the means resulting from additive × dominance epistasis, and dd = the amount of variation among the means resulting from dominance × dominance epistasis.

In addition to the genetic analysis, phenotypic correlations among traits on an individual plant basis over all generations were calculated for each cross.

Table 1. Phenotypic correlations among selected traits for the crosses Bates × Mo.06234 (B × M) and Bates × Allen (B × A) over all generations

	Plant height	Tiller (no.)	Percent leaf reddening
Seed yield			
(B × M)	0.54**[a]	0.47**	−0.35**
(B × A)	0.67**	0.61**	−0.17**
Plant height			
(B × M)	···	0.47**	−0.26**
(B × A)	···	0.43**	−0.02
Tiller no.			
(B × M)	···	···	−0.19**
(B × M)	···	···	−0.11**

[a]** = Significant $P = 0.01$.

RESULTS AND DISCUSSION

The phenotypic correlation coefficients among traits in both crosses are given in Table 1. In all correlations except percent leaf reddening for the cross Bates × Allen, the values were highly significant. Plant height, tiller number, and seed yield were positively correlated with each other. Percent leaf reddening was negatively correlated with the other three traits. This was as expected, because plants with less BYD resistance should show more leaf symptom expression and be shorter, have fewer tillers, and yield less.

The generation means and the mean squares for the crosses Bates × Allen and Bates × Mo.06234 are listed in Tables 2 and 3, respectively. The disease reactions of the three parental lines involved in the two crosses conformed to our expectations. Allen, thought to be susceptible to BYD, had half the seed yield of Bates and showed significantly more leaf reddening. Bates and Mo.06234, both considered resistant to BYD, did not differ significantly for seed yield or leaf reddening.

The values of the genetic effects fitted to a three-parameter model for both crosses are presented in Table 4. Only leaf reddening from the Bates × Allen cross showed an acceptable fit to this model. Because in the other cases we found a chi-square value high enough to reject the model, we concluded epistasis to be present in the inheritance of these traits. Higher chi-square values for the Bates × Mo.06234 cross than for the Bates × Allen

Table 2. Generation means and analysis of variance for four traits in generations derived from the oat cultivars Bates and Allen

Generation	Plant height (cm)	Tillers (no.)	Seed yield (g/plant)	Leaf reddening (arc sine $\sqrt{p}$)
Bates	49.1 b[y]	6.5 a	2.5 a	0.69 c
Allen	43.9 d	4.9 c	1.1 d	0.94 a
F_1	47.9 bc	5.5 b	2.0 b	0.82 b
F_2	52.2 a	5.8 b	2.6 a	0.77 bc
Bates × F_1	47.3 c	5.5 b	1.9 bc	0.73 c
Allen × F_1	41.8 d	4.8 c	1.4 cd	0.78 bc
Mean squares				
Replication	20.0	12.3*[z]	1.3	0.45**
Generation	1,425.0**	55.6**	60.7**	1.42**
Error	43.0	3.1	1.5	0.04

[y]Within a column, any two means having a letter in common are not significantly different at $P = 0.05$ according to Duncan's multiple range test.
[z]* = Significant at $P = 0.05$ and ** = significant at $P = 0.01$.

Table 3. Generation means and analysis of variance for four traits in generations derived from oat cultivars Bates and Mo.06234

Generation	Plant height (cm)	Tillers (no.)	Seed yield (g/plant)	Leaf reddening (arc sine $\sqrt{p}$)
Bates	48.4 a[y]	5.9 b	2.7 b	0.50 ab
Mo.06234	44.0 c	6.7 a	2.6 b	0.62 a
F_1	45.4 bc	5.9 b	2.7 b	0.48 bc
F_2	48.8 a	6.6 a	3.5 a	0.41 d
Bates × F_1	45.7 b	5.3 c	2.5 b	0.45 c
Mo.06234 × F_1	40.8 d	5.6 bc	1.9 c	0.43 cd
Mean squares				
Replication	1,934.4**[z]	16.6**	63***	0.07*
Generation	1,349.4**	49.7**	41**	0.32**
Error	36.1	3.3	3.3	0.02

[y]Within a column, any two means having a letter in common are not significantly different at $P = 0.05$ according to Duncan's multiple range test.
[z]* = Significant at $P = 0.05$ and ** = significant at $P = 0.01$.

cross suggested that epistasis was of greater importance in the Bates × Mo.06234 cross.

In Table 5, the values of the genetic effects for the six-parameter model are presented. We cannot explain why no genetic effects were significant for leaf reddening in the Bates × Mo.06234 cross. Possible causes of error that would go undetected in this study were trigenic epistasis and linkage; either of them could bias the derived genetic values. In all other cases but one, tiller number in the Bates × Allen cross, the epistatic effects additive × additive and dominance × dominance were significantly different from zero. The genetic effect additive × dominance was significantly different from zero in only the Bates × Mo.06234 cross for the traits plant height and seed yield.

In general, inheritance was more complex in the Bates × Mo.06234 cross. The greater amount of epistasis present in this cross, however, could be due to the nondirectional distribution of alleles in the two parents. They were derived from different parentage and could have different sources of BYD resistance. Further testing would have to be done to test for epistasis or dispersion of resistance alleles.

Our results coincide with the findings of Landry et al (5), who crossed Lamar, a cultivar susceptible to BYD, with resistant lines of *A. sterilis* and found larger additive than dominance effects based on F_1, F_2, and parental means. In our study, we detected larger additive than dominance effects for three of the four traits with a three-parameter model for the cross Bates × Allen. This cross is similar in form to their crosses because it is also a cross of resistant with susceptible genotypes. We found no reason to expect epistasis in the inheritance of the trait they studied, leaf reaction or reddening.

Cisar et al (2) found significant general and specific combining abilities for yield reduction and disease reaction in a diallel cross among resistant, intermediate, and susceptible wheat cultivars. Our results are similar in that additive effects were more predominant in the Bates × Allen cross, with epistasis being more important in the Bates × Mo.06234 cross. Additive effects and general combining ability describe additive gene action, whereas epistasis and specific combining ability deal with other types of gene action.

Both Landry et al (5) and Cisar et al (2) concluded that resistance could be increased by selection. We conclude from our results that selection of resistant progeny in oats is possible but difficult because of probable epistasis. Further, breeders interested in obtaining BYD-resistant inbred lines will contend with dominance effects and dominance × dominance epistatic effects that by definition involve nonfixable, heterozygous loci. Although in our study, percent leaf reddening fitted a nonepistatic model, selection on this criterion would be inefficient because of its low correlation with grain yield.

Table 4. Estimates of genetic effects for four traits in the oat crosses Bates × Mo.06234 and Bates × Allen fitted to a three-parameter model with weighted means

Trait / Cross	m[x]	a	d	Chi-square value[y]
Plant height				
Bates × Mo.06234	45.90**[z]	2.30**	−0.90	94.0
Bates × Allen	47.80**	2.30**	2.00**	78.0
Tiller number				
Bates × Mo.06234	6.00**	−0.41**	−0.50*	34.0
Bates × Allen	5.50*	0.75**	−0.32	15.0
Leaf reddening				
Bates × Mo.06234	0.46*	−0.004	−0.07**	53.0
Bates × Allen	0.78**	−0.13**	−0.05*	6.7
Seed yield				
Bates × Mo.06234	2.82**	0.09	−0.02	70.0
Bates × Allen	1.86**	0.14**	0.19	47.0

[x]The mean, additive, and dominance genetic effects for the model $y = m + a + d$, where y equals the generation means.
[y]For values higher than 7.81, the probability of a fit is less than 0.05.
[z]* And ** = estimate larger than its standard error by a factor of 2 and 3, respectively.

Table 5. Estimates of genetic effects for four traits in the oat crosses Bates × Mo.06234 and Bates × Allen fitted to a six-parameter model

Trait / Cross	m[y]	a	d	aa	ad	dd
Plant height						
Bates × Mo.06234	49.00**[z]	4.90**	−23.00**	−22.00**	2.70**	31.00**
Bates × Allen	53.00**	5.50*	−30.00**	−31.00**	2.90	42.00**
Tiller number						
Bates × Mo.06234	6.60**	−0.20	−4.80**	−4.40**	0.20	6.80**
Bates × Allen	5.80**	0.70	−2.80*	−2.60*	0.10	4.40
Leaf reddening						
Bates × Mo.06234	0.42**	0.02	0.05	0.01	0.03	0.14
Bates × Allen	0.77**	−0.08	−0.14	−0.12	0.05	0.39
Seed yield						
Bates × Mo.06234	3.60**	0.60**	−5.30**	−5.30**	0.60*	7.20**
Bates × Allen	2.60**	0.60*	−3.80**	−4.00**	−0.10	5.20**

[y]The mean, additive, dominance, additive × additive, additive × dominance, and dominance × dominance genetic effects for the model $y = m + a + d + aa + ad + dd$, where y equals the generation means.
[z]* And ** = estimate larger than its standard error by a factor of 2 and 3, respectively.

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