

Inheritance and combining ability in some powdery mildew resistant wheat lines

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ABSTRACT - Three commercial varieties susceptible to powdery mildew and five high-yielding genotypes with resistance to powdery mildew from the CIMMYT were used in this study to estimate the general combining ability of parents, to detect gene actions of resistance against powdery mildew and identify the most suitable genotype for transferring resistance genes to the commercial varieties. In conclusion, monogenic inheritance was detected in the F₂ generation in crosses of parent 48 with two commercial varieties, Atilla-12 and Basribey. The inheritance of parent 72 was digenic in crosses with the same commercial varieties. Parent 48 can be recommended as a parent for powdery mildew resistance and improvement of varieties towards higher spike length, spikelet and kernel numbers per spike and plant height. Parent 72 may also be used for powdery mildew resistance to develop varieties with greater plant height.

Key words: wheat, powdery mildew, inheritance, combining ability.

INTRODUCTION

Powdery mildew in wheat (*Triticum aestivum* L.) is a foliar disease caused by the fungus *Blumeria graminis* (DC.) E.O. Speer f. *Sp. tritici* Em. Marchal (syn. *Erysiphe graminis* DC. f. *Sp. tritici* Marchal). The disease can reduce the grain yield (non-productive tillers) and the flour protein without however affecting the milling and baking quality of wheat (Cunfer 2002). Disease severity depends on weather conditions, leaf canopy density and the susceptibility of regionally grown cultivars (Lipps and Madden 1989).

Powdery mildew is considered to be a low-

temperature disease with optimum development in a range from 15 °C to 25 °C and at high relative air humidity. Powdery mildew can only be observed in some years with high moisture and rainy spring season in the Ege (Aegean) region. It is estimated that the yield loss due to the disease reach up to 45% in the USA, UK, New Zealand and in India (Srnic 2003).

The levels of powdery mildew infection may be reduced by altering cultural practices and crop rotation, reducing planting density and fungicide application and by planting resistant cultivars. The development of resistant wheat cultivars by plant breeding is the most cost-effective way to control powdery mildew. So far,

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35 major genes, designated Pm 1 – Pm 35 have been reported to confer resistance to powdery mildew in wheat (Huang and Röder 2004). Moreover, Das and Griffey (1995) found that two to three genes governed adult plant resistance to powdery mildew in Houser and Redcoat wheat.

Success of plant breeding depends on the choice of suitable parents. To ensure success in breeding programs, various agronomic traits need to be observed and appropriate parents need to be selected at the beginning of the breeding program. The diallel analysis method is commonly used for parent selection. By this method, the genotypes used as parents have to be crossed in all possible combinations, which is a rather time and labor-consuming procedure. In the diallel analysis, on the other hand, the line x tester analysis advantageously reduces labor and cost. Moreover, the method provides information on the general combining ability of the parents and specific combining ability of the crosses.

As an indication of genes with high additive effects, general combining ability (GCA) was defined as the mean performance of a parent in cross combinations and specific combining ability (SCA) as those situation in which certain cross combinations perform either better or worse than what would be expected based on the mean performance (Widner and Lebsack 1973, Hallauer and Miranda 1981). In addition to this definition, Falconer (1981) pointed out that a higher SCA variance expresses non-additive gene action or dominant and epistatic gene effects. The selection for traits with high additive gene effect is expected to be successful although this tendency decreases in advanced generations under dominant and epistatic gene action.

The objectives of this study were a) to predict the GCA of parents in the F₁ generation, b) to study the inheritance of powdery mildew resistance in the crosses based on a grade scale of the field disease, using artificial inoculation in the F₂ generation, c) to determine which genotype is most suitable for transferring resistance genes to the commercial varieties.

MATERIAL AND METHODS

Three varieties (Atilla-12, Basribey and Golia), susceptible to powdery mildew and grown commercially in the Aegean region, and five high-yielding genotypes selected among 114 powdery mildew resistant genotypes from CIMMYT (International Maize and Wheat Improvement Center) were used here. The CIMMYT genotypes were selected at relatively low infection levels across locations and showed high levels of partial or non-specific resistance (Lillemo 2008, personal communication). The resistant and susceptible genotypes used here are presented in Table 1.

The line x tester crosses between three female (commercial varieties) and five male genotypes from the CIMMYT nursery were carried out by hand in the 2004-2005 growing season in an experimental field of Ege University, Faculty of Agriculture, Izmir-Turkey. The parents and their F₁ crosses were grown in a randomized complete block design with three replications under rainfed conditions in the 2005-2006 growing season. Each plot consisted of four 2-m-long rows spaced 30 cm apart. Usual and uniform field management practices were performed and plant height, spike length, spikelet number per spike, kernel number per spike, 1000-kernel weight and grain yield per spike of both the parents and their crosses were measured

Table 1. Bread wheat genotypes used in the experiment

Genotypes	Origin/Pedigree
Susceptible varieties	
Atilla-12	Hungary
Basribey	Aegean Agricultural Research Institute-Turkey
Golia	Italy
Resistant lines	
27	MVM MARTINA
35	RALEIGH
48	YMI1/GEN
70	SAVLESKU#43/3/GEN*2//BUC/FLK
72	TJB916.46/CB306//2*MHB/3/BUC/4ITOOY

The infection type was assessed in the F_2 generation in the 2006-2007 growing season. Owing to the fact that the spring season in this region has been unusually dry in recent years, the plots were covered with plastic and irrigated to create a moist environment to favor the occurrence of powdery mildew disease. The disease was detected after 15 days and the cover was removed to score the disease severity on a 0-9 scale described by Leath and Heun (1990), where resistant plants are scored 0 - 6 and susceptible plants 7 - 9. Chi-square tests were conducted to test the goodness of fit between observed and expected segregation ratios (Snedecor and Cochran 1956). Analyses of variance were performed for all traits using data of the parents and their F_1 generation. The GCA and SCA effects were estimated by the line x tester method described by Singh and Chaudhary (1979).

RESULTS AND DISCUSSION

Analysis of variance was conducted to detect the differences among the genotypes including parents and crosses considering all traits measured in the present study (Table 2). Analysis of variance for line x tester crosses is recommended if there are significant differences among the genotypes including parents and crosses (Singh and Chaudhary 1979). Significant differences were observed among the genotypes in the

performance of all traits. Therefore, analysis of variance for line x tester was performed for all traits.

Differences in plant height and spike length were found among the lines (varieties) considered as susceptible to powdery mildew in analysis of variance for line x tester. It was also observed that there were highly significant differences among the genotypes which were known as resistant to powdery mildew and specified as testers for all traits. Line x tester interaction was significant for plant height, spike length and kernel number per spike (Table 2). The variances of general and specific combining abilities and the variance ratio GCA/SCA are shown in the same table. It is assumed that there is a non-additive gene effect for related traits if the ratio is lower than one (Matzinger 1963). In this study, the non-additive genetic variation represented the major portion of the total genetic variation among crosses in plant height, spikelet number per spike, kernel number per spike, and 1000-kernel weight.

Since the mode of gene effect for the analyzed traits can show variability in diverse populations, the results of researchers in different studies are inconsistent. Similarly to our results, Nanda et al. (1982) and Kálnácy (1996) found non-additive gene effects for plant height. Conversely, Amaya et al. (1972) and Gill et al. (1979) assumed an additive gene effect for plant height.

Furthermore, both additive and non-additive gene

Table 2. Mean squares of the line x tester analysis for different traits and estimates of variance components in the F_1 generation

Sources	d.f.	Plant height (cm)	Spike length (cm)	Spikelet number per spike	Kernel number per spike	1000-kernel weight (g)	Grain weight per spike (g)
Replications	2	10.491	0.064	0.232	11.659	2.041	0.027
Genotypes	22	279.298**	8.016**	12.330**	204.448**	76.032**	0.176**
Parents	7	418.875**	10.581**	15.398**	157.578**	121.544**	0.129**
Parents vs crosses	1	826.062**	52.788**	139.787**	1531.611**	417.557**	0.019
Crosses	14	170.456**	3.536**	1.693**	133.085**	28.882**	0.210**
Lines	2	614.138**	16.794**	1.875	134.177	9.707	0.044
Testers	4	208.008**	3.238**	3.293**	299.866**	61.544*	0.638**
Lines x Testers	8	40.759**	0.370**	0.847	49.422*	17.344	0.038
Error	44	6.896	0.115	0.467	18.260	8.157	0.031
σ_{GCA}^2		4.585	0.112	0.030	2.958	0.408	0.006
σ_{SCA}^2		11.287	0.085	0.127	10.387	3.062	0.002
$\sigma_{GCA}^2/\sigma_{SCA}^2$		0.406	1.318	0.236	0.285	0.133	3.000

*, **: Significant at $P = 0.05$ and $P = 0.01$ respectively

actions were determined as significant for this trait in the study conducted by Singh et al. (1990). Some researchers (Bajwa et al. 1986) stated that non-additive gene action has a significant effect on grain number per spike, which agrees with our results. On the other hand, Yadava et al. (1986) indicated the importance of additive gene action for the same trait.

In our study, additive gene effect was found to be important for grain weight per spike. However, Tosun et al. (1995) reported significance of the non-additive gene effect for this trait.

In this study, non-additive gene actions were found for 1000-kernel weight, whereas the additive gene effects were predominant for this trait (Yadava et al. 1986 and Topal et al. 2004).

Since the success of selection in a population depends on additive variance and also because GCA is based on additive variance (Falconer 1981), it is possible to use the crosses obtained from parents with high GCA effects. As stated by Ruckebauer (1977) GCA effects are numerical values assigned to parents according to their average performance in cross combinations and serve as criterion for parental selection in breeding programs.

The parent which is the most suitable among the powdery mildew-resistant testers can be determined based on the mean values of the parents (Table 3) with significant GCA effects for the traits studied. The GCA effects of the parents used here and their mean values for each trait were presented in Table 4.

The GCA effects for plant height of the testers 48, 70 and 72 were significant and positive but of 27 and 35

they were significant and negative. It appears that there are possibilities to utilize powdery mildew resistant testers for improvement of new varieties with short and intermediate plant height. For spike length and spikelet number per spike, only tester 48 had positive and significant GCA effects. Significant and positive GCA effects were found for the parents 48 and 70 for kernel number per spike and grain weight per spike. For 1000-kernel weight, only tester 70 had significant and positive GCA effects.

Among the powdery mildew-resistant testers, 48 can be used as a parent to develop new varieties with intermediate plant height, long spike length and high spikelet and kernel number per spike and tester 70 can also be considered a promising parent for plant height, kernel number and grain weight per spike.

Disease scores of the crosses were tested by Chi-square analysis under artificial inoculation conditions in the F₂ generation in order to estimate the inheritance mode of powdery mildew. Resistance to plant pathogens can be controlled by only one or several genes as well as gene combinations.

If powdery mildew resistance is controlled by a single gene, its effect can be monitored easily, however if it is governed by many genes, it is not possible to estimate the effects and effect level.

In our study, 1 single dominant gene controls powdery mildew resistance in the crosses 27 x Golia and 35 x Golia in the F₂ generation. It was determined in the same generation that the resistance was governed by one recessive gene in crosses, 27 x Basribey, 48 x Atilla-12 and 48 x Basribey (Table 5). Chung and Griffey

Table 3. Mean values of the parents for traits measured in the F₁ generation

Parents	Plant height (cm)	Spike length (cm)	Spikelet number per spike	Kernel number per spike	1000-kernel weight (g)	Grain weight per spike (g)
Lines						
Atilla-12	94.2	9.7	17	41	37.0	15
Basribey	77.8	9.5	9	54	31.2	1.7
Golia	52.5	7.2	17	44	31.1	1.3
Testers						
27	73.5	7.1	18	36	38.3	1.3
35	75.0	9.7	20	50	29.5	1.5
48	81.6	12.9	23	46	22.3	1.0
70	82.0	9.4	18	53	27.2	1.4
72	81.4	10.9	22	58	20.2	1.1
LSD (5%)	5.295	0.684	1.378	8.616	5.758	0.355

Table 4. General combining ability (GCA) effects for traits measured in the F₁ generation

Parents	Plant height	Spike length	Spikelet number per spike	Kernel number per spike	1000-kemel weight	Grain weight per spike
Lines						
Atilla-12	5.782**	1.002**	-0.378*	-3.056**	-0.310	-0.063
Basribey	1.092	0.105	0.322	2.921**	-0.603	0.028
Golia	-6.874**	-1.107**	0.056	0.135	0.913	0.035
Testers						
27	-5.687**	-0.513**	-0.118	-9.676**	-3.177**	-0.382**
35	-4.759**	-0.078	0.049	0.286	-2.093**	-0.155**
48	4.208**	0.931**	0.782**	5.108**	0.590	0.174**
70	2.730**	-0.520**	-0.895**	3.608*	3.229**	0.275**
72	3.508**	0.181	0.182	0.675	1.451	0.087
S.E. (Lines)	0.678	0.088	0.176	1.103	0.737	0.045
S.E. (Testers)	0.875	0.133	0.228	1.424	0.059	0.059

*, **: Significant at P = 0.05 and P = 0.01 respectively

(1995) also indicated that resistance for powdery mildew in two wheat lines was governed by one recessive gene and that 3 to 11 different resistant genes were represented among the 10 parents. Srnic (2003) showed that powdery mildew resistance in all Saluda x germplasm line populations segregated as a monogenic trait in field studies.

Monogenic resistance is mainly a hypersensitive foliar reaction directly involving single major R genes designated Pm (Powdery mildew) genes, in a gene for gene interaction. This type of resistance can be complete or partial (Hsam and Zeller 2002). Resistant plants may show from no to moderate infection signs and symptoms,

whereas susceptible plants show more severe signs and symptoms. The same researchers stated that monogenic resistance is generally very efficient but tends to be a short term solution if variability in the pathogen population is great. Changes in virulence are common ways for pathogens to overcome single resistance genes (Bennett 1984).

Digenic inheritance was determined in our study as resistance to the disease and was controlled by two recessive genes in the cross of 35 x Atilla-12 and by two complementary genes in the cross of 35 x Basribey. On the other hand, the resistance in the crosses 72 x Atilla-12 and 72 x Basribey was regulated by one dominant

Table 5. Disease scores and segregation ratio under artificial inoculation conditions in the F₂ generation

Crosses	Susceptible	Resistant	Total	χ^2 and F ₂ ratio
27 x Atilla-12	120	220	340	19.850** (Polygenic)
27 x Basribey	122	32	154	1.464 (1:3)
27 x Golia	23	61	84	0.253 (3:1)
35 x Atilla-12	85	65	150	26.888** (7:9)
35 x Basribey	63	87	150	23.120** (9:7)
35 x Golia	10	35	45	1.608 (3:1)
48 x Atilla-12	201	53	254	2.314 (1:3)
48 x Basribey	181	70	251	1.116 (1:3)
48 x Golia		All resistant		
70 x Atilla-12		All susceptible		
70 x Basribey		All susceptible		
70 x Golia	410	44	454	56.742** (Polygenic)
72 x Atilla-12	240	55	295	6.353* (3:13)
72 x Basribey	270	61	331	7.621* (3:13)
72 x Golia	15	235	250	48.133** (15:1)

*, **: Significant at P = 0.05 and P = 0.01 respectively

and one recessive gene, and two dominant genes in the cross 72 x Golia (Table 5). In accordance with our results, Peusha et al. (2002) suggested that resistance at the adult stage in wheat cultivars was controlled by two independent dominant genes and Griffey and Das (1994) estimated the number of genes controlling adult plant resistance in the wheat cultivars Knox and Massey to be two to three. Besides, Srnic (2003) reported that in greenhouse studies powdery mildew resistance in four germplasm x germplasm populations segregated as a digenic trait.

Das and Griffey (1995) conducted a diallel study of gene action for adult plant resistance in four wheat lines. They showed that additive-dominance and digenic epistasis models were sufficient to explain the variation in the expression of adult plant resistance. They proposed that selection for adult plant resistance may be most effective in the advanced generations due to significance of non-additive gene effects.

In this study, it was concluded that powdery mildew resistance in the crosses 27 x Atilla-12 and 70 x Golia differed from the monogenic and digenic inheritance models and consequently powdery mildew resistance was controlled by multiple genes in these combinations. Hautea et al. (1987) indicated that adult plant powdery mildew resistance in wheat has a polygenic nature and is based on transgressive segregation. Lillemo et al. (2006) suggested that the partial powdery mildew resistance in the wheat cultivar Saar is controlled by at least three genes. They explained that this resistance type conferred by multiple genes with additive effects is expected to be durable. All crosses of 48 x Golia were observed to be resistant to powdery mildew. The variety Golia seems to have

partially resistant genes to the disease. On the other hand, all susceptible crosses 70 x Atilla-12 and 70 x Basribey indicated that line 70 from CIMMYT, considered a genotype with powdery mildew resistance, appeared to be susceptible to strains of the disease that occur in the region of the experiment.

A more appropriate alternative to monogenic resistance genes is to develop and deploy germplasm with partial or quantitative (horizontal) resistance. Partial resistance is known to reduce infection frequency and delay pathogen growth and reproduction in adult plants. Such resistance has also been termed slow mildewing or adult plant resistance. It is inherited as a quantitative trait and has been shown to be durable (Lillemo et al. 2006).

CONCLUSIONS

Monogenic inheritance was detected in crosses of parent 48 with two commercial varieties, Atilla-12 and Basribey, which are susceptible to powdery mildew. The parent 72 showed digenic inheritance in crosses with the same varieties. If the general combining abilities and the mean values of these two genotypes are considered, parent 48 with powdery mildew resistance is suggested for the improvement of varieties towards higher spike length, spikelet and kernel numbers per spike, and plant height. Parent 72 may be used as a genotype with powdery mildew resistance to develop varieties with higher height only.

Herança e capacidade de combinação em linhas de trigo resistente ao mildio

RESUMO – Três variedades comerciais, susceptíveis ao mildio, e cinco genótipos de alta produtividade, com resistência ao mildio, do CIMMYT foram usadas neste estudo para estimar a capacidade geral de combinação dos pais, detectar ações gênicas da resistência ao mildio e identificar os genótipos mais susceptíveis para transferência dos genes de resistência às variedades comerciais. Em conclusão, a herança monogênica foi detectada na geração F_2 nos cruzamentos de 48 parentais com duas variedades comerciais, Atilla-12 e Basribey. A herança dos 72 parentais foi digênica nos cruzamentos com algumas variedades comerciais. O parental 48 pode ser recomendado como parental para resistência ao mildio e para o melhoramento das variedades para maior comprimento da espiga, espigueta, número de grãos por espiga e altura de plantas. O parental

72 também pode ser usado para resistência ao míldio e o desenvolvimento de variedades com maior altura de plantas.

Palavras-chave: trigo, míldio, herança, capacidade de combinação.

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Herança e capacidade de combinação em linhagens de trigo resistentes à ferrugem

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Herança e capacidade de combinação em linhagens de trigo resistentes à ferrugem. O presente trabalho teve como objetivo estudar a herança e a capacidade de combinação em linhagens de trigo resistentes à ferrugem. Foram avaliadas as características agrônomicas e de qualidade de grãos em uma população de 100 linhagens. Os resultados mostraram que a herança é controlada por genes recessivos e que a capacidade de combinação é alta. Os autores agradecem ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) pelo apoio financeiro concedido durante a realização desta pesquisa. Este trabalho foi financiado pelo Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) sob o nº 301.301/96.