Euphytica **47**: 203–214, 1990.

Inheritance of resistance to two *Septoria tritici* isolates in spring and winter bread wheat cultivars

T. Danon & Z. Eyal
Department of Botany, the George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel

Received 24 May 1989; accepted in revised form 27 August 1989

Key words: Triticum aestivum, wheat, *Septoria tritici*, septoria tritici blotch, resistance, *Mycosphaerella graminicola*

Summary

All possible crosses (including reciprocals) were made among four winter bread (Aurora, Bezostaya 1, Kavkaz, and Trakia) and two Israeli spring wheat cultivars (spring × winter diallel), and among two South American spring wheats (Colotana and Klein Titan) with the same Israeli cultivars (spring × spring diallel) to study the inheritance of resistance to septoria tritici blotch. Parents, F_1, F_2 and backcrosses were grown in two separated blocks in the field over two years. One block was inoculated with isolate ISR398A1 and another with ISR8036. Each plant was assessed for plant height (cm), days to heading (from emergence or transplanting), and percent pycnidia coverage on the four uppermost leaves. Plant height and maturity had insignificant effects on pycnidia coverage. No cytoplasmic effects could be detected. In the spring × winter diallel general combining ability (GCA) was the major component of variation. Significant specific combining ability (SCA) was present in all cases. Partial dominance was operative in populations inoculated with ISR398A1. Resistance in the winter wheats was controlled by a small number of genes (usually two). The four winter wheats derive their resistance to ISR398A1 from their common parent Bezostaya 1 which lacks the 1B/1R wheat-rye translocation. Their resistance is readily overcome by ISR8036. Inheritance of the South American wheats can be explained by additive effects, with a small number of genes of recessive mode affecting resistance to both isolates. Breeding strategies that favor additive, and additive × dominance gene action should be pursued.

Introduction

Septoria tritici blotch of wheat caused by the fungus *Mycosphaerella graminicola* (Fuckel) Schroeter (anamorph, *Septoria tritici* Rob. ex Desm.) is a major wheat disease in many parts of the world causing severe losses in yield (Eyal, 1981).

Breeding for resistance is the most economically feasible disease control measure. The incorporation of resistance to *S. tritici* into agronomically acceptable spring bread wheat (*Triticum aestivum* L.) cultivars has been slow and insufficient in providing adequate level of protection under disease outbreaks. Physiologic specialization in the pathogen can be attributed in part to the deficiency in protection. In spring bread wheat breeding, the most reliable and wide spread sources of resistance were derived from winter or from South American spring wheats (Rajaram et al., 1984, 1988). Seedling resistance to a world-wide virulence spectrum of *S. tritici* isolates was reported (Eyal et al., 1985) in the winter wheat cultivars Bezostaya 1 and

in Aurora and Kavkaz, both possess the 1B/1R wheat-rye translocation (Mettin et al., 1973). A single hypothetical gene for resistance were assigned to each of these cultivars (Eyal et al., 1985). Wheat cultivars possessing Aurora and Kavkaz germplasm expressed the highest overall level of resistance among the tested spring bread wheat germplasm. The resistance in Bezostaya 1 to isolate ISR398A1 of *S. tritici* was reported to be controlled by relatively few genes (Danon et al., 1982). The resistance to *S. tritici* in Frontana-derived South American wheat cultivars is effective in geographical regions other than South America (Eyal & Levy, 1987). It is likely that the Frontana-derived accessions Colotana, IAS 20, Klein Titan and Veranopolis which were used in several Septoria breeding programs, all had origin in the two land cultivars Alfredo Chaves in Brazil and Americano 44D in Uruguay (Roelfs, 1988). Resistance to *S. tritici* in IAS 20 and in Veranopolis was reported to be simply inherited (Rosielle & Boyd, 1985; Rosielle & Brown, 1979; Wilson, 1979).

The objectives of this study were to determine the mode of inheritance of resistance in winter wheat accessions possessing Bezostaya 1 germplasm and the 1B/1R wheat-rye translocation, as well as in Colotana and Klein Titan, subjected to distinct *S. tritici* virulences.

Materials and methods

Genetic material

Four winter bread wheat cultivars which possess resistance to *Septoria tritici* in Israel (Danon et al., 1982) and two susceptible spring bread wheat cultivars were crossed in all possible combinations including reciprocals to produce F_1 and F_2 seeds. The winter bread wheats all of which possess Bezostaya 1 germplasm were as follows: Aurora (PI167407), Bezostaya 1 (PI345685), Kavkaz (Lutescens 314 H174/Bezostaya 1) and Trakia (Bezostaya 1/ Elia// Rousalka). The sib selections Aurora and Kavkaz both possess the 1B/1R wheat-rye translocation. In addition a second diallel was prepared in which the two resistant South American spring bread wheat cultivars Colotana (CI13556) and Klein Titan (CI12615) were crossed with the same two susceptible parents: Hazera 2230 (Tzpp-Paloma × 7C/ Emek 132) and Lakhish (Yt//Nrn/Bvr/3/FA).

Field trials

Seeds from populations of parents, F_1, F_2 and backcrosses were sown in two separated blocks and spaced within each row. Twenty plants from each parent, 20 F_1 plants, 200–300 F_2 plants and 15 plants of BC were sown for each combination in each block. The two blocks were separated from one another by a 10 m buffer crop. Winter wheat parents and their derived populations were transplanted in the trial after vernalization for 8 weeks at 4° C. The trials were conducted during the 1984/1985 and 1985/1986 growing seasons.

Isolates and inoculation

The *S. tritici* isolates ISR398A1 (non-virulent on the resistant cultivars) and ISR8036 (virulent on all the winter wheat cultivars) were used in the two trial years. Each isolate was assigned to a specific field block. Each block was uniformly inoculated with 10^7 spores per ml suspension once or twice a week on rainy days and/or dewy nights using a low volume/low pressure Ulva 8 sprayer as described previously (Eyal et al., 1987). The inoculation was initiated when early-maturing parents reached the growth stage where flag leaf was just visible (GS 37) and terminated when the late-maturing parents reached the end of the milk-stage (GS 76).

Data collection

Each plant in the trials was assessed for the following parameters: plant height (cm), days to heading (from seedling emergence or transplanting) and percent pycnidia coverage on the four uppermost leaves recorded at GS 86 using a standard drawing scale (Eyal & Brown, 1976).

Data analysis

The effects of cultivars, isolates and years and the interactions were estimated using a two way analysis of variance. The relationship between plant height and maturing and pycnidial coverage was assessed for the combined F_2 populations of either winter wheats and the spring South American spring wheats each crossed with either one of the two Israeli spring wheat cultivars. Such an analysis is needed to distinguish between phenological – physiological and genetical effects. The Griffing (method 1, model I) and Hayman diallel analyses of variance were performd (Mather & Jinks, 1971a; Mather & Jinks, 1971b). Due to inequality of variances the transformation $1/\sigma^2$ as suggested by Draper & Smith (1966) was used in the multiple regression analyses to determine the general combining ability (GCA), specific combining ability (SCA) and other variance components. The reciprocal crosses were analyzed for the presence or absence of maternal effects which is a necessary assumption in the diallel analysis. Since no maternal effects were involved, the relations between Vr and Wr and between W'r were used to determine the genetic dominance effects and the relations within the parental lines. Vr is the variance of all the offsprings of each parent in each array (complete row or column), Wr is the covariance between these offspring and their nonrecurrent parents, and W'r is the covariance of the offspring in each array with the array means (Allard, 1956). These main statistics were used to test the underlying assumptions of the additive-dominance model. Narrow sense heritability was estimated using Warner (1952) approach:

$$h^2_{ns} = [2\sigma^2F_2 - (\sigma^2BC_1 + \sigma^2BC_2)]/\sigma^2F_2$$

in which σ^2F_2 denotes the variance of the F_2 population, σ^2BC_1 and σ^2BC_2 the variances of the backcrosses to F_1 by either one of the two parents. The standard error of h^2_{ns} was calculated according to Ketata et al. (1976):

$$SEh^2ns = \{2/\sigma^2F_2[(\sigma^2BC_1 + \sigma^2BC_2)^2/ dfF_2 + (\sigma^2BC_1)^2/dfBC_1 + (\sigma^2BC_2)^2/dfBC_2]\}^{1/2}$$

where dfF_2, $dfBC_1$ and $dfBC_2$ = degrees of freedom of the F_2, BC_1 and BC_2 populations, respectively.

The number of genetic factors segragating in the F_2 generation was estimated by the formulas of Falconer (1981), and Burton (1951).

The Falconer formula:

$$n = \bar{V}F_2/VF_2$$

in which n is the estimated number of segragation loci in the F_2 generation, VF_2 is the predicted variance in a segregating F_2 whose genetic resistance is governed by a single locus, and $\bar{V}F_2 = V_B + V_W$ where V_B = the variance between groups, and V_W is the variance within groups. VF_2 is the observed variance of the F_2 generation. The genetic variance of a quantitative trait is equal to $\bar{V}F_2/n$ if the n controlling loci are identical in effect, additive, unlinked, not dominant and if one parental line contribute all plus factor. If these conditions are not maintained the true genetic variance will be greater than the VF_2 and the formula will underestimate n.

The Burton formula:

$$n = 1/4(3/4 - h + h^2)D^2/(VF_2 - VF_1)$$

in which n is the estimated number of segregating loci in the F_2 generation. VF_2 is the observed variance of the F_2 generation, VF_1 is the observed variance of the F_1 generation, $D = P_1 - P_2$, $h = (F_1 - P_1)/D$, V_B is the predicted genetic variance in the segragating F_2 whose genetic resistance is governed by a single locus, and $V_B = 1/4P_1 + 1/4P_2 + 1/2F_1$.

Results

Parents

Performance of parents

The winter wheat cultivars Aurora, Bezostaya 1, Kavkaz and Trakia (Table 1) expressed rather low pycnidia coverage (5–16%) to inoculation by ISR 398A1 as compared to 56–71% pycnidia coverages by ISR8036. The two Israeli spring bread wheats

Hazera 2230 and Lakhish expressed high pycnidia coverages (60–70%) to the two isolates. The South American spring bread wheat cultivars Colotana and Klein Titan expressed low pycnidia coverage to ISR398A1 during the two years (6–11%). A shift in pycnidia coverage of these two cultivars occurred in 1985/1986 as compared to 1984/1985 when inoculated with ISR8036.

Isolates × cultivar × year interactions

In the analysis of variance of the pooled parental data (excluding Aurora) for the two trial years, the main effect due to isolates explained 67% of the variance (Table 2), whereas 20% the total variance could be explained by cultivar effect. The isolate × cultivars interaction explained 8.5% of the variance, while the year effect, though significant was rather small (< 1.0% of total variance).

Crosses

Plant height-maturity relationship

The effect of height on disease expression (Table 3) in crosses with the winter wheats (Aurora, Bezostaya 1, Kavkaz and Trakia) was small and in most cases statistically not significant. The correlations between the two Israeli cultivars (Hazera 2230 and Lakhish) and the tall statured South American spring wheats (Colotana and Klein Titan) were higher and in some cases significant.

The correlation coefficients between disease severity and maturity level expressed in days to heading for the F_2 populations are presented in Table 4. The effect of maturity level on disease expression in crosses with the winter wheats was small. The correlations with the late maturing South American spring cultivars were higher and in some cases significant. In crosses between Lakhish and the two South American cultivars tested in 1984/85 an r = 0.505** was recorded, which was not reproduced in 1985/6 (r = 0.056 ns).

Comparisons of reciprocals

In most crosses the differences between reciprocals were not significant for the F_1 and the F_2 populations for both isolates. There is no indication that parental cytoplasm confers greater or lesser pycnidial coverage to either *S. tritici* isolate.

Hayman analysis of spring × winter diallel

The GCA and SCA effects derived from the Hayman analysis of variance (Hayman, 1954) for the two *S. tritici* isolates in F_1 and F_2 populations were highly significant (Table 5). The mean squares for GCA in this diallel inoculated with ISR398A1 were much greater than those for SCA and b in both years indicating a preponderance of additive gene

Table 1. Pycnidial coverages on the four uppermost leaves of wheat parents by *Septoria tritici* isolates ISR398A1 and ISR8036, tested over two years

Cultivar	Isolate ISR398A1		Isolate ISR8036	
	1984/85	1985/86	1984/85	1985/86
spring wheat:				
Hazera 2230	64.4 ± 0.6[a]	57.2 ± 1.3	65.2 ± 0.4	70.2 ± 0.7
Lakhish	67.2 ± 0.6	59.8 ± 0.8	64.5 ± 0.7	67.2 ± 0.7
Colotana	5.7 ± 0.5	11.1 ± 0.6	8.4 ± 1.2	45.1 ± 2.6
Klein Titan	8.9 ± 0.9	10.9 ± 0.9	24.4 ± 1.8	48.2 ± 2.9
winter wheat:				
Aurora	13.0 ± 0.7	–	68.8 ± 0.6	–
Bezostaya 1	6.2 ± 0.4	16.0 ± 0.9	56.1 ± 0.9	63.9 ± 1.5
Kavkaz	5.4 ± 0.5	13.7 ± 1.0	61.2 ± 0.8	71.4 ± 0.9
Trakia	5.6 ± 0.4	12.9 ± 0.8	57.4 ± 0.9	67.0 ± 0.9

[a] Pycnidial caverage on four uppermost leaves and standard errors.

Table 2. Analysis of variance of wheat cultivar response (pycnidial coverage) to two *Septoria tritici* isolates tested over two years

Source	df	Mean square
cultivar	6[a]	223498.9**
isolate	1	742345.1**
year	1	24745.3**
cultivar × isolate	6	94318.7**
cultivar × year	6	5513.4**
isolate × year	1	14673.3**
cultivar × isolate × year	6	1816.1**

** = significant at the 0.01 level of probability.
[a] Aurora excluded from analysis.

effects for host response to this isolate. The magnitude of the mean squares for GCA in spring × winter F_1 and F_2 populations inoculated with ISR8036 was much smaller and the ratio between GCA and SCA ($2ms_{GCA}/(2ms_{GCA} + ms_{SCA})$) (Baker, 1978) in all cases was smaller than 1.0. The mean squares for the reciprocals in both *S. tritici* isolates though significant was rather small for the F_1 and F_2 populations.

In the calculation of the relationship between the array variance (Vr's) and the covariance of each parental array with the nonrecurrent parents (Wr's) for the F_1 and F_2 populations in the spring × winter diallel (with Aurora excluded) inoculated with ISR398A1, the regression line slope was not significantly different from unity. The winter wheat parents are nearer to the origin, indicating that these parents carry dominant alleles, while the spring wheat parents are further from the origin. The F_1 regression line intercepts the Wr axis above the origin indicating a partial dominance. The F_2 intercept is above the F_1 intercept, as is expected when there is dominance (Fig. 1A). Analysis of F_1 and F_2 populations of the spring × winter diallel inoculated with ISR8036 resulted in regression line slope greater than unity, with parents concentrating near the origin (Fig. 1B).

The relationship between Wr and the covariance of the offsprings in each array with the array means (W'r) for F_1 and F_2 populations inoculated with ISR398A1 indicate that all the winter wheat parents (Aurora excluded) are near the origin with little spread among them especially in F_1's, with the spring wheat parents furthest from the origin. The regression line slopes of both F_1 and F_2 are about the same (b = 0.44 and b = 0.46, respectively). The winter wheat parents are removed from the origin, thus dominance is not full and undirectional while the spring wheat parents occupy a reccessive position (Fig. 1C). The magnitude of W'r is much smaller in F_1 and F_2 populations inoculated with ISR8036, and the means of the parents are not spread and concentrate somewhat near the origin (Fig. 1D).

Hayman analysis of spring × spring diallel

A similar trend, namely a large GCA effect for populations inoculated with ISR398A1 as compared to the SCA and b values were observed in the South American spring × Israeli spring wheat diallel (Table 5). The ratio between mean squares of

Table 3. Correlations between plant height and percent coverage by pycnidia of *Septoria tritici* isolates in F_2 populations over two years

Populations	Isolate ISR398A1		Isolate ISR8036	
	1984/85	1985/86	1984/85	1985/86
Hazera 2230 × WBW[a]	− 0.022 ns[c]	− 0.039 ns[d]	0.027 ns	0.012 ns
Hazera 2230 × SBW[b]	− 0.236**	− 0.184**	− 0.251**	0.128**
Lakhish × WBW	0.027 ns	− 0.091**	− 0.006 ns	0.029 ns
Lakhish × SBW	0.038 ns	− 0.050 ns	− 0.114*	0.115**

[a] Combined F_2 populations in crosses with the winter wheat cultivars Bezostaya 1, Kavkaz and Trakia.
[b] Combined F_2 populations in crosses with the South American spring wheat cultivars Colotana and Klein Titan.
[c] Correlation coefficient (r).
[d] ns = not significant, * = significant at P = 0.05, ** = significant at P = 0.01.

GCA in population inoculated with ISR8036 in 1984/85 were more than twice larger than the SCA and b. The ratio between GCA and SCA and b in populations with ISR8036 in 1985/86 were less than 1.0. In the 4 × 4 diallel, the mean squares for reciprocals was calculated for the F_1 population inoculated with ISR398A1 in 1984/85. The effect was small though significant.

In analyzing the Vr, Wr relationships, the two South American parents Colotana and Klein Titan assumed a position furthest from the origin for the F_1 and F_2 populations inoculated with either ISR 398A1 and or with ISR8036 (Figs. 2A, 2B). The Israeli wheat parents Hazera 2230 and Lakhish assumed a more dominance position relative to the South American accessions. The four spring wheat parents assumed the same position in the Wr, W'r relationship when subjected to isolate ISR398A1 (Fig. 2C). The South American parents were placed in a recessive position relative to Hazera 2230 and Lakhish when exposed to ISR8036 (Fig. 2D).

Heritability

The heritability in the narrow sense (h^2_{ns}) in crosses between the four winter parents and Lakhish were significant and ranged from 0.68 to 0.95. The heritability values in crosses with Hazera 2230 were significant only for Aurora while the values for the other 3 parents ranged from 0.47 to 0.56. Values for crosses among the winter parents and among the spring parents themselves were not significant. Significant heritability values were obtained in the spring × spring diallel between Hazera 2230 crosses with either Colotana or Klein Titan, and between Lakhish × Klein Titan.

The number of genetic factors segregating in the F_2 generation

In crosses between the winter parents and the two susceptible spring wheats, and between the South American cultivars and the same two Israeli spring wheats, a small number of segragating loci (one or two) was estimated with some differences manifested by the Burton (1951) and Falconer (1981) formulas (Table 6).

Discussion

The incorporation of resistance to *S. tritici* remains a high priority breeding objective. Russian winter wheats (e.g. Aurora, Bezostaya 1, and Kavkaz) and South American accessions (e.g. IAS 20, and Veranopolis) which were used as sources for resistance to other foliar pathogens, were claimed to provide acceptable level of protection against *S. tritici* in many parts of the world (Rajaram et al., 1984).

Virulence on these groups of cultivars varied according to geographical region, sampling procedure and probably influenced by the genetical source from which *S. tritici* isolates were secured (Eyal et al., 1985; Eyal & Levy, 1987). Analyses of

Table 4. Correlations between days to heading (maturity) and percent coverage by pycnidia of *Septoria tritici* isolates in F_2 populations over two years

Populations	Isolate ISR398A1		Isolate ISR8036	
	1984/85	1985/86	1984/85	1985/86
Hazera 2230 × WBW[a]	0.013 ns[c]	−0.069*[d]	0.015 ns	0.006 ns
Hazera 2230 × SBW[b]	0.028 ns	−0.171**	−0.132**	−0.089*
Lakhish × WBW	0.013 ns	−0.016 ns	−0.107**	−0.112**
Lakhish × SBW	0.505 ns	−0.056 ns	−0.213**	−0.252**

[a] Combined F_2 populations in crosses with the winter wheat cultivars Bezostaya 1, Kavkaz and Trakia.

[b] Combined F_2 populations in crosses with the South American spring wheat cultivars Colotana and Klein Titan.

[c] Correlation coefficient (r).

[d] ns = not significant, * = significant at P = 0.05, ** = significant at P = 0.01.

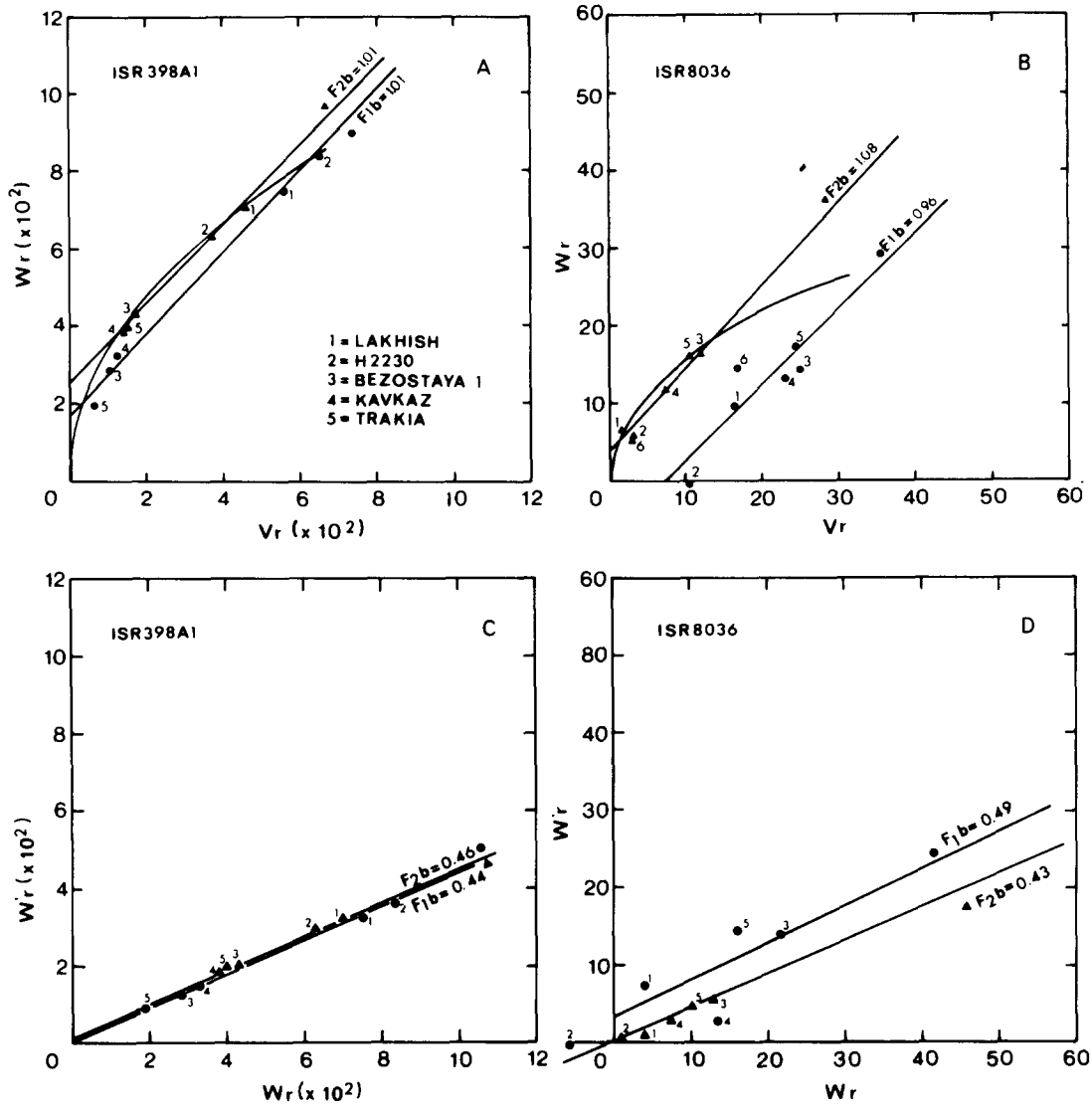

Fig. 1. The linear relationship between parents in F_1 (●) and F_2 (▲) populations of a 5 × 5 spring × winter diallel (spring wheat: 1 = Lakhish, and 2 = Hazera 2230; winter wheat: 3 = Bezostaya 1, 4 = Kavkaz, and 5 = Trakia) infected with *Septoria tritici* isolates ISR398A1 and ISR8036 in 1984/85. A, B = variance-covariance graph (Vr, Wr); C, D = covariance-covariance graph (Wr, W'r). Vr is the variance of all the offspring of each parent in each array, Wr is the covariance between these offspring and their nonrecurrent parents and W'r is the covariance of the offspring in each array with the array means. Slopes (b) are significant at P = 0.05.

world-wide virulence patterns revealed that the frequency of virulence on the Russian winter wheat cultivar Aurora, Bezostaya 1 and Kavkaz was rather high among isolates from Montana and Oregon in the U.S.A. and Ethiopia, but rather low among isolates from European and Mediterranean countries (Eyal et al., 1985). On the other hand, the frequency of virulence on the Frontana-derived South American accessions Colotana, Frontana and Klein Titan was rather high in South American countries and in Ethiopia. Such virulence analyses have hypothesized similar genes for resistance in Bezostaya 1 and Kavkaz, which differed from the Bezostaya 1-derived winter wheat cultivar Trakia by one hypothesized gene (Eyal & Levy, 1987). The South American Frontana-derived wheats

Colotana, IAS 20 and Klein Titan differed from one another in their response and in the hypothesized genes for resistance upon exposure to 42 *S. tritici* isolates from Israel (Eyal & Levy, 1987).

In the present study the four Bezostaya 1-derived winter wheat cultivars namely, Aurora, Bezostaya 1, Kavkaz and Trakia, and the two Frontana – derived South American spring wheat cultivars Colotana and Klein Titan responded rather similarly within each cultivar group (winters and South American) to the two Israeli *S. tritici* isolates. The main effect due to isolates was more than 3 times larger than the effect due to cultivars. The differences in virulence between ISR398A1 and ISR8036 were previously elucidated (Yechilevich-Auster et al., 1983), and further examplified in the present study. The level of infection during the second year was higher and is expressed in a relatively high year effect. The significant cultivar × isolate interaction assumes an 8.5% portion of the total variation, or 2.6% of the mean squares values due to partitioned effect. The magnitude of the year effect on both cultivar and isolates was relatively small, though significant.

Genetical analysis could be further carried out in view of the insignificant effect of either plant stature or maturity level on symptoms expression.

Reciprocal differences within generations were of low frequency in both years in all families thus host response is controlled by nuclear genetic factors, and there is no indication for the role of the cytoplasm in resistance. These conclusions therefore satisfy some of the assumptions for the diallel analysis (Allard, 1956). The general combining ability (GCA) which contains mainly additive effects was found to be the major component of variation, although significant specific combining ability (SCA) which is composed of dominance plus interallelic interaction or epistatic variance was present in all cases. The analysis of Wr, Vr and Wr, W'r graphical statistics in both F_1 and F_2 provided detailed information on the interrelations between the parents in each of the two diallels. In no case there was an indication for epistasis, or that the parents are not completely homozygous. The positive Wr intercept of both F_1 and F_2 regression lines in the graphic analysis indicates partial dominance. The presence of dominance was indicative in significant b values (dominance component mean squares) in the Hayman analyses of variance for the two diallels during the 2-year trials for both *S. tritici* isolates. In the spring × winter diallel inoculated with isolate ISR398A1 the inheritance is composed of both additive and partial dominance components. The number of genes controlling resistance to isolate ISR398A1 was rather small (usu-

Table 5. Mean squares of Hayman's analysis of variance of per cent pycnidia coverage in complete spring × winter and spring × spring diallel crosses of wheat infected with *Septoria tritici* isolates ISR398A1 and ISR8036 in 1984/85 and 1985/86

Diallel	Isolate	Year	F_1			F2		
			GCA[1]	SCA[2]	ratio[3]	GCA	SCA	ratio
S × W[4]	ISR398A1	1984/5	3285.9**	27.6**	0.99	4565.0**	14.0**	0.99
	ISR398A1	1985/6	655.3**	139.4**	0.90	1157.8**	72.7**	0.97
	ISR8036	1984/5	38.1**	18.2**	0.81	85.3**	5.2**	0.97
	ISR8036	1985/6	20.5**	17.9**	0.69	45.6**	20.8**	0.81
S × S	ISR398A1	1984/5	3378.2**	11.0**	0.99	4314.3**	3.9**	0.99
	ISR398A1	1985/6	1146.9**	18.9**	0.99	1873.6**	13.4**	0.99
	ISR8036	1984/5	549.0**	190.7**	0.85	1063.0**	40.9**	0.98
	ISR8036	1985/6	13.3**	33.2**	0.44	29.4**	33.8**	0.63

[1] GCA = General combining ability.
[2] SCA = Specific combining ability.
[3] Ratio = $2ms_{GCA}/(2ms_{GCA} + ms_{SCA})$ according to Baker (1978).
[4] S × W = spring × winter wheat diallel, S × S = spring × spring wheat diallel.
** = significant at P = 0.01.

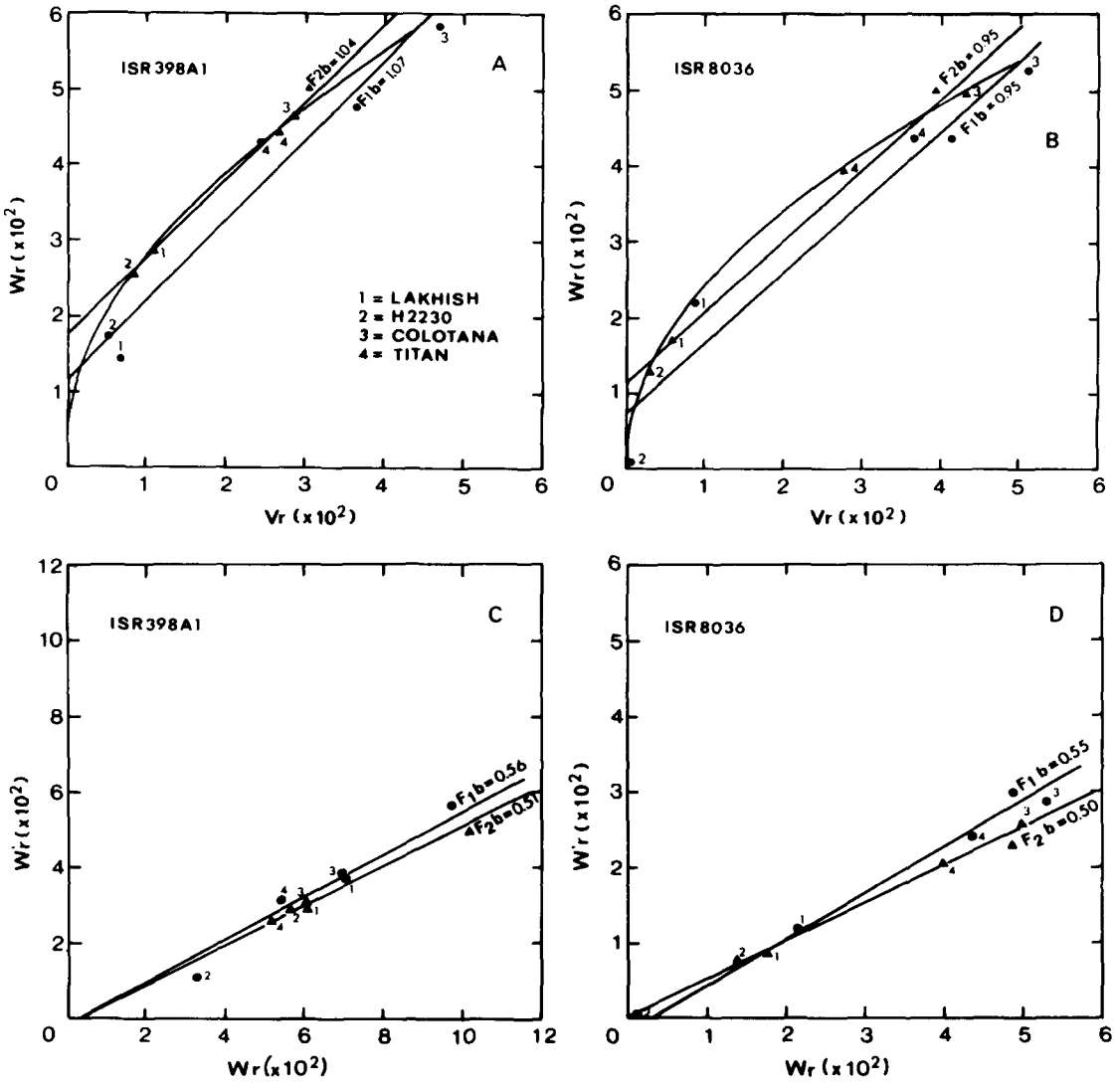

Fig. 2. The linear relationship between parents in F_1 (●) and F_2 (▲) population of a 4 × 4 spring × spring diallel (1 = Lakhish, 2 = Hazera 2230, 3 = Colotana, and 4 = Klein Titan) infected with *Septoria tritici* isolates ISR398A1 and ISR8036; A, B = variance – covariance graph (Vr, Wr); C, D = covariance – covariance graph (Wr, W'r). Vr is the variance of all the offspring of each parent in each array; Wr is the covariance between these offsprings and their nonrecurrent parents, and W'r is the covariance of the offspring in each array with the arrays means. Slopes (b) are significant at P = 0.05.

ally 2 genes). There were no significant differences in the number of genes in crosses among these parents. It is therefore concluded that the Bezostaya 1-derived winter wheat parents all carry the Bezostaya 1 genes for resistance to ISR398A1. Resistance in Aurora and Kavkaz is not associated with 1B/1R wheat-rye translocation which is lacking in Bezostaya 1 and Trakia. It is probable that the four winter parents derive their resistance to isolate ISR398A1 from their common parent Bezostaya 1.

Resistance of the winter wheats is readily overcomed by *S. tritici* isolate ISR8036. The GCA and SCA values for this isolate though significant, are several folds smaller than that of ISR398A1. Based on the significant cultivar × isolate interaction it is

probable that the two *S. tritici* isolates possess different genes for virulence.

In the spring × spring diallel there is a large additive effect to both isolates, though much larger to ISR398A1. This is due to the fact that *S. tritici* isolate ISR8036 is not as virulent on the South American spring wheats as it is on the winter wheats. The South American cultivars Colotana and Klein Titan carry resistance factors to both isolates which is mostly additive with a very small dominance components. The resistance is governed by a small number of genes, probably two, which have a recessive effect. No differences were observed among the two South American cultivars in the calculated number of genes for resistance, which may be indicative of their common parent Frontana.

Rosielle and Brown (1979) assigned a single dominant gene for resistance to IAS 20, which possess Frontana germplasm. Wilson (1985) found that a two recessive gene model fitted better than a single dominant gene affecting inheritance of IAS 20. The discrepancy may derive from differences in the *S. tritici* isolates used in the various studies.

It is of interest to note that a small number of hypothesized complementry genes (two) were designated to Aurora, Bezostaya 1 and Kavkaz in a gene-for-gene analysis of a 97 isolate × 35 cultivar matrix (Eyal et al., 1985) whereas Colotana was assigned one gene and Klein Titan 2 hypothetical genes. A much larger number of hypothesized genes (8–9) were assigned to Bezostaya 1, Kavkaz and Trakia in a 42 Israeli isolates × 16 wheat cultivars (Eyal & Levy, 1987). In the later study Colotana was designated two hypothetical genes and Klein Titan 7 genes.

The dissimilarities between the two *S. tritici* isolates used in the present study suggest that a gene-for-gene relationship may be operative in the *S. tritici* – *Triticum aestivum* cultivars used in this study, and thus the two isolates differ in virulence rather than in their aggressiveness sensu Van der Plank (1968). The presence of significant dominant component in the winter wheat cultivars detected upon exposure to isolate ISR398A1 strengthen the virulence rather than aggressiveness explanation (M. van Ginkel & A.L. Scharen, 1987, 1988a, 1989b). Choice of cultivars and isolates may strongly influence the conclusions.

The fact that isolate ISR8036 overcome the resistance of the winter wheats, combined with the relatively high world-wide virulence frequency of

Table 6. Estimated number of segregating loci in F_2 crosses populations of spring × winter and spring × spring wheat families inoculated with *Septoria tritici* isolates ISR398A1 and ISR8036 in two seasons

Cross	ISR398A1				ISR8036			
	1984/85		1985/86		1984/85		1985/86	
	n_B[a]	n_F	n_B	n_F	n_B	n_F	n_B	n_F
Lakhish × Hazera 2230	0.1	0.8	0.1	2.1	0.1	0.5	0.3	0.9
× Aurora	1.5	–	–	–	0.2	–	–	–
× Bezostaya 1	5.6	1.5	1.9	1.5	1.2	1.6	0.1	1.2
× Kavkaz	2.9	1.2	1.3	1.1	0.1	1.2	0.1	0.6
× Trakia	1.6	1.3	1.1	1.1	0.2	1.3	0.0	0.5
Lakhish × Colotana	1.1	1.6	1.4	1.3	–	1.4	2.0	2.4
× Klein Titan	–	–	1.1	1.0	–	1.1	−2.5	7.6
Hazera 2230 × Aurora	0.9	–	–	–	0.4	–	–	–
× Bezostaya 1	2.1	1.6	2.0	2.3	1.9	0.8	0.9	1.1
× Kavkaz	0.9	1.1	1.4	1.3	0.4	1.1	0.1	0.7
× Trakia	1.3	1.0	1.2	1.0	1.8	0.6	0.2	0.7
Hazera 2230 × Colotana	1.6	1.7	1.9	1.4	1.8	2.5	−7.6	2.5
× Klein Titan	1.7	1.5	−4.1	1.5	2.9	1.2	−2.2	2.9

[a] n_B = Burton (1951) formula = $n^2 1/4(3/4 - h + h^2)D^2/(VF_2 - VF_1)$; n_F = Falconer (1981) formula = $\bar{V}F_2/VF_2$.

Bezostaya 1 – Kavkaz (Eyal et al., 1985), suggests that these sources of resistance do not provide sufficient protection where virulence is present. It may provide some protection where virulence frequency is low or under low – moderate Septoria epidemic levels. Combining these resistance sources with other sources such as expressed in Bobwhite"S" (Au//Kal/BB/3/Wop"s", CM33203) or KVZ-K4500 L.A.4 may provide better and more widely adapted protection. The use of specific *S. tritici* virulences to challange resistance sources serve as a powerful tool in elucidating the presence or absence of incorporated resistance in breeding programs and in genetical studies.

Acknowledgements

The assistance of Ora Zvielli and U. Cohen of the department of Botany, and of Ilana Gelerenter and Dr. D.M. Steinberg of department of Statistics, Tel Aviv university is gratefully acknowledged. This research was supported by a grant from DPO/OT, the ministry of Foregin Affairs, The Hague, the Netherlands, in cooperation with CIMMYT, Mexico and IPO, Wageningen, the Netherlands.

References

Allard, R.W., 1956. Biometrical approach to plant breeding. p. 69–85. In: Genetics in plant breeding. Symposia in Biology No. 9. Brookhaven National Laboratory, Upton, NY. 236 pp.

Baker, R.J., 1978. Issues in diallel analysis. Crop Science 18: 533–536.

Burton, G.W., 1951. Quantitative inheritance in pearl millet (*Pennisetum glaccum*). Agronomy Journal 43: 409–417.

Danon, T., J.M. Sacks, & Z. Eyal, 1982. The relationships among plant stature, maturity class, and susceptibility to Septoria leaf blotch of wheat. Phytopathology 72: 1037–1042.

Draper, W.R. & H. Smith, 1966. Applied regression analysis. John Wiley & Sons, Inc., NY. 407 pp.

Eyal, Z., 1981. Integrated control of Septoria diseases of wheat. Plant Disease 65: 763–768.

Eyal, Z. & M.B. Brown, 1976. A quantitative method for estimating density of *Septoria tritici* pycnidia on wheat leaves. Phytopathology 66: 11–13.

Eyal, Z. & E. Levy, 1987. Variation in pathogenicity patterns of *Mycosphaerella graminicola* within *Triticum* spp. in Israel. Euphytica 36: 237–250.

Eyal, Z., A.L. Scharen, M.D. Huffman & J.M. Prescott, 1985. Global insights into virulence frequencies of *Mycosphaerella graminicola*. Phytopathology 75: 1456–1462.

Eyal, Z., A.L. Scharen, J.M. Prescott & M. van Ginkel, 1987. The Septoria diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico, 52 pp.

Falconer, D.S., 1981. Introduction to quantitative genetics. Longman House, Essex, UK. 340 pp.

Hayman, B.I., 1954. The theory and analysis of diallel crosses. Genetics 39: 789–809.

Ketata, H., L.H. Edwards & E.L. Smith, 1976. Inheritance of eight agronomic characters in winter wheat cross. Crop Science 16: 19–22.

Mather, K. & J.L. Jinks, 1971a. Biometrical genetics. Chapman and Hall., London, UK. 382 pp.

Mather, K. & J.L. Jinks, 1971b. Introduction to biometrical genetics. Cornell University Press. Ithaca, N.Y. 231 pp.

Mettin, D., W.D. Bluthner & G. Schlegel, 1973. Additional evidence of spontaneous 1B/1R wheat-rye substitutions and translocations. p. 179–184. Proc. 4th Int. wheat Genet. Symp., Colombia, Mo., USA.

Rajaram, S., B. Skovmand & B.C. Curtis, 1984. Philosophy and methodology of an international wheat breeding programm. p. 33–60. In: J.P. Gustafson Ed. Gene manipulation in plant improvement. Plenum Publ. Corp.

Rajaram, S., R.P. Singh & E. Torres, 1988. Current CIMMYT approaches in breeding wheat for rust resistance. p. 101–118. In: N.N. Simmonds & S. Rajaram (Eds.). Breeding strategies for resistance to the rusts of wheat. CIMMYT, Mexico. 151 pp.

Roelfs, A.P., 1988. Resistance to leaf and stem rusts in wheat. p. 10–22. In: N.N. Simmonds & S. Rajaram (Eds.). Breeding strategies for resistance to the rusts of wheat. CIMMYT, Mexico, 151 pp.

Rosielle, A.A. & A.G.P. Brown, 1979. Inheritance, heritability and breeding behavior of three sources of resistance to *Septoria tritici* in wheat. Euphytica 28: 385–392.

Rosielle, A.A. & W.J.R. Boyd, 1985. Genetics of host-pathogen interactions to the *Septoria* species of wheat. p. 9–12. In: A.L. Scharen (Ed.). Septoria of cereals Proceedings of the Workshop. Montana State University, 116 pp.

Van Der Plank, J.E., 1968. Disease resistance in plants. Academic press, N.Y. 201 pp.

Van Ginkel, M. & A.L. Scharen, 1987. Generation mean analysis and heritabilities of resistance to *Septoria tritici* in durum wheat. Phytopathology 77: 1629–1633.

Van Ginkel, M. & A.L. Scharen, 1988a. Diallel analysis of resistance to *Septoria tritici* isolates in durum wheat. Euphytica 38: 31–37.

Van Ginkel, M. & A.L. Scharen, 1988b. Host-pathogen relationships of wheat and *Septoria tritici*. Phytopathology 78: 762–766.

Warner, J.N., 1952. A method for estimating heritability. Agronomy Journal 44: 427–430.

Wilson, R.E., 1979. Resistance to *Septoria tritici* in two wheat

cultivars, determined by independent, single dominant genes. Australian Plant Pathology 8: 16–18.

Wilson, R.E., 1985. Inheritance of resistance to *Septoria tritici* in wheat. Pages 33–35. In: A.L. Scharen (Ed.). Septoria of cereals: Proceeding of the workshop. Montana State University, Bozeman. 116 pp.

Yechilevich-Auster, M., E. Levi & Z. Eyal, 1983. Assessment of interactions between cultivated and wild wheats and *Septoria tritici*. Phytopathology 73: 1077–1083.